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Impacts of rubber plantations on community assembly of ants (Hymenoptera: Formicidae): a case study from monsoonal tropics of Xishuangbanna, southwest China

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Abstract. Rubber plantation has become one of the most dominant human-modified landscape features in continental Southeast Asia. Xishuangbanna, a monsoonal tropical region of southern Yunnan in China, is a hotspot of rubber cultivation and represents the northern margins of rubber expansion in Asia. Here, we compared the species richness, beta diversity patterns, and assemblage composition of ants from a rubber plantation and two forest types (alluvial and limestone forest) common in Xishuangbanna. We hypothesized that species richness is higher in forest habitats than the rubber plantation. Due to habitat similarities between the limestone forest and the rubber plantation (tree defoliation, dry condition, thinner soil), we hypothesized that ant assemblages in these habitats are similar, and beta diversity is driven by nestedness. We found the highest ant species richness in the alluvial forest, followed by the limestone forest and rubber plantation. Ant assemblages were similar between alluvial and limestone forests but different in the rubber plantation. Beta diversity estimation showed that beta diversity patterns were driven by species turnover in all three habitats. Our results showed that the rubber plantation was species-poor and harbored unique ant assemblages compared to forest habitats. Moreover, the assemblages in the rubber plantation were often dominated by numerically dominant and aggressive taxa. Our study highlights: biodiversity changes associated with forest conversion into monoculture rubber plantations; the conservation value of limestone forests, a common yet understudied forest type in Southeast Asia; and the importance of considering species identities when determining the impacts of habitat modification on ant diversity.

Keywords: biodiversity, Formicidae, *Hevea brasiliensis*, IndVal, Menglun, Southeast Asia, Winkler extractor.

Introduction

The ever-increasing demand for natural rubber has promoted widespread forest conversion into monoculture rubber plantations across Southeast Asia (Ahrends et al. 2015, Warren-Thomas et al. 2015). The rubber in the region corresponds to 84% of the global area for rubber planting and produces 97% of the global supply of natural rubber. The rise in rubber prices in the early 2000s also triggered its northward expansion into Cambodia, Vietnam, Laos, Myanmar, and Xishuangbanna in Southwest China (Hurni & Fox 2018, Warren-Thomas et al. 2018), where rubber planting became a major contributor to poverty reduction and local economic growth (Wigboldus et al. 2017, Zhang et al. 2019). Latex prices have crashed in the market since 2011, resulting in rubber 'greening' (sensu Wigboldus et al. 2017, Kenney-Lazar et al. 2018) or conversion into other cash crops (Zhang et al. 2019), but rubber plantation expansion remains among the biggest threats to biodiversity in the region (Warren-Thomas et al. 2018).

Rubber plantations have come at the expense of evergreen and deciduous forests (Hurni & Fox 2018), converting diverse

plant communities into homogenized communities, typically without understory vegetation (Barnes et al. 2017, Rembold et al. 2017). Aside from changes in plant diversity and community structure, it has led to losses of the diversity of vertebrates (Zhang et al. 2017), ground invertebrates (Liu et al. 2019, Singh et al. 2019, Potapov et al. 2020), and soil microbiota (Monkai et al. 2018, Schulz et al. 2019, Sun et al. 2020), causing subsequent losses of ecosystem functions (Clough et al. 2016, Drescher et al. 2016). In addition, assemblages in rubber plantations are functionally distinct (Brinkmann et al. 2019, Lee et al. 2020), with a higher prevalence of tramp species (Lee et al. 2020, Nazarreta et al. 2020). Species found in rubber plantations are also often generalists with more widespread distributions and low conservation values than those found in forest habitats (Sreekar et al. 2016, Paoletti et al. 2018, Alcantara et al. 2019).

Ants are one of the most common terrestrial invertebrate groups which play important ecological roles in natural and man-made habitats (Wielgoss et al. 2010). They are a key component of food web interactions and are important in maintaining certain ecosystem processes (Tiede et al. 2017, Griffiths et al. 2018). They tend to reflect habitat conditions

and are often used as bioindicators of environmental change (Nakamura et al. 2007, Lee et al. 2020, Nazarrreta et al. 2020). Lastly, ants have a well-known taxonomy and are very easy to sample (Burbidge et al. 1992), making ants an ideal group to study the ecological impacts of rubber plantations. However, there are still few studies on the ecological impacts of rubber plantations on ant fauna. Many investigated the diversity and species composition within forest and rubber plantation habitats. Most studies reported reduced species richness and altered assemblages in rubber plantations (e.g., Liu et al. 2016, Lee et al. 2020, Nazarrreta et al. 2020). Little attention has been paid to the effects of forest conversion to rubber plantation on other aspects of ant ecology (see Liu et al. 2016, Alcantara et al. 2019).

