ORIGINAL CONTRIBUTION

Weeds mediate the level of intraguild predation in arthropod food webs

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Abstract

Intraguild predation, which is common for generalist predators, is a specific form of omnivory that may suppress the biological control of a pest. The dietary flexibility of a given organism depends on the choice of the C3 (banana crop) and the C4 (weeds) pathways they use and on the trophic level on which they feed. Understanding the conditions in which intraguild predation decreases biological control is a major issue in agroecosystems. We tested whether the contribution of different primary producer pathways in diets of generalist predators mediates the level of intraguild predation. We studied 10 agroecosystems in which banana plants (C3 metabolism) were diversely associated with weeds (C4 metabolism). Diversity in litter macrofauna was relatively low, with a mean between three and eight species per trap. Measurement of stable isotopes showed a significant decrease in the $\delta^{15}N$ values of generalist predators when the C4 pathway contributed more than the C3 pathway to their diet. We rejected hypotheses that an increase in the abundance of prey and that a decrease in prey's $\delta^{15}N$ values occur when the C4 pathway contributes more than the C3 pathway to their diet. The results are consistent with the diet modification hypothesis, that is, intraguild predation is lower when the C4 (weeds) pathway is preferred to the C3 pathway. Our results suggest that when the C4 pathway of weeds is more exploited by herbivores (or detritivores), generalist predators tend to consume these herbivores and thus neglect the intraguild prey. The diverse C4 plant community probably supports a diverse herbivore community that provides alternative prey. Our results provide evidence that increasing plant diversity in agroecosystems should decrease intraguild predation of generalist predators and should therefore improve pest regulation. In an applied perspective, plant diversity could be increased by establishing a more diverse cover-crop community.

Introduction

Intraguild predation is a specific form of omnivory that may suppress the biological control of pests, especially when the intraguild prey is a better competitor than the intraguild predator for the shared prey (Daugherty et al. 2007). Omnivory is not only the response to a lack of resources at a lower trophic level, it is also a more general strategy to optimize the exploitation of resources in terms of quality (energetics) and abundance (Diehl 2003). Omnivory is particularly common for generalist predators, which often consume herbivores, intraguild prey and sometimes even plants (Denno and Fagan

2003). This is the case for many species of ants (Carroll and Janzen 1973; Wise et al. 2006). Diversity and abundance of prey may alter the omnivory of predators (Hunter 2009). Intraguild predation is common among generalist predators (Arim and Marquet 2004; Rickers et al. 2006), and an increase in productivity or a decline of diversity may change intraguild predation (Post and Takimoto 2007). The dietary flexibility of generalist predators can therefore affect the biological control in agroecosystems. The dietary flexibility of a given organism depends on the choice of the pathways they use (e.g. detritic vs. phytophagous, or C3 vs. C4 plants) and the trophic level on which they feed (e.g. plants, primary or secondary consumers). Enhancing biological control depends on understanding interactions between exploited pathways and trophic levels.

Stable isotopes of C and N can be used to understand how food webs are structured and how the omnivory of predators varies. Variations in the natural abundance of stable isotopes of C and N can reveal the trophic structure of food webs. Values of $\delta^{13}C$ are useful for determining the identity of the primary producer at the base of the food web. In our study, primary producers included C3 banana plants, which are the main primary producers with a $\delta^{13}C$ deviation close to -26.5% (Yakir and Israeli 1995), and weeds, which are mainly C4 plants with a $\delta^{13}C$ deviation from -17.0% to -9.0% (Staddon 2004). Regular enrichment of ^{15}N along trophic chains allows the use of $\delta^{15}N$ values to estimate the trophic level of organisms. Intraguild predation increases the $\delta^{15}N$ values of predator taxa (Ponsard and Arditi 2000) relative to predators that feed only on herbivores.

