



Plant richness enhances banana weevil regulation in a tropical agroecosystem by affecting a multitrophic food web



Charlotte Poeydebat^{a,b}, Philippe Tixier^{b,c}, Luc De Lapeyre De Bellaire^b, Dominique Carval^{a,b,*}

^a CIRAD, UPR GECO, F-97285 Le Lamentin, Martinique, France

^b CIRAD, UPR GECO, F-34398 Montpellier, France

^c Departamento de Agricultura y Agroforestería, CATIE, CR-30501 Turrialba, Costa Rica

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ABSTRACT

Field-scale plant diversification of agroecosystems is a promising way to enhance ecological pest regulation. Existing studies, however, have provided inconsistent results and have generally focused on only a few trophic groups or a few levels of plant diversification. Using field data from banana agroecosystems and structural equation modelling, we assessed (i) the effects of plant species richness (two height strata) and soil cover (% of living plant cover and % of litter cover) on a multitrophic arthropod food web, (ii) the links among five trophic groups of arthropods (detritivores, herbivores, non-ant omnivores, omnivorous ants, and predators) and (iii) the effect of natural enemies on the abundance and the damage of the banana weevil, *Cosmopolites sordidus*. Plant species richness of low strata (< 1.5 m high) had a positive bottom-up effect on herbivore prey abundance, which in turn enhanced the abundance of non-ant omnivores and of predators. Litter cover promoted the abundance of detritivore prey, which in turn enhanced predators and omnivorous ants. The latter two trophic groups were negatively related to weevil damage and probably reduced damage by consuming weevil eggs and larvae. Finally, on the basis of our results, we suggest how the plant community and soil cover within the field could be managed to enhance ecological regulation of the banana weevil.

1. Introduction

Field-scale plant diversification of agroecosystems has been proposed as a promising means of restoring ecological pest regulation and of reducing environmental and health problems resulting from pesticide applications (Gurr et al., 2003; Malezieux et al., 2009; Ratnadass et al., 2012). Several recent reviews have concluded that plant species richness has a generally positive effect on the regulation of herbivorous pest abundance or damage (Dassou et al., 2015; Letourneau et al., 2011). Some studies, however, have reported that plant species richness may have neutral or negative effects on the regulation of herbivores (Letourneau et al., 2011; Poveda et al., 2008). A limitation of many studies on this topic is that they focus on the abundance and/or richness of only one or two trophic groups (for instance, herbivorous pests and their natural enemies) even though changes in ecosystem services very likely result from changes in the abundance and richness of many interacting trophic groups (Soliveres et al., 2016). The latter authors showed that the consideration of only a small number of trophic groups has caused researchers to greatly underestimate the importance of ecosystem services provided by higher levels of plant richness. Here,

using a multitrophic approach as described by Soliveres et al. (2016), we assessed the effect of field-scale plant species richness on the regulation of the abundance and the damage of an oligophagous pest of banana, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae).

The banana weevil, *Cosmopolites sordidus*, is the most important insect pest of bananas and plantains (Cuillé, 1950; Gold et al., 2001), which together are the second most important global fruit crop and the fourth most important global food commodity (after rice, wheat, and maize) in terms of production (Echezona et al., 2011). *Cosmopolites sordidus* is a narrowly oligophagous pest, attacking wild and cultivated clones of *Musa* and *Ensete* (Gold et al., 2001). Free-living adult weevils are nocturnal and disperse by walking, usually for short distances (Carval et al., 2015; Gold et al., 2001; Vinatier et al., 2010). Females lay eggs near the soil surface in the corm or at the base of the pseudostem of banana plants. The larvae bore galleries in the corm to feed (Cuillé, 1950; Koppenhöfer, 1993b), causing severe damage to the crop (Gold et al., 2001). Previous studies reported the potential for the control of the abundance or damage of *C. sordidus* by natural enemies (Abera-Kalibata et al., 2008; Carval et al., 2016; Dassou et al., 2015; Koppenhöfer et al., 1992; Mollot et al., 2012). Some of these studies

* Corresponding author at: CIRAD, UPR GECO, F-34398 Montpellier, France.

E-mail address: dominique.carval@cirad.fr (D. Carval).

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have indicated that the regulation of *C. sordidus* could be affected by plant species richness possibly via effects on the arthropod community (Carval et al., 2016; Dassou et al., 2015; Mollot et al., 2012). However, it is difficult to draw general conclusions on the effect of plant richness on banana weevil regulation from these studies because (i) they did not consider a gradient of plant species richness and/or (ii) they only considered one species or group of species at a single trophic level of the arthropod food web. Here, we analysed the relationships between plant species richness, the abundance of five arthropod trophic groups (detritivores, herbivores, non-ant omnivores, omnivorous ants, and predators) and the regulation of *C. sordidus* abundance and damage. We hypothesised that i) field-scale plant species richness has positive bottom-up effects that increase the abundance of potential natural enemies and that ii) non-ant omnivores, omnivorous ants, and predatory arthropods reduce the abundance of adult banana weevils and the corm damage. To test these hypotheses, we collected data from banana agroecosystems covering a gradient of plant species richness. We then used structural equation modelling and generalised mixed-effects models to investigate i) the links between plant species richness in two height strata and the abundance of arthropod trophic groups and ii) the effects of plant species richness on the regulation of banana weevil abundance and damage.

