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Species Richness, Density, Activity, and Composition of Ground-dwelling Ants in the Humid Forest Zone of Southern Cameroon: Role of Vegetation Cover and Abiotic Factors

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Abstract

The destruction of natural habitats is among the major factors responsible for the decrease in species diversity and distribution. This study focused on the effect of vegetation and its interaction with the season on ant species richness, density, activity, and composition in the three dominant habitats – forest, fallow, and mixed crop field – prevailing in southern Cameroon. Ants were sampled using two sampling techniques –pitfall trap and quadrat – in fallows, forest, and mixed crop fields from May 2007 to April 2008. Average ant species richness did not differ between fallow and forest, but the number of species in both habitats was higher compared with mixed-crop field. Species richness was also higher during the short dry season compared with other seasons. Species density was higher in mixed-crop field and in the long dry season. Species activity was similar in the three habitats, but it was higher during the long-wet season. Species richness, activity, and density were lower at low altitude. Vegetation and season affected the composition of ant species, but not the interaction between the two factors. The highest dissimilarity index was observed between mixed crop-field and forest while between seasons, it was between the short-wet and the long dry season. These results suggest that vegetation cover and abiotic factors interact to determine the distribution, density, activity, and composition of ant species. Identifying key drivers among environmental factors could help to understand the response of species to the variation of those factors in the context of climate change.

Key words: altitude, biodiversity, pitfall trap, quadrat, habitat, land use

How species are affected by land management remains an important concern in ecology and nature conservation (Grevé et al. 2018). The magnitude by which ecosystem management affects microclimate can inform the response of the affected taxa to the disturbance (Pérez-Sánchez et al. 2018). In the Tropics, the most noticeable consequence of the structural changes in the forest due to human activities is the modification of plant species composition (Zapfack et al. 2002, Dolan et al. 2015), and the change in abiotic factors due to the discontinuity in canopy covers which are among the most important physical factors affecting ecological processes (Brown and Whitmore 1992, Campbell 1994, Christianini and Oliveira 2013, Bohn et al. 2018, Salles et al. 2018). Several studies have attributed the difference in the diversity of insects to the disparities of ecological factors between vegetation types and species richness generally declined with increasing disturbance (Belshaw and Bolton 1993, Eggleton and Bignell 1995, Eggleton et al. 1996, Watt et al. 1997, 2002; Callist Kundy 2015, Norris 2016, Giam 2017, Papworth et al. 2017, Zhang et al. 2018). However, the direction of change of many organisms following forest clearance is uncertain and there is a need to directly measure the impact of deforestation on insect diversity (Murphy and Romanuk 2014, Chase et al. 2019).

Terrestrial and marine invertebrates, because of their dominant biomass, and diversity and their fundamental importance in the ecosystem, are often used as Indicators of the environmental changes (Disney 1986, Rosenberg et al. 1986, Andersen 1993, King et al. 1998, Hoffmann et al. 2000, Andersen et al. 2002, Majer and Kaspari 2010, Parmar et al. 2016). Because they are so sensitive to habitat variation and respond quickly to changes in habitat quality, ants' abundance, diversity, and activity are important for monitoring ecosystems including interactions with other organisms at multiple trophic levels (Alonso and Agosti 2000, Underwood and Fisher 2006, Lawes et al. 2017). Ants are excellent indicators of land management practices and restoration efforts (Andersen et al. 2002, Ottonetti et al. 2006, Majer and Kaspari 2010, Lawes et al. 2017). The composition of ant assemblages is responsive to biotic and abiotic factors including interspecific competition (Davidson 1977), variation in resource availability and habitat quality (Palmer 2003, Boulton et al. 2005, Dauber et al. 2005), and temporal changes in activity (Herbers 1985, 1989; Albrecht and Gotelli 2001). It is widely recognized that several plant attributes (e.g., richness, biomass, and percentage of cover) affect ants' diversity, abundance, species richness (Fisher and Robertson 2002). The vegetation in southern Cameroon is characterized by a mosaic of vegetation which includes 1) short fallows dominated by *Chromolaena odorata* (L. King & H.E. Robins, Asterales, Asteraceae) primary and secondary forests (Maley and Brenac 1998), and 3) slash-and-burn dominant farmlands dominated by mixed-crop fields. Mixed crop field are planted with cassava *Manihot esculenta* (Crantz, Malpighiales, Euphorbiaceae) groundnuts *Arachis hypogeae* (L., Fabales, Fabaceae) maize *mays* (L., Poales, Poaceae), plantain *Musa acuminata* (Colla, Zingiberales, Musaceae), cocoyam (*Xanthosoma mafafa* Schott., Alismatales, Araceae), and taro (*Colocassia esculenta* [L] Schott., Arales, Araceae). In previous study, we demonstrated that diversity decreased with increasing deforestation, and this also affected ant functional groups (Fotso Kuate et al. 2015b). Therefore, measuring ant species richness, density, activity, and composition, considered as bioindicators in the three dominant habitats prevailing in southern Cameroon, will contribute to establish the role of biotic and abiotic interactions in the different ecosystems in the target zone. Such a finding could support the notion that the processes shaping ant community structure are context-dependent, and that both biotic and abiotic factors interact to determine the distribution and density of ant species among assemblages.

