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Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping

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HIGHLIGHTS

- Intercropping altered ant community structure in a plantain agroecosystem.
- Plant damage by *Cosmopolites sordidus* was linked to ant abundance.
- *Axinidris* sp., *Monomorium* spp., *Pheidole* spp. and *Tetramorium* sp. decreased damage.

GRAPHICAL ABSTRACT
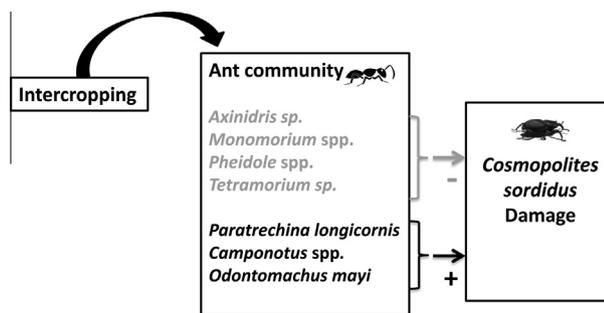
ABSTRACT

Intercropping is a practical way to increase plant diversity in agroecosystems and provide alternative food and habitat to arthropods, including generalist predators. In tropical agriculture, ants are important predators and have complex and often strong effects on pests. With the goal of optimizing control of the banana weevil, *Cosmopolites sordidus*, we studied maize (*Zea mays*), cocoyam (*Xanthosoma sagittifolium*), and bottle gourd (*Lagenaria siceraria*) as intercrops in a plantain field in Cameroon. We analyzed the effects of intercropping on ant abundance (by taxon) and on the damage caused by *C. sordidus* larvae to plantain corms. We also analyzed the relationship between ant abundance and *C. sordidus* damage. When added singly, the three intercropped plants significantly affected the abundance of each of the seven ant taxa but the sign of the effect depended on the intercropped plant species and on the ant taxon. Intercropping had clear effects on ant abundance, which was negatively correlated with *C. sordidus* damage for the Myrmicinae and positively correlated for the Formicinae and Ponerinae. Intercropping in plantain agroecosystems has the potential to alter ant community structure which contributes to *C. sordidus* control, but the effect of intercropped plant species remain unclear and further investigations are needed.
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1. Introduction

Plant diversity alters arthropod food webs by increasing the abundance of most trophic groups except for pests and invaders, which tend to decrease (Scherber et al., 2010). Increasing plant diversity in agroecosystems is a promising way to improve pest control (Brown, 2012). The diversification of agroecosystems increases the availability of habitats, alternative prey or hosts,

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and shelter for natural enemies (Landis et al., 2000). Intercropping is a practical way to improve plant diversity in agroecosystems, and several studies have shown that intercropping tends to favor natural enemies of pests and thus enhance biological control (Berndt et al., 2006; Hooks and Johnson, 2003; Song et al., 2010). However, mechanisms linking intercropping and pest control are complex because they include both direct effects (the provisioning of resources for alternative prey of generalist predators) and indirect effects (the modification of the entire community structure and the alteration of habitats). Intercropped plants, for example, may alter the entire arthropod community (Liang and Huang, 1994) and reduce pest populations by increasing the abundance of natural enemies (Khan et al., 1997; Risch, 1983). Interaction among the generalist predators may also be modified by increased plant diversity, e.g., increased plant diversity can decrease intraguild predation among generalist predators (Tixier et al., 2013) and thereby increase control of herbivores. Plant diversity may also increase the abundance of alternative prey, which usually enhances pest control but may reduce pest control if the pest is not the preferred prey (Koss and Snyder, 2005). Here, we investigate the effects of intercropping on the community of ants in plantain and on the damage of the banana weevil, *Cosmopolites sordidus* (Germar), to this crop.

C. sordidus is a major pest in most banana and plantain production areas (Gold et al., 2001) including Cameroon (Okolle et al., 2009). Females lay their eggs on the plantain corm, and eclosing larvae bore galleries and feed in the corm (Koppenhöfer, 1993). If there is no management of the weevil population and infestation levels are high, the damage can be substantial and may even result in the death of banana plants (Rukazambuga et al., 1998). In commercial banana plantations, pheromone traps have been successfully used to reduce populations (Duyck et al., 2012). However due to the significant cost of pheromone trapping, this method is not suitable for small-scale plantain farmers in Centre Africa, and is not practical on large scale farms where control of *C. sordidus* is needed (Alpizar et al., 2012; Rhino et al., 2010).

