Intensive agroforestry practices negatively affect ant (Hymenoptera: Formicidae) diversity and composition in southeast Sulawesi, Indonesia

Wara Asfiya[1,2*], Lori Lach[3,4], Jonathan D. Majer[5],
Brian Heterick[5], and Raphael K. Didham[1,6]

[1] School of Animal Biology, The University of Western Australia,
35 Stirling Highway, Crawley WA 6009, Australia
[2] Bogor Zoological Museum, Research Center for Biology,
Indonesian Institute of Sciences, Gd. Widyasatwaloka, Jl. Raya Jakarta-Bogor
Km. 46 Cibinong 16911, Indonesia
[3] School of Plant Biology, The University of Western Australia,
35 Stirling Highway, Crawley WA 6009, Australia
[4] Centre for Tropical Biodiversity and Climate Change,
James Cook University, Cairns, Qld 4870 Australia
[5] Department of Environment & Agriculture, Curtin University,
Kent Street, Bentley, WA 6102, Australia
[6] CSIRO Land & Water Flagship, Centre for Environment and Life Sciences,
Underwood Ave, Floreat WA 6014, Australia

*Corresponding author's e-mail: wara.asfiya@lipi.go.id

ABSTRACT. Many natural forests in southeast Asia have been replaced by agroforestry systems with increasingly intensive management practices. To test the effects of intensive agroforestry practices on the retention of rainforest biodiversity, we quantified ant diversity and composition in three cocoa plantations versus three rainforest remnants in the remote Mekongga Mountains of southeast Sulawesi, Indonesia. Using three complementary sampling methods (pitfall trapping, leaf litter sifting, and baits) we found substantially more species, in total, at rainforest sites (67 spp.) than at the cocoa sites (43 spp.), and for all sampling methods there was significantly greater ant richness and diversity in rainforest habitats compared with cocoa plantations. Moreover, only 23 out of the total 87 species were shared between habitat types and an ANOSIM analysis showed that forest ant assemblages were significantly different from cocoa ant assemblages, with an average of 89.8% dissimilarity of species relative abundances between rainforest fragments and cocoa plantations. Whereas rainforest fragments were dominated by a diverse array of native species in the genera *Pheidole*, *Prenolepis*, *Odontomachus* and *Tetramorium*, cocoa plantations were dominated by the tramp ant species *Anoplolepis gracilipes*, *Monomorium floricola* and *Nylanderia vaga*. The results of this study suggest that intensive agroforestry can have a dramatic influence on ant species composition, promoting the establishment of invasive tramp ant species and the loss of rainforest specialist species. This contrasts with previous findings from lower intensity, shade grown cocoa, which suggest that agroforestry can be a 'win-win' for both biodiversity conservation and agricultural production. Our results suggest that intensive production practices have strong negative effects on native biodiver-

sity in plantation agroforests, and effective conservation strategies should focus on limiting land use conversion to more intensive agroforestry systems.

Keywords: biodiversity, cocoa plantation, Formicidae, invasive ants, land use, rainforest, Sulawesi.

INTRODUCTION

Tropical rainforests support at least two-thirds of all terrestrial plant and animal species on Earth and also provide significant economic, environmental, and social benefits to humans. However, the future of tropical forests has never been more uncertain, as many rainforests in the tropics are being rapidly destroyed and degraded through various forms of human impact, such as infrastructure development, agricultural expansion, and timber extraction (Gardner *et al.* 2009). Of all the tropical regions of the world, the extensive forests of southeast Asia are under greatest pressure, with recent deforestation rates of around 1.0% annually between 2000 and 2010 (Miettinen *et al.* 2011).

A wide variety of different land uses have expanded in the human-modified landscapes surrounding tropical rainforest remnants, led in particular by conversion to industrial-scale agricultural crops and plantation forests in Asia and South America (Bhagwat *et al.* 2008). Moreover, human population pressure and increasing demand for food, combined with the shift from small-scale independent producers to large-scale agribusiness, have promoted conversion from traditional low intensity agricultural practices (i.e. use of a small quantity of chemical pesticides and fertilizers, and a small quantity of supplementary livestock) to much more intensive agricultural practices (i.e. clearing native vegetation, monocropping, application of large quantities of chemical pesticides and fertilizers, and overgrazing by livestock) (Attwood *et al.* 2008). With continuing land use intensification, there is serious international concern about ecosystem resilience and loss of biodiversity (Bos *et al.* 2007a; Bhagwat *et al.* 2008; Gibbs *et al.* 2010).

Many studies have documented the negative impact of tropical deforestation and intensification of land use on invertebrate communities, including a collapse in termite species richness and abundance along a land-use intensification gradient (Jones *et al.* 2003) and a change in species richness and composition of different animal groups with increasing habitat modification (Lawton *et al.* 1998). Others have identified that habitat modification and land use intensification can negatively affect ant communities (e.g. Watt *et al.* 2002; Kone *et al.* 2012). Changes in the successional stage of the habitat, diversity and heterogeneity of vegetation, soil and litter characteristics, age of habitat, and proximity to colonization sources are all factors that might explain the dissimilarity of invertebrate assemblages between agroforestry and rainforest sites (Roth *et al.* 1994). However, few studies, have provided such information for ants (e.g. Roth *et al.* 1994; Ottonetti *et al.* 2010).