Material and Methods

Study Areas

Sampling plots were established in three locations in southern Cameroon across the following altitude gradients: Higher altitude – Awae II (3.59° N, 11.61° E, 680 m; 3.58° N, 11.56° E, 615 m, mid altitude – Matomb (3.80° N, 11.06° E, 588 m; 3.75° N, 11.05° E; 597 m; ~97 km from Awae II); and low altitude – Boga (3.89° N, 10.77° E, 201 m; 3.89° N, 10.71° E, 245 m; ~39 km from Matomb and 136 from Awae II).

The climate in the three study sites is equatorial, with a bimodal rainfall distribution, and 4 seasons: 2 humid seasons – from August to November (long rainy season) and from March to June (short rainy season); and 2 dry seasons – from November to February (long dry season) and from July to mid-August (short dry season). Annual rainfall is 1,500–2,000 mm. Mean daily temperature ranges from 19.2 to 28.6°C, with higher temperature at low altitude (Thenkabail 1999, Molua and Lambi 2006). The average annual relative humidity is around 78.6 ± 6.5 %.

General Sampling Method

In each location, two complementary techniques pitfall trap and quadrat sampling were used to sample ants in plots of 400 m^2, delimited in each of the 3 habitats – forest, fallow, and mixed-crop field. Sampling was conducted at 2-month intervals from May 2007 to April 2008, for a total of 6 samplings dates for the entire study period. In each location, each habitat was replicated four times, making 72 plots for each habitats. Ten quadrats of 1 × 1m and 10 pitfall traps (160 mm deep, 21 mm top internal diameter) were used for sampling in each plot on 400 m^2, delimited in each habitats. A total number of 720 samples from quadrats and 720 from pitfalls traps were processed from each habitats.

Environmental Parameters

Daily temperature and humidity were recorded with HOBO Pro v2 Temperature/Relative Humidity data logger (Onset Comp. Corp., MA), set in an appropriately protected location each habitats. We recorded soil temperature using thermocouple thermometer (Barnant) in the morning and, in the afternoon, in unshaded and shaded areas within each habitats. We used Tru-Chek rain gauge (Edwards Manuf. Co., MN) to record daily rainfall (Fig. 1). From Fig. 1, we delimited 6 seasons during which the 6 sampling events occurred: Short-wet season (SW1 for year 1 and SW2 for year 2), short dry season (SD), long-wet season (LW), and long dry season (LD1 for year 1 and LD2 for year 2).

Data Analysis

Ant Species Richness, Density, and Activity

Ant species richness was expressed as a total number of species recorded per habitats using the two sampling methods. We estimated ant species density as the number of species collected in the 1 × 1 m quadrat and species activity as the number of pitfall traps in which any species was recorded, to make our data and results comparable with other studies (Gotelli and Colwell, 2001, Deblauwe and Dekoninck, 2007).