Because of their relatively simple communities, banana plantations are a useful model for studying food webs and omnivory in the context of pest regulation in agroecosystems. In banana agroecosystems, two primary producers may be defined: the banana crop (C3 plant) and weeds (mainly C4 plants). Dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export have long been cultivated intensively in monocultures on bare soil (Blazy et al. 2009), but cover crops are increasingly used (Tixier et al. 2011). In most production areas, the main pest of banana plant is the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Gold et al. 2001). The litter in *Musa* spp. plantings contains a number of generalist predators such as spiders, earwigs, ants and ground beetles (Koppenhofer et al. 1992; Koppenhofer 1993; Abera-Kalibata et al. 2006; Duyck et al. 2011). These predators may also feed on other predators. This is the case for ants and

spiders, which are reciprocal intraguild predators (Sanders and Platner 2007). Ground beetles are also often involved in intraguild predation interactions (Davey et al. 2013). A key question in banana agroecosystems is how to enhance the biological control of the banana weevil.

Duyck et al. (2011) showed that when a cover crop is present in an experimental banana plot, the generalist predators tend to use the cover crop as a new basal resource. The comparison of two situations (banana with bare soil vs. banana with a single species of cover crop) did not permit the detection of differences in $\delta^{15}N$ values, and thus, the authors could not determine whether a cover crop modified the trophic level at which the generalist predators feed. A change in the trophic level at which generalists feed should change their potential to control prey at lower trophic levels, that is, their potential to control pests will be lower if their participation in intraguild predation increases. On real farms, alternative basal resources include more than a single cover crop species, although those alternative basal resources are mostly C4 weeds in banana fields. On real farms, the contribution of weeds to the macrofauna food web and their effects on intraguild predation and biological control remain unknown.

In this manuscript, we tested whether the contribution of a C4 weed pathway in the diet of generalist predators mediates the level of intraguild predation. We attempted to measure the effect of C4 weeds (vs. C3 banana plants) on intraguild predatory by assessing predator $\delta^{15}N$ values. We also explored the following possible causes of variation in intraguild predation: (i) a modification in prey abundance, (ii) a modification in prey $\delta^{15}N$ values and (iii) a modification in type of prey. To this end, we analysed 10 fields that were managed as commercial banana plantings; the fields differed in stage (i.e. in time since planting), but all fields had the same soil and climate. First, we describe the variation of diversity of macrofauna living in litter in these banana agroecosystems. Then, we studied the variation in the $\delta^{15}N$ values of predator and potential prey taxa (indicating their trophic level) in relation to their $\delta^{13}C$ values (indicating the relative contributions of the C3 vs. C4 pathways).

Materials and Methods

Location and description of the study site

All fields were located in the Habitation Macouba farm (14°52′ 26.05′N; 61°08′ 45.24′W) in Martinique, French West Indies. In this area, the soil consists of

recent volcanic deposits and is classified as andosol with pumice. The average annual rainfall in Macouba is 2250 mm. We sampled 10 banana fields whose ages ranged from 0 years (fallows before planting) to 12 years (before destruction). None of these fields received insecticide application during the 4 years before sampling. The fields were treated homogeneously using intensive cultural practices, with 250 kg of nitrogen per ha applied each year and a moderate weed control of two to four applications of herbicide (glyphosate) each year. The wet tropical climate of this area in Martinique provides relatively constant conditions throughout the year. During banana cropping, weeds were almost exclusively C4 plants (*Cynodon dactylon* and *Brachiaria decumbens*). In fallow plots (age = 0 years), weed cover was 100% and was dominated by the C4 plants *C. dactylon* and *B. decumbens* with lower representation by the C3 plants *Amaranthus spinosus*, *Commelina diffusa* and *Centrosoma pubescens*. In all other plots (age = 0.2–12.3 years), the percentage of weed cover ranged from 30 to 50%.

Sampling of litter macrofauna

In each field, eight pitfall traps (0.2 m diameter) distributed every 20 m were used during 48 h to measure the macrofauna in the litter. All fields were sampled in July 2009. We captured 980 individuals from 26 taxa. Only eight taxa (those with more than seven individuals) were kept for abundance and isotopic analyses. The abundant species were identified to family or species. For each taxon, we recorded the number of individuals captured in each trap.

