Article

Dissimilarity of Ant Communities Increases with Precipitation, but not Reduced Land-Use Intensity, in Indonesian Cacao Agroforestry

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Abstract: Land-use degradation and climate change are well-known drivers of biodiversity loss, but little information is available about their potential interaction. Here, we focus on the effects of land-use and precipitation on ant diversity in cacao agroforestry. In Central Sulawesi, Indonesia, we selected 16 cacao agroforestry plots with a shaded *vs.* unshaded plot in each of eight villages differing in precipitation (1032–2051 mm annual rainfall). On each plot, 10 cacao trees with similar size and age (7–10 years) were selected for hand collection of ants on each cacao tree and the soil surface. In total, we found 80 ant species belonging to five subfamilies. Land-use intensification (removal of shade trees) and precipitation had no effect on species richness of ants per cacao tree (alpha diversity) and, in an additive partitioning approach, within-plot beta diversity. However, higher precipitation (but not shade) significantly increased ant species dissimilarity across cacao trees within a plot, with ant species showing contrasting responses to precipitation. Reduced precipitation causing drought stress appeared to contribute to convergence of ant community structure, presumably via reduced heterogeneity in cacao tree growth. In conclusion, reduced precipitation greatly influenced ant community dissimilarity and appeared to be more important for ant community structure than land-use intensification.

Keywords: alpha diversity; beta diversity; community dissimilarity; land-use; precipitation

1. Introduction

Land-use degradation and climate change are well-known drivers of biodiversity loss [1]. Temperature increase and reduced precipitation can have an effect on the distribution, reproduction and behavior of species [2], and may even favor invasive species that are able to adapt to this altered environment [3]. However, little is known of the interaction of land-use degradation and climate change, although both together may greatly increase biodiversity losses [4].

In agricultural ecosystems, land-use intensification, exacerbated by climate change effects, may severely affect functional biodiversity, for example, natural enemies providing successful biological control. Increasing carbon dioxide and temperature can also facilitate the presence of pests and diseases in agricultural habitat and reduce agrobiodiversity [5]. In addition, climate change can have direct effect on crop plant growth through increased temperature, drought, rainfall and tropical storms [5].

Agroforestry systems can provide suitable habitat for biodiversity [6] and may mitigate effects of climate change [7]. However, this depends on the management. Agroforestry intensification by shade tree removal [7,8] and pesticide application [9] has particularly adverse effects on biodiversity. This may have functional consequences, especially if organisms important for pest regulation, such as ants [10], are affected. Bos *et al.* [11] found that decreasing shade-tree cover negatively affects ant diversity in cacao agroforestry. Wielgoss *et al.* [12] suggest that ant diversity in cacao agroforestry is affected more by temperature than decreasing numbers of shade trees. In general, however, the joint role of climate and shade-tree loss in affecting ant species communities has not been addressed, despite its potential significance in ecosystem response to changing rainfall patterns and land-use change.

In this study, we analyze how land-use change and precipitation affect ant diversity in agroforestry. We selected 16 cacao agroforestry plots located in eight villages around Lore Lindu National Park (LLNP) in Central Sulawesi, Indonesia. In each village, we studied one shaded and one unshaded agroforestry system, while the eight villages were situated along a precipitation gradient. We asked the following questions: (i) How does ant community structure change along land-use intensity and precipitation gradients? (ii) Does the ant communities on the cacao tree and on the ground show different responses? (iii) Which ant species show the strongest responses to the precipitation gradient?

2. Experimental Section

2.1. Study Sites

The 16 studied plots were cacao agroforestry systems located in eight villages around the Lore Lindu National Park (LLNP), Central Sulawesi, Indonesia (Figure 1). The agroforestry systems differed in land-use intensity (shaded *vs.* unshaded) and the villages in precipitation (1032 to 2051 mm/year) (Table 1).

