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Extrafloral nectary-bearing leguminous trees enhance pest control and increase fruit weight in associated coffee plants

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ABSTRACT

Plant diversification is a strategy for pest management in agroecosystems. However, a major hurdle in the adoption of this management practice by farmers is related to doubts concerning its effects on crop productivity. Here we assess coffee production and natural control of coffee pests in the presence or absence of leguminous trees bearing extrafloral nectaries (*Inga edulis*). We compared coffee yield, coffee damage caused by coffee leaf miners (*Leucoptera coffeella*) and coffee berry borers (*Hypothenemus hampei*) and parasitism and predation of coffee leaf miners in a replicated field experiment. To evaluate the effect of proximity of the nectar source on natural control, we also assessed pest control and production along transects of 50 m extending from the *Inga* trees. Production per coffee plant was equal in both systems but coffee fruits were heavier in coffee consorted with *Inga* trees. In the most productive year, coffee production was higher on plants closer to the *Inga* trees. Damage caused by coffee leaf miners and coffee berry borers was lower in coffee with *Inga* trees and increased with distance from the trees. Parasitism of coffee leaf miners and predation by wasps did not increase in coffee consorted with *Inga*, neither decreased with distance from the trees. Therefore, *Inga* trees enhanced coffee production and increased natural control of coffee pests.

1. Introduction

Tree diversity increases productivity in natural ecosystems and several studies reveal that biodiversity can be used to enhance agricultural production (Bullock et al., 2001; Liang et al., 2016; Nesper et al., 2017). Agroforestry is based on increasing tree diversity in agricultural fields, thus providing important ecosystem services such as carbon sequestration, nutrient cycling, soil fertility, drought resistance, weed and pest control and even mitigate effects of rising temperatures due to climate change (Gomes et al., 2020; Jha et al., 2011; Perfecto et al., 2007, 1996; Pumariño et al., 2015; Souza et al., 2012; Zhang et al., 2007). The major bottleneck in implementation of agroforestry systems and other plant diversification strategies is that they do not always translate into increased yield (Poveda et al., 2008; Zhang et al., 2007).

Indeed, some studies show that increased diversification in crop fields can lead to lower crop production (Letourneau et al., 2011; Poveda et al., 2008), whereas a recent meta-analysis shows that increased plant diversification in agricultural systems does not result in overall significant yield loss (Tamburini et al., 2020). Yet, on-farm diversification has to be designed to support functional biodiversity, provide intended ecosystem services (Landis et al., 2000) and maintain or increase production (Poveda et al., 2008).

Crop production is often constrained by pest attacks. Therefore, one of the most important and desired ecosystem services is the natural control of crop pests (Chaplin-Kramer et al., 2011; Lewis et al., 1997; Zhang et al., 2007). Increasing plant diversification in agricultural systems usually results in decreases of herbivore densities, enhancement of natural enemy efficiency and reduction of crop damage which,

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ultimately, may increase crop production (Andow, 1991; Bianchi et al., 2006; Isbell et al., 2017; Letourneau et al., 2011). Several hypotheses have been put forward to explain how vegetation diversity can enhance pest control. Increased plant diversity may attract pests away from the crops and increase mortality of the pest due to enhancement of natural enemies (Begg et al., 2017; Gurr et al., 2017; Perović et al., 2018; Poveda et al., 2008; Root, 1973). The underlying ecological mechanisms that explain aggregation and improvement of natural enemies in more diversified habitats are not completely explored (Perović et al., 2018). The main explanation suggested so far is the availability of refuges, favorable microclimatic conditions, and the presence of alternative prey and food, such as pollen and nectar, for natural enemies (Begg et al., 2017; Bianchi et al., 2006; Landis et al., 2000; Perović et al., 2018; van Rijn and Wäckers, 2016). The management of tree species in agroforestry systems can affect conservation and enhancement of natural enemies, improve pest control and increase crop productivity (Jezeer et al., 2018; Muschler, 2001; Somporn et al., 2012; Vaast et al., 2006). In this paper, we assess coffee production in the presence or absence of young leguminous trees with extrafloral nectaries in a replicated field experiment. In addition, we compared the damage and natural control of coffee pests in the presence and absence of young trees.