Isotopic analyses

All sampled arthropods were lyophilized for 48 h and ground into a fine powder; a 1 mg sample of the powder was placed in a tin capsule for analysis. For each taxon, we measured one pooled sample per trap (allowing the linking of abundance and isotopic values of a given species in a given trap). Isotope ratios were determined by an isotope ratio mass spectrometer SerCon 20/20 coupled to an ANCA-GSL elemental analyser at the Scottish Crop Research Institute laboratory for stable isotope analysis (Dundee, Scotland). All stable isotope values are reported in the δ notation, with δ^{13}C or δ^{15}N calculated as $[(R_{sample}/R_{standard}) -1] \times 1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards were PeeDee Belemnite (Peterson and Fry 1987) and atmospheric air (Mariotti 1983) for C and N, respectively. To evaluate the reliability of isotopic

measurements, five replicates of the same sample were analysed. This was performed for one sample of *C. sordidus*, one sample of banana and one sample of *B. decumbens*. For *C. sordidus*, banana, and *B. decumbens*, standard errors of δ^{13}C were 0.40, 0.02 and 0.02‰, respectively, and standard errors of δ^{15}N were 0.14, 0.08 and 0.04‰, respectively.

Statistical analyses

For each trap, the number of taxa collected was analysed by a GLM with Poisson error as a function of the age of the field or of the stage of the crop (fallow or banana). We analysed the effect of δ^{13}C and age of banana fields on δ^{15}N and on the abundance of captured individuals of each taxon using GLM with Poisson error. All analyses were performed in R version 2.14 (R Development Core Team 2012). Models used for linear regression between δ^{15}N and δ^{13}C only included significant tested variables.

Results

Species richness and food web structure of litter macrofauna at the plot scale

The diversity of taxa collected (table 1) differed between plots (fig. 1). An average of three to eight species was collected. More taxa were collected in fallows just before planting (age = 0) than during banana cropping (GLM with Poisson error: Δdev = 23.94, Residual dev = 47.09, d.f. = 78; 1, P < 0.0001). The mean number of taxa collected was 8.0 in fallows and 2.5 to 4.5 in banana cropping fields. There was no significant correlation between the number of taxa measured in plots in banana and the time since the plots were planted (GLM with Poisson error: Δdev = 1.15, Residual dev = 43.01, d.f. = 70; 1, P = 0.284).

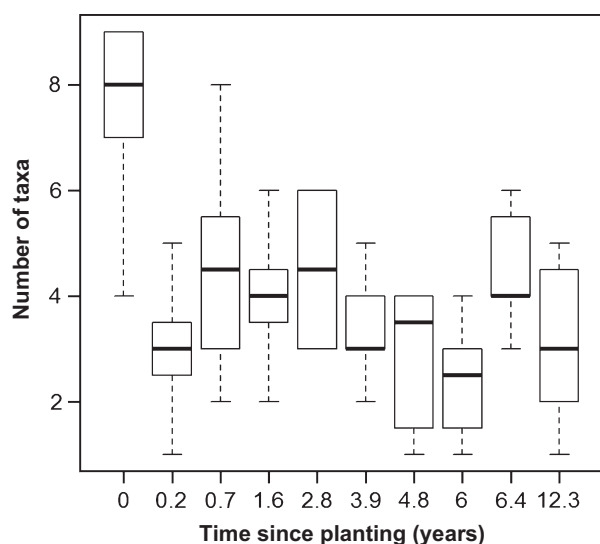The δ^{15}N values varied widely with the trophic level (δ^{15}N) of each taxon (fig. 2). The δ^{15}N value of the two primary resources was −0.19 for banana and 0.93 for C4 weeds. The mean δ^{15}N values ranged from 1.6 to 4.7‰ for phytophagous or detrivorous taxa and from 4.5 to 9.0‰ for predators. Spiders were at the highest trophic position, and earwigs and ground beetles were below. Among phytophagous or detrivorous taxa, locusts, Paradoxosomatidae and Rhinocricidae were at the intermediate trophic level, and banana weevils and crickets were at the lowest trophic level.