Figure 1. Location map of the 16 cacao agroforestry plots in eight villages with different precipitation levels. Villages are located around Lore Lindu National Park, Central Sulawesi, Indonesia.
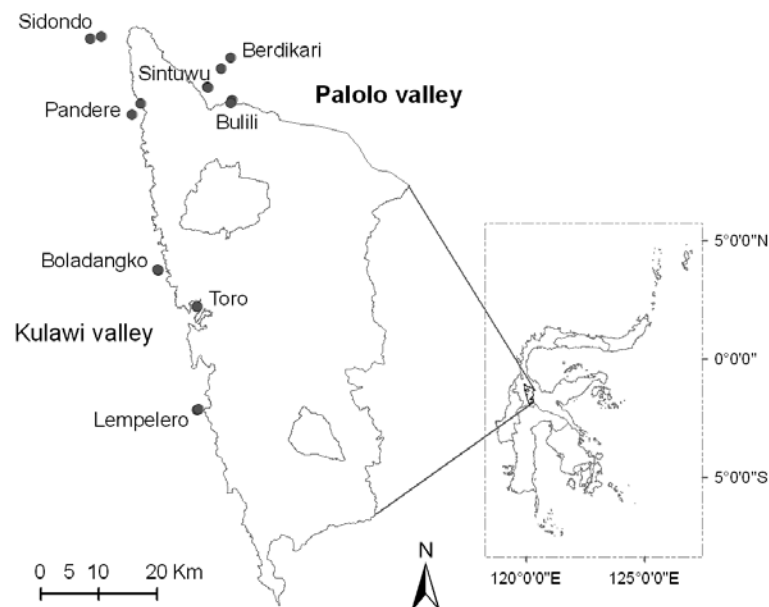

Table 1. Observed and estimated ant species richness of the 16 plots with different land-use (A: shaded; B: unshaded cacao agroforestry) and different precipitation located in eight villages around Lore Lindu National Park, Central Sulawesi, Indonesia.

No	Village	Land-use	Latitude (°S)	Longitude (°E)	Altitude (m asl)	Precipitation (mm/year)	Observed species	Estimated species (%)*
1.	Berdikari	A	01.11693	120.09266	646	2,051	24	28.5 (84.2)
		B	01.13420	120.07861	603		17	25.0 (68.0)
2.	Sintuwu	A	01.16213	120.05642	554	1,430	26	32.8 (79.4)
		B	01.16339	120.05790	567		20	52.0 (38.5)
3.	Bulili	A	01.18261	120.09550	582	1,504	17	29.3 (58.1)
		B	01.18738	120.09239	652		18	22.2 (81.2)
4.	Pandere	A	01.18844	119.95393	179	1,160	21	23.1 (91.0)
		B	01.20482	119.94063	102		18	19.5 (92.3)
5.	Sidondo	A	01.08366	119.89272	41	1,032	23	35.3 (65.2)
		B	01.08764	119.87599	27		16	17.5 (91.4)
6.	Boladangko	A	01.44530	119.98057	523	1,590	24	44.3 (54.2)
		B	01.44499	119.98001	558		18	20.7 (87.1)
7.	Toro	A	01.50238	120.04055	800	1,704	26	32.4 (80.2)
		B	01.50237	120.04109	797		21	24.1 (87.0)
8.	Lempelero	A	01.66104	120.04093	432	1,742	14	16.7 (84.0)
		B	01.66035	120.04307	438		22	30.1 (73.1)

* Predicted number of species based on Chao estimator of the 10 cacao trees as sampling unit; %, sampled species as a percentage of predicted number of species.

2.2. Plots Selection and Ant Sampling

Each cacao agroforestry plot differed in agricultural management because it belonged to a different farmer. On each plot (5 m × 15 m), 10 cacao trees with similar size and age (7–10 years) were selected for ant observation. Ants were sampled on all strata *i.e.*, the tree trunk and the soil surface (within area 1 m distance from base of cacao tree) using hand collecting combine with baiting (using tuna and sugar) lasted a maximum of 10 min per tree and conducted both in the morning and afternoon. Hand collection is the best method to record all of ant species inhabiting an area by searching and collecting ants in different microhabitats [13]. Hand collecting was conducted twice in the same cacao trees, in November 2009 and June 2010, to quantify ant species diversity on each cacao tree per plot in different seasons.

Ant specimens were sorted and identified to genus using [14] or were separated according to their external morphology as morphospecies [15]. Some of the ants could be identified to species level with the help of websites (e.g. [16]).

