



# Tree species richness and density affect parasitoid diversity in cacao agroforestry

Carlos Frankl Sperber<sup>a,\*</sup>, Kazuiyuki Nakayama<sup>b,c</sup>, Maria Júlia Valverde<sup>c</sup>, Frederico de Siqueira Neves<sup>b</sup>

<sup>a</sup>*Departamento de Biologia Geral, Universidade Federal de Viçosa, Brazil*

<sup>b</sup>*Entomology Graduation Program, Departamento de Biologia Animal, Universidade Federal de Viçosa, 36570-000 Viçosa, MG, Brazil*

<sup>c</sup>*CEPLAC/CEPEC/SECEN, Rodovia Ilhéus, Itabuna, km. 22, CP: 7, 45.600-000 Itabuna, BA, Brazil*

## KEYWORDS

Biodiversity hotspot;  
Brazilian Atlantic  
Forest;  
Cabruca;  
Canopy;  
Habitat heterogeneity;  
LME;  
Seasonality;  
Wasps

## Summary

In Brazil, cacao is mostly planted beneath shade trees. The diversity of shade trees varies from monospecific to highly diverse canopies, characteristic of pristine Atlantic Forest. This study evaluates the relationships between family richness of Hymenoptera-Parasitica and Chrysidoidea, and tree species richness and density, the species richness of herbaceous understorey, and the area and age of the cacao agroforestry system. We sampled 16 cacao agroforestry systems, with canopy diversity ranging from one to 22 tree species per hectare, in three seasons: summer (March), winter (August) and spring (November). Parasitoids were sampled using eight Malaise-Townes traps per site. Tree species richness and density were enumerated within 1 ha at each site, and herbaceous plant species richness was calculated in eight 1 m<sup>2</sup> plots, within the hectare. The number of parasitoid families increased with tree species richness and density in spring and summer, but decreased in winter. Neither species richness of herbaceous plants nor area and age of the system affected parasitoid family richness. We suggest that the increase of parasitoid diversity with tree species richness and density in warmer seasons reflects increasing heterogeneity and availability of resources. The decrease in parasitoid family number with tree density in winter may be due to local impoverishment of resources, leading to parasitoid emigration to neighbouring forest remnants. This result implies that a higher diversity of shade trees will help to maintain high parasitoid levels and, in consequence, higher levels of natural enemies of cacao pests, particularly in the warmer seasons. This prediction is borne out in the experience of cacao producers. The proper management of shade tree diversity will play a vital role in maintaining the sustainability of cacao agroforestry production systems in the tropics and, concurrently, will maintain high biodiversity values in these locations.

© 2004 Elsevier GmbH. All rights reserved.

\*Corresponding author. Tel.: +55-31-3899-2556; fax: +55-31-3899-2549.

E-mail addresses: [sperber@ufv.br](mailto:sperber@ufv.br) (C.F. Sperber), [kazuo@cepec.gov.br](mailto:kazuo@cepec.gov.br) (K. Nakayama), [fneves@insecta.ufv.br](mailto:fneves@insecta.ufv.br) (F.S. Neves).

## Zusammenfassung

In Brasilien wird Kakao meist unter Schattenpflanzen angepflanzt. Die Diversität der Schattenbäume variiert von monospezifischen bis zu äußerst diversen Kronendächern, die charakteristisch für ursprüngliche atlantische Wälder sind. Diese Studie bewertet die Beziehung zwischen dem Familienreichtum der Hymenoptera-Parasitica sowie Chrysoidea und der Baumartenzahl und -dichte, der Artenzahl des krautigen Unterwuchses sowie der Fläche und dem Alter des Kakao-Waldfeldbausystems. In 16 Kakao-Waldfeldbausystemen mit einer Variation der Kronendachdiversität von einer bis 22 Arten pro Hektar nahmen wir in drei Jahreszeiten Proben: Sommer (März), Winter (August) und Frühjahr (November). Die Parasitoide wurden unter Verwendung von acht Malaise-Townes-Fallen pro Probefläche gesammelt. Die Baumartenzahl und -dichte wurden innerhalb eines Hektars für jede Probefläche gezählt und die Artenzahl der krautigen Pflanzen wurde über acht 1 m<sup>2</sup>-Probeflächen innerhalb des Hektars berechnet. Die Zahl der Parasitoidenfamilien stieg mit der Baumartenzahl und -dichte im Frühjahr und Sommer, nahm im Winter jedoch ab. Weder die Artenzahl der krautigen Pflanzen noch die Größe oder das Areal des Systems beeinflusste die Zahl der Parasitoidenfamilien. Wir schlagen vor, dass die Zunahme der Parasitoidendiversität mit der Baumartenzahl und -dichte in den wärmeren Jahreszeiten die zunehmende Heterogenität und Verfügbarkeit der Ressourcen widerspiegelt. Die Abnahme der Anzahl der Parasitoidenfamilien mit der Baumdichte im Winter könnte auf die lokale Verarmung der Ressourcen zurück zu führen sein, die zu einer Emigration der Parasitoide in benachbarte Waldreste führt. Diese Ergebnisse zeigen, dass eine höhere Diversität der Schattenbäume besonders in den warmen Jahreszeiten helfen wird, hohe Bestände von Parasitoiden und als Konsequenz höhere Bestände natürlicher Feinde der Kakaoschädlinge aufrecht zu erhalten. Diese Vorhersage wird von der Erfahrung der Kakaoproduzenten getragen. Das richtige Management der Schattenbaumdiversität wird eine wichtige Rolle bei der Aufrechterhaltung der Nachhaltigkeit des Kakao-Waldfeldbaus in den Tropen spielen und gleichzeitig hohe Biodiversitätswerte an diesen Orten aufrecht erhalten.

© 2004 Elsevier GmbH. All rights reserved.