The need to balance the negative effects of land use intensification on biodiversity versus the socioeconomic benefits derived from increased agricultural production has become an extremely contentious issue (Green *et al.* 2005; Fischer *et al.* 2008; Fischer *et al.* 2011). In this debate, agroforestry development has been promoted as a 'win-win' for both agricultural production and biodiversity conservation, particularly in shade-grown coffee and cocoa agroforestry systems (Delabie *et al.* 2007; Clough *et al.* 2011; Waldron *et al.* 2012). There are several examples in which low-intensity agroforestry systems have been shown to have similar invertebrate richness to adjacent rainforest, such as for canopy ants and beetles in low-intensity cocoa agroforestry in Indonesia (Bos *et al.* 2007b) and leaf litter ants in Ghanaian cocoa (Belshaw & Bolton 1993). Even though low-intensity agroforestry can have high levels of biodiversity (Bos *et al.* 2007a; Steffan-Dewenter *et al.* 2007; Kessler *et al.* 2009), there can be strong pressure for farmers to increase production yield using more intensive agroforestry practices (Clough *et al.* 2011). Consequently, not all agroforestry development will necessarily have a low impact on biodiversity (e.g. Wielgoss

et al. 2010; Rizali *et al.* 2013), but this has not been well investigated.

In some studies, intensification of cocoa agroforestry practices was shown to result in an increased abundance of tramp species such as *Anoplolepis gracilipes*, the yellow crazy ant (Bos *et al.* 2008). In turn, forest ant richness decreased significantly with increasing density of *A. gracilipes* (Bos *et al.* 2008). Similarly, the richness and relative frequency of forest ground ants occurring in oil palm plantations in Sabah (Malaysia) was strongly negatively affected by the occurrence of *A. gracilipes*, and other tramp species such as the flower ant *Monomorium floricola* (Brühl & Eltz 2010). These findings are in line with widespread evidence that habitat modification can promote species invasion and influence the composition of native species (Didham *et al.* 2007).

Here, we contribute to a wider understanding of the role that tropical agroforestry can play in biodiversity conservation in human-modified landscapes, by testing how intensive land use management affected ant species diversity and composition, and whether intensive agroforestry promotes the colonization and establishment of invasive ant species.

METHODS

Study sites

The study was conducted within the Mekongga Mountains, located in the province of Sulawesi Tenggara in Indonesia (3° 38'S, 121°4'E), between 23 June and 1 July 2010. The climate is humid tropical, with monthly average temperatures varying between 23.2 and 30.9°C and an annual average rainfall of 2143 mm (www.meteo.bmkg.go.id). The forest in this region has a mostly intact canopy, but with obvious signs of human activity, such as selective logging, intensive agriculture (cocoa, coffee, maize, and paddy) and road-building (Cannon *et al.* 2005).
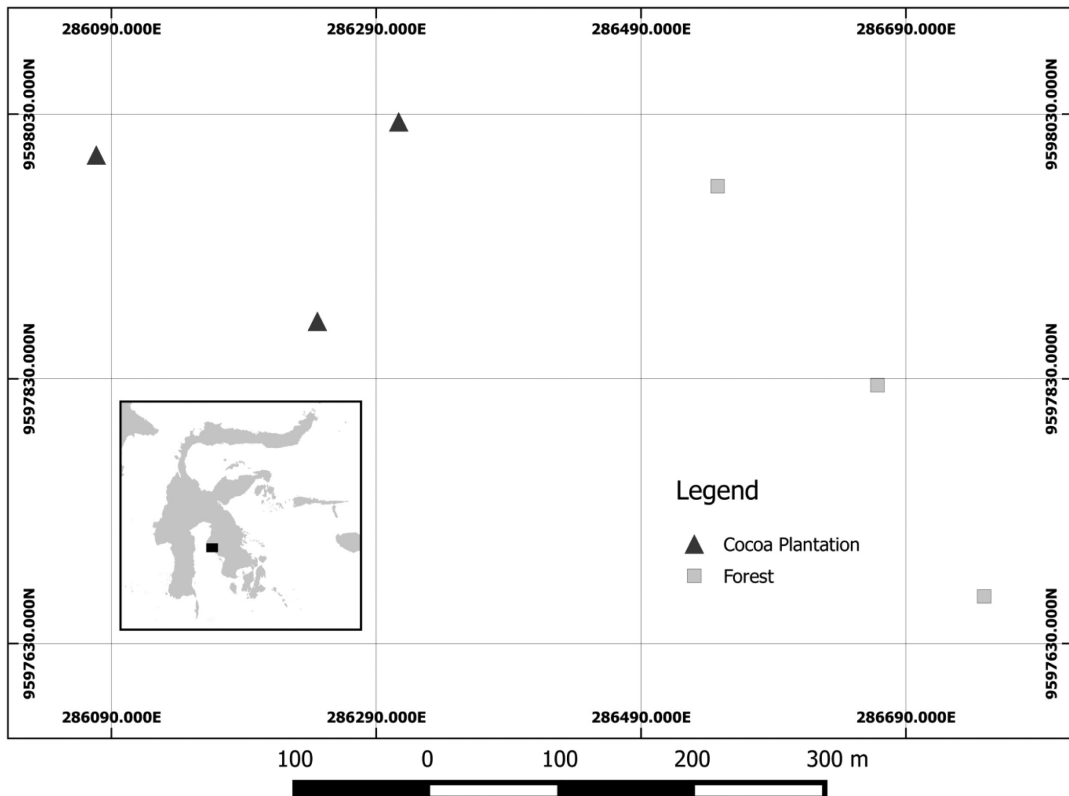

Fig. 1. Map of the locations of sampling sites in the Mekongga Mountains, Sulawesi (CRS: WGS84/UTM Zone 51S).

Comparisons of ant assemblages were made among three 90-m transects within separate rainforest remnants and three 90-m transects within separate cocoa plantations (Fig. 1). Each of the six transects was separated by at least 200 m to ensure that sampling of ant assemblages was as independent as possible, given logistical difficulties of access and the small patch sizes (1-2 ha) of both rainforest remnants and cocoa plantations in this area. Moreover, it was not possible to establish all sites at similar elevations since most human disturbance (plantation establishment) was clustered on flat terrain, leaving rainforest remnants unavoidably located on steeper slopes of the mountains. Due to these study site constraints, our land use type treatment was unavoidably confounded with elevation, but we make the assumption that the most parsimonious explanation for treatment differences is land use intensification, rather than just historical variation in ant assemblage composition with elevation.

