

The role of integrating agroforestry and vegetable planting in structuring communities of herbivorous insects and their natural enemies in the Neotropical region

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Abstract The integration of agroforestry plots with ephemeral crops such as vegetables on the farm scale can probably serve as a refuge and source of beneficial insects. Therefore, agroforestry systems possibly represent an alternative that favors ecosystem services and help growers in the transition process from conventional to agro-ecological agriculture. This study aimed to understand the role of introducing agroforestry systems in structuring insect communities, with consequences for the abundance of herbivore and natural enemies, contributing to farm management and favoring biological control as an ecosystem service. Field surveys showed that agroforestry

systems can harbor more species than horticultural crops, independent of the functional group. They also contain a greater diversity of herbivores and an even greater diversity profile of natural enemy communities. Agroforestry systems served as a source of natural enemies that can colonize horticultural crops when herbivores are present. As a consequence, natural enemies can establish a numerical response to herbivore abundance, but their communities are also affected by stochastic factors related to climatic conditions. Thus, agroforestry systems and agro-ecological practices might favor an agriculture based on the maintenance and conservation of ecosystem services.

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Introduction

The targets of biodiversity conservation and food production have taken a new perspective since the Millennium Ecosystem Assessment in 2005 (Perrings et al. 2010, 2011, Ferreira et al. 2012; Melo et al. 2013). It was proposed that the efforts of conservation should focus on the services that biodiversity can provide, instead of only on the conservation of taxonomic diversity per se (Perrings et al. 2010, 2011). These ecosystem services are provided not only

in natural landscapes such as agricultural ones, but also in human-dominated landscapes such as urban centers (Melo et al. 2013). Moreover, landscapes worldwide are a mixture of natural and agricultural areas. For example, Brazil is considered a mega-diverse country as well as being one of the main producers of food and fiber of the world (Ferreira et al. 2012). Thus, it provides an opportunity to integrate the needs of food production with nature conservation, by changing farm design based on an agro-ecological concept. Originally, the agro-ecological concept is defined as the application of ecological principles to agriculture, in order to use ecosystems services provided by the biodiversity conservation instead of artificial external outputs in farm management. (Altieri et al. 1983; Gliessman 2007). The first step to accomplish this is to identify the needs of the people involved and select plants that will compose the agro-system's diversity in a functional way (Altieri 1999; Lin et al. 2011; Perrings et al. 2011).

A major problem in agro-ecological systems is herbivore insect outbreaks that can cause production loss because growers are not permitted to spray chemical insecticides (Ratnadass et al. 2011). The problem with insect pest outbreaks is more evident when a conventional grower is moving towards an agro-ecological system. During this "transition" phase, several changes in the insect communities can occur until it reaches an acceptable level of dynamic equilibrium with a well-established pool of species in the area (Altieri and Nicholls 2009). Due to this, growers need to manage the farm to favor the ecosystem services, such as nutrient and water cycling, herbivory, pollination and, specially, biological control of pest and disease (de Groot et al. 2002). This latter ecosystem service will depend mainly on understanding the dynamics of herbivores and their natural enemies on the farm scale and how specific traits of each functional group can be favored (Andow 1991; Scherber et al. 2010; Vandewalle et al. 2010).

There are several agricultural management practices that can be used to favor biological control conservation, such as enhancing diversity of crops (poly-cultures and intercropping) instead of monoculture crops, planting different varieties of the same crop, management of non-crop vegetation (e.g. weeds) inside the crop plots (Gurr et al. 2003; Sujii et al. 2010). Nevertheless, the magnitude of these effects varies according to the strategy used (Letourneau et al.

2011). Thus, increasing plant diversity within the plot is considered one of the main techniques to favor biological control (Ratnadass et al. 2011; Chaplin-Kramer and Kremen 2012). In some ephemeral crops such as vegetables, the efficiency of these strategies can be conditioned to the pool of species available in the area (Tylianakis et al. 2005). Therefore, it is necessary to understand the functional group interactions at the plot level. Interactions with habitats in the landscape and abiotic conditions also play an important role in biological control efficiency and in understanding why the enhancement of vegetation diversity can affect this service (Tscharntke et al. 2007).

The establishment of agroforestry systems is one of the strategies that can be considered important to integrate conservation and food production needs and also favor biological control (Pastur et al. 2012). These agroforestry systems are characterized by a mixture of different species of plants that can be native or introduced, used for multiple purposes including crop production, fruit harvesting, timber extraction, native species conservation outside of reserves and also human well-being (Tscharntke et al. 2011). In tropical region, agroforestry systems also serve as a refuge for many species of animals. According to Bhagwat et al. (2008), for some animal taxa such as insects, there is a great similarity in species between natural areas and agroforestry systems. Therefore, increasing the diversity of plants in the agricultural landscape, by the introduction of an agroforestry system plots among ephemeral plots of vegetables, can provide alternative resources such as pollen and nectar, herbivore preys and other favorable conditions to natural enemies, and serve as source of these beneficial insects in the farm. Thus, it is possible that agroforestry systems represent an alternative to favor ecosystem services and help growers in the transition process from conventional agriculture to agro-ecological systems.

To test these assumptions, in 2008, some small growers from the Federal District in Brazil engaged in the agro-ecological transition from conventional to an ecological-based model of vegetable production. To accomplish this, a research institution together with a federal university and a local extension agency worked with these growers to change farm design in a participatory way. Strips of agroforestry systems were planted as the first step of this process on all farms. This study was conducted in areas located in the Cerrado biome, the Brazilian tropical savanna. The

Cerrado is the second major vegetation type in Brazil, occupying about one quarter of the Brazilian land area. As well as its importance as the second major vegetation type in Brazil and a hotspot of biodiversity (Myers et al. 2000), the Cerrado is also considered the main agricultural frontier in the country (Sparovek et al. 2010). Consequently, the Cerrado presents a highly fragmented landscape that is permeated by extensive monocultures of soybean, cotton, corn and pastures (Sparovek et al. 2010). However, in Brazil, the food produced for internal consumption is produced mainly by small growers on small areas (0.4–12 ha). These farmers have a high diversity of products per area (IPD 2010). Due to this, these small growers might represent the major agents for Cerrado biodiversity conservation if they use ecosystem services instead of conventional practices for crop management (Ferreira et al. 2012).