C. sordidus adults disperse by walking over the soil during the night (Vinatier et al., 2010) and may suffer significant mortality from generalist predators on the soil surface. For example, predation on *C. sordidus* by the ants *Odontomachus brunneus* and *Pheidole fallax* was observed in the field in Martinique (Carval pers. Com.). The egg stage is particularly vulnerable to generalist predators such as ants (Abera-Kalibata et al., 2007). Larval stages develop within the banana plant (Abera-Kalibata et al., 1999) and are consequently inaccessible to many predators. However, Abera-Kalibata et al. (2006) observed predation of *C. sordidus* larvae by the ant *Myopopone castanea* Smith (Ponerinae). Generalist predators such as ants, earwigs, and ground beetles are all potential sources of mortality for *C. sordidus* (Abera-Kalibata et al., 2006; Mollot et al., 2014). Insect parasitoids of *C. sordidus* are scarce, and attempts at classical biological control of *C. sordidus* with them have been unsuccessful (Gold et al., 2001).

In Africa, plantains are grown in association with annual crops (root, tuber, and vegetable crops) and perennial crops (cocoa, coffee, palm, and others). Studies have shown that cover crops, used in banana plantations to reduce herbicide applications and erosion, increase primary productivity and diversify the basic resources available for higher arthropod trophic levels Duyck et al. (2011). In another study, addition of a cover crop also increased the abundance of the fire ant *Solenopsis geminata* (Myrmicinae) and, in turn, improved predation by this ant on eggs of *C. sordidus* (Mollot et al., 2012). Sweet potatoes and maize intercropping are known to increase *C. sordidus* natural enemies such as *Pheidole* sp., *Camponotus* sp., *Dorylus* sp., *Forficula* sp., and some tenebroinids (Uronu, 1992). However, other studies showed that the legume intercrops did not affect *C. sordidus* populations and damage (McIntyre et al.,

2001). Intercropping may also alter *C. sordidus* damage indirectly because competition for nutrients with other plants may increase the susceptibility of plantains to *C. sordidus* (Gold et al., 2001; Rukazambuga et al., 2002). Here, we focus on annual crops as intercrops in plantain systems with the goal of understanding how their presence affects arthropod community structure and pest control in plantain agroecosystems with low chemical inputs.

Ants have been increasingly recognized as important predators in agricultural systems in the tropics and subtropics (Perfecto and Castineiras, 1998; Way and Khoo, 1992). Ants have complex and often strong effects on lower trophic levels (Philpott et al., 2008) and may be useful in pest management (Perfecto, 1991). The potential for ants to control insect herbivores, however, can depend on the structure of their community and on their feeding behavior. In banana agroecosystems in French Antilles, Mollot et al. (2012) documented the carpenter ant *Camponotus sexguttatus* feeding on *C. sordidus* and in Cuba, Roche and Abreu (1983) showed that *Tetramorium guineense* ants reduced *C. sordidus* populations in heavily infested banana plantations. In Uganda, Abera-Kalibata et al. (2008) found that *Pheidole* sp. and *Odontomachus troglodytes* Santschi reduced the density of *C. sordidus* eggs but not of larvae in banana suckers. Castenieras and Ponce (1991) reported that *T. guineense* (Nylander) reduced *C. sordidus* populations in plantations with moderate to heavy *C. sordidus* infestations and that *Pheidole megacephala* (Fabricius) deterred *C. sordidus* oviposition on banana plants. Most studies have considered the effect of only one or few ant species on *C. sordidus* and no study has yet addressed the impact of a whole ant community on *C. sordidus* control.

In the experiment described in this study, we planted three annual crops (tuber, cereal, and cucurbits) with plantain in single, double, and triple-species combinations. The general goal of the study was to determine whether and how intercropping may alter biological control of *C. sordidus* in plantain fields. The broad objectives were: (i) to understand how these intercrops modify ant community structure in plantain fields and (ii) to determine whether *C. sordidus* damage to plantain is correlated with the abundance of particular ant species. We also considered mechanisms of how intercropping might enhance biological control of *C. sordidus* in plantain fields.

