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2   STRUCTURAL CHANGES IN ARBOREAL ANT ASSEMBLAGES IN AN AGE-

3   SEQUENCE OF COCOA PLANTATIONS IN THE SOUTHEAST OF BAHIA,

4   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 characterize 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 analyzed in terms behavioural dominance and the Berger-Parker's dominance index (here based on frequency data), and also by PCA 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 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 dominance and this could in part be related to which species initially colonized the plantation. PCA 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: *Theobroma cocoa*, competition, territoriality, dominance, Formicidae

INTRODUCTION

Plantations of cocoa (*Theobroma cocoa* L., Malvaceae) tend to be characterized 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 monopolized 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, insolated stratum where resources are more abundant (Ribeiro *et al.*, 2013). The assemblage of arboreal ants associated with cocoa plantations, focussing on the mosaic structure, was first studied in Ghana, West Africa (Leston 1973; Majer, 1976a; 1976b) and since then in other countries such as Papua New Guinea (Room, 1975), Central America (Adams 1994), and 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 organization 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 defense 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

88 of such situations include the exotic *Wasmannia auropunctata* in Africa (Mikissa *et al.*,

89 2013), *Pheidole megacephala* in Asia (Greenslade, 1971) and *Monomorium floricola* in

90 Brazil (Wetterer, 2010; this study).

91   The dynamic nature of the ant assemblage can be better understood by assessing

92 the ontogenetic succession of species that nest or forage in trees representing several

93 ages of development, and assessing the accompanying changes in those biotic and

94 abiotic factors that might provide ecological conditions favourable for new species to

95 enter the canopy (Kenne *et al.*, 2003; Dejean *et al.*, 2008).

96   Perennial arboreal crops offer an excellent opportunity to study the processes

97 involved in assemblage organization and how this can result in the formation of a

98 mosaic, since this type of agriculture favours a diverse ant fauna. The structure of

99 arboreal ant assemblages of cocoa plantations in the southeast of Bahia is considered to

100 be close to that of the original Brazilian Atlantic forest (Majer & Delabie, 1993; Delabie

101 & Mariano, 2000; Delabie *et al.*, 2007). This may be because cocoa trees are often

102 planted under the original forest trees (the "cabruca" system) or are located near

103 remnant areas of primary or secondary forest (Majer & Delabie, 1993; Delabie &

104 Mariano, 2000; Delabie *et al.*, 2007). Thus, like coffee, cocoa is a crop that contributes

105 to the preservation of ant biodiversity (Perfecto *et al.*, 1996; Kone *et al.*, 2012), as well

106 as that of invertebrates (Delabie *et al.*, 2000; 2007) and certain other organisms

107 (Cassano *et al*., 2009; Schroth *et al*., 2011). This reinforces the interest in supporting

108 this crop as a major agricultural activity in the southeast of Bahia, ensuring the

109 preservation of a representative fraction of the biodiversity of the Atlantic Forest. In this

110 region, the "derruba" system, in which the original forest trees is totally cleared and

111 shade trees are planted concurrently or prior to cocoa establishment (for details see

112 Delabie *et al*., 2007; Cassano *et al*., 2009; Schroth *et al*., 2011), is also commonly used

113 by cocoa producers (Delabie *et al*., 2007); this also contributes, albeit to a lesser extent,

114 to maintaining invertebrate diversity.

115   Studies on ant assemblages and mosaics are extremely important, especially for

116 revealing how their structure tracks the development of the vegetation. Such studies

117 may contribute to our understanding of the factors governing ant assemblage

118 organization, not only in cocoa plantations, but also in many other perennial tree crops

119 and natural forests (Philpott *et al.*, 2008; Ribeiro *et al.*, 2013; Rizali *et al.*, 2013). For

120 example, the plant provides a range of conditions that change according to the tree's

121 development, influencing the activities of the ant assemblages that develop on it, and
122 their interactions with other insects, to name just two. Another benefit is that
123 conservation of ant diversity in cocoa contributes to improving the local economy, as
124 some species act as biological control agents for protecting the plant (Delabie *et al.*,
125 2007). This is because dominant species can determine the distribution of certain pests
126 by processes such as exclusion, selective predation or competition (Seguni *et al.*, 2011).