The objective of this study was to describe the insect communities, classified into two functional groups, herbivores and natural enemies, when a plot of agroforestry system was introduced into a vegetable production farm to enhance local plant diversity. The scientific questions that oriented our study were: (1) Do less-disturbed habitats such as agroforestry systems, favor the establishment of insect communities with higher species diversity and abundance evenness compared with horticultural crops? (2) Do agroforestry system play a role in structuring insect communities, within the functional groups of herbivores and natural enemies, in vegetable production plots? (3) Is the balance in the abundance of herbivores and natural enemies throughout the year, affected by either functional group or by stochastic factors such as meteorological conditions? We expected that by answering these questions we could understand the role of agroforestry systems in structuring insect communities, with consequences for the abundance of herbivores and natural enemies that contribute to the agro-ecosystem management and favor biological control as an ecosystem service.

Materials and methods

Study area

This study was conducted on four small farms located, at least 18 km distant from each other, in the Brazilian

Federal District, Brazil. These farms are characterized by the employment of mainly familiar labor in the management of crop production. When this study started growers from Farm I, II and III were interested in moving from the conventional model of vegetables production to agro-ecological model of crop production. As the first step in this “transition” process rows of agroforestry systems were introduced in each farm nearby and among vegetable planting plots to increase plant diversity in the farms. Only Farm IV (see below) had an early stage agroforestry system already established when this study started. The farmers selected the species for the agroforestry systems including native non-crop species, fruit trees, crop species based on personal experience for marketable crops and species for multiples usages, such as timber extraction, medicine and own use preference. Adaption to soil and climate conditions in the region was considered in addition (Table 1).

Farm I (11 ha) is located at the Planaltina region (15°34′39″S; 47°44′27″W), the grower has been planting, mainly, green corn (*Zea mays* L., Poaceae) (6 ha), in a conventional and irrigated monoculture system since 2005. Pest control and other agronomic practices have been performed by applying chemical products such as insecticides and synthetic fertilizers. When the grower engaged in the agro-ecological transition process, some rows of green corn were intercropped with beans. A strip of agroforestry system measuring about 0.6 ha was established at the beginning of sampling dates in this study. Farm II (8 ha) is located in the Ceilândia region (15°49′25″S; 48°15′09″W), main activity was the production of chayote (*Sechium edule* Swartz, Cucurbitaceae) (3 ha). Other crops produced on a smaller scale, such as eggplant and some leafy vegetables, were used for subsistence. Spontaneous vegetation and medicinal plants were present within and around the planted plots. The farmer stopped using pesticides to control pests and a strip of agroforestry system measuring about 0.4 ha was established around the vegetables plots as the first step toward the agro-ecological transition process. Additionally, some fruit trees were planted in farm, as a way of enhancing the diversity of plants in the farm. Farm III (14 ha) is located in the Paranoá region (47°38′13″W; 15°49′42″S) and leafy vegetables was cultivated with medicinal plants and herbs (e.g. coriander and parsley) (0.6 ha) for personal consumption and subsistence. The plants were grown

Table 1 List of main species planted in each agroforestry system on farms in December of 2008, Federal District, Brazil

Scientific name	Plants			Farms ^a			
	Plant use	Architecture	Life cycle	I	II	III	IV
Bromeliaceae							
<i>Ananas comosus</i>	Food crop	Herbaceous	Semiperennial	X	X	X	X
Caricaceae							
<i>Carica papaya</i>	Food crop	Herbaceous	Semiperennial	X	X	X	X
Cucurbitaceae							
<i>Sechium edule</i>	Food crop	Herbaceous	Perennial				X
Dioscoreaceae							
<i>Dioscorea</i> sp.	Food crop	Herbaceous	Perennial	X	X	X	X
Euphorbiaceae							
<i>Manihot esculenta</i>	Food crop	Herbaceous	Annual	X	X	X	X
<i>Ricinus communis</i>	Oil plant	Shrub	Annual		X	X	X
Fabaceae							
<i>Cajanus cajan</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Canavalia ensiformes</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Crotalaria breviflora</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Crotalaria juncea</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Crotalaria spectabilis</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Leucaena</i> sp.	Fodder	Tree	Perennial	X	X	X	X
<i>Mucuna pruriens</i>	Cover crop	Herbaceous	Annual	X	X	X	X
<i>Piptadenia</i> sp.	Native	Tree	Perennial				X
Malvaceae							
<i>Gossypium</i> sp.	Fiber	Herbaceous	Annual	X	X		X
Meliaceae							
<i>Swietenia</i> sp.	Native	Tree	Perennial	X	X	X	X
Moraceae							
<i>Morus alba</i>	Food crop	Tree	Perennial	X	X	X	X
Musaceae							
<i>Musa speciosa</i>	Food crop	Shrub	Perennial	X	X	X	X
Palmaceae							
<i>Bactris gasipaes</i>	Native	Tree	Perennial	X	X		X
Passifloraceae							
<i>Passiflora edulis</i>	Food crop	Herbaceous	Semiperennial		X	X	X
Poaceae							
<i>Saccharum</i> sp.	Cover crop	Herbaceous	Semiperennial		X		X
<i>Sorghum vulgare</i>	Cover crop	Herbaceous	Annual		X		
<i>Zea mays</i>	Food crop	Herbaceous	Annual	X	X	X	X
Punicaceae							
<i>Punica granatum</i>	Medicinal	Shrub	Perennial			X	
Rubiaceae							
<i>Coffea arabica/conilon</i>	Food crop	Shrub	Semiperennial	X	X	X	X
Species (N ^o)				16	20	17	21

