

New primary resource increases predation on a pest in a banana agroecosystem

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- Abstract**
- 1 Primary resources may affect the structure of species assemblages in upper trophic levels of food webs. These bottom-up effects may involve important ecological processes that affect pest control. For example, population densities of natural enemies may increase when alternative preys are favoured by a new resource.
 - 2 Ants, particularly *Solenopsis geminata* Forel (Myrmicinae), are recognized as effective predators of herbivores eggs. In the present study, we tested the hypothesis that the addition of a primary resource in a banana agroecosystem will increase pest control of the banana weevil *Cosmopolites sordidus* Germar (Coleoptera, Curculionidae) by ants.
 - 3 Using stable isotope analyses, we showed that *S. geminata* used the new resource pathway provided by the addition of a cover crop. This change was revealed by increased $\delta^{13}\text{C}$ values ($^{13}\text{C}/^{12}\text{C}$) in a cover crop treatment (C4 plant) compared with a banana (C3 plant) in bare soil treatment.
 - 4 We also showed that the abundance of *S. geminata*, as measured with pitfall traps, was 4.8–5.4-fold higher in the cover crop treatment than in the bare soil treatment. Estimation of egg predation rates was in the range 7.8–70.3%, which occurred in plots with the lowest and highest *S. geminata* numbers, respectively.
 - 5 The addition of a new primary resource in this system changed the origin of the carbon consumed by predators and increased their densities. The increased ant abundance resulted in increased predation of weevil eggs, which was consistent with our hypothesis. These results will be useful for the design of cropping systems that enhance the biological regulation of pests.

Keywords Apparent competition, *Cosmopolites sordidus*, cover crop, diet, *Musa* spp., predation rate, *Solenopsis geminata*, stable isotope.

Introduction

Top-down and bottom-up effects are both acknowledged as regulatory mechanisms in food webs (Elton, 1927; Rosenheim, 1998). In terms of pest control, top-down effects by natural enemies have often been emphasized because of their direct role in decreasing pest numbers (Carter & Rypstra, 1995; Cardinale *et al.*, 2003; Bell *et al.*, 2010). The bottom-up effect of primary resources (i.e. plants or plant-derived materials) may, however, also be important in pest control. In a recent 8-year experiment,

Scherber *et al.* (2010) found that plant diversity in agroecosystems has particularly strong effects on upper trophic levels in that an increase in plant species richness caused an increase in parasitism of pests (i.e. species-rich systems enhanced the potential for biological control). New primary resources in the agroecosystem may provide alternative prey for upper trophic levels and thereby increase population densities of natural enemies and pest control (Wise *et al.*, 2006; Barberi *et al.*, 2010).

An increase in predation when alternative preys are present may result from apparent competition (Holt, 1977). In this case, apparent competition would refer to the positive effects of two noncompeting prey on predator abundance. The increase in abundance induced by the consumption of the first prey could

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increase predation on the second prey (van Veen *et al.*, 2006). In arable crops, indirect interactions between pest and non-pest arthropods through a shared enemy (a biological control agent) can lead to a decrease in pest abundance (Evans & England, 1996). The effectiveness of pest consumption by generalist predators could increase when the nonpest prey maintains higher numbers of the predator and when predation on the pest improves consumer fitness (Polis & Strong, 1996). On the other hand, when preference is lower for the pest than for the nonpest prey, predators should switch their diet to the alternative prey and the pest population could increase (Koss & Snyder, 2005).

The addition of straw, cover crops or similar primary resources to agroecosystems may increase predator abundance and foraging activity, and thus reduce herbivore abundance (Symondson *et al.*, 2002). For instance, Mathews *et al.* (2004) showed that the addition of composted mulch to an apple orchard supported greater densities of alternative prey, which were positively correlated with increased predator abundance. Similarly, cover crops, which are usually employed to limit erosion and the leaching of organic matter, are assumed to support nonpest populations that might act as alternative prey for predators. This has already been demonstrated in a rice-based tropical cropping system in which a wood-debris mulch was found to increase the abundance of spiders, carabids, staphylinids and ants (Afun *et al.*, 1999). Such results are in agreement with the prediction of the apparent competition theory in the case where the pest constitutes the preferred prey (Holt & Kotler, 1987).