## Introduction

Tropical landscapes are dominated by agroecosystems, but the potential value of such agroecosystems for the conservation of species is often overlooked (Klein, Steffan-Dewenter, & Tscharrtk, 2002). Investigations of the determinants of biodiversity, especially in managed areas within high diversity regions, must be of high priority so that conservation values can be maximised and impacts minimised in these irreplaceable areas.

At the local spatial scale, species diversity may be influenced by area, species interactions, disturbance, resource availability, and habitat heterogeneity (Ricklefs & Schluter, 1993; Begon, Harper, & Townsend, 1996). It is expected that diversity will increase with habitat heterogeneity (Strong, Lawton, & Southwood, 1984). Levels of parasitism may increase with landscape complexity (Kruess, 1994; Marino & Landis, 1996; Thies & Tscharrtk, 1999; Menalled, Marino, Gage, & Landis, 1999), and ant species richness has been shown to increase

with tree species richness (a surrogate for 'habitat heterogeneity') (Ribas, Schoederer, Pic, & Soares, 2003).

The highest priority areas for conservation have been designated 'biodiversity hotspots' (Myers, Mittermeyer, Mittermeyer, Fonseca, & Kent, 2000). Brazil's Atlantic Forest is one of these biodiversity hotspots, with a wealth of endemic species, and high levels of past, present and potential degradation. In two sites near Ilhéus, southern Bahia, more than 44% of the tree species (Angiospermae) are endemic to the coastal forest and more than 26% are endemic to southern Bahia and northern Espírito Santo (Thomas, Carvalho, Amorim, Garrison, & Arbeláez, 1998).

One of the most significant factors which contribute to the loss of biodiversity in forested areas is the introduction of intensive agricultural systems (Mahar, 1989). One way to ameliorate such impacts while maintaining agricultural productivity is the promotion of less environmentally 'aggressive' agroecosystems such as those which combine elements of forestry, particularly of local tree

species, with other crops ('agroforestry'). (Altieri, 1987; Nair, 1993). In Brazil, cacao (*Theobroma cacao* L., Sterculiaceae) is mostly planted within agroforestry systems. The shade trees may be planted, or the canopy of the native forest thinned and the cacao planted as an understorey. Planted overstorey trees are most commonly *Erythrina fusca* Lour. (Leguminosae: Papilionoideae) and *Hevea brasiliensis* (Wild.) Muell.-Arg. (Euphorbiaceae). When cacao is cultivated beneath native forest trees, it is referred to as *cabruca* (Vinha, Ramos, & Hori, 1976; Rosand, Santana, & Zevallos, 1987). In Brazil most cacao is grown in areas currently or once covered by Atlantic rainforest (Coimbra-Filho & Câmara, 1996). Accordingly where *cabruca* systems are in place the overall agroecosystems may present high levels of tree richness and, potentially at least, be of high conservation value.

Tropical insects show accentuated seasonality (Wolda, 1989, 1992), probably related to tree phenological events, such as leaf shedding and budding, flowering and fruiting (Janzen, 1975; Larcher, 2000). These may influence the number of parasitoid families directly or indirectly, and may well affect the relationship between parasitoid diversity and tree diversity.

In this study we evaluate whether the number of Hymenoptera families of the Parasitica series and of the Chrysidoidea superfamily, increase with the richness and density of tree species in the overstorey, herbaceous plant species richness in the understorey, and the area and age of the cacao agroforestry system. We also evaluate if these relationships are affected by season.

## Materials and methods

### Study area and sites

The sampling sites were located in Bahia, Brazil, in a polygon which includes remnants of Atlantic forest (bounded by: 15°17'S, 39°04'W; 15°25'S, 39°19'W; 15°25'S, 39°39'W; 15°05'S, 39°20'W), in a climatic region regarded as optimal for cacao agroforestry (Sá, Almeida, Silva, & Leão, 1982). The mean annual temperature is 24°C, with lowest temperatures (monthly mean = 20°C) in June to August (winter) and highest temperatures (monthly mean = 26°C) in December to March (summer). There are pronounced differences between wet and dry seasons, with total annual precipitation below 750 mm (Rosand et al., 1987).

We compared 16 cacao agroforestry systems, between 7 and 55 km apart (Table 1). The systems chosen presented levels of richness of shade trees ranging from one (*Erythrina fusca* or *Hevea brasiliensis*) to 22 species per hectare (Lauraceae, Leguminosae, Meliaceae, Moraceae, Sapotaceae, and others).

### Plants

In each cacao agroforestry system we determined tree species richness, tree density and the richness of herbaceous plants. Tree species richness was determined by counting all tree species within a single hectare. All trees with a crown which overtopped the cacao plants, were included. Tree density was calculated by counting the number of trees in this site. Herbaceous plant species richness

**Table 1.** Locations and characteristics of the cacao agroforestry systems which were sampled.

Tree species richness	Farm name	Localization	Age (years)	Area (ha)
1	Bolandeira 3	15°21'S; 39°00'W	27	20
1	Bolandeira 4	15°20'S; 39°02'W	24	18
1	Cachoeira 1	15°11'S; 39°01'W	35	25
1	Piruna 2	15°17'S; 39°06'W	40	20
1	Puaia 4	15°02'S; 39°20'W	47	20
9	Conceição	15°23'S; 39°18'W	30	50
14	São Roque 2	15°06'S; 39°16'W	25	16
15	Bolandeira 1	15°20'S; 39°01'W	28	80
15	Piruna 1	15°17'S; 39°07'W	20	20
15	São Roque 1	15°05'S; 39°17'W	60	20
15	Serra Boa	15°30'S; 39°39'W	45	20
16	Bolandeira 2	15°19'S; 39°03'W	25	60
16	Cachoeira 2	15°12'S; 39°02'W	40	70
18	Puaia 2	15°03'S; 39°19'W	45	20
21	Puaia 3	15°04'S; 39°19'W	35	30
22	Puaia 1	15°02'S; 39°20'W	25	20

was calculated by counting the number of species of herbs in 1 m<sup>2</sup> plot, located in the core of each 1-ha site. When in doubt, identification was confirmed by comparing field material with the herbarium collection of Centro de Pesquisas da Lavoura Cacaueira (CEPLAC). All collected material was incorporated subsequently in the CEPLAC collection.

