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ORIGINAL PAPER

Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil

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Abstract By maintaining a forest-like structure, shaded cocoa plantations contribute to the conservation of ants that usually live in the soil, leaf litter or canopy of tropical forests. Here we synthesize the available information on the diversity and community structure of

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ants in shaded cocoa plantations in the Atlantic forest region of Brazil, compare ant assemblages in cocoa agroforests with forests and other forms of agriculture, and discuss how these shaded plantations contribute to the conservation of the ants in the Atlantic Forest region. We also discuss ants of economical importance and of special interest, including *Camponotus*, *Dolichoderus*, *Gnamptogenys*, *Pachycondyla*, *Pseudomyrmex* and other litter dwelling genera. We discuss the situation of the tramp ant *Wasmannia auropunctata* in the Bahian cocoa-producing region where it is considered as native, and that of the two cryptobiotic genera *Thaumatomyrmex* and *Typhlomyrmex*, as well as that of proven and possible endangered army ant and Ponerini species. A total of 192 ant species from four strata were found in extensive sampling of a cocoa plantation with a relatively simple shade canopy (comprised primarily of *Erythrina*). Species richness in the cocoa plantations corresponded roughly to that of low diversity native forests, and species composition of cocoa plantations was most similar to native habitats (forest and mangroves) while ant composition in other agricultural habitats was most similar to that of urban areas. Although occurrences of *Wasmannia auropunctata* were similar in cocoa plantations and forests, abundance of *Thaumatomyrmex* and *Typhlomyrmex*, generally thought to be rare ants, was relatively high in cocoa plantations. These results, from cocoa plantations with relatively simple shade, demonstrate the importance of cocoa for ant conservation in the Atlantic forest region of Brazil. It is likely that cocoa plantations with a greater number of vegetation strata and higher tree species richness (such as traditional cabruca plantations) provide even more important habitat for ants generally and for ant species of conservation concern.

Keywords Agroecosystem · Arboreal ants · Cabruca · Community structure · *Erythrina* · Forest · Ground-dwelling ants · Neotropical fauna · *Theobroma cacao*

Introduction

The Brazilian Atlantic biome is a biodiversity hotspot (Morellato and Haddad 2000, Galindo-Leal and Camara 2005), with a record endemism rate for plants estimated to be about 40% for Angiosperms (Thomas et al. 1998; Oliveira-Filho and Fontes 2000), and a high endemism for insects (Brown 1991), herbaceous plants (Jackson 1978), birds (Haffer 1974) and mammals (Mittermeier et al. 1982; Faria et al. 2006). Yet today, the Atlantic forest retains only about 8% of pristine vegetation due to an intensive, historical deforestation that began with the Portuguese colonization in the 16th Century (Dean 1995). Due to its high diversity and its low forest cover, the region is considered one of the highest priorities for biodiversity conservation within Brazil and is the site of many conservation and restoration projects (Ministério do Meio Ambiente, dos Recursos Hídricos e da Amazônia Legal 1995).

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In addition to being an area of high biodiversity, the region is the largest cocoa-growing area on the eastern coast of Brazil with around 400,000 hectares currently under cocoa (*Theobroma cacao* L., Malvaceae). Cocoa is native to the Amazon region and was introduced into southeastern Bahia in the 18th Century (Delabie 1990). During the cocoa boom of the 1960's and 1970's, approximately 650,000 ha of forest were converted to cocoa plantations thereby creating a greatly fragmented native forest ecosystem. In the 1980's cocoa production was one of the largest exports of Brazil. Yet, the future of the cocoa economy and the conservation of native forest remnants are increasingly threatened by a complex phytosanitary situation of the cocoa farms following the introduction of the witches' broom fungus (*Crinipellis perniciosa*) in 1989, and a continuous pressure for wood extraction in the region, especially for the timber trade (Alger and Caldas 1994; Rocha 2002).

There are two main cocoa production systems in Bahia which vary in vegetation structure and management. The traditional cocoa groves, called ''cabruca'', are established by planting cocoa under a thinned forest canopy and are, therefore, shaded by native trees (Rolim and Chiarello 2004). The vegetation structure and stratification of cabruca plantations are considered to be similar to, albeit less complex than, that of natural forests (Saatchi et al. 2001), and plant richness is among the highest for agricultural systems (Rolim and Chiarello 2004). The cabruca cocoa agroecosystem has received much recent attention because of its economic importance for the region, and also because cocoa cultivation in traditional, shaded systems favors the conservation of a high proportion (but evidently not all) species of the Atlantic Forest landscape (Delabie et al. 1999; Sperber et al. 2004; Faria and Baumgarten 2007). In the past 50 years, a new system called ''derruba total'' (total felling) where the original vegetation is completely eliminated before planting has been developed. In ''derruba total'', cocoa trees are planted at twice the density of cabruca systems, and cocoa plants are generally shaded with introduced leguminous *Erythrina* trees or sometimes with trees with economic value. There are very few cocoa plantations without shade in Bahia. Other forms of land use including pasture, coffee and eucalyptus are developing on the margins of the traditional cocoa production region and eucalyptus in particular has already expanded 200 km north from where it was reported by Johns (1999).

Ants are an extremely important component of tropical biodiversity in both natural and agricultural systems. Ants comprise a large fraction of the animal biomass and are among the major predators in tropical agroforestry systems. The ecology, diversity, and functional role of ants as providers of natural biological control of a range of organisms, has been extensively studied in coffee and cocoa farms (Way and Khoo 1992; Majer 1993; Philpott and Armbrecht 2006). Implicit in much of this work is that tropical agroforests are important for conservation of tropical ants. Using both original data and information collected from the literature, a summary of work on ant diversity, ecology, and conservation is provided here with a special emphasis on ants of the cocoa plantations of the Atlantic region of Brazil. First, original work examining species richness and composition of different components of the ant community in a cocoa plantation in Bahia is presented. Next, using a separate set of original data from the area around Ilhéus, we compare the species composition of ants in cocoa plantations and other common habitats in the Atlantic region. A review of existing literature on ant community organization in cocoa plantations follows, as does detailed information about the ecology and natural history of important ant genera found in cocoa plantations (*Wasmannia*, *Thaumatomyrmex* and *Typhlomyrmex*). As ants may damage crops, but also play extremely important functional roles as predators, we include a review on the economic importance of ants in cocoa plantations. Finally, we discuss the importance of cocoa plantations for the conservation of ant diversity both generally and for particular threatened genera in the Brazilian Atlantic Forest, at both habitat and regional scales.

Methodology

Field data collection was conducted in several habitat types in the surroundings and in the municipality of Ilhéus in Bahia. Ilhéus is situated at 15°S on the coast of the Atlantic Ocean and the region is covered by secondary and pristine coastal Atlantic forest, ‘‘restinga’’ (the typical vegetation of the sea shore related to the Atlantic forest), cultivated lands (mainly shaded cocoa plantations and pastures), mangroves and urban areas. The average temperature in Ilhéus is between 20°C and 28°C with annual precipitation between 1,300 and 2,000 mm, with decreasing values as the distance to the coast increases.

An extremely exhaustive sampling of the ant community in a cocoa plantation in Bahia was carried out in 1992 to 1996. First, a 1 ha plot was delimited in a 20 year old cocoa grove shaded by the introduced legume *Erythrina fusca* Loureiro (Fabaceae) and then ants were collected in all strata with 27 different methods over three years (for a presentation of methods and an analysis of the ground dwelling fauna, see Delabie et al. 2000b). Hypogeous species were collected in cubes of soil, epigeous species with baits and pitfall traps, leaf litter species by Winkler and Berlese extraction and by inspection of fallen twigs and all other favorable microhabitats, and arboreal species by chemical knockdown and beating of vegetation. The methods used did not always allow determining the actual activity (nesting, foraging, accidental presence) of the ants collected but were useful for calculating their frequency of occurrence in the respective strata.