2.3. Data Analysis

The completeness of sampling on each plot was calculated using the Chao estimator [17]. To test for spatial autocorrelation, we used the Mantel test [18, 19] based on the distance and ant similarity among plots. Alpha diversity was derived from mean ant species richness per tree, whereas beta diversity was calculated based on an additive diversity portioning approach [20] with beta diversity resulting from gamma diversity (total ant species in one plot) minus alpha diversity (species richness per tree). The Bray-Curtis dissimilarity index was used to calculate the dissimilarity of ant species communities between the ten cacao tree on each plot, using vegan package in R software [21]. Then, we calculated the community dissimilarity using ordihull within non-metric multidimensional scaling (NMDS) (vegan package). Analysis of variance (ANOVA) and linear models (LM) were used to relate ant diversity and community similarity to the land-use and precipitation gradients. Logit regression was performed to analyze the relationship between ant species presence or absence and the precipitation level. All analyses were conducted using R software [21].

3. Results

3.1. Ant Community Structure along Land-Use Intensity and Precipitation Gradients

In total, we found 80 species belonging to 5 subfamilies in the 16 cacao agroforestry plots (see supplementary material Table S1). The Chao estimate for each plot on almost all 16 sampled cacao agroforestry indicated that these sampling methods captured most of ant species richness (Table 1). Based on the Mantel test, we did not find spatial autocorrelation between similarity of ant communities with nearness distance of plots (Mantel statistic r = 0.161, P = 0.087). We found that mean ant species richness per tree (alpha diversity), beta diversity (richness per plot minus mean richness per tree) and ant species similarity (on the tree and on the soil surface) across the 10 trees per plot were not affected by the presence or absence of shade trees (Table 2). In contrast, precipitation levels significantly

affected ant community similarity on the tree (but not on the soil surface) in the cacao agroforestry (Table 2).

Table 2. Effects of shade-tree removal, precipitation and altitude on species richness per tree (alpha diversity), beta diversity and community similarity of ant communities in each stratum, based on 16 cacao agroforestry plots.
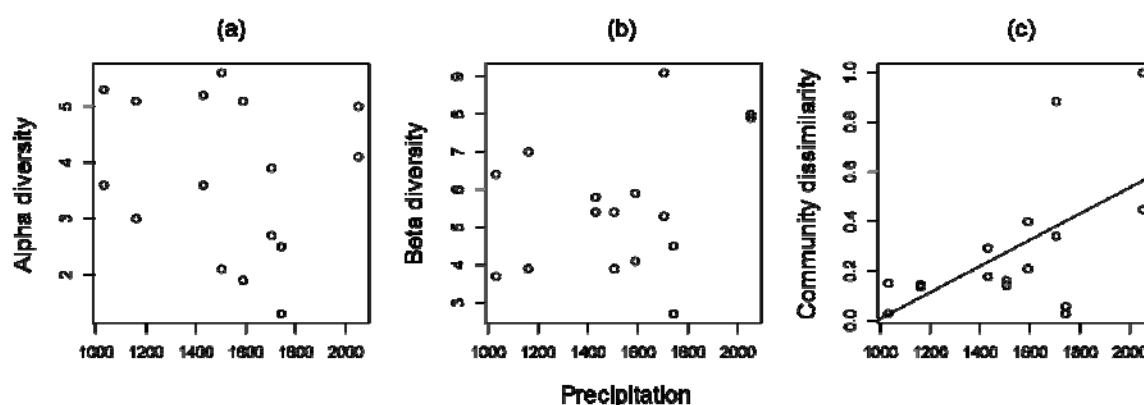
Parameters	Strata		
	Total	Tree	Soil surface
Alpha diversity			
Land-use	$F_{1,12} = 0.084, P = 0.777$	$F_{1,12} = 0.070, P = 0.796$	$F_{1,12} = 0.006, P = 0.940$
Precipitation	$F_{1,12} = 0.003, P = 0.957$	$F_{1,12} = 0.415, P = 0.532$	$F_{1,12} = 0.059, P = 0.813$
Altitude	$F_{1,12} = 0.001, P = 0.982$	$F_{1,12} = 0.014, P = 0.907$	$F_{1,12} = 1.372, P = 0.264$
Beta diversity			
Land-use	$F_{1,12} = 4.950, P = 0.046$	$F_{1,12} = 1.511, P = 0.243$	$F_{1,1} = 2.379, P = 0.149$
Precipitation	$F_{1,12} = 0.223, P = 0.645$	$F_{1,12} = 1.708, P = 0.216$	$F_{1,12} = 0.134, P = 0.721$
Altitude	$F_{1,12} = 2.779, P = 0.121$	$F_{1,12} = 0.286, P = 0.603$	$F_{1,12} = 1.980, P = 0.185$
Ant community similarity			
Land-use	$F_{1,12} = 0.277, P = 0.608$	$F_{1,12} = 1.854, P = 0.198$	$F_{1,12} = 0.576, P = 0.463$
Precipitation	$F_{1,12} = 5.032, P = 0.045$	$F_{1,12} = 7.613, P = 0.017$	$F_{1,12} = 0.008, P = 0.932$
Altitude	$F_{1,12} = 1.025, P = 0.331$	$F_{1,1 2} = 0.588, P = 0.458$	$F_{1,12} = 0.008, P = 0.932$