In Latin America, coffee was traditionally cultivated in agroforestry systems, but agronomic intensification resulted in a transformation of understory coffee to full-sun cropping (Jha et al., 2014, 2011; Perfecto et al., 1996). In Brazil, coffee has predominantly been cultivated in monocultures under full sun (DaMatta, 2004; Jha et al., 2011). However, environmental and social problems caused by conventional agricultural practices encouraged small-scale farmers to develop agroforestry coffee systems and to adopt agroecological practices, aiming to recover soil quality, reduce erosion, improve nutrient cycling and increase food security and sovereignty (Cardoso et al., 2001; Sales et al., 2013; Souza et al., 2012). The trees used for diversification of coffee agroforestry systems are chosen by family farmers based on compatibility with coffee, biomass production, nitrogen fixation, labor intensity and diversification of the production (Cardoso et al., 2001; Grossman, 2003; Souza et al., 2010). However, little information on the effect of trees on pest suppression is available (Staver et al., 2001). Although not selected with respect to this characteristic, many trees selected for intercropping with coffee possess extrafloral nectaries, some of the most common species belonging to the genus *Inga* Miller (Fabaceae) (Souza et al., 2010).

Extrafloral nectar can be an important source of carbohydrates, providing energy to insects (Koptur, 2005). Nectar may increase survival, fecundity, longevity and flight activity and also enhances foraging behavior of natural enemies, thus leading to increased control of herbivores (Jamont et al., 2014; Koptur, 2005; Lavandero et al., 2005; Tylianakis et al., 2004; Wäckers, 2005). Despite some evidence that defense provided by extrafloral nectaries extends to the plant community (Barbosa et al., 2009; Rudgers and Gardener, 2004), only a few recent studies suggested that plants bearing extrafloral nectaries could also provide protection to neighboring plants (Jamont et al., 2014; Jezorek et al., 2011). We previously showed that the production of extrafloral nectar by associated *Inga* trees was correlated with increased natural control of coffee pests (Rezende et al., 2014). Here, we performed a manipulative field experiment to confirm that the presence of nitrogen-fixing and nectar-producing *Inga* trees can enhance natural control of herbivores without negative effects on yield.

Pests causing major damage in coffee are the coffee leaf miner *Leucoptera coffeella* (Guérin-Mèneville) (Lepidoptera: Lyonetidae), which disrupts coffee photosynthesis due to premature drop of mined leaves, and the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae), which depreciates coffee fruits due to the galleries bored into coffee seeds (Damon, 2000; Pereira et al., 2007). Based on an earlier study (Rezende et al., 2014), we expected extrafloral nectary-bearing trees to contribute to the natural control of coffee pests, which we aimed to verify in this study. To this end, we compared coffee

damage and parasitism and predation of coffee pests between replicated coffee plots, half of which with young *Inga* trees, and along transects extending from the plots with trees. We also assessed the effects of the association of coffee plants with *Inga* on coffee yield.

2. Methods

2.1. Study area

Experiments were conducted on a 45 ha farm in the municipality of Paula Cândido, Minas Gerais, Brazil (20°48'24.47"S 42°59'01.85"W, altitude 777 m), within the Atlantic Rainforest domain. The predominant soil type is Oxisols and the region is characterized by a tropical highland climate (Ab'saber, 2012), with rainy summers and dry winters (mean annual temperature 18.5 °C mean rainfall 1400 mm). Within the farm, most land was cultivated with full-sun coffee but there were also natural forest fragments, none of them close to the experimental plots. The full-sun coffee was conventionally managed, with use of fertilizers and pesticides, but insecticides were not used during the study period.

To assess the effect of *Inga* trees on coffee production and natural control of coffee pests, we compared coffee (*Coffea arabica* L., variety "Oeiras") in monoculture with coffee consorted with *Inga* trees in eight field plots (20 × 20 m, four with and four without *Inga* trees; Supplementary material: Fig. A1) in a single full-sun coffee field and assessed the effect of distance from the trees on production and pest damage in four transects of 50 m. In November, 2012, 49 seedlings (height 60 cm) of *Inga edulis* Mart. (Fabaceae) were planted per plot, in seven rows per plot, 2.5 m apart. The other four plots served as control. Plots with and without *Inga* trees were interspersed and 22 m apart, thus minimizing differential effects of the environment on the plots. The experimental plots were surrounded by full-sun coffee plantations. Natural enemies of coffee pests and coffee damage were assessed between February 2013 and February 2014. Sampling was performed every fifteen days during 51 weeks. On every sample date, ten coffee plants in each plot were randomly chosen and sampled (excluding plants from the edge), and one coffee plant was sampled every 10 m in the transects (0–50 m).

2.2. Production

Coffee production was estimated by collecting all fruits from 10 coffee plants in each plot and from one coffee plant every 10 m along each transect in May 2013 and in May 2014 (104 coffee plants per year). Coffee production was expressed as the total fruit weight per coffee plant (kg/plant) and as the mean weight per fruit (yield, g/100 fruits per coffee plant). Seed weight is of special economic interest since it increases the total yield and has crucial impact on the quality and price of coffee (Classen et al., 2014).