In the present study, we tested the general hypothesis that the addition of a new primary resource, a cover plant, would increase pest control in a banana agroecosystem in Martinique. The main insect pest in bananas is the banana weevil *Cosmopolites sordidus* Germar (Coleoptera, Curculionidae). Females of this species lay eggs in the corm of the banana tree (Gold *et al.*, 2001). Because the larvae bore deeply into the corm, the egg appears to be the stage that is most accessible to natural enemies. Koppenhofer (1993a) showed that 58% of eggs are directly accessible to predators. Ants are effective predators of banana weevil eggs (Gold *et al.*, 2001; Abera-Kalibata *et al.*, 2007, 2008). Ant species identified in banana agroecosystems in Martinique include *Odontomachus bauri* Emery (Ponerinae), *Wasmannia auropunctata* Forel (Myrmicinae) and the fire ant *Solenopsis geminata* Forel (Myrmicinae), and our direct observations of predation in the field indicate that *S. geminata* is the dominant species feeding on weevil eggs in our field sites (G. Mollot, unpublished observations).

To study the effect of a cover plant on the potential of *S. geminata* to control the banana weevil, we tested specific hypotheses with respect to when a cover crop is added to the banana agroecosystem: (i) *S. geminata* is able to use the new resource pathway; (ii) the abundance of *S. geminata* increases; and (iii) predation on banana weevil eggs increases. To test the first hypothesis, we used stable isotope analysis of carbon and nitrogen to detect changes in trophic niche with respect to resource and trophic levels (Ponsard & Ardit, 2000; Post, 2002). To test the second and third hypotheses, we used trapping methods to quantify ants and we measured predation of banana weevil eggs that were placed in the field, mimicking the egg-laying behaviour of the banana weevil.

Materials and methods

Study sites

The present study was conducted in Martinique (French West Indies) during June and July of 2010. The two treatments were 'bare soil' (banana plantation with bare soil, which is the traditional system) and 'cover crop' (banana plantation with a cover crop). Two banana cropping sites were selected: the first site was an experimental farm in Rivière Lézarde (60°59'59"W; 14°39'45"N) with a bare soil plot (30 × 10 m) near a plot (16 × 23 m) cropped with *Brachiaria decumbens* Stapf (Graminaceae: Poaceae). The second site was the Leyritz farm in Basse-Pointe (61°07'20"W; 14°50'50"N) where a bare soil plot (30 × 15 m) was adjacent to a plot (31 × 16 m) cropped with *Cynodon dactylon* (L.) Persoon (Graminaceae: Poaceae). The two sites were separated by 24.4 km. The soil at the Rivière Lézarde site is a nitisol, and the site has a mean annual temperature of 26.5 °C and a mean annual rainfall of 2000 mm. The soil at the Leyritz site is an andosol with pumice, and the site has a mean annual temperature of 26 °C and a mean annual rainfall of 2500 mm. The plots at both sites were representative of intensive cultural management (i.e. banana trees were planted in double rows with approximately 4 m separating the double rows). None of these banana fields received any insecticide application during the 4 years before the experiment.

Stable isotopes analysis

Changes in predator diet may be indicated by changes in isotopic signature in ¹³C and ¹⁵N (Ponsard & Ardit, 2000; Oelbermann & Scheu, 2002; Vanderklift & Ponsard, 2003) and an analysis of ratios of stable isotopes has recently contributed to our understanding of ant feeding behavior (Mooney & Tillberg, 2005). To test for a change of resource pathway in predator diet with the addition of a primary resource to the banana agroecosystem, we first measured the isotopic signature of each primary resource (banana and cover crops) and of the predator. Seventy samples of banana trees, 24 samples of *B. decumbens*, 26 samples of *C. dactylon* and 28 samples of *S. geminata* were analyzed. Plant samples were collected with a scalpel, and ants were collected with a manual vacuum (for details of the trapping methods, see below). Each sample was conditioned in a dry pillbox and frozen at -20 °C until preparation for isotope analysis. Frozen samples were lyophilized for 48 h and ground into a fine powder before an appropriate mass was placed in a tin capsule for analysis. When one individual of *S. geminata* had sufficient biomass (0.4 mg), it was analyzed independently; otherwise, two individuals were pooled to make one sample. As noted, animals contain various ratios of the stable isotopes ^δ¹³C and ^δ¹⁵N, reflecting the isotopic composition of their diet (Ponsard & Ardit, 2000). Animal tissues tend to accumulate the heavier isotope compared with their diet. In our system, the cover crops consisted exclusively of C4 plants (*C. dactylon* and *B. decumbens*) that have a different ^δ¹³C isotopic signature from that of banana tree, which is a C3 plant (Staddon, 2004). Differences observed for ^δ¹³C values of primary resources reflect differences in carbon metabolism between C3 plants (banana trees), whose values usually range between -25‰

and -27% , and C4 plants (cover plants), whose values usually range between -9% and -17% (Staddon, 2004). $\delta^{13}\text{C}$ values of the predator reflect the origin of the carbon it has absorbed [i.e. whether the carbon resource was derived from the C3 pathway (banana trees), from the C4 pathway (cover plants) or from both]. Isotope ratios were determined with an isotope ratio mass spectrometer (SerCon 20/20; SerCon Ltd, U.K.) coupled to an ANCA-GSL elemental analyzer (PDZ Europa, U.K.) at The James Hutton Institute (U.K.). All stable isotope values are reported in the δ notation: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Standards are PeeDee Belemnite (Peterson & Fry, 1987) and atmospheric air.