Xishuangbanna Dai Autonomous prefecture at the tip of Yunnan, Southwest China, is a hotspot of rubber expansion, with rubber occupying just around 11% of the region's total land area in 2002 to a peak of almost 25% in 2014 (Zhang et al. 2019). Forests have remained mainly at higher elevations and on steep slopes where rubber planting is more labor intensive and less profitable (Liu & Slik 2014). These remaining forests in Xishuangbanna generally occur on alluvial and limestone-derived soils (Kitching et al. 2015). Floristically, forests on alluvial soils (hereafter alluvial forests) have higher tree species diversity, different tree species composition, and denser understory vegetation compared with forests on limestone-derived soils (hereafter limestone forests) (Cao & Zhang 1997, Liu & Slik 2014, Pasion et al. 2018). Canopy closure is similar in both forest types; however, limestone forest canopies become more open during the dry seasons due to many deciduous species shedding their leaves (Cao & Zhang 1997). Limestone forests also have a drier environment and shallower soils than the alluvial forests (Cao & Zhang 1997, Tang et al. 2011). On the other hand, rubber plantations in the region are mostly monoculture plantations without understory growth, especially in rubber rows (Li et al. 2012). The canopies are generally more open, and the soils are thin and compacted. Moreover, rubber trees lose all their leaves towards the end of the cold season due to cold stress (Lin et al. 2018). Rubber plantations may therefore represent habitats, at least structurally, similar to those of limestone forests in this region. Consequently, the fauna found in rubber plantations may represent subsets of those found in limestone forests.

This case study investigated the ecological impacts of rubber plantations on ant fauna in Xishuangbanna, Southwest China. Specifically, we compared alpha and beta diversities and ant assemblage compositions in the alluvial forest, limestone forest, and rubber plantation and evaluated indicator ant species for any particular habitat type. We hypothesize that (i) ant species richness is higher in both alluvial and limestone forests than in the rubber plantation; (ii) due to some similarities between limestone forests and rubber plantations (e.g., tree defoliation, shallower soil, drier conditions), assemblage composition and characteristic species found in rubber plantation is a subset of species found in limestone forest, and beta diversity is primarily driven by nestedness; and (iii) assemblage composition between the alluvial forest and rubber plantation is more dissimilar than in the limestone forest, and rubber plantation and beta diversity is driven by turnover rather than by nestedness.

Material and Methods

Study site and habitat characteristics

The study was conducted in three habitat types (an alluvial forest, a limestone forest, and a monoculture rubber plantation) within Xishuangbanna Tropical Botanical Garden (XTBG; 21°55'N, 101°15'E) in Menglun, Mengla, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, Southwest China. The area is around 600 m above sea level and experiences a monsoonal seasonal climate (Cao et al. 2006). The mean annual temperature is 21.4°C, and the mean annual precipitation is 1493 mm, of which > 80% falls during the rainy season (May to October).

The alluvial forest in our study area had the highest plant species richness, followed by the limestone forest (Pasion et al. 2018). *Millettia leptobotrya* (Fabaceae) and *Pittosporopsis kerrii* (Icacinaeae) were the dominant plant species in the alluvial forest. In contrast, those in the limestone forest include *Cleistanthus sumatranus* (Phyllanthaceae), *Lasiococca comberi* (Euphorbiaceae), and *Celtis philippensis* (Cannabaceae). The alluvial forest also had denser understory vegetation than the limestone forest (Pasion et al. 2018), while the rubber plantation was cleared of undergrowth, particularly at rubber rows. Humus and leaf litter are also thicker in the alluvial forest and limestone forest (average depth of 3.7 and 2.3 cm, respectively, measured at the survey plots described below) than in rubber plantation (1 cm deep). The alluvial and limestone forests had denser canopy cover (with ~98% canopy closure at the beginning of the dry season during ant sampling). In contrast, the rubber plantation, which defoliates during the cold season (Lin et al. 2018), had a relatively more open canopy (~90%).