The effects of associated *Inga* trees on coffee fruit weight and coffee yield (both $\log(x + 1)$ transformed) in the plots were analyzed with a linear mixed effects model (LME, package nlme in R) (Pinheiro et al., 2017) with the presence of *Inga* and the year as well as their interaction as fixed factors and plot as random factor. Coffee yield and fruit weight along the transects were analyzed with an LME model with the distance along the transect and the year as fixed factors and the transect as random factor. Significance of factors and interactions were assessed through model simplification and comparison of models using the anova function of R (R Development Core Team, 2017). Contrasts between treatments within each year were assessed with general linear hypothesis testing with the package lsmeans (Lenth, 2016).

2.3. Pest damage

Ten coffee plants were fortnightly sampled in each plot and one coffee plant was sampled every 10 m on each transect. Eight leaves were collected from primary plagiotropic branches at the center of the canopy of each plant. We sampled the fourth pair of leaves from each side of the

plant (north, south, east and west) (Pereira et al., 2007). The proportion of mined leaves per coffee plant was assessed based on a total sample size of 21632 leaves. These leaves were also used to assess predation of leaf miners (see 2.4. *Natural enemies* below). Because the proportion of mined leaves showed a strong seasonal trend and consisted of repeated measures through time, we used a generalized additive model (GAM, package *mgcv* for R) (Wood, 2017) for data analysis, with time as a smooth factor with plot or transect as random factor and the presence or absence of *Inga* trees (in plots) or distance (for transects) as fixed factors, with a binomial error distribution (logit link). We used the default thin plate regression splines as smoothing function (Wood, 2017) and a first-order autocorrelation model (Wood, 2017), typically used to account for temporal autocorrelation of the data. We first formulated the full model, checked its performance with the *gam.check* function, and then tested the significance of the fixed and random factors through model simplification using the *anova* function of R (R Development Core Team, 2017) and Akaike's information criterion (AIC). Contrasts were obtained by stepwise aggregating factor levels and testing them with the *anova* function and AIC. "Wiggly" models (Wood, 2017) were avoided by restricting the basis of the dimension of the smooth term.

Damage caused by coffee berry borers was calculated as the proportion of bored coffee berries. During the five months that plants carried fruits (between February and June of 2013), the same coffee plants as sampled for mined leaves were sampled non-destructively by checking fifty fruits (a total of 135200 berries) on one branch of each coffee plant for entrance holes of the borers (Souza and Reis, 1997). Because this sampling had to be non-destructively, we could not determine whether the holed fruits actually contained borers. Effects of trees on fruit borer damage were analyzed with GAM as above. Because of the low incidence of bored fruits, data of the transects were summed per distance, and the effect of distance on the proportion of bored fruits was analyzed with GAM as above.

After coffee harvesting, a new survey was conducted to evaluate damage caused by coffee berry borers on the harvested berries. The proportion of bored fruits per coffee plant was assessed based on a total of 10400 coffee fruits per year for two consecutive years. Because these were not repeated measures, we analyzed the effects of the presence of trees in the plots and of the distance from the trees in the transects with an LME (see 2.2. *Production*) with an arcsine transformation of the proportion of bored fruits.

2.4. Natural enemies

Death of coffee leaf miner larvae due to predation by predatory wasps can be observed because the predators tear the mines to reach the larvae (Lomeli-Flores et al., 2009; Pereira et al., 2007). The 21632 sampled leaves were examined for such torn mines in the laboratory. Data of the transects were combined per distance as explained above.

To assess parasitism of coffee leaf miners, we collected one leaf with an intact mine from 10 coffee plants in each plot fortnightly. We also collected one mined leaf every 10 m on each transect. Each mined leaf was incubated in the laboratory in a separate plastic vial with the petiole inserted in water to maintain turgidity (Pereira et al., 2007) until the emergence of leaf miners or parasitoids. Emerged parasitoids were stored in 70% ethanol for identification. A total of 2704 mined leaves were sampled and the parasitism rate per coffee plant was assessed. The proportions of parasitized leaf miners and of preyed mines were analyzed with a GAM as above.

