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To cite this article: Dominique Carval, Rémi Resmond, Anicet Gbéblonoudo Dassou, Violaine Cotté, Raphaël Achard & Philippe Tixier (2022): Influence of a cover crop on ants and dermapterans in banana plantations: consequences for the regulation of the banana weevil, International Journal of Pest Management, DOI: [10.1080/09670874.2022.2029972](https://doi.org/10.1080/09670874.2022.2029972)

To link to this article: <https://doi.org/10.1080/09670874.2022.2029972>



Published online: 25 Jan 2022.



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Influence of a cover crop on ants and dermapterans in banana plantations: consequences for the regulation of the banana weevil

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ABSTRACT

The banana weevil *Cosmopolites sordidus* Germar is the most important pest of banana and plantain. In banana agroecosystems, cover cropping is a practice that prevents the use of herbicides and may provide natural habitats for generalist predators. Here, we assessed the effect of a cover crop, *Paspalum notatum* Flügge on the ant community, dermapterans and *C. sordidus*. In investigating the dumps of *Pheidole jelskii* Mayr colonies, we found that most of carcasses belonged to other ant species (> 96%) and very few (< 1%) belonged to *C. sordidus*. In plots with banana plants and with and without a cover crop, the occurrences of almost all ant species were negatively correlated with each other, but the occurrence of ants was not correlated with weevil abundance. However, we found a negative relationship between the abundances of dermapterans and *C. sordidus*, both of which were negatively related to presence of the cover crop. These results indicate that dermapterans are probably the main biological control agents of *C. sordidus* and that cover cropping may increase *C. sordidus* regulation.

ARTICLE HISTORY

Received 8 June 2021
Revised 27 October 2021
Accepted 5 January 2022

KEYWORDS

Dermapterans;
biological control;
predation;
scavenging;
cover crop;
trophic network;
dump analysis

1. Introduction

Banana ranks 14th in terms of crop production and is the second most produced fruit worldwide (FAO 2018). The banana weevil *Cosmopolites sordidus* Germar is the most important pest of banana and plantain (Gold et al. 2001, Okolle et al. 2009). Banana weevil females lay eggs in small cavities in the corm or lower pseudostem of banana plants (Cuillé 1951). The larvae bore galleries as they feed on the corm, which weakens the plant and causes yield losses as high as 100% when plants topple before harvest (Gold et al. 2001).

Integrated pest management strategies to reduce weevil infestation include fallow, crop rotation, clean planting material, trapping and pesticides (Budenberg et al. 1993; Beauhaire et al. 1995; Gold et al. 2001; Rhino et al. 2010; Duyck et al. 2011; Okolle et al. 2020). Application of chlordecone in the French West Indies during two decades led to major public health problems (Devault et al. 2018; Joachim et al. 2019). Therefore, alternatives to pesticides must be found to complete the actual integrated pest management strategies. The conservational biological control represents a sustainable way to contribute to pest management.

As other parts of integrated pest management strategies (Kogan 1998), it can contribute to a reduction in pesticide use. The contribution of natural enemies to pest management was estimated as being more important than pesticides (Pimentel and Burgess 2014). The conservational biological control relies on the statement that diversity of natural enemies may be conserved or increased through maintaining natural habitats in agrosystems, and that, in return, natural enemies would contribute to pest regulation (Begg et al. 2017). Several studies have been conducted to look for natural enemies of *C. sordidus* (Tresson et al. 2021). Among the identified potential predators (see Tresson et al. 2021 for a review), dermapterans and ants seem to be of a particular interest in *C. sordidus* management (Koppenhöfer et al. 1992; Abera-Kalibata et al. 2006, 2007, 2008; Mollot et al. 2012; Carval et al. 2016; Tresson et al. 2019). Koppenhöfer et al. (1992) searched for potential predators of the banana weevil in Kenya and assessed their feeding capacity in laboratory experiments. They found that the earwig *Euborellia annulipes* Lucas (Dermaptera) was able to feed on egg and larval stages of the weevil. Abera-Kalibata et al. (2006)

conducted field surveys for natural enemies of *C. sordidus* in the Indo-Malay region, from which the banana weevil is supposed to have originated (Waterhouse 1998). Among the detected predators, the histerid *Plaesius javanus* Erichson larvae and adults attacked larvae and pupae of *C. sordidus* in laboratory experiments. Abera-Kalibata et al. (2006) also reported the direct observation of individuals of the predaceous ant *Myopopone castanea* Smith preying upon *C. sordidus* larvae in crop residues. Elsewhere, sentinel experiments have shown that the tropical fire ant *Solenopsis geminata* Fabricius prey upon eggs of *C. sordidus* (Mollot et al. 2012; Tresson et al. 2019). Abera-Kalibata et al. (2008) demonstrated the ability of two ant species (*Odontomachus troglodytes* Santschi and one species of the *Pheidole* genus) to prey upon naturally laid eggs in banana corms. In French West Indies, studies have identified the earwig *Eurborellia caraibea* Hebard (Dermaptera) and the ant species *S. geminata* and *Camponotus sexguttatus* Fabricius as potential predators of the banana weevil (Mollot et al. 2014; Carval et al. 2016).