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

134

135 **MATERIALS AND METHODS**

136 The study was carried out in a chronosequence of cocoa plantations aged 1, 3, 4,
137 8, 15 and 33 years, planted under the derruba system (supplementary material, Figure
138 1). These were located in the blocks E, F, G and H in the experimental areas of the
139 Cocoa Research Center (CEPEC - CEPLAC) (supplementary material, Figure 2),
140 Ilhéus, in the State of Bahia, Brazil (14º47'55"S 39º02'01"W).

141 Ilheus has a hot and humid climate type AF (Köppen, 1936), with annual
142 temperatures ranging between 20-25^{0}C (Santana *et al.,* 2003; IBGE, 2010). The
143 predominant ecosystem is the wet forest of the Brazilian Atlantic forest biome, with
144 regional precipitation varying between 2,000 and 2,400 mm per year, with the rain
145 irregularly distributed throughout the year. The terrain is flat or with gently rolling hills,
146 and consists of stratified layers of sand and clay sediments, with an average elevation of
147 60 m above sea level (Santana *et al.,* 2003).

148 All plantations were shaded with planted, non-native *Erythrina* spp. (Fabaceae)
149 shade trees. Broadly speaking, the *Erythrina* trees corresponded to the emerging canopy
150 trees of the original forest, while the cocoa trees represented the understorey layer. To
151 adequately describe the areas, litter thickness, the heights and canopy volumes of cocoa
152 trees and the heights of the *Erythrina* shade trees were measured for each age-class of

153 plantation. The cocoa trees had a height ranging from 1.94±0.35 m (1-year old trees),

154 increasing progressively to 7.29±1.01 m (33-year old trees), with a canopy volume

155 varying from 0.78±0.72 m^3 to 104.76±61.53 m^3 (Table 1). The *Erythrina* shade trees,

156 ranged from 11.45±6.06 m (15-year old plantation) to 19.23±9.97 m (4-year old

157 plantation); there was no relationship between shade tree height and age of plantation

158 because some areas had been established in previous cocoa plantations where the

159 original planted shade trees had been retained. The litter thickness varied from

160 1.05±0.60 cm (1-year old plantation), progressively increasing to 5.67±0.96 cm (33-

161 year old plantation).

162 Ants were sampled from September 2008 to March 2009, a period in which no

163 chemicals at all were used in the experimental areas. Furthermore, no insecticides had

164 been applied for the last 20 years in the region, partly due to economic considerations

165 that followed the introduction of the witches' broom disease in Bahia (Pereira *et al*.,

166 1990), although fungicides have been continuously and heavily used elsewhere. Fifty

167 trees were chosen randomly within each age class of plantation, with sampled trees

168 spaced at least 25 m apart (a distance greater than that recommended by Majer *et al*.,

169 1994). This was done to ensure relative independence of sampling, where the

170 probability of two successively sampled plants being occupied by the same ant colony

171 was almost zero. All trees conformed to a minimum distance of 25 m from the edge.

172 Although we cannot exclude the possibility that the shade trees contribute to structuring

173 part of the ant assemblage on the cocoa trees, ants were not sampled on them, a matter

174 which we discuss later. On each cocoa tree, four conventional methods for sampling

175 arboreal ants were applied according to the recommendations of Bestelmeyer *et al*.

176 (2000), namely: 1) sardine baits placed in an 50 ml plastic cup set at 1.5 m for 2 hours

177 during the earlier hours of the day (08:00-10:00 h); 2) honey baits set at the same height

178 and time; 3) manual collection on the trunk and foliage for 10 minutes per tree; and 4)

179 tree beating using a 9 m^2 sheet placed beneath each tree. For the bait sampling, all ants

180 on the bait at the end of the two hours were caught and sealed in vials of ethanol for

181 subsequent identification and counting. The number of baits occupied by different

182 species was recorded as well as the number of different species co-occuring on the same

183 baits at the same time. For the other sampling methods only a single or few individuals

