Agroforest Syst (2025) 99:1
https://doi.org/10.1007/s10457-024-01102-7

Conservation of ant communities in cashew tree-based agroforestry systems: key roles of tree density and diversity

Anicet G. Dassou · Charlemagne D. S. J. Gbemavo · Alexis Onzo · Sathurnin Kpoto · Corinne M. Anagonou · Alexandre Dansi · Philippe Tixier · Dominique Carval

Received: 4 November 2023 / Accepted: 28 November 2024
© The Author(s), under exclusive licence to Springer Nature B.V. 2024

Abstract Under the pressure exerted by humans on forest ecosystems, agroforestry is promoted to maintain a balance between forest and agricultural ecosystems. Agroforestry systems are the center of interactions between crops and other plants and between fauna and flora. Within this faunistic diversity, ants occupy a prominent place through their protective association with some tropical plant species as natural enemies of their arthropod pests. In this study, we analyzed the effects of the diversity of trees associated with cashew trees and of cashew tree density on ant abundance/diversity in cashew agroforestry systems. The study was conducted in 12 cashew orchards in central Benin. Data on the diversity and densities of ground-dwelling and arboreal ant species were collected using hand and bait traps. The diversity of trees in the orchards and cashew tree density were also determined. Twenty ant species were collected among which the most abundant were *Pheidole* spp., *Lepisiota* sp., *Paratrechina longicornis*, *Camponotus sericeus*, *Brachyponera sennaarensis*, *Camponotus* spp., and *Oecophylla longinoda*. Tree diversity and cashew tree density in those orchards had significantly positive effects on the ant densities but not on ant diversity. Structural equation modeling showed that the abundance of ants increased the diversity of ants, which decreased the herbivory index. Based on the important role of ants as biological pest control agents, it is worth promoting agroforestry systems in cashew orchards to increase ant abundance, thereby improving their productivity.

Keywords Orchards · Conservation biological control · Biodiversity · Ant · Forest conservation · Benin

A. G. Dassou (✉) · C. D. S. J. Gbemavo · S. Kpoto · C. M. Anagonou · A. Dansi
National High School of Biosciences and Applied Biotechnologies (ENSBBA), National University of Sciences, Technologies, Engineering and Mathematics (UNSTIM), BP 14 Dassa, Abomey, Benin
e-mail: dassoua5@gmail.com

A. Onzo
Faculty of Agronomy, University of Parakou, 02 BP 1003 Parakou, Benin

P. Tixier · D. Carval
CIRAD, UPR GECO, 34398 Montpellier, France

P. Tixier · D. Carval
GECO, Univ Montpellier, CIRAD, Montpellier, France

P. Tixier
UPR GECO, CIRAD, Vientiane, Laos, France

D. Carval
CIRAD, UPR GECO, 97455 Saint-Pierre, La Réunion, France

Introduction

In agricultural and forestry systems, Conservational biological control (CBC) can foster sustainable yields

Published online: 21 December 2024

at lower costs than alternative non-sustainable methods based on chemical pesticides (Offenberg 2015). One of the key components of CBC is the implementation of practices that maintain and enhance the reproduction, survival, and efficacy of natural enemies (predators, parasitoids, and pathogens) of pests (Van Lenteren 2000; Chailleux et al. 2013). In addition, recent studies in agroecosystems have revealed that generalist predators (single- and multiple-species assemblages) are the most involved in controlling herbivore abundance (79% of studies), thereby reducing plant damage and increasing plant yields (65% of studies) (Symondson et al. 2002; Dassou and Tixier 2016). Among these generalist predators, ants are an important and one of the most abundant and diversified groups, with an estimated world population of 10^{15} adults (Wilson 1971). In tropical ecosystems, ants may represent up to 80% of animal biomass (Hölldobler and Wilson, 1990). Given the potential role of ants as biological pest control agents in agroecosystems (Dassou et al. 2023), it is worth investigating the functionality of different tropical ecosystems to promote those that positively affect ant densities.

Tropical agroforestry systems are characterized by the presence of trees associated with the crop areas, thereby creating landscapes called "parks" or "agrosilvopastoral landscapes" (Zomboudré et al. 2005). These agroforestry systems capitalize on land use strategies that associate trees and cultivated plants in a random spatial arrangement (Sinclair 1999; Boffa 2000). This is precisely the case in Benin for well-known native savannah tree species such as *Parkia biglobosa* (Jacq.) Benth, the shea tree *Vitellaria paradoxa* CF Gaertn. F. (Gbemavo et al. 2010), and planted tree species such as cashew (*Anacardium occidentale* L), which are maintained together with food and cash crops (Agbahungba and Depommier 1989). Agroforestry systems are generally characterized by a canopy cover of shade trees below which a wide range of crop plants can be grown (Schroth et al. 2004). Consequently, in human-dominated deforested landscapes, agroforestry systems provide the only remaining habitat type with a substantial tree cover (Schroth et al. 2004).