In another study in the same region in the period 1997–2002, the species richness of ants found in a cocoa plantation shaded by *Erythrina fusca* was compared with that of three areas of native forest of low, medium and high ant diversity. These three areas were chosen as representative of the ant richness in regional forest remnants, out of a set of 60 sampled forest areas of the same region (Delabie et al., unpublished data). Each forest and cocoa plantation was sampled with identical methodology and sampling effort. Each forest was sampled with a series of mini-Winkler traps (50 independent samples of 1 m^2 in each area, according to the methodology described in Delabie, 1999), aiming to show the typical variation in ant diversity among forest areas of the Atlantic rain forest of Bahia.

To examine whether species composition varies with habitat type, species lists were created for various habitat types using museum collections, and richness and relative abundance of ant species were compared using the Sorensen index (Southwood 1978). An inventory of all ants at the collection of the Myrmecology Laboratory of the Brazilian Cocoa Research Center (CEPEC/CEPLAC) in Ilhéus/Itabuna was made using the biological material received mostly during the past 15 years (the collection is referred to as ‘‘CPDC’’ in taxonomic literature). Analyses were limited to those ant species found within a 1,750 km^2 area around Ilhéus and belonging to the genera *Camponotus* Mayr (Formicinae, Camponotini), *Dolichoderus* Lund (Dolichoderinae, Dolichoderini), *Gnamptogenys* Roger (Ectatomminae, Ectatommini), *Pachycondyla* Smith (Ponerinae, Ponerini) and *Pseudomyrmex* Lund (Pseudomyrmecinae, Pseudomyrmecini). From its collection history, each specimen collected in Ilhéus and presently found in the CPDC collection, regardless of species, was independently categorized into habitat classes (forest, ‘‘restinga’’, cocoa, pasture, mangrove, urban) according to the environment where it was found. These genera were chosen because they are among the most species rich in the cocoa producing region and because of their distinct characteristics. Most (but not all) species of *Camponotus*, *Dolichoderus* and *Pseudomyrmex* are arboreal. *Dolichoderus* and *Camponotus* commonly tend sap-sucking Hemiptera (Delabie 2001), and *Pseudomyrmex* do occasionally. *Gnamptogenys* are ground-dwelling and some *Pachycondyla* (those formerly in the genus

Neoponera, for example) are arboreal while others of the same genus are epigaeic or even live below ground. Nutritional ecology information about all these ants can be found in Fowler et al. (1991). Lists of species belonging to these genera at Ilhéus are available in Delabie et al. (1998; 2006), Fraga et al. (1999) and Majer and Delabie (1999). In order to minimize the overestimation for one or the other habitat due to the disparity of the collection efforts, the contribution of each species per habitat was recalculated on a hypothetical basis of 100 occurrences for the whole habitat.

Comparisons were made of the relative abundances of two important ant genera in cocoa plantations and surrounding habitats. Complete descriptions and justification for using each genus are given below. First, a dataset on *Wasmannia auropunctata* was obtained from standardized Winkler collections in native forest, shaded cocoa plantations, and pastures. Ants were sampled in 11 plots per habitat where each plot was located in a different landscape fragment. In each plot, 50 1-m^2 leaf litter samples were taken, each at 50 m intervals. Samples were randomly distributed in 12.5 hectares of a single fragment (Delabie 1999). In each area, the number of *W. auropunctata* occurrences was recorded (*i.e.* one observation means that one or more workers were found in a single Winkler sample). Second, comparisons of the frequency of occurrence of *Thaumatomyrmex* sp.1 were made in several land uses in the surroundings of Ilhéus. The data were obtained from standardized mini-Winkler collections in 16 native forest areas, 16 shaded cocoa plantations, and 14 pastures. Samples and plots were distributed as for *W. auropuncata* studies, and comparisons of occurrence done in the same way.

Finally, a range of new observations on *Typhlomyrmex* diversity and ecology was made between 1993 and 2006 in primary and secondary forests in various regions of Brazil and French Guyana (S. Lacau, unpublished), as well as in shaded cocoa plantations in Bahia.

Results and discussion

Ant diversity in shaded cocoa plantations

A total of 192 species were collected in ant samples in the shaded cocoa plantation sampled in Bahia (Table 1). A first analysis of the data allowed partitioning the ant species richness between the strata (Fig. 1). Many species of ants were found foraging and even nesting in several strata. Species richness reached no plateau at the end of the sampling program even after combining all samples ($n = 1458$; Fig. 1). The total species richness of the ant community of the 1 ha plot was estimated to be around 230 species (Fig. 1). The diversity of hypogeous and epigeous-foraging ants was similar (rarefied species richness for 212 occurrences [Coleman method] = 54 ± 1 and 55 ± 3, Fisher's alpha = 23.4 and 24.0, Simpson index = 20.2 and 27.5, respectively) and was lower than the diversity of leaf litter and arboreal-foraging species, which were close to each other (Coleman = 70 ± 4 and 71 ± 4, Fisher's alpha = 39.3 and 35.9, Simpson index = 44.5 and 47.1, respectively; Fig.1). Fewer than half (86 out of 192) of the species collected were found only foraging in a single stratum that corresponded generally to their nesting site: 5 out of 54 species collected in the soil, 44 out of 126 species collected in the leaf litter, 12 out of 88 species collected at the ground surface, and 25 out of 107 species found foraging on the cocoa tree (Table 1). Fifty one species (26%) were collected from two strata and a lesser proportion in three (17%) or four (11%) strata. Ants collected from all strata were mostly arboreal-nesting dolichoderines (*Azteca* spp.), the Neotropical tramp *Wasmannia auropunctata*

Table 1 Frequency of occurrence (0–100%, $n = 54$ quadrats) of ant species found in the hypogeous, leaf-litter, epigeous and arboreal strata in one hectare of a 20 year old cocoa plantation shaded by *Erythrina fusca* on the research station of the Brazilian Cocoa Research Center (CEPEC/CEPLAC), Ilhéus/Itabuna, Bahia, Brazil. The data were collected in 1992–1996 using 27 sampling methods as detailed in the text

	Hypogeous	Litter	Epigeous	Arboreal
AMBLYOPONINAE				
Prionopelta antillana		35		2
CERAPACHYINAE				
Cerapachys splendens	4			
DOLICHODERINAE				
Azteca alfari		2	7	
Azteca chartifex spiriti	2	6	6	6
Azteca longiceps				2
Azteca paraensis bondari	2		15	7
Azteca sp.A	4	4	11	17
Azteca sp. nr.*fasciata*		2		
Dolichoderus attelaboides			6	37
Dolichoderus bidens				2
Dolichoderus decollatus			2	4
Dolichoderus diversus				7
Dolichoderus imitator		2		
Dolichoderus lutosus				11
Dolichoderus schulzi				2
Linepithema sp.nr.*humile*	2	6	44	20
Tapinoma melanocephalum		54	17	11
Tapinoma sp.A				7
Tapinoma sp.B		2		
ECITONINAE				
Eciton burchelli			20	
Eciton mexicanum			2	
Labidus coecus			2	
Labidus praedator	4		30	7
Neivamyrmex pilosus				2
ECTATOMMINAE				
Ectatomma brunneum		6	6	
Ectatomma permagnum			2	
Ectatomma tuberculatum			22	17
Gnamptogenys annulata			4	
Gnamptogenys haenschi				2
Gnamptogenys moelleri		11	11	19
Gnamptogenys sp. nr.*horni*		2		2
Gnamptogenys sp.		6		
Gnamptogenys striatula		4		
Typhlomyrmex pusillus	39	4		
Typhlomyrmex sp.A	2			2
Typhlomyrmex sp.B	2	2		