184 of each species were collected, as only their identification was necessary. Each type of

185 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 analyzed 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. The Berger-Parker 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; Sofia & Suzuki, 2004; Magurran, 1988). 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 analyzed by Principal Components 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), for example, 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) (Pacheco *et al.*, 2009; Ribas &

219 Schoereder, 2002). Co-occurrence was assessed by the parameter indicated by Parr and

220 Gibb (2010); i.e. when the C-score is high compared with the null model, there is no

221 suggestion that the species that predominated in the assemblage were avoided, and

222 when it is low this suggests that the species tended to aggregate. We used this analysis

223 of co-occurrence as it allows verification of the occurrence of competition between

224 species in each plantation age-class. Using this analytical method, in conjunction with

225 our own and previous ethological observations, the detection of patterns in the

226 arrangement of arboreal ants during the development of the cocoa tree could be

227 ascertained, enabling us to understand cohabitation between species or their mutual

228 exclusion (see, for example, Davidson *et al*., 2007; Dejean *et al*., 2007).

229

230 **RESULTS**

231   A total of 113 ant species was found in the plantations (Supplementary

232 Appendix 1). Apart from lower numbers of species being found in the 1-year old

233 plantation (26), there was no consistent trend in richness with plantation age, with

234 values being 52, 45, 42, 62 and 51 passing through the rest of the age series.

235   When considering behavioural dominance, we cannot exclude the possibility

236 that a species found to be more abundant at a bait is because it is nesting close by, or

237 even because the hour of sampling (morning) coincides with its maximum activity

238 rhythm, rather than it exhibiting truly dominant behaviour. Notwithstanding this

239 possibility, the conservative cut-off of at least 7 at one or both bait types was considered

240 to genuinely signify behavioural dominance. As expected, since behavioural dominance

241 is based on abundance, three of the numerically dominant species also stood out as

242 being behaviourally dominant at baits (*Linepithema neotropicum*, *M. floricola* and *W.*

243 *auropunctata*), although *E. tuberculatum* also scored highly in this regard (Table 2).

244 *Linepithema neotropicum* dominated both bait types in the 1-year old plantation, as did

245 *W. auropunctata* in the 8-year old one. The influence of *E. tuberculatum* prevailed at

246 honey baits in the 8- old plantations, while *M. floricola* dominated in all but the

247 youngest and oldest plantations. Thus, only one species reached behavioural dominance

248 in most age classes of plantation, although this increased to three in the 8-year old one,

249 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 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 3a and b).

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 4. 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 the Berger-Parker dominance index values (Table 4), 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 dominance in the youngest plantation (Table 4). *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 dominance in the youngest plantation, whereas all other age classes contained one to three dominants (Table 4).

The ordering of sites on the PCA (Figure 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 plantations with *E. tuberculatum* and *W. auropunctata*.

283　　　　　When using the entire array of species, the variation in C-score values of co-
284　occurrence was significant in all but the youngest and oldest age groups of plantations
285　(3, 4, 8 and 15 years) (Table 5), which indicates the non-randomness of co-occurrence
286　among species in these areas. Using the analysis of the most frequent species, there was
287　significance in 3-, 8- and 15-year old cocoa plantations. When the entire array of species
288　without *M. floricola* was tested, we only detected significance in the 3- and 8-year old
289　cocoa plantations (Table 5).

290

291　**DISCUSSION**

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

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

305　　　　　Nevertheless, the dominance hierarchy, based on each species' competitive
306　ability, is clearly dynamic because factors such as resource type, host tree structure,
307　temperature, trophobionts or even the occurrence of parasitoids, can affect the ants'
308　status within this hierarchy (Parr & Gibb, 2010; Ribeiro *et al.*, 2013). These can change
309　their status as dominant or subdominant (Medeiros *et al.*, 1995; Armbrecht *et al.*, 2001).
310　Co-occurrence of dominants (*M. floricola*) could only be effectively detected in 4- to
311　15- year old cocoa trees. Probably, throughout the various stages of development of
312　cocoa trees, the populations of ants influence each other and settle in the spaces
313　available. This pattern of co-occurrence observations may result from the reduction in
314　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 organization 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 organization of the species under its influence.

