



## Structural changes in arboreal ant assemblages (Hymenoptera: Formicidae) in an age sequence of cocoa plantations in the south-east of Bahia, Brazil

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### Abstract

A study of succession of ant species in plantations of different ages and development may assist with our understanding of the dynamics of their assemblages. The aim of this study was to characterise the relationship between development of Brazilian cocoa plantations and the nature of their dominant ant assemblages. A chronosequence of cocoa plantations aged 1, 3, 4, 8, 15 and 33 years was sampled by several methodologies. Data were analysed in terms behavioural dominance and Berger-Parker's dominance index (here based on frequency data), and also by principal component analysis and analysis of co-occurrence. Apart from lower numbers of species being found in the 1-year-old plantation, there was no consistent trend in ant richness with plantation age. According to the criteria we adopted, only one species reached behavioural dominance in most age classes of plantation, although this increased to three in the 8-year-old one, before declining to zero in the oldest plantation. No species reached Berger-Parker's dominance in the youngest plantation, whereas all other age classes contained one to three dominants. Particular species showed non-age-related variations in their degree of Berger-Parker's dominance and this could in part be related to which species initially colonised the plantation. Principal component analysis axis 1 was partly related to plantation age, indicating an age-related change in assemblage composition. Ant species co-occurrence could only be effectively detected in cocoa plantations from 3 to 15 years of age. The arboreal ant assemblage is dynamic in nature, with the competitive hierarchy among species oscillating along the cocoa development chronosequence. The assemblage structure could be influenced by the initial founding ants, as well as by the invasive *Monomorium floricola*.

**Key words** competition, dominance, territoriality, *Theobroma cacao*.

### INTRODUCTION

Plantations of cocoa (*Theobroma cacao* L., Malvaceae) tend to be characterised by the occurrence of numerically and/or behaviourally dominant arboreal ants, distributed in a mosaic-like fashion (Leston 1973, 1978; Majer 1992; Majer *et al.* 1994; Hora *et al.* 2005). The establishment of large territories of dominant ants is a feature of plantations (Philpott 2006), in which food is plentiful and more easily monopolised than in forest where, due to the higher diversity of fauna and flora as well as higher vegetation structural complexity, resources are

much more dispersed and more diverse in composition. This can lead to competition for territory, with resources being more acute, and occupation of space by ant species being much more fragmented. Thus, in the understorey of forest areas with poor soil, low solar energy input, and where resources are dispersed, large, mutually exclusive territories of dominant ants tend not to be found (Floren & Linsenmair 2000), although this is not necessarily the case in the uppermost, insulated stratum where resources are more abundant (Ribeiro *et al.* 2013). The assemblage of arboreal ants associated with cocoa plantations, focusing on the mosaic structure, was first studied in Ghana, West Africa (Leston 1973; Majer 1976a,b) and since then in other countries such as Papua New Guinea (Room 1975), Central America (Adams 1994) and

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most recently in the Ivory Coast (Kone *et al.* 2012). It has also been extensively studied in Brazilian forests and cocoa plantations (Leston 1978; Majer & Delabie 1993; Majer *et al.* 1994; Medeiros *et al.* 1995; Delabie *et al.* 2000; Dejean *et al.* 2003).

Dominant ant species are numerically superior to other ant species and may mediate the structure of the rest of the community (Leston 1973; Majer & Delabie 1993; Majer *et al.* 1994), although another study suggests that they can disaggregate the organisation of other species (Sanders *et al.* 2007). Although the evidence is conflicting, non-dominant species can occur randomly, with their occurrence being governed by a mixture of factors (Majer *et al.* 1994). The establishment of ant territories is partly a function of which species arrive first (Egler 1954), and partly a function of the aggressiveness of the species, which is modulated by defence and conquest, and where competition with enemies is the main behavioural mechanism involved in regulating the assemblage. This can result in a mosaic-like structure (Hölldobler 1983). The nature of this mosaic can also be influenced by the presence of invasive ant species, which pose novel interactions with the native ant fauna. Examples of such situations include the exotic *Wasmannia auropunctata* in Africa (Mikissa *et al.* 2013), *Pheidole megacephala* in Asia (Greenslade 1971) and *Monomorium floricola* in Brazil (Wetterer 2010; this study).

The dynamic nature of the ant assemblage can be better understood by assessing the ontogenetic succession of species that nest or forage in trees representing several ages of development, and assessing the accompanying changes in those biotic and abiotic factors that might provide ecological conditions favourable for new species to enter the canopy (Kenne *et al.* 2003; Dejean *et al.* 2008).