The diversity data between the three habitats were compared using a sample based-species accumulative curves which allow

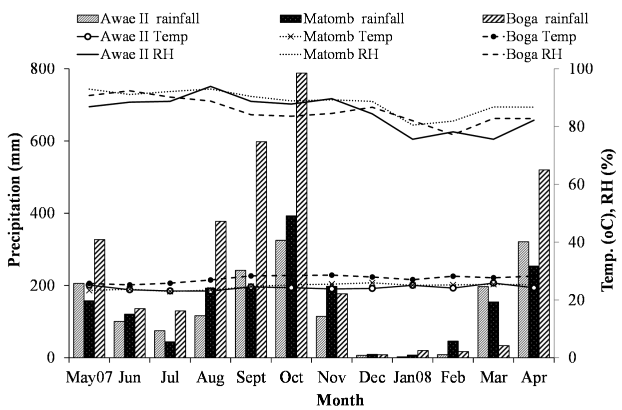

Fig. 1. Monthly rainfall patterns during the study period in the three locations – Awae II, Matomb, and Boga. The six sampling events are delimited with arrows on the horizontal line.

meaningful comparison of samples by interpolating data to a standardized number of sampling unit (Gotelli et al. 2011). We combined data for each habitat from the three locations to have a larger sample size and more power. Analysis was done with EstimateS software 9.1.0 that computes nonparametric, asymptotic species richness estimators for incidence-based data (e.g., Chao2) (Colwell 2013).

Dependent and Independent Variables

We used principal component analysis (PCA) to reduce the number of correlated parameters to three PCA axes. The analysis was done with the program JMP 8.0.2. Association between the environmental parameters was assessed based on eigenvectors (variable loadings). We considered the following main independent variables: the first three axes of the PCA analysis from abiotic variables, the type of vegetation, the season, and the interaction between the type of vegetation and season. The effect of these parameters on species richness, species density, and species activity was analyzed with one-way ANOVA. To check the relationship of species density and activity and species richness with the most significant axes of the PCA of the environmental parameters, we used multiple linear regressions – built using backward variable selection – to examine the joint effect of predictors on the dependent variables. We chose this method because adding any single predictor may have little effect and cause the construction of the model to stop; possibly overlooking many models that provide a better fit to the data (Graham 2003). Activity data was log-transformed in the analysis to reduce the variance that may be caused by highly populated species of a column of foragers (e.g., *Dorylus* species). The effect of habitats, season, and their interactions on ant species composition was analyzed using the permutational multivariate analysis of variance. The analysis was carried out with the software PERMANOVA 1.6 (Anderson 2005). Posteriori pairwise comparisons of means between habitats in general and within the season, and between seasons within the habitats were carried out. We also performed a distance-based test for homogeneity of multivariate dispersion with the program PERMDISP which compares the multivariate dispersions among groups based on any distance or dissimilarity measure (Anderson 2006). We chose the Bray-Curtis dissimilarity index with 9999 permutations in the program PERMDISP. Total occurrence of each species was transformed into presence/absence matrix before the analysis (Anderson 2005, Deblauwe and Dekoninck 2007).

Table 1. Eigen values, percentage (%) of variance explained, and eigenvector coefficients (EC) of the six environmental parameters for the three significant axes of the principal components analysis (PCA)

Parameter	Prin 1	Prin 2	Prin 3
Eigen value	3.78	1.18	0.42
% Variation	63.0	24.7	7.03
Air temperature	0.38	**−0.51**	0.27
Air humidity	−0.38	0.34	**0.76**
Soil temperature morning	**0.43**	−0.39	0.32
Soil temperature afternoon	0.38	**0.41**	−0.37
Soil temperature open	0.42	**0.43**	0.14
Soil temperature shade	**0.45**	0.35	0.29

Highest coefficient for each parameter is in bold.

Results

Environmental Parameters

The first 3 axes of the PCA significantly explained 94.7% of the variance in the 8 abiotic variables (Table 1). The first axis (Prin 1) was positively associated with all the parameters, except the air relative humidity. Prin1 is considered as the measure of soil temperature giving the higher load on these parameters. The second component (Prin 2) has a high negative coefficient (−0.51) on air temperature while the third component (Prin 3) has a high positive coefficient (0.76) on air relative humidity.

Species Richness

Species rarefaction and accumulation curves in the three habitats tended to completion, and showed that the forest habitat was more diverse, as the number of different species increase more