In the rainforest remnants, the three transects were located at 226, 275, and 273 m elevation. The dominant trees at these sites were *Mallotus floribundus*, *Macaranga hispida*, *Croton argyratus*, *Ficus ampelas, F. erythrosperma, F. minahassae, F. nervosa* subsp. *pubinervis, Lasianthus* sp.*, Psychotria viridiflora, Myrmeconauclea strigosa* and *Ixora timorensis* (E.A. Widjaja, personal communication). The rainforest remnants represented relatively undisturbed forest, although there had been selective logging in the past. In the cocoa plantations, the three transects were located at 185, 188, and 121 m elevation. These were 5-year-old plantations (established after complete clearing of sites) without native shade trees and with a heavy use of pesticides and fertilizer (three times every 2 months). There were also several other crops, such as coffee, capsicum, legumes, and mango grown within the cocoa plantations (E. A. Widjaja, personal communication). Leaf litter depth at the time of sampling ranged from 10-20 cm.

Sampling methods

To provide an adequate representation of ant species and assemblage structure in rainforest and cocoa plantations, ants were surveyed using three complementary methods: baits, pitfall traps, and litter extraction. Each method consisted of taking samples along a transect, but a separate transect line was used for each of the three methods, with the lines located 10 m apart to minimize interference among methods.

Baits were used to estimate the composition and richness of diurnally active ant foragers (Bestelmeyer *et al.* 2000; Bestelmeyer & Casanova 2010). Ten bait stations were spaced out along each transect, with an interval of 10 m between each stations. Small pieces of canned sardine (1-2 cm^3) were put on a laminated paper (10 cm^2) placed on the ground. Baits were observed at 20 minutes intervals for a total of 1 hour (in the order in which baits were laid). The ants attracted to the baits at all three times were collected with forceps and stored in 70% ethanol.

Pitfall trapping was used to estimate the abundance and composition of ground active ants (Bestelmeyer *et al.* 2000; Bestelmeyer & Casanova 2010). Ten pitfall traps were spaced out along each transect, with an interval of 10 m between each trap. Traps consisted of plastic drinking cups (7 cm internal diameter) filled with 70% ethanol to about one third of the cup volume and then placed in the ground with the cup lip flush with the surface of soil or leaf litter. Logistical constraints precluded allowing for a settling in period to avoid 'digging-in' effects (Greenslade 1973), so we disturbed the soil as little as possible while setting the traps. Traps were left in place for 4 days. After 4 days, all ants were removed, washed, and stored in 70% ethanol.

We used litter extraction to measure the abundance and composition of ants inhabiting a volume of leaf litter (Bestelmeyer *et al.* 2000; Bestelmeyer & Casanova 2010). Leaf litter samples (1 m^2) were collected at 10 m intervals along each transect. The leaf litter samples were sifted over a 1 cm square mesh and then the sifted litter was placed in a sample bag to be processed in mini-Winkler sacks. Ants moved out of the litter and fell into a plastic cup (70 mm internal diameter) filled with 70% ethanol as a receptacle. After 2 days, ants were removed from the cups and stored in 70% ethanol.

Table 1. Estimated model coefficients for the best-fit generalized linear model (GLM) for each response variable: (a) species richness, (b) species diversity (Shannon), and (c) proportion of samples containing the invasive yellow crazy ant *Anoplolepis gracilipes*. Methods of model fitting are described in the methods section. SE = standard error of parameter estimates; z = z-score testing whether the parameter estimate is significantly different from zero in Poisson and Binomial models; t = t-value testing whether the parameter estimate is significantly different from zero in Gaussian models; and P = probability of the observed z-score or t-value being greater than the critical value at '**' $P < 0.01$, or '***' $P < 0.001$.

Model	Parameter	Estimate	SE	z or t	P	
(a) Ant richness (Poisson model)						
	Intercept (Cocoa: baiting)	1.934	0.159	12.174	<0.001	***
	Habitat type (Rainforest)	0.344	0.124	2.786	0.005	**
	Sampling method (Litter)	0.884	0.168	5.257	<0.001	***
	Sampling method (Pitfall)	0.683	0.174	3.937	<0.001	***
(b) Ant diversity (Gaussian model)						
	Intercept (Cocoa: baiting)	1.689	0.112	15.061	<0.001	***
	Habitat type (Rainforest)	0.387	0.112	3.450	0.004	**
	Sampling method (Litter)	0.873	0.137	6.355	<0.001	***
	Sampling method (Pitfall)	0.598	0.137	4.353	<0.001	***
(c) Proportion of samples containing *Anoplolepis* (binomial model)						
	Intercept (Cocoa: baiting)	1.244	0.403	3.085	0.002	**
	Habitat type (Rainforest)	-4.049	0.537	-7.543	<0.001	***
	Sampling method (Litter)	-0.809	0.528	-1.533	0.125	
	Sampling method (Pitfall)	0.780	0.573	1.362	0.173	

Ant identification

All ant specimens were sorted, point-mounted, and identified to genus using Bolton (1994) and then separated into morphospecies. Where possible, species names were assigned using taxonomic publications. Voucher specimens have been deposited in the Museum Zoologicum Bogoriense (MZB) in Cibinong, Indonesia.

Statistical analyses

All data for analyses were expressed as presence-absence because ants are colonial and are strongly aggregated when sampling methods capture colonies or portions of colonies (Longino 2000).

Analyses were limited to ant workers, since the presence of queens or males in a sample does not necessarily signify the establishment of a colony of that species within the habitat (Fisher & Robertson 2002).