Ant sampling and taxonomic assignment

Ant sampling was conducted during the beginning of the dry season in November 2015. Ants were collected between 1300h and 1700h on warm sunny days using litter extraction and baiting methods to supplement the litter extraction samples. In each habitat type, we established five 10 m × 10 m plots, at least 50 m away from the habitat edge and at least 25 m away from other plots, to ensure the independence of leaf-litter samples (McGlynn 2006). Litter and loose topsoil were collected from four 0.5 m × 0.5 m quadrats in each plot. All collected materials were sifted through a 1-cm sieve, transferred to cotton bags, and brought back to the lab, where the fauna was extracted by Winkler extractors for three days using the shuffling technique (Guénard & Lucky 2011).

For baiting, we used three bait types (honey, lipid-based peanut butter, and water-based canned tuna) to attract ants. We randomly selected nine trees within each plot, with diameters ranging from 6 to 31 cm in the alluvial forest, 5 to 60 cm in the limestone forest, and 19 to 28 cm in the rubber plantation. Since rubber trees had smooth bark, we selected trees with relatively smooth bark in the alluvial and limestone forests to reduce the possible influence of bark roughness in our study. We prepared baits by placing 1.0 g honey, 1.5 g peanut butter, or 3.0 g tuna on 9 cm-diameter filter papers. To prevent the ants from taking the fish, we wrapped tuna in a 0.3 mm-mesh polystyrene net and attached the net to the filter paper using staple wires. In total, we placed 18 baits (six per bait type) per plot such that each bait type was attached to three trees on the trunks and the ground near the tree base. Ground baits were directly placed on the forest floor approximately 1m from the tree base. Arboreal baits were set by erecting the bottom half of filter papers at a right angle (to keep the baits from falling) to the tree trunks at around 1.3 m from the ground using metal wires. Baits were visited every 30 minutes for two hours, and all ants on the filter papers were collected into plastic tubes with 95% ethanol.

All ants collected from leaf litter and baiting samples were identified as species or morphospecies (hereafter species) using various literature (e.g., Eguchi et al. 2011, 2014, Fayle et al. 2014, Liu et al. 2015) and websites including AntWeb (2018) and an online pictorial record of ants in Xishuangbanna (Liu 2014). Where possible, we consulted taxonomists who have worked in the area for

confirmation of our identifications.

Data analyses

Ant data from the different methods (litter extraction, ground, and arboreal baiting) within each plot were pooled before analysis. For all analyses, we used incidence data (presence/absence) instead of abundance data, as the different sampling methods represent various ecological aspects (i.e., litter extraction shows the density of ants, whereas baiting tends to represent competitively dominant ants, Gotelli et al. 2011). All analyses were performed in R v3.6.1 (R Core Team 2019), and all graphics were produced using ggplot2 v3.3.2 (Wickham 2016) and ggpubr v0.2.3 (Kassambara 2019) packages.

We first generated sample-based completeness curves and species rarefaction curves to compare sampling sufficiency among habitats (Chao et al. 2014). The sample completeness curve estimates the sample coverage, which represents the proportion of the total number of individuals in the community that belongs to the sampled species as a function of sample size. On the other hand, the sample-based rarefaction curve computes diversity estimates for a given set of samples (sample size). We used sample-based instead of individual-based rarefaction curves since ant abundance often indicates the proximity of the sampling units to the ant colonies and does not reflect sampling intensity. We used 100 replicate bootstrapping for both curves to estimate 95% confidence intervals and extrapolated by doubling the number of reference samples. Rarefaction curves were generated using the iNEXT package v 2.0.19 (Hsieh et al. 2019) available in R.

To assess ant taxonomic diversity, we calculated the species richness (as a measure of alpha diversity) and beta diversity in the three habitats. The influence of habitat type on species richness was evaluated with a generalized linear model (GLM) using Poisson distribution. Differences among habitats were then analyzed using the glht function in the multcomp package v1.4-16 (Hothorn et al. 2008). Beta diversity was estimated using the beta.pair function in betapart package v1.5.2 (Baselga et al. 2020) in R. Total beta diversity (β_{sor}) was estimated using the Sørensen dissimilarity index and then decomposed into its turnover (β_{sim}) and nestedness (β_{sne}) components. β_{sim} was measured as Simpson dissimilarity, while β_{sne} was measured as the nestedness-resultant fraction of the Sørensen dissimilarity. We used PERMANOVA (999 permutations) to detect differences among the habitats based on total beta diversity and its turnover and nestedness components using the adonis function in the vegan package v2.5.7 (Oksanen et al. 2020). Pairwise comparisons were performed using the pairwise.adonis function in the

pairwiseAdonis package v0.0.1 (Martinez Arbizu 2017).