2. Materials and methods

2.1. Study sites and design

We conducted a field study in the Reserve of Talamanca (9°00′ – 9°50′ N, 82°35′ – 83°05′ W) in Costa Rica. In this area, banana agroecosystems mainly consist of diversified agroforestry, but also include systems ranging up to intensive monoculture. The different types of agroecosystems differ in terms of plant community structure and composition (*Musa* genotypes and non-crop plant species). Agroforestry systems are generally long-established, they may contain several cultivars of plantains and bananas, and can include remnant forest trees, cultivated trees (e.g., cocoa), medicinal plants, ground crops (e.g., taro, cassava), and weeds (Somarriba and Harvey, 2003). The mean annual temperature and air relative humidity measured at several points within our sampling area during the study were 24.8 ± 0.3 °C and $91 \pm 4.2\%$, respectively. The mean annual rainfall is about 3500 mm in this tropical-humid region (Deheuvels et al., 2012).

We monitored a network of 75 twenty-meters diameter circular plots distributed in 9 heterogeneous banana-based farmers' fields. Fields and plot locations were selected *a priori* to cover a wide range of plant species richness situations (Table 1). We installed one *in vitro*-propagated banana plant (*Musa* AAA, Cavendish subgroup, Grande Naine cultivar) in the center of each plot as a phytometer (Fig. 1). The phytometers are standardized plants (genetically similar) initially free of weevils and experimentally transplanted in contrasted situations to assess responses to environmental variables (Dietrich et al., 2013). Each phytometer was placed 1.5 m distant from an existing banana plant.

Table 1

Total, low-stratum and high-stratum plant species richness (mean number of species \pm standard-deviation of the plots), number of phytometers (or plots), *Musa* genotype richness and *Musa* density per hectare of the nine banana fields selected.

Field	Total plant species richness (\pm sd)	Low-stratum plant species richness (\pm sd)	High-stratum plant species richness (\pm sd)	Number of phytometers (\pm sd)	<i>Musa</i> genotype richness	<i>Musa</i> density per ha (\pm sd)
1	8 \pm 2	7 \pm 1	1 \pm 1	8	1	2898 \pm 287
2	10 \pm 4	7 \pm 4	3 \pm 1	5	6	1982 \pm 304
3	11 \pm 4	7 \pm 3	4 \pm 2	14	2	505 \pm 202
4	15 \pm 3	12 \pm 2	3 \pm 1	5	2	2166 \pm 287
5	15 \pm 4	8 \pm 2	7 \pm 4	8	10	1477 \pm 496
6	17 \pm 9	13 \pm 6	5 \pm 3	10	8	994 \pm 602
7	19 \pm 3	17 \pm 2	2 \pm 2	10	3	857 \pm 328
8	21 \pm 6	13 \pm 4	8 \pm 3	8	5	677 \pm 304
9	25 \pm 2	17 \pm 3	8 \pm 2	8	7	912 \pm 340

Within one field, adjacent phytometers were at least 20 m apart so that two adjacent plots never overlapped. The study began in July 2014 and ended in January 2016. There was no chemical control or pheromone trapping of weevils in any of the fields.

In each plot, we evaluated plant species richness below and above 1.5 m high, the abundance of various trophic groups of the ground-dwelling arthropod food web, the abundance of adult banana weevils, and the damage caused by the weevils to the phytometer corm.

2.2. Plot-scale plant community

Plant species richness is commonly used as an indicator of ecosystem biodiversity (Dassou et al., 2015; Letourneau et al., 2011). Within each plot, we subdivided the plant community into a low stratum (plant height at top of the crown < 1.5 m) and a high stratum (plant height at top of the crown \geq 1.5 m) to account for differential effects related to differences in plant traits such as height, growth rate, or lifespan. Plant species richness of the high-stratum was calculated as the number of plant species present in the plot after identification of each plant to species level. We evaluated the species richness of plants smaller than 1.5 m high along four transects of 10 m, going from the phytometer to the border of the plot and oriented toward the four cardinal points (Fig. 1). Plant species richness of the low stratum was obtained by averaging the four species richness values. Plants were identified using recent literature on the plants of Costa Rica (Gargiullo et al., 2008) and/or according to local, traditional knowledge (Cook et al., 2014). When a species was not identifiable, a morphospecies was assigned to the individual on the basis of morphological specificities, to allow for richness calculation. *Musa* genotype richness was assessed separately because of the particular role of this plant family in the life cycle of *C. sordidus* (Gold et al., 2001). Ultimately, we evaluated the percentage of living-plant soil cover and litter soil cover (including crop and other plant residues) within the plot as proxies for living and dead plant biomass, respectively.

