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Ant Community Evolution According to Aging in Brazilian Cocoa Tree Plantations

ES Conceição[1], TMC Della Lucia[2], AO Costa-Neto[3], ES Araujo[4], EBA Koch[5,6], JHC Delabie[6,7]

1 - Departamento de Ciências Exatas e da Terra, Universidade do Estado da Bahia, Bahia, Brazil
2 - Departamento de Biologia Animal, Universidade Federal de Viçosa. Viçosa-MG, Brazil
3 - Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana-BA, Brazil
4 - Programa de Pós-Graduação em Zoologia, Universidade Estadual de Santa Cruz, Ilhéus-BA, Brazil
5 - Programa de Pós-Graduação em Ecologia e Biomonitoramento, Universidade Federal da Bahia, Salvador-BA, Brazil
6 - Laboratório de Mirmecologia, CEPEC/CEPLAC, Itabuna-BA, Brazil
7 - Departamento de Ciência Agrárias e Ambientais, Universidade Estadual de Santa Cruz, Ilhéus-BA, Brazil

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Corresponding author
Eltamara Souza da Conceição
Departamento de Ciências Exatas e da Terra
Universidade do Estado da Bahia (UNEB)
CP 59, CEP 48.040-210 - Alagoinhas-BA, Brasil.
E-Mail: econceicao@uneb.br

Abstract
Agriculture is frequently held accountable for the depletion of biotic diversity, although a few agroforestry systems support the conservation of a number of organisms. Cocoa farming is noteworthy as an example of an agricultural activity that benefits or maintains species richness. However, the mechanism by which the biodiversity persists throughout the entire process of plant development remains obscure. In Southeastern Bahia, Brazil, cacao tree plantations support the conservation of a large amount of organisms native to the Atlantic Forest, between them the ants. This study aims at recording the relationship between cocoa tree development and ant community structure. The experiment was carried out in a series of six cocoa tree plantations aged one, three, four, eight, fifteen and 33 years, distributed across the experimental grounds of the Cocoa Research Center at Ilhéus. 1,500 ant samples were collected using the sampling techniques: hand collection, honey and sardine baits, entomological blanket and "pitfall". Highest values for diversity and richness were reported in the 15-years-old cocoa plantation. No significant correlations between diversity, richness or plant age were reported. Considering the faunistic composition, a statistical similarity was observed between the plantations close in age to one another. Plant aging did not exert any influence on the diversity gradient and richness in the succession process of the ant community. In young plantations, there are low differences between the ants found on the ground and the ones found on the young cocoa trees. In older plantations, the ant community divides in two distinct assemblages on the ground and on the trees. The variations observed in the ant community along the plant development were likely caused by the structural organization of the dominant species mosaic.

Introduction

Agricultural expansion is frequently blamed for significant reduction in local biodiversity (Norris et al., 2010), although many species manage to survive in habitats that are disturbed or subjected to agricultural processes (Lugo, 1988). However, a few agroforestry systems are rather similar to and act as natural forest ecosystems (Michon & De Foresta, 1995; Delabie et al., 2007). In such areas, many species are able to survive in the landscape even after the native forest becomes locally extinct, particularly at times when the following characteristics come together: planted species, natural secondary vegetation and proximity to remnants of native vegetation (Henriques, 2003; Cassano et al., 2009).

Southeastern Bahia is one of the largest cocoa growing regions in Brazil, with the structure of the arboreal ant

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communities rather identical to that of the Atlantic Forest, because of the occurrence of the cacao trees and their shading trees, frequently associated with undergrowth (Majer & Delabie, 1993; Roth et al., 1994; Delabie et al., 2000; Delabie & Mariano, 2001; Delabie et al., 2007; Cassano et al., 2009; Conceição et al., 2015). In this region, the "*cabruca*" (the traditional system of cocoa tree [*Theobroma cacao* L., Sterculiaceae] cultivation) and "*derruba total*" (integral knocked down trees) systems utilized in cocoa farming are examples of such kinds of agricultural management, "environmentally friendly". "*Cabruca*" involves planting the cocoa trees between indigenous trees which provide the necessary shade (Delabie et al., 2007; Cassano et al., 2009; Schroth et al., 2004). But, according the same authors, in the "*derruba total*" system, exotic trees such like *Erythrina fusca* Lour. (Fabaceae), are planted to ensure shading for the cacao trees. In both planting systems, therefore, there is a combination of planted species and secondary vegetation which supports and maintains local animal diversity, particularly ants (Delabie et al., 2000; Delabie & Mariano, 2001), in a manner which is close to a secondary forest community (Delabie et al., 2007).

Formicidae, the dominant invertebrates of tropical forests, contribute to maintain at low levels the populations of many other organisms being for that considered as "key components" (Bihn et al., 2008); in addition to that many species are seen as ecosystem engineers as they are responsible in great part for mixing up mineral and organic soil components (Folgarait, 1998). Furthermore, they have other traits which highlight the pivotal role of this family in the ecosystems, an important reason for focusing on them in biodiversity studies.

It is well established that environmental changes affect the ant community and other faunal components (Andersen, 1990, 1997). Ant population richness may be positively linked to vegetation density, as in the most heterogeneous habitats, there is a larger variety of nesting sites, food, microclimate and interspecific interactions (competition, predation, mutualism) than in the less complex habitats (Corrêa et al., 2006).