Among plant diversification practices, the addition of a cover crop represents the minimal increase of plant diversity in monocropping agrosystems. The first ecological service provided by cover crops is the replacement of herbicide treatment. Elsewhere, the cover crop may also increase the quantity of available resources (food and habitats) to alternative prey (Chailleux et al. 2014) and natural enemies, resulting in a modification of their diet (Duyck et al. 2011; Mollot et al. 2014). However, the modification of trophic networks induced by the addition of a natural habitat, such as a cover crop, does not systematically result in an increase of the regulation of a target pest (Tscharntke et al., 2016).

In the present study, we present a 3-year survey of an ant community, dermapterans, and *C. sordidus* in bare soil and cover cropped banana fields. We aim to (i) investigate on trophic relationships between the dominant ant species of the community and other ants, dermapterans and *C. sordidus* by analyzing colony dumps; (ii) assess the influence of the addition of a cover crop on the ant community, dermapterans and *C. sordidus*.

2. Materials and methods

2.1. Study site and experimental design

The experiment was conducted in Martinique (French West Indies) between July 2012 and April 2015 on an experimental farm in Rivière-Lézarde (14°39'45.04"N; 60°59'59.08"W) in an area initially free from weevil. Six plots were established, each

with an area of 361 m² and with 49 banana plants (Cavendish Grande Naine cultivar). The banana plants were planted on 24 July 2012. The cover crop *Paspalum notatum* was planted in three of the six plots on 11 June 2012, while the other three plots were maintained with bare soil. The plots with the cover crop and with bare soil are hereafter referred to as CCP and BSP, respectively. On 30 of October 2012, 70 banana weevils (sex ratio 1:1) were added to each plot. Each month, banana plants were uniformly fertilized, the cover crop was cut back and weeds were controlled with herbicide (glyphosate) in BSP.

2.2. Sampling of banana weevils and earwigs

Banana weevil and dermapteran abundances were estimated with banana pseudostem traps (pieces of pseudostems 30 cm long cut in half lengthwise) from December 2012 to April 2015, first monthly until November 2013 then in January 2014, April 2014, June 2014, October 2014 and April 2015. At each sampling date, new pseudostem traps, were deposited at the bottom of each banana plant (49 traps per plot), and weevils and earwigs found in the traps 7 days later were counted (Koppenhöfer et al. 1992; Gold et al. 2001). Two species of dermapterans were retrieved: *Euborellia caraibea* and *E. annulata* Dohrn (Brindle 1971). However, earwigs were counted and released at field, and it was impossible to distinct the two species during this sampling.

2.3. Ant sampling

Ant abundances and occurrences were estimated from July 2012 to April 2015, first monthly until November 2013 then in January 2014, June 2014, October 2014 and April 2015. We placed 12 white ceramic tiles (30×30 cm) in each plot at each sampling date. In each subplot, we measured ant occurrence by using canned tuna-honey baits. One bait, which had a diameter of 4 cm was placed in the centre of each ceramic tile. Each tile was sampled 15 and 90 minutes after the baits were deployed. At each sampling time, we identified and estimated the number of individuals of different species present on the tile using the following six-point scale of scores: 1 = 1 ant, 2 = 2-5 ants, 3 = 6-10 ants, 4 = 11-20 ants, 5 = 21-49 ants and 6 ≥ 50 ants (Andersen 1997; Parr 2008; Baccaro et al. 2010). From abundance data, we obtained presence-absence data and we calculated the occurrence of each species among a plot at each sampling time of each sampling date. Samples of all species were collected and conserved

in 70% alcohol then we performed identification to species. Sampling was performed between 7:00 and 11:00 in the morning.

2.4. Dominant analysis

We used the percentage of bait controlled as a measure of dominance (Bestelmeyer 2000; Baccaro et al. 2010). A bait was considered controlled by a species (i) if the number of individuals was > 20 and no other ant was present or (ii) if one species was at least twice as numerous as the second numerous taxa when several species were present, and the total number of individuals was > 20. Following Baccaro et al. (2010), an ant species was considered as a dominant species when (i) it occurred at a proportion of baits > 5%, (ii) it controlled a proportion of baits > 25% whenever it was present and (iii) it had a mean abundance score > 4. Conversely, an ant species was considered as a subdominant species when (i) it occurred at a proportion of baits > 5%, (ii) it controlled a proportion of baits > 20% whenever it was present and (iii) it had a mean abundance score > 2.5. All other species that did not meet all these criteria were considered as subordinate species.