^a X indicate plant species introduced in each the farm

together with herbaceous plants with few cultural practices; a low exploitation rate and no use of pesticides. The main business activity of the property was hay production in most of the remaining area. A strip of agroforestry system measuring about 0.4 ha was established at the beginning of this study. Farm IV (12 ha) is located in the Taguatinga region (15°49'49''S; 48°04'27''W), produces vegetables (5 ha) in crops rotation and intercropping organic system (>10 species per plot), with organic certification since 1999. Further, there are barriers and “windbreaks”, with floristic species separating the plots of vegetables. These are interspersed with agroforestry plots or orchards containing native tree species and fruit trees, associated with herbaceous, cultivated and spontaneous plants. All agroforestry systems, except the farm IV, were deployed in December of 2008.

The climate of the region is tropical semi-humid, with mean temperatures ranging from 22 to 27 °C and an average rainfall of 1,500 mm per year (Klink and Machado 2005). There are two well-defined seasons throughout the year. The wet season is usually from November to March, whereas the dry season occurs from May to September. As the Cerrado biome is characterized by seasonal fluctuations of rainfall throughout the year (Klink and Machado 2005), we hypothesized that rainfall might affect species abundance together with time. Thus, rainfall data were obtained from the weather station installed in the experimental field of Embrapa Vegetables in Federal District, Brazil (15°56'S; 48°08'W).

Sampling methods

The insect fauna was sampled in the agroforestry system and the nearby horticultural crop plot at each farm simultaneously in the same day (paired design) for two group of samplers that alternate each other among the farms and months randomly. The samplings were performed from February 2009 to January 2010, always in the first week of the month. The samplers established line transects crossing the plot in different directions, and all the plants (cropped or not) on transect was entirely and carefully inspected in order to find and captures insects in its above ground structures. The plants in the agroforestry system were sampled in the same strata (about 1 m) of the horticultural crop system in an attempt to standardize

the collection on both systems. The insects were captured using plastic pots, insect net or insect aspirator depending on their mobility and behavior. This procedure was adopted instead of other sampling methods such as traps because this way we could measure the insect fauna present only in the sampled area and on plants. In each area the plants were inspected during 120 min, totaling a sampling effort of 240 min per farm.

The insects were taken to the laboratory, where they were identified and separated into the functional groups of herbivores and natural enemies (predators and parasitoids). The identification was based on the literature and where there was a lack of published information, these were classified based on external morphology such as mouthpart morphology. Thus, an abundance of data for each selected functional group per sampling date was generated. The small insects like aphids, scale insects, mealybugs and whiteflies were not collected because they are usually in a higher scale of abundance and present an aggregate distribution in crop. These traits compromise the data analyses. Abundance of other insects such as ants and bees were not also measured because they are social insects, requiring specific sampling methods.

Data analysis

The diversity of insect communities in agroforestry systems and horticultural crop was initially compared by rarefaction curves to estimate the species richness for samples with a different number of individuals collected (Krebs 1999), and by the Rényi function to compare the diversity profile (Tóthmérész 1995). This latter function allows a continuum of possibilities of diversity measurement according to the parameter α , where $\alpha_0 = \log N$, where N is the total number of a community's species; α_1 is Shannon's entropy (Shannon 1948) and α_2 = Simpson's index (Simpson 1949). Further, “Rényi's entropy, differ in their sensitivity to the rare and abundant species in the community, becoming dominated by the commonest species for increasing values of the parameter α ” (see Ricotta et al. 2002; Ricotta 2003 for details). The curves plotted from this function could be compared and allow inferences concerning the differences in diversity patterns. However, when the curves of two or more communities intersect, they cannot be compared (Tóthmérész 1995).

Equitability (J) and dominance ($D = 1 - \text{Simpson index}$) were used to assess how species abundance is distributed among the taxa present in samples from agroforestry systems and horticultural systems (Legendre and Legendre 2012). All diversity analyses were performed using the PAST program (Hammer et al. 2001).

The effect of crop system (agroforestry system and horticultural crops) in the abundance of each functional group was assessed using a mixed effect linear model (GLMM). In this analysis, the sampling date was used as a random variable via the maximum likelihood method (Crawley 2007). We also used a GLMM to assess whether the monthly abundance of herbivores and natural enemies was affected by each other and by the rainfall period. To accomplish this, we used a hierarchical model, where the properties and the crop system inside the properties were used as random factors. In this way, we controlled the temporal pseudo-replication in the former analysis and the spatial pseudo-replication in the latter. In both analyses, the significance of each variable was tested and non-significant factors were removed from the model and compared with the previous model until it reached a minimum adequate model (Crawley 2007). This model was compared with a null model to investigate the biological significance of the analysis. The significance of variables was tested using an Analysis of Variance (ANOVA) with a chi squared test (Crawley 2007). Previous to using the GLMM on the rainfall data, we compared the mean rainfall per period using a one-way ANOVA. All analyses were performed using the software R (R Development Core Team 2012).

Results

Diversity of functional groups communities

A total of 12,506 insects were collected and classified into ten orders, 83 families and 554 morphospecies. Among these, 6,325 individuals (ten orders, 39 families and 302 species) were identified as herbivores. In this functional group, the most abundant taxa in the horticultural and agroforestry systems were: *Lagria villosa* (Fabricius, 1781) (Coleoptera: Lagriidae) (8.1 %), *Diabrotica speciosa* (Germar, 1824) (Coleoptera: Chrysomelidae) (7.9 %), *Euxesta* sp.