Perennial arboreal crops offer an excellent opportunity to study the processes involved in assemblage organisation and how this can result in the formation of a mosaic, since this type of agriculture favours a diverse ant fauna. The structure of arboreal ant assemblages of cocoa plantations in the southeast of Bahia is considered to be close to that of the original Brazilian Atlantic forest (Majer & Delabie 1993; Delabie & Mariano 2000; Delabie *et al.* 2007). This may be because cocoa trees are often planted under the original forest trees (the 'cabruca' system) or are located near remnant areas of primary or secondary forest (Majer & Delabie 1993; Delabie & Mariano 2000; Delabie *et al.* 2007). Thus, like coffee, cocoa is a crop that contributes to the preservation of ant biodiversity (Perfecto *et al.* 1996; Kone *et al.* 2012), as well as that of invertebrates (Delabie & Mariano 2000; Delabie *et al.* 2000, 2007) and certain other organisms (Cassano *et al.* 2009; Schroth *et al.* 2011). This reinforces the interest in supporting this crop as a major agricultural activity in the southeast of Bahia, ensuring the preservation of a representative fraction of the biodiversity of the Atlantic Forest. In this region, the 'derruba' system, in which the original forest trees are totally cleared and shade trees are planted concurrently or prior to cocoa establishment (for details see Delabie *et al.* 2007; Cassano *et al.* 2009; Schroth *et al.* 2011), is also commonly used by cocoa producers (Delabie *et al.* 2007); this also con-

tributes, albeit to a lesser extent, to maintaining invertebrate diversity.

Studies on ant assemblages and mosaics are extremely important, especially for revealing how their structure tracks the development of the vegetation. Such studies may contribute to our understanding of the factors governing ant assemblage organisation, not only in cocoa plantations, but also in many other perennial tree crops and natural forests (Philpott *et al.* 2008; Ribeiro *et al.* 2013; Rizali *et al.* 2013). For example, the plant provides a range of conditions that change according to the tree's development, influencing the activities of the ant assemblages that develop on it, and their interactions with other insects, to name just two. Another benefit is that conservation of ant diversity in cocoa contributes to improving the local economy, as some species act as biological control agents for protecting the plant (Delabie *et al.* 2007). This is because dominant species can determine the distribution of certain pests by processes such as exclusion, selective predation or competition (Seguni *et al.* 2011).

The aim of this study was to characterise the relationship between the development of Brazilian, derruba-type cocoa plantations with their dominant ant assemblage, and how the invasive tramp ant species *M. floricola* can influence its organisation as the plantation changes with age. Not only should this contribute to our understanding of ant assemblage and mosaic dynamics, it should also provide insight into why mosaics have not necessarily been observed in lower forest canopies (Floren & Linsenmair 2000).

## MATERIALS AND METHODS

The study was carried out in a chronosequence of cocoa plantations aged 1, 3, 4, 8, 15 and 33 years, planted under the derruba system (Fig. S1). These were located in the blocks E, F, G and H in the experimental areas of the Cocoa Research Center (CEPEC – CEPLAC) (Fig. S2), Ilhéus, in the State of Bahia, Brazil (14°47'55"S; 39°02'01"W).

Ilhéus has a hot and humid climate type AF (Köppen 1936), with annual temperatures ranging between 20°C and 25°C (Santana *et al.* 2003). The predominant ecosystem is the wet forest of the Brazilian Atlantic forest biome, with regional precipitation varying between 2000 and 2400 mm per year, with the rain irregularly distributed throughout the year. The terrain is flat or with gently rolling hills, and consists of stratified layers of sand and clay sediments, with an average elevation of 60 m above sea level (Santana *et al.* 2003).

All plantations were shaded with planted, non-native *Erythrina* spp. (Fabaceae) shade trees. Broadly speaking, the *Erythrina* trees corresponded to the emerging canopy trees of the original forest, while the cocoa trees represented the understorey layer. To adequately describe the areas, litter thickness, the heights and canopy volumes of cocoa trees and the heights of the *Erythrina* shade trees were measured for each age class of plantation. The cocoa trees had a height ranging from 1.94 ± 0.35 m (1-year-old trees), increasing progressively to 7.29 ± 1.01 m (33-year-old trees), with a canopy

**Table 1** Mean and standard deviation of environmental parameters in the cocoa plantations of different ages at Ilheus, Bahia, Brazil

Plot age (year)	1	3	4	8	15	33
Litter thickness (cm) $\pm$ SD	1.05 $\pm$ 0.60	1.61 $\pm$ 0.86	2.13 $\pm$ 1.17	2.9 $\pm$ 1.54	4.53 $\pm$ 0.43	5.67 $\pm$ 0.96
Height of cocoa trees (m) $\pm$ SD	1.9 $\pm$ 0.35	2.8 $\pm$ 0.64	3.1 $\pm$ 0.40	3.6 $\pm$ 0.69	3.9 $\pm$ 0.68	7.3 $\pm$ 1.01
Height of the cocoa tree crown (m) $\pm$ SD	0.9 $\pm$ 0.27	1.6 $\pm$ 0.43	1.8 $\pm$ 0.53	2.5 $\pm$ 0.67	3.1 $\pm$ 0.69	5.6 $\pm$ 1.23
Cocoa tree crown diameter (m) $\pm$ SD	1.6 $\pm$ 0.47	3.9 $\pm$ 0.43	4.3 $\pm$ 0.57	4.0 $\pm$ 0.53	5.8 $\pm$ 0.92	8.1 $\pm$ 1.77
Cocoa tree crown volume (m <sup>3</sup> ) $\pm$ SD	0.8 $\pm$ 0.72	6.6 $\pm$ 2.88	9.3 $\pm$ 5.51	10.8 $\pm$ 4.07	29.3 $\pm$ 15.21	104.8 $\pm$ 61.53
Height of shade trees (m) $\pm$ SD	14.3 $\pm$ 8.19	17.2 $\pm$ 10.24	19.2 $\pm$ 9.97	11.9 $\pm$ 8.51	11.4 $\pm$ 6.06	14.3 $\pm$ 6.53

