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Drivers of Parasitoid Wasps' Community Composition in Cacao Agroforestry Practice in Bahia State, Brazil

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1. Introduction

The world's total forest area is just over 4 billion hectares, and five countries (the Russian Federation, Brazil, Canada, the United States of America and China) account for more than half of the total forest area (FAO, 2010). Apart from their high net primary production, the world's forests harbour at least 50% of the world's biodiversity, which underpins the ecosystem services they provide (MEA, 2005). Primarily the plants, through their physiological processes, such as evapotranspiration, essential to the ecosystem's energy budget, physically dissipate a substantial portion of the absorbed solar radiation (Bonan, 2002), and sequester carbon from the atmosphere. The carbon problem, considered a trend concern around the world due to global warming (Botkin et al, 2007), can be minimized through the carbon sequestration by forests. Forests have the potential of stabilizing, or at least contributing to the stabilization of, atmospheric carbon in the short term (20–50 years), thereby allowing time for the development of more long-lasting technological solutions that reduce carbon emission sources (Sedjo, 2001).

Brazil's forests comprise 17 percent of the world's remaining forests, making it the third largest block of remaining frontier forest in the world and ranks first in plant biodiversity among frontier forest nations. However, deforestation, mainly due to land-use change, such as conversion of tropical forests to agricultural land, is one of the major threats to terrestrial biomes (Hoekstra, 2005). Globally, around 13 million hectares of forests were converted or lost through natural causes each year between 2000 and 2010. Brazil and Indonesia had the highest annual deforestation rates in the 1990s (FAO, 2010), and one of the most threatened ecosystems in Brazil is the tropical Atlantic Forest. Brazil has lost over 570,000 km² of its Amazonian forest.

The Atlantic Forest originally stretched from the Brazilian coastline to Argentina and Paraguay, including around 15% of Brazilian's territory (Rizzini, 1997). A significant portion of the original tropical Atlantic Forest currently supports about 50% of Brazil's human

population, resulting in intense habitat degradation and fragmentation (Conde, 2006). Unfortunately, less than 7% of the original Atlantic Forest area is still intact (Tabarelli, 2005), being considered one of the world's 25 biodiversity hotspots due to high rate of conversion and the occurrence of thousands of endemic animals and plants (Myers, 2000). Moreover, most of the original Atlantic Forest areas were cleared and replaced by sugarcane, coffee plantations, cattle ranching, *Eucalyptus* monocultures and cacao plantations (Colombo, 2010). Intensive land use in this biome reduces diversity of several useful species, such as predators, parasitoids and other organisms that are responsible for ecosystem service of pest control, for example (Perfecto, 2004).

Recent emphasis on biodiversity conservation, taking into account the agricultural landscape that surrounds most remnants of tropical forest ecosystems, triggered a revival of agroforestry systems (Perfecto, 2008). Agroforestry systems arose as an important tool for conservation, as far as they provided a high quality matrix habitat for the organisms, allowing for migration among natural habitat and remnant ecosystems (Perfecto, 2008; Stenchly, 2011).

Agroforestry systems can be defined as a set of land-use systems and technologies where woody perennials (trees, shrubs, palms, etc.) are deliberately grown on the same land as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence. Agroforestry systems provide a variety of ecosystem services beyond the production of food, including nutrients recycling, regulation of microclimate and local hydrological processes, and suppression of undesirable organisms and detoxification of noxious chemicals (Altieri, 1999; Sileshi et al. 2007). Agroforestry systems consisting of traditional cultivars, such as coffee, cacao and banana, are a part of an ancient knowledge and practice (Miller, 2006). For example, planting coffee crops under shade trees in the semi-arid regions of Brazil to avoid extreme micro-climatic fluctuations dates back to the 19th century (Severino, 1999).

Brazil is among the countries in Latin America with the highest cacao (*Theobroma cacao* L., Sterculiaceae) yields (Franzen, 2007) with an estimated production area of 697,420 hectares (Clay, 2004). Most (98%) of Brazil's cacao is produced in Bahia State, northeastern Brazil. These cacao fields are established within the Atlantic Forest domain (Johns, 1999; Schroth, 2007). Cacao is an Amazonian native tree and was introduced in Bahia in the 18th century, causing a fragmentation of the native forest ecosystem, particularly during its highest production eras, in the 1960's and 1970's (Delabie, 2007).

There are two main cacao management systems in Bahia State (Delabie, 2007): (i) the traditional management system, called *cabruca*, and (ii) the intensive management system, called *derruba total* (total clearing). The *cabruca* system involves planting cacao under a thinned forest canopy, using the native tree's canopy as shade (Greenberg 2000; Sperber, 2004; Franzen, 2007). The *derruba total*, developed in the last 50 years, involves complete clearance of the forest before cacao planting; cacao trees are shaded by introduced trees, planted afterwards. In this management system, the density of cacao plants is twice that attained in the *cabruca* system (Delabie, 2007). Obviously, this second method is not the most conservative for biodiversity because the native forest is completely destroyed, leading to habitat loss. Increased density of cacao plants has similar ecological impacts as other crop monocultures, especially those resulting from high crop density and low plant species richness. The introduction of a monoculture of shading trees, commonly *Erythrina* spp.

(Leguminosae: Papilionoideae) or *Hevea brasiliensis* (Wild.) Muell. - Arg. (Euphorbiaceae), generates overall landscape simplification.

The less management intensive cacao agroforestry system, *cabruca*, is considered a conservation management system because most native trees are maintained above the cacao crop. *Cabruca* allows the maintenance of endangered native tree species such as *Dalbergia nigra* (jacarandá), *Caesalpinia espinata* (pau-brasil), and *Cariniana brasiliensis* (jequitibá), all important hardwood species (Johns, 1999). Therefore, *cabruca* management system supports high plant species richness and multi-strata structure similar to natural forest (Rolim, 2004; Saatchi, 2001). The fauna is also positively affected in *cabruca* management systems. For instance, the species richness of bats, birds, beetles, ants and a wide range of soil fauna is higher in *cabruca* (Bos, 2007; Delabie, 2007; Moco, 2009; Schroth, 2007) than in *derruba total*. In addition, *cabruca* is frequently visited by mammals, such as the endangered gold lion marmoset (*Leontopithecus rosalia*) (Johns, 1999), and thus can represent a potential habitat for endangered species, contributing to Atlantic Forest species conservation. *Cabruca* systems can work as ecological corridors, linking forest remnants, and allowing organisms' dispersion among habitats (Schroth, 2007). Furthermore, the use of native forest shading trees in *cabruca* systems provides for continuous litter deposition above the soil, affecting the soil's chemical, physical and biotic characteristics, leading to high levels of soil organic matter content and improving soil conservation (Moco, 2009).