(Diptera: Ulidiidae) (6.4 %) and *Oxycarenus* sp. (Hemiptera: Lygaeidae) (4.8 %). The other 6,181 individuals (eight orders, 44 families and 252 species) were classified as predators or parasitoids (natural enemies) and the most abundant species were: *Condylostylus* spp. (Diptera: Dolichopodidae) (43.0 %), *Toxomerus lacrymosus* (Bigot, 1884) (Diptera: Syrphidae) (10.8 %), *Doru luteipes* (Scudder, 1876) (Dermaptera: Forficulidae) (5.9 %), and *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) (1.8 %). See details in Table 2.

When comparing the community richness by rarefaction curves, there were more herbivore and natural enemy species in the agroforestry system than the horticultural system (Fig. 1). However, the diversity in these systems (compared by the Rényi profiles), showed a different pattern between functional groups (Fig. 2). The herbivores had more diverse communities in agroforestry system areas than in horticultural systems (Fig. 2a), whereas the natural enemies only differ between agroforestry and vegetable crop systems for species richness and community evenness (Fig. 2b). For natural enemies, we could not infer an overall difference related to community diversity, because the Rényi profile curves touch each other at $\alpha > 1$ (Fig. 2b).

Structure of functional group communities

Regarding community structure, herbivores and natural enemies had an overall abundance concentrated in a few species in both crop systems (Fig. 3). However, the individual abundance within the herbivore community was better distributed among species in the agroforestry system than the horticultural system (Fig. 3a). This pattern was not related to the species composition in such habitats; there was no shift of dominant species in each system. When comparing the ten most abundant species in the herbivore community, seven were among the most abundant in both agroforestry system and horticultural systems, and all ten occurred in both crop systems. The 20 most abundant species, from 302 species collected, comprised 59.1 and 44.9 % of the individuals collected in horticultural and agroforestry systems, respectively. The similarity index between herbivore species collected in horticultural and agroforestry systems was for Sorensen = 0.78, and for Morisita = 0.75.

Table 2 List of the most abundant taxa collected on areas of Horticultural Crops (Hort. Crop.) and Agroforestry Systems (Agrof. Syst.), Federal District, Brazil

Order	Family	Functional group	Species	Abundance		Total
				Hort. Crop.	Agrof. Syst.	
Diptera	Dolichopodidae	Predator	<i>Condylostylus</i> sp.	1,604	1,045	2,649
Diptera	Syrphidae	Predator	<i>Toxomerus lacrymosus</i>	389	287	676
Coleoptera	Lagriidae	Herbivore	<i>Lagria villosa</i>	325	185	510
Diptera	Ulidiidae	Herbivore	<i>Euxesta</i> sp.	425	78	503
Coleoptera	Chrysomelidae	Herbivore	<i>Diabrotica speciosa</i>	350	149	499
Dermaptera	Forficulidae	Predator	<i>Doru luteipes</i>	325	41	366
Coleoptera	Chrysomelidae	Herbivore	<i>Colaspis joliveti</i>	169	143	312
Diptera	Syrphidae	Predator	<i>Ornidia obesa</i>	200	110	310
Hemiptera	Lygaeidae	Herbivore	Morphospecie 2.31	229	72	301
Hemiptera	Membracidae	Herbivore	Morphospecie 1.18	148	100	248
Coleoptera	Chrysomelidae	Herbivore	<i>Diabrotica viridula</i>	151	63	214
Hemiptera	Miridae	Herbivore	Morphospecie 2.34	177	20	197
Orthoptera	Gryllidae	Herbivore	Morphospecie 5.3	97	60	157
Hemiptera	Cicadellidae	Herbivore	Morphospecie 1.14	52	79	131
Hemiptera	Membracidae	Herbivore	Morphospecie 1.10	4	124	128
Diptera	Tachinidae	Parasitoid	Morphospecie 0.52	36	76	112
Coleoptera	Coccinellidae	Predator	<i>Harmonia axyridis</i>	107	3	110
Coleoptera	Curculionidae	Herbivore	Morphospecie 3.93	63	28	91
Diptera	Bombyliidae	Predator	Morphospecie 0.82	31	60	91
Hemiptera	Alydidae	Herbivore	<i>Neomegalotomas styrex</i>	22	66	88
Hemiptera	Miridae	Herbivore	Morphospecie 2.21	56	29	85
Hemiptera	Cicadellidae	Herbivore	Morphospecie 1.32	72	12	84
Hemiptera	Coreidae	Herbivore	Morphospecie 2.42	43	37	80
Coleoptera	Elateridae	Herbivore	Morphospecie 3.32	55	24	79
Coleoptera	Coccinellidae	Predator	<i>Cycloneda sanguinea</i>	52	23	75
Coleoptera	Coccinellidae	Predator	<i>Scymnus</i> sp.	22	49	71
Coleoptera	Coccinellidae	Predator	<i>Psyllobora gratiosa</i>	37	31	68
Hemiptera	Berytidae	Herbivore	Morphospecie 2.77	27	33	60
Hemiptera	Membracidae	Herbivore	Morphospecie 1.17	22	36	58
Hemiptera	Coreidae	Herbivore	Morphospecie 2.25	35	21	56
Hemiptera	Miridae	Herbivore	Morphospecie 2.19	21	34	55
Coleoptera	Chrysomelidae	Herbivore	Morphospecie 3.20	6	48	54
Coleoptera	Chrysomelidae	Herbivore	Morphospecie 3.194	41	11	52
Hymenoptera	Braconidae	Parasitoid	Morphospecie 4.64	46	5	51
Hemiptera	Coreidae	Herbivore	<i>Leptoglossus zonatus</i>	41	9	50