Interactions between ants and plants are a key phenomenon in moist agroforestry systems (Philpott and Armbrecht 2006; Gras et al. 2016). Ants reduce some undesirable pest populations by directly preying upon them, chemically deterring them, or causing them to drop off the host plants that they are attacking (Way and Khoo 1992). Therefore, most functional studies on these relationships have been devoted to the question of the protective value of ants on those plants, often using a rather general approach. For instance, whereas Offenberg (2015) showed that ants play important ecological roles in agroforestry systems, other studies reported that management practices can strongly influence ant behavior and their potential for providing biological pest control services (Armbrecht and Gallego 2007; Teodoro et al. 2010; Abdulla et al. 2016). Surprisingly, however, very few studies have examined the relationship between ant density and tree density or diversity in agroforestry systems. The study by Philpott et al. (2006) showed that ant diversity generally decreased with the intensification of coffee- and cocoa-based agroforestry systems. Another study has shown the interactions of ants with cashew trees and has specified that ants are often attracted to a large number of extrafloral nectaries on leaves, inflorescences, flowers and developing nuts (Rickson and Rickson 1998). In India, the ant species richness has been studied and their interactions with cashew trees (Vanitha et al. 2017), but did not show how other associated trees in the orchard environment could affect this ant species richness. However, the literature lacks a summary of the known mechanisms that govern the declining ant diversity and how this diversity loss may affect the role of ants as predators of insect pests. Moreover, the effect of tree richness (i.e., density and diversity) is not always positive on the predator community, as shown in Poeydebat et al. (2017), and thus still needs to be investigated.

Generally, agroforestry systems based on cashew trees (*A. occidentale*) are one of the most widespread in West Africa. Indeed, cashew is an important cash crop that attracts several growers and even developers as it significantly contributes to the gross national product of many countries. Because of this growing interest in cashew nut production and the need to increase its productivity, the predatory role of ants in cashew agrosystems is worth exploring. The hypothesis of our study is to show how the heterogeneity of cashew orchards with a gradient of tree diversity and cashew tree density could improve the conservation and abundance of predatory ant species. We also expected to find that conservation of ant species in cashew orchards would contribute to a reduction in herbivory in these cropping systems. In that respect, our study aimed to (i) determine the structure of ant communities in a cashew tree-based agroforestry system; (ii) assess the effect of tree density/diversity on the diversity of ant communities and herbivory index in a cashew tree-based agroforestry system; and (iii) determine the relationship between cashew tree locations and the abundance of ant populations.

Materials and methods

Study site

The study was conducted in the municipalities of Dassa-Zoumé (longitude: 2°10′59.99″E and latitude: 7°45′0.00″N), Glazoué (longitude: 2°14′14.40″E and latitude: 7°58′14.99″N), and Savalou (longitude: 1°58′32.09″E and latitude: 7°55′41.05″N) in the Department of Collines in Central Benin. The study covered a total area of 13,931 km^2, characterized by a series of bare hills with an average elevation of 200 m above sea level. The climate is of the subequatorial type, dominated by two rainy seasons and two dry seasons. The average annual rainfall oscillates between 960 and 1256 mm, whereas the average temperature varies between 24 and 29 °C (Adomou, 2011). Covered with natural vegetation, the municipality of Dassa-Zoumé is a peneplain with savannah and a shrubby cut of deciduous and semi-deciduous forests and some forest galleries along the rivers. The vegetation at Glazoué and Savalou is also made up of natural vegetation (riparian forests, gallery forests, dense forests, dry forests, clear forests, wooded savannahs, and savannahs), and teak plantations. Soils in the study area are tropical ferruginous with concretions at some places. There are also some hydromorphic soils and vertisols (Adomou, 2011).

Village selection criteria

The choice of villages was made based on cashew production and the size of the areas planted with cashew trees. This information was gathered from the villagers and complemented by our direct observations in each village. In each village, a plantation of around 2 ha in size and in associations with tress was selected. These criteria were used to compare the level of plant diversity between the selected plantations. In each of the three municipalities, four villages were selected, resulting in a total of 12 cashew orchards involved in the study. These included community as well as individual plantations, both of which exhibited several forms of flowering. In the study area, the first plantations were planted around 1965 while the young plantations were around 10 years old. We have selected young plantations that were set up by farmers with wide margins, thereby allowing intercropping with maize and groundnuts. These plantations were covered by weeds, principally *Andropogon gayanus* Kunth, *Panicum maximum* Jacq., and *Imperata cylindrica* (L.) Raeusch. The average cashew nut yield of 285 kg per ha (Arouna et al. 2010).

Characterization of the plots studied

In the study area, cashew trees were generally planted at a spacing of 12 m within each row and 12 m between rows; this spatial organization is recommended for the optimal use of products. The cashew trees were in flowering and fruiting phases. Cashew orchards were thinned with a periodicity of 5 years. In each village, the study objectives were explained to cashew farmers as a group. In the center of each orchard studied, an experimental plot of 1 ha was delimited. Then, cashew trees within this plot were counted to determine their abundance or density in these plantations. Other trees associated with cashew trees were also listed and counted to study the heterogeneity comprising the diversity of trees in these agroforestry systems.

Assessment of ant densities

The study was carried out for 2 months (from April to May) in the rainy season of 2017 and was repeated for two more months (November and December) in the dry season of the same year. Ants were collected in the morning, between 08:00 and 12:00, once during the rainy season and once in the dry season. Both the abundance and diversity of ant communities were assessed using two collecting methods: i) using a standardized attractive device consisting of a white ceramic tile (30 × 20 cm) to collect ground-dwelling ant species (Dassou et al. 2015) and ii) direct collection by hand to collect arboreal ant species on the trunk, branches, and leaves of cashew trees.