There is a positive correlation between precipitation and altitude ($F_{1,14} = 21.47, P = 0.0004, r^2 = 0.58$) (see supplementary material Figure S1). Nevertheless, the better predictor of ant species is precipitation (df = 5, AIC = −1.553) than altitude (df = 5, AIC = 2.465) based on the linear mixed effects model (LME). According to the linear model, we found that precipitation was not related to the number of ant species richness per tree (alpha diversity, Table 3, Figure 2a) and beta diversity on the tree (Table 3, Figure 2b). However, precipitation was closely correlated with the dissimilarity distance among cacao trees on each plot. Increasing precipitation was followed by increasing dissimilarity of ant communities on the tree in the cacao agroforestry systems (Table 3, Figure 2c).

Table 3. Linear model between precipitation and alpha diversity, beta diversity and community similarity in each stratum, based on 16 cacao agroforestry plots.

| Parameters	Strata		
	Total	Tree	Soil
Alpha diversity	$r^2 = -0.071, F_{1,14} = 0.003,$ $P = 0.954$	$r^2 = -0.036, F_{1,14} = 0.481,$ $P = 0.450$	$r^2 = -0.067, F_{1,14} = 0.062,$ $P = 0.808$
Beta diversity	$r^2 = -0.059, F_{1,14} = 0.159,$ $P = 0.697$	$r^2 = 0.047, F_{1,14} = 1.733,$ $P = 0.209$	$r^2 = -0.063, F_{1,14} = 0.114,$ $P = 0.740$
Ant community similarity	$r^2 = 0.223, F_{1,14} = 5.296,$ $P = 0.037$	$r^2 = 0.280, F_{1,14} = 6.828,$ $P = 0.021$	$r^2 = -0.071, F_{1,14} = 0.009,$ $P = 0.927$
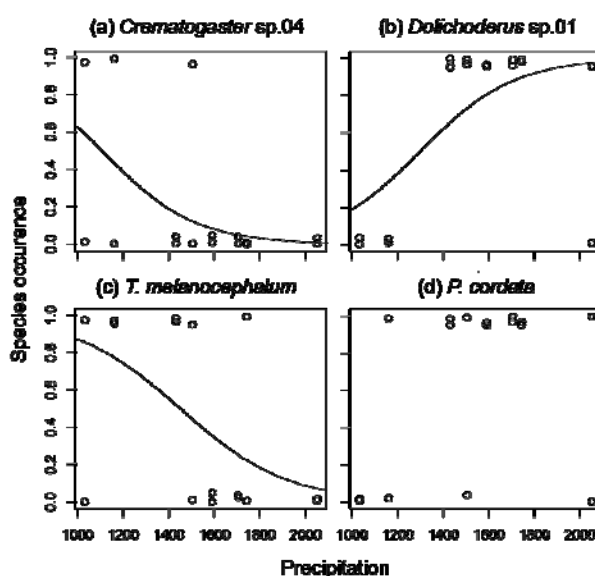
Figure 2. Linear model between precipitation and (**a**) the mean number species per tree (alpha diversity, $r^2 = -0.036$, $F_{1,14} = 0.481$, $P = 0.450$), (**b**) beta diversity ($r^2 = 0.047$, $F_{1,14} = 1.733$, $P = 0.209$) and (**c**) community dissimilarity ($r^2 = 0.280$, $F_{1,14} = 6.828$, $P = 0.021$) based on species found on all 10 trees per plot.