### Sampling of parasitoids

Each agroforestry system was sampled using eight Malaise-Townes traps (Townes, 1972), erected on the ground for one day, along a 100 m transect, in the core of each 1-ha site. We used a total of 32 traps, manipulated by two teams. Each team used 16 traps, sampling one or two sites per day. Each site was sampled on three occasions: summer (17–28 March 2001), winter (5–14 August 2001), and spring (22 November–2 December 2001). The whole study involved (16 sites × 8 traps × 1 day)—a total of 384 trap-days.

### Parasitoid diversity

Parasitoid diversity was calculated as the mean number of families of Hymenoptera-Parasitica series (Terebrantia) or of the Chrysidoidea superfamily, sampled per trap in each site. The *taxa* involved were almost all (>95%) parasitoids and contain most of the known hymenopterous parasitoids (Goulet & Huber, 1993). Families were identified using Goulet and Huber (1993) and Gibson, Huber, and Woolley (1997). We chose to work at the level of the family, because the taxonomy of parasitoids in tropical regions is poorly known at the genus and species level and, because the sheer number of specimens collected in this study obviated the use of any finer taxonomic level. Higher taxon diversity may be a good surrogate of species diversity (Humphries, Williams, & Vane-wright, 1995; Cabeza & Moilanen, 2001; Baldi, 2003).

### Statistics

We used linear mixed effect models, with tree species richness, season, herb richness, tree density, area and age of cacao agroforestry system as explanatory variables. The analyses also generated interaction terms.

All of the explanatory variables were put into the model as fixed effects (Table 1). The site of the cacao systems was regarded as random effect. Mixed-effects models enable us to model

correlations that may exist within grouped data (Pinheiro & Bates, 2000; Buckley, Briese, & Rees, 2003). Accordingly all the fixed effect variables were nested within the random effects of the site of the cacao agroforestry system, thus avoiding pseudoreplication (Crawley, 2002).

We used the natural logarithm of the number parasitoid family numbers as the response variable within the model to normalise the count errors and so meet the demands of the linear mixed effect model (Buckley et al., 2003).

Our analysis used both categorical and continuous variables and so was analogous to a multiple regression with an associated analysis of covariance (Crawley, 2002). We progressively simplified the model by removing non-significant terms in a stepwise fashion. We did this in an hierarchical manner beginning with the removal of the highest level interaction terms, then, the non-significant explanatory variables. Finally we amalgamated non-significant factor levels, using contrasts (see Crawley, 1993). We evaluated models using analyses of variance, *F*-tests of the maximum likelihood ratios within and between models. Finally we calculated and assessed the minimal adequate model (Crawley, 2002; Buckley et al., 2003). Tree species richness and density were present as explanatory variables in the adjusted minimal adequate model. We examined the correlation between these two variables with Pearson's product-moment correlation (Crawley, 2002). All analyses were done within the R statistical package, R 1.7.1 © 2003; The R Development Core Team (Ihaka & Gentleman, 1996).

## Results

In total we sampled 21,346 individual parasitoids (Hymenoptera-Parasitica and Chrysidoidea), belonging to 33 families (Table 2). The superfamilies Platygastroidea, Chalcidoidea, and Ichneumonioidea were most abundant.

In the complete model, only season, tree species richness, and the interaction term of season with tree species richness and of season with tree density were significant (Table 3). The minimal adequate model included all these significant variables plus tree density, which could not be removed from the model because it was included as part of a significant interaction term related to family richness (Table 4). Richness of herbaceous plants, the area and age of the cacao agroforestry system, and the interaction terms not included in

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

Taxon	Individuals	%	Taxon	Individuals	%
<i>Evanoidea</i>	287	1.34	<i>Ichneumonoidea</i>	3952	18.51
Gasteruptiidae	6	1.32	Braconidae	1921	9.00
Evaniidae	281	0.03	Ichneumonidae	2031	9.51
<i>Proctotrupoidea</i>	1400	6.56	<i>Platyastroidea</i>	6486	30.37
Monomachidae	99	0.46	Platygastridae	2745	12.85
Proctotrupidae	168	0.80	Scelionidae	3741	17.52
Diapriidae	1130	5.29	<i>Chalcidoidea</i>	5019	23.50
<i>Chrysoidea</i>	1369	6.41	<i>Perilampidae</i>	9	0.04
Sclerogibbidae	24	0.11	Eucharitidae	12	0.06
Dryinidae	104	0.49	Elasmidae	12	0.06
Chrysididae	57	0.27	Agaonidae	27	0.13
Bethyidae	1178	5.52	Torymidae	53	0.25
<i>Ceraphronoidea</i>	1049	4.91	Eurytomidae	69	0.32
Megaspilidae	66	0.31	<i>Eupelmidae</i>	136	0.67
Ceraphronidae	983	4.60	Signiphoridae	145	0.68
<i>Cynipoidea</i>	1793	8.40	Aphelinidae	242	1.13
Liopteridae	1	<0.01	Chalcididae	326	1.53
Figitidae	27	0.13	<i>Trichogrammatidae</i>	342	1.60
Eucoilidae	1765	8.27	Pteromalidae	368	1.72
			Eulophidae	789	3.69
			Encyrtidae	1083	5.07
			Mymaridae	1406	6.58

**Table 3.** Analysis of variance of the complete linear mixed effect model, before model simplification, to explain parasitoid (Hymenoptera of the Parasitica series or Chrysoidea superfamily) diversity in cacao agroforestry systems.