2. Materials and methods

2.1. Study site and experimental design

Our study site was located at the CARBAP Research Station (4° 34′ 11.33″ N; 9° 38′ 48.96″ E; 79 m a.s.l.) in Njombe, Cameroon, Central Africa. The climate is humid tropical with a monthly mean temperature ranging from 25.0 to 27.4 °C and a mean annual rainfall of 2610 mm. The young brown soil is derived from a volcanic platform (Delvaux et al., 1989). Seven intercropped treatments and one bare soil control treatment were tested in a field of plantain (AAB, *Musa acuminata* × *Musa balbisiana*, Batard variety) in its third cycle of production. Inside a 1 ha plantain field (surrounded by other plantain fields), four replicates of 22 m × 39 m were defined with 6 m of bare soil separating adjacent plots. Each replicate was divided into eight experimental units (4 m × 22 m), one for each treatment, and each unit had a row of plantains running lengthwise down the middle so that there was a 2 m strip on each side of the row; bare soil was maintained or the intercrops were planted in these 2 m strips. Each experimental unit included eight plantain plants and was separated from other experimental units by a 1-m strip of bare soil. The intercropped treatments included three plants frequently associated with plantain in Cameroon: cocoyam, *Xanthosoma sagittifolium*, maize, *Zea mays*, and gourd, *Lagenaria siceraria*, representing a tuber-root, a cereal, and a

cucurbit, respectively. The eight treatments included one control in which no other plant species was associated with the plantain, three single-species treatments with one companion plant, three double-species treatments with two companion plants, and one triple-species treatment. Plants in the double-species and triple-species treatments were homogeneously mixed around the plantains. Treatments were randomly assigned to experimental plots in each replicate. The intercropped plants were planted at the end of the third cropping cycle of plantain field and were maintained until the end of the fourth cropping cycle. To maintain continuous plant cover in the case of short-cycle maize and gourd crops, replanting was conducted as needed. The plantains were uniformly fertilized (20% nitrogen, 10% phosphorous, and 10% potassium) at 500 kg per ha per year and all suckers were removed early in the cropping cycle, except for one selected for the next cropping cycle. Weeds were controlled manually in intercropped treatments and with herbicide (glyphosate) in the bare soil control treatment. The experiment began on March 1, 2013 and ended on February 28, 2014.

2.2. Sampling methods

2.2.1. Ant abundance

We determined the abundance of each ant species between June 1, 2013 and August 30, 2013 during the rainy season (from mid-March to mid-November) and again between December 1, 2013 and February 28, 2014 during the dry-season (from mid-November to February). In each experimental unit, we measured ant abundance by using attractive, canned tuna-honey baits, which were placed 0.5 m distant from each of the eight plantain plants in a unit, alternating from one side to the other of each adjacent plantain. The bait had a diameter of 4 cm and was placed in the center of a 30×30 cm white ceramic tile All samples were obtained between 8:00 a.m. and 12:00 p.m. Ants were collected with an aspirator beginning 30 min after the baits were deployed. Ants on the ceramic tiles were counted, digitally photographed to later confirm the counts, and the ants identified using the Bolton key (Bolton and Ficken, 1994) and the PIAkey (Sarnat, 2009).

2.2.2. Ant abundance and corm damage by C. sordidus

At the end of the experiment, we measured the damage caused by C. sordidus larvae to plantain corms in experimental units. Damage assessment was done after shelling 2 cm of the corm surface from 10 cm above to 10 cm below ground over entire circumference of the corm. A 0–100 scoring system (Vilardebo, 1973) was used to score damage where 0 = no damage, 5 = 1 or 2 galleries per corm, and 10, 30, 40, 60, and 100 equaled 10%, 25%, 50%, 75%, and 100% of the corm circumference damaged, respectively. We also tested whether the Vilardebo method is reasonably correlated with real C. sordidus damage. On a total of 32 plants (one per experimental unit), we conducted a complete corm transverse section on which we measured the percentage of damage including deep galleries. There was a reasonable ($R^2 = 0.4864$) and significant ($P < 0.0001$) correlation between the percentage of damage on the corm section and Vilardebo damage index (Fig. S1).