The mean δ^{13}C values of banana weevils and locusts were between −25 and −27‰ (corresponding to the C3 plant signature). In contrast, mean δ^{13}C values of crickets, Paradoxosomatidae and Rhinocricidae

Table 1 Classification of taxa collected over the 10 banana fields in Martinique, French West Indies

Taxa	Trophic group	Class	Order	Family	Species	Individuals counted	Number of isotopic samples
Spider	Generalist predator	*Arachnida*	*Araneae*	*Lycosidae*	*	168	40
Earwig	Generalist predator	*Hexapoda*	*Dermaptera*	*Carcinophoridae*	*Euborellia caraibea*	34	13
Ground beetle	Generalist predator	*Hexapoda*	*Coleoptera*	*Carabidae*	Galerita tristis	74	18
Banana weevil	Herbivore (pest)	*Hexapoda*	*Coleoptera*	*Curculionidae*	*Cosmopolites sordidus*	20	13
Locust	Herbivore	*Hexapoda*	*Orthoptera*	*Grillidae*	*	17	11
Cricket	Herbivore	*Hexapoda*	*Orthoptera*	*Gryllidae*	*Grillus assimilis*	83	34
Paradoxosomatidae	Detritivore	*Myriapoda*	*Diplopoda*	Paradoxosomatidae	*	282	49
Rhinocricidae	Detritivore	*Myriapoda*	*Diplopoda*	Rhinocricidae	*	29	24

*Not identified.

Fig. 1 Number of taxa measured in eight pitfall traps per plot in each banana field.

ranged from −22 to −19‰, suggesting that they fed on both C3 and C4 plants. The $\delta^{13}C$ value of generalist predators (earwigs, ground beetles and spiders) was significantly affected by species but was not significantly affected by the age of banana field or by the interaction between species and age (table 2). The $\delta^{13}C$ value of herbivores (banana weevils, crickets, locusts, Paradoxosomatidae and Rhinocricidae) was significantly affected by species, age of banana field and their interaction (table 2).

$\delta^{15}N$ variation of generalist predators

The $\delta^{15}N$ values of spiders, earwigs and ground beetles decreased with the $\delta^{13}C$ values (fig. 3). Although the

$\delta^{15}N$ values were significantly related to $\delta^{13}C$ values, they were not significantly affected by the age of banana field (table 2). There was no interaction between the effect of the $\delta^{13}C$ values and the taxa (meaning that there was no effect of the taxa on the slope of the linear regression), and thus, the slopes of the linear regressions were considered equal (slope = −0.39).

Abundance and $\delta^{15}N$ variation of non-predator taxa

Figure 4 presents the abundance of non-predator taxa in relation to their mean $\delta^{13}C$ values. We did not observe any significant effect of $\delta^{13}C$ values on the abundance of any non-predator taxa (GLM quasi-Poisson, $\Delta dev = 6.67$, d.f. = 6; 1, P = 0.273; $\Delta dev = 99.54$, d.f. = 66; 1, P = 0.322; $\Delta dev = 7.65$, d.f. = 56; 1, P = 0.342; $\Delta dev = 2859.10$, d.f. = 18; 1, P = 130, for banana weevils, locusts, Paradoxosomatidae, Rhinocricidae and crickets, respectively). Figure 5 presents the $\delta^{15}N$ values of non-predator taxa in relation to their mean $\delta^{13}C$ values. $\delta^{15}N$ values were not significantly affected by $\delta^{13}C$ values or age of banana field (table 2).