Source	num. df	den. df	F	Pr (>F)	
(Intercept)	1	16	2885.06	<0.0001	*
Season	2	16	31.21	<0.0001	*
Tree species richness (S tree)	1	6	6.63	0.042	*
Herbaceous plant species richness (S herb)	1	6	2.12	0.196	ns
Tree density (N tree)	1	6	0.39	0.553	ns
Cacao agroforestry system area	1	6	2.13	0.195	ns
Cacao agroforestry system age	1	6	0.39	0.554	ns
Season × S tree	2	16	9.96	0.002	*
Season × S herb	2	16	3.23	0.066	ns
S tree × S herb	1	6	2.74	0.149	ns
Season × N tree	2	16	9.08	0.002	*
S tree × N tree	1	6	0.32	0.593	ns
S herb × N tree	1	6	0.01	0.930	ns
Season × S tree × S herb	2	16	1.15	0.343	ns
Season × S tree × N tree	2	16	0.74	0.494	ns
Season × S herb × N tree	2	16	0.76	0.482	ns
S tree × S herb × N tree	1	6	0.62	0.461	ns
Season × S tree × S herb × N tree	2	16	0.98	0.397	ns

Response variable = ln(number of parasitoid families); random effect = site.

the minimal model, did not affect the number of parasitoid families (Table 3). The number of parasitoid families increased with tree species richness and tree density in both spring and

summer, but decreased in winter (Table 5, Fig. 1). Tree species richness and tree density were strongly correlated (Fig. 2,  $r = -0.89$ ;  $t = 13.04$ ,  $df = 46$ ,  $p < 0.0001$ ).

**Table 4.** Analysis of variance of the minimal adequate linear mixed effect model, to explain parasitoid (Hymenoptera of the Parasitica series or Chrysoidea superfamily) diversity in cacao agroforestry systems.

Source	num. df	den. df	F	Pr (>F)
(Intercept)	1	26	2602.61	<0.0001
Season	2	26	26.27	<0.0001
Tree species richness (S tree)	1	13	5.99	0.0294
Tree density (N tree)	1	13	0.27	0.6100
Season × S tree	2	26	8.39	0.0015
Season × N tree	2	26	7.15	0.0033

Response variable = ln(number of parasitoid families); random effect = site.

**Table 5.** Parameter estimates and standard error, for the adjusted minimal adequate LME model.

Term	Estimate	Std. error
Winter	2.6216	0.2965
Spring	-0.6765	0.2481
Summer	-0.0617	0.2481
Tree species richness (S tree)	-0.0069	0.0157
Tree density (N tree)	-0.0015	0.0007
Spring × S tree	0.0389	0.0131
Summer × S tree	0.0094	0.0131
Spring × N tree	0.0020	0.0006
Summer × N tree	0.0015	0.0006

Response variable = ln (Parasitoid family number); fixed effects = Season (Summer × Winter × Spring) + Tree species richness (S tree) + Tree density (N tree) + Season × S tree + Season × N tree; random effect = site.

## Discussion

This work showed that the abundance of parasitoids in cacao agroforestry systems is astonishingly high, when compared with other systems. For example, we collected almost three times the number of individuals per unit trapping effort than did [Matlock and de la Cruz \(2002\)](#) in a mosaic of agriculture and forest remnants in the Caribbean.

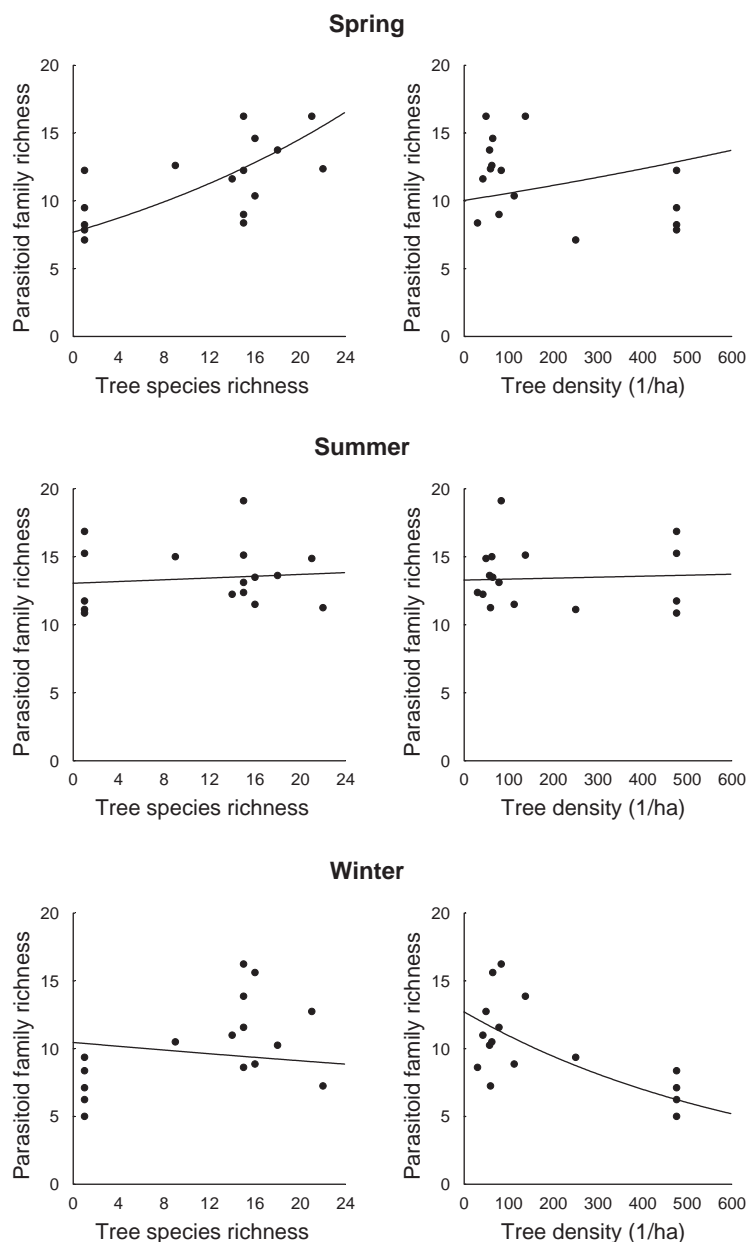
The family taxonomic level was sensitive to the effects of variables related to the canopy of shade trees, possibly due to their high levels of specialisation. Most parasitoid families prey upon a restricted range of insect orders ([Quicke, 1997](#)). It seems unlikely that the use of a lower taxonomic level for the parasitoids would show any different trend.