Abundance of *S. geminata*

Two trapping methods were used to assess the abundance of *S. geminata*: pitfall traps and pseudostem traps. Pitfall traps are the most commonly used method for capturing ground-dwelling arthropods in the field. Pitfall traps were filled with soapy water and regularly distributed over the study plots, with 4 m between traps. After 48 h, trapped individuals were identified and counted. Eight and nine pitfall traps per treatment were monitored at Rivière Lézarde and Leyritz sites, respectively. The pseudostem trap consists of one-half of a section of fresh banana pseudostem (approximately 50 cm in length) that is placed on the soil near the base of a banana tree. After 48 h, individuals under the pseudostem trap are removed, identified and counted. Twenty-eight and 23 pseudostem traps per treatment were monitored at Rivière Lézarde and Leyritz sites, respectively.

Predation on weevil eggs

We estimated predation rates from field measurements with corms that were artificially infested with eggs in plots with the bare soil and the cover crop treatments. Eggs were obtained from laboratory-reared *C. sordidus* adults that were maintained on fresh banana tissues in a plastic box ($20 \times 15 \times 5$ cm) at 25°C . These reared adults were initially collected from different sites in Martinique using dry pitfall traps (so that the weevils were alive when collected) containing sordidin, a synthesized aggregation pheromone (Jaramayan *et al.*, 1997). Females produce one to four eggs per week; the sex ratio in natural populations is 1 : 1; and the minimum duration of egg development to the first larval instar is 12 days under tropical conditions (Gold *et al.*, 2001). A total of 1940 weevils were collected and maintained to obtain a minimum of 200 freshly-laid eggs per day. The female lays eggs (approximately 1 mm long) in small cavities that she has previously chewed with her rostrum, within 1–2 mm of the corm or pseudostem surface (Koppenhofer, 1993b). We placed eggs on banana trees in the field to mimic placement by a female weevil. Each egg was individually deposited with a wet brush into a small cavity, which was dug with a stainless steel needle at the base of the banana tree. Each banana tree was artificially infested with five eggs (2 cm spacing between eggs), and there were 20 and 18 artificially infested banana trees per treatment at Rivière Lézarde site and Leyritz

farm site, respectively. Predation rates were estimated by counting remaining eggs after 1 h of exposure. To check for causes of egg removal other than predation (e.g. rain run-off), we established controls by applying tree glue (Pelton[®] 2; Scotts France SAS, France) around some eggs to protect them from ants. The percentage of remaining eggs in controls was significantly different between sites [generalized linear mixed (GLM) with binomial error: $\Delta_{\text{Deviance}} = 10.8$, d.f. = 1,23, $P = 0.001$] and between treatments ($\Delta_{\text{Deviance}} = 14.7$, d.f. = 1,24, $P < 0.001$). At Rivière Lézarde, the percentage of remaining eggs in controls was $100 \pm 0\%$ ($n = 8$ banana trees) and $75 \pm 16\%$ ($n = 8$ banana trees) for the bare soil treatment and cover crop treatment, respectively. At the Leyritz farm, the percentage of remaining eggs in controls was $100 \pm 0\%$ for both the bare soil treatment ($n = 5$ banana trees) and the cover crop treatment ($n = 5$ banana trees).

Statistical analysis

Although $\delta^{13}\text{C}$ values were significantly but only slightly higher for *B. decumbens* than for *C. dactylon* (d.f. = 1,49; $F = 106.57$; $P < 0.001$; for $\delta^{13}\text{C}$ values, see Results), $\delta^{13}\text{C}$ values for *S. geminata* did not differ between the two cover crop plots (d.f. = 1,24; $F = 0.4178$, $P = 0.5278$). The two cover crop species were pooled under the factor 'cover crop'; this pooled effect was used to examine the main effect of cover crop and the interaction between cover crop and site in the subsequent analyses. Values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, abundance in pitfall traps, abundance in pseudostem traps and predation rate were analyzed using generalized linear mixed-effects models (GLMM; Bolker *et al.*, 2009) as a function of treatment (bare soil or cover crop) with normal, Poisson and binomial errors for isotope, abundance and predation data, respectively. We treated 'site' as a random effect because we assumed that plots contained unobserved heterogeneity and also to account for pseudo-replication. Overdispersion was taken into account by using 'sample identifier' as an individual-level random variable. The GLMMs were fitted by the Laplace approximation using the 'glmer' function in 'lme4' (Bates & Maechler, 2011) with statistical software R 2.12.1 (R Development Core Team, 2009).