Despite both cacao crop systems being less harmful to the environment than herbaceous monoculture crops, they are vulnerable to a large number of pest species. The economically most important pest is generated by a fungus - especially the one called "witches' broom disease", caused by *Moniliophthora perniciosa* and *Moniliophthora roreri* (Oliveira, 2005). Other cacao enemies, like herbivorous insects, can contribute to economic losses in cacao crops. In Brazilian cacao crops, important cacao herbivores are Lepidoptera (e.g. *Stenoma decora*, *Cerconota dimorpha*), Coleoptera (e.g. *Theoborus villosulus*, *Taimbezinhia theobromae*), Thysanoptera (e.g. *Selenotnnpis rubrocinctus*) and Heteroptera (e.g. *Monalonion annulipes*, *Toxoptera aurantili*) (Silva-Neto, 2001). There is, also, a diverse insect fauna that has no economic impact or may, even, be beneficial to cacao farmers. Beneficial agents are insects responsible for pollination and pest control. Among pest control agents, there are insect predators, like ants (Delabie, 2007), and parasitoids that control caterpillars' populations (Silva-Neto, 2001).

In this context, the Hymenoptera wasps of the Parasitica series and Chrysoidea superfamily, may have an important function as parasitoids of cacao pests. Wasps are part of the biodiversity associated to cacao crops, whose maintenance may be differentially linked to the two cacao management systems. Trees, which provide shade to the cacao crop as their direct function, may also attract and maintain wasps (indirect function) (Vandermeer, 1995). Besides, the maintenance of native forest trees may stabilize the microclimate along yearly seasonal changes, dampening insects' diversity and abundance fluctuations (Shapiro, 2000).

The Hymenoptera include more than 115,000 described species, but this is far from being a representative sample of the group's actual diversity (Hanson, 1995). Parasitoid wasps are one of the most species rich and abundant components of terrestrial ecosystems, and represent the highest species richness within the Hymenoptera (LaSalle, 1992). Parasitoids

are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects, causing the death of the parasitoid's host (Godfray, 1994) in most of the cases. They play a crucial role in natural pest population regulation (LaSalle, 1992). The world literature on the group is vast, and there was a huge effort to understand parasitoid community structure in Atlantic rain forests (Azevedo, 2000; Azevedo, 2002; Azevedo, 2003; Perioto, 2003; Perioto, 2005; Alencar, 2007; Gnocchi, 2010). We have some knowledge on the environmental drivers of parasitoid wasps' diversity in cacao agroforestry: parasitoid wasp's diversity responds to shading tree species richness and density, and these relationships are altered among seasons (Sperber, 2004). However, there is almost no understanding on the environmental drivers of parasitoid wasp's community composition in agroforestry systems. This work contributes to the understanding of the effect of agroforestry design on biodiversity and the ecosystem services provided by parasitoids. We present original results on the drivers of parasitoid wasps' (Hymenoptera of the Parasitica series and Chrysididae superfamily) community composition in cacao agroforestry systems in Brazilian Atlantic Forest.

We evaluated the following potential drivers of parasitoid community composition: (Fig. 1) (i) seasonality (summer *versus* winter *versus* spring); (ii) kind of disturbance ('cabruca' *versus* total clearing); (iii) amount of resource availability, estimated by shading tree density; (iv) resource amplitude availability, estimated by shading tree species richness; (v) resource amplitude availability, estimated by herbaceous species richness; (vi) resilience or habitat degradation, estimated by cacao plantation age; (vii) and regional species pool, estimated by cacao plantation area. We expect that the detection of environmental drivers of wasps' community composition may enhance our understanding of the mechanisms driving these organisms' ecology, and provide knowledge which sustainable crop management actions.

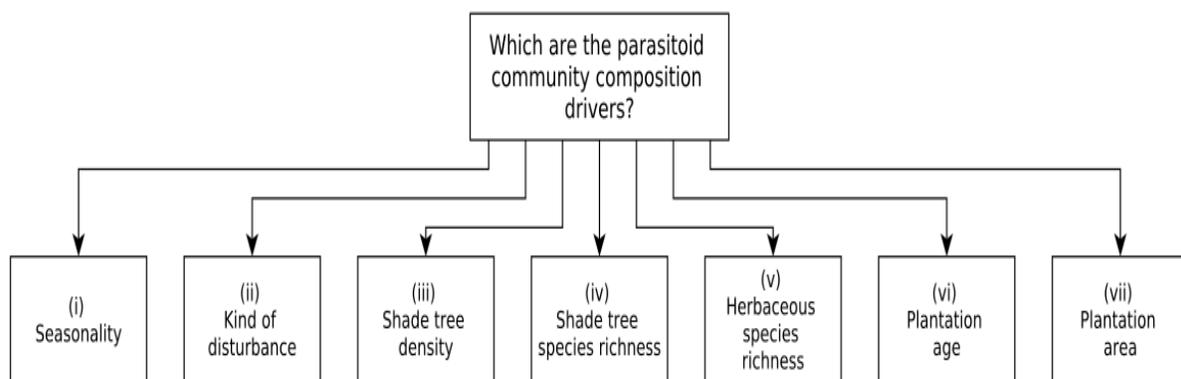


Fig. 1. Hypotheses of the drivers of parasitoid community composition in cacao plantation.

2. Materials and methods

2.1 Study site

The studied cacao plantations were located in Ilhéus, Bahia, Brazil (14°46' S - 39°29' W) within the Atlantic Forest ecosystem. Mean annual temperature is 24°C, with lowest temperatures (20°C monthly mean) in June to August (winter) and highest temperatures

(26°C monthly mean) in December to March (summer). Annual precipitation ranges from 2000mm to 2400mm near the coastline, and around 700mm in the hinterland (Santana, 2003).

We sampled 16 cacao agroforestry farms, with areas varying ranging from 16 to 80 ha. The farms were 20 to 60 years old (Table 1). Farm selection was arbitrary, prioritizing replication of 'total clearing' management (n=5), and those *cabruca* farms where it was allowed to carry out the study (n=11). Distances between sampled farms ranged from 7 to 55 km. The shade tree species richness in sampled plantations varied from one (total clearing- native forest falling- with either *Erythrina fusca* or *Hevea brasiliensis*) to 22 tree species ha⁻¹ (*cabruca* native forest canopy shading trees, Fig 2). Table 1 shows tree species (Lauraceae, Leguminosae, Meliaceae, Moraceae, Sapotaceae, and other, less common, plant families) in the sampled cacao farms. Herbaceous plant species richness was estimated by counting the number of species of herbs in a 1m x 1m plot, located in the core of each sampled 1-ha plot, within each sampled farm. Tree species richness was determined by counting all trees with canopy above the cacao plants, in each sampled 1-ha area. All trees with crowns which over-topped the cacao plants were included. Tree density was determined by counting the number of trees in each sampled 1-ha plot. Tree identification was confirmed by comparing field material with the herbarium collection of CEPLAC (Centro de Pesquisas da Lavoura Cacaoeira - Cacao Crop's Research Center). All collected materials were incorporated in the CEPLAC collection.

