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Extrafloral nectaries of associated trees can enhance natural pest control

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ABSTRACT

Plant diversity may increase natural enemy populations because some plants can provide alternative food to natural enemies. Extrafloral nectar is such an alternative food and plants producing extrafloral nectar are known to suffer less from herbivory. Little is known about the effect of plants with extrafloral nectaries on herbivory of neighbouring plants. Here, we investigated whether extrafloral nectaries of an associated tree (*Inga subnuda* subsp. *luschnathiana*) can enhance natural pest control in coffee agroforestry systems. We assessed the effect of nectar availability from Inga trees on parasitism of coffee leaf miners (*Leucoptera coffeella*) and on damage caused by coffee leaf miners and coffee berry borers (*Hypothenemus hampei*). Most of the nectary visitors were either parasitoids or predators, with most predators being natural enemies of coffee pests. Coffee plants were sampled every metre along a transect of 10–15 m extending from each Inga tree. The distance of the coffee plants from the Inga trees did not significantly correlate with coffee leaf miner parasitism, proportion of mined leaves or with the proportion of bored coffee berries. We subsequently used abundance and species richness of those nectary visitors without known association with leaf miners and borers as indirect measures of nectar availability. Whereas species richness had no significant effect on natural pest control, leaf miner parasitism increased significantly with the abundance of nectary visitors (excluding natural enemies of the coffee pests), and the proportion of mined leaves decreased significantly with this abundance. The proportion of bored fruits decreased with increasing abundance of visitors, but this trend was not significant. Together, these results suggest that Inga trees provide alternative food to natural enemies of coffee pests, resulting in increased natural control. Thus, extrafloral nectaries of associated trees can enhance natural pest control in agroforestry systems.

1. Introduction

Natural pest control is one of the most important ecosystem services and has been associated with increased habitat complexity (Bianchi et al., 2006). Diversified agroecosystems are shown to increase natural enemy abundance and enhance pest control (Langellotto and Denno, 2004; Bianchi et al., 2006). Herbivore abundance and crop damage are also lower in more diversified agroecosystems compared to lower diversity crops (Letourneau et al., 2011). The underlying ecological mechanisms that explain aggregation and improvement of natural enemies in more diversified habitats are not completely explored (Langellotto and Denno, 2004). The main explanation suggested so far is the availability of refuges, favourable microclimatic conditions, and the presence of alternative prey and food for natural enemies (Landis et al., 2000; Gurr, 2003; Langellotto and Denno, 2004; Bianchi et al., 2006).

Alternative food such as pollen and nectar is utilized by parasitoids and predators for survival in periods of prey scarcity (Landis et al., 2005). Moreover, many predators can also reproduce on such alternative food (Wäckers, 2005). The availability of nectar and pollen from flowers consorted or adjacent to crops can increase natural enemy diversity and abundance, which may lead to reduction of herbivory on crop plants (Van Rijn et al., 2002; Tylianakis et al., 2004; Koptur, 2005). Nectar from extrafloral nectaries is also a food source for natural enemies (Bentley, 1977). Plants

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bearing extrafloral nectaries enhance the diversity and abundance of arthropod assemblages, which decreases herbivory and increases fitness of these plants (Cuautle and Rico-Gray, 2003; Kost and Heil, 2005; Mathews et al., 2007; Brown et al., 2010). Nectar-feeding insects respond positively to increases in nectar flow rate and sugar content, adjusting their visitation frequency according to nectar availability (Heil et al., 2001; Ness, 2003; Schilman and Roces, 2003; Kost and Heil, 2005). In return to the food provided by the extrafloral nectaries, the natural enemies protect plants against herbivory (Whitney, 2004; Koptur, 2005). Extrafloral nectaries are therefore considered an indirect plant defence (Sabelis et al., 2005). Elucidating how such indirect plant defence could be used for crop protection may help implement more sustainable practices for agroecosystem management (Heil, 2008).

Although extrafloral nectaries are thought to affect arthropod communities (Atsatt and O'Dowd, 1976; Pemberton and Lee, 1996; Rudgers and Gardener, 2004; Barbosa et al., 2009), little is known about the effect of nectaries on herbivory on neighbouring plants. If nectar availability increases the number of natural enemies, resulting in less herbivory on plants bearing extrafloral nectaries (Heil et al., 2001; Kost and Heil, 2005), neighbouring plants could also profit from the visitors (Jezorek et al., 2011). Here, we investigated whether the presence of associated plants with extrafloral nectaries increases natural control of pests in an agroforestry coffee crop.