Results

Stable isotope analysis

The mean $\delta^{13}\text{C}$ values of the primary resources were $-26.9 \pm 0.2\%$ for banana trees, $-12.4 \pm 0.1\%$ for *B. decumbens* and $-13.6 \pm 0.1\%$ for *C. dactylon*. $\delta^{13}\text{C}$ values for *S. geminata* were significantly greater in the cover crop treatment ($-17.6 \pm 0.4\%$) than in the bare soil treatment ($-21.4 \pm 0.4\%$), indicating a diet shift from a banana to a cover crop pathway (Table 1). The mean $\delta^{15}\text{N}$ values of the primary resources were $4.1 \pm 0.2\%$, $2.1 \pm 0.5\%$ and $2.1 \pm 0.3\%$, for banana trees, *B. decumbens* and *C. dactylon*, respectively. $\delta^{15}\text{N}$ values of *S. geminata* were not significantly different between bare soil ($7.9 \pm 0.2\%$) and cover crop treatments ($8.5 \pm 0.4\%$), and the effects of site and interactions were not significant.

Table 1 Effect of treatment (bare soil or cover crop) on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, abundance in Pitfall traps, abundance in pseudostem traps and predation rate, as analyzed by generalized mixed-effect models

Variables	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Abundance in pitfall traps	Abundance in pseudostem traps	Predation rate
Distribution error	Normal	Normal	Poisson	Poisson	Binomial
AIC	141.35	103.92	79.92	263.38	183.69
ΔAIC	-13.65	0.67	-14.12	-23.02	-9.27
Log-likelihood	-59.85	-48.30	-35.96	-127.69	-87.84
<i>P</i>	<0.0001	0.248	<0.0001	<0.0001	0.0007

All models include two random effects: 'sample identifier' and 'site'. All models present 3 degrees of freedom and $\Delta\text{d.f.} = 1$. Distribution errors are indicated for each analyzed variable. ΔAIC corresponds to the Akaike information criteria (AIC) value of the presented model minus AIC of the model without treatment.

Abundance of *S. geminata*

The mean abundance of *S. geminata* ranged from 0.6 ± 0.2 individuals ($n = 8$) to 10.9 ± 2.9 individuals ($n = 9$) per pitfall trap and from 0.3 ± 0.1 individuals ($n = 23$) to 10.0 ± 1.6 individuals ($n = 28$) per pseudostem trap (Fig. 1). The abundance of *S. geminata* measured with pitfall traps was 4.8- and 5.4-fold higher in the cover crop treatment than in the bare soil treatment at the Rivière Lézarde site and the Leyritz farm site, respectively. The values with pseudostem traps were 1.6- and 13.6-fold higher in cover crop than in bare soil at the Rivière Lézarde site and the Leyritz farm site, respectively (Table 1). Overall, the abundance of ants was higher at the Rivière Lézarde site than at the Leyritz farm site, based either on pitfall or pseudostem traps.

Predation on weevil eggs

Predation rates (percentage of weevil eggs removed from corms) were lowest in the bare soil treatment at the Leyritz site ($7.8 \pm 3.3\%$, $n = 18$ banana trees) and highest in the cover crop treatment at the Rivière Lézarde site ($70.3 \pm 3.8\%$, $n = 20$ banana trees) (Fig. 2). The predation rate was 1.28-fold higher in the cover crop treatment than in the bare soil treatment at Rivière Lézarde and 6.28-fold higher at the Leyritz farm site; the effects of treatment and site were significant but the interaction was not (Table 1). Although predation by individual species of predators was not quantified, we did observe *S. geminata* removing eggs from corms that were artificially infested with eggs.

Discussion

Solenopsis geminata uses the new primary resource pathway

When the only primary resource in the agroecosystem was the banana tree (bare soil treatment), *S. geminata* mainly fed in the C3 pathway, although not exclusively because its $\delta^{13}\text{C}$ value on bare soil was different from that of banana trees. The generalist nature of this ant and its ability to explore its environment allow it to prey outside the plot, where C4 plants can be present. When a new resource (i.e. the cover crop) was added to the system, an additional change in the origin of