Research conducted on diversity patterns is significant for developing strategies for species conservation. It also enables predicting the effects of environmental changes, such like fragmentation and simplification of habitats (Retana & Cerdá, 2000; Graham et al., 2009). Thus, studies done on the diversity patterns and population richness in agroforestry systems such like cocoa tree plantations may contribute to a clearer understanding of the variations that can occur throughout the plant development. A first assessment of the dominance consequences of certain species on the other ants has been done earlier, which appears as a function of plant ontogeny (Conceição, 2015). In this new study, we intend to reveal the mechanisms responsible for this variation, according to the growth of the cocoa trees in the plantations of Southeastern Bahia, Brazil.

Material and Methods

This study was carried out on the experimental grounds of the Cocoa Research Center – CEPEC/CEPLAC (14º47'S, 39º02'W), in the municipality of Ilhéus, state of Bahia, Brazil. Located in the south-eastern coastal microregion of Bahia, this area is characterized by a warm and humid climate of AF-type (Köppen, 1936), with an annual temperature ranging between 20 and 25 ºC (Santana et al., 2003); rain forest is the principal regional ecosystem, included in the *Mata Atlântica* (Brazilian Atlantic Forest Biome), with an annual regional rainfall from 2,000 to 2,400 mm on average and at an altitude of around 60 m a.s.l. (Santana et al., 2003).

Areas of cocoa plantations were chosen in different developmental stages, planted under the "derruba total" system with *Erythrina* sp. as shade; they were all subjected to similar agronomic management and edaphoclimatic conditions. The plants were located in the experimental blocks E, F, G and H (CEPEC nomenclature) (Fig 1). The selected areas were planted with trees of 1, 3, 4, 8, 15 and 33 years of age, each of them with a surface of at least four hectares.

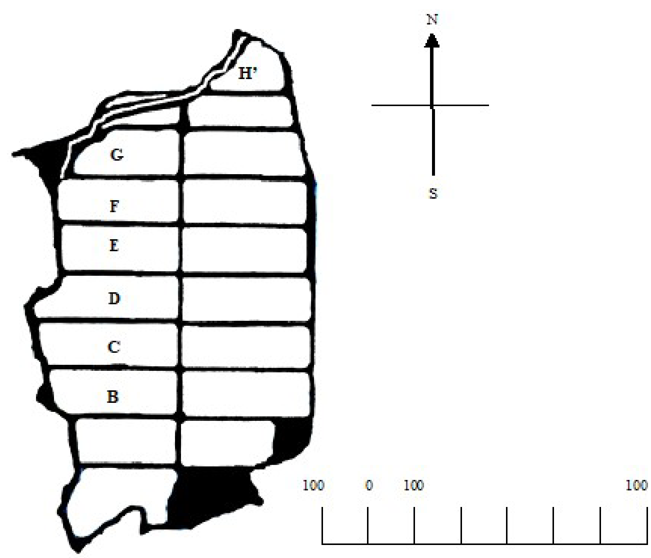

Fig 1. Map of experimental areas of the Cocoa Research Center (CEPEC), Ilhéus, Bahia, Brazil (adapted from Silva & Melo (1968), identifying the blocks where the ants were sampled).

The samples were collected between September 2008 and March 2009. Three hundred cacao trees were randomly selected from within the planted areas. With at least 25m intervals between the trees, 50 trees were selected per planting age category, maintaining a minimum of 25m distance from the border. The canopy volume of cocoa trees was assessed using the measurements of the crown height and diameter to evaluate the observed changes according to plant ontogeny (Fig 2). In each of the trees five conventional ant collection methods were applied: 1) sardine baits, 2) honey baits; 3) hand collection; 4) entomological sheet and 5) "pitfall" traps (Bestelmeyer et al., 2000). A total of 1,500 samples were collected.

The same collection method was applied, during the same period and conditions for each developmental plant stage. At the base of each plant, pitfall traps were installed for 24 hours to capture the ants, aiming to facilitate a comparison with the arboreal fauna. The baits (sardine or honey) were put into containers (disposable plastic glasses) positioned at two extreme points on the branches of the canopy of each sampled cocoa tree. Two hours later, they were taken down and the foragers were collected and packed into vials in 70% alcohol. Hand collection involved the use of forceps to pick up the ants foraging on each tree trunk, up to 1.50 m in height, in 10 minutes of observation. Finally, the trunk of each tree was subjected to 10 shakes and the Formicidae were captured on an entomological sheet placed on the ground.

After screening, all the biological material was identified with the help of the taxonomic keys and compared with the reference collection of the Laboratory of Myrmecology (CPDC acronym) at the Cacao Research Center (CEPEC-CEPLAC). Nomenclature followed Bolton (2003), Bolton et al. (2007), Antcat (Bolton, 2017) and Antweb v6 13.3.

The richness was estimated with the Chao 2 index, thanks to the software EstimateS version 7.5 (Colwell, 2005). The Shannon-Winner index was calculated using PAST (Paleontological Statistics) program, version 1.97 (Hammer et al., 2001). To calculate the arboreal ant matrices, in each plant age class, the indexes of diversity and richness were assessed by combining the data of the litter sample, hand collection and honey and sardine baits per sample. Calculation of the same indices was done separately for the epigeal ants.