For the first method, a total of 10 white ceramic tiles were randomly placed around the base of 10 cashew trees in each experimental plot. In the center of each tile, 10 g of bait (5 cm in diameter) composed of honey mixed with sardine (Dassou et al. 2015, 2016, 2017) was deposited to attract the ants. After 10 min, a picture was taken using a high-resolution camera, and the ants on the tile were counted and identified. Following observations on each tile continued for at least 60 min, which allowed other ants to be recorded and counted after the departure of the dominant species. The ants that fled from the bait were identified and counted in the laboratory using the images taken by the camera.

Direct collection by hand was used to assess the abundance and diversity of arboreal ants. All the ant samples were kept separately per tree and orchard and were preserved in 70% ethanol and brought to the laboratory for their identification. The ant samples were identified at the entomology laboratory of CIRAD, Montpellier using the identification key "Ants of Africa and Madagascar" by Fischer and Bolton (2016). Ant densities were estimated by considering the number of each species per ha of cashew orchard by pooling together hand-collected and bait-collected samples.

Assessment of herbivory

The herbivory by insects was also evaluated. The mean leaf herbivory index was identified as follows: 0 = no damage; 1 = little damage (pinholes and/or small holes); 2 = mean damage (some larger holes and/or larger leaf edge areas eaten); and 3 = heavy damage (many larger holes and/or larger leaf edge areas eaten). This score was assigned to each cashew plant based on an overall observation of the damage level to the leaves. The evaluation of herbivory was made using the 10 cashew trees selected for the ant density measurements in each experimental plot. Visual observation of the damage was carried out by the same person throughout the experiment.

Data analyses

Catches from the traps were examined and counted to identify the dominant ant species. We used a Poisson generalized linear model (GLM) to test the effects of tree diversity and cashew tree densities in the selected orchard on (i) the species richness of the ant communities; (ii) the density of the ant communities; and (iii) the density per ant species. The GLM was also used to test the effects of locality on (iv) the species richness of the ants and (v) the density of the ants. Visualizations of the relationships between variables were performed using the ggplot function of the ggplot2 package (Wickham, 2016). GLMs of the Poisson family were made using the GLM function of the "car" package (Fox and Weisberg, 2011). In the event of overdispersion, the quasi-Poisson family was used to perform the analyses. The cashew tree density variable did not follow the normal distribution and was transformed using the log (x) + 1 function. Tree diversity was assessed with the Shannon index. The relationships between tree diversity, cashew tree density, and diversity/abundance of ants and between the abundance/diversity of ants and herbivory index were analysed using structural equation modeling (SEM) with the lavaan package (Rosseel 2012). Marginal R^2 was used as an absolute value for the goodness-of-fit of the models (Nakagawa and Schielzeth 2013). All statistical analyses were carried out with R software version 4.2 and an alpha level of 0.05 (R Core Team 2019).

Results

Ant density in cashew tree-based agroforestry systems

From the 12 study sites, a total of 3,472 individual ants belonging to 20 different species were collected during the study period. The most abundant species or morphospecies, with densities greater than 100 individuals per ha, were *Pheidole* sp.1 (578 individuals), *Lepisiota* sp. (502 individuals), *Paratrechina longicornis* (430 individuals), *Camponotus sericeus* (412 individuals), *Pheidole* sp.2 (398 individuals), *Brachyponera sennaarensis* (282 individuals), *Camponotus* sp.5 (278 individuals), *Oecophylla longinoda* (134 individuals), *Pheidole megacephala* (114 individuals), and *Camponotus* sp.1 (110 individuals) (Fig. 1).

Influence of the diversity of trees associated with cashew trees and of cashew tree density on ant density and diversity

Many trees were associated with cashew trees in sampled orchards (Table 1). Overall tree diversity (Df = 118, AIC = 511.6, p = 0.24) and cashew tree

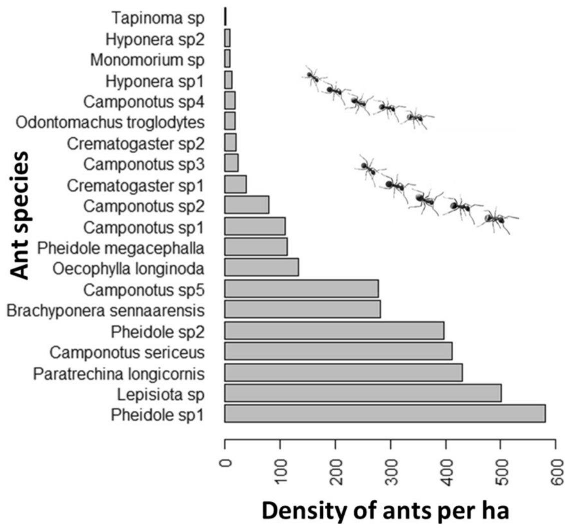

Fig. 1 Density of ant species collected from cashew tree-based agroforestry systems. This shows the density of each ant species per hectare of cashew plantation

density (Df = 117, AIC = 512.3, p = 0.3600) had no significant effects on the species richness of the ant communities in this agroforestry system. In contrast, the diversity of the associated/intercropped trees (Df = 118, AIC = 4741, $p < 0.00001$) and cashew tree density (Df = 118, AIC = 4533, $p < 0.00001$) had significant effects on ant densities, which increased with cashew tree densities (Fig. 2). More specifically, tree diversity had significant effects on the densities of the ant species *C. sericeus*, *Camponotus* sp.1, *Camponotus* sp.2, *Camponotus* sp.5, *Lepisiota* sp., *Odontomachus troglodytes*, *Pheidole* sp.1, and *Pheidole* sp.2 (Table 2). However, the effects were negative on *O. troglodytes*, *Lepisiota* sp., *Camponotus* sp.1, and *Camponotus* sp.2 (Fig. 3).