consumed carbon was observed. Our results on stable isotope ratio show that *S. geminata* used the new primary resource pathway. This could be explained in two ways: either the diet of the predator changed or the diet of the main prey of *S. geminata* changed. Generalist predators are able to consume a large spectrum of prey and, by definition, are not specialized on pest prey (Begon *et al.*, 2006). Supplemental sampling was performed with a suction sampler (D-vac®; Rincon-Vitova Insectaries, Inc., Ventura, California) to determine potential alternative prey supported by the cover crop at the Rivière Lézarde site. Although several specimens belonging to various orders and families were identified, the most abundant specimens were leafhoppers (Hemiptera: Cicadellidae), which were present only in the cover crop treatment (G. Mollot, unpublished data). Shifts in the resource pathway by generalist predators after an increase in alternative primary resources have been documented for different species (Wise *et al.*, 2006; Kuusk & Ekbom, 2010; Messelink *et al.*, 2010; Duyck *et al.*, 2011). Using isotope analyses, Duyck *et al.* (2011) found that different generalist predators changed their trophic position when a cover crop was present in the banana agroecosystem. A diversity of food sources appears to be essential for generalist predators, which require some levels of diversity in food to obtain an optimal composition of nutrients (Kuusk & Ekbom, 2010).

Increase in abundance of *S. geminata*

We found that the abundance of *S. geminata* was always higher in banana plots with cover crops than in plots with bare soil, regardless of the site or trapping method. This is consistent with the concept that cover plants support the development of alternative prey. In the present study, we suspect that the main alternative prey was leafhoppers. In addition to acting as prey, leafhoppers also produce honeydew that may support the increased *S. geminata* abundance. Ant-hemipteran mutualistic interactions have been frequently documented (Styrsky & Eubanks, 2007). In these relationships, ants protect hemipteran species from natural enemies, such as predators or parasitoids, and collect hemipteran honeydew. Menke *et al.* (2010) showed that ant colonies with access to honeydew have lower $\delta^{15}\text{N}$ values than ant colonies without access to honeydew. In our system, we found no difference between $\delta^{15}\text{N}$ values of *S. geminata* in bare soil versus cover crop plots. Additional research

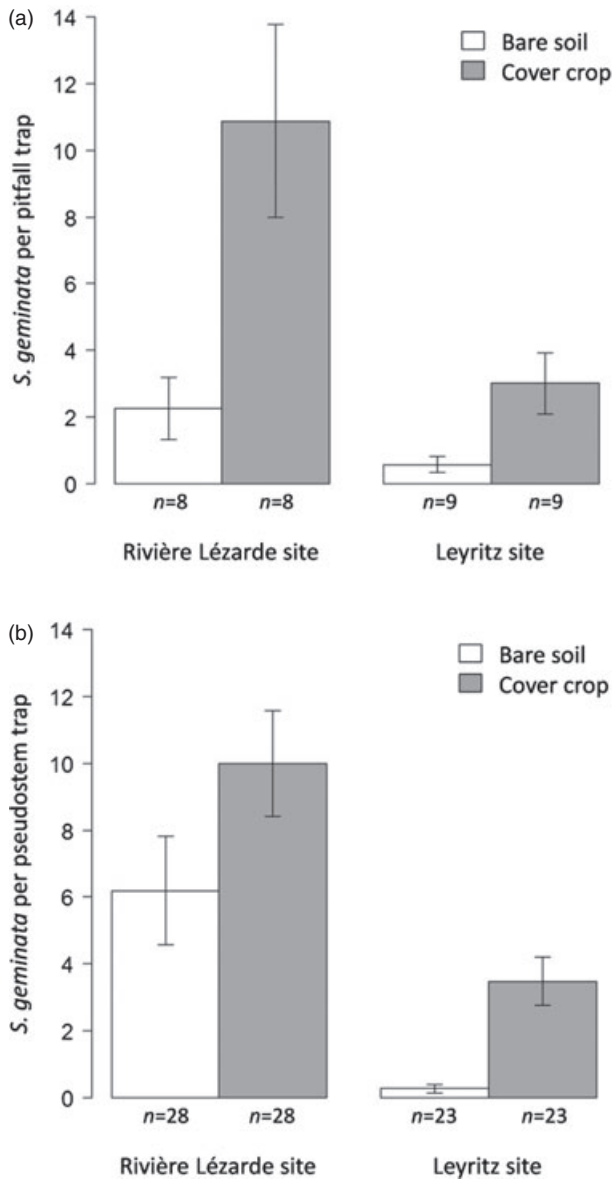


Figure 1 Abundance (mean \pm SE) of *Solenopsis geminata* in banana plots with bare soil or cover crops in two sites assessed by (a) pitfall traps and (b) pseudostem traps. Sample sizes (n) are annotated under bars. Statistics are provided in Table 1.

is required to confirm and understand the relationship between *S. geminata* and leafhoppers in banana plantations.