3. Results

3.1. Coffee production

The average fruit weight was significantly higher from plants associated with *Inga* trees than from unassociated plants (Fig. 1a, LME, $\text{Chi}^2 = 8.18$, d.f. = 1, $P = 0.0042$), and was significantly higher in 2013

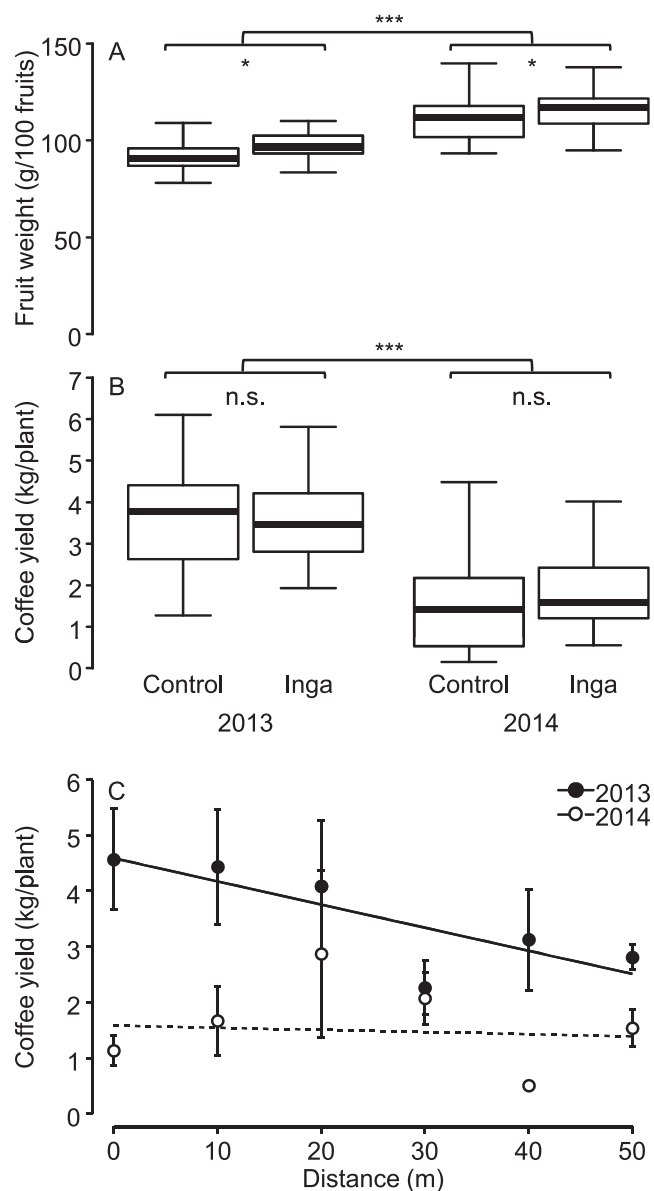


Fig. 1. Production by coffee plants in monoculture (Control) or associated with the leguminous tree *Inga edulis* (Inga). Shown are (a) the weight of coffee fruits (per 100 fruits) and (b) the coffee yield per coffee plant for two years (2013 and 2014) in plots with or without (Control) *Inga* trees. Thick lines indicate medians, boxes show 25 and 75 percentiles, whiskers show interquartile ranges, and points are individual outliers. Asterisks below accolades show significance of the difference between treatments within each year, asterisks above accolades show significance of the difference between years. (c) Average (\pm s.e.) coffee yield along transects extending from 0 to 50 m from an *Inga* tree. Lines are fits from a linear mixed effects model (see text). *: $P < 0.05$; ***: $P < 0.001$; n.s.: Not significant.

than in 2014 ($\text{Chi}^2 = 96.5$, d.f. = 1, $P < 0.0001$). The yield per coffee plant did not differ between plots with and without *Inga* trees (Fig. 1b, LME, $\text{Chi}^2 = 0.59$, d.f. = 1, $P = 0.44$), but was significantly higher in 2013 than in 2014 ($\text{Chi}^2 = 85.9$, d.f. = 1, $P < 0.0001$).

The distance from *Inga* trees did not affect coffee fruit weight (2013: average weight \pm s.e. per 100 fruits 95.1 ± 1.4 ; 2014: 118.7 ± 2.2 , LME, $\text{Chi}^2 = 1.24$, d.f. = 1, $P = 0.26$). There was a significant effect of the interaction of distance with year on coffee yield (Fig. 1c, LME, $\text{Chi}^2 = 4.69$, d.f. = 1, $P = 0.03$). This was caused by coffee yield decreasing significantly with distance in 2013 (LME, $\text{Chi}^2 = 10.7$, d.f. = 1, $P = 0.011$), but not in 2014 (Fig. 1c, LME, $\text{Chi}^2 = 0.0015$, d.f. = 1,

P = 0.97). Coffee yield was significantly higher in 2013 than in 2014 (contrasts after LME).