Discussion

The diversity of captured taxa was unrelated to the age of banana fields in this study. Nevertheless, we clearly observed more taxa in the fallow just before planting (age = 0) than in the fields with banana. This observation could be due to the larger plant diversity during fallow, which may sustain a more diverse macrofauna community. From a general point of view, diversity was relatively low compared with other tropical ecosystems (Decaens et al. 2004). This low diversity
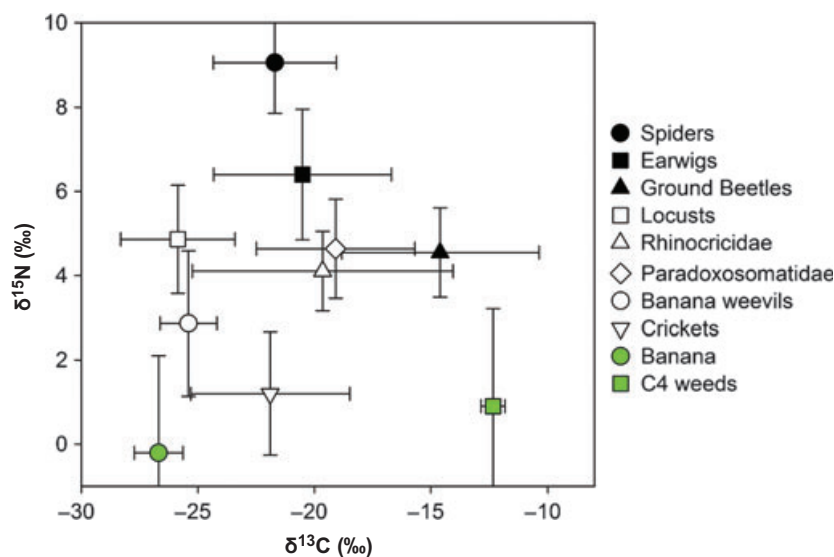
Fig. 2 The δ^{13}C and δ^{15}N means values of macrofauna taxa collected in 10 banana fields; bars indicate standard deviations. Black symbols represent predacious taxa, white symbols represent phytophagous and detrivorous taxa and green symbols represent plants.

Table 2 General test of the effect of taxa (taxa), age of banana fields (age) on δ^{13}C values (A and B), and the effect of species, age of banana fields and δ^{13}C values on δ^{15}N values (C and D), for predators and non-predators

Tested variable	d.f.	Deviance	Residual d.f.	Residual deviance	F	P-value
A- δ^{13}C~sp × age (Predators)						
NULL			70	1385.95		
Taxa	2	635.89	68	750.06	28.564	<0.0001
Age	1	9.07	67	740.99	0.815	0.36990
Taxa:age	2	17.50	65	723.49	0.786	0.45990
B- δ^{13}C~sp × age (Non-predator)						
NULL			130	2700.30		
Taxa	4	1081.10	126	1619.20	24.583	<0.0001
Age	1	170.58	125	1448.60	15.515	0.00013
Taxa:age	4	118.31	121	1330.30	2.690	0.03430
C- δ^{15}N~δ^{13}C × sp × age (Predator)						
NULL			70	371.50		
δ^{13}C	1	211.25	69	160.25	232.785	<0.0001
Taxa	2	90.32	67	69.92	49.767	<0.0001
Age	1	3.05	66	66.87	3.359	0.07172
δ^{13}C:taxa	2	1.39	64	65.48	0.767	0.46864
δ^{13}C:age	1	7.29	63	58.19	8.031	<0.0001
Taxa:age	2	2.83	61	55.36	1.561	0.21805
D- δ^{15}N~δ^{13}C × sp × age (Non-predator)						
NULL			130	341.88		
δ^{13}C	1	0.76	129	341.12	0.549	0.46016
Taxa	4	141.28	125	199.84	25.462	<0.0001
Age	1	0.70	124	199.13	0.508	0.47734
δ^{13}C:taxa	4	21.69	120	177.44	3.908	0.00517
δ^{13}C:age	1	8.48	119	168.97	6.110	0.01490
Taxa:age	4	9.45	115	159.52	1.702	0.15421

d.f., degrees of freedom; ':',indicate the interaction between two variables; NULL, test of the null model.