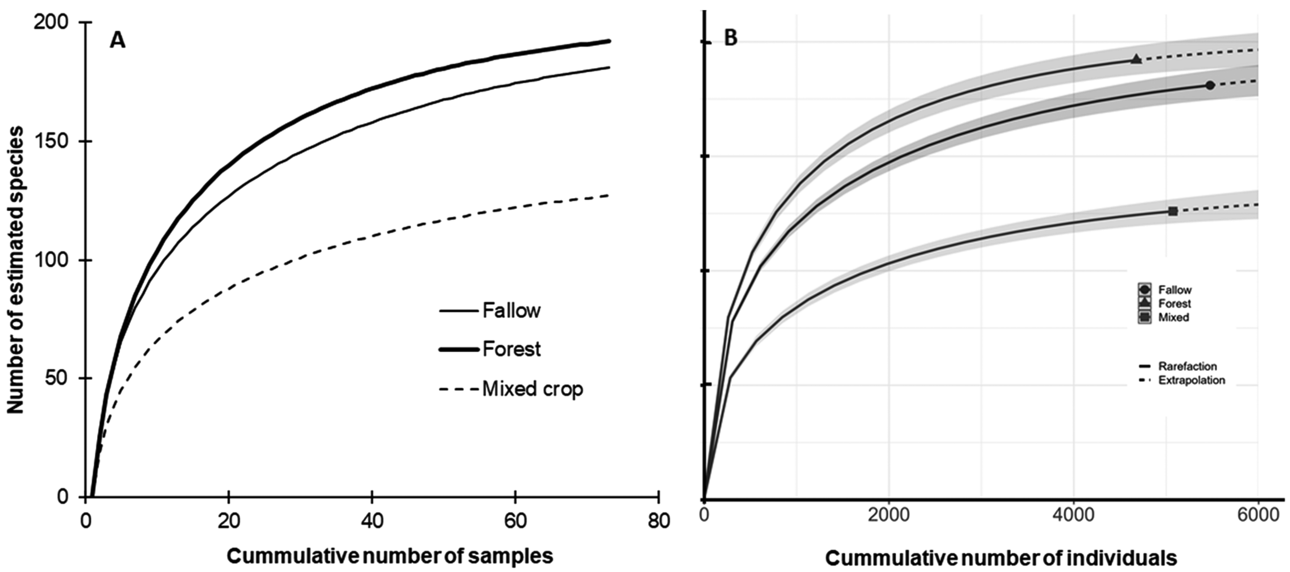

Fig. 2. Sample-based species accumulation curve (A) and rarefaction curve (B) in the three habitats. Sampling efficiency based on Chao 2 estimates is 92% in the fallow, 96% in forest and 93% in mixed crop field habitats.

than in other habitats, with increasing number of samples. In contrast the mixed-crop field is less diverse, as the number of species does not increase very much regardless of the number of samples (Fig. 2A and B). Average ant species richness in the fallow did not differ between fallow and forest (fallow vs forest: t = 0.15, df = 159; p = 0.44), but both were at least 28% higher than species richness in the mixed-crop field (fallow vs mixed crop: t = 5.3, df = 154; p < 0.001) (forest vs mixed crop: t = 5.2, df = 155; p < 0.001) (Table 2).

Average species richness was higher in the short dry season SD and lower during the long dry season LD1 (Fig. 3A; Table 2). Species richness was significantly different between the short dry season SD and the other seasons, except the short-wet season SW1: SD versus short wet season SW2 (t = 3.2, df = 154, p = 0.001), SD versus long wet season LW (t = 2.6, df = 154, p = 0.01); SD versus long dry season LD2 (t = 2.8, df = 154, p = 0.006); SD versus long dry season LD1 (t = 3.7, df = 154, p < 0.001).

Average species richness was 29% higher at the higher altitude of Awae II compared with the lowland altitude of Boga (F = 8.8; df = 2,154, p = 0.002) (Table 2).

Species Density

Ant species density was at least 16% higher in mixed-crop field compared with densities in the other two land uses – fallow and forest (p < 0.001; Fig. 3B; Table 2). Average species density was higher in the long-wet season LW compared with the other seasons: LW versus LD1 (t = 4.9, df = 154, p < 0.001), LW versus LD2 (t = 3.7, df = 154, p < 0.001); LW versus SD (t = 4.0, df = 154, p < 0.001), LW versus SW1 (t = 3.3, df = 154, p = 0.001), LW versus SW2 (t = 3.7, df = 154, p < 0.001).

Average species density was at least 12% higher at higher and mid altitude (Awae II and Matomb) compared with lowland in Boga (F = 9.8; df = 2, 154, p < 0.001 (Table 2).