2.5. Investigation of dumps of *P. jelskii* colonies

Since we identified the ant *P. jelskii* as the dominant species (Table 1), we searched the dumps of 27 colonies with the objectives to find out arthropod carcasses to identify competitive and trophic links in which *P. jelskii* is involved. Dumps were sampled using a Cordless Insect Vacuum (BioQuip® Products, Inc. Bioquip) and conserved in a plastic bag. Then, in laboratory, we looked for hard fragments of carcasses with focusing on identifiable fragments

according to a collection of arthropod samples from the same field communities: we counted (i) the number of head capsules of each identifiable ant species, (ii) the number of left and right forceps of dermapterans and (iii) the number of cephalothorax, the number of left and right elytra and legs of weevils. We kept information on the number of dermapterans at the genus taxonomic level because we cannot identify to the species level on the basis of the forceps.

2.6. Statistical analysis

Based on the literature, the investigation of dumps of *P. jelskii* colonies and the population dynamics data, we defined a set of a priori hypotheses describing the relationships within the arthropod community, the effect of treatment (bare soil vs. cover crop) and the sampling time (months). We restricted this analysis to the occurrence of *P. jelskii*, the occurrence of the four ant species identified in the dumps of *P. jelskii* (*S. geminata*, *Paratrechina longicornis* Latreille, *C. sexguttatus*, *Odontomachus ruginodis* Smith) and to the abundance of *Euborellia* spp. and banana weevils, over the common sampling period (15 sampling dates). From these hypothetical links, we constituted a global path model composed of a set of 5 linear sub-models (Table 3). According to response variable distributions, we used binomial generalized models (GLM) for the occurrence of ant species and negative binomial GLM for the abundance of *Euborellia* spp. and *C. sordidus* (Zuur et al. 2009). To consider the influence of population dynamics and temporal autocorrelation, we added the sampling time to each statistical model, from linear to cubic polynomial of time. We then used structural equation modelling (SEM) (Grace 2006) with the piecewiseSEM R-package (Lefcheck 2016)

Table 1. Occurrence of dominant, subdominant, and subordinate ants at baits in all plots.

Species	Baits recorded (%)			Baits controlled (%)			Mean abundance score		
	All	BS	CC	All	BS	CC	All	BS	CC
Dominant	76.2	74.2	78.2	47.1	53.1	41.4	4.0	4.2	3.8
<i>Pheidole jelskii</i>									
Subdominant	21.0	23.3	18.7	33.0	37.1	27.9	3.1	3.2	2.9
<i>Paratrechina longicornis</i>									
<i>Solenopsis geminata</i>	15.9	15.9	15.8	22.3	25.3	19.2	2.8	2.9	2.7
Subordinate	55.2	52.8	57.5	13.9	11.5	16.1	2.8	2.6	3.1
<i>Brachymyrmex patagonicus</i>									
<i>Camponotus sexguttatus</i>	22.2	16.3	28.0	0.3	0.0	0.5	1.6	1.4	1.6
<i>Cardiocondyla obscurior</i>	16.6	18.4	14.9	0.6	0.4	0.9	1.6	1.6	1.5
<i>Odontomachus ruginodis</i>	10.9	11.2	10.6	0.9	0.6	1.2	1.5	1.4	1.5
<i>Nylanderia guatemalensis</i>	9.3	10.0	8.7	1.4	0.0	3.1	1.7	1.7	1.8
<i>Wasmannia auropunctata</i>	5.7	3.6	7.7	9.4	9.3	9.4	2.4	2.2	2.5
<i>Nylanderia fulva</i>	4.3	4.2	4.4	2.3	1.6	3.0	2.0	1.9	2.0
<i>Monomorium ebeninum</i>	3.1	4.6	1.7	35.8	41.4	20.0	3.4	3.6	2.6
<i>Pheidole vallifica</i>	1.7	1.3	2.1	7.8	15.8	3.1	2.1	2.1	2.1
<i>Tetramorium bicarinatum</i>	1.6	0.2	3.0	18.8	0.0	20.0	2.6	1.3	2.7
<i>Tapinoma melanocephalum</i>	1.5	3.0	0	11.1	11.1	–	2.5	2.5	–

(All), in bare soil plots (BS) and in cover crop plots (CC).

to perform a confirmatory test of our global path model and identify the significant relationships. Shipley's tests of direct separation were used to test for missing paths, a Fisher's C statistic was then calculated from the p-values of those tests (Shipley 2009), and finally, we ran a chi-squared test on the C statistic. The global path model is considered to represent the data well when the p-value of this chi-squared test is greater than the significance threshold (Lefcheck 2016). All statistical analyses were performed with R 4.1.0 (R Core Team 2021) and with a significance threshold of 0.05.

3. Results

3.1. Dominant analysis

We recorded 14 species during bait samplings. We identified the ant *P. jelskii* as the dominant species since it had a high occurrence, controlled a large proportion of baits and had a high mean score abundance (Table 1). We identified the ant species *P. longicornis* and *S. geminata* as subdominant species because they had a high occurrence, controlled a moderate proportion of baits and had a moderate mean score abundance (Table 1). We identified all other species as subordinate species (Table 1).