cannot be explained by pesticide applications, because no insecticide had been applied in the 4 years before the study. The low level of plant diversity (banana and weeds) may explain this low diversity of the macrofauna community. Indeed, plant species richness is known to influence invertebrate herbivory and community structure (Stein et al. 2010). However, the relatively simple banana ecosystem is valuable for
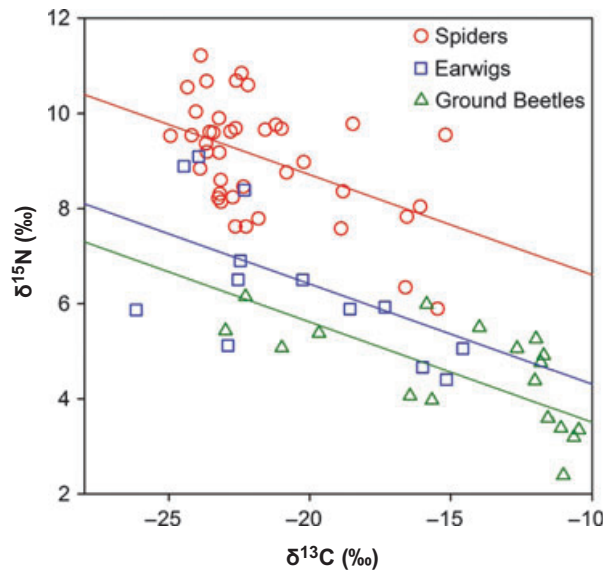
Fig. 3 The $\delta^{13}C$ and $\delta^{15}N$ values of predators. Each point represents the isotopic values of individuals (pooled) of one taxon in a given trap.
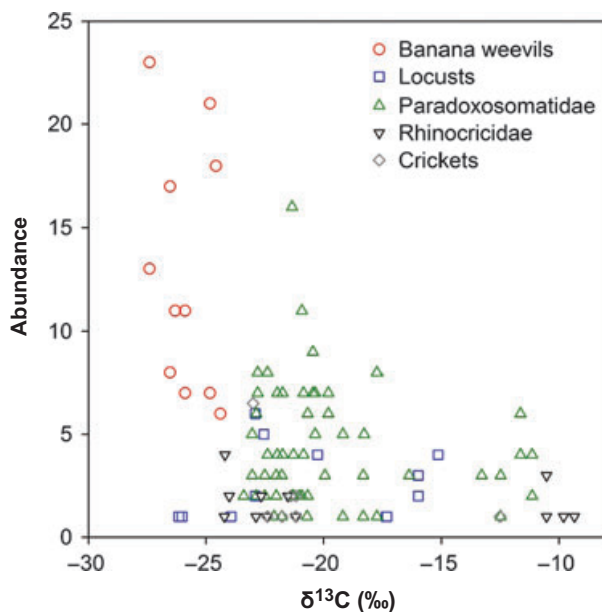

Fig. 4 Relationship between the abundance of non-predator taxa and their $\delta^{13}C$ values. Each point represents the abundance and the isotopic value of individuals (pooled) of one taxon in a given trap.

Fig. 5 Relationship between the $\delta^{15}N$ values of non-predator taxa and their $\delta^{13}C$ values. Each point represents the isotopic values of individuals (pooled) of one taxon in a given trap.

measuring a switch between two pathways: the C3 (banana crop) and the C4 (weeds) pathways.

