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Temperature and a dominant dolichoderine ant species affect ant diversity in Indonesian cacao plantations

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ABSTRACT

Agricultural land conversion and climate change play a major role in shaping tropical landscapes, but the direct and indirect links to biodiversity and species community composition remain little understood. We tested how landscape and environmental factors and management techniques, affect the diversity of ground and tree living ants in cacao plantations in Sulawesi (Indonesia). In addition, we investigated the occurrence of an aggressive, numerically dominant dolichoderine ant species (genus *Philidris*). Half of the 43 study plots, which differed in canopy cover, shade tree diversity, cacao tree age and their distance to the nearest rainforest, were weeded manually every 3 month, the others biannually. Each plot was divided into two subplots, one was fertilized twice a year whereas the other remained unfertilized. Using protein and sugar-solution baits, we examined species richness, abundances and interspecific interactions of ants on the ground and in cacao trees. In total we collected 160 ant morphospecies. Reduced ant species richness on the ground and in the trees was significantly correlated with higher mean temperatures while the other factors, including number of shade trees did not have any significant influence. The abundant and aggressive *Philidris* species, reduced arboreal ant species richness. It occurred more frequently in warmer, less shaded plots and on older cacao trees, which offer more nesting sites. In our study we show, that micro-climatic conditions and the occurrence of single ecologically dominant species are the major factors predicting species diversity in tropical agricultural ecosystems.

1. Introduction

Unlike many crop monocultures, complex agroforestry systems in tropical forest-agriculture landscapes, like well shaded cacao, may harbour high species richness, and have the potential to raise connectivity between forest fragments (Bhagwat and Willis, 2008; Klein et al., 2002; Perfecto et al., 2008). This has been shown for birds and bats (Harvey and Villalobos, 2007; Waltert et al., 2004), primates (Estrada, 2005), arthropods (Bos et al., 2007b; Johnson, 2000; Perfecto and Vandermeer, 2002; Perfecto et al., 2003), and plants (Mendez et al., 2007; Sonwa et al., 2007). As in other cacao producing countries (Rice and Greenberg, 2000), Indonesian farmers have been intensifying cacao agroforestry by reducing shade tree diversity and density, as well as applying insecticides, fungizides and fertilizers and removing weeds manually and by using herbizides (Siebert, 2002). Full-sun cacao monocultures may no longer provide the large biodiversity of complex agroforestry systems, increasing the negative effect of agricultural activity and potentially compromising these important ecosystem services, like e.g. biological pest control, seed dispersal and pollination (Klein et al., 2002; Rice and Greenberg, 2000). Nitrogen fertilization, however, can have a positive effect on the abundance of sap sucking insects like aphid and coccids (e.g. Jahn et al., 2005; Krauss et al., 2007; Schutz et al., 2008). For most ants in the tropics tend trophobionts for (Hölldobler and Wilson, 1990), fertilization could influence the ant fauna secondarily via changed trophobiont abundances.

In the tropics ants play an important ecological role in both natural and agricultural habitats (Delabie et al., 2007). They show a wide range of multitrophic interactions with plants and insects, ranging from parasitism to mutualism (Hölldobler and Wilson, 1990). As efficient predators ants may limit herbivore populations, including potential insect pests in agroecosystems (Armbrecht and Gallego, 2007; Philpott and Armbrecht, 2006; Van Mele, 2008). The diversity of ant communities has been shown to decline when a

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natural habitat is disturbed (Brühl et al., 2003; Floren and Linsenmair, 2005) or agricultural land-use is intensified (Armbrecht et al., 2005; Philpott et al., 2006). The observed simplification of cacao agroforestry in Indonesia may not only cause losses in functional ant diversity, but also increase the risk of outbreaks of pest insects and plant diseases (Bos et al., 2007a; Schroth and Harvey, 2007; Tscharntke et al., 2005). The removal of shade trees and higher frequency of weeding accompanying intensification of tropical agroforestry systems may increase nest-site limitation of many ant species (Armbrecht and Perfecto, 2003; Armbrecht et al., 2006; Philpott and Armbrecht, 2006; Philpott and Foster, 2005), which is often associated with a impoverishment of the ant community in favor of a few dominant species like e.g. *Anoplolepis gracilipes* (Smith) (formerly *Anoplolepis longipes*, Jerdon) (Bos et al., 2008).