Species Activity

Ant species activity in the mixed-crop field was similar to species activity in the fallow and the forest (Fig. 3C; Table 2). Species activity across land uses was correlated with species density (Spearman ρ = 0.44, n = 163, p < 0.001). Season, however, had a significant effect on species activity, as average species activity was higher in the long-wet season LW and lower during the short-wet season SW1 (p < 0.001) (Table 2). Species activity was similar during the short dry season SD and the long-wet season LW (t = 0.2, df = 154, p = 0.88), but species activity was higher during the latter two seasons than during the other seasons (p < 0.001). No differences in species activities were found between the three altitudes (p = 0.36).

Table 2. Average (±SE) species richness, density, and activity in the 3 study locations and their associated habitats and season

	Ant species variable		
Environmental factor	Richness	Density	Activity
Vegetation			
Fallow	26.7 ± 1.1[a]	2.6 ± 0.15[b]	15.5 ± 3.1[a]
Forest	26.5 ± 1.3[a]	2.3 ± 0.12[b]	12.5 ± 2.1[a]
Mixed-crop field	19.2 ± 0.6[b]	3.1 ± 0.21[a]	18.1 ± 2.3[a]
Season			
Long dry (LD1)	21.5 ± 1.3[c]	2.3 ± 0.2[b]	12.0 ± 1.8[b]
Long dry (LD2)	23.4 ± 1.9[bc]	2.6 ± 0.2[b]	9.69 ± 1.5[b]
Long wet (LW)	23.5 ± 1.73[bc]	3.4 ± 0.3[a]	22.5 ± 5.1[a]
Short dry (SD)	28.9 ± 2.0[a]	2.5 ± 0.2[b]	23.2 ± 5.3[a]
Short wet (SW1)	26.1 ± 2.3[ab]	2.4 ± 0.2[b]	15.3 ± 2.2[ab]
Short wet (SW2)	22.5 ± 0.9[bc]	2.6± 0.22[b]	10.1 ± 1.73[b]
Location			
Awae II	26.7 ± 1.0[a]	2.8 ± 0.1[b]	14.6 ± 1.9[a]
Matomb	24.2 ± 1.1[ab]	3.2 ± 0.2[a]	19.2 ± 2.5[a]
Boga	20.7 ± 1.1[b]	2.4 ± 0.1[c]	13.9± 2.9[a]

Values followed by the same letter in a column are not significantly different at p < 0.05 following a t test.

Ant Species Composition

Vegetation and the season affected the composition of ant species, but without an interaction between the two factors (Table 3). The test for homogeneity of multivariate dispersions showed

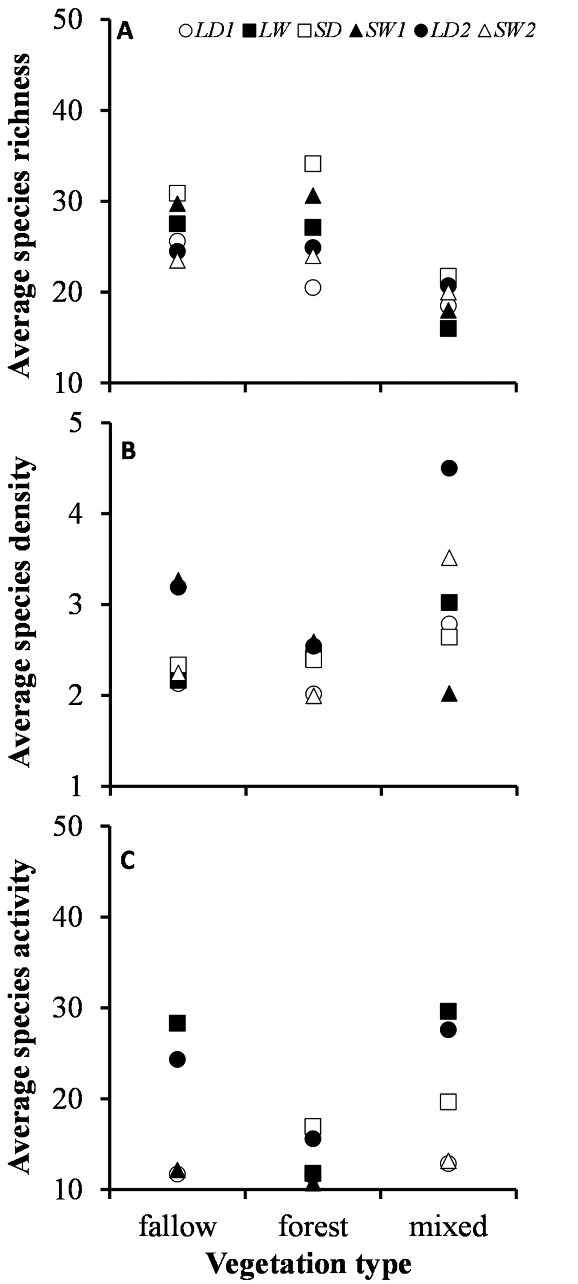

Fig. 3. Average species richness (A), density (B), and activity (C) in the three habitats across the season