The similarity indices were determined using the PAST Program version 1.97 (Hammer et al., 2001), where the ant fauna found on trees were compared with that of soil at each class of age and subsequently its variation was observed throughout the course of the plant development. Next, we performed a selection of models to verify which one (linear or nonlinear) best fits the relationship of similarity between ground-dwelling and arboreal ant communities and the age of planting. For the choice of the best model, the Akaike criterion (AIC) was used. The analyses were performed using software R v. 3.5.0 (R Development Core Team 2018).

In order to address the species composition, a Multidimensional Non-Metric Ordering (NMDS) was performed. Bray-Curtis index was used, which is based on the frequency of occurrence of ant species in each one of the tree age classes. This analysis was performed in the software R v. 3.4.3 (R Development Core Team 2018). Then, a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001) was performed in which the presence/absence of ant species in each one of the tree age classes was the response variable, while the predictor variable was tree age classes. We also performed the post-hoc comparison test to show which pairs of assemblages differ in composition.

Finally, we tested if there is variation in the number of ant species found per plant according the plantation ages, and if the difference between vegetation and soil varies, using two-way ANOVA, followed by Fisher´s pairwise multiple comparison tests. All these analyses were performed in the software R v. 3.4.3 (R Development Core Team 2018).

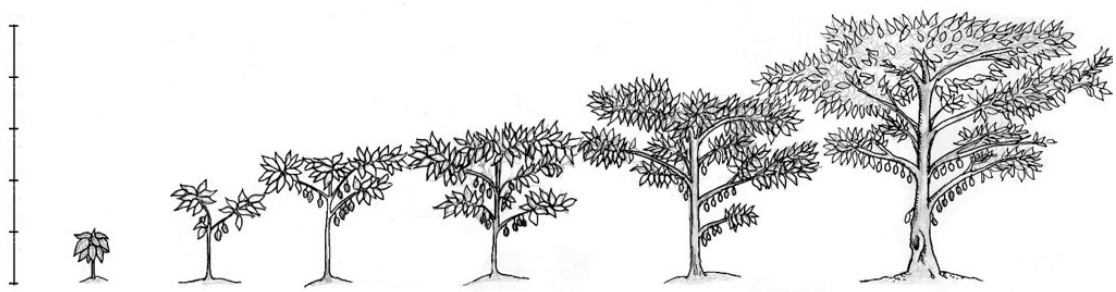

Fig 2. Comparative growth of cocoa tree plantations according to age, with 1, 3, 4, 8, 15, 33 years.

Results

The commonest ant species in all the plant ages appear *in bold* in Table 1. The number of occurrences varied greatly according to the developmental stages of the plants. Regarding ground-dwelling ant species, both diversity and richness indexes were unexpectedly higher in younger cocoa trees (plantations of one, three and four-years-old, Table 2). On the other hand, arboreal ants showed the highest diversity index on 15-years-old cocoa trees, whereas species richness was the lowest on one-year-old trees, the highest on 33-years-old trees and intermediate on the other tree age classes (Table 2). The diversity and richness indices showed no tendency either for growth or for decrease (Table 2, in response to tree development).

A greater similarity in the faunal composition was confirmed between the areas with 3- and 4-years-old trees. The same was observed for both ground-dwelling and arboreal ant assemblages. In general, the younger areas stretch towards a similar composition (Figs 3 and 4). Soil and crown fauna show greater similarity when the cacao trees are younger. The pattern of distribution that best suited to explain the similarity between the assemblages of ground-dwelling and arboreal ants according to cocoa tree age follows the Michaelis-Menten's model [$y = 0.24835x / (-0.19347 + x)$]. In the initial ages the similarity between the two strata is very high, and then it falls and continues stable along the aging of plantations (Fig 5). PERMANOVA confirmed significant differences between plantations of different ages (Table 3). The most important change is observed in the 8 years-old plantation which corresponds to the closure of the canopy cover.

Table 1. Frequency of arboreal ant species (maximum: 50) found on cocoa trees in plantations of different ages. Ilhéus, state of Bahia, Brazil. September 2008 to March 2009. Bold highlights the commonest species.