Although stable isotope analyses indicated that the effect of the cover crop on *S. geminata* abundance was based at least in part on trophic relationships, the cover crop could also have increased *S. geminata* abundance by buffering temperature and moisture on the soil surface (Hölldobler & Wilson, 1990) (i.e. by providing a more stable and favourable habitat for *S. geminata* and its prey). The abiotic environment might also explain why *S. geminata* was more abundant at the Rivière Lézarde site than at the Leyritz farm site. The rainfall patterns of the two experimental sites were relatively similar, although the soil types were different, and soil type is likely to affect soil

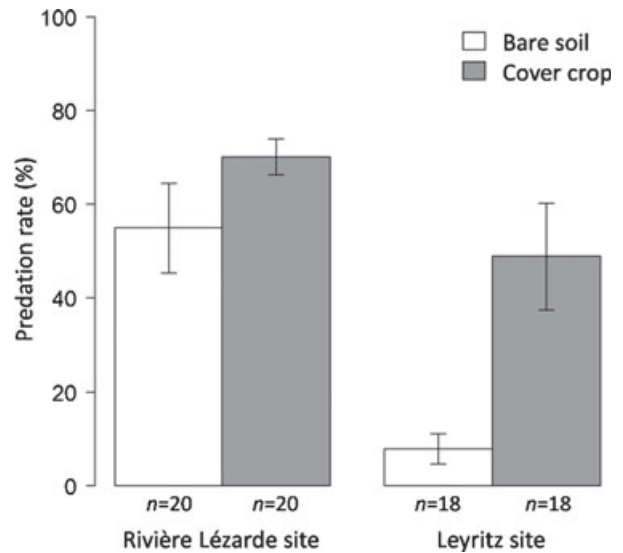


Figure 2 Percentage (mean \pm SE) of weevil eggs removed from banana corms (predation rate) after 1 h of exposure in plots with bare soil or cover crop at two sites (Rivière Lézarde and Leyritz farm). Sample sizes (n) are annotated under bars. Statistics are provided in Table 1.

moisture levels. The site with the lower abundance of *S. geminata*, the Leyritz farm site, has an andosol with pumice, which drains quickly and may therefore expose ants to desiccation.

Increased predation of *C. sordidus* eggs

Our estimations of egg predation relied on observations in natural situations corrected by results obtained in controls. The removal of eggs in controls may be explained by run-off, predation by large terrestrial predators that were not stopped by tree glue or by flying predators promoted by the cover crop. Estimation of egg predation rates was in the range 7.8–70.3%, which occurred in plots with the lowest and highest *S. geminata* abundance values, respectively. This suggests a causal link between *S. geminata* abundance and the rate at which *C. sordidus* eggs were predated. The predation rate was very low in the plots where banana was intensively cropped and where herbicide was applied to remove weeds. By contrast, predation of banana weevil eggs by *S. geminata* may be very efficient when a cover crop is present. Although a trophic link between *S. geminata* and *C. sordidus* eggs should be confirmed with other methods, we did observe *S. geminata* removing many eggs from corms. Our results are consistent with other studies reporting that ants can cause high levels of predation of pest eggs. For example, *S. geminata* also removes eggs of two pod-sucking bugs of soybean (Vandenberg *et al.*, 1995). Although well known as an invasive and dominant species, *S. geminata* is also recognized as an egg predator of *Diabrotica* spp. on several annual crops in Costa Rica (Risch, 1981) and of *Pseudoplusia includes* Walker on soybean in the U.S.A. (Nickerson *et al.*, 1977). The characteristics that allow invasive ants to spread may be advantageous for biological control. Helms *et al.* (2011) suggest that the success of invasive ants is greater when they form associations with honeydew-producing hemipterans

whose populations could be supported by a cover crop. Invasive ants often have a strong relationship with honeydew-producing hemipterans, which can supply up to half of the colony's energy requirements (Grover *et al.*, 2008; Helms & Vinson, 2008). An association with honeydew-producing hemipterans could therefore help ensure that *S. geminata* is abundant when *C. sordidus* initially infests the banana plantation. The benefit that the ants acquire from plant-based carbohydrates in honeydew may increase their ability to forage for protein-rich food such as other arthropods, including arthropod pests in agriculture.