2.3. Multiple trophic groups of ground-dwelling arthropods

Ground-dwelling arthropods were sampled using pitfall traps (Cosmotrack®, Calliope) containing water with a few drops of detergent (commercial dish cleaner) to weaken water surface tension. One trap was buried 50 cm away from each phytometer, and the trapped arthropods were retrieved 2 days later. Ants were identified to species using keys (Baccaro et al., 2015; Bolton, 1994; Bolton, 2000; Dash, 2011; Feitosa et al., 2008; Fernández, 2007; Jiménez et al., 2007; LaPolla and Fisher, 2014; Longino and Fernández, 2007; Mackay and Mackay, 2010; Pacheco and Mackay, 2013; Wild, 2005; Wilson, 2003). Other arthropods were identified to family (Delvare and Aberlenc, 1989), but a morphospecies was attributed to each individual based on morphological specificities, allowing further calculation of richness (Barratt et al., 2003). Each individual was assigned to one of the following trophic groups according to its species or family: detritivores,

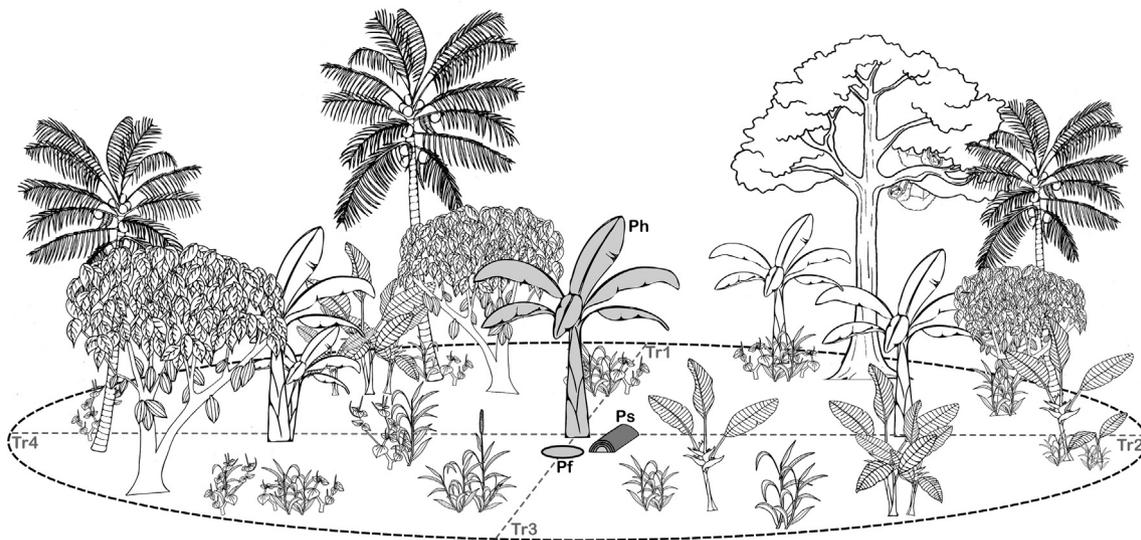


Fig. 1. Plot configuration. The phytometer (Ph) is placed in the center of the 20-meters diameter circular plot (dark dashed line). Gray dashed lines represent the four transects (Tr1, Tr2, Tr3, Tr4) used to assess low stratum plant species richness. Pseudostem (Ps) and pitfall traps (Pf), used for weevil and arthropod sampling respectively, are represented.

herbivores, non-ant omnivores, omnivorous ants, and predators. Pitfall sampling was performed twice in April 2015. For analyses, the abundances of each group at both sampling events were summed to obtain a single estimate for each arthropod group.

2.4. Banana weevil abundance and damage

The abundance of adult banana weevils was assessed using 30 cm-long pieces of banana pseudostem (*Musa* AAA, Gros Michel subgroup, Gros Michel cultivar) that were cut in half longitudinally and used as attractive traps (Gold et al., 2001). Pseudostem traps were first kept under controlled conditions outside the fields for one week, during which time they decomposed and thereby became more attractive to the weevil (Mestre and Rhino, 1997). One pseudostem trap was placed at the base of each phytometer where it was left for one week. The traps were surveyed six times every 2 days in April 2015, and each time the adult weevils present on the trap were counted. For analysis, the six counts were summed to obtain a single estimation of adult weevil abundance per phytometer.