Species	**Age of the plantation (year)**					
	1	**3**	**4**	**8**	**15**	**33**
Atta cephalotes (Linnaeus, 1758)	0	1	0	1	3	0
Azteca chartifex Forel, 1912	0	0	0	0	0	3
***Azteca paraensis* Borgmeier, 1937**	**0**	**6**	**10**	**0**	**6**	**9**
Brachymyrmex heeri Forel 1874	3	4	2	7	3	7
***Brachymyrmex admotus* Mayr** ,1887	**13**	**6**	**3**	**1**	**3**	**0**
Brachymyrmex sp.1	1	0	0	0	0	0
Brachymyrmex sp.2	4	4	0	0	0	0
Brachymyrmex sp.3	0	0	0	1	0	0
Camponotus atriceps (forma 1) (Fr. Smith, 1858)	0	0	0	0	6	0
Camponotus atriceps (forma 2) (Fr. Smith, 1858)	0	0	0	0	1	0
Camponotus balzani Emery, 1894	0	0	0	0	1	0
Camponotus bidens Mayr, 1870	0	0	3	0	0	0
Camponotus chartifex (Fr. Smith, 1860)	0	0	1	0	0	3
Camponotus cingulatus (Mayr, 1862)	0	1	3	0	0	1
***Camponotus fastigatus* Roger, 1863**	**2**	**9**	**12**	**4**	**11**	**2**
Camponotus sexguttatus (Fabricius, 1793)	0	0	0	0	1	0
Camponotus trapezoideus Mayr, 1870	0	3	0	1	2	0
***Camponotus crassus* Mayr, 1862**	**4**	**10**	**19**	**4**	**11**	**1**
Camponotus (Myrmobrachys) canescens Mayr, 1870	0	0	0	0	1	2
Camponotus (Myrmobrachys) sp.1	0	1	0	0	0	3
Camponotus (Myrmobrachys) sp.2	0	0	1	2	0	0
Camponotus (Myrmobrachys) sp.3	0	0	0	0	2	0
Camponotus (Myrmobrachys) sp.4	0	0	0	0	2	0
Cardiocondyla minutior (Forel, 1899)	1	4	2	1	1	0
Cardiocondyla obscurior (Wheeler, 1929)	0	1	0	0	0	0
Cephalotes angustus (Mayr, 1862)	0	1	0	0	0	0
***Cephalotes atratus* (Linnaeus, 1758)**	**5**	**13**	**14**	**7**	**20**	**3**
Cephalotes goeldii (Forel, 1912)	0	1	0	0	0	0
Cephalotes maculatus (Fr. Smith, 1876)	0	1	1	0	1	0
Cephalotes pallens (Klug, 1824)	0	0	0	1	0	0
Cephalotes pavonii (Latreille, 1809)	0	3	0	1	4	0
Cephalotes pusillus (Klug, 1824)	0	0	2	0	1	0
Cephalotes umbraculatus (Fabricius, 1804)	0	1	0	0	0	0
Crematogaster acuta (Fabricius, 1804)	0	2	2	0	0	7
Crematogaster carinata (Mayr, 1862)	0	1	7	2	0	11
***Crematogaster curvispinosa* Mayr, 1862**	**2**	**6**	**5**	**18**	**1**	**11**
***Crematogaster erecta* Mayr, 1866**	**2**	**24**	**20**	**12**	**22**	**0**
Crematogaster limata Fr. Smith, 1858	0	0	0	2	0	3
Crematogaster longispina (Forel, 1904)	0	7	9	1	2	9
Crematogaster moelleri (Forel, 1912)	0	0	0	0	0	6
Crematogaster sp. near *crucis*	0	0	0	0	2	0
Crematogaster tenuicula (Forel, 1904)	0	0	0	0	0	3
Crematogaster victima Fr. Smith, 1858	0	6	5	0	0	0
Dolichoderus attelaboides (Fabricius, 1775)	1	2	6	4	3	9
Dolichoderus bidens (Linnaeus, 1758)	0	0	0	0	7	0

Table 1. Frequency of arboreal ant species (maximum: 50) found on cocoa trees in plantations of different ages. Ilhéus, state of Bahia, Brazil. September 2008 to March 2009. Bold highlights the commonest species. (Continuation)

Species	**Age of the plantation (year)**					
	1	**3**	**4**	**8**	**15**	**33**
Dolichoderus bispinosus (Olivier, 1792)	1	9	3	0	0	3
Dolichoderus diversus Emery, 1894	1	0	0	1	0	0
Dolichoderus imitator Emery, 1894	0	0	0	2	0	0
Dolichoderus lutosus (Fr. Smith, 1858)	2	3	0	0	1	1
Dorymyrmex thoracicus (Fr. Smith, 1860)	0	0	0	0	1	0
Ectatomma brunneum Fr. Smith, 1858	0	0	0	1	0	0
Ectatomma permagnum Forel, 1908	0	0	1	0	1	0
Ectatomma tuberculatum (Olivier, 1791)	0	0	0	26	22	15
Gnamptogenys annulata Mayr, 1887	0	0	0	0	0	1
Hypoponera sp.1	0	0	0	1	0	0
Hypoponera sp.5	0	0	0	0	1	0
Linepithema humile (Mayr, 1866)	2	3	0	2	5	1
***Linepithema neotropicum* Wild, 2007**	**31**	**16**	**10**	**12**	**3**	**3**
Megalomyrmex goeldii Forel, 1912	0	0	0	0	0	1
***Monomorium floricola* (Jerdon, 1852)**	**2**	**25**	**16**	**16**	**31**	**1**
Mycocepurus smithi Forel, 1893	2	0	1	0	0	0
Nesomyrmex spininodis Mayr, 1887	0	0	0	0	1	0
Nesomyrmex asper (Emery, 1896)	0	1	1	4	1	1
Nylanderia fulva (Mayr, 1862)	2	3	4	4	2	5
Nylanderia guatemalensis (Forel, 1885)	0	1	0	1	0	4
Nylanderia sp.1	0	0	0	0	0	1
Nylanderia sp.2	0	0	1	0	8	0
Odontomachus haematodus (Linnaeus, 1758)	0	0	0	0	1	0
Odontomachus meinerti Forel, 1905	0	0	0	0	0	1
Neoponera crenata (Roger, 1861)	0	2	1	2	0	0
***Neoponera inversa* (F. Smith, 1858)**	**0**	**0**	**0**	**0**	**8**	**13**
Neoponera moesta Mayr, 1870	0	1	1	0	0	0
Neoponera curvinodis (Forel, 1899)	0	1	0	1	7	0
Neoponera unidentata (Mayr, 1862)	0	3	2	0	1	3
Neoponera villosa (Fabricius, 1804)	0	0	0	0	0	1
Paratrechina longicornis (Latreille, 1802)	0	0	0	0	5	0
Pheidole diligens (Smith, 1858)	0	0	1	0	0	0
Pheidole flavida Mayr, 1887	0	0	0	0	1	2
Pheidole manuana Wilson, 2003	1	1	1	0	0	1
Pheidole midas Wilson, 2003	0	0	0	0	1	1
Pheidole nitidula Emery, 1888	0	3	2	0	0	0
Pheidole radoszkowskii Mayr, 1884	1	1	0	0	0	0
Pheidole sp.1 gp. *Fallax*	3	6	2	3	4	0
Pheidole sp.10 gp. *Fallax*	0	0	0	0	0	1
Pheidole sp.11 gp. *Fallax*	0	0	0	0	1	0
Pheidole sp.12 gp. *Fallax*	0	0	0	0	1	1
Pheidole sp.15 gp. *Flavens*	0	0	0	0	3	1
Pheidole sp.4 gp. *Flavens*	0	0	0	2	3	0
Pheidole sp.5 gp. *Fallax*	0	0	0	0	0	1
Pheidole sp.8 gp. *Flavens*	0	0	0	0	0	3