2.3. Data analysis

We used generalized linear mixed models (GLMMs) with a Poisson error (O'Hara and Kotze, 2010) to analyze the effect of the intercropped plants and their interactions (double and triple) on each ant taxon and on the corm damage index. In all analyses, the statistical unit was the plantain plant on which measurements were taken. When local ant communities are dominated by one or a few species, ground baits can give misleading estimates of biodiversity (Folgarait, 1998). To consider the potential influence of

locally abundant species on the effect of the intercropped plant(s) and the abundance of ant taxa, we included the sum of the local abundances of other ant species as a random factor. We verified the normality of the distribution of models' residuals (Tables S1 and S2). We verified that data followed a Poisson distribution and log-transformed the ant abundance data to homogenize variation between species with small and large colonies. We considered the plantain plant as a random, individual effect. The HSD test (de Mendiburu and de Mendiburu, 2014) was used to group treatments according to level of C. sordidus damage.

We examined the need to include random effects using likelihood ratio tests (LRTs) (Bolker et al., 2009). Then, we removed non-significant fixed-effect parameters in a backward, stepwise process using LRTs, removing non-significant interactions first, and then non-significant variables. This procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). All GLMMs were estimated using the 'glmer' function in the 'lme4' package (Bates et al., 2012), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009). Statistical analyses were performed with R 2.15.0 (R Development Core Team, 2014) and with an alpha level of 0.05.

3. Results

3.1. Ant abundance

Ant abundance was similar in both the rainy and the dry season (Table S1) so the data was pooled for further analysis. A total of 12,197 ants belonging to 14 species were observed. We reduced the 14 taxa to seven by combining species by genera into three groups: *Pheidole* spp., *Monomorium* spp., and *Camponotus* spp. *Pheidole* spp. was the most abundant taxon with 4681 individuals, followed by *Paratrechina longicornis* with 2577 individuals, *Tetramorium* sp. with 2182 individuals, *Monomorium* spp. with 1555 individuals, *Camponotus* spp. with 755 individuals, *Axinidris* sp. with 390 individuals, and *Odontomachus mayi* with 57 individuals. The ants were distributed among treatments as follows: 2767 in cocoyam, 2064 ants in cocoyam-gourd, 1989 ants in gourd, 1901 ants in controls, 1170 ants in cocoyam-maize, 821 ants in maize, 803 ants in cocoyam-maize-gourd and 682 ants in maize-gourd treatment. Intercropping of plantain with one plant (maize, cocoyam, or gourd) significantly affected all seven ant taxa in all but one of the 21 cases (cocoyam did not affect *P. longicornis*) (Fig. 1). The effect of intercropping with more than one plant was significant for 12 of 21 cases with two added plants and for 2 of 7 cases with three added plants (Fig. 1 and Table S3). Intercropping with gourd reduced the abundance of all seven ant taxa except *Pheidole* spp., whereas intercropping with maize and cocoyam reduced or increased ant abundance depending on the ant taxon (see Table 1).