At the end of the study, each phytometer was unearthed, and corm damage was assessed by stripping the entire circumference of the corm. The percentage of the corm circumference with weevil galleries was used as a corm damage score (0–100 scale; modified from Vilardebo (1973)). This method has been proved to be representative of the true level of corm damage (Dassou et al., 2015). Because of accidental cutting of phytometers by farm workers before the end of the study, only 56 of the 75 phytometers were evaluated for damage.

2.5. Data analysis

On the basis of the literature, we identified the *a priori* most probable hypotheses for the causal links among the variables describing the plant community and the abundances of the trophic groups of the food web of ground-dwelling arthropods. From these hypothetical links among the variables, we constituted a global path model composed of a set of 5 linear sub-models (Table 2). According to response variable distributions, all sub-models were Poisson general linear mixed models (GLMMs). To address the non-independence of sampling between fields, we added field identity as a random intercept effect in all sub-models (Zuur et al., 2009). We used structural equation modelling (SEM) (Grace, 2006) to realise a confirmatory test of our global path model and identify the significant relationships. Because the application of traditional SEM is restricted to normally distributed data, we

used the *piecewiseSEM* R-package (Lefcheck, 2016), which generalises the method to a larger range of distribution families. In the piecewise SEM approach, Shipley's tests of direct separation are used to test for missing paths and a Fisher's C statistic is calculated from the p-values of those tests (Shipley, 2009). The confirmatory test of the global path model consists in running a chi-squared test on the C statistic. According to the piecewise SEM method described in Lefcheck (2016), 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. In addition, the *piecewiseSEM* package provides a coefficient for each path and two types of R^2 (the marginal R^2_m , which is the variance explained by fixed effects, and the conditional R^2_c , which is the variance explained by both fixed and random effects) as indicators of the goodness-of-fit of each sub-model (Nakagawa and Schielzeth, 2013).

We used Poisson GLMMs to assess i) the effect of each group of predatory arthropods (non-ant omnivores, omnivorous ants, and predators) and the effect of *Musa* abundance and richness on the abundance of adult weevils, and ii) the potential effects of the abundance of adult weevils and the abundance of each group of predatory arthropods on weevil corm damage score. We included field identity as a random intercept effect (Zuur et al., 2009) to account for uncontrolled field-scale effects. In each case, we selected the best model by removing non-significant fixed-effect parameters in a backward-stepwise process using likelihood ratio tests (LRTs) (Bolker et al., 2009). Following Nakagawa and Schielzeth (2013), we used R^2 as an absolute value for the goodness-of-fit of the models. We tested for potential correlation between total plant species richness and *Musa* abundance using linear regression.

All GLMMs were estimated using the 'lme4' package (Bates et al., 2011), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009). All statistical analyses were performed with R 3.3.1 (R Development Core Team, 2016) and with a significance threshold of 0.05.

3. Results

3.1. Plot-scale plant community

Plant richness in the plots ranged from 2.5 to 22.5 species in the low stratum and from 0 to 16 species in the high stratum. Total plant richness ranged from 4.5 to 32.25 species. *Musa* abundance and total plant species richness were negatively but weakly correlated ($R^2 = 0.10$; p-value < 0.001). In decreasing order of frequency, the

Table 2

Set of GLMMs constituting the global path model based on *a priori* hypotheses regarding the relationships between response variables (trophic group abundances) and explanatory variables (environmental variables). D: Detritivore abundance; H: Herbivore abundance; OA: Omnivorous ant abundance; O: Non-ant omnivore abundance; P: Predator abundance; LSR: Low-stratum plant richness; HSR: High-stratum plant richness; LC: % of litter cover; PC: % of living-plant cover.

Response variable	Explanatory variables	Hypothesized mechanisms	References
D	LSR ¹ + HSR ¹ + LC ¹	¹ Positive bottom-up effect of plant richness and% of litter cover	Landis et al. (2000), Birkhofer et al. (2008)
H	LSR ² + HSR ² + PC ²	² Positive bottom-up effect of plant richness and% living-plant cover	Landis et al. (2000), Birkhofer et al. (2008)
OA	H ³ + D ³ + LSR ⁴ + HSR ⁴ + PC ⁴ + P ⁵	³ Positive bottom-up effect of prey abundance ⁴ Positive bottom-up effects (trophic and non-trophic) of plant richness and% of living-plant cover ⁵ Intraguild predation by predators	Landis et al. (2000), Zehnder et al. (2007) Landis et al. (2000) Gagnon et al. (2011)
O	H ⁶ + D ⁶ + LSR ⁷ + HSR ⁷ + PC ⁷ + P ⁸	⁶ Positive bottom-up effect (trophic and non-trophic) of plant richness and% of living-plant cover ⁷ Positive bottom-up effect of prey abundance ⁸ Intraguild predation by or competition with predators and omnivorous ants	Landis et al. (2000) Landis et al. (2000), Zehnder et al. (2007) Gagnon et al. (2011)
P	H ⁹ + D ⁹ + LSR ¹⁰ + HSR ¹⁰ + PC ¹⁰	⁹ Positive bottom-up effect of prey abundance ¹⁰ Positive bottom-up effect of plant richness and% of living-plant cover	Landis et al. (2000), Zehnder et al. 2007 Landis et al. (2000), Birkhofer et al. (2008)

Musa genotypes present in the study plots were Gros Michel, Cavendish, Plantain, Quadrado, Lacatan, Fressinette, Chopo Colorado, Chopo Blanco, and Cocori.