The taxonomic composition of the hymenopteran assemblage in our study was similar to that in natural forest of the same biome. Sampling an Atlantic forest reserve, [Azevedo and Santos \(2000\)](#) collected 8305 individuals, in 30 families. The number of families was almost the same in their study and ours—the most abundant super-families were the same, with the same order of abundance. Scelionidae was the most abundant family in both

studies, Platygasteridae, Ichneumonidae, Braconidae, and Eucolidae were among the ten most abundant families in [Azevedo and Santo's \(2000\)](#) study.

Our results showed that parasitoid family numbers are affected by the richness and density of the shade trees which form the canopy of the agroecosystem. Similar trends have been demonstrated for other predatory insects. In sclerophyllous *cerrado* vegetation in Brazil, ant species richness increased with tree species richness and tree density ([Ribas et al., 2003](#)). In general, tree species richness is probably a surrogate for resource heterogeneity ([Tilman & Pacala, 1993](#); [Ribas et al., 2003](#)). So, for example, [Lill, Marquis, and Ricklefs \(2002\)](#) showed that some parasitoid species are specialized with respect to tree species—each new tree species provides a different set of direct and indirect resources for parasitoids. Direct resources include supplementary food such as pollen, nectar, and honeydew ([Thompson, 1999](#); [Wackers, 2001](#); [Beach, Williams, Hendrix, & Price, 2003](#); [Gentry, 2003](#)), enemy free space ([Russell, 1989](#)), suitable microhabitats ([Lawton, 1983](#); [Bell, McCoy, & Mushinsky, 1991](#); [Ribas et al., 2003](#)), and herbivorous hosts associated with the trees ([Hawkins, 1990](#); [Godfray, 1993](#); [Hawkins & Mills, 1996](#); [Quicke, 1997](#)).

The species richness of insect herbivores is probably positively correlated with tree species richness ([Erwin, 1982](#); [Novotny, Basset, & Kitching, 2003](#)). The greater the herbivore specialisation and the faunal turnover among tree species, the stronger will be the correlation of herbivorous species richness with tree species richness ([Basset, Samuelson, Allison, & Miller, 1996](#)). The percentage of monophagous herbivorous insects in the canopy may be as low as 4% ([Novotny, Basset, Miller, Drozd, & Cizek, 2002](#)) or as high as 26% ([Barone, 1998](#)); the faunal overlap among tree species canopies is generally high ([Basset & Novotny, 1999](#)). Tree diversity is correlated with faunal composition ([Brehm, Homeier, & Fiedler, 2003](#)). The richness of herbivores on any one tree will be affected not

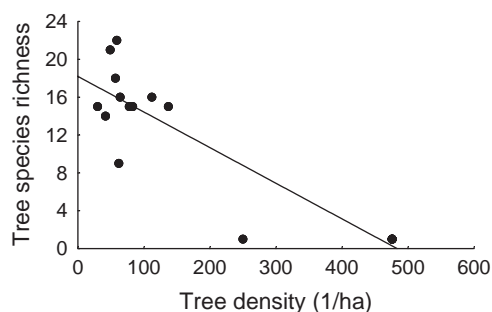


**Figure 1.** Number of Hymenoptera-Parasitica and Chrysoidea families in cacao agroforestry systems with different shade tree diversity, in three seasons: Spring, Summer, and Winter. Left: parasitoid family number against shade tree species richness; right: parasitoid family number against shade tree density. Curves were based on parameters (Table 5) of the fitted minimum adequate linear mixed effect model (Table 4).

only by the identity of the tree species itself but by the pattern of adjacent canopies (Basset & Novotny, 1999). In addition, variation in plant traits among plant species may well promote the development of a characteristic functional assemblage of insect herbivores associated with each plant species (Peeters, Read, & Sanson, 2001).

Why, then, did the number of parasitoid families increase with tree density in the warm seasons? For tropical forest figs, significant predictors of insect species richness include tree density (Basset &

Novotny, 1999). In experimentally manipulated agroecosystems, shade structures have a strong effect on enemy and herbivore trophic levels (Dyer & Stireman, 2003). Klein et al. (2002), studying a cacao agroforestry system, showed that the abundance and species richness of entomophagous insects diminished with land-use intensity: an effect which the authors ascribed to reduced species richness of shade trees as well as increased temperature, decreased canopy cover and lower humidity. Increased tree density maintains a mesic



**Figure 2.** Scatter-plot of shade tree species richness against tree density, in cacao agroforestry systems. Line: fitted linear regression. Pearson's product-moment correlation,  $r = -0.89$ ,  $t = 13.04$ ,  $df = 46$ ,  $p < 0.0001$ .

microclimate, which [Fernandes and Price \(1991, 1992\)](#) have hypothesised to favour parasitoids of herbivores.

We are confident that the effect of tree species richness and density upon the numbers of families of parasitoids is not merely a spurious correlation. There was a significant correlation of tree species richness with tree density, but this was negative rather than the positive trend that has been observed in other systems ([Ribas et al., 2003](#)). This negative correlation is probably the result of human interventions within the cacao agroecosystem. Locations with the lowest tree richness have canopies composed of planted trees—in other words their minimal richness is entirely anthropogenic.