During a pre-study in one cacao plantation in the same study area (A. Wielgoss, Y. Clough, 2006, unpublished data) a dolichoderine ant species of the genus *Philidris* has found to be the most abundant species of the ant fauna with high colony densities having polydomous, polygynous nests on nearly every cacao tree of the plantation. It showed aggressive behavior towards other ant species, excluding them from baits and formed a uniform ant community with relatively few species.

In this study we use ant data collected in 43 cacao plantations in Sulawesi (Indonesia) differing in shade tree density, tree diversity and temperature, distance to natural forest as well as frequency of manual weed removal and fertilization. We addressed the following questions: Which environmental variables and management techniques affect species richness of ground- and tree-dwelling ants in cacao plantations? Does the presence of dominant ants like *Philidris* sp. cause a decline in species richness arboreal or ground living ants? Can environmental or management variables be used to predict the presence of this dominant ant species in cacao plantations of the study area?

2. Methods

2.1. Study area/study plots

The survey was conducted from the end of July to the end of November 2007 in Kulawi and Palolo valley at margin of the Lore Lindu National Park, the largest NP (2.290 km^2) in Central Sulawesi, Indonesia (Appendix Fig. A). The climate is humid and diurnal with no pronounced seasons. The daytime temperature in these areas ranges from 26 to 32 °C. The annual rainfall ranges from 2000 to 3000 mm.

We selected 43 cacao plantations in the two valleys differing in distance to nearest primary rainforest (0–2500 m), canopy cover, number of shade trees (mean: 32 shade trees per plot; min: 4; max: 125), shade tree diversity (mean: 9 shade tree species per plot; min: 3; max: 25), cacao tree age (mean: 14 years; min: 8; max: 22) and altitude above sea level (400–900 m). Each of the 40 m × 40 m plots was divided into two subplots, of which one was fertilized twice with 100 kg/ha urea (43% nitrogen) in December 2006 and June 2007 and the other remained unfertilized. Fertilizer was applied at each cacao tree of the subplot dug in five locations into the ground (15 cm depth; 1.5 m distance from tree). In each subplot five representative cacao trees were chosen as focal trees (total 10 test trees per plot, 5 fertilized, fife unfertilized). Half of the plots were weeded manually every 3 months the others biannually. No herbicides, fungicides or insecticides were applied since August 2006. The distance of the study plots to the nearest rainforest fragment was measured using georeferenced satellite images and Arcview 3.2 (ESRI). We used data quantifying the canopy cover per plot by vertical digital photography with a fish-eye lens. Per test tree two pictures were taken: one above, and one below the cacao tree canopy (5.80 m and 1.30 m above the ground, respectively). We calculated the mean shade cover per plot above and below the cacao canopy for each plot using Winscanopy (© Regent Instruments Inc.). Per plot two temperature dataloggers (Thermochron® iButton®, Maxim–Dallas Semiconductor) were placed at breast height in different cacao trees, recording the temperature every 2 h from June 2006 until June 2007. For the analysis we used the mean of the average daily temperature per plot over that time period.

2.2. Ant sampling

We used plastic observation plates (25 cm diameter), which were equipped with two baits of 2 cm^3 of tuna in oil and two sponges saturated with 70% sugar solution, to determine the abundance of ant morphospecies. One plate was placed in the main ramification of each experimental cacao tree (if the main ramification was too high it was fixed at breast height on the stem with elastic rubber band; approximately one of ten cases) and one set on the ground, 1.70 m north of the stem. All plates of one subplot (five in trees, five on the ground) were observed by the same person simultaneously, walking from plate-to-plate spending 1 min at each bait. Of every ant species appearing on the plate 5–10 specimens were caught with forceps and conserved in 70% ethanol for later identification. For abundant ant species we waited with the sampling until 10–20 individuals were recruited to the baits. Ant species that occurred as singletons were sampled immediately to avoid missing them. All observed interspecific ant interactions were recorded. At 15, 30, 45 and 60 min after placing the plates at the observation sites, the abundance of all ant species occurring at the baits was counted at each plate (separately for ants feeding on fish or sugar). After each use the plates were washed with clean water to remove pheromones and remaining sugar or fish.