3.2. Effects of plant species richness and soil cover on multitrophic food web of ground-dwelling arthropods

Our global path model represented the data well (Fisher's C = 21.17, d.f. = 14, χ^2 test $p = 0.097$), and 10 of the 23 links tested were significant. SEM results, including pathway coefficients and significance levels, are presented in Table 3. The significant causal relationship between trophic group abundances and

Table 3

Pathway coefficient estimates and p values from the structural equation modelling. D: Detritivore abundance; H: Herbivore abundance; P: Predator abundance; LSR: Low-stratum plant richness; HSR: High-stratum plant richness; LC: % of litter cover; PC: % of living-plant cover.

Response variable	Explanatory variable	Estimate (± SE)	p value
Detritivores	LSR	0.012 (± 0.020)	0.5565
	HSR	-0.007 (± 0.026)	0.7866
	LC	1.024 (± 0.342)	0.0027
Herbivores	LSR	0.054 (± 0.025)	0.0297
	HSR	-0.045 (± 0.032)	0.1695
	PC	0.051 (± 0.462)	0.9123
Omnivorous ants	H	-0.001 (± 0.018)	0.9587
	D	0.028 (± 0.009)	0.0038
	LSR	0.045 (± 0.0153)	0.0031
	HSR	0.010 (± 0.017)	0.5368
	PC	-0.371 (± 0.219)	0.0901
	P	-0.015 (± 0.008)	0.0705
Non-ant omnivores	H	0.178 (± 0.056)	0.0014
	D	-0.074 (± 0.053)	0.1644
	LSR	0.083 (± 0.043)	0.0517
	HSR	-0.019 (± 0.038)	0.6253
	PC	0.289 (± 0.832)	0.7288
	P	-0.103 (± 0.042)	0.0147
Predators	H	0.045 (± 0.020)	0.0262
	D	0.027 (± 0.010)	0.0087
	LSR	-0.046 (± 0.016)	0.0054
	HSR	-0.047 (± 0.020)	0.0201
	PC	0.436 (± 0.238)	0.0668

Values in bold are statistically significant at an alpha level of 0.05.

environmental variables are summarised in the path diagram in Fig. 2. The arthropod orders found in the plots are listed in Table 4.

3.3. Biological control of the banana weevil by natural enemies

Adult weevil abundance was positively related to the abundance of *Musa* (χ^2 (df = 1) = 4.56, $p = 0.033$) but was not related to *Musa* genotype richness (χ^2 (df = 1) = 0.27, $p = 0.604$), the abundance of omnivorous ants (χ^2 (df = 1) = 1.07, $p = 0.299$), the abundance of non-ant omnivores (χ^2 (df = 1) = 1.06, $p = 0.304$), or the abundance of predators (χ^2 (df = 1) = 1.18, $p = 0.277$). The marginal and conditional R^2 values (including the random intercept effect) of the selected model were 0.12 and 0.61, respectively.

The corm damage score was negatively related to the abundance of omnivorous ants (χ^2 (df = 1) = 329.20, $p < 0.001$) and to the abundance of predators (χ^2 (df = 1) = 139.01, $p < 0.001$) (Fig. 3). However, it was not related to the abundance of adult weevils (χ^2 (df = 1) = 0.53, $p = 0.465$) or to the abundance of non-ant omnivores (χ^2 (df = 1) = 1.20, $p = 0.272$). The selected model explained a large percentage of the variance with a marginal R^2 of 0.59 and a conditional R^2 of 0.97.

4. Discussion

4.1. Effect of plant species richness and soil cover on multitrophic food web of ground-dwelling arthropods

We found that the food web of ground-dwelling arthropods was shaped by both a detritivory and an herbivory bottom-up cascade that propagated up to the predaceous trophic levels and affected the abundance of the potential natural enemies of the banana weevil. In the case of the herbivory pathway, the low-stratum plant species richness had a positive bottom-up effect on the abundances of herbivores and of omnivorous ants but had no direct effect on the abundance of omnivores, although a substantial portion of the diet of opilions, which represented 83% of this group, includes fruits and other plant materials (Halaj and Cady, 2000; Schaus et al., 2013). Omnivorous ants combine predation, scavenging, and consumption of plant-based resources to meet their nutritional requirements. Plant-based resources used by ants are various and mostly consist of honeydew (from association with trophobionts), extra-floral nectaries, and seeds (Bluthgen and Feldhaar, 2010). The importance of plant-based resources in the diet of omnivorous ants