volume varying from  $0.78 \pm 0.72 \text{ m}^3$  to  $104.76 \pm 61.53 \text{ m}^3$  (Table 1). The *Erythrina* shade trees ranged from  $11.45 \pm 6.06 \text{ m}$  (15-year-old plantation) to  $19.23 \pm 9.97 \text{ m}$  (4-year-old plantation); there was no relationship between shade tree height and age of plantation because some areas had been established in previous cocoa plantations where the original planted shade trees had been retained. The litter thickness varied from  $1.05 \pm 0.60 \text{ cm}$  (1-year-old plantation), progressively increasing to  $5.67 \pm 0.96 \text{ cm}$  (33-year-old plantation).

Ants were sampled from September 2008 to March 2009, a period in which no chemicals at all were used in the experimental areas. Furthermore, no insecticides had been applied for the last 20 years in the region, partly due to economic considerations that followed the introduction of the witches' broom disease in Bahia (Pereira *et al.* 1990), although fungicides have been continuously and heavily used elsewhere. Fifty trees were chosen randomly within each age class of plantation, with sampled trees spaced at least 25 m apart (a distance greater than that recommended by Majer *et al.* 1994). This was done to ensure relative independence of sampling, where the probability of two successively sampled plants being occupied by the same ant colony was almost zero. All trees conformed to a minimum distance of 25 m from the edge. Although we cannot exclude the possibility that the shade trees contribute to structuring part of the ant assemblage on the cocoa trees, ants were not sampled on them, a matter that we discuss later. On each cocoa tree, four conventional methods for sampling arboreal ants were applied according to the recommendations of Bestelmeyer *et al.* (2000), namely (1) sardine baits placed in an 50 mL plastic cup set at 1.5 m for 2 h during the earlier hours of the day (08:00–10:00 h); (2) honey baits set at the same height and time; (3) manual collection on the trunk and foliage for 10 min per tree; and (4) tree beating using a 9 m<sup>2</sup> sheet placed beneath each tree. For the bait sampling, all ants on the bait at the end of the 2 h were caught and sealed in vials of ethanol for subsequent identification and counting. The number of baits occupied by different species was recorded as well as the number of different species co-occurring on the same baits at the same time. For the other sampling methods, only a single or few individuals of each species were collected, as only their identification was necessary. Each type of sampling was performed once on each tree, since we consider that weather conditions during this warmer part of the year have a minimum influence on our data. Ants were placed into 70% alcohol and returned to the laboratory for determination using the CEPLAC (CPDC) reference collection, where vouchers are deposited.

Ant occurrence matrices for each species (1: presence; 0: absence) were first compiled for each collecting method in each age class of plantation. A presence/absence matrix was then prepared for all methods combined.

Behavioural dominance of species was analysed according to recommendations of Blüthgen and Stork (2007) and Parr and Gibb (2010), and was based on abundances at honey and/or sardine baits. The criterion for behavioural dominance was arbitrarily set at one third of the maximum value obtained, this being 7. This conservative criterion captured the species that we know from previous observations are behaviourally dominant. Berger-Parker's index of dominance of the most frequently occurring ant species, as well as the less frequent *Crematogaster carinata* and *Ectatomma tuberculatum* (both of them considered as dominant in Majer *et al.* 1994), was calculated using frequency in samples values (May 1975; Magurran 1988; Sofia & Suzuki 2004). Once again, the criterion for Berger-Parker dominance was conservatively set at one third of the maximum value, resulting in a cut-off of 0.193.

The data (ant species frequency) were analysed by principal component analysis (PCA) using the program PAST version 1.97. This analysis allowed us to check how the species frequency ordered according to plantation age. This method is used to sort samples according to the criterion of Majer (1976a), e.g. by the number of occurrences of a species. The species chosen for this analysis were the most frequently occurring according to the 95 percentile.