Farm	Kind of disturbance	Tree species richness	Plantation age	Area (ha)
1	total clearing	1	27	20
2	total clearing	1	24	18
3	total clearing	1	35	25
4	total clearing	1	40	20
5	total clearing	1	47	20
6	<i>cabruca</i>	9	30	50
7	<i>cabruca</i>	14	25	16
8	<i>cabruca</i>	15	28	80
9	<i>cabruca</i>	15	20	20
10	<i>cabruca</i>	15	60	20
11	<i>cabruca</i>	15	45	20
12	<i>cabruca</i>	16	25	60
13	<i>cabruca</i>	16	40	70
14	<i>cabruca</i>	18	45	20
15	<i>cabruca</i>	21	35	30
16	<i>cabruca</i>	22	25	20

Table 1. Management system, shading tree species richness, plantation age (years) and planation area of the studied cacao farms.



Fig. 2. Cacao plantation under cabruca management system, CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira) farm, Ilhéus, BA, Brazil. Photo: Pollyanna Santos.

2.2 Hymenoptera sampling

Each agroforestry farm was sampled using eight Malaise-Townes interception traps (Townes, 1972), erected on the ground for a 24h-period, along a 100m transect, in the core of a 1-ha plot, within each sampled farm. All sites were sampled three times during the year of 2001: summer (March), winter (August) and spring (November - December). The whole study involved an accumulated sampling effort of 16 sites x 8 traps x 3 seasons; two samples from *cabruca* were lost, resulting in 382 sampling days. Since our aim was not to detect area effects (Schoereder et al. 2004), we uniformly sampled farms to avoid sampling effects on diversity estimation (Hill et al., 1994). Parasitoid diversity was estimated as the number of Parasitica and Chrysididae (Hymenoptera) families, which are mostly (>95%) parasitoids, and contain most of the hymenopterous parasitoids (Goulet & Huber, 1993). Hymenoptera families were identified using the taxonomic keys provided by Goulet & Huber, (1993) and Gibson et al., (1997). We worked at the family level due to lack of information about taxonomy of genus and species of parasitoids in tropical regions (LaSalle, 1992).

2.3 Data analyses

2.3.1 Parasitoid community composition

To evaluate the effects of selected environmental drivers on parasitoid family composition, we performed longitudinal data analyses for repeated measures, adjusting generalized linear mixed models (GLMM), with binomial errors. Sampling date (March, August and November - December) was adjusted as repeated measure, and sampling site (n=16) as grouping random factor. The use of mixed effects models, adjusting sampling site as random effect, enabled avoidance of pseudo-replication (Crawley, 2007).

We used occurrence in each Malaise trap at each site (n = 128), per sampling date, as binary response variable. Binary logistic analyses are not subject to overdispersion, are robust to zero-inflated data (Zuur, 2009) and the results are more conservative, in comparison to

abundance as response variable. Family identity was adjusted as fixed effect, together with the tested environmental variable and an interaction term.

2.3.2 Testing the environmental drivers

To evaluate if any of the environmental variables, presented in Figure 1, worked as drivers of parasitoid community composition, we adjusted separate statistical models for each variable. A significant effect of an environmental variable on community composition should lead to significance of the interaction term between the environmental variable and the factor 'parasitoid family identity'. Similarly, a significant interaction between a family identity level and an environmental variable should result from differences in the response of wasps families' occurrence to the environmental variable. For example, whereas the occurrence of some families increased with increasing values of the environmental variable, other families' occurrence decreased.

Significance was evaluated by model comparison, deleting non-significant fixed effects (Crawley, 1993). Models were further simplified by amalgamating factor levels, using contrast analyses. To detect which factor levels could be amalgamated, we fitted generalized linear models (GLM), with binomial errors, not considering pseudoreplication, and used the "coms.R" procedure from the RT4Bio package, developed by Ronaldo Reis Jr. (Unimontes, Montes Claros, MG, Brazil). Amalgamation suggested by GLM was tested adjusting the corresponding GLMM. When the substitution of the current by the simplified model did not alter significantly model deviance, we accepted the simplification (Crawley, 2007). Families whose responses were amalgamated within the same factor levels (groups) presented similar occurrence levels and responses to the tested environmental variable.

Seasonality (i) and kind of disturbance (ii) were adjusted as categorical (=nominal) explanatory variables. Amount of resource availability (iii), resource amplitude availability (iv and v), resilience or habitat degradation (vi), and regional species pool (vii) were adjusted as continuous explanatory variables.

Categorical environmental variables were analyzed through two-way binary logistic analyses of variance (ANOVA); continuous environmental variables (shading tree density, shading tree species richness, plantation age, herbaceous species richness, plantation area), were analyzed through binary logistic analyses of covariance (ANCOVA).

To evaluate if composition was altered by kind of disturbance, we used the whole set of observations (each observation corresponds to the presence or absence of each family, in each trap; n.obs. = 11,460; n.groups = 16). If there was significant effect of kind of disturbance on parasitoid family composition, we tested the remaining environmental variables separately within each kind of disturbance (*cabruca*: n.obs. = 7,860; n.groups = 11); '*derruba total*': n.obs. = 3,360; n.groups = 5). We analyzed the effects of tree density and cacao plantation area, exclusively within *cabruca* management system, as far as total clearing management involved only two tree densities (250 and 476 trees per ha) and three plantation areas (18, 20 and 25ha), whereas in the *cabruca* management systems, there were sites with eleven different tree densities (30 - 137 trees per ha) and seven different plantation areas (16, 20, 30, 50, 60, 70, 80). Effects of shade tree species richness were evaluated exclusively among *cabruca* sites.

Although we considered 5% level of significance, we presented the exact p-values for all analyses, as recommended by Iacobucci (2005), among others. To visualize the effects of the

environmental drivers on the parasitoid wasps' community composition, we plotted the amalgamated families groups' occurrence means (procedure 'interaction plot' within R) of the minimal adequate models. Information criteria indices (Akaike Information Criteria – AIC, and Bayesian Information Criteria – BIC) were used to compare alternative explanatory models. The smallest AIC and BIC values indicated better models (Crawley, 2007). All statistical analyses were done under R (R Development Core Team, 2010).

3. Results

3.1 Parasitoid community composition

We collected a total of 21,346 individuals, of 30 families (Table 2), 16,567 in *cabruca* and 4,779 in 'total clearing' management. Individuals in the Platygastroidea taxa were the most abundant, while those in the Evanioidea family were the least abundant. Two parasitoid families were exclusive of *cabruca*: Gasteruptiidae and Liopteridae.