3.2. Coffee damage

The proportion of mined leaves showed a clear seasonal trend (GAM, effect of smoothed factor time: $\chi^2 = 597$, estimated d.f. = 31.4, $P < 0.0001$), decreasing during the rainy season and increasing during the dry period (Fig. 2a). A lower proportion of leaves in the plots with *Inga* had mines than in the plots without trees ($\chi^2 = 19.1$, estimated d.f. = 1, $P < 0.0001$), especially when leaf miners caused most damage, i. e. during the dry season (Fig. 2a). A similar seasonal trend was observed along the transects (Fig. 2b, GAM, effect of time, $\chi^2 = 266$, estimated d.f. = 24.1, $P < 0.0001$). Coffee plants closer to *Inga* trees had a lower proportion of leaves with mines than plants further away (GAM, $\chi^2 = 6.82$, est. d.f. = 1, $P = 0.009$). There was no significant effect of distance beyond 20 m from the trees (Fig. 2b, contrasts after GAM).

The proportion of bored fruits varied significantly through time (GAM, $\chi^2 = 488$, est. d.f. = 27.5, $P < 0.0001$) and was also lower for coffee with *Inga* trees than for coffee without trees (Fig. 3a, GAM, $\chi^2 = 31.2$, est. d.f. = 1.8, $P < 0.0001$). The proportion of bored fruits increased significantly with distance from the trees (Fig. 3b, GAM, $\chi^2 = 44.0$, est. d.f. = 1, $P < 0.0001$), and again, there was no significant

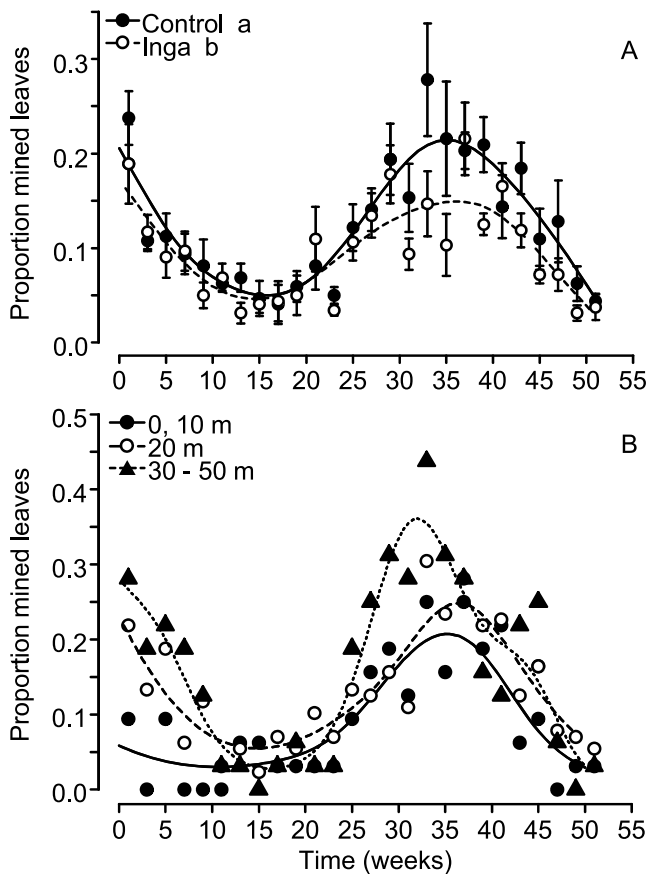


Fig. 2. (a) The average proportion (\pm s.e.) of coffee leaves attacked by the leaf miner *Leucoptera coffeella* as a function of time in plots with (*Inga*, open circles) or without (Control, closed circles) trees planted in between the rows of coffee plants. There was a significant difference between the two treatments (indicated by letters in the legend, contrasts after GAM). (b) The average proportion of leaves with mines as a function of time in transects extending 50 m from an *Inga* tree. Standard errors are left out for reasons of clarity. Three groups of distances could be discerned (0 + 10 m, closed circles; 20 m, open circles, 30 + 40 + 50 m, closed triangles). The three groups differed significantly from each other (contrasts after GAM).