As for cashew tree density, there were significant relationships between this parameter and the densities of most ant species but non-significant for *Camponotus* sp.5, *Crematogaster* sp.1, *Hypoponera* sp.2, *Pheidole* sp.1, and *Tapinoma* sp. (Table 3). Specifically, the relationship was positive between cashew tree density and the density of *Camponotus* sp.1, *O. longinoda*, *Crematogaster* sp.2, *O. troglodytes*, *Camponotus* sp.2, *Monomorium* sp., *Hypoponera* sp., *P. megacephala*, *Camponotus* sp.3, *Camponotus* sp.4, and *Pheidole* sp.2, but it was negative between cashew tree density and the density of *B. sennaarensis*, *C. sericeus, Lepisiota* sp., and *P. longicornis* (Fig. 4).

SEM analyses showed that a high density of cashew trees increased ant density and also herbivory by insects. High ant diversity leads to high ant density, which was negatively related to the herbivory index. Tree diversity was negatively related with the herbivory index but had no significant effect on ant diversity and abundance (Table 4; Fig. 5).

Influence of locality on the species richness and density of ants

Locality had a significant effect on ant diversity (Df = 2, AIC = 69.69, LRT = 34.16, p < 0.00001), ant species richness (Df = 2, AIC = 513.16, LRT = 96.378, $p < 0.00001$), and ant density (Df = 2, AIC = 4787.7, LRT = 552.46, $p < 0.00001$). The municipality of Glazoué had the highest ant density with 1824 ants followed by Dassa-Zoumé with 898 ants and Savalou with 752 ants.

Table 1 Plant species associated with cashew trees in the three locations studied

Associated trees	Common names	Orders	Families	Genus and species	Densities
1	Cashew tree	Sapindales	Anacardiaceae	*Anacardium occidentale*	5514
2	Lemon tree	Sapindales	Rutaceae	*Citrus limon*	30
3	Mango tree	Sapindales	Anacardiaceae	*Mangifera indica*	314
4	Neem	Sapindales	Meliaceae	*Azadirachta indica*	112
5	Orange tree	Sapindales	Rutaceae	*Citrus sinensis*	114
6	Oil palm tree	Arecales	Arecaceae	*Elaeis guinense*	100
7	Locust bean tree	Fabales	Mimosaceae	*Parkia biglobosa*	138
8	Teak	Lamiales	Lamiaceae	*Tectona grandis*	70

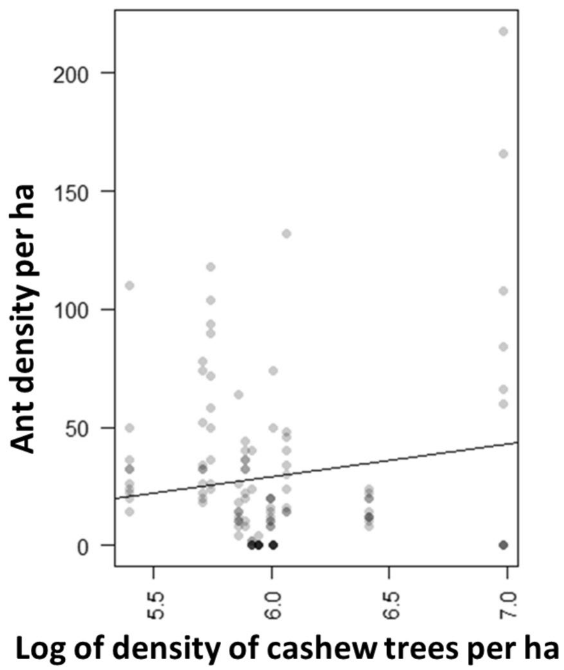

Fig. 2 Influence of cashew tree density on ant density. A correlation was realized between the density of cashew trees and the density of ants collected. To normalise the data, the cashew tree density was transformed using the function log (x) + 1

Table 2 Effect of tree diversity on the density of each ant species. LRT: likelihood ratio test; Df: degrees of freedom; AIC: Akaike information criterion; Pr: probability

Ant species	Df	AIC	LRT	Pr (> Chi)
Brachyponera sennaarensis	1	810.12	1.65	0.198
Camponotus sericeus	1	1045.90	6.29	0.012 *
Camponotus sp.1	1	337.24	26.17	< 0.00001***
Camponotus sp.2	1	448.25	49.27	< 0.00001***
Camponotus sp.3	1	170.25	0.02	0.874
Camponotus sp.4	1	91.63	0	0.999
Camponotus sp.5	1	973.30	82.13	< 0.00001***
Crematogaster sp.1	1	391.74	0.058	0.809
Crematogaster sp.2	1	83.97	0	0.999
Hypoponera sp.1	1	72.96	0	0.999
Hypoponera sp.2	1	103.71	0.014	0.903
Lepisiota sp.	1	1500.40	8.36	0.003 **
Monomorium sp.	1	54.20	0	0.999
Odontomachus troglodytes	1	86.79	4.35	0.036 *
Oecophylla longinoda	1	237.07	0	0.999
Paratrechina longicornis	1	1066.80	3.05	0.081
Pheidole megacephala	1	471.86	0	1
Pheidole sp.1	1	1345.20	4.16	0.041 *
Pheidole sp.2	1	1343.30	65.66	< 0.00001***
Tapinoma sp.	1	4	0	1