In order to test whether the interactions between species progressively changes with increasing age of plantation, an analysis of co-occurrence was performed with the aid of *EcoSim* software (Gotelli & Entsminger 2012), testing for non-randomly co-occurring species using the array of presence/absence ant data (Gotelli 2000). Species with a non-random occurrence were examined using three different groups of species, namely the entire array of species, the most frequently occurring species (95 percentile) and the entire array of species excluding the invasive ant *M. floricola*. The default program for random samples was used (C-score index, where the expected values simulate a critical point in the distribution of probability, corresponding to the null model, fixed columns and rows, and 1000 arrays) (Ribas & Schoereder 2002; Pacheco *et al.* 2009). Co-occurrence was assessed by the parameter indicated by Parr and Gibb (2010); i.e. when the C-score is high compared with the null model, there is no suggestion that the species that predominated in the assemblage were avoided, and when it is low this suggests that the species tended to aggregate. We used this

analysis of co-occurrence as it allows verification of the occurrence of competition between species in each plantation age class. Using this analytical method, in conjunction with our own and previous ethological observations, the detection of patterns in the arrangement of arboreal ants during the development of the cocoa tree could be ascertained, enabling us to understand cohabitation between species or their mutual exclusion (see, e.g. Davidson *et al.* 2007; Dejean *et al.* 2007).

## RESULTS

A total of 113 ant species was found in the plantations (Appendix S1). Apart from lower numbers of species being found in the 1-year-old plantation (26), there was no consistent trend in richness with plantation age, with values being 52, 45, 42, 62 and 51 passing through the rest of the age series.

When considering behavioural dominance, we cannot exclude the possibility that a species found to be more abundant at a bait is because it is nesting close by, or even because the hour of sampling (morning) coincides with its maximum activity rhythm, rather than it exhibiting truly dominant behaviour. Notwithstanding this possibility, the conservative cut-off of at least 7 at one or both bait types was considered to genuinely signify behavioural dominance. As expected, since behavioural dominance is based on abundance, three of the numerically dominant species also stood out as being behaviourally dominant at baits (*Linepithema neotropicum*, *M. floricola* and *W. auropunctata*), although *E. tuberculatum* also scored highly in this regard (Table 2). *Linepithema neotropicum* dominated both bait types in the 1-year-old plantation, as did *W. auropunctata* in the 8-year-old one. The influence of *E. tuberculatum* prevailed at honey baits in the 8-year-old plantations, while *M. floricola* dominated in all but the youngest and oldest plantations. Thus, only one species reached behavioural dominance in most age classes of plantation, although this increased to three in the 8-year-old one, before declining to zero in the oldest plantation (Table 2).

*Monomorium floricola* and *W. auropunctata* were the most frequent in co-occurrence (same time, same place). The ages at which these co-occurred with other species, ranked by their number of co-occurrences, were 8, 3, 4, 15 and 33 years. In the 8-year-old cocoa plantation, there were a larger number of occurrences of more than a single species at the same time. This is precisely the age at which we observed the co-occurrence of species in all situations tested (Tables 3,4).

There was considerable variation in the frequency of individual ant species in relation to the stage of plantation development. The most frequent species, regardless of plantation age (5% most frequent, all the plantations together), are shown in Table 5. Most of these species tended to be more frequent in different age bands, with *W. auropunctata* predominating in mid-aged and oldest plantations, *M. floricola*

and *Crematogaster erecta* being more frequent in the young and mid-aged plantations, and *Cr. carinata* predominating in the oldest plantation.

These trends were partly reflected by Berger-Parker's dominance index values (Table 5), although these were extremely variable through time. Nine of the 13 most frequently occurring species failed to reach dominance in any of the plantations (*A. paraensis*, *B. patagonicus*, both *Camponotus* spp., *Ce. atratus*, *Cr. curvispinosa*, *E. tuberculatum*, *L. neotropicum* and *Pa. inversa*). No species reached our criteria for Berger-Parker's dominance in the youngest plantation (Table 5). *Crematogaster erecta*, *M. floricola* and *W. auropunctata* reached dominance in the 3-year-old plantation and the first mentioned maintained dominance in the 4-year-old plantation. *M. floricola* once again attained dominance in the 15-year-old plantation. *Crematogaster carinata* reached dominance status in the oldest plantation only, where once again *W. auropunctata* attained dominance status. In conclusion, no species reached Berger-Parker's dominance in the youngest plantation, whereas all other age classes contained one to three dominants (Table 5).

The ordering of sites on the PCA (Fig. 1) did not exhibit a clear chronosequence, although the 15-year-old plantation received the highest positive score on component 2 and the 1-year-old plantation the lowest. The 3- and 4-year-old plantations scored low on component 1 and the 8- and 33-year-old plantations scored high. The separation of the 15-year-old plantation was associated with the frequency of *M. floricola*, *Cr. erecta* and *Ce. atratus*, the youngest plantations with *L. neotropicum* and the 8-year-old plantations with *E. tuberculatum* and *W. auropunctata*.

When using the entire array of species, the variation in C-score values of co-occurrence was significant in all but the youngest and oldest age groups of plantations (3, 4, 8 and 15 years) (Table 6), which indicates the non-randomness of co-occurrence among species in these areas. Using the analysis of the most frequent species, there was significance in 3-, 8- and 15-year-old cocoa plantations. When the entire array of species without *M. floricola* was tested, we only detected significance in the 3- and 8-year-old cocoa plantations (Table 6).