After the last count the ant trails were followed to locate the nests when possible and nests were characterized by location (ground/tree), type (e.g. within dead wood or myrmecophytic plants) and if they were poly- or monodomous. This survey was conducted in all 43 cacao plots twice: once in the morning (9:00–11:00 a.m.) and once in the afternoon (13:00–15:00 p.m.) with a minimum of two weeks intermission between the two samples. The sampling order of plots was random. In pre-studies we found that most ant species reduced their activity under very wet conditions, so no surveys were conducted during and just after rain.

2.3. Identification of ants/definition of dominant ant species

Ant species identification literature for Sulawesi is lacking. Therefore we identified the samples to genera using the key by Bolton (1994), and further separated the ants to morphospecies level using external morphological features.

Dominant ants characteristically have populous colonies which build large or polydomous nests (Richard et al., 2001). They tend to have high rates of carbohydrate feeding on honeydew excreted by trophobionts (Bluthgen et al., 2004), exclude other species from their territory and from baits and frequently have a high level of aggressiveness (Hölldobler and Wilson, 1990). We used these indicators and checked nest sizes, polydomy, body size, interspecific behavior and worker recruitment rates at the baits. According to that criteria we identified nine arboreal ant morphospecies that could have the potential to ecologically dominate the arboreal ant fauna in the single cacao trees of the studied plantations: two morphospecies of the genus *Philidris*, *Oecophylla smaragdina*, *A. gracilipes*, *Dolichoderus thoracicus* and 4 *Crematogaster* morphospecies. However only *Philidris* sp.1 was present at a sufficient number of test trees, to include its presence/absence as explanatory variable in the statistical analysis.

Table 1
Sampling success and species distribution of ants in Indonesian cacao plantations.

	Arboreal ant morphospecies	Ground-dwelling ant morphospecies	Ubiquitous ant morphospecies	Total
Kulawi	28	36	51	115
Palolo	30	36	57	123
Region overlap	11	19	48	78
Total	47	53	60	160

Number of ant morphospecies found visiting the tuna + sugar baits (43 study sites, 10 ground- and 10 tree baits per plot, two repeats; arboreal = found only on tree baits, ground-dwelling = found only on ground baits, ubiquitous found at ground and tree baits; region overlap = species occurring in both areas).

2.4. Statistical analyses

Dependent and explanatory variables used in our analyses are detailed in Appendix B. We used mean daily temperature instead of altitude, because both variables are strongly correlated (Pearson's product-moment correlation; $r = -0.89$; $df = 41$; $p < 0.0001$). We used regression modeling with a Poisson error structure and log link junction to explain tree- and ground-dwelling ant morphospecies richness with environmental variables using multi-model inference (MMI) approach. This model selection method allows to compare models with all possible combination of explanatory variables of the full model, in order to rank the relevant variables by their explanatory power.

Best-subset models were then chosen based on information–theoretic methods (Burnham and Anderson, 2004). First, we analyzed data on the fertilization subplot level in a linear mixed model, with plot as a random grouping variable. As we did not find a significant influence of fertilization, we combined subplots differing in fertilizer treatments and continued the analysis on plot level with general linear models (glm). Model adequacy was ascertained using diagnostic plots on full models, to ensure homoscedasticity, normality of errors, and absence of outliers. The models of all possible permutations of the variables used in the full model were calculated and were ranked by their explanatory strength using AICc (Akaike's Information Criterion corrected for small sample sizes, Burnham and Anderson, 2004). We identified and ranked the set of best models with ΔAICc values ≤ 2 (i.e. the difference of AICc of the best model to the AICc of the model of interest). For each model in this top set of models we calculated the pseudo-R^2, the negative log-likelihood (NLL) and the AICc-weight (AICcw), which is the relative likelihood for the model of being the best of the set (Burnham and Anderson, 2004). For a model averaging, we calculated ΣAICcw, the sum of the AICcw of the top-set models in which a predictor variable appears. This value is a good indicator to rank the variables by their relative explanatory power. For each relevant predictor variable we calculated the average of the estimates and standard errors of the top set of models, for the most relevant explanatory variables. We additionally did a linear regression to confirm our results of the model selection method.