A number of analyses were used to examine ant species richness, diversity and composition in cocoa plantations and forest sites. First, richness of ant species was calculated as the total number of species occurring in the 10 samples (pooled together) for each of the three sampling methods at each of the three sites per habitat type (i.e. n = 18 richness values). We used a generalized linear model (GLM) with Poisson error structure to test the effects of sampling method and habitat type (and their interaction) on ant

richness, using the 'stats' package in R3.1.2 (R Core Team 2014). Model simplification was performed using an information theoretic approach in which we compared the goodness of fit of competing models containing all possible subsets of fixed effects, and selected the 'best' model with the lowest bias-corrected Akaike Information Criterion (AICc) score, calculated in the 'AICcmodavg' package in R (Mazerolle 2015). For the final best-fit model, we used the package 'AER' in R (Kleiber & Zeileis 2008) to confirm that there was no overdispersion of poisson model residuals.

Second, we carried out a comparable GLM analysis on the effects of sampling method and habitat type (and their interaction) on ant diversity, based on the Shannon diversity metric (Jost 2006) for the relative incidence of each ant species in the 10 pooled samples per method per site (calculated using the 'vegan' package in R; Oksanen *et al*. 2015). The diversity GLM used a Gaussian error structure, and we tested the best-fit model (following the model simplification procedure described above) to confirm normality and homogeneity of variances in the 'stats' package in R.

Third, a sample-based rarefaction procedure was carried out using the program EstimateS version 8.0 (Colwell 2013) to compare the pattern of species accumulation with increasing sampling effort among habitat types. Data used for this analysis were the number of occurrences of species at baits or traps per site (n = 0–30; which provided a measure of relative incidence) and the interpolated number of species, which was calculated using 100 random draws with replacement. Sample-based accumulation curves were re-scaled to species incidence on the x-axis and number of species observed (Mao Tau) on the y-axis. This approach allowed direct comparison of results between groups that were sampled using different techniques (Barlow *et al.* 2007). The number of species sampled was compared with the total extrapolated richness of ants using the Chao2 asymptotic richness estimator, as recommended by Gotelli and Colwell (2010).

Fourth, variation in assemblage composition between habitat types was analyzed using non-metric multidimensional scaling (NMDS) ordination with a Bray–Curtis dissimilarity met-

ric on ant incidence data, in the program Primer version 6.0, using the standard default settings (Clarke & Gorley 2006). Two-way Analysis of Similarity (ANOSIM in Primer v6.0) was used to test for significant differences in composition among sampling methods and habitat types (Clarke & Gorley 2006). Similarity Percentage (SIMPER in Primer v6.) analysis was also used to calculate the percentage dissimilarity within and among habitat types, and determine which species of ants contributed most to the statistical difference between rainforest sites and cocoa plantations (Clarke & Gorley 2006).

Lastly, any difference in the relative frequency of occurrence of the dominant invasive ant, *A. gracilipes*, among sampling methods or between cocoa plantations and forest sites, was tested using a GLM with binomial error structure conducted in the 'stats' package in R. Following the model simplification procedure (as described above) the best-fit model was determined to have overdispersion of model residuals (based on the ratio of residual deviance to residual degrees of freedom). Therefore, we used the glm.binomial. disp function in the 'dispmod' package in R (Scrucca 2012) to calculate final model coefficients for overdispersed binomial logit models.

RESULTS

Ant diversity in rainforest remnants versus cocoa plantations

A total of 87 species of ants in 42 genera and seven subfamilies were collected. Most of the ant species belonged to the subfamily Myrmicinae (15 genera, 44 species), followed by Ponerinae (9 genera, 21 species), Formicinae (8 genera, 11 species), Dolichoderinae (5 genera, 6 species), Proceratiinae (2 genera, 2 species), Ectatomminae (1 genus, 2 species), and Dorylinae (1 genus, 1 species) (Appendix 1). Twenty species were found only in cocoa sites, 44 species were found exclusively in forest sites, and 23 species were found in both habitat types. Forest sites had a higher total number of species (67) than cocoa sites (43) (Fig. 2), and in the final most-parsimonious GLM model (which excluded the non-significant interaction effects between habitat type and sampling

Table 2. Rank order of ant species occurrence in cocoa plantations and rainforest sites in the Mekongga mountains, Sulawesi, sampled using baits (B), pitfall traps (PT), and leaf litter sampling (LS). The list shows only the 10 most common species in each site. Values indicate the sampling incidence of each species out of 30 samples collected with each sampling method.

Rank	Species	Cocoa			Rainforest		
		B	PT	LS	B	PT	LS
Cocoa plantations							
1	*Anoplolepis gracilipes*	24	27	17	1	3	2
2	*Pheidole* sp. WA035	3	9	9			
3	*Brachyponera* sp. WA061	2	8	6			
4	*Nylanderia vaga*	7	3	5			
5	*Monomorium intrudens*	2	9	4	1	1	7
6	*Pheidole* sp. WA027	1	5	6	0	1	6
7	*Monomorium floricola*	7	1	3			8
8	*Tetramorium* sp. WA042	2	3	6			
9	*Tetramorium* sp. WA044	4	1	6	1		
10	*Odontomachus* sp. WA056		4	4	3	9	6
Rainforest remnants							
1	*Pheidole* sp. WA025				5	9	16
2	*Prenolepis* sp. WA012	2			9	4	6
3	*Odontomachus* sp. WA056		4	4	3	9	6
4	*Solenopsis* sp. WA037			4	2	5	9
5	*Tetramorium* sp. WA041				4	3	8
6	*Aphaenogaster* sp. WA014				4	6	2
7	*Pheidole* sp. WA031				3	6	3
8	*Strumigenys* sp. WA040			5			10
9	*Monomorium intrudens*	2	9	4	1	1	7
10	*Hypoponera* sp. WA050					3	6

method; AICc = 101.43, Akaike weight = 0.89), habitat type had a significant effect on average richness per site (Table 1a).