During succession, the colonization of plants by ants moves from a relatively homogeneous occupation to a random one, where the organization becomes more complex, with segregation among species and assemblages (Zorrila *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 organization, 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 colonized (Zorrila *et al.*, 1986). Ant species that co-occur tend to differ in their adaptations and strategies for gathering, handling and defense 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

348   exotic ant (Delabie et al., 2006). This may be due to its diminutive size or its behaviour,

349   by which workers avoid directly encountering arboreal dominant ants, thus allowing co-

350   occurrence or avoidance of competition for food or nesting sites (Delabie et al., 2006).

351   It appears to be a dominant species that influences the use of food or maybe the nesting

352   resources by the other species. The invasiveness of this species may be a condition for

353   species coexistence, by which it can increase within a stable or persistent population of

354   another ant (Kotler & Brown, 2007). This influence of *M. floricola* particularly occurred

355   in 4- and 15-year old cocoa plantations (Table 2). As previously mentioned, *M. floricola*

356   showed behavioural dominance in almost all of the plantation ages, with the exception

357   of 1- and 33-year old plantations. These are precisely the ages where it was not possible

358   to define what was the main factor regulating the community structure. This suggests

359   that the species can remain in this state throughout most of the plantation's

360   development, influencing and changing the organization of other species. This occurs

361   most effectively when its frequency is higher, especially in relation to *W. auropunctata*.

362   Although this ant is not usually considered dominant and invasive (Way & Bolton,

363   1997), the occurrence of *M. floricola* can be particularly prominent in habitats where

364   competition with other arboreal ants is very low (Wetterer, 2010). Invasive species can

365   contribute to the reconfiguration of the entire network of interactions and lead to

366   changes in ecosystem balance (Croll *et al.*, 2005).

367   *Wasmannia auropunctata* showed remarkable variation in its frequency as a

368   function of plant development. Although of Neotropical origin, it is generally

369   considered invasive, even in its home range (Medeiros *et al.*, 1995, Le Breton *et al.*,

370   2004; Grangier *et al.*, 2007), and in some circumstances this ant is able to eliminate

371   virtually the entire ant fauna of a particular location (Hölldobler & Wilson, 1994; Ward

372   & Beggs, 2007). The aerial parts of the plants are only dominated by this ant under

373   certain conditions, especially when the surrounding trees are not occupied by dominant

374   ants, such as those of the genera *Azteca*, *Crematogaster*, or *Ectatomma* (Majer *et al.*,

375   1994, Delabie & Mariano, 2000).

376   Small-scale spatial variations in structural complexity have an effect on resource

377   use by many of the ant species (Luque & Lopez, 2007). This suggests that the nature of

378   microhabitats may be a factor influencing the outcome of dominance hierarchies among

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

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

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Table 2. Behavioural dominance (according 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 with exceptionally high behavioural dominance values (≥ 7 in at least one of the two bait types) are boldfaced.