Coffee-based agroforestry systems are complex agroecosystems that usually contain a high diversity of tree species (Tscharntke et al., 2011). Trees can provide refuges for natural enemies and more diversified agroforestry systems are usually related to positive effects on coffee pest control (Armbrecht and Perfecto, 2003; Philpott et al., 2008; Teodoro et al., 2009; Pardee and Philpott, 2011). Several plant species within coffee agroforestry systems possess extrafloral nectaries, but one of the most common tree genera consorted with coffee and bearing foliar nectaries is *Inga* Miller (Leguminosae) (Soto-Pinto et al., 2007; Souza et al., 2010). Coffee plants are attacked by at least 850 insect species, the major pests in the Neotropics being the coffee leaf miner *Leucoptera coffeella* (Guérin-Mèneville) (Lepidoptera: Lyonetiidae) and the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) (Le Pelley, 1973; Vega et al., 2009). Coffee leaf miners are small moths, whose larvae feed on the palisade parenchyma cells of coffee leaves; coffee berry borers mine galleries in coffee seeds (Souza et al., 1998; Vega et al., 2009). We investigated the effect of the presence of nectar-producing Inga trees and the visitors of extrafloral nectaries on the natural control of these two coffee pests.

2. Materials and methods

The study was conducted between January and May 2010 in five coffee agroforestry systems in the municipality of Araponga, state of Minas Gerais, Brazil (42°31′14″W, 20°40′01″S), located in the domain of the Atlantic Rainforest (Ab'Sáber, 2003). The agroforestry systems form part of a long-term experimentation carried out by a non-governmental organization (Centre of Alternative Technologies of Zona da Mata) and local farmers since 1993 (Cardoso et al., 2001). The diverse vegetation within the agroforesty systems is managed based on compatibility with coffee, biomass production, labour intensity and production diversity (Souza et al., 2010). Several plant species consorted with coffee, such as *Senna* sp., *Piptadenia gonoacantha* (Mart.) J.F. Macbr. and *Ricinus communis* L., possess extrafloral nectaries. We choose Inga trees as a model because it is common in coffee agroforestry systems and farmers reported its capacity to help in coffee pest control. Hence, all systems studied here had Inga trees, but each agroforestry had a unique plant species composition (Souza et al., 2010). The management of these agroforesty systems was based on agroecological principles (Cardoso et al., 2001). The region has a tropical highland climate with rainy summers and dry winters. Annual rainfall is 1200–1800 mm, the mean annual temperature is 18 °C (Golfari, 1975; ENGEVIX, 1995). The altitude of the studied agroforestry systems varies from 800 to 1070 m, with slopes up to 45% and the soil types are predominantly Oxisols (Golfari, 1975).

2.1. Abundance and richness of nectary visitors

Twenty-five Inga trees (*Inga subnuda* subsp. *luschnathiana* (Benth.) T.D. Penn.) were selected, five in each coffee agroforestry system. Thirty leaves per tree were checked for arthropods feeding on the nectaries during five minutes, every two hours, from 6 to 18 h. All five trees in each study site were sampled during the same day. Visitors were collected in 70% ethanol for identification of morphospecies. For purposes of analysis, tree size (circumference at breast height) was scored in three classes: small: [5.0–31.6 cm); medium: [31.6–70.0 cm); large: [70.0–131.0 cm]. To evaluate whether abundance of natural enemies visiting the nectaries varied with the time of day (6–18 h), we used linear mixed effects models (LMEs). Because it is known that visitation of nectaries by ants has a maximum around noon (Koptur, 1984), we entered both time of day and time of day squared as factors. The abundance of all visitors, parasitoids, ants and other predators were $\log(x+1)$-transformed and used as response variables. The effect of tree size on the abundance and species richness of nectary visitors (excluding the natural enemies of the two coffee pests) was analyzed with a generalized linear model (GLM) with a Poisson error distribution.

2.2. Effect of Inga trees on coffee pest control

We aimed to elucidate the extent to which extrafloral nectaries result in aggregations of natural enemies and reduce damage of crop plants. The expectation was that coffee plants closer to the Inga trees would be more protected against herbivory. We therefore assessed the proportion of herbivory and frugivory and the rate of parasitism of leaf miners on ten coffee plants on a transect extending from the Inga trees that were sampled for nectary visitors (above). Coffee plants were sampled at intervals of one metre, starting with the plant closest to the Inga tree. When a coffee plant did not have leaves or berries, we sampled an extra plant, thus extending the transect with one metre for each plant without leaves or berries. This resulted in 5 transects per field site (one per tree) extending 10–15 m from the Inga trees. It was not possible to assess the effect of Inga trees beyond this range because of the limited distances among the trees.

From each designated plant on the transect, the damage caused by coffee leaf miners was assessed by collecting 20 leaves distal from the fifth pair of leaves from four different branches per coffee plant (Souza et al., 1998). The four branches were located in the centre of the shrub and pointed to the four cardinal directions (Souza et al., 1998). A total of 5000 coffee leaves were sampled (200 per transect) and the proportion of mined leaves was assessed.

To estimate the damage caused by the coffee berry borer, nine fruits were randomly collected from the top, centre and lower parts of the plants per designated coffee plant on each transect (Souza and Reis, 1997). We sampled fully developed green, yellow and red fruits, which are all suitable for attacks by the coffee berry borer (Vega et al., 2009). A total of 2250 fruits were sampled (90 per transect) and the proportion of bored fruits per coffee plant was assessed.

To assess the parasitism rate of leaf miners, one mined leaf was collected from each coffee plant along the transects (10 leaves per