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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 Agroforesteria, 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 ± 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. 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 ≥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,

Table 1
Total, low-stratum and high-stratum plant species richness (mean number of species ± 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 (± sd)	Low-stratum plant species richness (± sd)	High-stratum plant species richness (± sd)	Number of phytometers (± sd)	*Musa* genotype richness	*Musa* density per ha (± sd)
1	8 ± 2	7 ± 1	1 ± 1	8	1	2898 ± 287
2	10 ± 4	7 ± 4	3 ± 1	5	6	1982 ± 304
3	11 ± 4	7 ± 3	4 ± 2	14	2	505 ± 202
4	15 ± 3	12 ± 2	3 ± 1	5	2	2166 ± 287
5	15 ± 4	8 ± 2	7 ± 4	8	10	1477 ± 496
6	17 ± 9	13 ± 6	5 ± 3	10	8	994 ± 602
7	19 ± 3	17 ± 2	2 ± 2	10	3	857 ± 328
8	21 ± 6	13 ± 4	8 ± 3	8	5	677 ± 304
9	25 ± 2	17 ± 3	8 ± 2	8	7	912 ± 340

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