The trophic level of predators, revealed by $\delta^{15}N$ values, was highest for spiders; earwigs and ground beetles were below. Locusts, Paradoxosomatidae and Rhinocricidae were at an intermediate trophic level, and banana weevils and crickets were at the lowest
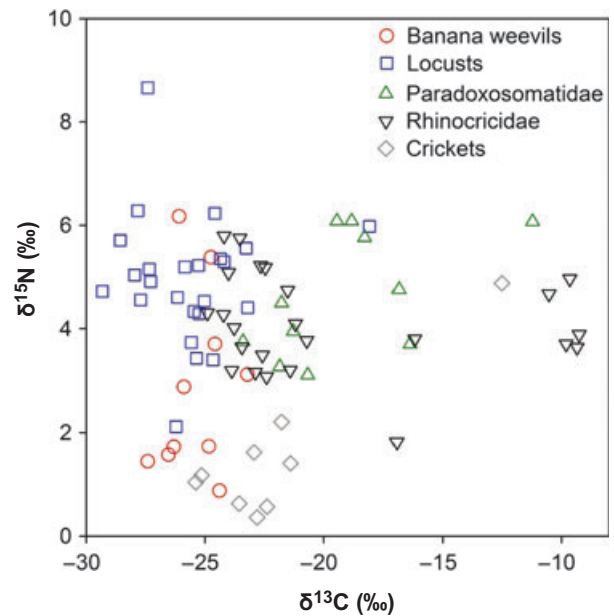
trophic level. There was a good agreement between the trophic levels of these taxa and results from studies in other banana fields (Duyck et al. 2011). The mean $\delta^{13}C$ values allowed us to identify the primary resource pathway of taxa: banana weevils and crickets fed mostly on C3 plants (most probably banana, the most abundant plant), and millipedes fed on both C3 and C4 plants; spiders and earwigs fed on herbivores associated with both C3 and C4 plants. Like Duyck et al. (2011), we found that ground beetles occupy a very low trophic position in the food web (although they are reported as predators). Furthermore, ground beetles fed almost exclusively on a C4 pathway. This suggests that ground beetles fed on another basal resource (possibly outside the banana field) or that their enrichment in ^{15}N compared with their prey is much lower than in other predators. Spiders and earwigs have wide ranges of diet (mixing C3 and C4 pathways) and of trophic level. These results show that generalist predators have flexible diets. Stable isotopes demonstrate that the diet of some species can be more general than field observations and the literature suggest (O' Grady et al. 2011).

The significant decrease in the $\delta^{15}N$ values of generalist predators when the C4 pathway contributed to their diet (fig. 3) could be explained by a diet modification hypothesis (a decrease in intraguild predation or cannibalism) or by two alternative hypotheses: i) an increase in the abundance of prey when the C4

pathway is more important and ii) a decrease in the prey δ^{15}N values when the C4 pathway is more important. Figure 4 does not support the first alternative hypothesis because, according to the GLM with Poisson error, the abundance of captured individuals was not significantly related to taxa or δ^{13}C value. Contrarily, we observed a trend (non-significant) with a decrease in the abundance of herbivores when the C4 pathway is more important. We conclude that predators do not consume more non-predator taxa in the C4 pathway because of higher non-predator abundance. Figure 5 does not support the second alternative hypothesis; we did not observe any significant relation between δ^{15}N values of the most abundant non-predator taxa in relation to their mean δ^{13}C values. We conclude that predators that consumed prey that feed more in the C4 than in the C3 pathway should not have lower δ^{15}N values because these prey have lower δ^{15}N values. That the results were inconsistent with the two alternative hypotheses suggest that the decrease in predator δ^{15}N values when they consumed prey that fed in the C4 pathway (fig. 3) can be explained by a modification of diet and more specifically by a decrease in intraguild predation.

The inability of pitfall traps to capture other alternative prey that live above the litter did not allow us to identify other potential alternative prey, for example, flying insect dwelling on C4 weeds. Another study focussing on ants suggested that leafhoppers (Hemiptera: Cicadellidae) or the honeydew they produce may be alternative resources for *Solenopsis geminata* (Mollot et al. 2012). While the latter study concerned a different generalist predator and a simpler system (with and without plant cover), it also supported the hypothesis that the addition of new resources in an agroecosystem results in diet modification of generalist predators. As the C/N ratio of consumed species may alter the enrichment in ^{15}N of the consumer, such variations in prey consumed by generalist predators represent a limitation of our study in that C/N ratios were not measured.