The switch in direction in the relationship between parasitoid richness and overstorey richness that we observed across seasons is probably related to differences in resource availability. In the warmer, growing seasons, there is an increased availability in new meristematic tissue, new leaves and fruits which are often preferred resources for herbivores ([Wolda, 1989, 1992](#); [Novotny et al., 2003](#); [Wagner, 2001](#)) which, in turn, are a resource for parasitoids. Flowering phenology may also be implicated. Many tropical tree species flower synchronously ([Augspurger, 1985](#); [Kirmse, Adis, & Morawetz, 2003](#)), which may well be reflected in an apparent seasonality in their directly or indirectly dependent insect associates ([Basset, Novotny, Miller, & Kitching, 2003](#); [Didham & Springate, 2003](#); [Itioka et al., 2003](#)).

The negative relationship between parasitoid family numbers and tree species richness and density in the winter is more difficult to explain. The lower parasitoid diversity in the systems with monospecific shade trees may have a landscape-level explanation possibly involving the emigration of the parasitoids to neighbouring forest remnants ([Ricklefs & Schluter, 1993](#); [Chesson, 2000](#)) in search

of scarce resources. Natural habitat remnants may harbour most of the animal diversity of agriculturally managed systems ([Duelli & Obrist, 2003](#)). In addition, in the winter, temperature is lower and rainfall less ([Rosand et al., 1987](#)), which will likely reduce plant growth and flowering, with consequent negative impacts upon populations of insect herbivores both directly (as development rates decrease) and indirectly through comparable negative impacts upon resources ([Ferro, 1987](#)).

Although the traps we used were located at ground level, parasitoid diversity was unaffected by species richness of herbaceous plants. This contrasts with multiple cropping systems or crops intermingled with weeds, where parasitoid diversity is correlated to herbaceous plant diversity ([Andow, 1990](#), and references therein).

Our results showed that parasitoid diversity was not affected by the area or the age of the cacao agroforestry system and this result agrees with what previous information exists on the topic (see the results of [Matlock and de la Cruz \(2002\)](#), from Central Sulawesi). This may be the result of different parasitoid species responding to different spatial scales ([Roland & Taylor, 1997](#)).

Our results have direct implications for herbivore regulation and sustainable management of cacao agroforestry systems. Cacao agroforestry systems using natural forest as shade trees maximise parasitoid family numbers in the warm seasons, when herbivore populations are higher ([Ferro, 1987](#)) increasing the likely efficiency of natural pest control. [Klein et al. \(2002\)](#), studying tropical cacao agroforestry systems and natural forests, showed that the predator–prey ratio was reduced with land-use intensity. Use of insecticides and nematicides reduces species richness and abundance of parasitoids in a mosaic of agricultural habitats and forest remnants ([Matlock & de la Cruz, 2002](#)). In less diverse cacao habitats, the abundance of particular herbivorous *taxa*, such as rhizophagous Coleoptera, is higher than in cacao under natural forest ([Garcia & Silveira-Neto, 1980](#); [Benton, 1984](#)). There is also evidence that cacao planted under shade trees, irrespective of tree species richness, experiences a lower frequency of pest outbreaks ([Abreu, 1972](#); [Benton, 1984](#); [Medeiros, Fowler, & Bueno, 1995](#)), and requires lower levels of pesticide use ([CEPLAC, 1980](#)). Therefore, vegetational diversity can lead to suppression of pests via 'top-down' enhancement of natural enemy populations, as well as longer term benefits for sustainability of the farming system and, ultimately, broad societal benefits including aesthetics and conservation of flora and fauna ([Gurr, Wratten, & Luna, 2003](#)).



The maintenance of natural forest canopy as shade trees in the cacao agroforestry system may have conserved, or even enhanced (see Sax & Gaines, 2003), the naturally occurring number of parasitoid families. This has been demonstrated in comparisons with natural systems. Accordingly the use of natural mixtures as shade for cacao is not only good sense from the point of view of reducing pest numbers but also has considerable positive implications for conservation. This is particularly important in regions such as the Atlantic forest which is recognised as a biodiversity 'hotspot' (Myers et al., 2000).

## Acknowledgements

This work was done as part of the requisites for the PhD thesis of K. Nakayama, who was supported with a grant from CNPq (Conselho Nacional de Pesquisa). We thank Celso O. Azevedo for training in taxonomy, José Henrique Schoereder for manuscript review, Og DeSouza for the initial ideas, Carla Galbiati for helping with the statistical analyses, and Roger L. Kitching, for English revision. Two anonymous referees, gave valuable critics and suggestions which improved the manuscript substantially.