Table 3. PERMANOVA table with the response of the Euclidian distances of ant species richness, density, activity (log-transformed), and of the Bray-Curtis dissimilarities of ant species composition to habitat and season

Source of variation	DF	SS	MS	F ratio
Species richness				
Vegetation	2	2,140	535	20.6***
Season	5	953	95	3.7**
Vegetation × Season	10	660	33	1.30
Residual	144	7,477	52	
Species density				
Vegetation	2	16	4	13.2***
Season	5	22	2	7.3***
Vegetation × Season	10	27	1	4.4***
Residual	144	87	1	
Species activity				
Vegetation	2	6	209	4.5*
Season	5	10	495	2.9*
Vegetation × Season	10	10	113	1.50
Residual	144	95	1	
Species composition				
Vegetation	2	440,816	22,408	20.2***[a]
Season	5	23,232	4,646	4.2***[a]
Vegetation × Season	10	11,009	1,100	0.99[a]
Residual	72	79,974	1,100	

[a]Evidence of heterogeneity in dispersions (PERMDISP, $p < 0.01$).

Table 4. PERMANOVA of a posteriori comparisons of ant species composition among seasons, within habitat, and among habitats within seasons using the permutation calculated t statistic (numbers in table) within season or within habitats

Within season	LD1	LD2	LW	SD	SW1	SW2
Fallow-Forest	1.67*	1.89**	1.74**	1.85**	1.94**	1.96**[a]
Fallow-Mixed crop field	1.71**[a]	1.93**[a]	1.54*[a]	1.82**	1.94*	1.50*[a]
Forest-Mixed crop field	2.51**[a]	2.79**[a]	2.34**[a]	2.32**	2.19**	2.62**[a]
Within habitat	Fallow	Forest	Mixed-crop field			
LD1-LD2	1.13[a]	1.19	1.62**			
LD1-LW	0.93	1.14	1.17			
LD1-SD	1.24	1.23	1.30*			
LD1-SW1	1.70**[a]	1.74**[a]	2.27**			
LD1-SW2	1.10[a]	0.96	1.51**			
LD2-LW	1.32[a]	1.20	1.65**[a]			
LD2-SD	1.5*	1.45*	1.66**[a]			
LD2-SW1	2.08**	1.79**	1.43**[a]			
LD2-SW2	1.28*	0.98	1.48**			
LW-SD	1.11	1.24	1.17			
LW-SW1	1.55**[a]	1.48*[a]	1.73**			
LW-SW2	1.15[a]	0.96	1.19[a]			
SD-SW1	1.54**[a]	1.59**	1.66**			
SD-SW2	1.36	1.08	1.47*[a]			
SW1-SW2	1.86**[a]	1.43*[a]	1.94**[a]			

*$p < 0.05$; **$p < 0.001$.

[a] Evidence of heterogeneity in dispersions (PERMDISP, $p < 0.01$).

that the significant differences between vegetation and seasons were due to differences in dispersion; we also have some evidence of heterogeneity in dispersions for the interaction terms (all $p < 0.01$) (Table 4). The Bray-Curtis dissimilarity index showed at least 55.8% species dissimilarity between habitats and at least 53.9% between seasons. The highest dissimilarity index between vegetation (69.6%) was observed between mixed-crop field and forest, while between seasons (63.7%) dissimilarity was observed between the short-wet season SW1 and the long dry season LD1.

Correlation with Environmental Parameters

Species richness was negatively correlated with the first axis of PCA (Soil temperature) (−0.61) while species density was negatively correlated with the second axis (Air temperature) (−0.45). Multiple regressions showed that the number of species decreased with Prin 1 and the model *RICHNESS = 24.6 − 2.58*Prin 1* ($R^2 = 0.43$; $F = 9.4$, df = 3, 38, $p = 0.008$) in mean species richness per habitats. We also observed that species density could be predicted by Prin 2 and Prin 3 (Air relative humidity) according to the model *DENSITY = 2.5 − 0.38*Prin 2 − 0.3*Prin 3* ($R^2 = 0.38$; df = 3, 38, $F = 5.77$, $p = 0.002$)

in mean density per square meter. Species activity was not correlated with any of the PCA axes.