## DISCUSSION

It was observed that while the dominance of some arboreal species is higher during certain periods as the plantation matures, they can be less dominant at other times. The existence of this oscillation is not congruent with the observations on African pioneer trees by Dejean *et al.* (2008), where there is a tendency for species to change their level of dominance in a more orderly fashion as the plants mature. There is no evidence of a consistent trend in the hierarchical relationship between ant species, although *M. floricola* maintained behavioural dominance throughout much of the developmental period.

**Table 2** Behavioural dominance (according to Parr & Gibb 2010), based on abundance of arboreal ant species at honey and sardine baits in cocoa plantations ordered according to their ages at Ilhéus, Bahia, Brazil

Species	1 year		3 years		4 years		8 years		15 years		33 years	
	Honey	Sardine	Honey	Sardine	Honey	Sardine	Honey	Sardine	Honey	Sardine	Honey	Sardine
<i>Azteca chartifex</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Azteca paraensis</i>	0	0	0	1	1	2	0	0	0	0	0	3
<i>Brachymyrmex heeri</i>	0	0	1	0	0	0	1	0	1	0	1	0
<i>Brachymyrmex patagonicus</i>	3	0	1	0	2	0	1	0	0	0	0	0
<i>Brachymyrmex sp.2</i>	1	0	1	0	0	0	0	0	0	0	0	0
<i>Camponotus bidens</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Camponotus cingulatus</i>	0	0	1	0	0	0	0	0	0	0	0	0
<i>Camponotus fastigatus</i>	0	0	1	1	0	2	2	0	3	0	1	0
<i>Camponotus crassus</i>	0	0	2	4	5	2	2	0	2	1	0	0
<i>Camponotus trapezoides</i>	0	0	1	0	0	0	0	0	1	0	0	0
<i>Cephalotes atratus</i>	0	1	0	2	2	4	0	4	3	3	0	0
<i>Crematogaster acuta</i>	0	0	0	0	0	1	0	0	0	0	0	1
<i>Crematogaster carinata</i>	0	0	0	0	0	0	0	1	0	0	0	2
<i>Crematogaster curvispinosa</i>	0	0	0	0	0	0	3	2	0	1	0	0
<i>Crematogaster erecta</i>	0	0	3	4	0	6	3	5	2	4	0	0
<i>Crematogaster limata</i>	0	0	0	0	0	0	1	1	0	0	0	0
<i>Crematogaster longispina</i>	0	0	0	0	0	2	0	0	0	0	0	1
<i>Crematogaster near crucis</i>	0	0	0	0	0	0	0	0	0	1	0	0
<i>Crematogaster victima</i>	0	0	0	1	2	0	0	0	0	0	0	0
<i>Dolichoderus attelaboides</i>	0	0	0	0	0	1	1	1	0	0	0	1
<i>Dolichoderus bidens</i>	0	0	0	0	0	0	0	0	2	1	0	0
<i>Dolichoderus bispinosus</i>	0	0	0	2	0	0	0	0	0	0	0	0
<i>Dolichoderus imitator</i>	0	0	0	0	0	0	0	1	0	0	0	0
<i>Ectatomma brunneum</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Ectatomma permagnum</i>	0	0	0	0	0	1	0	0	0	0	0	0
<b><i>Ectatomma tuberculatum</i></b>	0	0	0	0	0	0	<b>11</b>	5	3	4	1	0
<i>Gnamptogenys annulata</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Hypoponera sp.1</i>	0	0	0	0	0	0	0	1	0	0	0	0
<b><i>Linepithema neotropicum</i></b>	<b>10</b>	<b>14</b>	0	2	4	2	4	3	0	1	1	0
<b><i>Monomorium floricola</i></b>	0	1	<b>7</b>	<b>9</b>	0	<b>9</b>	6	<b>11</b>	<b>9</b>	<b>21</b>	1	0
<i>Mycocepurus smithi</i>	0	0	0	0	0	1	0	0	0	0	0	0
<i>Pachycondyla inversa</i>	0	0	0	0	0	0	0	0	1	0	3	4
<i>Pachycondyla subversa</i>	0	0	0	0	0	0	1	0	0	1	0	0
<i>Pachycondyla unidentata</i>	0	0	0	0	0	0	0	0	0	0	2	0
<i>Nylanderia fulva</i>	1	0	0	0	0	0	3	1	0	0	0	0
<i>Nylanderia guatemalensis</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Paratrechina longicornis</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pheidole diligens</i>	0	0	0	0	1	0	0	0	0	0	0	0
<i>Pheidole manuana</i>	1	0	0	0	0	0	0	0	0	0	0	1
<i>Pheidole nitidula</i>	0	0	0	0	0	2	0	0	0	0	0	0
<i>Pheidole radoszkowskii</i>	0	0	0	1	0	0	0	0	0	0	0	0
<i>Pheidole gp. fallax sp.1</i>	2	0	2	1	0	0	0	0	2	0	0	0
<i>Pheidole gp. flavens sp.4</i>	0	0	0	0	0	0	1	0	0	2	0	0
<i>Pheidole gp. fallax sp.9</i>	1	2	2	2	0	0	2	1	0	0	0	0
<i>Pheidole gp. flavens sp.15</i>	0	0	0	0	0	0	0	0	0	1	0	0
<i>Pseudomyrmex gracilis</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pseudomyrmex oculatus</i>	0	0	0	0	0	0	1	0	0	0	0	0
<i>Pseudomyrmex termitarius</i>	0	0	0	0	0	0	0	0	1	0	0	0
<i>Solenopsis geminata</i>	0	1	0	0	1	0	1	0	0	0	0	0
<i>Solenopsis saevissima</i>	0	0	0	0	0	0	0	0	0	0	1	0
<i>Solenopsis sp.2</i>	0	0	0	0	0	0	0	0	0	2	1	2
<i>Solenopsis sp.3</i>	0	0	1	0	1	1	3	2	0	1	0	0
<i>Tetramorium simillimum</i>	0	0	0	0	0	0	0	0	0	1	0	0
<b><i>Wasmannia auropunctata</i></b>	0	0	1	2	1	2	<b>11</b>	<b>12</b>	0	1	2	4
<i>Wasmannia rochai</i>	0	0	0	0	0	0	1	0	0	1	0	0
No. of species exhibiting behavioural dominance	1		1		1		3		1		0	