Importance of primary resources for biological control by natural enemies

In the present study, we used a mechanistic approach, which combined stable isotope analyses and measurements of predator abundance and predation rates in the field, aiming to study the increase of pest predation when a cover crop was added to an agroecosystem. The results obtained suggest that *S. geminata* is an important predator of *C. sordidus* eggs in the banana plantations in Martinique. Although predation of the eggs by ants was not quantified, *S. geminata* was observed to carry away eggs that had been artificially deposited at the base of banana trees. Additional research is required to quantify predation of weevil eggs by *S. geminata* and other species. The present study also indicates that adding a cover crop increases egg predation. We suspect that it increases egg predation by *S. geminata* by changing the ant's resource pathway and increasing both its abundance and predation rate. Apparent competition could be the underlying mechanism, with the cover crop supporting a nonpest alternative prey and thus providing additional nutrients and enabling an increase in *S. geminata* numbers. The effects of nonpest alternative prey on the numerical responses of a predator have been demonstrated for a lycosid spider in cereal and leys on organic farms (Kuusk & Ekbohm, 2010). These previous studies tested whether the presence of *Collem-bola* spp. (an alternative food for lycosid spiders) affects aphid predation by these spiders. Their results indicated that *Collem-bola* spp. increase lycosid spider abundance at the same time as reducing lycosid spider predation on cereal aphids. When reviewing the effect of resource addition to agroecosystems on herbivore mortality from predation or parasitism, Russell (1989) showed that nine studies found that mortality rates were positively related with plant diversity, two studies found that mortality rates were negatively related with plant diversity, and two studies found no relationship. Determining the effect of the added resource on predator abundance appears to be important for understanding how plant diversity can enhance biological control by generalist predators. In a banana agroecosystem, fallowing between rotations and planting a cover crop when the banana trees are planted may provide resource early in the crop cycle, and may thereby promote *S. geminata* establishment. When the pest infests the banana trees, the removal of the cover crop by mowing would suppress honeydew resource and leave high numbers of *S. geminata*, which would presumably attempt to compensate for the lost resource by increasing their predation on arthropods including the pest. Future research should consider the dynamics of *S. geminata* establishment in banana

plantations with the goal of optimizing how cover crops are managed to maximize biological control.

Additional research is also needed to identify the alternative prey supported by different cover crops in the banana agroecosystem, as well as to quantify predation according to predator species. By using polymerase chain reaction-based analysis of gut contents, researchers can identify diet composition and may be able to characterize the trophic relationships between species (King *et al.*, 2008). Ultimately, this knowledge should help in the development of cropping systems in which pest abundance is reduced by the management of primary resources.

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References

- Abera-Kalibata, A.M., Gold, C.S., Van Driesche, R.G. & Ragama, P.E. (2007) Composition, distribution, and relative abundance of ants in banana farming systems in Uganda. *Biological Control*, **40**, 168–178.
- Abera-Kalibata, A.M., Gold, C.S. & Van Driesche, R. (2008) Experimental evaluation of the impacts of two ant species on banana weevil in Uganda. *Biological Control*, **46**, 147–157.
- Afun, J.V.K., Johnson, D.E. & Russell-Smith, A. (1999) The effects of weed residue management on pests, pest damage, predators and crop yield in upland rice in Cote d'Ivoire. *Biological Agriculture and Horticulture*, **17**, 47–58.
- Barberi, P., Burgio, G., Dinelli, G., Moonen, A.C., Otto, S., Vaz-zana, C. & Zanin, G. (2010) Functional biodiversity in the agricultural landscape: relationships between weeds and arthropod fauna. *Weed Research*, **50**, 388–401.
- Bates, D. & Maechler, M. (2011) *lme4: Linear Mixed-Effects Models Using S4 Classes*. R package version 0.999375-39 [WWW document]. URL <http://CRAN.R-project.org/package=lme4>.
- Begon, M., Townsend, C.R. & Harper, J.L. (2006) *Ecology: From Individuals to Ecosystems*. Wiley-Blackwell, U.K.
- Bell, J.R., King, R.A., Bohan, D.A. & Symondson, W.O.C. (2010) Spatial co-occurrence networks predict the feeding histories of polyphagous arthropod predators at field scales. *Ecography*, **33**, 64–72.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, **6**, 857–865.