Discussion

Few studies have addressed the spatiotemporal patterns of ants in the tropics (Levings 1983, Kaspari and Weisser 2000, Coelho and Ribeiro 2006, Deblauwe and Dekoninck 2007). According to these studies, moisture availability increases ant species activity and density. In our study species activity was higher in the mixed-crop fields and during the long rainy season, while higher density was observed during the long dry season. Usually, species activity follows species density (Levings 1983, Basu 1997). This was the case in our study with the high correlation between the two parameters. Although high moisture promotes ant activity, long rains can alter species density (Levings 1983, Kaspari and Weisser 2000), which supports our findings of higher species density in the dry season compared with the long rainy season.

Ant species richness, activity, and density are indirectly affected by habitat disturbance through changes in habitat structure, microclimate, resource availability and competitive ability of ant species (Andersen 2002). Ant species respond differently to climatic change depending on their physiological tolerance levels, ecological requirement, and competitive ability (Deblauwe and Dekoninck 2007, Barrow and Parr 2008). Forests can therefore be considered as the habitat offering less disturbance and favorable microclimate which promote higher species richness. Three niche factors – space, food type, and time – can affect ant distribution and activity (Schoener 1974, Albrecht and Gotelli 2001). Most competitive species, through their numerical dominance, may partly control the distribution of competitively inferior species. Therefore, density and abundance of the subordinate species are expected to be lower in the presence of their competitors, which, for example, monopolize food resources (nectaries or honeydew-producing hemiptera aggregation) (Blüthgen et al. 2000, Fotso Kuate et al. 2015a).

The results presented here also suggest that conversion of forests to farmland resulted in a decrease in average ant species richness and a change in species composition. Species richness in the mixed-crop field was significantly lower compared with that of the forest; however, the difference was not as pronounced as presented in other studies where species richness in disturbed areas is 50% less than that in undisturbed areas(Mackay et al. 1991, Roth et al. 1994, Nepstad et al. 1995, Vasconcelos 1999). This low difference can be attributed to the contiguity of the different habitats, which displays a mosaic pattern (Nounamo and Yemefack 2002, Yemefack et al. 2005, 2006; 2019). Mixed-crop fields are nearly always surrounded by a fallow or a forest and generalist ant species which can nest in several sites or use a broad range of food items, can be found in both vegetations (Mackay et al. 1991). However, as observed in a previous study (Fotso Kuate et al. 2015b), despite the contiguity of habitats, some species were restricted to specific vegetation with the highest number of restricted species found in the forest. Habitat-associated ant assemblages can be comprised of species adapted to the microclimate within their habitat (Fisher and Robertson 2002) or species with narrow or specialized feeding or nesting habits (Wheeler and Bailey 1920, Hölldobler and Wilson 1990, Dejean et al. 2014); hence, some species are mostly recorded in a specific habitat.

The difference in ant species composition could also be attributed to structural differences among habitats (e.g., absence of trees in the mixed-crop fields). Some studies have shown that disturbance affects ant assemblages by altering shade regimes (King et al. 1998, Hoffmann et al. 2000), vegetation structure (Greenslade and Greenslade 1977), and plant species richness (Hoffmann et al. 2000). Trees, for example, reduce the amount of water and light reaching the soil surface (Belsky and Amundson 1992, Fisher and Robertson 2002). In our study, shade regimes and vegetation structure are all altered during the conversion of forest to farmland. Soil and air temperature in our study were always higher in the mixed-crop fields compared with fallows and forests, whereas air humidity was always lower during the day. These differences in environmental factors between habitats may affect the occurrence and diversity of ant species (Fisher and Robertson 2002).

This study has provided data on how biotic and abiotic factors can interact to shape the richness, activity, density, and composition of ants. Species richness and density were influenced by air temperature, soil temperature, and air relative humidity. However, no effect of these environmental factors on ant activity was detected. These findings open ways to the study of the response of most abundant species to variation of factors such as temperature and relative humidity in the context of climate change.

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