Species with exceptionally high behavioural dominance values ( $\geq 7$  in at least one of the two bait types) are boldfaced.

**Table 3** Number of baits occupied by co-occurring ant species at Ilhéus, Bahia, Brazil

Age	Number of co-occurrences	
	Honey	Sardine
1 year	2 (16)†	1 (18)
3 years	4 (19)	5 (26)
4 years	2 (18)	8 (31)
8 years	20 (36)	8 (39)
15 years	3 (29)	6 (40)
33 years	1 (13)	4 (17)

†In the brackets, total number of baits with ants.

**Table 4** Number of species that co-occur on the same baits at the same time on cocoa trees at Ilhéus, Bahia, Brazil

Age	Number of co-occurrences	
	Honey	Sardine
1 year	7	1
3 years	1	6
4 years	2	7
8 years	10	10
15 years	3	6
33 years	1	4

The presence of pre-existing mature shade trees in some plantations may have obscured the pattern of succession in the ant assemblage, as such trees may have harboured colonies of ants which spread on to the cocoa trees, regardless of their state of maturity. Ideally, investigations such as this should be performed in plantations in which shade trees had been planted close to the period of plantation establishment.

Nevertheless, the dominance hierarchy, based on each species' competitive ability, is clearly dynamic because factors such as resource type, host tree structure, temperature, trophobionts or even the occurrence of parasitoids, can affect the ants' status within this hierarchy (Parr & Gibb 2010; Ribeiro *et al.* 2013). These can change their status as dominant or subdominant (Medeiros *et al.* 1995; Armbrrecht *et al.* 2001). Co-occurrence of dominants could only be effectively detected in 4- to 15-year-old cocoa trees. Probably, throughout the various stages of development of cocoa trees, the populations of ants influence each other and settle in the spaces available. This pattern of co-occurrence observations may result from the reduction in degree of interactions between species in older cocoa plantations. According to Blüthgen and Stork (2007), the co-occurrence analysis between species can be used to detect the occurrence of a mosaic. A significant pattern of co-occurrence does not necessarily indicate that competition is the structuring mechanism in the mosaic, because certain environmental factors are also important (Parr & Gibb 2010). According to some analyses, no significant patterns of co-occurrence were detected in many of the assemblages that have been studied (Pacheco *et al.* 2009; Dejean *et al.* 2010), including some mosaics of cocoa trees, so stochastic factors, such as the nature of the founding species, may also mediate the assemblage organisation or preclude its detection. The

influence of founding species could certainly explain why *W. auropunctata* rises and falls in frequency in an inconsistent manner throughout the chronosequence.

The variations in size and crown volume of cocoa trees as a function of development (Table 1) showed less effect on mosaic structuring than did the influence of the dominant species such as *M. floricola*. This is probably because this species dominated the available resources, displacing other species. The randomness of space occupation by other ants must have caused changes in the organisation of the species under its influence.

During succession, the colonisation of plants by ants moves from a relatively homogeneous occupation to a random one, where the organisation becomes more complex, with segregation among species and assemblages (Zorrilla *et al.* 1986). In the mosaic of cocoa tree ants, although variations occur depending on the tree age, there may be reversals in the structural hierarchy of specific organisation, mainly due to the invasion or proliferation in the crop of invasive species such as *M. floricola*.