We repeated the analysis with the presence/absence data of *Philidris* sp. at the bait locations as additional explanatory variable. We also tested factors that influence the probability of *Philidris* sp.1 presence in the plots with the same glm-MMI-analysis, but with a binomial error structure and a logit-link. All analyses were conducted in *R* (R Core Development Team, 2008), with additional functions of original unpublished *R* codes for the multi-model inference procedure (available on request from YC).

3. Results

3.1. Sampling success

We sampled in total 160 ant morphospecies belonging to 33 genera (Table 1). The observed species richness per study plot varied between 2 and 23 for ants found at ground baits (mean ± SD: 13.7 ± 4.28) and between 1 and 19 for ant species sampled from cacao trees (9.2 ± 4.98). Per single tree we found a mean of 2.2 ant species (±1.25; min: 1; max: 8), while a single ground bait was visited by a mean of 3.4 species (±1.47; min: 2; max: 10).

In Fig. 1(a) and (b) we give an overview of the frequency of occurrence of the15 most common morphospecies at trees and ground bait locations plotted against their mean worker recruitment rate at the baits (mean of the maximal numbers counted at baits during 1 h observation time). At the baits placed in the trees we sampled in total 107 morphospecies of ants belonging to 20 genera. *Philidris* sp.1 was by far the most frequent morphospecies, occurring on 65% of the 430 test trees cacao test trees (82% of the plots). With a mean recruitment of 120.6 workers per tree bait, it was one of the most abundant ant species.

At the ground baits we sampled 113 morphospecies out of 32 genera. The most frequent was *Paratrechina longicornis* (74% of ground baits), with a mean recruitment of 12.2 workers. The tree nesting *Philidris* sp.1 was the second most frequent (28% of baits) ant species on the ground with relatively high abundances (mean 82.2 workers), followed by *A. gracilipes*, present at 26% of the ground observation sites, mean of 33.7 workers.

3.2. Factors affecting species richness

The mean daily temperature in the study plots was correlated negatively with the ant species richness on the ground and on the trees (Table 2a and b), as variable with the highest explanatory power ΣAICc.w (The sum of AICc.w can take values from 0 to 1. A value of 1 means that the variable entered in all of the top set of models as significant variable). We confirmed these findings with linear regressions (Ground: $N = 43$, $F = 6.56$, p-value < 0.01, adjusted R^2: 0.12; Tree: $N = 43$, $F = 6.73$, p-value < 0.01, adjusted R^2: 0.12, see Appendices D and E). The cacao trees of the region Palolo were more species-rich on average than those in Kulawi. We could detect a negative influence of canopy openness on the ant species richness on the ground (Table 2b), but with a lower explanatory strength (ΣAICc.w) than the mean temperature (non-significant in regression, $N = 43$, $F = 1.33$, p-value: 0.26, adjusted R^2: 0.01). In our analysis the number of shade trees and the distance to rainforest did not enter as relevant variables the top set of models to predict arboreal or ground living ant species richness. Number of shade tree species per plot did not have significant effect on ant species richness on the ground or on the trees (Ground: $N = 43$, $F = 0.36$, p-value: 0.54, adjusted $R^2 = -0.019$; Tree: $N = 43$, $F = 0.35$; p-value = 0.56, adjusted $R^2 = -0.019$).

For details of explanatory variables and full models see Appendices B and C.

3.3. Influence of Philidris sp.1

Integrating the presence of the dominant ant *Philidris* sp.1 as an additional explanatory variable in the full model (Appendix C)