Table 1 continued

	Hypogeous	Litter	Epigeous	Arboreal
FORMICINAE				
Acropyga berwicki		2		
Acropyga sp. nr.*berwicki*	22	11	2	
Acropyga urichi	15	2		2
Brachymyrmex heeri	19	24	9	4
Brachymyrmex pictus	30	9	19	
Brachymyrmex sp.		4	2	
Camponotus crassus	2	13	17	2
Camponotus atriceps		6	2	19
Camponotus bidens				11
Camponotus blandus			4	24
Camponotus canescens		11		24
Camponotus chartifex				59
Camponotus cingulatus		35	9	30
Camponotus claviscapus		2		
Camponotus novograndensis		2		7
Camponotus renggeri				2
Camponotus sexguttatus		2	2	6
Camponotus sp.A				17
Camponotus sp.B				2
Camponotus trapezoideus				15
Camponotus vittatus				4
Paratrechina fulva		50	11	33
Paratrechina longicornis		20	22	6
Paratrechina sp.A	4	74	9	11
Paratrechina sp.B	6		19	13
Paratrechina sp.C		35	17	4
Paratrechina sp.D	7	31	20	9
MYRMICINAE				
Acanthognathus ocellatus		20		2
Acromyrmex subterraneus brunneus		19	41	9
Apterostigma sp.*pilosum complex*		4		
Cardiocondyla obscurior			2	2
Carebara panamensis	4	22		
Carebara urichi		2		
Cephalotes angustus				7
Cephalotes atratus			17	33
Cephalotes frigidus				4
Cephalotes maculatus				7
Cephalotes minutus			4	2
Cephalotes pallens				2
Cephalotes simillimus				2
Crematogaster acuta				7

Table 1 continued

	Hypogeous	Litter	Epigeous	Arboreal
Crematogaster curvispinosa				46
Crematogaster erecta		4	28	19
Crematogaster evallans		6	6	
Crematogaster limata	6	26	13	35
Crematogaster sp. nr.*curvispinosa*		6		
Crematogaster sp. nr.*limata*		2		
Crematogaster victima	4	6	9	7
Cyphomyrmex peltatus		4		
Cyphomyrmex rimosus		22	4	
Cyphomyrmex transversus		4		
Eurhopalothrix clypeata		2		
Hylomyrma sagax		2		
Lachnomyrmex plaumanni		4		
Leptothorax tristani		2	6	4
Megalomyrmex silvestrii				2
Monomorium floricola	11	28	9	6
Mycocepurus smithi	2	22	24	2
Octostruma balzani		11		
Octostruma jheringhi	4	11	4	2
Octostruma stenognatha		4		
Pheidole cataractae		2		
Pheidole cornutula		7	19	6
Pheidole fabricator		4	7	2
Pheidole fallax		4	4	4
Pheidole fimbriata	15	50	70	2
Pheidole megacephala	4	7	13	19
Pheidole mendicula		44		
Pheidole midas		28	24	9
Pheidole sp. nr.*tristis*				15
Pheidole sp.1		15		
Pheidole sp.3		2		
Pheidole sp.4		2		
Pheidole sp.A		2		2
Pheidole sp.B			2	
Pheidole sp.C			2	6
Pheidole sp.D	2	2		
Pheidole sp.E			4	4
Pheidole sp.F	2	4	7	2
Pheidole sp.G	2		2	6
Pheidole sp.H			2	
Pheidole sp.I	2	61	19	15
Pheidole sp.J			13	9
Pheidole sp.K	4	2		

Table 1 continued

	Hypogeous	Litter	Epigeous	Arboreal
Pheidole sp.L	13			4
Pheidole sp.M		2		
Pheidole sp.N		2		2
Pheidole tachigaliae	2	11	7	39
Pheidole transversostriata	2		41	31
Procryptocerus marginatus				2
Pyramica alberti		4		2
Pyramica denticulata		4		
Pyramica eggersi		2		2
Pyramica rugithorax		4		
Pyramica schulzi	2	6		2
Pyramica subedentata	2	15		
Rogeria besucheti		2		
Rogeria foreli		2		
Rogeria micromma	2	9		
Rogeria scobinata		4		
Rogeria subarmata		6	2	11
Sericomyrmex bondari	7	33	56	6
Sericomyrmex sp.			2	
Solenopsis (Diplorhoptrum) sp.A		24		
Solenopsis (Diplorhoptrum) sp.B			2	
Solenopsis (Diplorhoptrum) sp.C	43	100	83	30
Solenopsis (Diplorhoptrum) sp.D		35	54	31
Solenopsis geminata		4	11	
Solenopsis pollux		24	4	2
Solenopsis saevissima		4		
Solenopsis sp.A	2		2	
Solenopsis virulens			2	
Stegomyrmex vizottoi		2		
Strumigenys carinithorax		2		
Strumigenys dolichognatha		19		
Strumigenys elongata	2	52		
Strumigenys louisianae		19		2
Strumigenys perparva		2		
Strumigenys smithi		2		
Trachymyrmex cornetzi		2		
Trachymyrmex relictus	2			
Wasmannia auropunctata	24	96	93	76
Wasmannia rochai	2		6	7
PONERINAE				
Anochetus mayri	2			2
Anochetus simoni		2		
Hypoponera foreli		4		

Table 1 continued

	Hypogeous	Litter	Epigeous	Arboreal
Hypoponera sp.A		4		
Hypoponera sp.B	39	2		
Hypoponera trigona	4	63		
Leptogenys arcuata	4	11		2
Leptogenys bohlsi		2		
Leptogenys crudelis	2			
Odontomachus haematodus	2	76	76	37
Odontomachus meinerti		30	7	
Pachycondyla apicalis		6	13	2
Pachycondyla arhuaca	2	7		2
Pachycondyla bucki		2		
Pachycondyla carinulata			2	7
Pachycondyla constricta		20	9	
Pachycondyla crenata		2		15
Pachycondyla harpax		31	56	7
Pachycondyla holmgreni	7			
Pachycondyla sp. nr.*venusta*	2			
Pachycondyla striata		2	2	
Pachycondyla striatinodis		2	4	
Pachycondyla unidentata		2		48
Pachycondyla villosa	2	11	7	46
Thaumatomyrmex sp.1		13		
Thaumatomyrmex contumax		2		2
PSEUDOMYRMECINAE				
Pseudomyrmex elongatus			2	
Pseudomyrmex gracilis	2		4	22
Pseudomyrmex oculatus			4	
Pseudomyrmex simplex		2	2	
Pseudomyrmex sp.A *gp. pallidus*		2		
Pseudomyrmex sp.B*gp. pallidus*			4	4
Pseudomyrmex tenuis			6	11

(Myrmicinae; Blepharidattini), and some arboreal-nesting *Crematogaster* (Myrmicinae; Crematogastrini).

Applying a similarity coefficient to these data shows a dichotomy between the ground and the arboreal-dwelling fauna (Fig. 2). The hierarchy of similarities confirms that some soil-nesting species forage in the leaf litter and some litter ants forage in the soil (i.e. *Sericomyrmex* spp.; Myrmicinae; Attini). An even greater number of arboreal-nesting species were found foraging at the ground surface, explaining the similarity between the arboreal and epigeous fauna (Fig. 2). The overall high faunal similarity estimated by the Chao-Sorensen incidence-based index reflects the fact that the majority of species are found in two or more strata.