For natural enemies, the abundance distribution among species was more similar between agroforestry and horticultural systems. The values of dominance and equitability were smaller for this functional group than those obtained for the herbivore group (Fig. 3b). When comparing the ten most abundant species in the

natural enemy community, five are equally the most abundant in both agroforestry and horticultural systems, and all of them occurred in both crop systems. The 20 most abundant species from the 255 species collected, comprised 83.1 and 75.4 % of the individuals collected in horticultural and agroforestry

Fig. 1 Species richness estimate by rarefaction curves of herbivore (a) and natural enemies (b) communities in horticultural crops and agroforestry system on farms in the Federal District, Brazil, 2009/2010

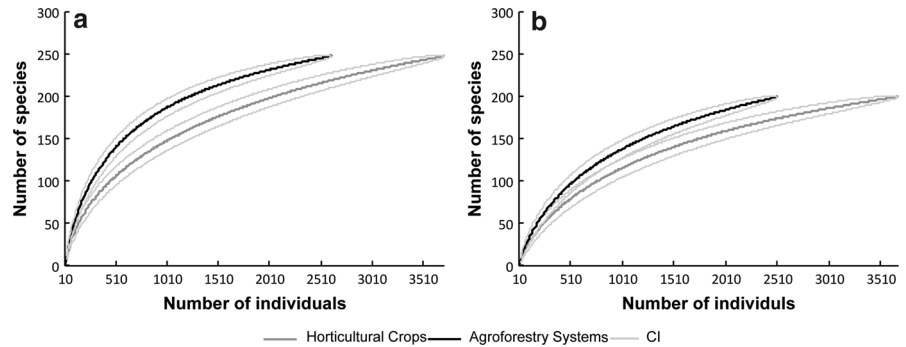


Fig. 2 Rényi entropy describing diversity curves of herbivore (a) and natural enemies (b) communities in horticultural crops and agroforestry system on farms in the Federal District, Brazil, 2009/2010

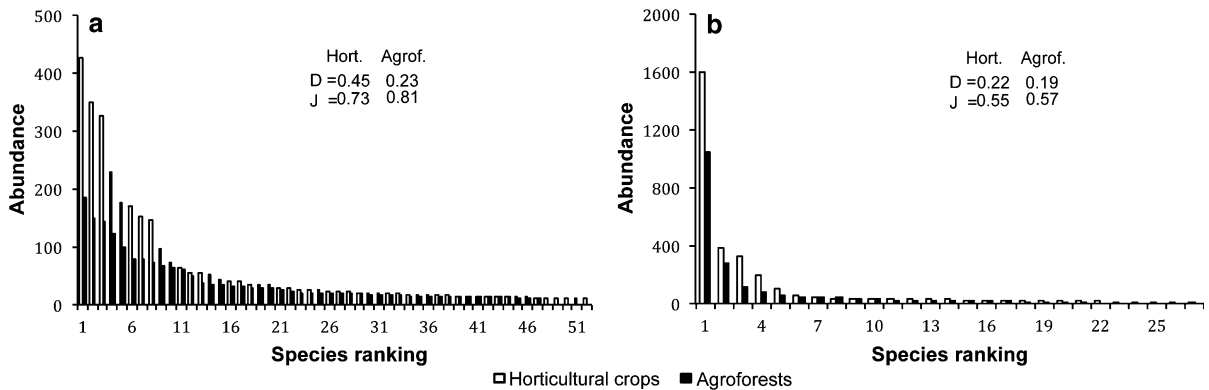
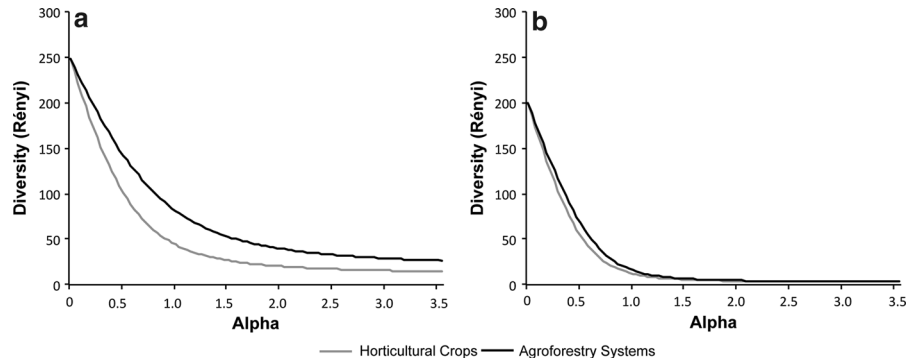


Fig. 3 Abundance distribution among species of herbivores (a) and natural enemies (b) in horticultural crops (Hort) and agroforestry system (Agrof.). *D* indicates the values of species

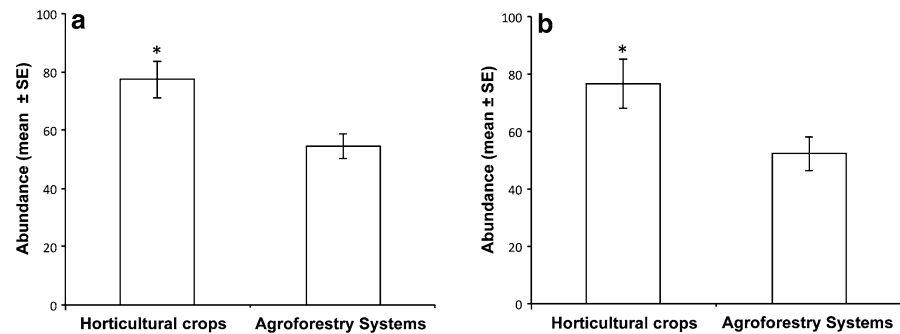
systems, respectively. We also observed a higher similarity of natural enemy species than herbivores collected between the systems (Sorensen = 0.88 and Morisita = 0.99).