## References

- Abreu, J. M. (1972). Flutuações de populações de coleópteros nocivos ao cacauero no Espírito Santo, Brasil. *Revista Theobroma*, 2, 45–55.
- Altieri, M. A. (1987). *The scientific basis of alternative agriculture*. Boulder: Westview Press.
- Andow, D. A. (1990). Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology*, 71, 1006–1017.
- Augsburger, C. (1985). A cue for synchronous flowering. In E. Leigh, A. Rand, & D. Windsor (Eds.), *The ecology of a tropical forest: Seasonal rhythms and long-term changes* (pp. 133–150). Washington: Smithsonian Institution.
- Azevedo, C. O., & Santos, H. S. (2000). Perfil da fauna de himenópteros parasitóides (Insecta, Hymenoptera) em uma área de Mata Atlântica da Reserva Biológica de Duas Bocas, Cariacica, ES, Brasil. *Boletim do Museu de Biologia Mello Leitão*, 11/12, 117–126.
- Baldi, A. (2003). Using higher taxa as surrogates of species richness: A study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves. *Basic and Applied Ecology*, 4, 589–593.
- Barone, J. A. (1998). Host-specificity of folivorous insects in a moist tropical forest. *Journal of Animal Ecology*, 67, 400–409.
- Basset, Y., & Novotny, V. (1999). Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of the Linnean Society*, 67, 477–499.
- Basset, Y., Novotny, V., Miller, S., & Kitching, R. (2003). *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy*. Cambridge: Cambridge University.
- Basset, Y., Samuelson, G. A., Allison, A., & Miller, S. E. (1996). How many species of host-specific insects feed on a species of tropical tree? *Biological Journal of the Linnean Society*, 59, 201–216.
- Beach, J. P., Williams, L., Hendrix, D. L., & Price, L. D. (2003). Different food sources affect the gustatory response of *Anaphes iole*, an egg parasitoid of *Lygus* spp. *Journal of Chemical Ecology*, 29, 1203–1222.
- Begon, M., Harper, J. L., & Townsend, C. R. (1996). *Ecology: Individuals, populations and communities* (3rd ed.). Oxford: Blackwell Science.
- Bell, S. S., McCoy, E. D., & Mushinsky, H. R. (1991). *Habitat structure: The physical arrangement of objects in space*. London: Chapman & Hall.
- Benton, P. F. (1984). Abundância estacional dos coleópteros fitófagos do cacauero do sul da Bahia e Espírito Santo. *Revista Theobroma*, 14, 85–102.
- Brehm, G., Homeier, J., & Fiedler, K. (2003). Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, 9, 351–366.
- Buckley, Y. M., Briese, D. T., & Rees, M. (2003). Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology*, 40, 481–493.
- Cabeza, M., & Moilanen, A. (2001). Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution*, 16(5), 242–248.
- CEPLAC. (1980). Contribuições da pesquisa para atualização dos pacotes tecnológicos recomendados para a região cacauera. Comissão Executiva do Plano da Lavoura Cacaueira, Ilhéus.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Coimbra-Filho, A. F., & Câmara, I. G. (1996). Os limites originais do bioma Mata Atlântica na Região Nordeste do Brasil. Fundação Brasileira para a Conservação da Natureza, Salvador.
- Crawley, M. J. (1993). *Glim for ecologists*. Oxford: Blackwell Scientific Publications.
- Crawley, M. J. (2002). *Statistical computing: An introduction to data analysis using S-Plus*. Chichester: Wiley.
- Didham, R., & Springate, N. (2003). Determinants of temporal variation in community structure. In Y. Basset, V. Novotny, S. Miller, & R. Kitching (Eds.), *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy* (pp. 28–39). Cambridge: Cambridge University.

- Duelli, P., & Obrist, M. K. (2003). Regional biodiversity in an agricultural landscape: The contribution of semi-natural habitat islands. *Basic and Applied Ecology*, 4, 129–138.
- Dyer, L. A., & Stireman, J. O. (2003). Community-wide trophic cascades and other indirect interactions in an agricultural community. *Basic and Applied Ecology*, 4, 423–432.
- Erwin, T. (1982). Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, 36, 74–75.
- Fernandes, G., & Price, P. W. (1991). Comparison of tropical and temperate galling species richness: The roles of environmental harshness and plant environmental status. In P. Price, T. Lewinsohn, G. Fernandes, & W. Benson (Eds.), *Plant–animal interactions: Evolutionary ecology in tropical and temperate regions* (pp. 91–115). New York: Wiley.
- Fernandes, G., & Price, P. W. (1992). The adaptive significance of insect gall distribution: Survivorship of species in xeric and mesic habitats. *Oecologia*, 90, 14–20.
- Ferro, D. (1987). Insect pest outbreaks in agroecosystems. In P. Barbosa, & J. Schultz (Eds.), *Insect outbreaks* (pp. 195–215). San Diego: Academic Press.
- Garcia, J. J. S., & Silveira-Neto, S. (1980). Estudo faunístico de coleópteros e hemípteros associados ao cacauero no Estado do Pará. *Revista Theobroma*, 10, 15–23.
- Gentry, G. (2003). Multiple parasitoid visitors to the extrafloral nectaries of *Solanum adherens*. Is *S. adherens* an insectary plant? *Basic and Applied Ecology*, 4, 405–411.
- Gibson, G. A. P., Huber, J. T., & Woolley, J. B. (1997). In *Annotated keys to the genera of nearctic Chalcidoidea (Hymenoptera)*. Ottawa: NRC Research.
- Godfray, H. C. J. (1993). *Parasitoids: Behavioral and evolutionary ecology*. Princeton: Princeton University.
- Goulet, H., Huber, J. T. (Eds.), (1993). *Hymenoptera of the World: An identification guide to families*. Ottawa: Agriculture Canada Research Branch.
- Gurr, G. M., Wratten, S. D., & Luna, J. M. (2003). Multi-function agricultural biodiversity: Pest management and other benefits. *Basic and Applied Ecology*, 4, 107–116.
- Hawkins, B. A. (1990). Global patterns of parasitoid assemblage size. *Journal of Animal Ecology*, 59, 57–72.
- Hawkins, B. A., & Mills, J. L. (1996). Variability in parasitoid community structure. *Journal of Animal Ecology*, 65, 501–516.
- Humphries, C. J., Williams, P. H., & Vanewright, R. I. (1995). Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics*, 26, 93–111.
- Ihaka, R., & Gentleman, R. (1996). A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, 5, 299–314.
- Itioka, T., Kato, M., Kaling, H., Merdek, M., Nagamitsu, T., Sakai, S., Mohamad, S. U., Yamane, S., Hamid, A. A., & Inoue, T. (2003). Insect responses to general flowering in Sarawak. In Y. Basset, V. Novotny, S. Miller, & R. Kitching (Eds.), *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy* (pp. 126–134). Cambridge: Cambridge University.
- Janzen, D. H. (1975). *Ecology of plants in the tropics*. London: Edward Arnold.
- Kirmse, S., Adis, J., & Morawetz, W. (2003). Flowering events and beetle diversity in Venezuela. In Y. Basset, V. Novotny, S. Miller, & R. Kitching (Eds.), *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy* (pp. 256–268). Cambridge: Cambridge University.
- Klein, A. M., Steffan-Dewenter, I., & Tschardt, T. (2002). Predator–prey ratios on cocoa along a land-use gradient in Indonesia. *Biodiversity and Conservation*, 11, 683–693.
- Kruess, A. (1994). Habitat fragmentation, species loss, and biological-control. *Science*, 264, 1581–1584.
- Larcher, W. (2000). *Ecofisiologia vegetal*. São Carlos: Rima.
- Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, 28, 23–39.
- Lill, J. T., Marquis, R. J., & Ricklefs, R. E. (2002). Host plants influence parasitism of forest caterpillars. *Nature*, 417, 170–173.
- Mahar, D. J. (1989). *Government policies and deforestation in Brazil's Amazon region*. Washington: The World Bank.
- Marino, P. C., & Landis, D. A. (1996). Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications*, 6, 276–284.
- Matlock, R. B., & de la Cruz, R. (2002). An inventory of parasitic Hymenoptera in banana plantations under two pesticide regimes. *Agriculture Ecosystems & Environment*, 93, 147–164.
- Medeiros, M. A., Fowler, H. G., & Bueno, C. O. (1995). Ant (Hym., Formicidae) mosaic stability in Bahian cacao plantations: Implications for management. *Journal of Applied Entomology*, 119, 411–414.
- Menalled, F. D., Marino, P. C., Gage, S. H., & Landis, D. A. (1999). Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecological Applications*, 9, 634–641.
- Myers, N., Mittermeyer, R. A., Mittermeyer, C. G., Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- Nair, P. R. (1993). *An introduction to agroforestry*. Dordrecht: Kluwer Academic.
- Novotny, V., Basset, Y., & Kitching, R. (2003). Herbivore assemblages and their food resources. In Y. Basset, V. Novotny, S. Miller, & R. Kitching (Eds.), *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy* (pp. 40–53). Cambridge: Cambridge University.
- Novotny, V., Basset, Y., Miller, S. E., Drozd, P., & Cizek, L. (2002). Host specialization of leaf-chewing insects in a New Guinea rainforest. *Journal of Animal Ecology*, 71, 400–412.