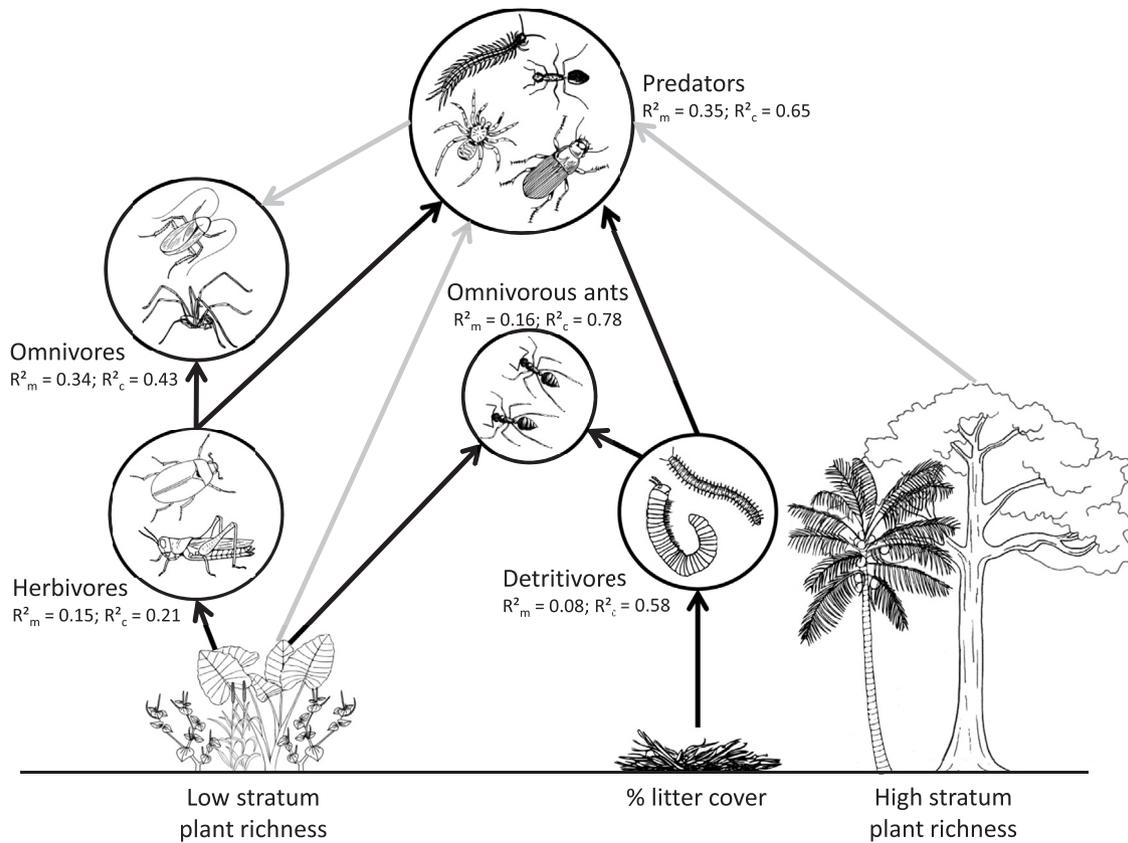


Fig. 2. Structural equation model of a multitrophic ground-dwelling arthropod food web. Structural equation model of the relationships among ground-dwelling arthropod trophic groups, low-stratum and high-stratum plant species richness, % of living plant cover, and % of litter cover. Black and grey arrows represent significant ($p < 0.05$) positive and negative relationships, respectively. The % of living-plant cover had no effect on any trophic group and is not shown. Non-significant relationships ($p > 0.05$) are not shown. Marginal (m) and conditional (c) R^2 values for each response variable are indicated.

Table 4
List and total abundance of arthropod orders of each trophic group sampled during the field study.

Trophic group	Class	Order	Individuals	
Detritivores	Insecta	Collembola	201	
		Coleoptera	26	
	Diplopoda	Polydesmida	63	
		Spirobolida	8	
		Julida	7	
		Stemmiulida	3	
	Malacostraca	Isopoda	42	
		Orthoptera	77	
Herbivores	Insecta	Hemiptera	66	
		Coleoptera	36	
		Homoptera	15	
		Hymenoptera	3	
		Lepidoptera	2	
		Thysanoptera	1	
		Insecta	Hymenoptera (ants)	904
			Blattodea	10
Arachnida	Opiliones	49		
	Hymenoptera (ants)	331		
Predators	Insecta	Coleoptera	92	
		Hemiptera	19	
		Dermoptera	4	
		Mantodea	1	
	Arachnida	Araneae	309	
		Scorpiones	1	
	Chilopoda	Lithobiomorpha	2	