Table 1. Frequency of arboreal ant species (maximum: 50) found on cocoa trees in plantations of different ages. Ilhéus, state of Bahia, Brazil. September 2008 to March 2009. Bold highlights the commonest species. (Continuation)

Species	Age of the plantation (year)					
	1	3	4	8	15	33
Pheidole sp.9 gp. *Fallax*	5	6	0	4	0	0
Procryptocerus spiniperdus Forel, 1899	0	0	0	0	2	1
Pseudomyrmex elongatus (Mayr, 1870)	0	1	0	0	0	0
Pseudomyrmex gracilis (Fabricius, 1804)	1	2	3	0	6	1
Pseudomyrmex holmgreni Wheeler, 1925	0	0	2	0	0	0
Pseudomyrmex kuenckeli (Emery, 1890)	0	0	1	0	0	0
Pseudomyrmex oculatus (Fr. Smith, 1855)	0	0	1	1	3	1
Pseudomyrmex pupa (Forel, 1911)	0	1	0	0	1	0
Pseudomyrmex sericeus (Mayr, 1870)	0	1	0	0	0	0
Pseudomyrmex sp.1 gp. *Pallidus*	0	0	0	1	0	0
Pseudomyrmex tenuis (Fabricius, 1804)	0	0	0	0	0	1
Pseudomyrmex termitarius (Fr. Smith, 1855)	0	5	4	3	8	0
Sericomyrmex bondari Borgmeier, 1937	0	0	0	0	0	1
Solenopsis geminata (Fabricius, 1804)	3	3	4	4	8	0
Solenopsis saevissima (Fr. Smith, 1855)	0	0	0	0	0	1
Solenopsis sp.1	0	0	0	0	1	0
Solenopsis sp.2	0	2	1	1	8	3
Solenopsis sp.3	0	3	4	7	2	5
Strumigenys elongata Roger, 1863	0	0	0	0	1	0
Strumigenys spathula Lattke and Goitia, 1997	0	0	1	0	0	0
Tetramorium simillimum (Fr. Smith, 1851)	0	0	0	0	3	0
***Wasmannia auropunctata* (Roger, 1863)**	**1**	**12**	**6**	**29**	**3**	**12**
Wasmannia rochai Forel, 1912	0	1	0	1	2	0
Number of trees investigated	**50**	**50**	**50**	**50**	**50**	**50**
Number of species by age of the plantation	**26**	**52**	**45**	**42**	**62**	**51**
Total number of species			**113**			

Table 2. Diversity index (Shannon Wiener H') and richness estimator (Chao 2), assemblages of arboreal and epigeic ants in cocoa tree plantations of different ages. CEPEC experimental areas, Ilhéus, Bahia, Brazil. September 2008 to March 2009.

Age	Arboreal		Epigeic	
	H'	Chao 2	H'	Chao 2
1 year	2.55	30.92	3.0	102.6
3 years	3.44	79.60	3.53	75.71
4 years	3.22	55.07	3.48	80.99
8 years	3.02	55.08	3.17	38.41
15 years	3.49	75.50	2.85	33.43
33 years	3.41	113.99	2.92	38.98

There are important variations in the ant richness according the cocoa tree increases (expressed by its height; Fig 6a) and the cocoa tree canopy (Fig 6b). Basically, in the first stages, the number of ant species increases according to the age of the plantation, but when the cocoa tree canopies began to touch each other, the diversity of ground-dwelling ants decreases while the diversity of arboreal ants increases (Fig 6).