*Low significant; ** mean significant; *** high significant

Discussion

Overall, 20 species of ants were collected in the sampled fields; the most abundant species were *Pheidole* spp., *Lepisiota* sp., *P. longicornis*, *Camponotus* spp., and *O. longinoda*. These ant species were also reported by Agboton et al. (2014) as being dominant in cashew systems in Benin. Their abundance could be explained by the fact that these species have competitive traits, and their large numbers could have favored them in the event of interspecific competitions with other ant species for space (Sarty et al. 2006). They are also known to occupy most of the trees in cocoa plantations while excluding the less competitive species with which they share ecological niches (Room 1971). Ants are acknowledged as playing an important role in protecting plants/trees against phytophagous insects, including phyllophagous, carpophagous, sapro-xylophagous, and xylophagous insects (Fiala et al. 1989; Del-Claro et al. 1996). Dominant ant species can reduce the species richness of natural enemies and the ecological stability of the food web because of their aggressive behavior, which excludes other species from their territory and food sources (Gibb and Hochuli 2003).

The diversity of other tree species encountered within the cashew orchard did not influence the diversity of ant species. This observation could be explained by a higher preference of ants for cashew trees, but also by a possible reduction in ant diversity by the most dominant ant species through competitive displacement of the less competitive species. Our results are in line with those by Poeydebat et al. (2017), who showed that tree richness did not increase the abundance of predators in tropical agroforestry systems. However, they contrast with those reported by previous studies that showed that heterogeneous landscapes increase the diversity and richness of ant communities (Ribas et al., 2007; Pacheco and Vasconcelos 2012).

Cashew tree-based agroforestry systems are very complex. Cashew trees are associated with other large trees such as *P. biglobosa*, *V. paradoxa*, and

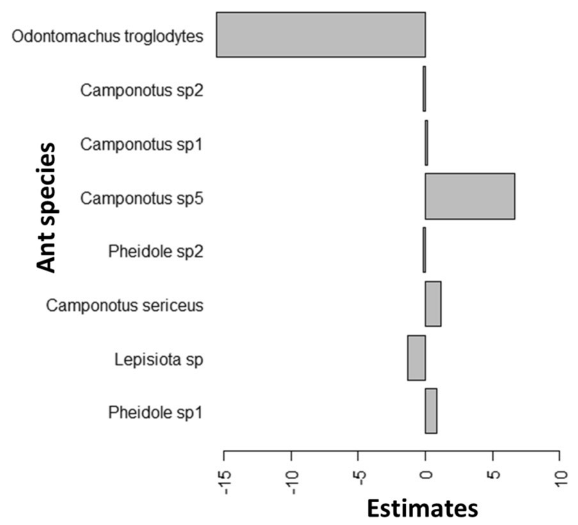

Fig. 3 Variation in the effect of tree diversity on the density of ant species. The estimates of the models used show the direction of variation in the effects of plant diversity on ant abundance. These estimates are used to make the histgram to show the positive or negative effect of plant diversity on the abundance of each ant species

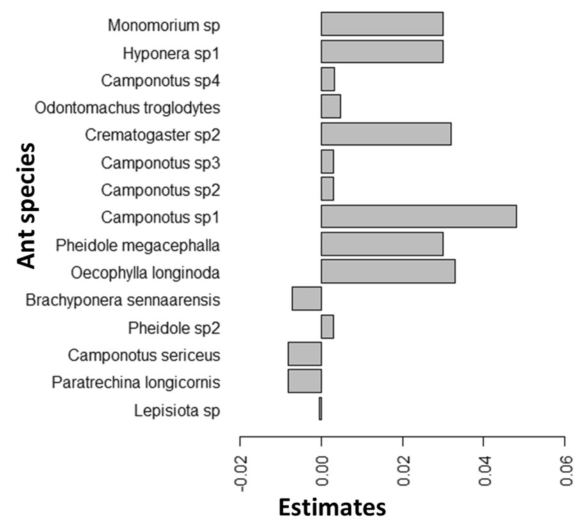

Fig. 4 Variation in the effect of the density of the cashew trees on the density of ants. The estimates of the models used show the direction of variation in the effects of cashew density on ant abundance. These estimates are used to make the histgram to show the positive or negative effect of cashew density on the abundance of each ant species

Table 3 Effect of cashew tree density on the density of each ant species. LRT: likelihood ratio test; Df: degrees of freedom; AIC: Akaike information criterion; Pr: probability

Ant species	Df	AIC	LRT	Pr (> Chi)
Brachyponera sennaarensis	1	956.27	147.81	< 0.00001
Camponotus sericeus	1	1259.20	219.57	< 0.00001
Camponotus sp.1	1	568.46	257.38	< 0.00001
Camponotus sp.2	1	492.06	93.08	< 0.00001
Camponotus sp.3	1	198.18	27.95	< 0.00001
Camponotus sp.4	1	151.62	59.99	< 0.00001
Camponotus sp.5	1	893.80	2.62	0.104
Crematogaster sp.1	1	392.28	0.61	0.436
Crematogaster sp.2	1	150.63	66.65	< 0.00001
Hypoponera sp.1	1	119.62	46.65	< 0.00001
Hypoponera sp.2	1	103.84	0.15	0.697
Lepisiota sp.	1	1496	3.96	0.046 *
Monomorium sp.	1	87.54	33.33	< 0.00001
Odontomachus troglodytes	1	124.31	41.86	< 0.00001
Oecophylla longinoda	1	683.66	446.59	< 0.00001
Paratrechina longicornis	1	1322.90	259.12	< 0.00001
Pheidole megacephalla	1	851.80	379.93	< 0.00001
Pheidole sp.1	1	1342.60	1.49	0.222
Pheidole sp.2	1	1439.60	162.01	< 0.00001
Tapinoma sp.	1	4	0	1