Taxa	Abundance
Ceraphronoidea	1049
Ceraphronidae	983
Megaspilidae	66
Cynipoidea	1793
Figitidae	1792
Liopteridae	1
Chalcidoidea	5019
Agaonidae	27
Aphelinidae	242
Chalcididae	326
Eucharitidae	12
Encyrtidae	1083
Eulophidae	801
Eupelmidae	136
Eurytomidae	69
Mymaridae	1406
Perilampidae	9
Pteromalidae	368
Signiphoridae	145
Torymidae	53
Trichogrammatidae	342
Chrysoidea	1369
Bethylidae	1178
Chrysididae	57
Dryinidae	104
Sclerogibbidae	24
Evanioidea	287
Evaniidae	281
Gasteruptiidae	6
Ichneumonoidea	3952

Taxa	Abundance
Braconidae	1921
Ichneumonidae	2031
Platygastroidea	6486
Platygastridae	6486
Proctotrupoidea	1400
Diapriidae	1130
Monomachidae	99
Proctotrupidae	168

Table 2. Number of individuals of Hymenoptera Parasitica series and Chrysoidea superfamily in sampled cacao agroforestry systems.

3.2 Evaluation of environmental drivers

3.2.1 Seasonality

Community composition differed among seasons (Figure 3), both for 'total clearing' management ($p < 0.0001$) and *cabruca* shade trees management ($p < 0.0001$). Parasitoid taxa could be amalgamated to a minimum of 11 levels in 'total clearing' (Groups A - K, in Figure 4, and 16 levels in *cabruca* (Groups A - P, in Figure 5) cacao systems. Season levels could not be amalgamated.

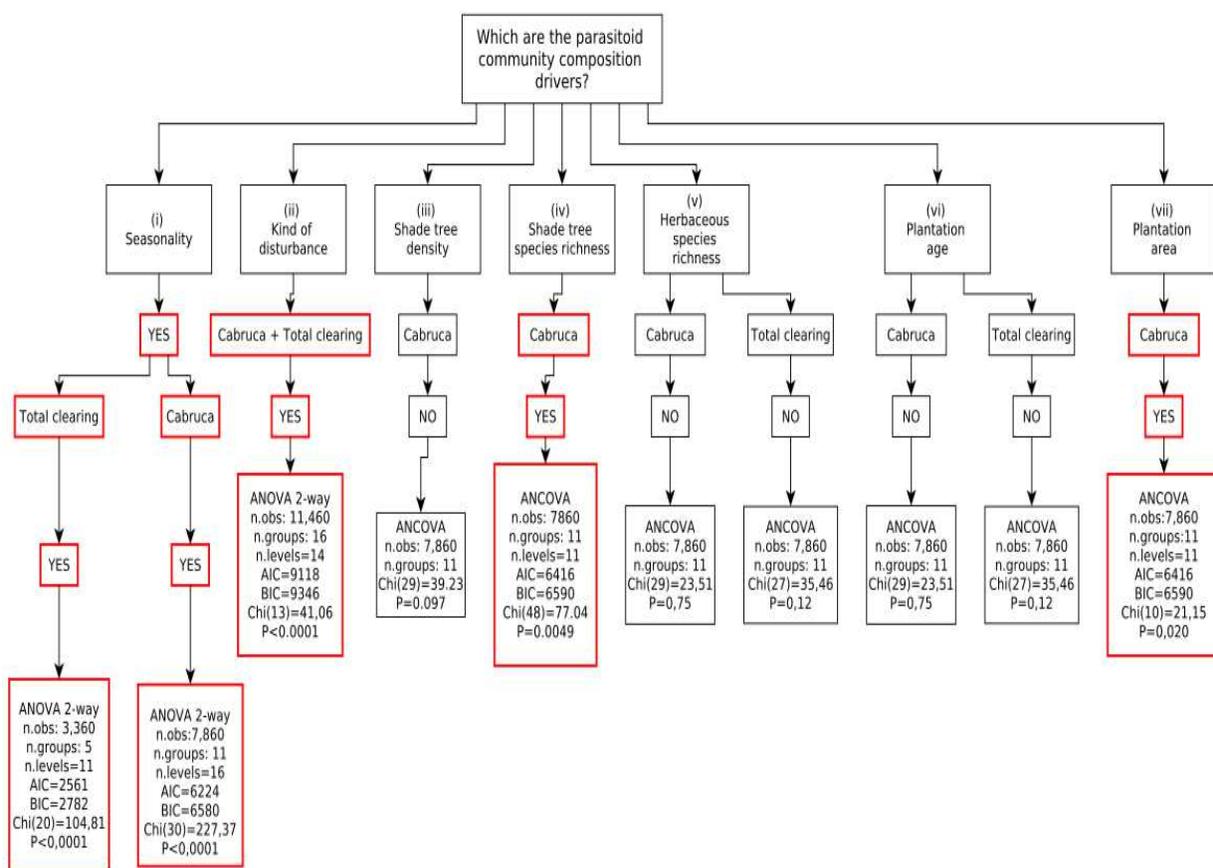


Fig. 3. Summary of the drivers of parasitoid community in cacao plantation. In red we highlighted the significant results.

In 'total clearing' management system, only the parasitoid families Ichneumonidae + Platygasteridae did not respond to season (Figure 4, Group A). Most families presented lowest occurrence in winter and highest abundance in summer (Figure 4, Groups B, C, D, E, F, G, H), whereas two wasp families - Proctotrupidae and Monomachidae - presented highest occurrence in winter (Figure 4, Groups I and K). Agaonidae + Eucharitidae + Perilampidae + Sclerogibbidae + Torymidae + Chrysididae (Group J, Figure 4) presented lowest occurrence in both winter and spring.

In *cabruca*, Platygasteridae, Figitidae, and Eulophidae were most abundant in spring (Figure 5, Groups A, C, E), while two of them (Platygasteridae and Figitidae - were least abundant in summer (Figure 5, Groups A, C). As in 'total clearing', individuals in Proctotrupidae and Monomachidae taxa were observed in largest numbers in winter (Figure 5, Groups J, N) than in other seasons. There were no significant differences in abundance of Braconidae + Ichneumonidae, Encyrtidae + Ceraphronidae, and Gasteruptiidae + Liopteridae + Perilampidae + Eucharitidae (Figure 5, Groups B, F, O) across seasons. Other parasitoid families were least abundant in winter, and most abundant in summer (Figure 5, Groups D, G, H, I, K, L, M, P).