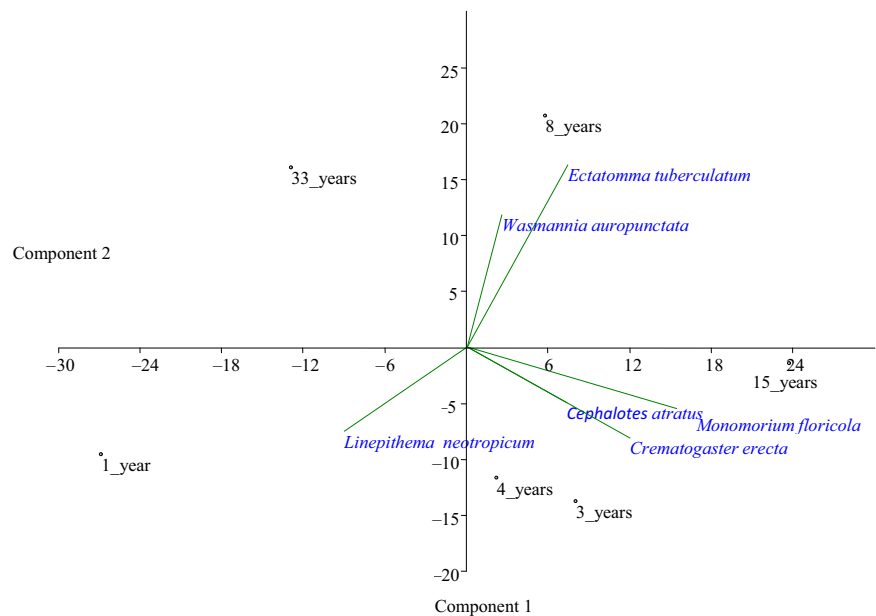
According to the concept of ontogenetic succession, the age of the vegetation type and size of plants seems to play an important role in the composition of mosaics (Djiéto-Lordon *et al.* 2004; Dejean *et al.* 2008; Kone *et al.* 2012). However, the cooperative interactions and competition between species influence the spatial relationship, which reflects the way in which a given habitat is colonised (Zorrilla *et al.* 1986). Ant species that co-occur tend to differ in their adaptations and strategies for gathering, handling and defence of food resources, and this reflects the dynamics of mosaic (Lynch 1981).

*Monomorium floricola* is able to reduce the populations of other insects (Wetterer 2010), and in Brazilian mangroves, this ant was twice as common as any other exotic ant (Delabie *et al.* 2006). This may be due to its diminutive size or its behaviour, by which workers avoid directly encountering arboreal dominant ants, thus allowing co-occurrence or avoidance of competition for food or nesting sites (Delabie *et al.* 2006). It appears to be a dominant species that influences the use of food or maybe the nesting resources by the other species. The invasiveness of this species may be a condition for species coexistence, by which it can increase within a stable or persistent population of another ant (Kotler & Brown 2007). This influence of *M. floricola* particularly occurred in 4- and 15-year-old cocoa plantations (Table 2). As previously mentioned, *M. floricola* showed behavioural dominance in almost all of the plantation ages, with the exception of 1- and 33-year-old plantations. These are precisely the ages where it was not possible to define what was the main factor regulating the community structure. This suggests that the species can remain in this state throughout most of the plantation's development, influencing and changing the organisation of other species. This occurs most effectively when its frequency is higher, especially in relation to *W. auropunctata*. Although this ant is not usually considered dominant and invasive (Way & Bolton 1997), the occurrence of *M. floricola* can be particularly prominent in habitats where competition with

**Table 5** Berger-Parker's index of ant dominance, based on frequency data, for the most frequently occurring species in the cocoa plantations ordered according to their ages at Ilhéus, Bahia, Brazil

Species	Age of cocoa plantation (years)					
	1	3	4	8	15	33
<i>Azteca paraensis</i>	0.000	0.002	0.031	0.000	0.005	0.086
<i>Brachymyrmex patagonicus</i>	0.054	0.022	0.002	0.000	0.001	0.000
<i>Camponotus fastigatus</i>	0.003	0.006	0.006	0.001	0.005	0.002
<i>Camponotus crassus</i>	0.004	0.005	0.026	0.000	0.004	0.000
<i>Cephalotes atratus</i>	0.000	0.008	0.019	0.000	0.017	0.002
<b><i>Crematogaster carinata</i></b>	0.000	0.004	0.009	0.000	0.000	<b>0.214</b>
<i>Crematogaster curvispinosa</i>	0.002	0.003	0.001	0.010	0.001	0.024
<b><i>Crematogaster erecta</i></b>	0.002	<b>0.211</b>	<b>0.201</b>	0.104	0.177	0.000
<i>Ectatomma tuberculatum</i>	0.000	0.000	0.000	0.019	0.023	0.030
<i>Linepithema neotropicum</i>	0.058	0.058	0.062	0.042	0.006	0.001
<b><i>Monomorium floricola</i></b>	0.085	<b>0.284</b>	0.167	0.063	<b>0.440</b>	0.036
<i>Pachycondyla inversa</i>	0.000	0.000	0.000	0.000	0.002	0.006
<b><i>Wasmannia auropunctata</i></b>	0.003	<b>0.213</b>	0.001	<b>0.579</b>	0.070	<b>0.250</b>
Number of species exhibiting dominance	0	3	1	1	1	2

Species with exceptionally high dominance values ( $\geq 0.193$ ) are boldfaced.