3.2. Ant species Responses to Precipitation Gradients

Based on logit regressions for each species, we found that three ant species were related to the precipitation gradients. *Crematogaster* sp.04 (df = 1, Chi-square = 3.84, P = 0.04, Figure 3a) and *Tapinoma melanocephalum* (df = 1, Chi-square = 4.59, P = 0.03, Figure 3c) was mainly found in cacao agroforestry with low precipitation (Figure 3c). In contrast, *Dolichoderus* sp.01 was mainly found in cacao plots with high precipitation (df = 1, Chi-square = 5.06, P = 0.02, Figure 3b). The dominant Dolichoderinae, *Philidris cordata*, did not show a clear pattern related to precipitation (df = 1, Chi-square = 2.41, P = 0.12, Figure 3d).

Figure 3. Logit regression of ant species with precipitation. (a) *Crematogaster* sp.04 (df=1, Chi-square=3.84, P=0.04), (b) *Dolichoderus* sp.01 (df=1, Chi-square=5.06, P=0.02), (c) *Tapinoma melanochephalum* (df=1, Chi-square=4.59, P=0.03) and (d) *Philidris cordata* (df=1, Chi-square=2.41, P=0.12).

4. Discussion

Our results showed that higher levels of precipitation were associated with higher dissimilarity, but not species richness, of ant communities in cacao agroforestry systems, whereas land-use changes such as losses of shade trees from the cacao agroforestry systems were not related to ant community dissimilarity or diversity. These findings support the results of Wielgoss *et al.* [12] in the same study region that decreasing shade trees did not affect ant diversity. However, the study by Bos *et al.* [11] showed that reduced numbers of shade trees can negatively affect ant diversity, in particular of forest ants, in cacao agroforestry. In the study region of Bos *et al.* [11], but not Wielgoss *et al.* [12], natural rainforest surrounded their cacao agroforestry systems. Adjacent rainforests (of the national park) provide high forest ant diversity colonizing cacao agroforestry if characterized by high canopy cover from shade-trees. Therefore, shade trees presumably to be particularly important when rainforest habitat is surrounding cacao agroforestry as a nearby source of forest ants. In this study, the cacao agroforestry systems were not surrounded by, but rather isolated from rainforests, explaining why shade-tree level was not a predictor of ant diversity.

Precipitation did not affect number of ant species per tree (alpha diversity) in cacao agroforestry. This result is similar to that of Delsinne *et al.* [22], who did not find a relationship between precipitation and local ant species richness in arid ecosystems. In our research, the gradient of precipitation was limited (1032 to 2051 mm/year), which may explain why alpha diversity did not show a positive correlation of precipitation and ant diversity [23,24]. Nevertheless, we found that increasing precipitation decreased similarity of ant communities in the cacao agroforestry systems.

High precipitation may influence ant communities because of its negative relationship to ant nesting site availability, which is an important stressor for ants [25]. Nesting site limitation can shape ant community composition, affecting co-existence in addition to factors such as competition, environmental stress and disturbance [26]. In addition, higher precipitation caused higher heterogeneity of ant communities, which should be due to higher heterogeneity of cacao tree growth when drought stress is no longer a dominant and homogenizing factor. Reduced precipitation can be an important stress shaping ant communities in a similar way, *i.e.*, converging ant communities, whereas higher precipitation appeared to allow divergence of ant community structure across trees. Higher precipitation is part of environmental instability affecting the similarity of coexisting species [27].

The ant species differed in their response to the precipitation level. *Dolichoderus* sp.01 tended to be mainly found in cacao agroforestry with higher precipitation. As generalized foragers and distributed mainly in tropical region [28], this species can be expected to suffer most from El Nino (ENSO) droughts, which are common in the region [29]. In contrast, *T. melanocephalum*, a tramp or human commensal species [30] and *Crematogaster* sp.04, an arboreal species and nesting in hollow tree trunks [28] were only found in cacao agroforestry with low precipitation, benefiting from droughts. The dominant and invasive species *P. cordata* was not affected by high precipitation and drought, which may be a reason why this species spread widely and became dominant in cacao agroforestry in Sulawesi.

5. Conclusions

Land-use intensity and precipitation gradients did not affect the ant diversity per cacao tree (alpha diversity) and beta diversity in agroforestry systems in Sulawesi. However, high precipitation enhanced ant community dissimilarity, presumably via increased heterogeneity in cacao growth with increasing precipitation and subsequent differences in ant colonization, with ant species responding differently to precipitation level. Our results show that changes of precipitation, which are expected to occur in the study region due to El Nino (ENSO) droughts, should contribute to the homogenization of ant community structure.