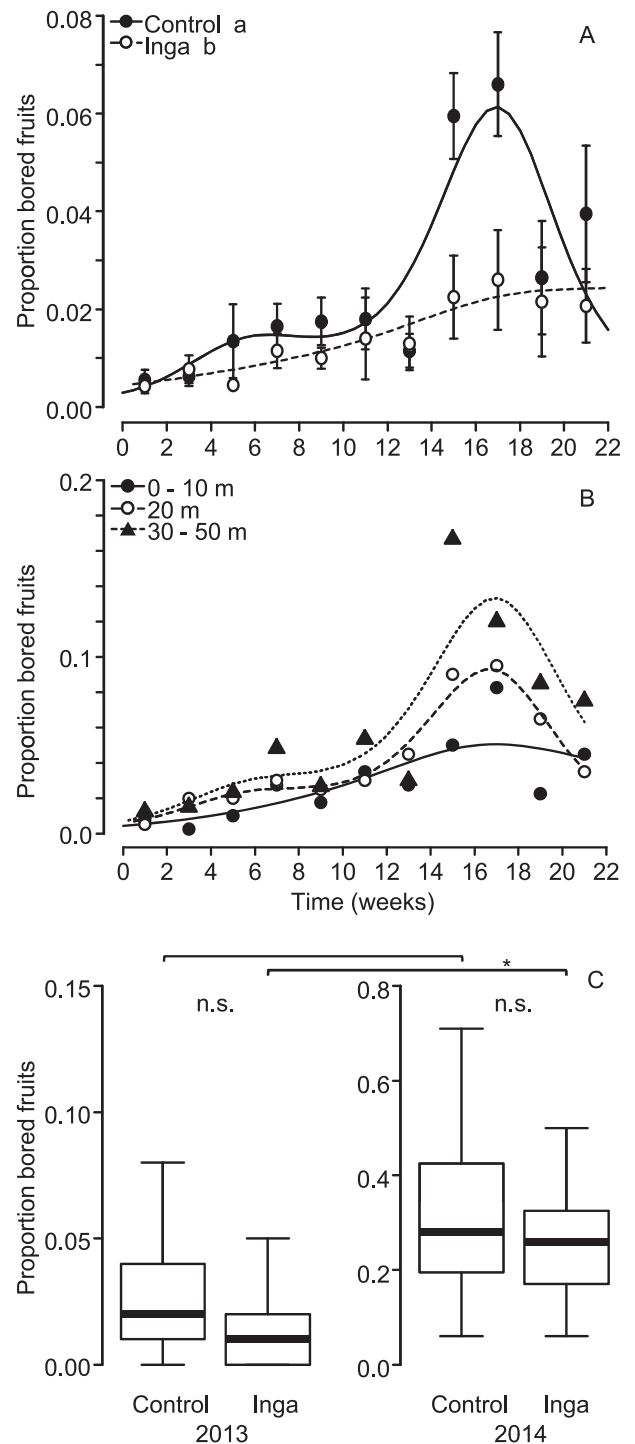


Fig. 3. (a) The average proportion (\pm s.e.) of coffee berries attacked by the coffee berry borer *Hypothenemus hampei* as a function of time in plots with (*Inga*, open circles) or without (Control, closed circles) trees planted in between the rows of coffee plants. There was a significant difference between the two treatments (indicated by letters in the legend, contrasts after GAM). (b) The average proportion (\pm s.e.) attacked berries as a function of time in transects extending 50 m from an *Inga* tree. Three groups of distances could be discerned (0 + 10 m, closed circles; 20 m, open circles, 30 + 40 + 50 m, closed triangles). The three groups differed significantly from each other (contrasts after GAM). (c) The proportion of bored fruits after harvesting in 2013 (left) and 2014 (right) in plots with (*Inga*) or without (Control) associated trees. See text for significant differences.

effect of distance beyond 20 m from the trees (Fig. 3b, contrasts after GAM). The proportion of bored fruits in the transects showed a significant trend with time (Fig. 3b, GAM, $\text{Chi}^2 = 266$, est. d.f. = 3.44, $P < 0.0001$).

After harvesting, a higher infestation by coffee berry borers was observed in the second year (Fig. 3c, LME, $\text{Chi}^2 = 204$, d.f. = 1, $P < 0.0001$), and overall, the proportion of bored fruits was lower on coffee plants associated with *Inga* (LME, $\text{Chi}^2 = 4.51$, d.f. = 1, $P = 0.034$). However, the difference in the proportion of bored fruits per year was not significant (Fig. 3c, contrasts after LME). There was no significant effect of distance on the proportion of bored, harvested fruits (2013: $2.9 \pm 0.7\%$ bored; 2014: $18.9 \pm 2.5\%$ bored, LME, $\text{Chi}^2 = 0.28$, d.f. = 1, $P = 0.59$).