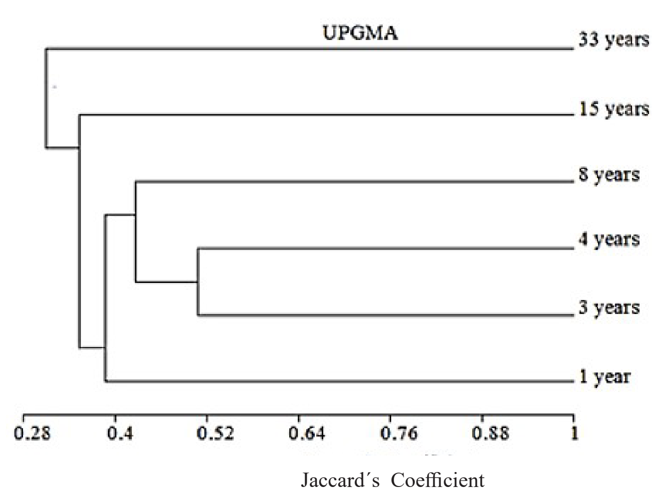

Fig 3. Dendrogram of similarity of arboreal ant assemblages in cocoa plantations according the age of the plantation (1 to 33 years old). CEPEC experimental areas, Ilhéus, Bahia, Brazil. September 2008 to March 2009.

Table 3. Post-hoc correlation of multiple comparisons showing the differences between the ant fauna composition according the age of the cocoa plantations. CEPEC experimental areas, Ilhéus, Bahia, Brazil, from September 2008 to March 2009. P-values in bold are significant (<0.05).

Age (years)	1	3	4	8	15	33
1	-	**0.0000629**	**0.0010204**	0.6368319	**0.0343438**	**0.0009982**
3		-	0.9838423	**0.0213842**	0.4617723	0.9818033
4			-	0.1303235	0.8742881	1.0000000
8				-	0.7082823	0.1308828
15					-	0.8780006
33						-

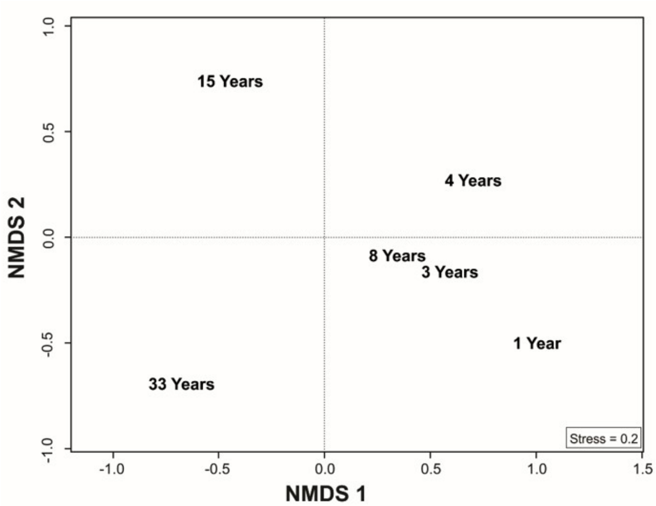

Fig 4. Non-metric multidimensional ordering (NMDS), ordering cocoa plantations (Bray-Curtis similarity) based on the frequency of occurrence of ant species in each one of the areas. CEPEC experimental areas, Ilhéus, Bahia, Brazil, from September 2008 to March 2009. PERMANOVA p <0.001.

We found significant differences in the average number of ant species recorded per plant according to the plantation age ($F = 11.30$, $df = 5$, $p < 0.001$) and stratum ($F = 32.405$, $df = 1$, $p < 0.001$), as well as a significant interaction between age and stratum ($F = 11.901$, $df = 5$, $p < 0.001$). In older and already producing plantations, the assemblages of ants living on the ground and on the trees are significantly different (Fig 7).

The Fisher's LSD test showed that the average number of ants living in the arboreal stratum was significantly lower in the one-year-old plantation than the other ages. In addition, 15 and 33 years-old plantations did not differ in their average number of species per plant, but presented a significantly larger number of ant species than plantations of intermediate ages (three to eight-years-old). The observed number of ants in the epigeic stratum was significantly lower in the one-year plantation compared to the three and four-years-old ones, however it was not significantly different from the other ages. The number of ants found was significantly higher for the intermediate ages (three and four-years-old) in relation to older plantations (Table 4).

Table 4. Post-hoc Fisher's PLSD comparisons showing the differences between the numbers of ant species per plant according to the age of the cocoa plantations. CEPEC experimental areas, Ilhéus, Bahia, Brazil, September 2008 to March 2009. P-values in bold are significant ($p < 0.05$).

Arboreal ants						
Age (years)	**1**	**3**	**4**	**8**	**15**	**33**
1	-	**0.004**	**0.0013**	**0.0015**	**<0.0001**	**<0.001**
3		-	0.7381	0.7131	**0.0181**	**0.0071**
4			-	0.9733	**0.0071**	**0.0025**
8				-	**0.0064**	**0.0023**
15					-	0.7381
33						-
Epigeic ants						
Age (years)	**1**	**3**	**4**	**8**	**15**	**33**
1	-	**<0.0001**	**<0.0001**	0.2926	0.6735	0.3435
3		-	0.1557	**<0.0001**	**<0.0001**	**<0.0001**
4			-	**<0.0001**	**<0.0001**	**<0.0001**
8				-	0.5275	0.9161
15					-	0.5985
33						-