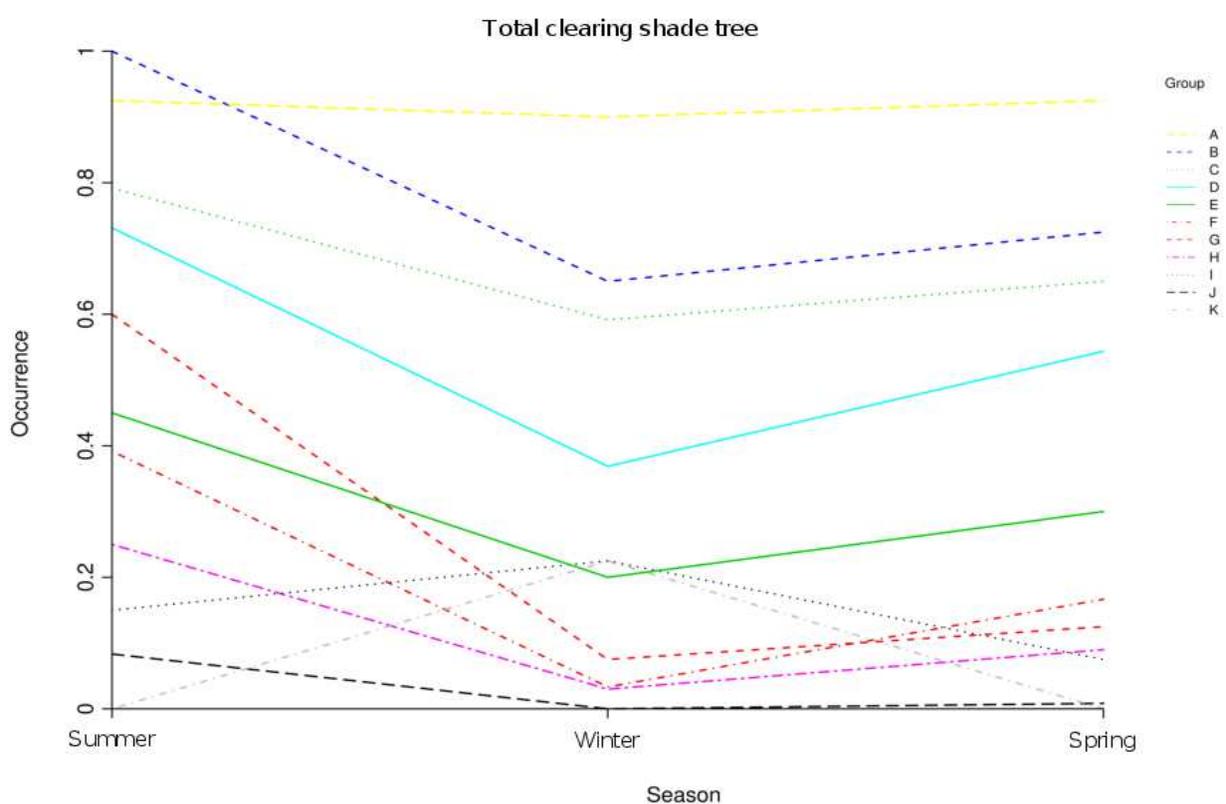


Fig. 4. Changes in occurrence ($p < 5\%$, mean of presence (1)/absence (0) per trap) of parasitoid families in monospecific 'total clearing' shading trees' cacao management, along three seasons. Groups are A: Ichneumonidae + Platygasteridae, B: Braconidae, C: Bethylinidae + Mymaridae + Figitidae, D: Encyrtidae + Ceraphronidae + Eulophidae + Diapriidae, E: Trichogrammatidae, F: Dryinidae + Aphelinidae + Chalcididae, G: Pteromalidae, H: Eurytomidae + Ceraphronidae + Eulophidae + Diapriidae, I: Proctotrupidae, J: Agaonidae + Eucharitidae + Perilampidae + Sclerogibbidae + Torymidae + Chrysididae, K: Monomachidae.

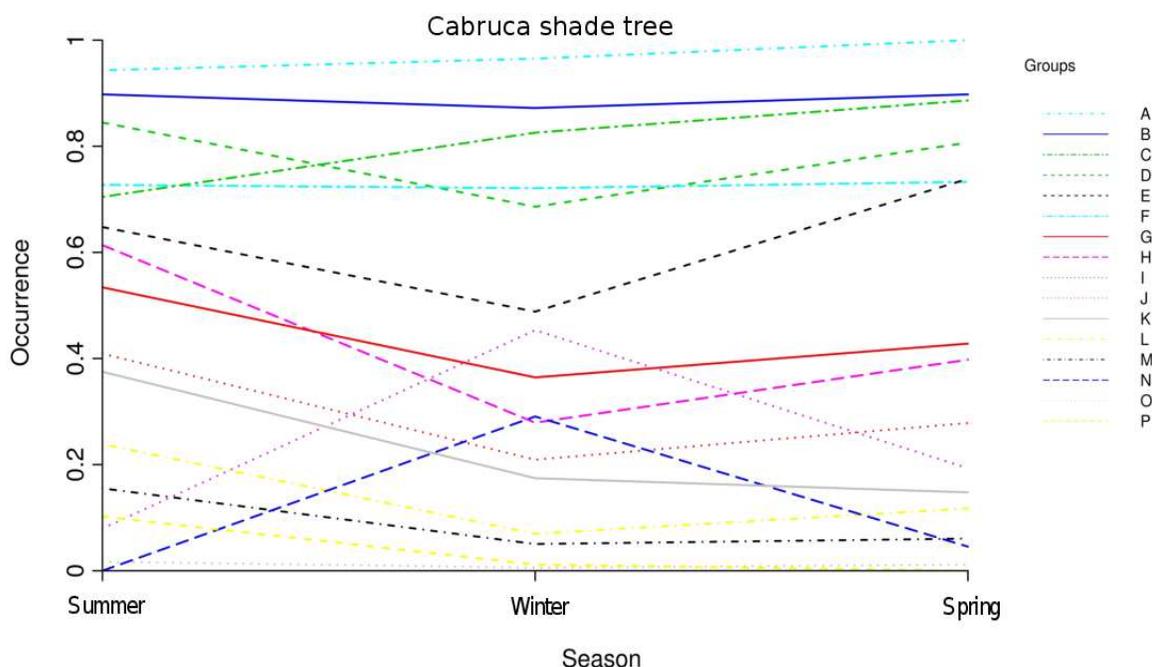


Fig. 5. Changes in occurrence ($p < 5\%$; mean of presence (1)/absence (0) per trap) of parasitoid families in *cabruca* shading trees' cacao management across seasons. Groups are A: Platygasteridae, B: Braconidae + Ichneumonidae, C: Figitidae, D: Mymaridae + Bethyridae + Diapriidae, E: Eulophidae, F: Encyrtidae + Ceraphronidae, G: Pteromalidae + Trichogrammatidae + Evaniidae, H: Chalcididae, I: Aphelinidae + Eupelmidae, J: Proctotrupidae, K: Signiphoridae, L: Torymidae + Eurytomidae + Dryinidae, M: Agaonidae + Chrysididae + Megaspilidae, N: Monomachidae, O: Gasteruptionidae + Liopteridae + Perilampidae + Eucharitidae, P: Sclerogibbidae.