3.3. Natural enemies

A total of 1365 parasitoids of the coffee leaf miner emerged from mined leaves (Supplementary material: Table A1). In monoculture coffee systems, 37.53% of leaf miners were parasitized, compared to 41.74% coffee consorted with *Inga* trees. However, the parasitism rate of coffee leaf miners did not differ between monoculture coffee and *Inga* consorted coffee (Supplementary material: Fig. A2, GAM, $\text{Chi}^2 = 0.086$, est. d.f. = 1.0, $P = 0.15$). Also, parasitism of coffee leaf miners did not decrease with distance from the trees ($\text{Chi}^2 = 0.63$, est. d.f. = 1.0, $P = 0.43$, data not shown). The proportion of mines preyed by wasps did not differ between monoculture and *Inga* consorted coffee (Supplementary material: Fig. A3, GAM, $\text{Chi}^2 = 0.05$, est. d.f. = 0.96, $P = 0.81$), and did not vary significantly with distance from the *Inga* trees (GAM, $\text{Chi}^2 = 0.0004$, est. d.f. = 1.0, $P = 0.98$, data not shown).

4. Discussion

Biodiversity can increase productivity in agroecosystems (Bullock et al., 2001; Nesper et al., 2017). However, restoration of species richness in agroecosystem is often perceived as being costly because of losses in agricultural production (Bullock et al., 2001). Sometimes diversification strategies indeed do result in lower crop production (Letourneau et al., 2011; Poveda et al., 2008), which may be caused by the reduced density of the main crop due to the presence of non-crop plants (Letourneau et al., 2011), but on average, crop yield is not significantly affected by crop and non-crop diversification in agricultural systems (Tamburini et al., 2020). Through a manipulative field experiment, lasting only two years, in which the density of the main crop was not reduced, we show here that coffee plants consorted with *Inga* trees produced heavier fruits than unconsorted coffee plants. In the first year, plants near *Inga* trees had higher yield, but such a trend was not observed in the second year, when coffee production was lower. In contrast to our findings, other studies showed that *Inga*-shaded coffee has lower yield compared to intensive monoculture coffee (Haggart et al., 2011). Coffee has a biennial production trend, alternating between high and low flowering and this may have been the cause of the difference in production between the two years (DaMatta, 2004). Such biennial fluctuations of crop yields occur predominantly in unshaded coffee (DaMatta, 2004), and our trees were still relatively low (max 2.5 m at the end of the experiment), providing little shade. We suggest that even if unshaded plantations have higher yields per harvest in some years, this could be compensated by more regular crop harvests in shaded plantations (DaMatta, 2004). In agreement with our results, other studies have also shown increases in coffee bean weight and bean size in shaded coffee (Muschler, 2001; Nesper et al., 2017; Somporn et al., 2012; Vaast et al., 2006).

The increased coffee fruit weight in coffee with *Inga* may have been caused by increased nutrient cycling in the plots with the trees, because the trees root deeper than the coffee plants and can access nutrients from more profound soil layers (Cardoso et al., 2003), and these nutrients become available to the coffee through the leaf litter of the trees (Duarte

et al., 2013). Nitrogen-fixing trees such as *Inga* can also increase production of associated coffee plantations (Grossman et al., 2006; Roskoski, 1982). Although N-fixation is high in adult *Inga* trees (Duarte et al., 2013), it appears to be low in young *Inga* trees as those used in our experiment (Grossman et al., 2006). Shade provided by the trees can also affect abiotic conditions and other factors, such as soil water and nutrient content, which might affect coffee yield (Classen et al., 2014; DaMatta, 2004; Lin, 2009; Meylan et al., 2017; Moreira et al., 2019). Moreover, the trees can also reduce soil erosion (Cardoso et al., 2001). As remarked above, the trees in our experimental plots were young and small and therefore did not root deeply. We therefore suggest that the effects of the trees on nutrient cycling, nitrogen fixation, protection against erosion and the provision of shade were rather small, but these ecosystem services will become more important with increasing tree age. This should be confirmed with longer manipulative field experiments.

The increased production can also have been caused by the decreased damage of coffee plants associated with trees. Damage caused by coffee berry borers can significantly reduce coffee fruit weight and quality (Damon, 2000), and coffee leaf miners decrease the photosynthesizing foliar area, which also reduces the weight of coffee beans (Pereira et al., 2007). The presence of *Inga* trees could have directly influenced pest populations by modifying local abiotic parameters that affect their dynamics (Avelino et al., 2012; Lomelí-Flores et al., 2010; Rice, 2018; Teodoro et al., 2008). For instance, planting trees associated with coffee resulted in lower densities of coffee berry borers compared to treeless systems (Mariño et al., 2016). Temperature affects coffee berry borer infestations (Jaramillo et al., 2009) and trees can effectively reduce temperature in coffee fields (Gomes et al., 2020). Intercropping rubber trees (*Hevea brasiliensis* Müell. Arg.) with coffee lowered coffee leaf miner infestations due to unfavorable microclimate conditions for the pest (Androcioli et al., 2018). The authors pointed out that the shade of rubber trees may result in changes in the coffee leaf structure that may impair coffee leaf miner survival.