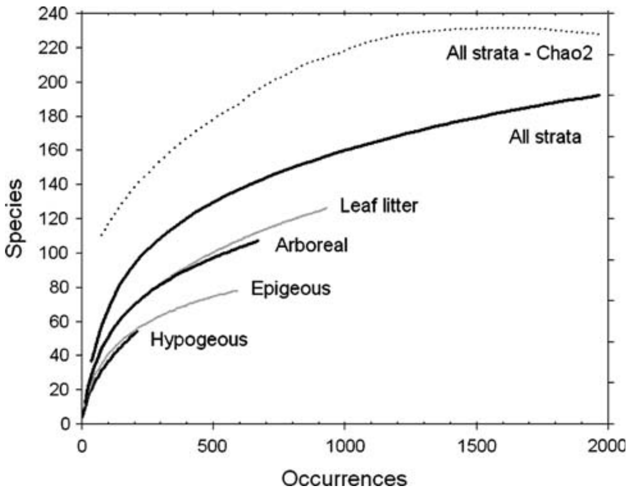


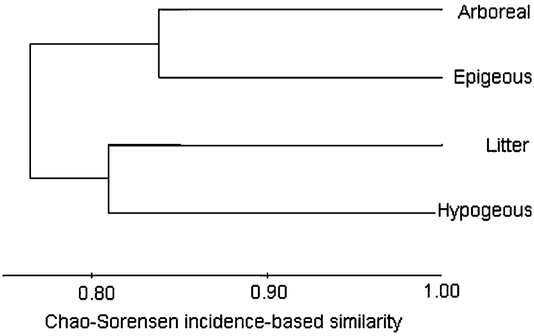
Fig. 1 Partitioning of ant species richness between the hypogeous, epigeous, leaf litter and arboreal strata of a 1 ha sampling plot in a cocoa plantation shaded by *Erythrina fusca* near Ilhéus, Bahia, Brazil (see Table 1). Accumulation curves were obtained by rarefaction (Coleman method). The total species richness for all strata combined was estimated with Chao2 (Colwell 2000)

The ant species richness in the cocoa plantation shaded by only *Erythrina fusca* corresponded to that of a native forest of low diversity (Fig. 3). It is reasonable to expect that the ant diversity of a cocoa grove shaded by native trees (cabruca) in the same region would be at least equal to that of native forest. However, it is clear that some ant species are negatively affected by the opening of the forest vegetation to plant cocoa trees, while others, which are more adapted to clearings or open habitats, benefit. This is highlighted below for a few ant genera.

Diversity and composition of selected ant genera in native and human-managed habitats near Ilhéus, Bahia

Within the 10,000 km^2 surrounding Ilhéus, 442 ant species have been reported, most of them known from native environments and shaded cocoa plantations (Delabie et al. 1999).

Fig. 2 Similarity between the hypogeous, epigeous, leaf litter and arboreal-foraging ant fauna of a 1 ha sampling plot in a cocoa plantation shaded by *Erythrina fusca* near Ilhéus, Bahia, Brazil (see Table 1). Similarities were calculated with the Chao-Sorensen incidence-based similarity index appropriate for incompletely inventoried assemblages



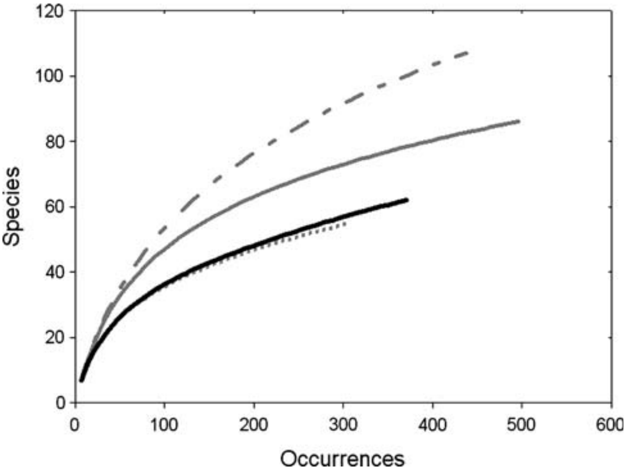


Fig. 3 Comparison of the ant species richness (Coleman method) between a cocoa plantation shaded by *Erythrina fusca* (*black line*) and native forests of Bahia, with low (Canavieiras—area 2 A60, *dotted grey line*), medium (Uruçuca—Serra Grande A15, *continuous grey line*) and high diversity (Canavieiras—Oiticica A55, *dashed grey line*). Species were extracted from leaf litter with mini-Winkler traps (50 1 m^2 quadrats collected in each forest plot and 54 quadrats in the cocoa plantation)

A similarity analysis among the several habitat types (including primary and secondary forests, restinga, cocoa plantations, pastures, mangroves, and urban areas) showed that the regional ant fauna is organized in two clusters: the first cluster consists of the native environments and the shaded cocoa plantations, and the second cluster consists of agricultural land uses other than cocoa groves and urban areas (Fig. 4). Most of the ants that contribute to the first cluster (natural habitats and shaded cocoa plantations) are currently assumed to be native to the Atlantic rain forest, while a large proportion of those of the second cluster (the more intensively managed areas) are exotic (Delabie 1993) or possibly originate from other drier Neotropical biomes, such as cerrado, caatinga or pampa (Delabie, unpublished data).

Among the genera *Dolichoderus*, *Gnamptogenys* and *Pachycondyla*, species found in shaded cocoa plantations were very similar to those found in native habitats (Fig. 4). By contrast, *Camponotus* species in cocoa were more similar to those found in human-managed habitats or in mangroves. Mangroves are an environment where the terrestrial fauna is strongly dependent on the surrounding vegetation: if pristine, the ants colonizing the mangrove trees will belong to the original native fauna; if degraded, most of these ants will be typical of human-managed (or disturbed) habitats (Delabie et al., 2006). As mangroves are well inserted in the urban area of Ilhéus, it is not surprising that a large part of the species of *Camponotus* and *Dolichoderus* are common with these strongly human-managed habitats (Fig. 4).

Ant community organization in shaded cocoa plantations

Ant community organization in cocoa plantations has been the subject of many publications because of the ecological dominance of ants in this agroecosystem and the relative ease with which ants can be studied in cocoa plantations compared to native ecosystems.

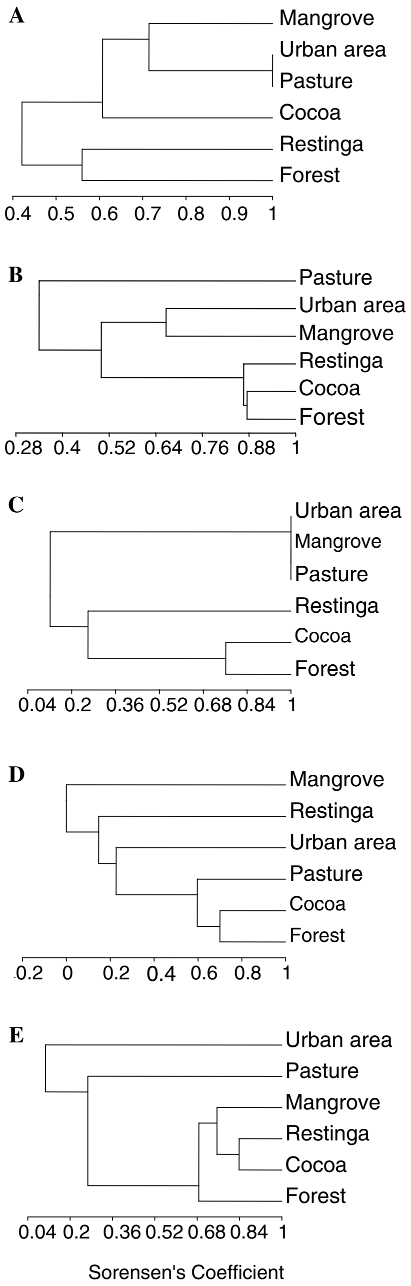


Fig. 4 Similarity between ant assemblages of five genera occurring in various habitats in the region of Ilhéus, Bahia, Brazil, CPDC collection data. A: *Camponotus* (*n* = 32 species); B: *Dolichoderus* (*n* = 9); C: *Gnamptogenys* (*n* = 14); D: *Pachycondyla* (*n* = 27) and E: *Pseudomyrmex* (*n* = 22). ''Unweighted Pair Group Method with Arithmatic Mean'' [UPGMA] algorithm.