3.2. Ant abundance and corm damage by C. sordidus

There was a significant effect of intercropping treatment on C. sordidus damage ($P < 0.0001$) but no treatment was significantly less damaged than controls (Table 2). Overall, the mean damage score was 34.69 ± 2.17 and ranged from 0 to 100. Although the damage demonstrated no clear relationship with intercropping, it was significantly related to the abundance of each ant taxon (Fig. 2). Damage was negatively related to the abundance of *Axinidris* sp. (LRT: $P < 0.001$, $\chi^2 = 11.15$, df = 1), *Monomorium* spp. (LRT: $P < 0.001$, $\chi^2 = 13.95$, df = 1), *Pheidole* spp. (LRT: $P < 0.001$, $\chi^2 = 16.06$, df = 1), and *Tetramorium* sp. (LRT: $P < 0.01$, $\chi^2 = 7.83$, df = 1). In contrast, damage was positively related to the abundance of *Camponotus* spp. (LRT: $P < 0.001$, $\chi^2 = 27.67$, df = 1),
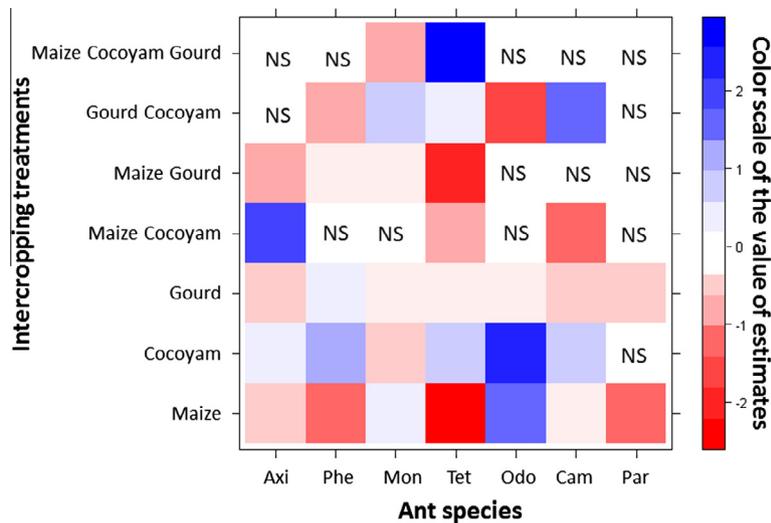
Fig. 1. Estimates of the strength and direction of effects of seven intercropping treatments on ant abundance. Blue indicates positive effects and red indicates negative effects, with color intensity indicating the strength of the effect (darker color = stronger) and positive and negative values indicating the fold-change in ant abundance. NS indicates a non-significant effect of intercropping on ant abundance. Axi: *Axinidris* sp.; Phe: *Pheidole* spp.; Mon: *Monomorium* spp.; Tet: *Tetramorium* sp.; Odo: *Odontomachus mayi*; Cam: *Camponotus* spp.; Par: *Paratrechina longicornis*. Details of the statistical analysis are provided in Table S3.

Table 1
Mean numbers of various ant species observed in each treatment and their standard errors.

Ant species	Maize	Cocoyam	Gourd	Maize cocoyam	Maize gourd	Cocoyam gourd	Maize cocoyam gourd	Control
Axinidris sp.	0.265 ± 0.165	0.75 ± 0.274	0.64 ± 0.236	2.765 ± 0.137	0.265 ± 0.137	0.484 ± 0.229	0.359 ± 0.284	0.5625 ± 0.2615
Camponotus spp.	1.359 ± 0.363	2.25 ± 0.872	0.563 ± 0.243	0.578 ± 0.309	0.969 ± 0.365	3.640 ± 1.515	1.750 ± 0.547	0.6875 ± 0.1780
Monomorium spp.	4.140 ± 1.075	1.530 ± 0.408	2.040 ± 0.434	4.480 ± 1.084	3.010 ± 0.910	3.250 ± 0.968	3.340 ± 0.916	2.4843 ± 0.9085
Odontomachus mayi	0.125 ± 0.085	0.156 ± 0.067	0.015 ± 0.015	0.453 ± 0.212	0.062 ± 0.049	0.030 ± 0.021	0.031 ± 0.021	0.0156 ± 0.0162
Paratrechina longicornis	3.609 ± 0.654	8.609 ± 1.860	6.062 ± 1.043	2.156 ± 0.488	1.984 ± 0.413	7.170 ± 1.330	1.922 ± 0.425	8.7500 ± 1.4524
Pheidole spp.	2.421 ± 0.960	25.180 ± 6.130	12.015 ± 3.340	7.640 ± 2.931	4.156 ± 1.123	10.234 ± 2.254	4.296 ± 0.948	7.1875 ± 2.3397
Tetramorium sp.	0.906 ± 0.350	4.750 ± 2.480	9.734 ± 3.596	0.203 ± 0.132	0.203 ± 0.134	7.437 ± 2.700	0.8437 ± 0.465	10.0156 ± 4.0967

Table 2
Mean damage indices and standard errors for *C. sordidus* damage in each treatment. Means bearing different letters were significantly different from others (Tukey's HSD, $\alpha = 0.05$). Estimates, Z and P values were calculated with GLM with controls as the reference treatment.