3.2. Investigation of dumps of *P. jelskii*

We retrieved seven identifiable taxa from the 27 colonies (Table 2). The most frequently retrieved species was the ant *S. geminata*, followed by the ants *P. longicornis* and *C. sexguttatus*, the dermapterans of *Euborellia* spp., the ant *O. ruginodis* and the small banana weevil *Polytus mellerborgii* Boheman, and finally *C. sordidus* (Table 2). The highest number of retrieved individuals was associated to the ant *S. geminata* (64.5%), followed by the ant *P. longicornis* (20.8%), then the ant *C. sexguttatus* (10.4%). The numbers of retrieved individuals of other taxa were lower and *C. sordidus* counting for 0.5% of retrieved individuals (Table 2).

3.3. Correlations between species and cover crop

Our global path model represented the data well (Fisher's C=8.18, d.f. = 10, χ^2 test: p=0.611), and 21 of the 34 links tested were significant. SEM results are presented in Table 4 and are summarized in the path diagram in Figure 1. The presence of the cover crop was positively related to the occurrence of *C. sexguttatus*, negatively related to the occurrence of *P. longicornis* and had no significant

Table 2. Results from the investigation of dumps of 27 colonies of *P. jelskii*.

Species / Taxon	Percentage of <i>P. jelskii</i> colonies with carcasses	Number of individuals
<i>Solenopsis geminata</i>	89	1348
<i>Paratrechina longicornis</i>	63	434
<i>Camponotus sexguttatus</i>	85	217
<i>Odontomachus ruginodis</i>	44	22
<i>Cosmopolites sordidus</i>	30	10
<i>Polytus mellerborgii</i>	44	23
<i>Euborellia</i> spp.	48	31

relationship with the occurrence of the remaining ant taxa. We found a negative relationship between the cover crop and the abundances of *C. sordidus* (Figure 2) and *Euborellia* spp. The occurrence of *P. jelskii* was negatively related to the occurrences of all the ant species except that of *O. ruginodis*. *P. longicornis* occurrence was negatively correlated with the occurrence of *S. geminata*. The occurrence of *S. geminata* was negatively related to that of *C. sexguttatus*. The abundance of the *Euborellia* spp. was negatively related to that of *C. sordidus*, while we found no significant relationship between the occurrence of ant taxa and *C. sordidus*. Finally, the time was correlated to all response variables (Table 4 and Figure 3).

4. Discussion

In the present study, we present a 3-year survey of an ant community, dermapterans and *C. sordidus* in bare soil and cover cropped banana fields. We aimed to (i) investigate on competitive and trophic relationships between the dominant ant species of the community and other ants, dermapterans and *C. sordidus* by analyzing colony dumps; (ii) assess the influence of the addition of a cover crop on the ant community, dermapterans and *C. sordidus*.

4.1. Colony dumps investigation

We found *P. jelskii* as being the dominant ant species of our community. By investigating dump of colonies of this species, we were able to access qualitative and quantitative information on its competitive and trophic relationships with other invertebrate species of the community. We found that the majority of identified carcasses belonged to other ant species (> 96%). Similarly, Retana et al. (1992) also found that ants represent respectively 71% and 43% of animal preys in *Pheidole pallidula* Nylander and *Tetramorium semilaeve* André, two omnivorous species. Although the search of dumps does not allow to differentiate between scavenging, predation or deadly combat in

Table 3. Set of GLMs constituting the global path model based on a priori hypotheses regarding the relationships between response variables and explanatory variables. Hypothesis are based on literature and raw data.

Response variable	Explanatory variable	Hypothesis	References	
<i>C. sordidus</i>	<i>P. jelskii</i> <i>C. sexguttatus</i> <i>O. ruginodis</i> <i>Euborellia</i> spp. <i>P. notatum</i>	Top-down control by predators	Mollot et al. 2014; Poeydebat et al., 2017	
	Time Time ²	No effect of the cover crop because of the oligotrophy of <i>C. sordidus</i> Population dynamics	Gold et al. 2001; Duyck et al. 2011 Raw data (Figure 3)	
	<i>C. sexguttatus</i>	<i>P. jelskii</i> <i>P. notatum</i> Time	Negative effect of intraguild predation by <i>P. jelskii</i> Positive bottom-up effect of the cover crop Population dynamics	Dumps of <i>P. jelskii</i> colonies Duyck et al. 2011 Raw data (Figure 3)
<i>O. ruginodis</i>		<i>P. jelskii</i> <i>P. notatum</i> Time Time ²	Negative effect of intraguild predation by <i>P. jelskii</i> Positive bottom-up effect of the cover crop Population dynamics	Dumps of <i>P. jelskii</i> colonies Duyck et al. 2011 Raw data (Figure 3)
		<i>Euborellia</i> spp.	<i>P. jelskii</i> <i>P. notatum</i> Time Time ² Time ³	Negative effect of intraguild predation by <i>P. jelskii</i> Positive bottom-up effect of the cover crop Population dynamics
	<i>S. geminata</i>		<i>P. jelskii</i> <i>P. longicornis</i> <i>P. notatum</i>	Negative effect of intraguild predation by <i>P. jelskii</i> Competition Positive bottom-up effect of the cover crop
<i>P. longicornis</i>			<i>P. jelskii</i> <i>P. notatum</i> Time	Negative effect of intraguild predation by <i>P. jelskii</i> Positive bottom-up effect of the cover crop Population dynamics
		<i>P. jelskii</i>	<i>P. notatum</i> Time	Positive bottom-up effect of the cover crop Population dynamics