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
Azteca chartifex	0	0	0	0	0	0	0	0	0	0	0	1
Azteca paraensis	0	0	0	1	1	2	0	0	0	0	0	3
Brachymyrmex heeri	0	0	1	0	0	0	1	0	1	0	1	0
Brachymyrmex patagonicus	3	0	1	0	2	0	1	0	0	0	0	0
Brachymyrmex sp.2	1	0	1	0	0	0	0	0	0	0	0	0
Camponotus bidens	0	0	0	0	0	1	0	0	0	0	0	0
Camponotus cingulatus	0	0	1	0	0	0	0	0	0	0	0	0
Camponotus fastigatus	0	0	1	1	0	2	2	0	3	0	1	0
Camponotus crassus	0	0	2	4	5	2	2	0	2	1	0	0
Camponotus trapezoideus	0	0	1	0	0	0	0	0	1	0	0	0
Cephalotes atratus	0	1	0	2	2	4	0	4	3	3	0	0
Crematogaster acuta	0	0	0	0	0	1	0	0	0	0	0	1
Crematogaster carinata	0	0	0	0	0	0	0	1	0	0	0	2
Crematogaster curvispinosa	0	0	0	0	0	0	3	2	0	1	0	0
Crematogaster erecta	0	0	3	4	0	6	3	5	2	4	0	0
Crematogaster limata	0	0	0	0	0	0	1	1	0	0	0	0
Crematogaster longispina	0	0	0	0	0	2	0	0	0	0	0	1
Crematogaster near *crucis*	0	0	0	0	0	0	0	0	0	1	0	0
Crematogaster victima	0	0	0	1	2	0	0	0	0	0	0	0
Dolichoderus attelaboides	0	0	0	0	0	1	1	1	0	0	0	1
Dolichoderus bidens	0	0	0	0	0	0	0	0	2	1	0	0
Dolichoderus bispinosus	0	0	0	2	0	0	0	0	0	0	0	0
Dolichoderus imitator	0	0	0	0	0	0	0	1	0	0	0	0
Ectatomma brunneum	0	0	0	0	0	0	1	0	0	0	0	0
Ectatomma permagnum	0	0	0	0	0	1	0	0	0	0	0	0

Species	1	2	3	4	5	6	7	8	9	10	11	12
Ectatomma tuberculatum	0	0	0	0	0	0	**11**	5	3	4	1	0
Gnamptogenys annulata	0	0	0	0	0	0	0	0	0	0	0	1
Hypoponera sp.1	0	0	0	0	0	0	0	1	0	0	0	0
Linepithema neotropicum	**10**	**14**	0	2	4	2	4	3	0	1	1	0
Monomorium floricola	0	1	**7**	**9**	0	**9**	6	**11**	**9**	**21**	1	0
Mycocepurus smithi	0	0	0	0	0	1	0	0	0	0	0	0
Pachycondyla inversa	0	0	0	0	0	0	0	0	1	0	3	4
Pachycondyla subversa	0	0	0	0	0	0	1	0	0	1	0	0
Pachycondyla unidentata	0	0	0	0	0	0	0	0	0	0	2	0
Nylanderia fulva	1	0	0	0	0	0	3	1	0	0	0	0
Nylanderia guatemalensis	0	0	0	0	0	0	1	0	0	0	0	0
Paratrechina longicornis	0	0	0	0	0	0	0	0	1	0	0	0
Pheidole diligens	0	0	0	0	1	0	0	0	0	0	0	0
Pheidole manuana	1	0	0	0	0	0	0	0	0	0	0	1
Pheidole nitidula	0	0	0	0	0	2	0	0	0	0	0	0
Pheidole radoszkowskii	0	0	0	1	0	0	0	0	0	0	0	0
Pheidole gp. *fallax* sp.1	2	0	2	1	0	0	0	0	2	0	0	0
Pheidole gp. *flavens* sp.4	0	0	0	0	0	0	1	0	0	2	0	0
Pheidole gp. *fallax* sp.9	1	2	2	2	0	0	2	1	0	0	0	0
Pheidole gp. *flavens* sp.15	0	0	0	0	0	0	0	0	0	1	0	0
Pseudomyrmex gracilis	0	0	0	0	0	0	0	0	1	0	0	0
Pseudomyrmex oculatus	0	0	0	0	0	0	1	0	0	0	0	0
Pseudomyrmex termitarius	0	0	0	0	0	0	0	0	1	0	0	0
Solenopsis geminata	0	1	0	0	1	0	1	0	0	0	0	0
Solenopsis saevissima	0	0	0	0	0	0	0	0	0	0	1	0
Solenopsis sp.2	0	0	0	0	0	0	0	0	0	2	1	2
Solenopsis sp.3	0	0	1	0	1	1	3	2	0	1	0	0
Tetramorium simillimum	0	0	0	0	0	0	0	0	0	1	0	0
Wasmannia auropunctata	0	0	1	2	1	2	**11**	**12**	0	1	2	4
Wasmannia rochai	0	0	0	0	0	0	1	0	0	1	0	0
No. of species exhibitig behavioural dominance		1		1		1		3		1		0

Table 3. Number of (a) baits occupied by co-occurring ant species and (b) number of species that co-occur on the same baits at the same time on cocoa trees at Ilhéus, Bahia, Brazil.