Sampling method also had a significant effect on average species richness in the GLM analysis (Table 1a), with baits yielding a total of 31 species, while pitfall trapping collected a total of 54 species, and litter sampling collected a total of 67 species. Species accumulation curves (Fig. 2) showed that rainforests had a higher estimated species richness for a given frequency of occurrence than cocoa plantations, although only for litter sifting were the 95% confidence limits non-overlapping (Fig. 2a-c). Across all methods and transects combined, species richness increased significantly faster with increasing sampling intensity in rainforests than in cocoa plantations (Fig. 2d), but the level of completeness of sampling was correspondingly lower (rainforest: 53.1% of the Chao2 incidence-based asymptote of 128 ± 33 S.D.; cocoa plantation: 88.5% of the Chao2 incidence-based asymptote of 49 ± 5 S.D.).
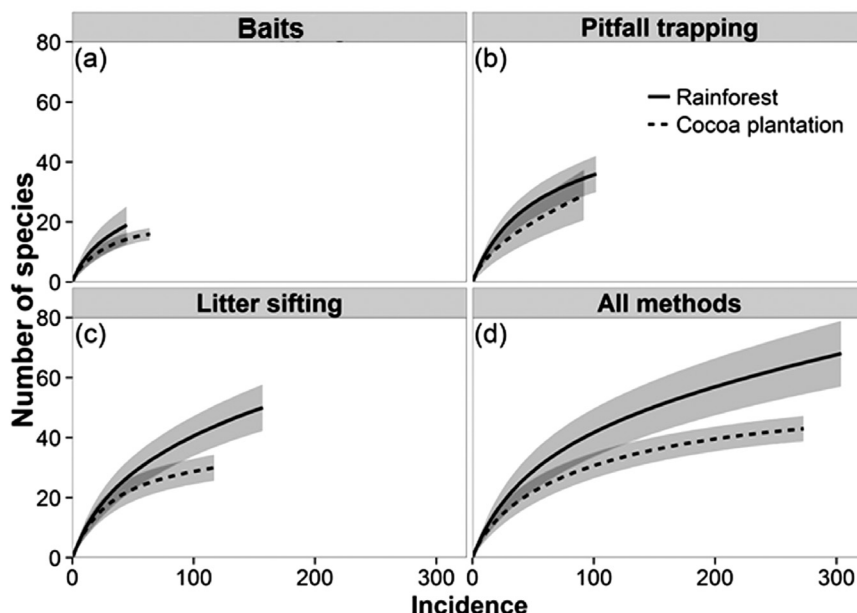
Fig. 2. Sample-based species accumulation curves (re-scaled to cumulative incidence of ant species) for each sampling method and for all sampling methods combined. Cumulative species richness for (a), (b), (c) is calculated with 100 random draws with replacement from a total of 30 samples, while for (d) richness is calculated with 100 random draws with replacement from a total of 90 samples.

Comparable patterns of variation in Shannon species diversity were observed across habitat types and sampling methods (Table 1b), with the final most-parsimonious GLM model again excluding the non-significant interaction effect (AICc = 9.86, Akaike weight = 0.96) and again showing significantly higher Shannon diversity in rainforest sites compared to cocoa plantations, and in pitfall and litter samples compared with bait samples (Table 1b).

Change in ant assemblages between rainforests and cocoa plantations

Based on frequency of occurrences, the most common species in rainforest sites were *Pheidole* sp. WA025 (9.9% of all ants collected from forest sites), *Prenolepis* sp. WA012 (6.3%), *Odontomachus* sp. WA056 (5.9%), *Solenopsis* sp. WA037 (5.3%), and *Tetramorium* sp. WA041 (4.9%), and these differed markedly from dominant species in cocoa plantations, such as *A. gracilipes* (24.9% of all ants collected from cocoa sites), *Pheidole* sp. WA035 (7.7%), *Brachyponera*

sp. WA061 (5.9%), *Nylanderia vaga* (5.5%), and *Monomorium intrudens* (5.5%) (Table 2). As a result of these differences, the NMDS ordination analysis showed a clear separation in species composition between rainforest sites and cocoa plantations (Fig. 3). A two-way ANOSIM analysis showed that rainforest ant assemblages were significantly different from cocoa ant assemblages (Global R = 0.921, P < 0.001), but there was no significant difference in the ant assemblages captured using different sampling methods within the same habitat type (Global R = 0.117, P < 0.219).

A one-way SIMPER analysis (combining all sampling methods) showed that rainforest and cocoa sites were, on average, 89.84% dissimilar in ant species composition. The species contributing strongly to the characteristic structure of rainforest assemblages were *Pheidole* sp. WA025, *Prenolepis* sp. WA012, *Odontomachus* sp. WA056, *Tetramorium* sp. WA041, *Pheidole* sp. WA031, *Solenopsis* sp. WA037, *Aphaenogaster* sp. WA014, *Diacamma* sp. WA047, *Hypoponera* sp. WA050, *M. intrudens*, *Leptogenys* sp.
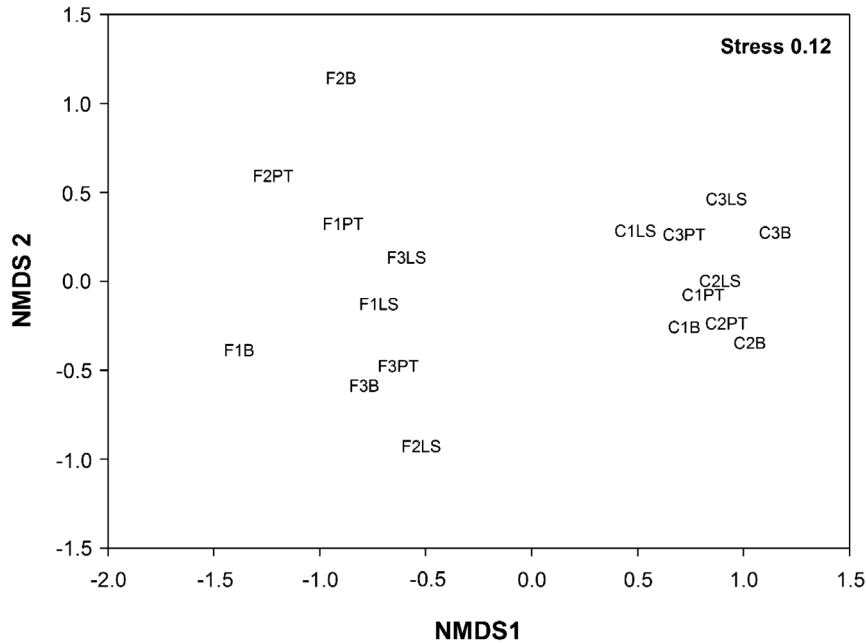
Fig. 3. Non-metric multidimensional scaling (NMDS) analysis of variation in ant species composition between rainforest remnants (F1-F3) and cocoa plantations (C1-C3) in the Mekongga Mountains, Sulawesi. The ordination is based on Bray-Curtis dissimilarities calculated from species incidence (not abundance) in each bait or trap. Sampling methods: B = baits, PT = pitfall traps, and LS = litter sifting.