| Treatments	Mean of damage	Estimate	Z	P
(Intercept)	–	3.383	47.12	<0.0001
Cocoyam gourd	45.78 ± 5.29a	0.433	10.40	<0.0001
Maize	42.66 ± 5.40b	0.362	8.58	<0.0001
Gourd maize	38.28 ± 4.03c	0.254	5.88	<0.0001
Gourd	34.53 ± 4.17d	0.151	3.42	<0.0001
Cocoyam	29.06 ± 4.58e	−2.128	−0.46	0.644619
Cocoyam maize	29.69 ± 4.15e	1.588e−07	0.00	0.999997
Gourd maize cocoyam	27.81 ± 4.17e	−0.065	−1.40	0.161974

Z and P values were obtained from the Chi-square test.

O. mayi (LRT: $P < 0.001$, $\chi^2 = 19.42$, df = 1), and *P. longicornis* (LRT: $P < 0.001$, $\chi^2 = 30.83$, df = 1).

4. Discussion

4.1. Ant abundance

Our results show that intercropping plantain with maize, cocoyam, or gourd significantly affected ant abundance but that the sign of this effect (positive or negative) depended on the
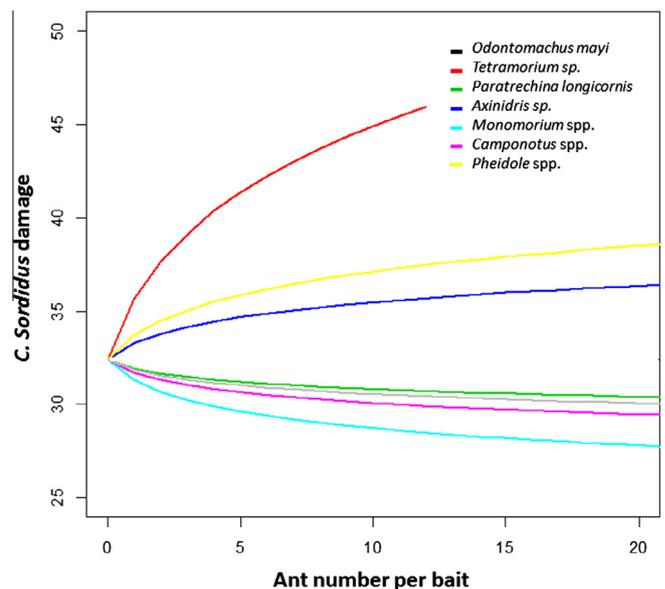
Fig. 2. Relationship between damage by *C. sordidus* to plantain corms and the abundance of seven ant taxa as predicted by a Poisson GLMM.

intercropped plant(s) and on the ant taxon. The similarity of the ant community structure between seasons (Table S1) suggests that climatic conditions were not a main factor structuring the ant

community. Maize had a positive effect on the abundance of *Camponotus* spp., *Monomorium* spp., and *O. mayi*, suggesting that these ant taxa may directly consume maize, may consume prey feeding on maize, or may otherwise benefit from maize habitat. The hypothesis that maize provides alternative prey for predators is supported by other studies. For example, Perfecto and Sediles (1992) showed that pupae of armyworm, *Spodoptera frugiperda*, and corn leafhopper, *Dalbulus maidis*, were more abundant in a maize agroecosystem when ant abundance had been reduced with insecticides, suggesting that these pests were ant prey. Dejean et al. (2000) documented competitive interference between the ants *Camponotus acvapimensis*, *Crematogaster* sp., *P. megacephala*, and *Myrmicaria opaciventris*; because of this interference, the maize pest *Peregrinus maidis* was more abundant when attended by multiple species of ants rather than by a single species. Another study showed that maize attracted predatory ants which, in turn, reduced maize damage by termites (Sekamatte et al., 2003).

In contrast to its positive effects on *Camponotus* spp., *Monomorium* spp., and *O. mayi*, maize had strong negative effects on *P. longicornis*, *Pheidole* spp., *Tetramorium* sp., and *Axinidris* sp. These could be partly due to the intensive cultural practices required by maize. Because of its short, 3 month cycle in our plots it was frequently reseeded, which may have caused disturbance of ants. The intensive farming practices of maize (weed control, irrigation, fertilization, tillage, and reseeding) may also have disturbed these particular ant taxa. Several studies have shown that agricultural practices such as heavy grazing, irrigation, drainage, fertilization, tillage, and planting can all reduce ant biodiversity and abundance (Díaz, 1991; Folgarait, 1998; Perfecto and Snelling, 1995).