3.2.2 Kind of disturbance

Parasitoid family composition differed between cacao management systems ($p < 0.0001$, Figure 3). Parasitoid taxa could be amalgamated to a minimum of 14 levels (Groups A – N, in Figure 6). Whereas Ichneumonidae and Dryinidae were more abundant in 'total clearing' management (Groups A and H, in Figure 6), other parasitoid families were less abundant in 'total clearing' management (see Groups C, D, F, G, I and J, in Figure 6). Platygasteridae, Eucharitidae + Sclerogibbidae, and Gasteruptionidae + Liopteridae + Perilampidae did not differ significantly ($p > 0.0001$) between systems (Groups A, L and N, in Figure 6).

3.2.3 Shade tree density and plant species richness

Shade tree density had no significant effect on parasitoid community composition ($p=0.097$). Shade tree species richness affected parasitoid community composition ($p = 0.0049$; Figure 7). Parasitoid taxa could be amalgamated to a minimum 11 levels (Groups A – K, in Figure 7). The abundance of Aphelinidae + Chalcididae + Trichogrammatidae + Evaniidae + Pteromalidae, Agaonidae + Megaspilidae + Chrysididae + Monomachidae, and Gasteruptionidae + Liopteridae + Eucharitidae + Perilampidae, increased with increasing tree species richness (Figure 7, Groups F, I, K); other families decreased in their occurrence with increasing tree species richness (Figure 7, Groups A – E, G, H, J). Herbaceous plant species richness had no effect on parasitoid community composition in both agroforestry systems ($p = 0.058$).

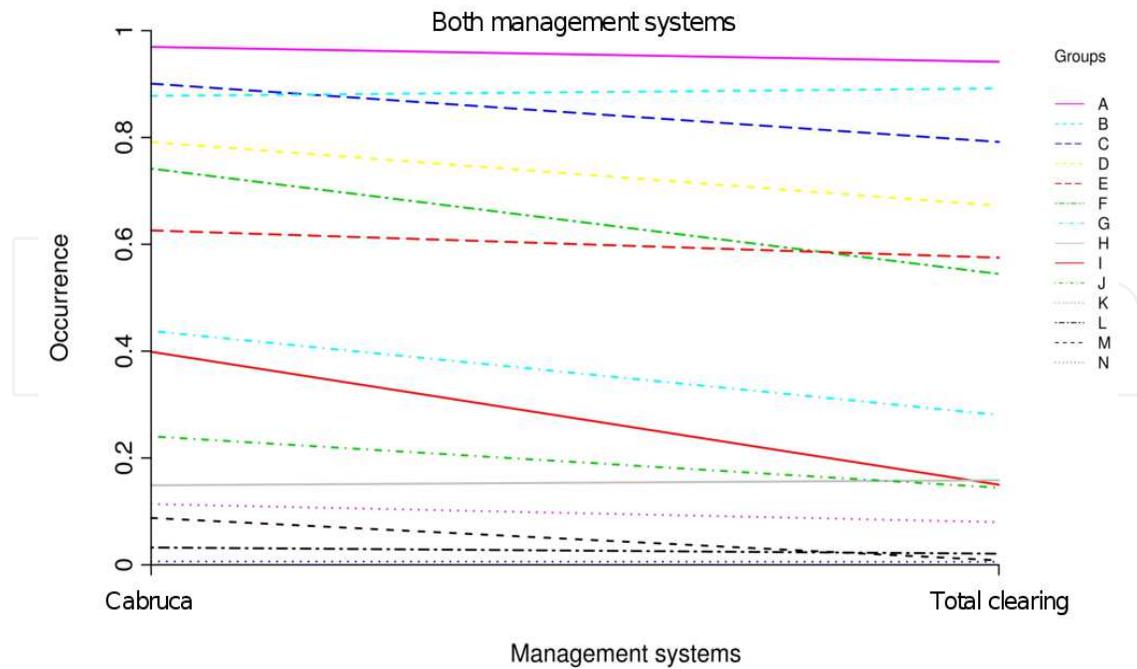


Fig. 6. Effect of cacao management system (cabruca versus 'total clearing') on the occurrence (mean of presence (1)/absence (0) per trap) of parasitoid families in both cacao management systems. Groups are A: Platygastridae, B: Ichneumonidae, C: Braconidae, D: Mymaridae + Diapriidae + Figitidae, E: Eulophidae, F: Encyrtidae + Ceraphronidae + Bethyidae, G: Chalcididae + Trichogrammatidae + Pteromalidae, H: Dryinidae, I: Aphelinidae + Evaniidae, J: Signiphoridae + Proctotrupidae + Eupelmidae, K: Megaspilidae + Chrysididae + Monomachidae + Torymidae + Eurytomidae, L: Eucharitidae + Sclerogibbidae, M: Agaonidae, N: Gasteruptionidae + Liopteridae + Perilampidae.

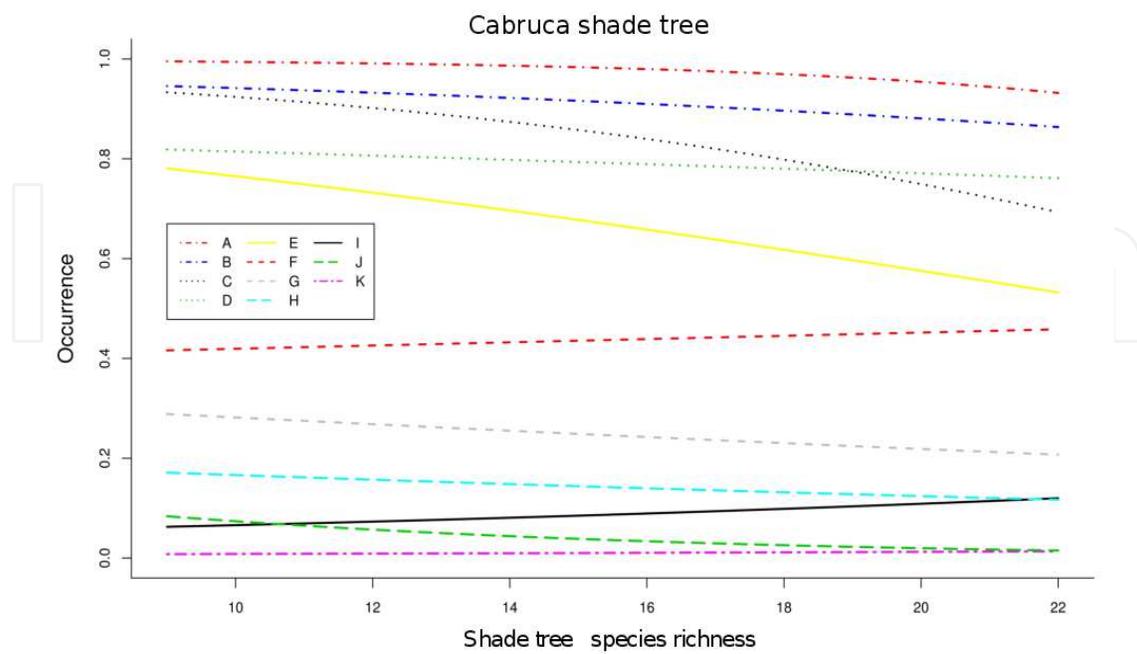


Fig. 7. Effect of shading tree species richness on the occurrence (mean of presence (1)/absence (0) per trap) of parasitoid families in cabruca shading trees' cacao management.