The factors related to local management practices can affect the abundance of functional groups. The herbivore abundance ($F_{1,86} = 11.07$; $P = 0.001$) and

dominance and *J* the equitability values for each functional group. Insects collected on farms in the Federal District, Brazil, 2009/2010

natural enemies ($F_{1,86} = 7.54$; $P = 0.007$) was affected by crop system. As the crop system appears to be one of the main factors controlling insect abundance, we compared the mean (\pm standard deviation) abundance of both functional groups in agroforestry and horticultural systems separately. This analysis showed that natural enemies ($F_{1,91} = 5.37$;

Fig. 4 Mean abundance of herbivores (a) and natural enemies (b) on horticultural crops and agroforestry system on farms in the Federal District, Brazil, 2009/2010. Asterisk above bars indicates significant differences between treatments by model contrast analysis ($P < 0.05$)



$P = 0.022$) and herbivores ($F_{1,91} = 9.87$; $P = 0.002$) were more abundant in horticultural than in agroforestry systems (Fig. 4).

Biotic and abiotic factors affecting herbivores and natural enemy abundance

We initially compared the rainfall distribution along the year. There was a seasonal fluctuation in the rainfall, which produced three distinct periods that were significantly different ($F_{1,11} = 1.85$; $P = 0.003$). An initial period, with a great quantity of rainfall (246.55 ± 29.94 mm) (October 2009–January 2010), a second half of the rainfall period with lower precipitation (112.98 ± 108.85 mm) (February 2009–May 2009) and a dry season (20.93 ± 16.88 mm) (June 2009–September 2009) (Fig. 5).

The mixed effect model analysis showed that the abundance of natural enemies and herbivores was regulated by different factors with time. The natural enemy abundance was affected by herbivore abundance ($F_{1,85} = 14.89$; $P < 0.000$) and the rainfall season ($F_{1,85} = 7.34$; $P = 0.008$), but not by the interaction between these factors ($F_{1,85} = 1.93$; $P = 0.168$). Alternatively, the herbivore abundance with time was affected by the natural enemy abundance ($F_{1,85} = 3.99$; $P = 0.048$) and no effects of the rainfall season ($F_{1,85} = 0.18$; $P = 0.672$) or the interaction between these variables ($F_{1,85} = 0.35$; $P = 0.554$) was observed. A numerical response of natural enemies to herbivore abundance was evaluated by regression analysis, which showed that natural enemy abundance was positively related to that of herbivores, when considering the overall abundance of each functional group (Fig. 6).

Discussion

The most abundant species of each functional group were characterized as generalist insects. Such insects tend to be more mobile organisms than specialists because they can feed upon many plant species and therefore, tend to constantly move between horticultural crops (ephemeral habitats) and agroforestry systems (perennial habitats) (Jonsen and Fahrig 1997; Rand and Tschardtke 2007; Tschardtke et al. 2007). For example, the coleopteran *L. villosa* is a common herbivore found in the soil of different agroecosystems and is a secondary pest of strawberries and other vegetables in Brazil (Liz et al. 2009). Another coleopteran, *D. speciosa*, is considered an important pest of beans, soybean, corn, and potatoes (Walsh 2003). Similarly, *Euxesta* sp. is found mainly on maize crops, but individuals also occur on other hosts and in habitats such as weeds, orchards and natural areas (Cruz et al. 2011; Goyal et al. 2012). In terms of natural enemies, the dipterous *Condylostylus* sp. and *T. lacrymosus*, and the coccinellid *H. axyridis* are also highly mobile predators that feed on soft-body insects acting as biological control agents. The dipterous adults also feed on pollen and nectar and many coccinellids can complement their diet with these same foods from plants (Amaral et al. 2013). These resources are usually found in different patches and finding a suitable habitat for feeding and reproducing requires great mobility (Evans 2003; Evans and Toler 2007; Van Rijn and Sabelis 2005). Due to the ephemeral nature of horticultural crops and their resources, we can infer that the functional groups can colonize or become locally extinct at predictable rates in such habitats. However, agroforestry systems are more constant and perennial

Fig. 5 Mean abundance of herbivores and natural enemies (*lines*) and total rainfall (*bars*) distribution along the year on farms in the Federal District, Brazil, 2009/2010

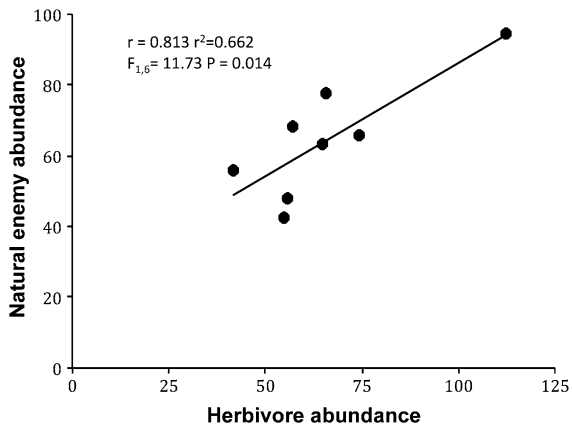
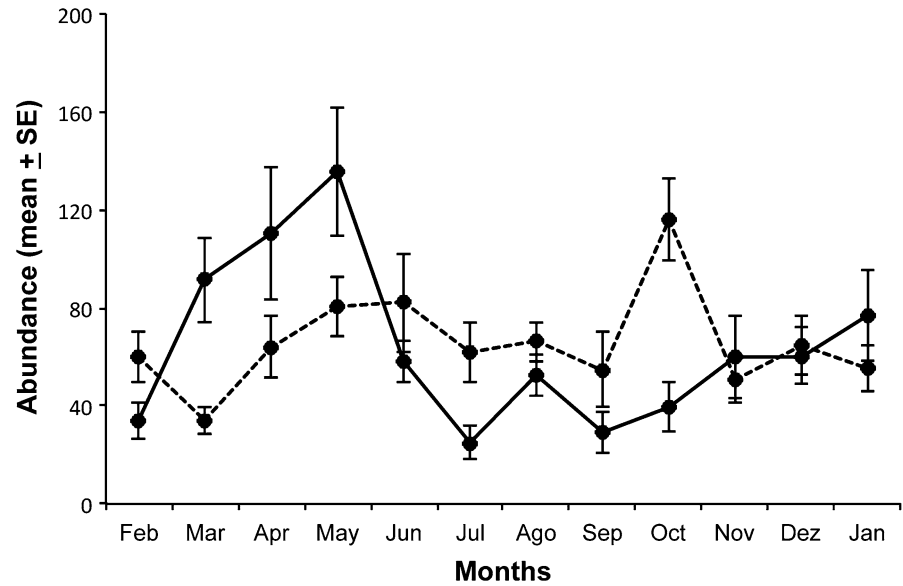