Cocoyam had a positive effect on the abundance of *Axinidris* sp., *Camponotus* spp., *O. mayi*, and *Pheidole* spp., but a negative effect on the abundance of *Monomorium* spp. and *Tetramorium* sp. Overall, ants were more abundant in plots intercropped with cocoyam than the other two crops. Tubers and ants are known to be involved in mutualisms (Giusto et al., 2001) where ants defend the plant from insect defoliators and the plant provides nesting sites for the ants (Heil and McKey, 2003; Rosumek et al., 2009). Such a mutualism between ants and cocoyam is likely to play an important role in shaping the ant community.

Gourd plants reduced the abundance of all ant taxa except *Pheidole* spp. Gourd is a tendril-bearing, annual plant with unisexual flowers that are visited by many insects, including ants (Kost and Heil, 2005). Agarwal and Rastogi (2010) showed that *Pheidole* sp. was one of the most abundant ants visiting leaves, bracts, bracteoles, calyces, and flowers of gourd, protecting them against herbivores. Several studies showed a negative interaction between *Pheidole* spp and other predators involved in pest control (González-Hernández et al., 1999; Reimer et al., 1993). *Pheidole* spp. display often an aggressive behavior towards subordinate species, which combined with its numerical dominance on various plant parts (Agarwal and Rastogi, 2010), probably contributed to its rapid colonization of baits.

Ant abundance was more affected by intercropping with gourd- cocoyam than with gourd-maize or cocoyam-maize. The gourd-cocoyam treatment had a positive effect on *Camponotus* spp., *Monomorium* spp., and *Tetramorium* sp. and a negative effect on *O. mayi* and *Pheidole* spp. We suspect that ant abundance was more affected by gourd and cocoyam than by maize because these plants have longer crop cycles than maize. Surprisingly, intercropping with all three crops significantly affected the abundance of only two of the seven ant taxa, *Tetramorium* sp. and *Monomorium* spp. These two taxa, which are dominant ant taxa in many habitats (Gonalves and Pereira, 2012; Gunawardene et al., 2009; Ślipiński et al., 2012; Stringer et al., 2007), are particularly sensitive to plant diversity and often respond to increasing resource heterogeneity (Stringer et al., 2007). Scherber et al. (2010), in contrast, found that

plant diversity decreased ant abundance (Supplementary Fig. 1 in Scherber et al., 2010). Yet another study documented a positive correlation between the numbers of ant species and plant diversity in coffee plantations (Perfecto and Snelling, 1995). Our findings are consistent with the latter study in that intercropping with one plant type almost always increased or decreased the abundance of each ant taxon.

The diversification of cropping systems through intercropping often alters arthropod community structure, reduces the numbers of herbivore pests (Baliddawa, 1985), and increases the abundance of generalist predators (Andow, 1991; Song et al., 2010). In our study, however, the intercropping of plantain with two or three other crops failed to consistently increase ant abundance, suggesting that interactions between ant species such as intraguild predation are of primary importance in structuring the ant community. Other studies have shown that intercropping can increase intraguild predation while relative abundance of ant species remain unchanged, (e.g., (Skovgård and Päts, 1996). Ant communities often contain a dominant species that can structure the ant assemblage by interfering with the foraging activity of other species (Savolainen and Vepsäläinen, 1988). Wielgoss et al. (2014) showed that ant species richness and evenness depend on the ecologically dominant species. Thus, the tramp ant, *P. longicornis*, can dramatically reduce ant diversity and abundance where it is invasive (Wetterer et al., 1999). Plant diversity may also change the abundance of dominant species and thereby have a major impact on ant assemblages (Djieto-Lordon and Dejean, 1999). Another alternative hypothesis is that plant diversity may provide favorable habitats for ants and enhance the availability of primary resources and alternative prey for predatory ants. An increase in the availability of alternative prey can change the abundance and the competitive ability of an ant species and thus affect its ability to control pests (Vasconcelos et al., 2008).