*: low significant; **: mean significant; ***: high significant

Mangifera indica L, which are known to occupy relatively large land spaces. This complexity of the system may hinder the dispersal capacity of some ant species, thereby limiting their species richness. Resources in simple habitats are more accessible than those in more complex habitats (Gibb 2005). Therefore, in such complex habitats, smaller and less competitive ant species may be prone to disappear (Fewell 1988). Other factors that could interfere with, or reduce ant diversity, in cashew systems include the destruction of some plants that shelter ants by bushfires that are intentionally or accidentally made by farmers, especially during the dry season, to clear their field plots from weeds. Indeed, slow ground ant species may be killed during these bushfire events. Cashew plantations in Savalou and Dassa-Zoumè have fewer ants than those in Glazoué. This shows that farmers in these two localities do not use good practices that could improve the conservation of ants in cashew plants.

Whereas tree diversity within the cashew orchards did not influence the diversity of ant communities. This result can be justified by the fact that cashew plantations are fairly large and we did not select several experimental sites in order to observe a gradient in the diversity of trees associated with

Table 4 Pathway coefficient estimates, critical values, and p-values from the SEM of relationships between the diversity of trees or density of cashew trees and the abundance/diversity of ants and herbivory index in cashew cropping systems

Responses	Predictors	DF	Critcal-value	Estimate	*p* value
Abundance of ants	Density of cashew trees	117	2.62	0.23	0.009**
Diversity of ants	Diversity of trees	117	−0.41	−0.03	0.68
Abundance of ants	Diversity of trees	117	−0.07	−0.89	0.94
Diversity of ants	Abundance of ants	117	9.72	0.18	< 0.00001***
Index of herbivory	Diversity of trees	117	−3.11	−3.11	0.0023**
Index of herbivory	Density of cashew trees	117	2.49	2.8	0.0138**
Index of herbivory	Diversity of ants	117	−0.007	−0.12	0.99
Index of herbivory	Abundance of ants	117	−0.3	−0.21	0.0001***

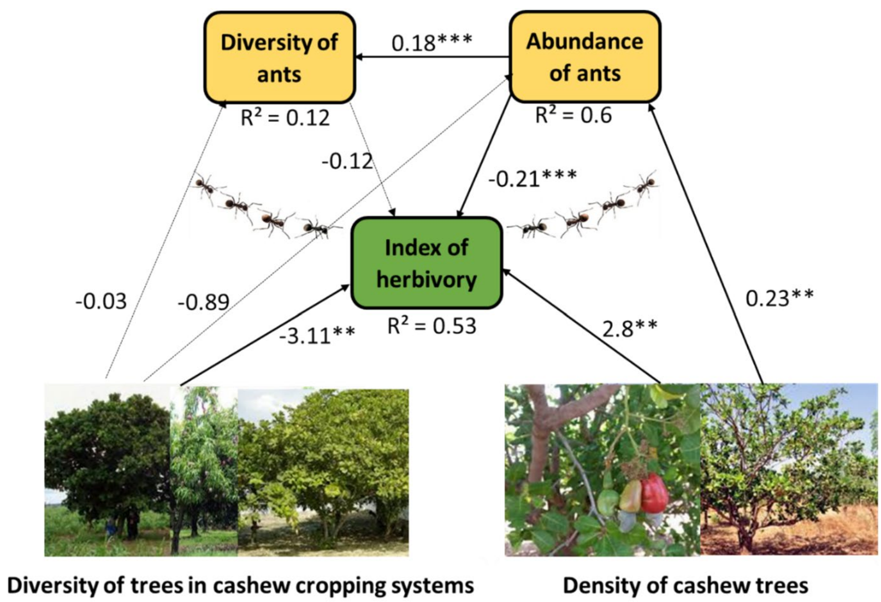

Fig. 5 Structural equation model (SEM) of the relationships between the diversity of trees or density of cashew trees and abundance/diversity of ants and herbivory index in cashew cropping systems. Full and dashed arrows represent ($p < 0.05$) significant and ($p > 0.05$) non-significant relationships, respectively. Marginal R^2 values for each response variable are indicated

the plantations and to better appreciate their influence on ant communities. Our study showed that both the diversity of trees associated with cashew trees and the density of cashew trees within an orchard were associated with an increase in the population densities of ant species. These findings are supported by Vasconcelos et al. (2008), who reported that vegetation composition can influence the availability of food resources (i.e., the presence of plants with extrafloral nectars) and ant nesting sites, as well as the species' ability to compete. Likewise, Davidson and Mickey (1993) explained that ants maintain many interactions with plants because some ant species live in mutualism with host plants and protect them against herbivores (Bronstein 1998; Cushman, 1991). Our results showed that ant abundance was negatively correlated with the herbivory index. This means that ants reduce the damage caused by herbivorous insects in cashew plants. In that respect, *Pheidole* spp. and *P. longicornis* are considered as developing mutualistic interactions with their host plants (Horvitz and Schemske 1990), as is the case for the majority of ant species that are predators of herbivorous insects. One such example is that of *Lepisiota* sp., which is found in agroforestry systems including cashew trees (Rickson and Rickson 1998; Agboton et al. 2014) and has been shown to be a predator of herbivores in banana-based cropping systems in Uganda (Abera-Kalibata et al. 2007). The presence of *O. longinoda* in these cashew tree-based agrosystems is not surprising because this ant species is a predator of some cashew pests (Dwomoh et al. 2009; Vaysieres et al., 2015).