Our results suggest that when herbivores or detritivores increasingly exploit the C4 pathway of weeds, generalist predators tend to consume these herbivores and thus neglect the intraguild prey. This relationship was particularly clear for spiders, which are known to be involved in intraguild predation with ants or other intraguild prey or in cannibalism (Halaj et al. 2005). This feeding behaviour of spiders indicated here is consistent with other studies (Wise et al. 2006; Sanders and Platner 2007). Duyck et al. (2011) showed that the addition of a cover crop to banana fields changes the δ^{15}N values of earwigs sig-

nificantly but not of other generalist predators. Here, the more diverse and numerous situations studied provided evidence of changes in the level of intraguild predation. We hypothesize that the C4 pathway corresponds to diverse additional resources compared with the most abundant one (i.e. the banana plants). Although the weed community in this system is composed of two main species (*Cynodon dactylon* and *Brachiaria decumbens*), it inevitably includes some other species of weeds with low abundance. This community of diverse C4 primary producers probably supports a diverse community of herbivores, probably in low abundance and maybe not exhaustively sampled in our study. This potential diversity of prey in the C4 pathway potentially constitutes an important pool of alternative prey, leading to the diet modification of predators observed in this study and a reduction in intraguild predation. In addition to potentially providing an increased diversity of prey, C4 weeds probably provide a habitat that differs from that provided by the banana plant and bare soil. In this 'weed habitat', predators may hide and protect themselves from the predation of other predators (Blubaugh et al. 2011; Amaral et al. 2013). This 'habitat effect' probably enhances the observed mechanism of diet flexibility, that is, it enhances predation of herbivores rather than of intraguild prey. Our results are consistent with other studies that suggest that predator and prey diet may exert subtle influences on intraguild predation (Mendel and Schausberger 2011). Modelling approaches showed that the provision of alternative prey to the intraguild prey increases the disruptive effect on the shared prey (potentially a pest) (Daugherty et al. 2007).

In our case, the exploitation of the C4 pathway by intraguild prey may enhance their control of species at lower trophic levels. Cardinale et al. (2006) showed that prey suppression is generally higher in diverse than in simple predator communities. To improve the regulation of pest herbivores by generalist predators, it should be possible to make the food web more complex by adding plants to agroecosystems. This could be achieved by cultivating mixtures of cover crops (rather than a monospecific cover crop), which are known to modify generalist predators (Costello and Daane 2003; Hooks and Johnson 2004). Diversified cover-crop communities are not yet implemented at a large scale. While our results provide evidence that increasing plant diversity in agroecosystems should help decrease intraguild predation of generalist predators and should therefore improve pest regulation, there are some possible drawbacks to a more

diversified agroecosystem. In addition to the risk of competition between the cultivated crop and the cover crops (Ripoche et al. 2012), there is the risk that the pest herbivores will consume the new plant resources and thereby increase their numbers. This risk is unlikely to be realized in the case of the banana weevil because its diet is strictly limited to *Musa* spp. (Gold et al. 2001). Another risk of diversifying the plant community is that the altered habitat may increase pest dispersal capacity (Vinatier et al. 2011).

Isotopic tools were used in the current study, but molecular tools can also be useful for disentangling trophic interactions and for establishing trophic links. For example, PCR-based techniques can be used to accurately distinguish and identify prey items in stomach, gut and faecal samples (Harper et al. 2005; Traugott et al. 2008). Isotopic and molecular approaches are complementary; isotopes provide integrative measures of food webs, and PCR-based techniques provide a very specific measure of trophic links (Carreon-Martinez and Heath 2010).

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Author Contributions

PT supervised the study and wrote the manuscript. DD carried out the field measurements. GM and FV participated in the design of the experiment and helped in species identification. PFD helped to analyse the data and provided editorial advice.

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