4.2. Ant abundance and corm damage by C. sordidus larvae

We found that the damage caused by *C. sordidus* larvae to plantain corms was correlated with ant abundance for each of the seven taxa. The correlation was negative for *Axinidris* sp., *Monomorium* spp., *Pheidole* spp., and *Tetramorium* sp., taxa which are mostly omnivorous and predaceous (Hanson and Gauld, 1995), and thus potentially direct predators of *C. sordidus*. The potential of *Pheidole* sp. to control *C. sordidus* was demonstrated in Uganda (Abera-Kalibata et al., 2008), and *P. megacephala* and *T. guineense* have been used in the biological control of *C. sordidus* in Cuba (Castineiras and Ponce, 1991; Perfecto and Castineiras, 1998). Single individuals of the invasive ant *P. megacephala* are able to capture a wide range of insects including relatively large prey such as *C. sordidus* (Dejean et al., 2008). For *Camponotus* spp., *O. mayi*, and *P. longicornis*, however, ant abundance was positively correlated with corm damage caused by *C. sordidus* larvae. We hypothesize that these species may be involved in intra-guild predation or competition with other predators of *C. sordidus*. Although molecular analysis of gut contents demonstrated that *C. sexguttatus* can consume *C. sordidus* (Mollot et al., 2014), *Camponotus* spp. are considered to be largely scavengers (Hanson and Gauld, 1995), and so we suspect that the trophic link between *C. sexguttatus* and *C. sordidus* may reflect consumption of *C. sordidus* eggs or dead adults. This is consistent with the low detection frequency of *C. sordidus* in guts of this species (Mollot et al., 2014). *P. longicornis* may have only a weak ability to reduce *C. sordidus* numbers because this ant species must recruit multiple workers to capture and transport large prey like *C. sordidus* (Kenne et al., 2005). The positive relationship between *P. longicornis* and *C. sordidus* damage may also reflect the ability of this ant to decrease ant diversity and abundance (Wetterer, 1999). Surprisingly, we found a positive

relationship between corm damage and the abundance of the predaceous ant *O. mayi*. In their molecular analysis of gut contents, Mollot et al. (2014) found no trophic link between *O. bauri* and *C. sordidus*. However, we hypothesize that the positive relationship between this species and damage is in part because *C. sordidus* larvae are inaccessible to these large ants. This is consistent with the inferences of Way and Khoo (1992), who concluded that predation on both *C. sordidus* eggs and larvae is required to significantly reduce damage. Abera-Kalibata et al. (2008) found that predaceous *O. troglodytes* can reduce *C. sordidus* numbers below damaging levels, depending on *C. sordidus* population density and life stage distribution. The potential for a given species of ant to control *C. sordidus* may also depend on plantation age, plant diversity, and diversity of other arthropods. Indeed, the epigeal surface structure and plant community may also alter control potential for by affecting ant access to inner parts of the banana corm, and therefore to eggs and larvae of *C. sordidus* (Abera-Kalibata et al., 2008). Because of the relatively long period *C. sordidus* larvae spend in the corm (ca. 2 months), some of the observed damage might have been caused by larvae hatching from eggs laid before the experiment began or before companion plants were fully established. Thus, our results probably underestimate the regulatory effects of the ant community. Longer-term experiments should be carried out in future, and perhaps on a broader scale to reduce the edge effects.

In summary, intercropping plantain with maize, cocoyam, or gourd did not significantly affect damage to plantain corms by *C. sordidus* larvae but it did increase the numbers of some ant species and decrease the numbers of others. The damage caused by *C. sordidus* larvae was either positively or negatively correlated with the abundance of the seven individual ant taxa. Numbers of *Monomorium* spp., *Tetramorium* spp., *Axinidris* sp., and *Pheidole* spp. were negatively correlated with *C. sordidus* damage and these ants appear to be the best candidates for *C. sordidus* biological control. Finally, crop diversification in the plantain agroecosystem altered the composition of ant communities which, in turn, altered the level of *C. sordidus* damage, but the effect of the individual companion plants on *C. sordidus* abundance remains unclear. Additional, longer-term experiments will be needed to further improve management recommendations.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocontrol.2014.11.008.

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