interspecific encounters, the high number of carcasses of *S. geminata*, *P. longicornis* and *C. sexguttatus* species suggests that direct intraguild predation by *P. jelskii* occurs on these three species. On the contrary, our results suggest low level of intraguild predation by *P. jelskii* on the *Euborellia* spp., which account for less than almost 1.5% of the identified carcasses. Similarly, the banana weevils, *C. sordidus* and *P. mellerborgii* account respectively for almost 0.5% and 1% of the identified carcasses, suggesting that *P. jelskii* ants play a marginal role in the regulation of adult weevils. Such investigation presents the advantage to bring diet information on a species while being non-lethal. In comparison, gut content assays of arthropod predator imply the trapping and killing of several individuals for post-mortem analysis (Mollot et al. 2014; Hagler 2019). Furthermore, we easily obtained both qualitative and quantitative assessment of prey consumption by a predator, while molecular gut content analysis provide only frequency as a proxy for quantitative evaluation of predation. However, both methods do not allow to discriminate between scavenging and true predation (Foltan et al. 2005; Juen and Traugott 2005). This problem can be circumvented by tagging arthropods

and taking repeated samples from dumps. It is also worthy to note that when studying ant diet, molecular gut content analysis of foraging workers may not reveal real colony diet since animal preys may mainly be consumed by other life stages (Cassill and Tschinkel 1999). All being said, we argue that colony dump investigation may be a cost-efficient, non-lethal and complementary method to obtain information on trophic relationships occurring in a community of ants.

4.2. SEM and trophic relationships

4.2.1. Cover crop

In agroecology, it is hypothesized that biological control may be enhanced through bottom-up modification of the agrosystems. Here, we compared one-species plant plots to two-species plant plots. We found that this addition of a cover crop did not affect most of the omnivorous and predaceous ant occurrences. This may be partly explained by the fact that the experimental set-up may not be adequate for species that forage on large distances such as *S. geminata*, which may forage at least up to 20 m (Way and Heong 2009). However, we found

Table 4. Pathway coefficient estimates and p-values from the structural equation modelling.

Response variable	Explanatory variable	Estimate (\pm SE)	p value
<i>C. sordidus</i>	<i>P. jelskii</i>	-0.1307 (\pm 0.5635)	0.8166
	<i>S. geminata</i>	-0.3932 (\pm 0.6812)	0.5638
	<i>P. longicornis</i>	-0.0068 (\pm 0.4938)	0.9890
	<i>C. sexguttatus</i>	0.0903 (\pm 0.4938)	0.8522
	<i>O. ruginodis</i>	-0.7152 (\pm 0.8448)	0.3972
	<i>Euborellia</i> spp.	-0.0147 (\pm 0.0035)	<0.0001
	<i>P. notatum</i>	-0.4769 (\pm 0.1775)	0.0072
	Time	0.2846 (\pm 0.0528)	<0.0001
	Time ²	-0.0070 (\pm 0.0016)	<0.0001
<i>Euborellia</i> spp.	<i>P. jelskii</i>	0.7612 (\pm 0.6703)	0.2561
	<i>P. notatum</i>	-0.5443 (\pm 0.2034)	0.0075
	Time	0.3518 (\pm 0.1206)	0.0035
	Time ²	-0.0227 (\pm 0.0101)	0.0064
	Time ³	0.0006 (\pm 0.0002)	0.0188
<i>O. ruginodis</i>	<i>P. jelskii</i>	-0.3658 (\pm 0.4550)	0.4214
	<i>S. geminata</i>	-1.2260 (\pm 0.6448)	0.0573
	<i>P. longicornis</i>	-0.2548 (\pm 0.4150)	0.5392
	<i>P. notatum</i>	0.1067 (\pm 0.1432)	0.4562
	Time	0.4011 (\pm 0.0493)	<0.0001
<i>C. sexguttatus</i>	Time ²	-0.0133 (\pm 0.0016)	<0.0001
	<i>P. jelskii</i>	-1.0494 (\pm 0.3608)	0.0036
<i>P. longicornis</i>	<i>S. geminata</i>	-1.7783 (\pm 0.4828)	0.0002
	<i>P. longicornis</i>	-0.2703 (\pm 0.3160)	0.3922
	<i>P. notatum</i>	0.8982 (\pm 0.1103)	<0.0001
	Time	0.8982 (\pm 0.1103)	<0.0001
<i>S. geminata</i>	<i>P. jelskii</i>	-2.5269 (\pm 0.3254)	<0.0001
	<i>P. notatum</i>	-0.2249 (\pm 0.1142)	0.0490
	Time	0.0831 (\pm 0.0085)	<0.0001
<i>P. jelskii</i>	<i>P. jelskii</i>	-2.4107 (\pm 0.4634)	<0.0001
	<i>P. longicornis</i>	-1.3174 (\pm 0.4634)	0.0064
	<i>P. notatum</i>	-0.0693 (\pm 0.1263)	0.5830
<i>P. jelskii</i>	Time	-0.1255 (\pm 0.0178)	<0.0001
	<i>P. notatum</i>	0.2056 (\pm 0.1070)	0.0548
<i>P. jelskii</i>	Time	-0.0888 (\pm 0.0065)	<0.0001