Indirectly, the presence of *Inga* trees can reduce pest densities by favoring biotic natural pest control through the provision of resources to natural enemies. Elsewhere, we showed that extrafloral nectaries of *Inga* trees attract natural enemies, resulting in increased control of pests on associated coffee plants (Rezende et al., 2014), which is in line with the results presented here. Damage caused by the two main coffee pests was lower in coffee with *Inga* trees. Similar trends were observed at distances near from *Inga* trees (until 20 m). This result could help designing optimal planting of shade trees.

Many studies have reported seasonal fluctuations in coffee leaf miner densities, as was found here (Lomelí-Flores et al., 2010; Pereira et al., 2007). Rainfall is one of the main mortality factors of coffee leaf miners and this might explain most of the variation in the proportion of mined leaves (Pereira et al., 2007). Also, the abundance of natural enemies can vary among seasons. For example, ants can be more abundant in the wet season, which can also contribute to decreased damage of coffee (Philpott et al., 2006a). In the dry season, when coffee leaf miners cause most damage, the difference in proportions of mined leaves between coffee with and without associated trees was pronounced. Mortality rates of coffee leaf miners during the dry season are mainly due to natural enemies (Pereira et al., 2007). Therefore, enhancement of natural enemies due to provision of sugar-rich nectar might explain the decreased damage in coffee plants with *Inga* trees.

The higher fruit weight from plants associated with *Inga* found here could also be a result of increased pollination due to recruitment of insect pollinators by *Inga* nectaries. Although *C. arabica* is autogamous, it can benefit from insect pollination and yield can be increased up to 30% due to pollination, which results in higher fruit set and heavier fruits (Classen et al., 2014; Hipólito et al., 2018; Vergara and Badano, 2009). We did not directly measure pollination, but we expect an increased pollinator community in consorted plots, since low-input farming and shaded coffee plantations are correlated to increased diversity of

pollinators and crop production (Hipólito et al., 2018; Prado et al., 2018). Natural enemies such as ants and wasps found on *Inga* nectaries are known to pollinate coffee flowers and increase fruit weight (Philpott et al., 2006b). Ants can also increase pollination indirectly via their interactions with flying pollinators (Philpott et al., 2006b).

Besides offering ecosystem services such as enhanced pest control and shade, which also creates a better working environment for the farmers, agroforestry systems also produce secondary products, such as fruits and timber, which can play an important role in terms of both use and for exchange with other products (Rice, 2011, 2008; Souza et al., 2010). Thus, diversified coffee systems provide a more stable income due to the provision of fruits and timber, require fewer inputs and enhance functional biodiversity, carbon sequestration, soil fertility, drought resistance, weed and pest control (Jha et al., 2011; Souza et al., 2012) and mitigate effects of climate change (Gomes et al., 2020). Our results show that *Inga* species are potentially important elements of diversity in coffee systems because they enhance pest control (Rezende et al., 2014) and can increase coffee production.

Although we found trends towards increased natural control of the coffee pests in plots with trees, the differences in predation and parasitism were not significant. However, the lower damage incidence in plots with trees may also have been caused by the increased presence of natural enemies. Coffee pests may have avoided plots with trees and the associated natural enemies and pest individuals may have been attacked before causing significant damage. Other studies showed that parasitoids were attracted by nectaries, resulting in an increase in the number of parasitized hosts near patches providing food (Jamont et al., 2014; Tylianakis et al., 2004). Wasps are also known to feed on extrafloral nectar and benefit the nectary-bearing plants due to predation of their herbivores (Cuautle and Rico-Gray, 2003; Alves-Silva et al., 2013). In well-developed coffee agroforestry systems, the availability of nectar in *Inga* trees increased parasitism of coffee leaf miners (Rezende et al., 2014). It should be considered that the intercropping with *Inga* trees was recent and the trees were small, hence, natural pest control may increase more in the presence of larger trees. In any case, a better estimation of the natural control of coffee pests with and without *Inga* should be obtained experimentally, using sentinel plants with known and equal pest densities.

Uncovering the ecosystem services provided by individual plant species will help in understanding the mechanisms which enhance pest control in diversified systems (van Rijn and Wäckers, 2016). It can also help in the design of pest-suppressive coffee systems (Staver et al., 2001). Therefore, *Inga* trees should be used to enhance crop protection in concert with other plant species that will provide further ecosystem services. Our findings strengthen the hypothesis that indirect plant defenses provided by extrafloral nectaries can indeed decrease herbivory on neighboring plants and sustain the use of agroforestry systems with extrafloral nectary-bearing trees for crop protection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107538.

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