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Supplementary Material

Table S1. The occurrence of ant species (proportion of trees occupied, 10 cacao trees observed) collected in the 16 cacao agroforestry plots in eight villages (1: Berdikari, 2: Sintuwu, 3: Bulili, 4: Pandere, 5: Sidondo, 6: Boladangko, 7: Toro, and 8: Lempelero) with different land-use (A: shaded, B: unshaded cacao agroforestry). Morphospecies were based on the different of external morphology.
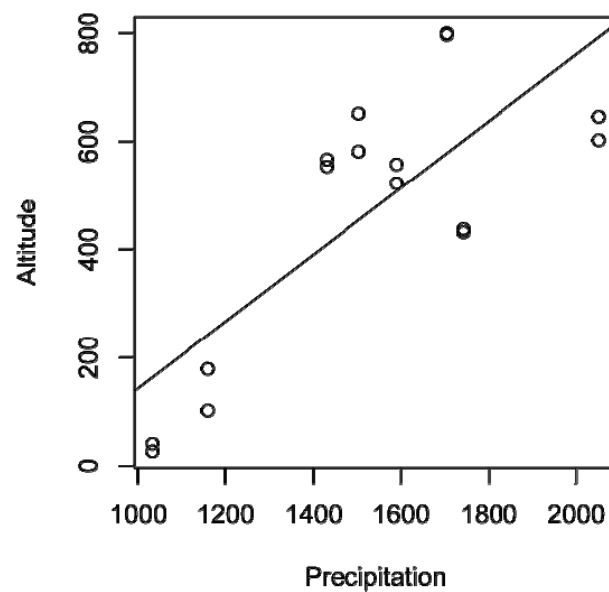
No	Species	Village															
		1		2		3		4		5		6		7		8	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Dolichoderinae																	
1.	*Dolichoderus* sp.01		0.5	0.4	0.5	0.2	0.7					0.9	0.2	0.5	0.2	0.1	0.2
2.	*Dolichoderus thoracicus*						1				1						
3.	*Philidris cordata*		0.7	1	1	1		1				0.7	1	0.9	1	1	1
4.	*Tapinoma melanocephalum*			0.2	0.7		0.3	0.3	0.9	1							0.2
5.	*Tapinoma* sp.01	0.4	1	0.2				0.7			0.9	0.1	0.7	0.8	0.7		0.2
6.	*Technomyrmex albipes*			0.3			1					0.9			0.2		
7.	*Technomyrmex* sp.01														0.3		
Formicinae																	
8.	*Anoplolepis gracilipes*		0.1						0.5		1	0.8	0.3	0.5	0.4		
9.	*Camponotus recticulatus*		0.4	0.9	0.2	0.7	0.1	0.1				0.3	0.6	0.1			0.5
10.	*Camponotus* sp.01	0.9			0.1	0.1	0.1	0.1	0.1			0.1	0.1				0.1
11.	*Camponotus* sp.02				0.1												
12.	*Echinopla lineata*	0.1		0.8		0.5											
13.	*Oecophylla smaragdina*		0.1	0.2	0.1				1								