Implications of the study for the conservation of ant communities

Although the weaver ant, *O. longinoda*, has long been considered as a biological pest control agent of some cashew pests, few studies have investigated the role played by other ant communities in the cashew agroecosystems. Our study revealed the occurrence of a high abundance of other predatory ant species that dominate cashew tree-based agroecosystems. Therefore, how these ant species interfere/interact with *O. longinoda* in cashew orchards needs to be investigated for the sustainability of CBC programs involving cashew pests. In addition, the diversity of trees in cashew tree-based agroforestry systems was shown to increase ant density and could, therefore, be a development lever for the sustainability of these systems.

Conclusion

Our study is carried out to better understand the interactions between trees and ant communities in cashew-based agroforestry systems for their sustainability. The study showed an increase in ant abundance through an increase in tree diversity and density. These trophic and non-trophic interactions have contributed to reducing insect herbivory.

Acknowledgements This work was financially supported by a Rufford Small Grant for Nature Conservation (United Kingdom) provided to Anicet G. Dassou in 2017. We thank the cashew farmers who participated in our interviews and made their orchards available for experiments.

Author contribution AGD and CDSJG conceived the study, SK and CMA conducted the experiments and collected the data with assistance from AGD, AD, AGD, CDSJG. AGD, DC, PT analyzed the data. AGD, CDSJG wrote the first version paper with revisions from AO, AD, DC and PT.

Funding Rufford Foundation, 002

Declarations

Competing Interests The authors declare no competing interests.

References

Abdulla NR, Rwegasira GM, Jensen KM, Mwatawala MW, Offenberg J (2016) Control of mango seed weevils (*Sternochetus mangiferae*) using the African Weaver Ant (*Oecophylla longinoda* Latreille; Hymenoptera: Formicidae). J Appl Entomol 140(7):500–506

Abera-Kalibata AM, Gold CS, Van Driesche RG, Ragama PE (2007) Composition, distribution, and relative abundance of ants in banana farming systems in Uganda. Biol Control 40(2):168–178

Adomou AC, Agbani OP, Sinsin B (2011) Plantes. Protection de la nature en Afrique de l'Ouest: Une liste rouge pour le Bénin. In: Nature conservation in West Africa: red list for Bénin, pp 21–46

Agbahungba G, Depommier D (1989) Aspects du parc à karités-nerés (Vitellaria paradoxa Gaertn. f.- *Parkia biglobosa* Jacq. Benth) dans le sud du Borgou (Bénin). Bois Forets des Trop 22(2):41–54

Agboton C, Onzo A, Ouessou FI, Goergen G, Vidal S, Tamo M (2014) Insect Fauna associated with *Anacardium occidentale* (Sapindales: Anacardiaceae) in Benin. West Africa J Insect Sci 14(1):1–11

Armbrecht I, Gallego MC (2007) Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. Entomol Exp Appl 124(3):261–267

Arouna A, Adegbola PY, Adekambi SA (2010) Estimation of the economic efficiency of cashew nut production in Benin, No. 308–2016–5130, pp 1–17

Boffa JM (2000) Les parcs agroforestiers en Afrique de l'Ouest : clés de la conservation et d'une gestion durable. Unasylva 51(200):11–17

Bronstein JL (1998) The contribution of Ant-Plant Protection studies to our understanding of Mutualism 1. Biotropica 30(2):150–161

Chailleux A, Bearez P, Pizzol J, Amiens-Desneux E, Ramirez-Romero R, Desneux N (2013) Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. J Pest Sci 86(3):533–541

Cushman JH, Whitham TG (1991) Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. Am Nat 138(4):851–865

Dassou AG, Tixier P (2016) Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. Ecol Evol 6(4):1143–1153

Dassou AG, Carval D, Dépigny S, Fansi G, Tixier P (2015) Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping. Biol Control 81:51–57

Dassou AG, Dépigny S, Canard E, Vinatier F, Carval D, Tixier P (2016) Contrasting effects of plant diversity across arthropod trophic groups in plantain-based agroecosystems. Basic Appl Ecol 17(1):11–20

Dassou AG, Tixier P, Dépigny S, Carval D (2017) Vegetation structure of plantain-based agrosystems determines numerical dominance in community of ground-dwelling ants. PeerJ 5:e3917

Dassou AG, Loko YLE, Toffa J, Gbèmavo C, Adjahossou N, Tchakpa C, Agboyi L, Sanon A, Dansi A, Brévault T (2023) Within-field crop diversity and landscape complexity decrease the abundance of fall armyworm larvae in maize cropping systems. Biol Control 183:105260

Davidson DW & McKey D (1993) The evolutionary ecology of symbiotic ant-plant relationships. pp 1–28