Fig. 6 Relationship between herbivore and natural enemy abundance on farms in the Federal District, Brazil, 2009/2010

habitats in the landscape. As the functional groups are dominated by organisms with high dispersal abilities, insect communities can use both habitats in the landscape in a patch-dynamics approach (Leibold et al. 2004; Pandit et al. 2009).

This mobility among habitat types in the landscape is one of the main factors that might have affected the patterns of species richness and diversity in different habitats (Mouquet and Loreau 2003; Cadotte 2006). In general, our study demonstrated that agroforestry systems can harbor more species than horticultural crops, independently of the functional group and also

have a greater diversity of herbivores. Despite this, the difference in the diversity profiles of the natural enemy communities between agroforestry systems and horticultural systems is clear only at richness and evenness level of the community. Although dispersal is important, these results suggest that the factors that structure the communities of functional groups in agroforestry systems and horticultural systems are quite different.

This finding is reinforced by the fact that the community dominance, equitability and similarity between agroforestry systems and horticultural crops are higher for natural enemies than for herbivores. Nevertheless, for both functional groups, individual abundance is better distributed among species in agroforestry systems than in horticultural crops. In agroforestry systems, there is a higher plant diversity, habitat structural diversity (several plant strata with different architectures) and there are many perennial and annual plants and weeds. These traits favor the coexistence of more species that use different types of resources within different patches of the same habitat and a lower species turnover (Tschamtkke et al. 2011). Agroforestry systems are also habitats with a low disturbance rate (e.g. harvesting and insecticide application), which can also contribute to their higher diversity and richness of insects. However, natural enemies, especially generalists, can find more prey in agroforestry systems, as well as shelter, oviposition

sites and plant-provided foods such as pollen and nectar (Lundgren 2009; Amaral et al. 2013). In horticultural crops, these resources and habitat conditions are found at a lower diversity and abundance or do not exist.

Herbivores can find similar advantages in agroforestry systems regarding niche availability. In contrast, the resources used by them in the agroforestry system are mixed with others. As a general trend, agroecosystems with a higher diversity of plants have negative effects on herbivore abundance, which benefits their natural enemies (Andow 1991; Letourneau et al. 2011, 2012). In such diversified habitats, herbivores need to deal with more visual, olfactory and structural stimuli (Randlkofer et al. 2010). When exposed to mixed sensory stimuli, generalist herbivores usually have more difficulty in making choices, because their capacity to integrate information is less accurate than that of specialist herbivorous insects (neural limitation) (see Bernays 2001; Tosh et al. 2009; Togni et al. 2010b). Some herbivores also tend to remain for long periods in monocultures rather than in diversified habitats, because their hosts are more apparent and predictable as hypothesized by Root (1973). The combination of resources and conditions that are unfavorable to herbivores and favorable to natural enemies, results in agroecosystems based on the use of ecosystem services, mainly biological control (Fiedler et al. 2008).

Thereby, both functional groups were affected by the crop system (agroforestry systems or horticulture crops), with a higher abundance of insects on horticultural crops always being present than in agroforestry systems. The horticultural crops, as mentioned above, are more suitable habitats for some herbivores (Randlkofer et al. 2010; Letourneau et al. 2011), where they can achieve high reproduction rates (Altieri 1999). Horticultural crops are usually mainly colonized by species such as caterpillars, aphids, herbivorous coleopterans (i.e. *D. speciosa*) and whiteflies (Oliveira et al. 2001; Walsh 2003; Blackman and Eastop 2007). In some instance, our sampling methodology might have underestimated the presence of some of these insects. The high abundance that these groups can occur in some occasions may attract their natural enemies. Together, the predators *Condylostylus* sp., *T. lacrymosus*, *D. luteipes* and *H. axyridis* comprised 61.5 % of the sampled natural enemies, and all of these species are known natural enemies of the

non-sampled herbivore groups. These predators were found in both habitats, but were more abundant on horticultural crops where they are important predators amongst these herbivores. It is thus reasonable to assume that these natural enemies might have found more prey in the horticultural crops, which favored their colonization, establishment, reproduction and consequently their abundance. Thus, horticultural crops are habitats that favor only some species of herbivores and natural enemies, permitting their establishment in this ephemeral habitat when compared with agroforestry system. However the lack of data the non-sampled herbivores limit our inferences about this pattern and should be better investigated in further studies.