(a)

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.

(b)

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

Table 4. 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 with exceptionally high dominance values (≥ 0.193) are boldfaced.

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

Table 5. 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. Boldfaced numbers correspond to the index of co-occurrence values that are significant at $p \leq 0.05$.

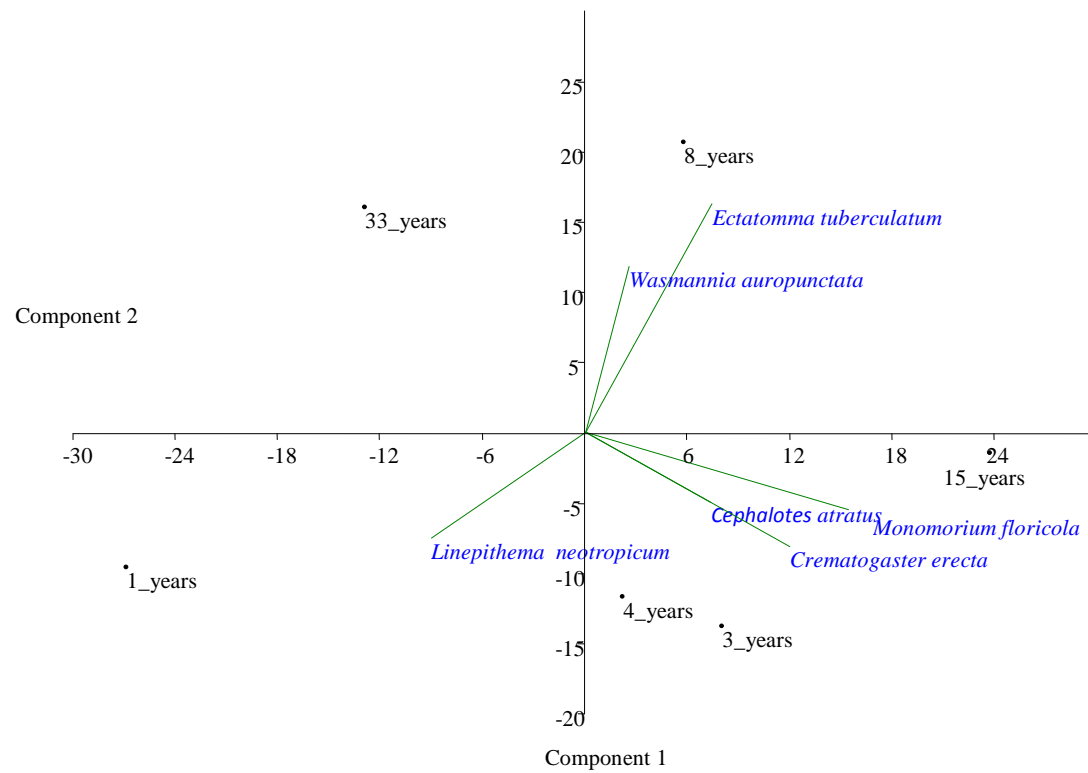| Age of cocoa plantation (years)	Selection of species								
	The entire array			The most frequent species			The entire array excluding *Monomorium floricola*		
	C-score	Null	P	C-score	Null	P	C-score	Null	P
1 year	7.06	6.64	0.15	15.69	14.18	0.07	7,28	6.82	0.08
3 years	**10.29**	**10.06**	**0.001**	**57.18**	**55.48**	**0.003**	**9.05**	**8.90**	**0.02**
4 years	**12.16**	**11.89**	**0.01**	65.33	65.49	0.59	10.91	10.75	0.09
8 years	**10.01**	**9.52**	**0.003**	**62.28**	**60.71**	**0.01**	**9.33**	**8.89**	**0.001**
15 years	**10.68**	**10.23**	**0.001**	**50.15**	**48.48**	**0.01**	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

Figure 1. Principal components analysis of the various plantations, analyzed 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.