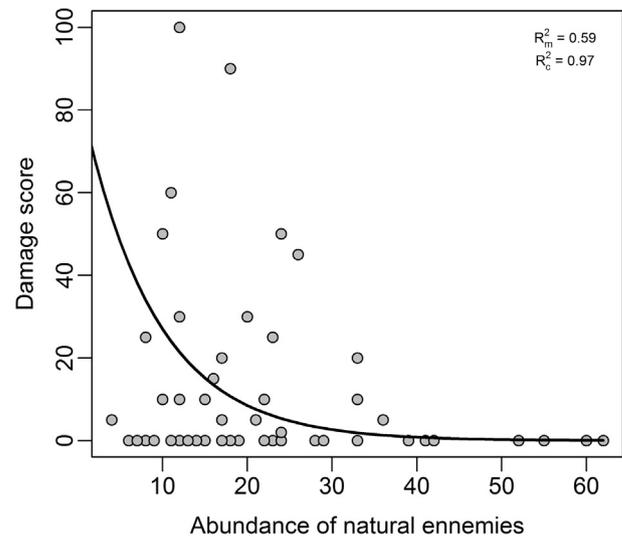


Fig. 3. Weevil damage vs. natural enemies' abundance. Relationship between damage by *C. sordidus* and the abundance of natural enemies (i.e. the sum of the abundance of omnivorous ants and predators, which were found to be both negatively correlated to the damage score). Circles: observed data; Line: relationship predicted by a Poisson GLMM.

is consistent with our finding that plant richness had a positive effect on the abundance of omnivorous ants.

We found no effect of the percentage of living-plant cover, which

served as a proxy for plant biomass, on any trophic group. This is consistent with Scherber et al. (2010), who found that herbivore and omnivore abundances were positively related with plant richness but not with plant biomass. Because the percentage of living-plant cover was not associated with arthropod abundances, we infer that the effect of plant richness on arthropod groups was more likely due to niche

diversity and complementarity rather than to resource abundance. In addition, the abundance of detritivores increased with the percentage of litter cover, likely because of increases in the availability of food and shelter.

Surprisingly, our study detected a negative effect of high- and low-strata plant richness on the abundance of predators. Malumbres-Olarte et al. (2013) found that the response to tussock cover differed among ground-active spider families and even among species within the Lycosidae family, which was the most represented spider family in our study. Such inconsistent responses to plant characteristics among spiders, which represented 42% of the predator group, suggest that the global negative effect of plant richness on predators in the current study may have masked the positive response of the abundance of certain spider species. However, pitfall trapping reflects relative arthropod activities, which depend on population density and activity (Curtis, 1980), rather than absolute abundances. Therefore, the global negative effect of plant richness on predators that we observed may also be explained by trapping bias. Higher plant species richness is expected to increase the structural complexity of vegetation, which may reduce the capacity or the need for predators to move to find shelter, mates, or food. Reduced movement may reduce trapping probability and lead to an underestimation of predator abundance. By manipulating the vegetation structure, Birkhofer et al. (2008) demonstrated that increasing vegetation complexity led to a decrease in the activity and abundance of ground-active spiders in a winter wheat field.

We found a positive, indirect bottom-up effect of the low strata plant richness on the abundance of omnivores and predators through the increase in the availability of alternative herbivore prey. In addition, predators seemed to benefit substantially from the detritivory pathway in that their abundance was positively related to the abundance of detritivores. A previous study showed that spiders, which were the second most abundant taxa within the predator group of the current study, can feed on both herbivory and detritivory pathways (Oelbermann et al., 2008).

Among the predaceous ants, which represented 45% of the predator group, 66% were *Ectatomma ruidum*. These large ants feed on herbivores, detritivores, and omnivores (Ibarra-Nunez et al., 2001) and are able to attack opilions and other large preys. This suggests that the negative effect of predator abundance on non-ant omnivore abundance was driven by intraguild predation of opilions by *Ectatomma ruidum*, especially given that those two taxa accounted for large proportions of their respective groups.

Our results support the hypothesis that the positive effects of vegetation on higher trophic levels are primarily driven by additional alternative prey rather than by structural complexity and highlight the potential role of plant-based resources on natural enemies, especially on omnivorous ants (Landis et al., 2000; Wackers et al., 2007).