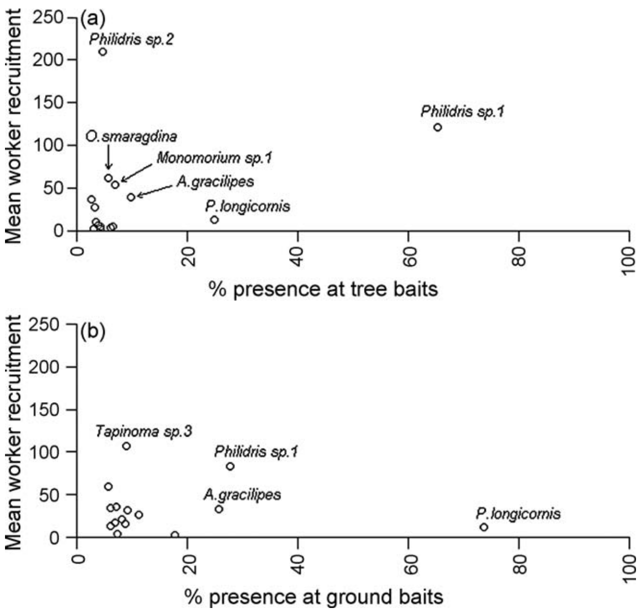

Fig. 1. (a) and (b) Occurrence and recruitment rates of most common ant species in trees and on the ground. Mean of the observed worker recruitment rate of the 15 most common ant species at tuna + sugar baits in the trees (a) and on the ground (b) plotted against percentage of occurrence at the baits (1 h observation time; $N = 430$, two repeats).

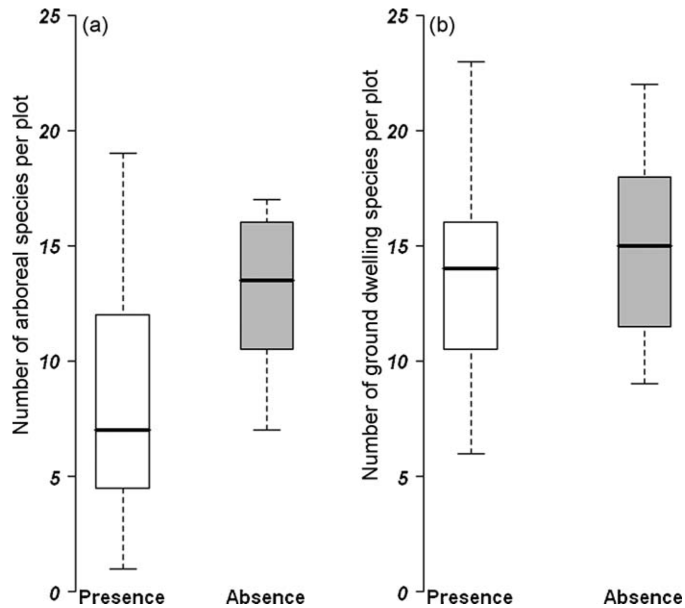

Fig. 2. Effects of ecologically dominant ant *Philidris* sp.1 on ant species richness. (a) Species richness of ants sampled in trees in cacao plantations in the presence and absence of the invasive ant *Philidris* sp.1: *t*-test: 95% confidence interval: 1.16–7.76; $df = 13.2$, p-value < 0.01. (b) Species richness of ants sampled on the ground in cacao plantations in the presence and absence of the invasive ant *Philidris* sp.1: *t*-test: 95% confidence interval: -0.70 to 4.11; $df = 35.1$, p-value = 0.16.

reveals that the presence of *Philidris* sp.1 was negatively correlated with the species richness of arboreal ants, being the most relevant explanatory variable (Table 2c). On average we found seven instead of 14 ant species per cacao tree when *Philidris* sp.1 was present (*t*-test: 95% confid. interval: 1.16–7.76; $df = 13.2$, p-value = 0.012; Fig. 2). There is also a negative influence of *Philidris* on species richness of ground-dwelling ant (Table 2d, Appendix C) relevant factor in generalized model, but non-significant in *t*-test (Fig. 2; *t*-test: 5% confid. interval: -0.70 to 4.11; $df = 35.1$, p-value = 0.16).

The probability of the presence of *Philidris* sp.1 in a study plot was positively correlated with the age of the cacao trees and the mean daily temperatures in the plot, and negatively with shade below the cacao canopy (Table 2e, Appendix C).

4. Discussion

We have shown that increasing temperatures in cacao plantations in Sulawesi was the main predictor of diversity of ground-dwelling and arboreal ants. The number of shade trees per

Table 2
Results of model selection for predicting ant species richness in Indonesian cacao plantations.