Del-Claro K, Berto V, Réu W (1996) Effect of herbivore deterrence by ants on the fruit set of an extrafloral nectary plant, *Qualea multiflora* (Vochysiaceae). J Trop Ecol 12(6):887–892

Dwomoh EA, Afun JV, Ackonor JB, Agene VN (2009) Investigations on *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae) as a biocontrol agent in the protection of cashew plantations. Pest Manag Sci Former Pestic Sci 65(1):41–46

Fewell JH (1988) Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behav Ecol Sociobiol 22(6):401–408

Fiala B, Maschwitz U, Pong TY, Helbig AJ (1989) Studies of a South East Asian ant-plant association: protection of Macaranga trees by *Crematogaster borneensis*. Oecologia 79(4):463–470

Fisher BL, Bolton B (2016) Ants of Africa and Madagascar: a guide to the genera. Univ of California Press, Oakland

Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Heiberger R (2012) Package 'car.' Vienna R Found St Comput 16(332):333

Gbemavo DSJC, Glèlè Kakaï R, Assogbadjo AE, Katary A, Gnanglè P (2010) Effet de l'ombrage du karité sur le rendement capsulaire du coton dans les agroécosystèmes coton-karité du Nord Bénin. Tropicultura 28(4):193–199

Gibb H (2005) The effect of a dominant ant, *Iridomyrmex purpureus*, on resource use by ant assemblages depends on microhabitat and resource type. Austral Ecol 30(8):856–867

Gibb H, Hochuli DF (2003) Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. Oikos 103(3):469–478

Gras P, Tscharntke T, Maas B, Tjoa A, Hafsah A, Clough Y (2016) How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. J Appl Ecol 53(3):953–963

Hölldobler B, Edward OW (1990) The ants. Harvard University Press, Cambridge

Horvitz CC, Schemske DW (1990) Spatiotemporal variation in insect mutualists of a neotropical herb. Ecology 71(3):1085–1097

John F and Sanford W (2011) An {R} Companion to applied regression, second edition. In: Thousand Oaks CA: Sage. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Method Ecol Evol 4:133–142

Offenberg J (2015) Ants as tools in sustainable agriculture. J Appl Ecol 52(5):1197–1205

Pacheco R, Vasconcelos HL (2012) Habitat diversity enhances ant diversity in a naturally heterogeneous Brazilian landscape. Biodivers Conserv 21(3):797–809

Philpott SM, Armbrecht I (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecol Entomol 31(4):369–377

Poeydebat C, Tixier P, de Lapeyre de Bellaire L, Carval D, (2017) Plant richness enhances banana weevil regulation in a tropical agroecosystem by affecting a multitrophic food web. Biol Control 114:125–132

R Core Team (2019) R: A language and environment for statistical computing [Internet]. Vienna, Austria; 2014

Ribas CR, Schoereder JH (2007) Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. Biodivers Conserv 16(5):1511–1520

Rickson FR, Rickson MM (1998) The cashew nut, *Anacardium occidentale* (Anacardiaceae), and its perennial association with ants: extrafloral nectary location and the potential for ant defense. Am J Bot 85(6):835–849

Room PM (1971) The relative distribution of ant species in Ghana's cocoa farms. J Anim Ecol 40:735–751

Rosseel Y (2012) lavaan: An R package for structural equation modeling. J Stat Softw 48:1–36

Sarty M, Abbott KL, Lester PJ (2006) Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149(3):465–473

Schroth G, Harvey CA, da Fonseca GA, Vasconcelos HL, Gascon C, Izac AMN (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington

Sinclair FL (1999) A general classification of agroforestry practice. Agrofor Syst 46(2):161–180

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47(1):561–594

Teodoro AV, Sousa-Souto L, Klein AM, Tscharntk T (2010) Seasonal contrasts in the response of coffee ants to agroforestry shade-tree management. Environ Entomol 39(6):1744–1750

Van Lenteren JC (2000) Success in biological control of arthropods by augmentation of natural enemies. Biological control: measures of success. Springer, Dordrecht, pp 77–103

Vanitha K, Bhat PS, Raviprasad TN, Srikumar KK (2017) Species composition of ants in cashew plantations and their interrelationships with cashew. Proceed Nat Academy Sci India Section b: Biol Sci 87:399–409

Vasconcelos HL, Leite MF, Vilhena JM, Lima AP, Magnusson WE (2008) Ant diversity in an Amazonian savanna: relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecol 33(2):221–231

Vayssières JF, Ouagoussounon I, Adandonon A, Sinzogan A, Korie S, Todjihoundé R, Goergen G (2015) Seasonal pattern in food gathering of the weaver ant *Oecophylla longinoda* (Hymenoptera: Formicidae) in mango orchards in Benin. Biocontrol Sci Tech 25(12):1359–1387

Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edn. Springer, New York

Way MJ, Khoo KC (1992) Role of ants in pest management. Annu Rev Entomol 37(1):479–503

Wilson EO (1971) The insect societies. The insect societies. Belknap Press, Cambridge, p 548

Zomboudré G, Zombré G, Guinko S, Macauley HR (2005) Réponse physiologique et productivité des cultures dans un système agroforestier traditionnel: cas du maïs (Zea mays L.) associé au karité (Vitellaria paradoxa Gaertn.) dans la Zone Est du Burkina Faso. BASE 1(6):75–85

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.