Many researchers have examined characteristics of the ant fauna of cocoa plantations in several producer countries including Brazil, Cameroon, Ghana, Papua New Guinea, and Trinidad. Much of the research in cocoa plantations examines the community structure of arboreal-nesting species, and a few recent studies have examined the completely different organization of ground-nesting colonies (Belshaw and Bolton 1993; Delabie et al. 2000a; Fisher et al. 2000). The study of the leaf litter ant communities has been greatly facilitated over the last years due to the adaptation of the Winkler collector, initially developed for the collection of soil fungi and beetles, to a smaller version, the mini-Winkler (Fisher 1998). Mini-Winkler use has become widespread as the traps are recognized as extremely efficient in capturing ground and litter-dwelling ants (Bestelmeyer et al. 2000; Delabie et al. 2000b; Parr and Chown 2001; Longino et al. 2002; Underwood and Fisher 2006).

Studies of the structure of arboreal ant communities in cacao plantations have formed the basis for much work examining the community assembly of ants. Cocoa plantations of Africa, Oceania, Mesoamerica and South America have provided perfect experimental fields for myrmecologists. In particular, many experiments have been carried out in the experimental plots of shaded cocoa plantations of the Brazilian Cocoa Research Center (CEPEC/CEPLAC) in Ilhéus/Itabuna, Bahia, beginning in the 1970's (Leston 1978; Winder 1978) and continuing to the present day. Only recently have these studies been extended to other forms of agriculture and to natural environments. The general pattern discovered is that a few competitively interacting ant species become numerically dominant in a given site or habitat, therein generating a horizontal and/or vertical stratification or mosaic formed by their non-overlapping territories (see the reviews of Majer 1993; Dejean et al. 2003; and the criticisms by Sanders et al. 2007). Furthermore, each dominant species often tolerates a series of non-dominant species, generating positive associations among dominants and non-dominants. Such mosaic patterns have been found in cocoa plantations across a wide range of producing countries. Yet, there are some doubts about whether mosaic patterns occur in the rainforest canopy because of changes in ant composition (complex community interactions), habitat complexity or resource availability, all of which may have strong effects on insect interactions. The mechanisms of species co-occurrence and maintenance of ant territories and mosaic patterns, which are much more discreet in the ground layers (Fowler and Delabie 1995; Delabie et al. 2000a), appear to be particularly complex on vegetation and may include competition, resource partitioning, or stochastic events (Majer et al. 1994; Sanders et al. 2007). Probably much of the variation in mechanisms results from the fact that each species may possess its own strategy for maintaining its status in the mosaic (see discussion in Ribas and Schoereder 2002). For example *Wasmannia auropunctata* Roger (Myrmicinae; Blepharidattini) can establish itself in extensive areas of cocoa plantations, occupying continuous areas of leaf litter (its natural habitat) and extending up to the tree canopy, where it acquires characteristics of a dominant arboreal ant (Majer and Delabie 1993; Majer et al. 1994; Souza et al. 1998). Its ecological and reproductive characteristics make *Wasmannia*, more than all other ant species that occur in cocoa plantations, the most successful competitor able to quickly fill an empty niche in the agroecosystem. Another interesting case is that of *Azteca chartifex spiriti* Forel (Dolichoderinae; Dolichoderini), which is extremely territorial and exhibits original defensive behaviors, inhibiting colonization by other ant species and competing for territory and tree resources by means of allomones (Medeiros and Delabie 1991). In contrast to canopy species in cocoa plantations, leaf litter ant species, although apparently sometimes positively and negatively associated, do not seem territorial (Delabie et al. 2000a).

The tramp *Wasmannia auropunctata* in Bahian shaded cocoa plantations

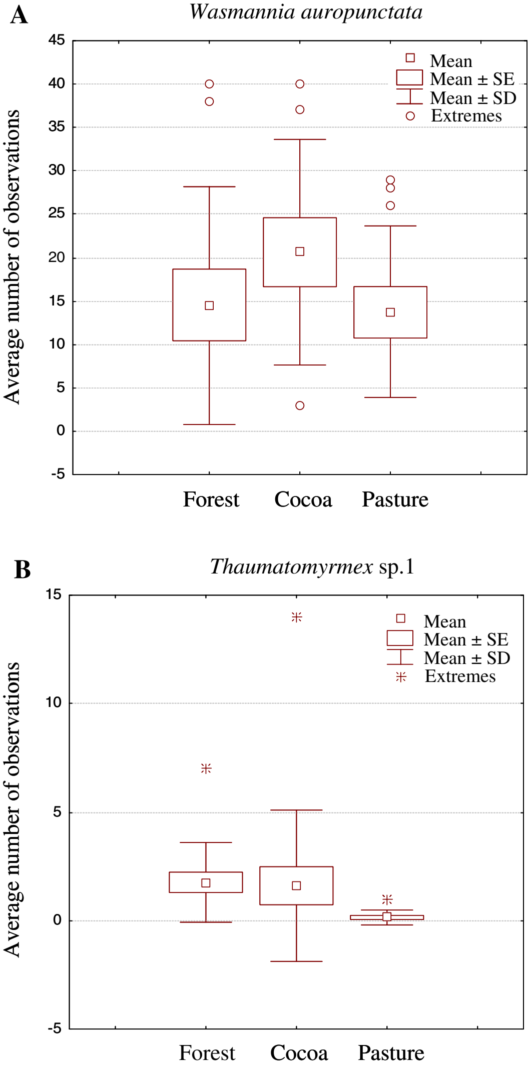
The Neotropical Myrmicinae *Wasmannia auropunctata* Roger is common in Bahia, where it can occur in any environment, including forests, urban areas, farms and beaches. This competitive ant is invasive in many tropical and subtropical countries (Le Breton et al. 2004; Errard et al. 2005), especially on islands where it has a strong negative effect on native fauna (Passera and Aron 2006). It can influence the mesofauna community structure discreetly in habitats in which it is native (Majer and Delabie 1993; Souza et al. 1998) and has stronger influences in areas where it has been introduced (Le Breton et al. 2003; Passera and Aron 2006). In the cocoa producing region of Bahia, the nests of this ant are found in rotten pieces of wood and other vegetation materials in the litter. In natural habitat, it is seldom found on arboreal vegetation (i.e., bark cavities, hanging soil associated with epiphytes) but in shaded cocoa plantations, the ant climbs on the cocoa trees where it forms a mutualistic association with the mealybug *Planococcus citri* Risso (Hemiptera; Auchenorrhyncha; Pseudococcidae; Delabie et al. 1994; Delabie 2001). The mealybug is apparently not associated with the ant in natural habitats (if associated, it must be very discreet) when the ant only lives in the litter, but the mealybug appears and its population strongly increases with the growth of the *W. auropunctata* population (information about the dynamics of the mealybug colonies on cocoa trees is given in Delabie et al. 1994). The effect of *W. auropunctata* on mealybug populations is more obvious when the mosaic of dominant ant species has been disturbed by abusive use of pesticides: *W. auropunctata* colonies frequently divide such that ants recolonize niches left empty by other ants regardless of the effect of pesticide on its own population (Delabie 1990).