MMI-analysis to predict	Explanatory variables included in top set of models	ΣAICc.w	Estimate	SE
(a) Effects of environmental factors on arboreal ant species richness	Mean temp.	0.74	−1.97	0.92
	Region	0.70	2.93	1.45
(b) Effects of environmental factors on ground-dwelling ant species richness	Mean temp.	1.00	−1.83	0.71
	Open (1.30)	0.29	−0.13	0.16
(c) Effects of invasive ant species *Philidris* sp.1 and environmental factors on arboreal ant species richness	P/A-Philidris	0.70	−3.45	1.82
	Mean temp.	0.63	−1.81	0.92
	Region	0.59	2.73	1.44
	Open (5.80)	0.08	0.05	0.05
	Dist_Forest	0.07	−0.05	0.06
(d) Effects of invasive ant species *Philidris* sp.1 and environmental factors on ground-dwelling ant species richness	Mean temp.	1.00	−1.78	0.72
	P/A-Philidris	0.27	−1.22	0.73
	Open (1.30)	0.21	−0.13	0.16
(e) Presence/absence of the *Philidris* sp.1	Mean temp.	1.00	1.34578	0.686
	Age cocoa	1.00	0.26811	0.123
	Open (1.30)	0.40	−0.219	0.169

Relevant explanatory variables of each analysis are ranked by their relative explanatory power ΣAICc.w. Estimates and standard errors predicting ant species richness at (a) tree baits and (b) on ground baits; analysis with inclusion of the presence/absence of the ant species *Philidris* sp.1 as factor, for species richness at (a) tree baits and (b) on ground baits; (c) factors affecting occurrence of *Philidris* sp.1. Estimates and standard errors rely on transformed data.

plot and the shade tree diversity did not have an influence on ant species richness on the ground or on the trees. Shade cover itself had no effect on the species richness of arboreal ants, but we found minor positive effect of shade on the species richness of ground-dwelling ants. This contrasts with other studies on ants conducted along shade cover gradients of cacao and coffee plantations in Latin America (Philpott, 2006) and Indonesia (Bos et al., 2007a), which showed that ant species richness decreased and/or the ant community composition simplified in study plots with less shade trees. That our findings only partly confirm these results, may be due to the more limited spatial extent and altitudinal range of the mentioned studies, and highlights the importance of large scale studies for identifying driving factors. The average daily temperatures, being the variable with the highest explanatory power for models predicting the arboreal and ground ant species richness, were determined by altitude. In the study area altitude is often correlated with landscape variables such as distance to forest, because settlements are mostly in the valleys and intact rainforest on elevations. But we accounted this hidden effect already when plots were chosen. In our study fertilization and weed management did not show an effect on ant species richness. In a study on lower canopy ants in the same study area (Bos et al., 2008) it was shown, that there is a general difference in species composition between natural forest and cacao agroforests. We can confirm these results, for at least half of the ant species found in cacao trees in our study were not found in the adjacent forest by Bos et al. As well we did not find a relationship of ant diversity to distance to rainforest which might suggest little linkage of rainforest to cacao plantations. So species richness alone should not be used as indicator for conservation value. We state that in this case mean temperature was a better predictor for ant species richness than shade cover, density and diversity of shade trees or management techniques.

In total we sampled 160 morphospecies in 43 Indonesian cacao plantations, of which 47 were exclusively arboreal, while 53 occurred only on the ground, and the other 60 occurring at both strata. Delabie et al. (2007) found a similar number of ant morphospecies (192) in cocoa plantations in Brazil. In a study of the ant fauna in oil palm plantations in Borneo and Peninsular Malaysia 53 ant species were found on a total of nearly 110 surveyed palms (Pfeiffer et al., 2008), suggesting, despite differences in sampling effort and methods complicate direct comparability between studies, that cacao plantations may harbor a more diverse ant community, than the more simply structured oil palm plantations.

We found one single ant species, *Philidris* sp.1, (Subfamily Dolichoderinae), to be extremely widespread in the study region, dominating the ant fauna in 36 of the 43 plots by abundance and aggressive behavior. It was present on 65% of all tested trees and 30% of the ground bait locations and recruited, relatively to other ant species, high numbers of individuals to the baits. This ant species shows a pronounced aggressiveness against intruders: farmers complain about serious annoyances by bites of *Philidris* sp.1 during harvest and pruning. *Philidris* sp.1 aggressively expelled other ant species from the observation plates and successfully defended the baits against other ants. During the whole study we observed no intraspecific aggression of ants of different *Philidris* colonies. This is the first time an ant species of the genus *Philidris* is reported to be such an ecologically dominant and abundant part of the ant fauna of a region.