Groups are A: Platygasteridae, B: Ichneumonidae + Braconidae, C: Figitidae, D: Encyrtidae + Ceraphronidae + Mymaridae + Bethyidae + Diapriidae, E: Eulophidae, F: Aphelinidae + Chalcididae + Trichogrammatidae + Evaniidae + Pteromalidae, G: Signiphoridae + Proctotrupidae + Eupelmidae, H: Torymidae + Dryinidae + Eurytomidae, I: Agaonidae + Megaspilidae + Chrysididae + Monomachidae, J: Sclerogibbidae, K: Gasteruptiidae + Liopteridae + Eucharitidae + Perilampidae.

3.2.4 Cacao plantation age and area

Cacao plantation age did not significantly affect parasitoid community composition in both 'total clearing' ($p = 0.12$) and *cabruca* ($p = 0.75$) shade tree management systems. By contrast, cacao plantation area significantly affected parasitoid community composition ($p = 0.020$; Figure 8). Parasitoid taxa could be amalgamated to a minimum 11 levels (Groups A - K, in Figure 8). The abundance of most parasitoid families increased with increasing plantation area (Figure 8, Groups A - C, E - H, J). The abundance of Ceraphronidae and Agaonidae + Megaspilidae + Chrysididae (Groups D and I, in Figure 8) decreased with increasing plantation area, whereas the abundance of Gasteruptiidae + Liopteridae + Perilampidae (Group K, in Figure 8) was not significantly affected by plantation area.

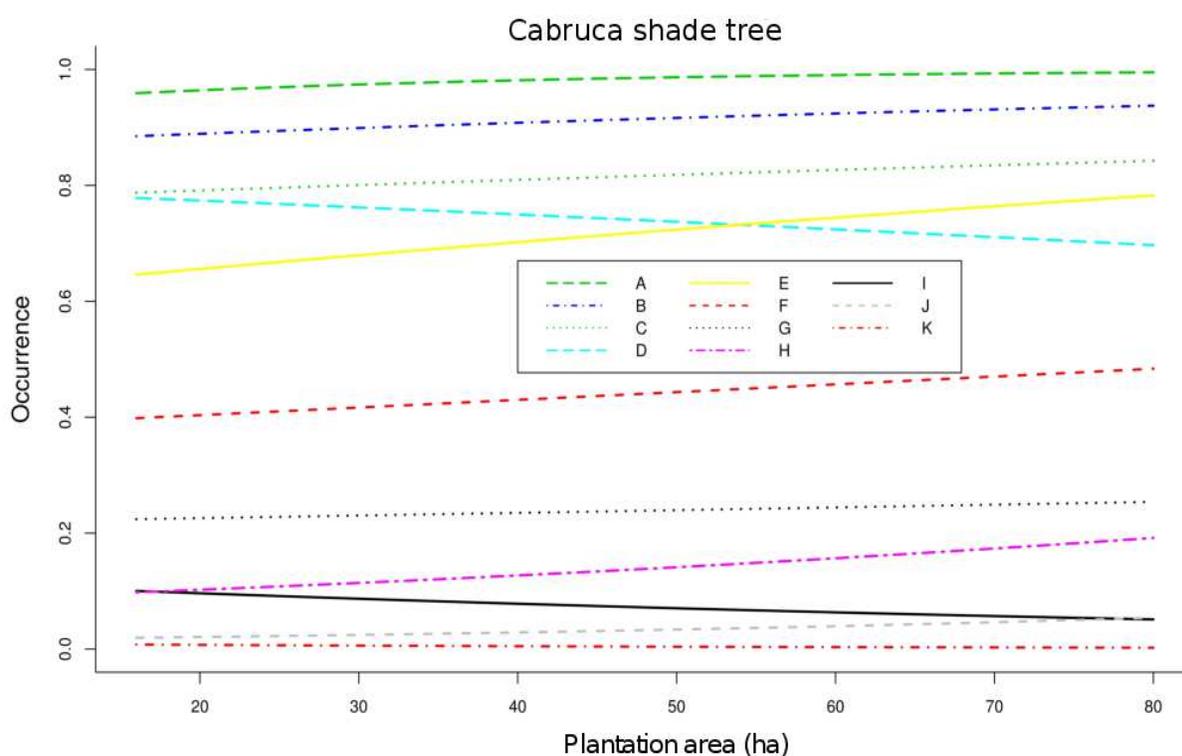


Fig. 8. Effect of cacao plantation area (ha) on the occurrence (mean of presence (1)/absence (0) per trap) of parasitoid families in cabruca shading trees' cacao management. Groups are A: Platygasteridae, B: Ichneumonidae + Braconidae, C: Mymaridae + Bethyidae + Diapriidae + Figitidae, D: Ceraphronidae, E: Eulophidae + Encyrtidae, F: Aphelinidae + Chalcididae + Trichogrammatidae + Evaniidae + Pteromalidae, G: Signiphoridae + Proctotrupidae + Eupelmidae, H: Monomachidae + Torymidae + Dryinidae + Eurytomidae, I: Agaonidae + Megaspilidae + Chrysididae, J: Eucharitidae + Sclerogibbidae, K: Gasteruptiidae + Liopteridae + Perilampidae.

Management system, seasonality, shade tree species richness and plantation area affected parasitoid community composition (Figure 3). For *cabruca* management system, we were able to compare the effects of alternative environmental Drivers – seasonality, tree species richness and plantation area – by comparing the information criteria values of the alternative models. The best models, depicted by the lowest AIC and BIC values, were those for tree species richness and plantation area, which presented exactly the same AIC and BIC values (Figure 3).

4. Discussion

In our statistical approach, we avoided the use of multivariate analyses, as commonly recommended for community composition studies (Hammer, 2001). The multivariate approach considers each taxon's occurrence as one dimension of a multidimensional 'entity', which would represent the ecological community (Manly, 1986; Harris, 2001). An assumption that is implicit in such an approach is that the set of studied taxa represents an actual interacting community. The multivariate approach would evaluate if the 'shap' of this abstract 'entity' differs among factor levels (e.g. non-metric multidimensional scaling – NMDS), or along a continuous variable's variation (e.g. multivariate regression). With our approach, we do not require such an abstract entity. Each taxon varies as a separate response variable, but this variation is not independent. In inserting 'sample site' as the random effect, we include a correlation structure for the errors (Zuur, 2009), such that sites with a high wasp occurrence will not generate a false effect related to more abundant wasp taxa in this site. Such an approach allowed us to attain a high statistical power, as depicted by the contrast between the amalgamation results obtained with pseudo-replicated GLM and the significant contrasts in GLMM analyzes. Furthermore, the amalgamation of family identity levels allowed us to distinguish families with differing occurrence levels, from those with similar occurrences, and the analyses of the 'interaction plots' allowed us to visualize and compare the different responses of community composition to each environmental driver. Therefore, we think our approach permits less stringent assumptions on the existence of interactions among the components of the assumed ecological community.