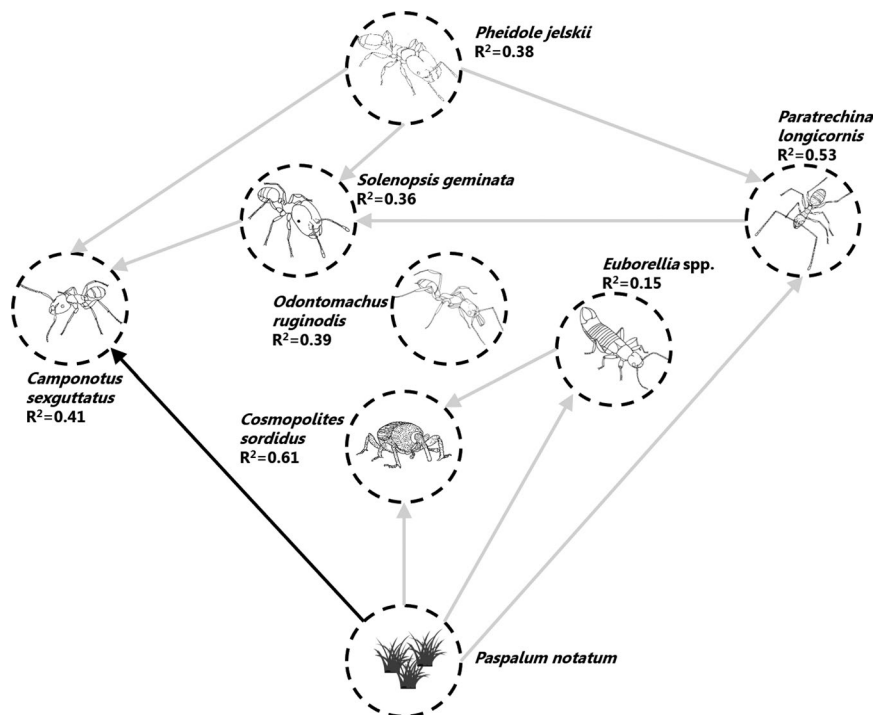


Figure 1. Structural equation model of exploring the relationships between the occurrence of the dominant ant *P. jelskii*, the subdominant ants *S. geminata* and *P. longicornis*, the subordinate ants *C. sexguttatus*, *O. ruginodis*, the abundance of *Euborellia* spp. and *C. sordidus*, and the cover crop *P. notatum*. Black and gray arrows represent significant ($p < 0.05$) positive and negative relationships, respectively. For clarity, the non-significant relationships between species and the relationships with the variable Time were not represent here (see Table 3).

that the carpenter ant *C. sexguttatus* occurrence is positively related to the presence of a cover crop. We observed that this subdominant species

primarily nests in dead or living standing banana pseudostems, suggesting that the negative relationship with *P. jelskii* and *S. geminata* is due to

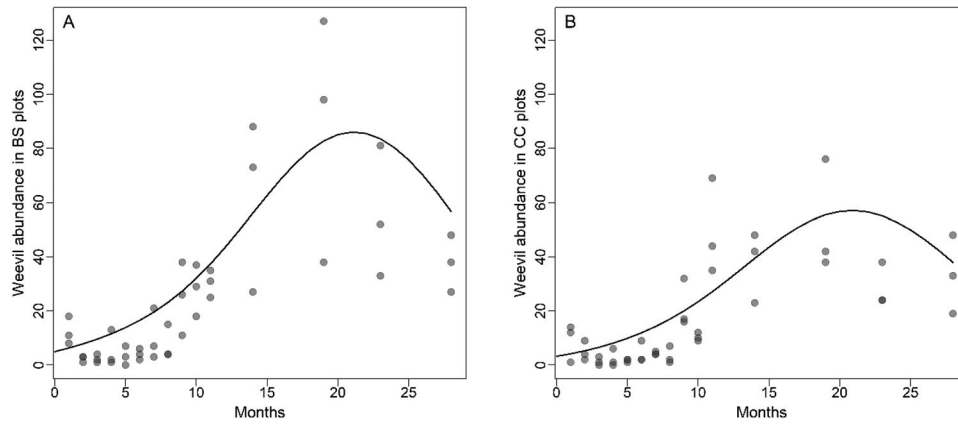


Figure 2. Weevil abundance in the bare soil (A) & cover crop plots (B). Curves are prediction from the fitted model.