4.2. Plant richness and the biological control of the banana weevil by natural enemies

Our results show that plant species richness is associated with a reduction of weevil abundance and corm damage (see Fig. 2 in Poeydebat et al. (submitted)), suggesting that the regulation of this pest might be enhanced by field-scale agroecosystem plant diversification. Such diversification may reduce pest abundance (Letourneau et al., 2011; Scherber et al., 2010; Symondson et al., 2002) through top-down effects associated with herbivore prey amplification and higher enemy abundance (Dassou et al., 2016; Letourneau et al., 2011; Poveda et al., 2008). However, we did not find a relationship between the abundance of *C. sordidus* adults and any potential natural enemy, i.e., we did not find evidence of top-down control of adults. In *C. sordidus*, the adult is cryptic and nocturnal and has a hard cuticle that may deter attack by predators (Koppenhöfer et al., 1992). Abera-Kalibata et al. (2006) searched for co-evolved natural enemies in the native region of *C. sordidus* but failed to find natural enemies that attacked adults. Adult

suppression associated with plant species richness may rely on other predators or pathogens. Consistent with the resource concentration hypothesis (Root, 1973), the abundance of *C. sordidus*, which is an oligophagous pest, decreased with the abundance of *Musa*. The negative relationship between plant species richness and *Musa* abundance in our study corroborates the role of host plant dilution in the regulation of weevil abundance.

Nevertheless, our results suggest that plant species richness enhance weevil corm damage regulation by promoting herbivorous and detritivorous preys and natural enemies that feed on immature stages of *C. sordidus*. Indeed, one may consider the damage score as a proxy for the incidence of immature stages (Carval et al., 2016). Researchers have reported that generalist predators consume banana weevil eggs and larvae (Abera-Kalibata et al., 2006; Koppenhöfer, 1993a; Koppenhöfer et al., 1992; Mollot et al., 2012) and that ants consume the eggs of various pest species (Way and Khoo, 1992).

In our study, the abundance of predators had a negative effect on the abundance of non-ant omnivores, which is likely a result of intraguild predation. Although intraguild predation may reduce predation on pests, this risk is thought to be relatively low (Chailleux et al., 2014; Rosenheim, 2007). In the current study, intraguild predation did not disrupt biological control because non-ant omnivores did not contribute to the control of weevil damage.

Because susceptibility to weevil attack varies among *Musa* cultivars (Kiggundu et al., 2007; Ortiz et al., 1995), we would have expected to detect positive (or negative) effects of *Musa* richness on weevil abundance if the cultivars were more susceptible (or more resistant) than the phytometer. In our study, the absence of an effect of *Musa* richness on the abundance of adult weevils may have resulted from a low variability in the susceptibility to the pest among the cultivars or from the balancing effect of a combination of more susceptible and more resistant cultivars compared to the phytometer.

Consistent with previous studies (Gold et al., 2001; Vilardebo, 1973), we found no relationship between weevil abundance and damage. This can be explained by the gap between the dispersal ability and lifespan of adults and immature stages and/or by the difference between the cumulative nature of the corm damage score, which integrates larval damage over time, and the punctual assessment of adult abundance.

5. Conclusions

Our results are consistent with the idea that pest regulation in agroecosystems can be enhanced through field-scale plant diversification. More specifically, our results suggest how the plant community and soil cover affect banana weevil regulation in banana and plantain agroecosystems. Omnivorous ants and predatory arthropods (including predaceous ants) were the groups likely responsible for the control of *C. sordidus* damage through eggs or larvae predation. The predator group contained different sub-groups of arthropods but was dominated by spiders, ants, and coleopterans. Plant species richness did not directly promote predator abundance, but indirectly, by supporting increases in omnivorous and herbivorous preys. Predators were also found to feed on detritivores, whose abundance was positively related to the percentage of litter cover. Ground-dwelling spiders and carabids prefer open habitat patches for movement and foraging (Birkhofer et al., 2008) but are also dependant on prey from plant diversified patches and litter patches. Omnivorous ants fed on detritivores and on plant-based resources, whose abundances positively depended on soil litter cover and plant richness, respectively. Additionally, bare soil has been shown to promote predation by ants (Jaffe et al., 1990). Finally, because the percentage of living-plant cover had no effect on any trophic group, we infer that plant richness rather than abundance is important for biological pest control. Thus, we suggest that future research should be conducted to evaluate the following three management strategies. First, the crop field should consist of a matrix that includes (i) plant-

diversified patches that promote the abundance and diversity of alternative herbivore preys and plant-based resources; (ii) crop and non-crop litter patches to promote the abundance of alternative detritivore prey; and (iii) bare soil patches to promote predator and omnivore foraging. Second, the plant species within the plant-diversified patches should be carefully selected because (i) plants that produce extrafloral nectaries can enhance biological control (Rezende et al., 2014), and (ii) some plant species may be hosts of other polyphagous pests of the crop (Zehnder et al., 2007) including plant-parasitic nematodes (Queneherve et al., 2006). Third, according to our results and to the resource concentration hypothesis (Root, 1973), farmers should reduce the planting density of the major cash crop(s) whenever it is economically viable and could compensate for the loss in production by planting other food crops or cash crops. Finally, the local fragmentation of habitats recommended here could be achieved with mixed systems that included annual, semi-perennial, and perennial crops.

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