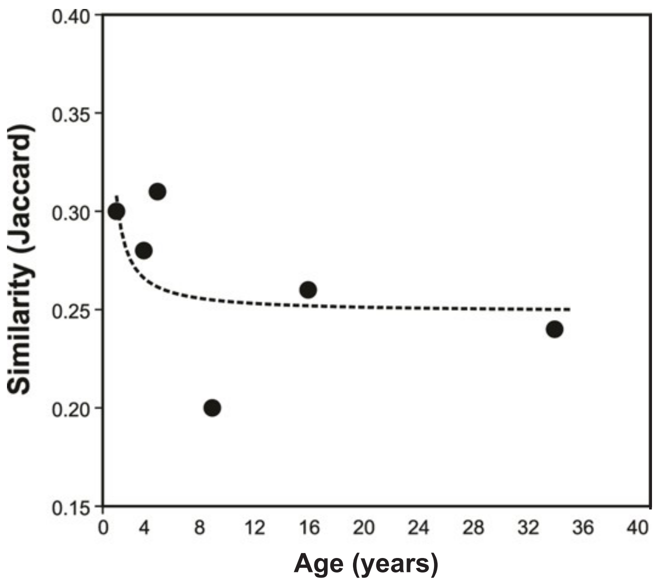

Fig 5. Similarity between soil and arboreal ant assemblages according to cacao plantations age, southeastern Bahia, Brazil, September 2008 to March 2009. The dotted line corresponds to the correlation analysis.

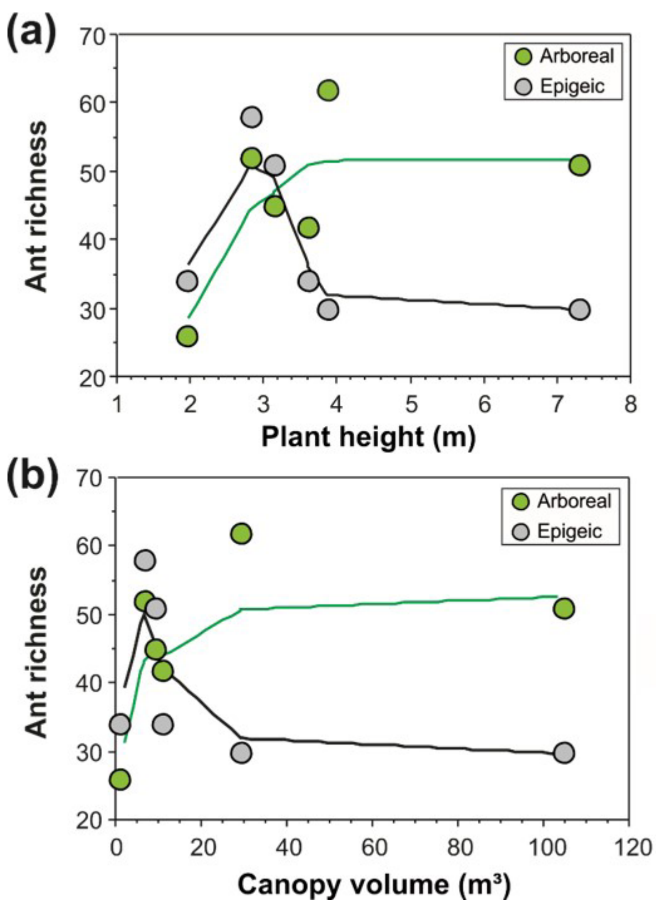

Fig 6. Influence of plant height (m) and crown volume (m^3) of cocoa in the arboreal and epigeic ant richness in cocoa plantations. Ilhéus, state of Bahia, Brazil. September 2008 to March 2009. Lines represent supersmoother display to each strata group.

Discussion

The ant species composition varies during succession, including the ones regarded as dominant in the mosaic of the cocoa trees such as the dolichoderines of the *Azteca* genus and some other competitive species of the genera *Monomorium* or *Crematogaster* (Majer et al., 1994; Delabie et al., 2000; Conceição et al., 2015). The *Wasmannia* genus revealed a highly irregular frequency of occurrence, even more clearly for *W. auropunctata*, which is native to the Neotropical Region and recognized as invasive in other parts of the world (Le Breton et al., 2004; Foucaud et al., 2010). The system of planting the cacao trees likely facilitates its population explosion while species of many other genera suffer from changes in land use.

The cocoa tree plantations showed no evident variation between the diversity indexes in relation to the plantation age. No clear trend of increase or decrease was evident, even with respect to species richness, such as in other similar studies (Majer & Camer-Pesci, 1991; Oliveira et al., 2011). The agroecosystem seems to boost the ant diversity, independently of the developmental stage of the trees. The lack of any upward variation, as first expected, in these indices in the older plantations compared to the younger ones suggests a trend similar to that seen in tropical forests, in which the succession of the arboreal ant communities is observed practically only until 25 years post deforestation (Neves et al., 2010).

Another noteworthy aspect is that the cacao tree crowns have no contact between them in the initial developmental years (Fig 2), while the crown of the trees reach in contact at around 8 years of age. These observations may influence species richness, although exert no effect on the diversity index. In terms of richness, this trend, although significant, may have been rather weak, to such an extent as not to reflect the relationship between these indices and the tree age.