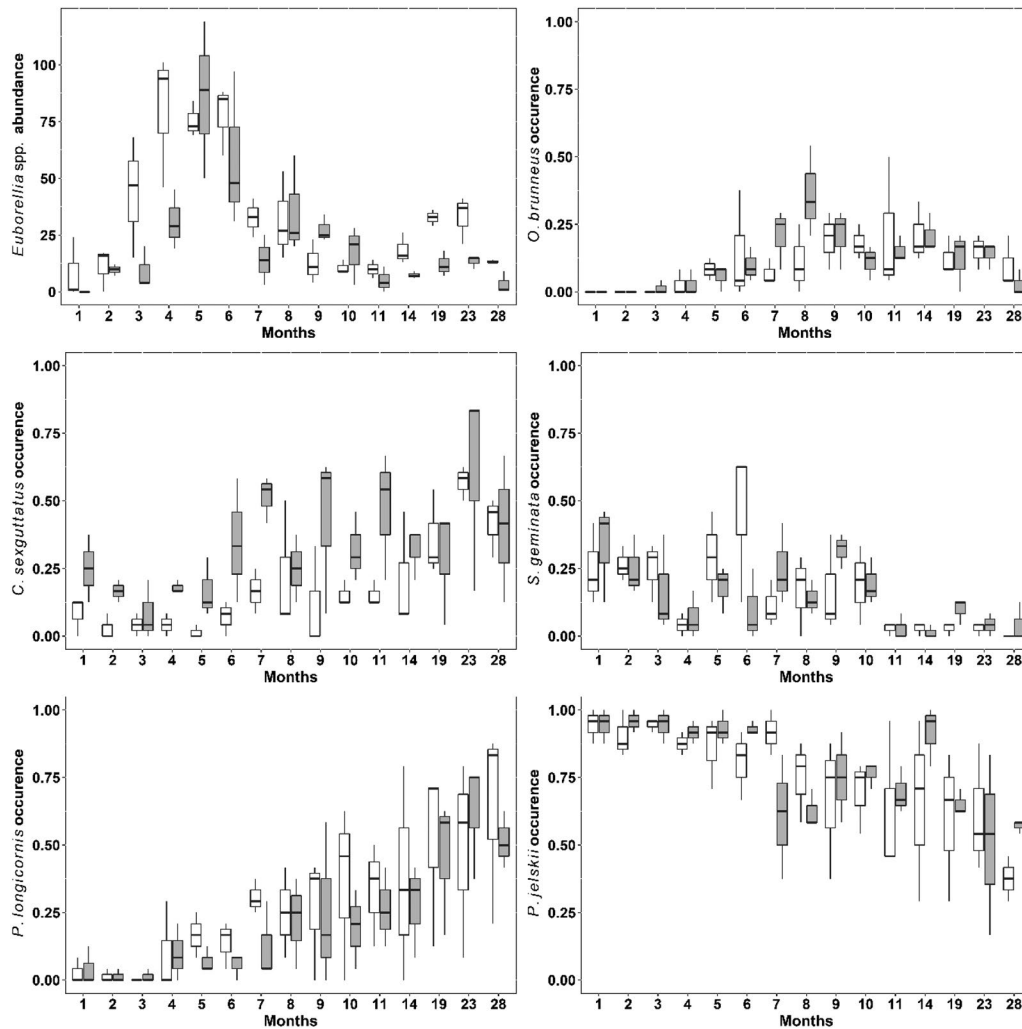


Figure 3. Abundances of *Euborellia* spp. and occurrences of the ants *O. ruginodis*, *C. sexguttatus*, *S. geminata* and *P. jelskii*. White boxes: Bare soil plots; Grey boxes: Cover crop plots. Note that scale of x-axis is not proportional.

competition in foraging since these two species are primarily ground-nesting species. *P. longicornis* was found to be scarce in the presence of other species (*P. megacephala*, *Wasmannia auropunctata* Roger) which, like *P. longicornis*, nest and compete with it at ground level (Way and Bolton 1997). However, *P. longicornis* may be a strong competitor in

non-native area and may replace native ant fauna (Wetterer et al. 1999).