A comparison between the number of occurrences of *W. auropuncata* in leaf litter in pasture, cocoa fields and forest areas showed few statistical differences among habitats (Fig. 5) [forest vs. cocoa plantation: $t(20) = 0.07$, $p = 0.30$; cocoa plantation vs. pasture: $t(20) = 1.41$, $p = 0.18$; forest vs. pasture: $t(20) = 0.16$, $p = 0.87$]. Although a strong difference between its occurrences in human-managed and in natural habitat was expected, these results show that this ant is distributed all over the region more or less independently of the land use. Nevertheless, *W. auropunctata* is less frequently encountered in natural habitat, where it forms smaller populations normally limited to the litter layers (Delabie, pers. obs.), than in disturbed habitat where it also inhabits plants and tends Hemiptera. This situation corresponds to what should be expected in many wet forest areas of the Neotropical region although the ant impact is drastically stronger in remote non-native areas (Jourdan 2003). The recently demonstrated peculiar reproductive system of this ant (Fournier et al. 2005) suggests that genetic mechanisms underlie the differentiated behavior and ecological aggressiveness in native and non-native areas of distribution.

The cryptic ant genus *Thaumatomyrmex* at Bahia: forest vs. shaded cocoa plantation and pasture

The ants of the genus *Thaumatomyrmex* Mayr (Ponerinae, Thaumatomyrmecini) have a noteworthy cephalic morphology in the family Formicidae. They have long mandibles forming fine sickles with three or four pin-shaped teeth (Kempf 1975). This architecture of their mouthparts represents a unique adaptation in the animal world for their specialized feeding habit: *Thaumatomyrmex* is among the rare arthropods known to predate Penicillata (Myriapoda; Diplopoda; Brandão et al. 1991) and able to circumvent their mechanic defenses. The genus *Thaumatomyrmex* includes eleven species (Baroni Urbani and De

Fig. 5 Occurrence of *Wasmannia auropunctata* (n = 11 plots per habitat) and *Thaumatomyrmex* sp.1 (n = 14–16 plots per habitat) in a series of 50 1 m^2 quadrats of leaf litter collected with a Winkler apparatus in the three ecosystems (native forest, shaded cocoa plantation, and pasture)



Andrade 2003; Jahyny et al. unpublished) or more, not taking into account Longino's (1988) revision of the *ferox* group. At least four of them occur in Brazil. These ants have been seldom collected because of their cryptic (*sensu* Andersen 1991) habits and their very small colonies; for that reason, their biology is little known. For most species, only the worker form has been described and no information is published for the gynes. Several hypotheses tentatively explain the small colony size and the reproduction system of these ants—they are assumed to be produced exclusively by fertilized egg-laying workers called ''gamergates'' (*sensu* Peeters and Crewe 1984). Except the cited taxonomic and specialized preying habit studies, only one study has been published on the genus' ecology, analyzing its frequency in shaded cocoa plantations and forest remnants of the southeastern Atlantic Forest of Bahia (Delabie et al. 2000c). The recent practice of studying the leaf litter ant communities with the Winkler extractor showed that the apparent rarity of these ants was in fact a sampling artifact at least for one species.

Three *Thaumatomyrmex* species are currently known in Bahia. *Thaumatomyrmex* sp.1 (formerly named *Thaumatomyrmex atrox* Weber in Brandão et al. (1991) and Delabie et al. (2000c)) is by far the most frequent species of the genus in the various ecosystems and agroecosystems of Bahia, while the larger *Thaumatomyrmex contumax* Kempf and *Thaumatomyrmex mutilatus* Mayr are seldom collected. These ants are generally found in the litter layer where their prey is abundant. At the local scale, two sympatric species occur: a small one (*Thaumatomyrmex* sp.1) and a second, much larger one. For example, in shaded cocoa plantations and Atlantic Forest remnants from Itabuna to Itororó, *Thaumatomyrmex* sp.1 and *T. contumax* are always found together (Brandão et al. 1991; Delabie et al. 2000c). Near the coast at Ilhéus or in the west transitional region (Itambé region), *T. mutilatus* coexists with *Thaumatomyrmex* sp.1 (Jahyny et al., unpublished).

Thaumatomyrmex sp.1 occurred significantly less in pasture compared to forest and shaded cocoa plantations where its occurrence was statistically similar (Fig. 5) [forest vs. cocoa plantation: $t(30) = 0.13$, $p = 0.90$; cocoa plantation vs. pasture: $t(28) = 1.58$, $p = 0.12$; forest vs. pasture: $t(28) = 3.20$, $p < 0.05$]. These results show that shaded cocoa plantations may represent a favorable environment even for highly specialized species since they can certainly find their prey in abundance in the plantations. The frequent occurrence of *Thaumatomyrmex* sp.1 can be considered as evidence of the efficiency of native or managed ecological corridors, at least at the soil mesofauna scale.

The rare *Typhlomyrmex* ants in Bahian shaded cocoa plantations

Typhlomyrmex Mayr, 1862 (Ectatomminae, Typhlomyrmecini) is a small genus of Neotropical ants, currently under revision (S. Lacau, unpublished). It is seldom represented in museum collections. The genus includes seven species for which the workers have a robust but elongated morphology, with a pale yellow to brown reddish color and an overall length from 1.5 to 5 mm (Lacau et al. 2004; unpublished). A few species have a wide distribution all over the Neotropics, while others are endemic to very small geographical areas. The biology of the genus remains very poorly known; however, the few available data show a great heterogeneity in the ecology of the species (Lacau et al. 2004). All species are cryptic. Some are general predators, while others practice specialized predation on several arthropods.

Observations of *Typhlomyrmex* diversity and ecology in primary and secondary forests revealed that the taxonomic knowledge of this small genus is not representative at all of its diversity. Furthermore, although these ants were previously considered rare, it is now believed they are in fact common in some microhabitats (rotten wood, tree rhizosphere) of the cocoa plantations (Lacau et al., unpublished). For example, just in the cocoa fields of the Cocoa Research Center at Ilhéus, Bahia, four species of *Typhlomyrmex* can be found, two of them undescribed.

The less rare species, *Typhlomyrmex rogenhoferi* Mayr, presents a singular autoecology: in forest, as well as in the shaded cocoa plantations, this epigaeic species nests exclusively in the rotten trunks of fallen trees or in large branches on the ground (Lacau et al. 2001; 2004). Adult colonies include two to three thousand individuals and most colonies are established inside the hardest parts of the trunk. *Typhlomyrmex rogenhoferi* can be relatively abundant in pristine or secondary forest areas of Bahia and other regions but is much rarer in shaded cocoa plantations. A logical explanation is that there is a low availability of fallen rotten trunks compared with the forests. The vegetation is obviously much denser and diversified in forest than in shaded cocoa plantations and only the dynamics of natural regeneration of forest allow the maintenance of this kind of micro-habitat. It was also observed that this ant is more abundant in cabruca groves than in plantations where the original vegetation was completely eliminated before planting. Cabruca ensures a constant renewal of the fallen wood according to the aging of the shade trees, whereas where vegetation is constantly removed, there is no dead wood on the ground leading to a lack of nesting opportunities for this ant. A major concern about this component of ant diversity in the traditional cabruca plantations is that forest trees are increasingly being substituted by pioneer vegetation or early secondary species (Rolim and Chiarello 2004) that possibly will not provide habitat for this ant genus over the long term.