**Fig. 1.** Principal components analysis of the various plantations, analysed according to the frequency (number of samples where the ant appeared) of the ant species within them. The diagonal lines show the ant species that have the most important influence on the separation of sites.

other arboreal ants is very low (Wetterer 2010). Invasive species can contribute to the reconfiguration of the entire network of interactions and lead to changes in ecosystem balance (Croll *et al.* 2005).

*Wasmannia auropunctata* showed remarkable variation in its frequency as a function of plant development. Although of Neotropical origin, it is generally considered invasive, even in its home range (Medeiros *et al.* 1995; Le Breton *et al.* 2004; Grangier *et al.* 2007), and in some circumstances this ant is able to eliminate virtually the entire ant fauna of a particular location (Hölldobler & Wilson 1994; Ward & Beggs 2007). The aerial parts of the plants are only dominated by this ant under certain conditions, especially when the surrounding trees are not occupied by dominant ants, such as those of the genera *Azteca*, *Crematogaster* or *Ectatomma* (Majer *et al.* 1994; Delabie & Mariano 2000).

Small-scale spatial variations in structural complexity have an effect on resource use by many of the ant species (Luque & López 2007). This suggests that the nature of microhabitats may be a factor influencing the outcome of dominance hierarchies among ants. The complexity of the habitat, even on a small scale, can produce differences among species that contribute to the sharing of resources and hence allow the subordinate species to avoid competition (Luque & López 2007).

In the cocoa plantations studied, the nature of ant dominance varied depending on age; although, generally, in intermediate-aged cocoa trees, the species present and their respective frequencies were relatively similar. Plant development in relation to age, along with differences in their life histories and the selective attraction they exert on the different species of arboreal ants, means that dominant ant assemblages are dynamic (Dejean *et al.* 2008; Kone *et al.* 2012). The

**Table 6** Index of co-occurrence of ant species, based on presence/absence, in cocoa plantations in relation to age of the plantation at Ilhéus, Bahia, Brazil

Age of cocoa plantation (years)	Selection of species								
	The entire array			The most frequent species			The entire array excluding <i>Monomorium floricola</i>		
	C-score	Null	<i>P</i>	C-score	Null	<i>P</i>	C-score	Null	<i>P</i>
1 year	7.06	6.64	0.15	15.69	14.18	0.07	7.28	6.82	0.08
3 years	<b>10.29</b>	<b>10.06</b>	<b>0.001</b>	<b>57.18</b>	<b>55.48</b>	<b>0.003</b>	<b>9.05</b>	<b>8.90</b>	<b>0.02</b>
4 years	<b>12.16</b>	<b>11.89</b>	<b>0.01</b>	65.33	65.49	0.59	10.91	10.75	0.09
8 years	<b>10.01</b>	<b>9.52</b>	<b>0.003</b>	<b>62.28</b>	<b>60.71</b>	<b>0.01</b>	<b>9.33</b>	<b>8.89</b>	<b>0.001</b>
15 years	<b>10.68</b>	<b>10.23</b>	<b>0.001</b>	<b>50.15</b>	<b>48.48</b>	<b>0.01</b>	9.26	9.18	0.17
33 years	8.85	8.83	0.39	24.38	24.25	0.32	9.05	9.05	0.42

Boldfaced numbers correspond to the index of co-occurrence values that are significant at  $P \leq 0.05$ .

age-related oscillation in the frequencies of these species may, in part, arise from this phenomenon.

Variations in the assemblage along the plantation age gradient were observed in terms of dominance among the species, with the mosaic on 15-year-old cocoa trees being possibly more structured (following the criteria of Majer *et al.* 1994). These variations occurred as a result of fluctuations in the dominance status of the species that comprise the mosaic. According to Armbrrecht *et al.* (2001), population fluctuations correspond to periodic pulses in the area of the territories of each species, with a consequent reduction or extension of each one, suggesting that the spaces occupied by each species do not have sharp boundaries; they are constantly reshaped.

We conclude that the assembly of arboreal ants of the cocoa plantations that we studied is extremely dynamic, with competitive hierarchy among species oscillating throughout the plantation's development, and with no obvious chronosequence linking plant development and ant species number. Thus, the dominance of certain ant species varies according the plant's growth, while an invasive species can greatly contribute to reconfiguring the assemblage structure.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

**Appendix S1** Absolute frequency of arboreal ant species, based on presence/absence, in cocoa plantations at Ilhéus, State of Bahia, Brazil ordered according to their ages. Bolding refers to species with higher frequency ( $\geq 10$  in at least one plantation).

**Fig. S1.** General views of each of the plantations surveyed during this study. Key: A = 1 years old; B = 3 years old; C = 4 years old; D = 8 years old; E = 15 years old; F = 33 years old.

**Fig. S2.** Map of the experimental area of the Cocoa Research Center (CEPEC) showing the blocks where the ant samples were collected. The letters correspond to the names of block in use at CEPEC: block E hosted the plantations aged of 1, 3 and 4 years; block F: 3 and 8 years; block G: 8 and 33 years; block H': 15 years (adapted from the Soil Map of Area CEPEC – CEPLAC, Ilheus – BA. Source: Silva & Melo (1970)).

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