We expected a positive relationship between the abundance of dermapterans and the addition of a cover crop because cover crop can sustain dermapterans by attracting alternative prey that dermapterans can feed on. Furthermore, cover crop also

supplies shading to arthropods thus providing a more suitable micro-climate than bare soil with less heat and more humidity, and a more suitable habitat for egg laying or larval development of dermapterans. However, we found a lower abundance of *Euborellia* spp. in cover crop plots than in bare soil crops. This may be due to a dilution effect affecting the sampling. Using an individual-based model of earwig-like foraging behaviour, Collard et al. (2018) have shown that the time spent by a generalist predator in the vicinity of banana plants decreases as the proportion of an alternative favourable habitat increases. In our case, the proportion of alternative habitat is maximal in cover crop plots. Since pseudostem traps were deposited at the bottom of banana plants, such dilution effect may have induced bias in the sampling by underestimating dermapterans abundance in cover crop plots.

4.2.2. Invertebrate community interactions

The results found by the SEM of the 3-years survey are consistent with the findings of the investigation of *P. jelskii* colony dumps. First, we found negative relationships between *P. jelskii* and the three ant species which were the most represented in the dumps of colonies. This suggests that the identified carcasses from dumps is a good quantitative representation of the intensity of competition and aggressive behaviour of *P. jelskii* towards its main competitors. Therefore, we argue that the retrieved carcasses are issued from direct attack or predation of this species on the others and that this aggressive behaviour explains partially the pattern of species occurrence during the survey, leading to the conclusion that interference competition is in our study case the main driver of community assemblage. The investigation of dumps of *S. geminata*, *P. longicornis* and *C. sexguttatus* colonies could have provided more information on the relationships between these species. For instance, we found that *C. sexguttatus* occurrence was negatively associated to *S. geminata* occurrence. This may be the result of interference competition and/or predation of *S. geminata* on *C. sexguttatus*, or due to exploitation competition. According to our results, none of the ant species seems to play a major role in the regulation of the banana weevil. Indeed, we found no significant relationships between *P. jelskii* occurrence and *C. sordidus* abundance, which is consistent with the very low number of carcasses retrieved from dumps. These results lead us to conclude that, even if *P. jelskii* is able to prey upon the banana weevils, this species probably plays a marginal role in the regulation of adult weevils and probably also on egg and larval stages of the weevils. *Solenopsis geminata* has

been previously reported as a potential effective agent of pest regulation (Jaffe et al. 1990, Sirjusingh et al. 1992, Way and Heong 2009, Bailly Maître et al. 2012) in general and in the case of *C. sordidus* in particular (Mollot et al. 2012, 2014) but our 3-year monitoring led to a contradicting conclusion. Previous studies on the predation of *C. sordidus* by *S. geminata* were conducted to search for a trophic link between this ant species and the pest through prey-sentinel experiments with *C. sordidus* eggs as prey items (Mollot et al. 2012) or through molecular gut content analysis (Mollot et al. 2012, 2014). While these studies showed that predation on *C. sordidus* by *S. geminata* is possible, ours shows that such predation events are probably too scarce and opportunistic to lead to an efficient regulation of the population of *C. sordidus* in banana agrosystems. The same reasoning holds for *C. sexguttatus* since it was previously identified as a potential predator of *C. sordidus* (Mollot et al. 2014) but we failed to found relationship between its occurrence and the abundance of *C. sordidus*.

However, these results alone do not allow to conclude that these species have no role on the *C. sordidus* regulation, only that it is probably weak. Exclusion experiments should be performed to assess quantitatively the impact of ants on the dynamics of *C. sordidus* populations. Contrary to ants, the dermapterans seem to play a role in the *C. sordidus* regulation. Indeed, we found a negative relationship between the abundance of *Euborellia* spp. and the abundance of the banana weevils. Previous studies have reported dermapterans as potential predators of *C. sordidus* (Koppenhöfer et al. 1992; Mollot et al. 2014; Carval et al. 2016).

Identifying predators that prey upon a pest and quantifying such relationships is a primary importance in conservational biological control. However, studying trophic interactions in invertebrate communities in nature is difficult because of the smallness of organisms, their possible cryptic and nocturnal behaviour such as *C. sordidus*. Through a 3-year survey, we found that the dermapterans of the genus *Euborellia* could play a role in the *C. sordidus* regulation while ant species encountered in these communities would not have any impact on *C. sordidus* population. Further studies should be carried out in different banana growing regions, through the combined use of the different methods available today: population monitoring, DNA analysis of stomach contents and faeces, analysis of dumps of ant colonies and image capture and analysis through deep learning. Such studies should also consider vertebrates as potential agents of biocontrol of *C. sordidus* (Tresson et al. 2021).

Acknowledgments

The authors thank J.J. Banidol, C. Hubervic, and M. Alier for help in the field. This work was supported by CIRAD and was funded by the Projects sustainable cropping systems design from E.U. FEDER (grants PRESAGE no. 31106, 32139, and 33157).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Data availability statement

Data and R analysis script are available on the Cirad dataverse at <https://doi.org/10.18167/DVN1/CMYEVA>.

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