The occurrence of *Philidris* sp.1 was the most important factor determining ant diversity, as in plots with *Philidris* present, ant species richness in the trees was significantly lower. Six of the nine best-subset models estimating ant species richness in the cacao trees included the presence of this ant species as an relevant explanatory variable. The effect of *Philidris* sp.1 on ground-dwelling ant species richness was weaker, but detectable. This species is tree nesting and most workers forage in the tree and only occasionally lower to the ground (present on 30% of the ground baits, but in 65% of the trees). Therefore, its influence on the arboreal ant fauna is stronger than on the ground living ants. It is known that aggressive ant species have a potential to contribute to changes in ant diversity and that they are frequently more abundant in more intensively managed agricultural habitats (Hölldobler and Wilson, 1990). The probability of occurrence of *Philidris* sp.1 was positively correlated with the mean temperature in the plot and the age of the cacao trees, and negatively with shade cover. The association with warm and little shaded cacao, together with its aggressiveness and numerical dominance, is reminiscent of the opposite results found for ant species richness. It strongly suggests that *Philidris* sp.1 drives out other ant species from cacao plantations.

Our results suggest that *Philidris* sp.1 is nest site limited on younger cacao trees. This ant species builds nests in hollow twigs and branch stumps remaining from pruning, as well as cracks in the bark of the cacao trees, sites that become more readily available as the trees age. Given the similarity in age of the cacao trees across the study area, with few plantations over 20 years and most between 4 and 15 years of age, the commonness of *Philidris* in cacao may be recent. Indeed, two studies conducted in our research area between 2001 and 2005 report *Philidris* as absent in one case, and as present but only very locally dominant in another (Bos et al., 2008; Hosang, 2004). Changes in ant communities as microsites in aging trees become available is known as "ontogenic succession" and has recently been described from a natural pioneer tree in West Africa (Dejean et al., 2008).

In our study area the invasive "Yellow crazy ant" *A. gracilipes* was present. This species is known for its ability to reach extreme high densities and pest status on islands in the Indian and Pacific Ocean (Greenslade, 1971; Hill et al., 2003; Abbott, 2005), causing great damages in invertebrate (Holway et al., 2002; Lester and Tavite, 2004) and vertebrate (Feare, 1999; Gerlach, 2004) communities. We found *A. gracilipes* to be only subdominant, being observed at only 10% of the trees and 27% of the ground bait locations. Compared with other ant species, *A. gracilipes* is recruiting relatively low numbers of individuals. This is in contrast with results to earlier surveys in our study region in 2004/2005 (Bos et al., 2008) reporting *A. gracilipes* to be the numerically dominant ant species in little shaded cacao plantations. A possible explanation for the subordinate role of this ant species in our study could be the cyclical variation of abundance of this species as reported from other invaded islands (Greenslade, 1971; K.E. Linsenmair, personal communication). We found the nests of *A. gracilipes* in cacao plantations mostly to be located on the ground under the leaf-litter. So this ant species could be more affected by the management intensification (including higher frequency of weeding, application of herbicides and insectizides), than *Philidris* sp., which is nesting more protected in cracks of the bark and dead wood. Comparing our sampling with previous studies (Hosang, 2004; Bos et al., 2008), it seems that *Philidris* sp.1 has spread in the study region in the past decade with the aging of cacao plantations (confirmed by questioned farmers) and has replaced *A. gracilipes* as the ecologically most dominant part of the ant fauna.

5. Conclusions

Our results highlight the threatening effects of ecologically dominant ant species on biodiversity in agricultural landscapes. We have shown that with higher mean temperatures and lower shade cover in the plantations a colonization of the studied dominant ant species becomes more likely. Hence, not only anthropogenic habitat modification, but also global and micro-climatic changes likely affect the further spread of dominant and/or invasive species. The age of a plantation is a crucial factor for the presence of the ecologically dominant ant *Philidris* sp.1. Therefore it is expected, that an invasion of this species in the younger plantations of the study area, associated with the linked species loss, may happen within the next years. In the case of our study mean temperature was a better predictor for ant species richness than management strategies or landscape factors.

It is important to acknowledge this link between climatic factors, anthropogenic habitat modification, and ecologically dominating species and their direct and indirect effects on species diversity in future studies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2009.10.003.

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