This study was conducted in the core of the Cerrado biome in Brazil. This region is characterized by alternate two well-defined seasons (rainy/dry) throughout the year that is common to all central regions of Brazil in the core of the Cerrado biome (Klink and Machado 2005). This seasonality is known to affect, for example, caterpillar abundance and their parasitism rate in natural habitats (Morais et al. 1999), as well as other insect orders (Silva et al. 2011). In this study, herbivore abundance was not affected by seasonality, but was affected only by natural enemy abundance (in agroforestry systems or horticultural crops). In a reciprocal way, the natural enemy abundance was affected by herbivore abundance as shown in Figs. 5, 6. Moreover, both functional groups were also affected by the rainfall period throughout the year. This suggests that population abundance is not only affected by biotic factors, but is also subject to stochastic process related to natural climate change, independent from prey availability. During the dry season, the climate is very dry, with air relative humidity reaching values below 15 % (Oliveira-Filho and Ratter 2002) and occasionally with no rainfall (see Fig. 5). Natural enemies appear to be more sensitive to these conditions than herbivores, because this factor did not interact with herbivore abundance. For example, Togni et al. (2010a) compared the natural enemy abundance and diversity in tomato fields planted in monocultures or intercropped with coriander and irrigated by drip or sprinkler irrigation systems during the dry season within the same biome in Brazil. They found that the more diverse plots—the intercropped ones—always had more species than monocultures. However, there was a greater diversity and abundance

of natural enemies when irrigated by sprinklers than when irrigated by the drip system. The natural enemy community structure was affected mainly by the irrigation system because the sprinklers created more favorable microclimate conditions for them (Togni et al. 2010a). Moreover, more pest outbreaks tend to occur during the dry season in this region than during other periods; there is probably a time-window during which herbivores can reproduce with a reduced pressure from their natural enemies (Morais et al. 1999; Marquis et al. 2002), even in agroecosystems.

The abundance of natural enemies was positively related to herbivore abundance, reinforcing the pressure that this functional group can create over the herbivore population. As a general trend, increasing plant diversity in the farm tends to produce a positive effect on natural enemy abundance and diversity and consequently a negative effect in herbivore populations (Letourneau et al. 2011). This pattern was previously observed in different tropical regions of the world. For example, in Kenya hedgerows crops with tree or shrub species reduced the abundance of major insect pests in maize and beans and favored the natural enemies' community (Girma et al. 2000). Rubber trees interspersed with coffee reduced leaf-miner damage to coffee planted in agroforestry systems in Brazil (Righi et al. 2013) and the tree richness and abundance in cocoa agroforestry systems can affect parasitoid diversity in cacao agro-forests also in Brazil (Sperber et al. 2004). Similarly, shade tree diversity reduced the herbivore damage in cocoa trees by benefiting specific guilds of natural enemies such as ants, wasps and spiders in West Africa (Bisseleua et al. 2013). Mixed species plantation of native tropical timber trees presented less herbivore damage than when planted in monocultures in Panama (Plath et al. 2011). This close relationship might be related to the characteristics of agroforestry systems and horticultural crops. When some vegetables are harvested, there is a high disturbance in the area, forcing the insects to move to adjacent areas such as agroforestry system, other crops and adjacent weeds. If a particular crop is replanted, there are considerable resources available for herbivores that can colonize this area. As the herbivore population increases, they tend to be more apparent, because cues such as semiochemicals, visual cues, and others, increase due to a numerical effect (Barbosa 1998). Herbivores usually arrive into a habitat before their natural enemies (Mazzi and Dorn

2012), after this initial event, there is a greater amount of prey available for natural enemies, which then move into these habitats to search for their prey/hosts (Gurr et al. 1998). Agroforestry system can thus serve as a qualitative source habitat of mainly beneficial insects that can then colonize horticultural crop habitats (Mouquet and Loreau 2003; Cadotte 2006; Leibold et al. 2004). The abundance of beneficial insects in vegetable plots is regulated not only by the proximity of colonization sources, but also by local agricultural practices that constrain the population dynamics of these species. The landscape complexity of different habitats (e.g. agroforestry system, natural areas and horticultural crops) can affect local pest numbers in horticultural crops (Chaplin-Kramer and Kremen 2012) and explain the positive relationship found in our study.

In conclusion, establishment of agroforestry systems nearby and surrounding vegetable crop plots enhanced the diversity of herbivores and natural enemies in vegetable production farms. Integrating of agroforestry systems to vegetable crop plots served as source of natural enemies that can colonize horticultural crops when herbivores are present. However, the establishment of these beneficial insects on the farm is also related to cultural practices of crop management. As a consequence, natural enemies can establish a numerical response to herbivore abundance, but their communities are also affected by stochastic factors relating to climatic conditions. Thus, agroforestry system and agro-ecological management practices of the crop can favor an agriculture based on the maintenance and conservation of ecosystem services.

We propose the establishment of rows of agroforestry systems nearby and surrounding vegetable crop plots as hedgerows and additional source of food and products contributing for food safety of small farmers. They also act as barrier crops, windbreak and for recovering natural areas in degradation process. Plant selection for agroforestry systems should consider the farmers usage for each plant in short and long term mixing annual and perennial species, such as those introduced in the farms of the present study, mimicking the early stage of the plant succession process. However, implementing agroforestry systems do not ensure that beneficial insects will colonize the crops. To this end it is necessary that growers use less intensive management practices such as maintain strips of weeds within or surrounding crops and

intercropping systems. Thus this will provide resources and conditions that can favor natural enemies and other beneficial insects attracting and retaining them in the crop. In regions such as the Cerrado biome in Brazil, the non favorable conditions during the dry season can be alleviated by agroforestry systems, serving as a refuge and source of natural enemies to more suitable seasons. Finally, we suggest that new efforts should be made in order to investigate the benefits involved in such agro-ecological management for other functional groups such as pollinators and decomposers and also with an interdisciplinary approach to select agricultural practices integrated to the landscape change.

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