WA052, and *Pheidole* sp. WA028 (average similarity among rainforest samples was 27.49%). Meanwhile, the species contributing strongly to the characteristic structure of cocoa assemblages were *A. gracilipes*, *Pheidole* sp. WA035, *Brachyponera* sp. WA061, *M.intrudens*, *N. vaga*, *Tetramorium* sp. WA042, *M. floricola*, and *Pheidole* sp. WA027 (average similarity among cocoa plantation samples was 41.17%).

Tramp ants at Mekongga

Overall, *A. gracilipes* was recorded in 74 of all 180 samples. A GLM analysis of the frequency of occurrences of *A. gracilipes* among sampling methods, and between rainforest versus cocoa plantation habitats showed no significant interaction effect between the variables (the most parsimonious model excluded the interaction effect: AICc = 66.18, Akaike weight = 0.73) and non-significant effects of variation among sampling methods (Table 1c). However, cocoa plantations had a significantly higher frequency of occur-

rence of *A. gracilipes* than rainforest sites (Table 1c), with *A. gracilipes* recorded at 68 of 90 collection sites in cocoa plantations, but only 6 of 90 collection sites in rainforest (Fig. 4).

Other tramp species, including *M. floricola* and *N. vaga*, were also recorded in the area at low frequencies. In cocoa plantations, *M. floricola* comprised 4% of all ants collected, whereas *N. vaga* comprised 5.5% of all ants collected. In forest sites, *M. floricola* comprised 2.6% of all ants collected, whereas *N. vaga* was not recorded in rainforests.

DISCUSSION

The study represents one of only a handful of moderately-intensive ant surveys ever conducted in Sulawesi (e.g. Wielgoss *et al.* 2010; Rizali *et al.* 2013) and the ant fauna remains poorly documented compared to other regions of the tropics. We recorded 87 species of ants at just three rainforest and three cocoa plantation sites, with 44

species found exclusively in rainforest sites. The most recent previous studies of ants in Sulawesi were conducted by Bos *et al.* (2008), Wielgoss *et al.* (2010) and Rizali *et al.* (2013) where 84, 160, and 87 ant species were recorded in cocoa plantations in Central Sulawesi, respectively, although sampling methods and sampling effort naturally varied among these studies. Unfortunately, the level of taxonomic identification is not yet sufficient to determine the degree of species overlap among these studies. Importantly, we note that the most recent taxonomic catalogue for Sulawesi only lists 138 ant species in total (Bolton *et al.* 2006), so many species are likely to remain undescribed.

The wide range of sampling methods we used may have contributed to the richness of species collected in our study, even though these methods predominantly sample ground-dwelling species and not arboreal species (Ryder Wilkie *et al.* 2010; Floren *et al.* 2014). In general, litter sifting was a more effective method compared to pitfall trapping and baiting in our study. Litter sifting collected 76% of the total number of ant species captured by all three methods in cocoa plantations and forests. This method also collected almost all genera found in both habitat types (85%), except *Aenictus*, *Camponotus*, *Cardiocondyla*, *Euprenolepis*, and *Philidris*, which were captured by pitfall trapping.

Ant richness was greater in rainforest sites than in plantation sites, and diversity and composition of the ant fauna were strongly affected by land use management. The high compositional dissimilarity between intensively-managed cocoa plantations and rainforests at Mekongga is similar to previous studies that have compared natural forests versus a wide range of timber and agroforestry plantations established following complete clearance of the original habitat (Kessler *et al.* 2009). For example, in southern Cameroon, the species richness of both leaf-litter and canopy ants was greater in plantations developed on partially-cleared sites than on completely-cleared sites (Watt *et al.* 2002), a finding that has been echoed in cocoa plantations of the Atlantic rainforest of Brazil (Delabie *et al.* 2007). Similarly, there were comparable shifts in native ant diversity and assemblage composition

along a land use intensification gradient in Nicaragua, Central America (Ottonetti *et al.* 2010). By contrast, in low-intensity cocoa agroforests in Central Sulawesi, Bos *et al.* (2007b) found no difference in the numbers of ant species compared to that found in adjacent rainforest, and lower compositional differences compared to those found at Mekongga. There are probably several reasons why our study presented a less favourable view of the value of cocoa plantations for the conservation of the local ant fauna than previous studies. Firstly, the system of plantation establishment used in our plots involved the complete clearing of rainforest trees, followed by their replacement with a low number of fruit trees, such as mango. This resulted in much lower habitat heterogeneity, both vertically and horizontally, and a less shaded environment. This loss of shade tree cover and diversity, along with the numerous ant-associated epiphytes they are associated with (Huxley 1980), undoubtedly contributed to the lower richness of ants in our plots, since some arboreal ant species can forage downwards and contribute to ground ant richness. Some of the cocoa plantations studied by Bos *et al.* (2007b) had also been totally cleared prior to establishment, but they were much older than our 5-year old areas. It may well be that if shade trees and their associated epiphytes are allowed sufficient time to develop, ant richness will start to build up, much like da Conceição *et al.* (2015) have observed in developing Brazilian cocoa plantations. However, at this stage we cannot be sure of this and urge caution in relying on intensively managed plantations for the conservation of biodiversity.