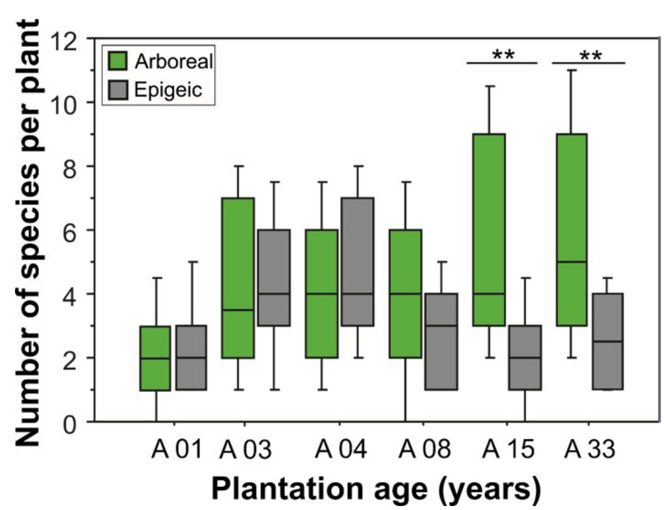

Fig 7. Variation of the average number of ant species per plant in the arboreal stratum (green) and on the ground (grey) according the plantation ages. Asterisks correspond to pair data significantly different.

The lowest diversity and richness indices values recorded in the one-year-old area definitely result from the straighter incidence of the sun on the ground, in comparison with all the others. Ants are susceptible to microclimatic variations like solar radiation, which can be determinant in the survival of certain species (Ríos-Casanova, 2006). Furthermore, species living in unfavorable environments most likely possess a better degree of physiological tolerance to variations of humidity and thermal amplitude, for example (Hölldobler & Wilson, 1990).

The similarity observed in the indices of species diversity among the cocoa tree plantations of very different ages, like those with 3, 15 and 33-years-old, suggest some kind of resilience common to all the parcels in the whole cocoa farm. Simultaneously, some species, either because of competition or stochastic factors, may not be present any longer in the environment, while others begin to arise into the community, inducing the observed variation between the diversity indexes. The ant community structure is dependent on the level of requireness or tolerance of each species, which in turn affects its distribution.

The species composition pattern during succession differed among plants of very different ages, although some similarities were observed in the cocoa tree plantations that were close in age. Thus, the assemblage structure which results from the advent of some species and the suppression of others, may have caused these variations (Majer et al., 1994; Sanders et al., 2007). These are natural oscillations that can also take place due to changes in the spatial distribution of certain populations, because although relatively stable over the time (Medeiros et al., 1995), the arboreal ant mosaic gets continuously restructured depending on the development of the host tree and other factors, such as local microclimate.

During the beginning of ecological succession in young plantations, the ant community varied greatly in composition with strong differences in the local distribution and in the abundance of arising species. During the later successional phases, however, a much less variation in the community composition was noted, similarly to what Dauber and Wolters (2005) observed in temperate grasslands.

In young plantations, the ants living on the ground and on the cocoa trees belong to the same assemblage and there are only low differences between the species found on the ground and the ones found on the young trees. In older plantations, it exists at least three congruent phenomena which contribute to diverge the cocoa ant community in two distinct assemblages on one side, on the ground and on the other, on the trees: i) in plantations older than 8 years, the canopies of neighboring trees tend to be closer from one tree to another, which facilitates to the arboreal ants colonizing the habitat and allowing the mosaic of dominant ants to become organized (see Majer et al., 1994); ii) the soil surface receives less and less direct sunlight according the plantation aging and; iii) there is low opportunities for ants living on and in the soil to tend mutualistic sap-sucking insects (Delabie, 2001), which is an important element of the success of arboreal ants in general. The rareness of sunlight certainly contributes to decrease the productivity of the soil biota but not its richness, and is possibly responsible for the strong specialization observed in many organisms living in this stratum, such as extremely specialized predation, fungus-growers and scavengers. The cocoa tree leaf litter is regarded as the stratum at which more specialized and the larger number of ant species inhabit (Delabie et al., 2000, 2007; Delabie & Mariano, 2001); the density of this stratum appears to have no effect either on the species diversity or richness (Delabie & Fowler, 1995). On the other hand, the organization of the arboreal species in function of the plant development is responsible for the mosaic of dominant ants which is typical of this kind of agroforestry (see Majer et al., 1994). Furthermore, the tree canopy may be colonized by an assemblage of typical arboreal species characteristic of the agro-ecosystem which distinctly diverges from the epigeal and edaphic faunal composition on its side closer from a forest assemblage (Vasconcelos & Vilhena, 2006; Delabie et al., 2007).

Therefore, the conclusion drawn is that, among the cocoa tree plantations of the Southeast of Bahia, no gradient of diversity and richness of the ant community is evident that even temporarily follows the course of the development of the host plant. However, gradual changes are seen in the faunal composition, with a pattern of species being structured during the various developmental stages; this pattern is very different when the younger and older cocoa trees are compared. The alterations in the species distribution and regulation of the ant populations take place according to the mosaic of the dominant arboreal ants at all the plant developmental stages. This is a structured and organized phenomenon (see Conceição et al., 2015), and is the most likely cause for the unequal variations observed in the species diversity and richness.

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