Another characteristic of *T. rogenhoferi* is that it is associated with larvae of several species of lampyrid beetles. These live inside ant nests, directly in contact with the ant larvae, constituting the framework of a narrow biotic association that is still not well understood (Lacau et al. 2001; Lacau, 2005). Lampyrid diversity is larger in forest than in the cocoa fields (Lacau, unpublished), but their overall abundance has a similar range in forest and cocoa fields.

It is noteworthy that the endemic *Typhlomyrmex meire* Lacau, Villemant and Delabie was recently described from the cocoa region of Ilhéus. This hypogeous species is locally found in the cocoa plantations, being even relatively frequent in cabruca, but was collected only once in a forest fragment. This interesting species always nests a few centimetres away from colonies of *Acropyga berwicki*, another dominant soil dwelling ant in the cocoa plantation, on which it is a specialized predator (Lacau et al. 2003). Considering the high density of *A. berwicki* nests in cocoa plantations (Delabie et al. 1991), this is one possible explanation for the high frequency of *T. meire*. Cocoa plantations therefore provide valuable habitat to maintain the diversity of certain hypogeous ants and their trophic interactions.

Economic importance of ants in Bahian shaded cocoa plantations

Several ant species are economically important in the shaded cocoa plantations of Bahia either because they act as biological control agents of cocoa pests or because they damage the cocoa crop (Delabie 1990). Of those groups considered pests to cocoa are the leaf-cutter ants and the fungus garden ants, each problematic for distinct reasons. Several species of leaf-cutting ants (Myrmicinae; Attini) such as *Atta cephalotes* Latreille, *Atta sexdens* Linnaeus and *Atta laevigata* Smith (Delabie et al. 1997), as well as *Acromyrmex balzani* Emery, *Acromyrmex rugosus* Smith and *Acromyrmex brunneus subterraneus* Forel (Delabie 1990) occur in cocoa plantations. All of these ant species are considered pests because they cut cocoa leaves, bark and small pods, especially on young plants (Delabie 1990; Delabie et al. 1993). Nevertheless, their impact on Bahian cocoa plantations is minimal, and in a certain manner, even beneficial, since these ants certainly contribute to the nutrient recycling in the cocoa farms, as well as in forests (Moutinho et al. 2003). They reportedly also attack shade trees in cocoa plantations but such damage is normally limited to a small number of plants. It can be inferred that, because leaf-cutters have a low diversity of plants from which to choose in cocoa plantations, they frequently do predate more on cocoa tree resources.

Azteca paraensis bondari Borgmeier (Dolichoderinae; Dolichoderini) is common both in cocoa groves and in natural forests of Bahia. This arboreal ant creates polydomous (multiple-nest) colonies that form ‘‘ant-gardens’’ with the epiphytic Gesneriaceae *Codonanthe uleana* Fritsch. In this mutualistic association—the only one of this kind recorded in the region—the ants disperse the epiphyte seeds to appropriate nest sites such that the epiphytes grow and flourish, thereby creating the ant nest structure through the development of their roots. This ant has long been considered the main pest of cocoa plantations in Bahia, due to strong physical damage inflicted to the trees by the ants as they rasp the plant buds in the upper levels of the trees to extract a gum used as a nest cement (Delabie 1990). This ant was extremely common in the cocoa region until the middle of the 20th century when intensive eradication campaigns were carried out regionally through mechanical elimination and insecticide application (Silva 1955; Delabie 1990). However, the species is becoming more common in the region as a result of the recent crisis of the regional economy, which caused many farmers to abandon their active control of this species.

Ants of the genus *Acropyga* (Formicinae; Plagiolepidini) live strictly belowground. They complete almost their entire life cycle inside their nests which consist of a series of galleries constructed along the superficial roots of several species of cultivated or native trees of the region (Delabie et al. 1991). The most commonly encountered species in Bahia is *Acropyga berwicki* Wheeler. *Acropyga* spp. tend minute mealybugs of the genus *Neochavesia* (Hemiptera; Auchenorrhyncha; Pseudococcidae) in their nest galleries in a mutualistic association (Delabie 2001; Johnson et al. 2001). During the nuptial flights, mated ant queens in search of new nest sites carry newly mated mealybug females that start the underground hemipteran colonies (Johnson et al. 2001). This kind of behavior exists convergently between a few other ant species and mealybugs (Delabie 2001). *Acropyga berwicki* is very abundant in shaded cocoa plantations and research on its biology was motivated by still unconfirmed reports from the first half of the 20th century that another species of *Acropyga* spreads coffee disease elsewhere in Brazil (Delabie 1990).

Azteca, *Acropyga* and many arboreous species in the genera *Camponotus*, *Dolichoderus*, *Wasmannia* and others (Delabie 2001) tend several species of Hemiptera (Auchenorrhyncha and Sternorrhyncha) on the cocoa pods or peduncles and young leaves. In some cases, this behavior can cause strong economic damage, although in Brazilian cocoa plantations this damage usually affects relatively small areas. This is not the case in cocoa producing countries on other continents, where the tending by ants of capsids (Miridae) or the Hemiptera that transmit the Swollen-Shoot-Virus cause producers enormous losses. Nevertheless, associations between ants and Hemiptera do not always have negative economic impacts. They may even benefit the host trees if the presence of the Hemiptera increases the ant activity and permanence on the trees, and if the ants act as predators against other phytophages (Delabie 2001; Philpott and Armbrecht 2006).

In fact, two ant species have a high potential for the biological control of cocoa pests in Bahia, thereby exerting a positive influence on cocoa production. *Azteca chartifex spiriti* Forel (Dolichoderinae; Dolichoderini) and *Ectatomma tuberculatum* Olivier (Ectatomminae; Ectatommini) can protect the cocoa plants from thrips *Selenothrips rubrocinctus* (Giard) (Thysanoptera; Thripidae) and mirids (Hemiptera) [*A. chartifex spiriti*], while the principal prey of *E. tuberculatum* are chrysomelid beetles, leaf-cutter ants, and caterpillars (Delabie 1990; Majer and Delabie 1993). It is to be noted, however, that the former species also facilitates the dissemination of the economically important black pod disease (*Phytophthora* spp.; Fungi, Oomycota, Pythiaceae; Medeiros et al. 1999; Delabie, unpublished), so the presence of this ant may involve some sort of trade-off from a production standpoint. Farmers in Bahia have promoted this species of *Azteca* in their plantations for its biological control activity since the beginning of the 20th century, in lieu of the mechanical and chemical control recommendations made by regional extension services over half a century, which have now been abandoned (Delabie 1990; Medeiros et al. 1999).

The positive influences of these and other ant species greatly benefit cocoa production. It is a fact that the Brazilian cocoa plantations are generally only little affected by insect pests. Contrary to the severe effects of diseases on the cocoa trees (mainly the witches' broom *Crinipellis perniciosa*), insect pest problems are at most local and limited. There are no recent reports of severely damaging pests of the cocoa tree or any special entomological problems in Bahia, and pesticide use continues to be limited. As an example, during the most recent economic crisis of cocoa production in Bahia, producers almost completely abandoned insecticide use but continued using fungicides (Ruf et al. 1994). The scarcity of insect pests is probably in part due to the predatory function exercised by many ant species on other organisms that are potentially damaging to cocoa production. Among the main groups of physical ecosystem engineers (Gutiérrez and Jones 2006), ants are certainly not the most diverse animal group in the tropical landscape, but they are the most constant and individually abundant and have the greatest impact on the habitat structure and the other organisms that live there. The ant abundance and diversity in shaded cocoa plantations of Bahia helps maintain the quality of the final product, usually without pesticide use, and is for the producer testimony to the equilibrium and health of this type of agriculture.