We separated the parasitoid wasps' families into groups of differing frequencies and responses to the environmental drivers. Whereas responses among some of these groups were different, responses for some of the parasitoid families could not be distinguished. A higher parasitoid family richness in both cacao management systems than found in natural Atlantic rain forest areas was evident. In four studies carried out in preserved forest areas, in the Espírito Santo state, an average of 28 families of parasitoid wasps was found (Azevedo, 2000; Azevedo, 2002; Azevedo, 2003; Alencar, 2007). In forest areas impacted by human activities, this number falls down to 19, as found by Perioto et al. (2000); Perioto, Lara, Santos & Selegatto (2002); Perioto, Lara, Santos & Silva (2002) in intensive management agroecosystems (soybean, cotton and coffee), suggesting that the current cacao agroforestry systems has a high conservation role for the parasitoid fauna.

Cacao plantations also keep the relative abundance of the families of parasitoid wasps. Platygasteridae, Braconidae, Ichneumonidae, Diapriidae, Bethylidae and Figitidae are usually abundant families in native forest, as we found in cacao plantations. For instance, Bethylidae is an uncommon family in intensive management agroecosystems, such as soybean, cotton and coffee, probably because these agroecosystems do not preserve the soil structure, as

Bethylidae are parasitoids of insects which depend somehow on the litter (Mugrabi, 2008). Intensive management of agroecosystems attracts less species and families of parasitoid wasps from the neighborhoods, which results in lower parasitoid family richness than in cacao plantations. For instance, according to Perioto et al., (2002), 54.2% of the total of parasitoid wasps in soybean crop belonged to three genera, *Telenomus*, *Trissolcus* and *Copidosoma*; the two formers are Platygasteridae, known as parasitoids of soybean bugs (*Nezara viridula*, *Piezodorus guildinii* and *Euschistus heros*), and the latter is an Encyrtidae known as parasitoid of soybean defoliator. This means that cacao plantation is better to conserve parasitoid fauna when compared to other crops cited above.

Although both cacao management systems sustained high parasitoid diversity, we detected that total clearing, followed by monospecific shading tree plantation, alters parasitoid wasps' community composition, in comparison to the more conservative *cabruca* management. Overall, frequency of the parasitoid families diminished, suggesting lower resource availability in these more intensively managed systems.

We detected an effect of seasonality on both 'total clearing' and *cabruca* shade tree systems, but changes in the more intensive management system were more pronounced. This may result from a higher dependency of immigration from neighboring forest areas to the more intensely managed 'total clearing' system, especially in winter. In contrast, the less altered *cabruca* habitat seemed to have a dampening effect on parasitoid occurrence. The higher availability of resource types in *cabruca* may be involved in this dampening, like that expected by the portfolio effect (Figge, 2004; Schindler, 2010).

Although insect seasonality has been studied for a long time, it is not settled which seasonal factors drive Hymenoptera communities, particularly in the tropics (Shapiro, 2000). Factors that affect these communities include host availability, adult food resource, habitat type and climate (English-Loeb, 2003; Tylianakis, 2004; Hoehn, 2008). In tropical forests, temperature varies little throughout the year, contrasting to the wide variation in rainfall and moisture, which explains the major importance of moisture as a key factor driving parasitoid wasps' community composition (Shapiro, 2000). Although the available studies on the effects of seasonality on Hymenoptera in the tropics have no replication of seasons among years (Shapiro, 2000; Sperber, 2004), both point to the conclusion that seasonality alters Hymenoptera communities.

In this study, most families' occurrence decreased during winter. However, two families of Proctotrupoidea - Monomachidae and Proctotrupidae - were most prevalent in winter. Monomachidae are often found during the winter time (Azevedo, 2001), in high altitudes or early in the morning (Masner, 1996). The Proctotrupidae are more abundant in high moisture and elevated areas (Masner, 1996). Both families are typical of low temperature areas, within the Neotropical region. The findings of this study were consistent with those published previously for these ecosystems.

The shade tree species richness altered the parasitoid composition mostly because the frequency of uncommon families increased and the frequency of common families decreased with shading tree species richness. This means that rare families benefited, probably because higher tree species richness enables more niches for those parasitoid species which are host species-specific. One example that supports such argument is Agaonidae. Members of Agaoninae are the fig-wasps which act as pollinators of the internal

fig flowers (the syconium) (Gibson, 1993), so the more fig-tree species, the more Agaoninae species and the more their abundance. The size of plantation area also altered the parasitoid composition, probably because an increase in *cabruca* plantation area correlates to increase in available shade tree species richness, especially as far as parasitoids are good flyers, being able to explore large plantation areas. The convergence of statistical models' AIC and BIC of plantation area and shade tree species richness supports this assertion.

5. Conclusion

Our results showed that cacao agroforestry provides suitable habitat for parasitoid communities. The drivers of parasitoid community composition include seasonality, kind of disturbance, shade tree species richness and plantation area, ranging from local spatial scale, at the farm's management system, through regional spatial scale, at the cacao plantation area. Further, our result highlight temporal (seasonal), categorical (management system) and continuous (tree species richness and plantation area) environmental drivers.

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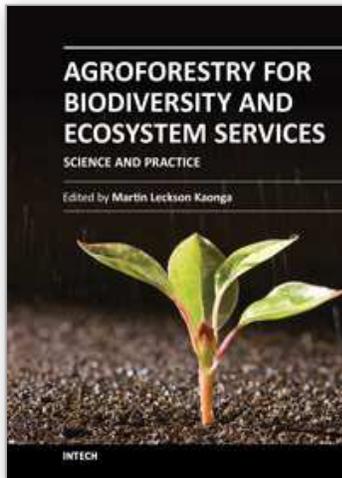
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Agroforestry for Biodiversity and Ecosystem Services - Science and Practice

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Agroforestry has great potential for reducing deforestation and forest degradation, providing rural livelihoods and habitats for species outside formally protected land, and alleviating resource-use pressure on conservation areas. However, widespread adoption of agroforestry innovations is still constrained by a myriad of factors including design features of candidate agroforestry innovations, perceived needs, policies, availability and distribution of factors of production, and perception of risks. Understanding the science, and factors that regulate the adoption, of agroforestry and how they impact the implementation of agroforestry is vitally important. *Agroforestry for Biodiversity and Ecosystem Services: Science and Practice* examines design features and management practices of some agroforestry practices and their impact on biodiversity and the ecosystem services it delivers. It also identifies policy issues for facilitating adoption of desirable agroforestry practices and gradual diminution of undesirable policies.

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