From our observation that rainforest sites contained several litter-dwelling genera that did not occur at all in cocoa plantations (e.g. *Aenictus*, *Gnamptogenys*, *Euprenolepis*, *Eurhopalothrix*, *Recurvidris*, *Acanthomyrmex*, *Myopias*, and *Discothyrea*), we can draw the conclusion that maintenance of native ant diversity depends on biotic and abiotic factors, such as habitat structure, microclimate or leaf litter resources that are not available in cocoa plantations, as suggested by Perfecto & Vandermeer (2002), Kaspari *et al.* (2003), and Brühl & Eltz (2010), respectively. However, a recent study showed a lack of association between heterogeneity, resource abundance
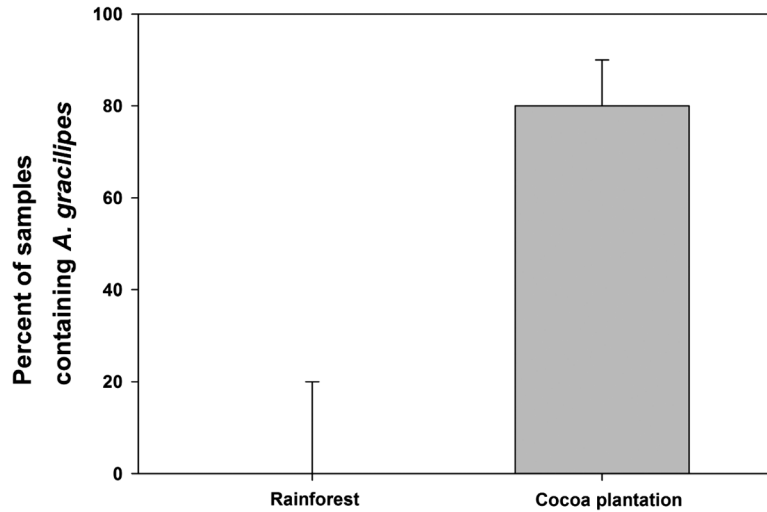
Fig. 4. Median (± range) values for the proportion of samples containing the invasive *A. gracilipes* in rainforest remnants and cocoa plantations.

or litter depth on litter arthropod diversity, including ants (Donoso *et al.* 2010). The ant genera found only in forest sites, such as the army ant *Aenictus*, have previously been used as biodiversity indicators because they are strongly affected by disturbance (Matsumoto *et al.* 2009). We avoid drawing strong conclusions on the basis of the two occurrences of *Aenictus* in our rainforest sites. Nevertheless, the occurrence of a third of the genera (14/42) and half of the species (44/87) in rainforest sites only in our study suggest that it is important to conserve even small patches of remnant rainforest, as they provide important habitat for a number of ant species that are sensitive to human disturbance. The results also suggest that the much greater impact of intensive agroforestry on ant diversity, compared to previous studies of low-intensity agroforestry systems, is due in large part to the intensity of ground-layer disturbance.

In contrast to rainforest, cocoa plantations were dominated by tramp species, such as *A. gracilipes*, *N. vaga*, and *M. floricola*. The yellow crazy ant, *A. gracilipes*, alone comprised 24% of the total number of ants collected and was found in 75% of samples in cocoa. Moreover, only the two forest sites with no *A. gracilipes* had high overall species richness (F1= 43 species, F2 = 41 species), whereas all the sites with *A. gra-*

cilipes (C1, C2, C3, and F3) had lower overall species richness (22 – 27). Both the decline in native species and dominance by invasive species may be an indirect result of habitat disturbance (Didham *et al.* 2007), but it is also possible that *A. gracilipes* may be competitively excluding other ants from the sites (Bos *et al.* 2008; Brühl & Eltz 2010; Hoffmann & Saul 2010; Mezger & Pfeiffer 2011). Although *A. gracilipes* is believed to be of southeast Asian origin (Wetterer 2005), it is invasive in many tropical and subtropical countries, and is thought to strongly influence the community structure of other ants in areas where it has been introduced (e.g. Bos *et al.* 2008; Brühl & Eltz 2010). For instance, Bos *et al.* (2008) reported that intensification of cocoa agroforests has increased the abundance of *A. gracilipes*. As a result, forest ant richness in three different types of cocoa agroforests (simple planted shade, diverse planted shade, and diverse natural shade) decreased significantly with increasing density of *A. gracilipes* (Bos *et al.* 2008). Moreover, the incidence and species richness of forest ground ants in oil palm plantations in Sabah was negatively affected by occurrences of *A. gracilipes* (Brühl & Eltz 2010).

Despite the overall difference in native ant diversity, it is important to note that co-

coa plantations also harboured ant species that were not found in adjacent rainforests, such as *Myrmoteras* sp. WA007 (n=1 individual) and *Probolomyrmex longiscapus* (n=2). This is a new record of *P. longiscapus* occurring in Sulawesi. These results suggest that even relatively intensive agroforestry plantations can harbour rarely-encountered ant species and ant species previously unknown from Sulawesi. However, this study only represents a snapshot of species occurrences in relatively young cocoa plantations, and there should be concern for the long-term persistence of these species if intensive production practices (such as high pesticide use) are not mitigated.