Ant conservation problems in a landscape composed of a mosaic of native habitats, cocoa plantations and agriculture

As shown, the shaded cocoa plantations, and especially the cabruca, contribute to maintaining a high diversity of ants in the cocoa-producing region of Bahia. This is especially important for the conservation of numerous species that need large territories to survive. A classic case are the army-ants of the genus *Eciton* (Ecitoninae) which need very large areas to forage, since they are very active predators, have nomadic habits and form very large populations with strong necessity for a constant supply of small prey items (mostly invertebrates) (Hölldobler and Wilson 1990). The fragmentation of the native forest, even as a rural landscape that forms a mosaic of cocoa plantations, forest remnants, pastures and other crops, is not particularly favorable to the maintenance of long-term viable populations of this type of ants (Freitas et al. 2006), chiefly for two reasons. First, agricultural areas do not support the large biomass of epigaeic invertebrates in the upper layers of the soil that could feed these ant colonies all year long, and second, fragmentation generates barriers (open places) that these ants cannot pass. In Panamanian coffee plantations, Roberts et al. (2000a, b) found that army ants only occur in shaded coffee plantations and forests, but not in sun coffee. At Bahia, cabrucas and the other types of cocoa plantations are certainly the only form of agriculture that can be used by these ants as ecological corridors, but only if they are adjacent to forested areas, or if individual blocks of plantations are large enough to harbor populations of these ants, consisting of several colonies. Of the three species of *Eciton* [*E. burchellii* (Westwood),*E. mexicanum* Roger and *E. vagans* (Olivier)] living in the cocoa producing region of Bahia, some may become endangered over the long term. Although these ants are not as common in Bahia as they are in the Amazon Basin where the forest is still largely continuous, they are still regularly observed. It is not known if other army-ants of the more diverse genus *Neivamyrmex* also occur frequently in the cocoa producing region, although there is no species in that genus with populations as large as those of *Eciton*. With eleven reported species, the Ilhéus region is exceptionally rich in *Neivamyrmex* (Delabie et al. 1998, Nascimento, in prep.).

Unfortunately, no data about *Neivamyrmex* biology are available as most of these ants have a cryptic nomadic life in soil galleries. Regardless, there is little doubt about the importance of army-ants on the regulation of populations of most of the soil surface invertebrates (Franks 1989) and their interactions with other animals, such as birds (Willis and Oniki 1978; Roberts et al. 2000b).

Other ants living in shaded cocoa plantations offer also specific conservation problems. The Ponerinae *Simopelta minima* Brandão, described from two series of samples collected in 1986–1987 on one experimental field of CEPEC/CEPLAC in Ilhéus, was recently inserted in the Brazilian official list of (presumably) extinct species, since its habitat, an old cabruca with no phytosanitary application for decades (located in a zone of regularly managed cocoa plantations), was irreversibly logged. The endangered giant ant *Dinoponera lucida* Emery (Ponerinae), also reported on the Brazilian red list, has been found on rare occasions in cabrucas in Bahia in the northern part of its natural geographic range (Campiolo et al., in prep.). However, these occurrences seem to depend on connectivity of the sampled cocoa plantations with areas of native habitat. This ant species, like the whole genus, has no gynes and the reproductive function is assumed exclusively by mated workers or ‘‘gamergates’’ (Peeters and Crew 1984). Gene flow depends thus only on males, which are the only winged individuals in the nest and apparently unable to fly in open habitats. New colony foundations occurs exclusively through fission of the mother colony in their immediate neighborhood. The fragmentation of the forest appears then unfavorable to the maintenance of viable populations of *D. lucida* for similar reasons to those discussed for the species of *Eciton*. Perhaps by leaving more cabruca habitat, these forest fragments could provide a suitable habitat at least for male dispersal.

Contributions of shaded cocoa plantations in the maintenance of regional diversity

The disruption of original connectivity in any landscape due to fragmentation has numerous implications for biological diversity, although it is obvious that each species has a particular response to habitat fragmentation (Wiens 1996). One implication is that gene flow can be limited due to the difficulty or inability of individuals to recolonize areas of other populations. Fragmentation thus contributes to the erosion of the genetic diversity of populations by increasing inbreeding, promoting local extinctions and possibly compromising the long-term viability of some species (Coyne et al. 2004). For most ants, shaded cocoa plantations appear adequate for species maintenance. The forest-like structure of this agroecosystem (even if extremely simplified as in plantations shaded by the exotic *Erythrina fusca*) offers a range of niches for most species, for several reasons. First, in the case of cabruca plantations, there is traditionally only limited use of fire to clear the understory of the native forest, so most of the original soil fauna where most of the ant diversity is represented (cryptic species living underground and soil-dwelling species) is preserved. This was the case when the use of native forest to install cabrucas was permitted. Today the Atlantic forest biome is protected by law. Second, the diversity of trees maintained in the plantation favors the diversity of Hemiptera (Auchenorrhyncha and Sternorrhyncha) as well as many other phytophageous insects, thereby guaranteeing the food supply for arboreous ants which mutualistically depend on the honeydew produced by many of these organisms (Delabie 2001). Third, the forest or introduced trees used to shade the plantations retain diverse and abundant populations of epiphytes, (often with their own dependent fauna) that form hanging soil layers where many arboreal and soil ant species live. Fourth, contrary to most other crops, not all of the vegetation strata of a cocoa plantation are simultaneously affected by pesticide application so that at least some of the insect diversity will survive even under pesticide abuse. For all these reasons, the fragmentation of the Atlantic forest of Bahia, if inserted in a matrix of cabrucas or other cocoa plantations with a forest-like structure, appears to have a relatively small effect on the native ant diversity. The high heterogeneity of the ant communities found in cabruca areas, not detailed here, is poorly understood and requires further research. The contribution of shaded cocoa plantations to the conservation of ant communities depends on the landscape characteristics (such as size of forest remnants and agroforestry plots and landscape connectivity) as well as on the range of climatic, pedological or other ecological factors that make the Bahian cocoa producing region unique.

Conclusions

The patterns of ant diversity in cocoa landscapes may reflect to a certain degree the patterns of many other organisms (Freitas et al. 2006), including organisms that are not directly dependent on ants but are in some way affected by the surrounding ant activities. Many organisms (such as birds, spiders, mites, most of the soil invertebrates, parasitoids and other wasps, most of the phytophagous insects and plants) are in one way or another strongly dependent on ants for their feeding or protection, for their own population regulation, and even in rare cases, for pollination (Fowler et al. 1991). Shaded cocoa systems, especially cabruca systems, protect a large number of ant species from several different components of the ant community. The species found therein are generally of more similar composition to forest assemblages than are ants in other agricultural systems. Further, many ant species in cocoa systems may have beneficial effects on the cocoa crop. Cocoa plantations in the Atlantic region of Brazil have been extremely important for the study of several interesting and rare genera, and for examining ant community assemblages. Finally, because of their forest-like structure and because they are the most complex cropping systems in Bahia, cocoa plantations make an ideal natural laboratory for studying the effects of human influence on rainforest ecosystems.

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