- Peeters, P. J., Read, J., & Sanson, G. D. (2001). Variation in the guild composition of herbivorous insect assemblages among co-occurring plant species. *Austral Ecology*, *26*, 385–399.
- Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-effects models in S and S-plus*. New York: Springer.
- Quicke, D. L. J. (1997). *Parasitic wasps*. New York: Chapman & Hall.
- Ribas, C. R., Schoereder, J. H., Pic, M., & Soares, S. M. (2003). Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, *28*, 305–314.
- Ricklefs, R. E., & Schluter, D. (1993). *Species diversity in ecological communities: Historical and geographical perspectives*. Chicago: University of Chicago.
- Roland, J., & Taylor, P. D. (1997). Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, *386*, 710–713.
- Rosand, P. C., Santana, M., & Zevallos, A. C. (1987). Associations between cacao (*Theobroma cacao*) and shade trees in southern Bahia Brazil. In J. W. Beer, H. W. Fassbender, & J. Heuveldop (Eds.), *Advances in agroforestry research* (pp. 137–154). Turrialba: Centro Agronómico Tropical de Investigación y enseñanza (CATIE)/Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ).
- Russell, E. P. (1989). Enemies hypothesis: A review of effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology*, *18*, 590–599.
- Sá, D. F., Almeida, H. A., Silva, L. F., & Leão, A. C. (1982). Fatores edafo-climáticos seletivos ao zoneamento da cacaucultura no Sudoeste da Bahia. *Revista Theobroma*, *12*, 169–187.
- Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution*, *18*, 561–566.
- Strong, D. R., Lawton, J. H., & Southwood, R. (1984). *Insects on plants: Community patterns and mechanisms*. Cambridge: Harvard University/Blackwell Scientific Publication.
- Thies, C., & Tschardtke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, *285*, 893–895.
- Thomas, W. M., Carvalho, W., Amorim, A. M. V., Garrison, A. M. A., & Arbeláez, J. (1998). Plant endemism in two forests in Southern Bahia, Brazil. *Biodiversity and Conservation*, *7*, 33–322.
- Thompson, S. N. (1999). Nutrition and culture of entomophagous insects. *Annual Review of Entomology*, *44*, 561–592.
- Tilman, D., & Pacala, S. (1993). The maintenance of species richness in plant communities. In R. E. Ricklefs, & D. Schluter (Eds.), *Species diversity in ecological communities: Historical and geographical perspectives* (pp. 13–25). Chicago: University of Chicago.
- Townes, H. A. (1972). A light-weight Malaise trap. *Entomological News*, *83*, 239–247.
- Vinha, S. G., Ramos, T. J. S., & Hori, M. (1976). Recursos Florestais. In: CEPLAC (Ed.), *Diagnóstico sócio-econômico da região cacauzeira*, Vol. 7. Ilhéus: Comissão Executiva do Plano da Lavoura Cacaueira.
- Wackers, F. L. (2001). A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *Journal of Insect Physiology*, *47*, 1077–1084.
- Wagner, T. (2001). Seasonal changes in the canopy arthropod fauna in *Rinorea beniensis* in Budongo Forest, Uganda. *Plant Ecology*, *153*, 169–178.
- Wolda, H. (1989). Seasonal cues in tropical organisms. Rainfall? Not necessarily!. *Oecologia*, *80*, 437–442.
- Wolda, H. (1992). Trends in abundance of tropical forest insects. *Oecologia*, *89*, 47–52.