We then generated a non-metric multidimensional scaling (NMDS) ordination to visualize assemblage compositions among the three habitats (Clarke 1993), using the metaMDS function in the vegan package (Oksanen et al. 2020). Ordination was performed on the Sørensen similarity matrix based on incidence data. Optimum configurations for the ordination were selected using 25 random restarts.

To find species characteristic of the habitats, we used the indicator value protocol (IndVal) developed by Dufrene and Legendre (1997), using the multipatt function in the indicpecies package v1.7.9 (De Caceres & Legendre 2009) in R. IndVal assesses individual species as indicators of certain habitat (or groups of habitats) by quantifying species habitat specificity and fidelity to a given habitat, expressed as a percentage. A maximum indicator value of 1.0 (or 100%) is given to a species if it achieves maximum specificity (it occurs only within the habitat of interest) and fidelity (it occurs in all sampling plots within that habitat). Species with significant indicator values ($P < 0.05$) based on 999 permutations of the samples were selected as indicators of the particular habitats. Indicator species with scores > 0.70 were then considered 'strong' indicators of the different habitats, following a suggestion from McGeoch et al. (2002).

Results

A total of 19,072 ant individuals from 89 species and 33 genera were sampled from the three habitats within XTBG (See Table S1 for full species list). More than half (10,453 individuals) were collected in the rubber plantation, 6,127 ants in the alluvial forest, and 2,492 in the limestone forest (Table 1). Sixty-eight species were collected from litter extraction (33 species were unique to this method), 49 species from ground baiting (nine unique species), and 28 species from arboreal baiting (five unique species). Based on the classification by Guénard & Dunn (2012), four potentially exotic species were found in our samples; of these, *Anoplolepis gracilipes* Smith, *Tapinoma melanocephalum* Fabricius and *Technomyrmex albipes* Smith were found only in the rubber plantation, and *Cardiocondyla wroughtonii* Forel was found only in the limestone forest.

Table 1 Abundance and species richness of ants in the three habitats. Superscripts indicate statistical difference among habitats after GLM and pairwise comparisons ($P < 0.05$). Values within parentheses represent 95% confidence interval of the mean.

	Alluvial forest	Limestone forest	Rubber plantation
Number of individuals collected	6,127	2,492	10,453
Number of species observed	62	48	37
Mean species richness	24.2 ^a (20.04–28.36)	21.2 ^{ab} (13.48–28.92)	16.0 ^b (12.17–19.83)

The sample completeness curve suggested that litter samples represent about 80% sample coverage in all habitats (86.4% in limestone forest, 80.4% in alluvial forest and 81.9% in rubber plantation; Fig. 1A). It also estimated an increase to over 90% of sample coverage in all habitats when the sample size was increased to 10 (Fig. 1A). Sample-based rarefaction curve showed the highest expected species richness in the alluvial forest, intermediate in the limestone forest, and the lowest in the rubber plantation, whose 95% confidence intervals overlapped with the limestone forest's (Fig. 1B).

Extrapolation to twice the number of samples also showed increased species richness in all habitats, although relative differences in species richness among the habitats did not change (Fig. 1B).

The total number of species was highest in the alluvial forest (62 species), intermediate in the limestone forest (48), and lowest in the rubber plantation (37; Table 1). Mean species richness (alpha diversity) was also highest in the alluvial forest (24.2 [95%CI = 20.04 – 28.36]), intermediate in the limestone forest (21.2 [95%CI = 13.48 – 28.92]), and lowest in

the rubber plantation (16.0 [95%CI = 12.17 - 19.83]; $\chi^2_{(2)} = 8.62$, $P = 0.013$). Pairwise analyses revealed that species richness in the alluvial forest was significantly higher than in rubber plantation and that species richness in limestone forest was like both the alluvial forest and rubber plantation (Table 1).