- Carter, P.E. & Rypstra, A.L. (1995) Top-down effects in soybean agroecosystems – spider density affects herbivore damage. *Oikos*, **72**, 433–439.
- Duyck, P.-F., Lavigne, A., Vinatier, F., Achard, R., Okolle, J.N. & Tixier, P. (2011) Addition of a new resource in agroecosystems: do cover crops alter the trophic positions of generalist predators? *Basic and Applied Ecology*, **12**, 47–55.
- Elton, C. (1927) *Animal Ecology*. Macmillan Co., New York.
- Evans, E.W. & England, S. (1996) Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. *Ecological Applications*, **6**, 920–930.
- Gold, C.S., Pena, J.E. & Karamura, E.B. (2001) Biology and integrated pest management for the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). *Integrated Pest Management Reviews*, **6**, 79–155.
- Grover, C.D., Dayton, K.C., Menke, S.B. & Holway, D.A. (2008) Effects of aphids on foliar foraging by Argentine ants and the resulting effects on other arthropods. *Ecological Entomology*, **33**, 101–106.
- Helms, K.R. & Vinson, S.B. (2008) Plant resources and colony growth in an invasive ant: the importance of honeydew-producing Hemiptera in carbohydrate transfer across trophic levels. *Environmental Entomology*, **37**, 487–493.
- Helms, K.R., Hayden, C.P. & Vinson, S.B. (2011) Plant-based food resources, trophic interactions among alien species, and the abundance of an invasive ant. *Biological Invasions*, **13**, 67–79.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Harvard University Press, Cambridge, Massachusetts.
- Holt, R.D. (1977) Apparent competition and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Holt, R.D. & Kotler, B.P. (1987) Short-term apparent competition. *American Naturalist*, **130**, 412–430.
- Jaramayan, S., Ndiege, I.O., Oehlschlager, A.C. *et al.* (1997) Synthesis, analysis, and field activity of sordidin, a male-produced aggregation pheromone of the banana weevil, *Cosmopolites sordidus*. *Journal of Chemical Ecology*, **23**, 1145–1161.
- King, R.A., Read, D.S., Traugott, M. & Symondson, W.O.C. (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. *Molecular Ecology*, **17**, 947–963.
- Koppenhofer, A.M. (1993a) Egg predators of the banana weevil, *Cosmopolites sordidus* (Germar) (Col, Curculionidae) in western Kenya. *Journal of Applied Entomology*, **116**, 352–357.
- Koppenhofer, A.M. (1993b) Observations on egg-laying behavior of the banana weevil, *Cosmopolites sordidus* (Germar). *Entomologia Experimentalis et Applicata*, **68**, 187–192.
- Koss, A.M. & Snyder, W.E. (2005) Alternative prey disrupt biocontrol by a guild of generalist predators. *Biological Control*, **32**, 243–251.
- Kuusk, A.K. & Ekbom, B. (2010) Lycosid spiders and alternative food: feeding behavior and implications for biological control. *Biological Control*, **55**, 20–26.
- Mathews, C.R., Bottrell, D.G. & Brown, M.W. (2004) Habitat manipulation of the apple orchard floor to increase ground-dwelling predators and predation of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). *Biological Control*, **30**, 265–273.
- Menke, S.B., Suarez, A.V., Tillberg, C.V., Chou, C.T. & Holway, D.A. (2010) Trophic ecology of the invasive Argentine ant: spatio-temporal variation in resource assimilation and isotopic enrichment. *Oecologia*, **164**, 763–771.
- Messelink, G.J., Van Maanen, R., Van Holstein-Saj, R., Sabelis, M.W. & Janssen, A. (2010) Pest species diversity enhances control of spider mites and whiteflies by a generalist phytoseiid predator. *Biocontrol*, **55**, 387–398.
- Mooney, K.A. & Tillberg, C.V. (2005) Temporal and spatial variation to ant omnivory in pine forests. *Ecology*, **86**, 1225–1235.
- Nickerson, J.C., Kay, C.A.R., Buschman, L.L. & Whitcomb, W.H. (1977) The presence of *Spissistilus festinus* as a factor affecting egg predation by ants in soybeans. *Florida Entomologist*, **60**, 193–199.
- Oelbermann, K. & Scheu, S. (2002) Stable isotope enrichment ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): effects of prey quality. *Oecologia*, **130**, 337–344.
- Peterson, B.J. & Fry, B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Ponsard, S. & Ardit, R. (2000) What can stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) tell about the food web of soil macro-invertebrates? *Ecology*, **81**, 852–864.
- Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.
- R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria.
- Risch, S.J. (1981) Ants as important predators of rootworm eggs in the neotropics. *Journal of Economic Entomology*, **74**, 88–90.
- Rosenheim, J.A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology*, **43**, 421–447.
- Russell, E.P. (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology*, **18**, 590–599.
- Scherber, C., Eisenhauer, N., Weisser, W.W. *et al.* (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.
- Staddon, P.L. (2004) Carbon isotopes in functional soil ecology. *Trends in Ecology & Evolution*, **19**, 148–154.
- Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 151–164.
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, **47**, 561–594.
- Vandenberg, H., Bagus, A., Hassan, K., Muhammad, A. & Zega, S. (1995) Predation and parasitism on eggs of two pod-sucking bugs, *Nezara viridula* and *Pizodorus hybneri*, in soybean. *International Journal of Pest Management*, **41**, 134–142.
- Vanderklift, M.A. & Ponsard, S. (2003) Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Oecologia*, **136**, 169–182.
- van Veen, F.J.F., Morris, R.J. & Godfray, H.C.J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187–208.
- Wise, D.H., Moldenhauer, D.M. & Halaj, J. (2006) Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, **16**, 865–876.

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