Table S1. *Cont.*

No	Species	Village 1		Village 2		Village 3		Village 4		Village 5		Village 6		Village 7		Village 8	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
14.	*Paratrechina longicornis*							1									0.4
15.	*Nylanderia* sp.01	1		0.9	1	1	1	0.6	1	0.8		1	0.8	1	1	1	0.9
16.	*Nylanderia* sp.02		1														
17.	*Nylanderia* sp.03									0.7							
18.	*Nylanderia* sp.04	0.1	0.8					0.3			1						
19.	*Plagiolepis* sp.01	0.9															
20.	*Polyrachis abdominalis*	0.3								0.2							
21.	*Polyrachis dives*			0.7	0.5	0.3		0.2						0.2			0.1
22.	*Polyrachis* sp.01			0.3	0.4												
23.	*Polyrachis* sp.02			0.5									0.4				
24.	*Polyrachis* sp.03	0.1															
25.	*Polyrachis* sp.04					0.2											
26.	*Polyrachis* sp.05	0.8															
27.	*Polyrachis* sp.06			0.1										0.2	0.1		
28.	*Polyrachis* sp.07	0.4															
29.	*Pseudolasius* sp.01											0.2		0.3	0.1		
30.	*Pseudolasius* sp.02														0.3		
Myrmicinae																	
31.	*Crematogaster* sp.01	0.6						0.1	0.7		0.6						
32.	*Crematogaster* sp.02		0.6	0.1		0.1	0.2	0.2	0.6	0.1	0.1	0.7	0.3	0.2	0.8	0.2	0.6
33.	*Crematogaster* sp.03			0.2													
34.	*Crematogaster* sp.04						0.2			0.9	0.8						
35.	*Crematogaster* sp.05													0.3	0.1		
36.	*Monomorium floricola*		0.7				0.7		1	0.3	1	0.3	0.2	0.1			
37.	*Monomorium* sp.01								0.2	0.1	0.2						
38.	*Monomorium* sp.02	0.4										0.1				0.3	
39.	*Monomorium* sp.03							0.2									
40.	*Monomorium* sp.04		0.1								0.1						
41.	*Monomorium* sp.05					0.1	0.2										
42.	*Monomorium* sp.06										0.1					0.1	
43.	*Pheidole* sp.01	0.3	0.7	0.1	0.3	0.3	0.3	0.7	0.7	0.7	0.6	0.3				0.5	0.2
44.	*Pheidole* sp.02	0.9				0.1	0.1	0.1				0.1			0.6	0.4	0.1
45.	*Pheidole* sp.03	0.4	0.9					0.7		0.7	0.5	0.1	0.4	0.1	0.3	0.1	
46.	*Pheidole* sp.04			0.1													
47.	*Pheidole* sp.05				0.5							0.1			0.6		
48.	*Pheidole* sp.06	0.1			0.4	0.1						0.1		0.2	0.2	0.2	
49.	*Pheidole* sp.07																0.1

Table S1. *Cont.*

No	Species	Village 1		Village 2		Village 3		Village 4		Village 5		Village 6		Village 7		Village 8	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
50.	*Pheidole* sp.08			0.1	0.1												
51.	*Pheidologeton* sp.01											0.1					
52.	*Pyramica paradoxa*									0.1							
53.	*Solenopsis geminata*									0.4							
54.	*Strumigenys* sp.01									0.1			0.1		0.1		0.1
55.	*Tetramorium bicarinatum*		0.9							0.1	0.4						
56.	*Tetramorium pasificum*	0.2					0.9					0.5		0.3			
57.	*Tetramorium smithi*						0.4				0.3		0.1	0.1	0.1		0.1
58.	*Tetramorium* sp.01								0.5								
59.	*Tetramorium* sp.02		0.2								0.2						
60.	*Tetramorium* sp.03	0.2								0.3							
61.	*Tetramorium* sp.04	0.4				0.1				0.1							
62.	*Tetramorium* sp.05			0.1	0.1					0.3			0.1	0.1		0.1	0.1
63.	*Tetramorium* sp.06												0.3		0.4		0.1
64.	*Tetramorium* sp.07														0.3		
65.	*Tetramorium* sp.08			0.2	0.1												
Ponerinae																	
66.	*Anochetus graeffei*						0.3	0.3	0.4	0.2			0.3		0.2		
67.	*Diacamma rugosum*							0.4	0.1	0.6	0.9						
68.	*Hypoponera* sp.01	0.2		0.1	0.1			0.2				0.1			0.2		
69.	*Hypoponera* sp.02			0.8	0.9	0.3	0.1					0.6	0.8	0.9	0.5	0.7	0.3
70.	*Hypoponera* sp.03			0.1						0.4		0.2					
71.	*Hypoponera* sp.04								0.2								1
72.	*Leptogenys* sp.01	0.1		0.2										0.1	0.3		
73.	*Odontomachus simillimus*	0.2	0.5	0.7	0.7	1		0.1	0.4	0.3		0.7	0.3	1	0.9	1	0.2
74.	*Pachycondyla* sp.01	0.4					0.1	0.2			0.2			0.1		0.2	0.4
75.	*Pachycondyla* sp.02	0.1															
76.	*Pachycondyla* sp.03								0.2								
77.	*Pachycondyla* sp.04									0.1							
78.	*Platythyrea* sp.01			0.1	0.1	0.1		0.2	0.1			0.1					
Pseudomyrmicinae																	
79.	*Tetraponera* sp.01		0.1														
80.	*Tetraponera* sp.02												0.2				0.1

Figure S1. Correlation between precipitation and altitude of the 16 plots of the study area ($F_{1,14} = 21.47$, $P = 0.0004$, $r^2 = 0.58$).