CONCLUSION

Small rainforest remnants retained a high diversity of native species, with several rarely-encountered ant genera and species. Because of this, it is important to prioritize these areas for conservation. In contrast, the low ant diversity, altered native species composition and dominance of tramp ant species in intensively-managed cocoa plantations reflected the high degree of land use disturbance compared to adjacent rainforest assemblages. This pattern may be caused by direct factors, such as intensity of pesticide application, lack of shade tree cover and disturbance of the leaf-litter layer, or by indirect factors, such as dominance and competition from invasive ant species. If we are to maintain native biodiversity within agroforestry plantations in the long-term, there is an urgent need to limit the intensity of agroforestry management practices.

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Appendix 1

Ant species and morphospecies incidence (out of 30 samples in each case) in cocoa plantations and forest sites in the Mekongga mountains, Sulawesi, sampled using baits (B), pitfall trapping (PT), and litter sifting (LS).

Species	Cocoa			Rainforest			Identification source[1]
	B	**PT**	**LS**	**B**	**PT**	**LS**	
Dolichoderinae							
Dolichoderus thoracicus (Smith, 1860)	1	1			7		Shattuck 1994
Ochetellus sp. WA001	3		2				
Philidris sp. WA002					1		
Philidris sp. WA003		1					
Tapinoma sp. WA004	2	1				1	
Technomyrmex kraepelini Forel, 1905		1	1				Bolton 2007
Dorylinae							
Aenictus cf *brevinodus* Jaitrong & Yamane, 2011					2		Jaitrong & Yamane 2011
Ectatomminae							
Gnamptogenys leiolabia Lattke, 2004					1		Lattke 2004
Gnamptogenys sp. WA005					2	1	
Formicinae							
Acropyga acutiventris Roger, 1862		2			2	2	LaPolla 2004
Anoplolepis gracilipes (Smith, 1857)	24	27	17	1	3	2	Smith 1857
Camponotus sp. WA006					2		
Euprenolepis procera (Emery, 1900)					1		LaPolla 2009
Myrmoteras sp. WA007				1			
Nylanderia vaga (Forel, 1901)	7	3	5				Forel 1901
Polyrhachis sp. WA008				1	1		

Species							Reference
Polyrhachis sp. WA009						1	
Polyrhachis sp. WA010		1			1		
Polyrhachis sp. WA011					3		
Prenolepis sp. WA012	2			9	4	6	
Myrmicinae							
Acanthomyrmex sp. WA013						2	
Aphaenogaster sp. WA014				4	6	2	
Cardiocondyla sp. WA015		2					
Carebara sp. WA016		1	4			7	
Carebara sp. WA017			2				
Carebara sp. WA018						6	
Carebara sp. WA019					2	2	
Carebara sp. WA020		1	1		1		
Crematogaster sp. WA021	2	1					
Crematogaster sp. WA022	1						
Eurhopalothrix heliscata Wilson & Brown, 1985						1	Taylor 1990
Eurhopalothrix omnivaga Taylor, 1990						3	Taylor 1990
Monomorium floricola (Jerdon, 1851)	7	1	3			8	Jerdon 1851
Monomorium intrudens Smith, 1874	2	9	4	1	1	7	Ogata & Bolton 1989
Monomorium sp. WA023		1					
Myrmecina sp. WA024			1			1	
Pheidole sp. WA025				5	9	16	
Pheidole sp. WA026					2	3	
Pheidole sp. WA027	1	5	6		1	6	
Pheidole sp. WA028		2	1	2	4	2	
Pheidole sp. WA029	1	1	2		2	1	
Pheidole sp. WA030				1		1	
Pheidole sp. WA031				3	6	3	
Pheidole sp. WA032				1	3		
Pheidole sp. WA033					1		
Pheidole sp. WA034						2	
Pheidole sp. WA035	3	9	9				
Pristomyrmex brevispinosus Emery, 1887					1	1	Wang 2003
Recurvidris hebe Bolton, 1992				1		3	Bolton 1992
Recurvidris sp. WA036				1		1	
Solenopsis sp. WA037			4	2	5	9	
Solenopsis sp. WA038						1	
Solenopsis sp. WA039						1	

Species							Reference
Strumigenys dantalion Bolton, 2000						1	Bolton 2000
Strumigenys emmae (Emery, 1890)		1	1				Bolton 2000
Strumigenys cf *fixata* Bolton, 2000			5			10	Bolton 2000
Strumigenys zapyx Bolton, 2000					1		Bolton 2000
Strumigenys sp. WA040			7				
Tetramorium sp. WA041				4	3	8	
Tetramorium sp. WA042	2	3	6				
Tetramorium sp. WA043						1	
Tetramoriium sp. WA044	4	1	6	1			
Tetramorium wroughtonii Forel, 1902		1		1		2	Bolton 1986
Vollenhovia sp. WA045						1	
Ponerinae							
Anochetus sp. WA046			4				
Diacamma sp. WA047				1	4	1	
Diacamma sp. WA048						1	
Hypoponera sp. WA049						1	
Hypoponera sp. WA050					3	6	
Hypoponera sp. WA051						1	
Leptogenys sp. WA052					5	2	
Leptogenys sp. WA053		1			1	2	
Leptogenys sp. WA054		1	2				
Myopias sp. WA055						1	
Odontomachus sp. WA056		4	4	3	9	6	
Odontomachus sp. WA057				1			
Odontomachus sp. WA058		1					
Bothroponera sp. WA059			1		1		Schmidt & Shattuck 2014
Brachyponera sp. WA060					1		Schmidt & Shattuck 2014
Brachyponera sp. WA061						1	Schmidt & Shattuck 2014
Brachyponera sp. WA062	2	8	6				Schmidt & Shattuck 2014
Ponera sp. WA063		1	2			3	
Ponera sp. WA064						1	
Ponera sp. WA065			5				
Ponera sp. WA066			4			5	
Proceratiinae							
Discothyrea clavicornis Emery, 1897						1	Emery 1897
Probolomyrmex longiscapus Xu & Zeng, 2000			2				Eguchi *et al.* 2006

[1] Literature sources:

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