NMDS ordination revealed that ant assemblages in the rubber plantation differed from alluvial and limestone forests (Fig. 2). PERMANOVA analyses statistically confirmed significant differences among the habitats based on β_{sor} and β_{sim} , but not for β_{sne} (Table 2). Pairwise comparisons further

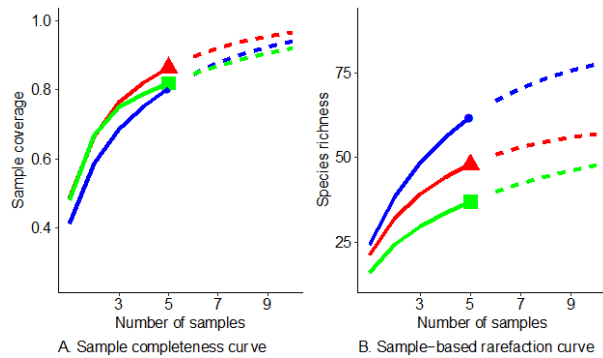


Figure 1 Sample completeness curve (A) and sample-based rarefaction curve (B) based on incidence data from the alluvial forest (blue circle), limestone forest (red triangle), and rubber plantation (green square). Solid and dashed lines represent rarefied and extrapolated (up to twice the reference sample) values.

showed that rubber plantation was significantly different from the alluvial and limestone forests, but no significant difference was detected between the alluvial and limestone forests (Table 2). Beta diversity estimation showed that the overall values of β_{sne} were very low compared with β_{sim} , indicating the small contribution of nestedness to the total beta diversity in our system (Fig. 3).

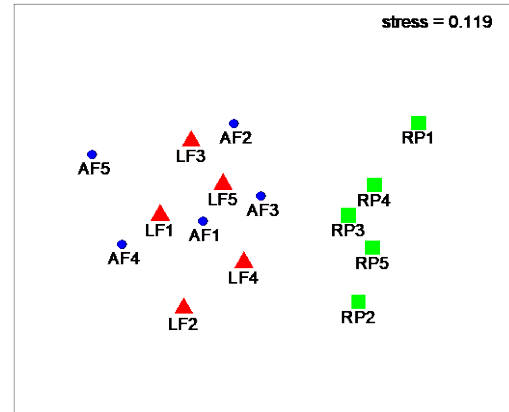


Figure 2 NMDS ordination showing the ant assemblage composition from the three habitats based on the Sørensen similarity matrix for incidence data. Blue circles represent alluvial forest sites (AF1-AF5), red triangles represent limestone forest sites (LF1-LF5), green squares represent rubber plantation sites (RP1-RP5).

Table 2 PERMANOVA results for ant communities sampled from the alluvial forest (AF), limestone forest (LF), and rubber plantation (RP) based on total beta diversity and its turnover and nestedness components. Statistical differences ($P < 0.05$) among habitats and between habitat pairs are highlighted in bold; -pairwise comparisons were not performed.

Beta diversity component	F-value	R ²	P	Pairwise comparisons (P)		
				AF-LF	AF-RP	LF-RP
Total	3.697	0.38	0.001	0.678	0.024	0.033
Turnover	3.855	0.39	0.002	1.000	0.018	0.018
Nestedness	0.192	0.031	0.741	-	-	-

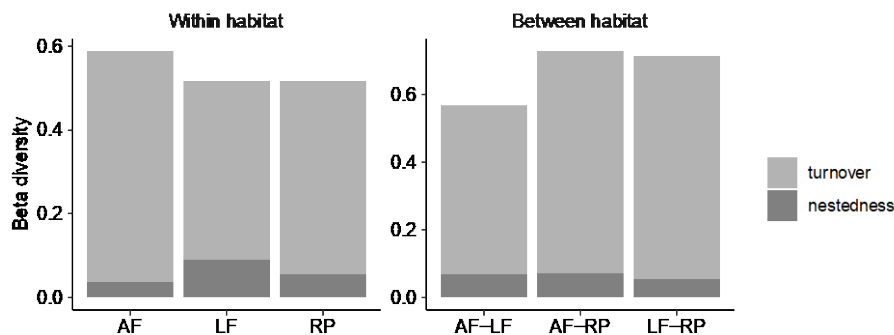


Figure 3 Mean of the total, turnover, and nestedness components of beta diversity within the same habitats and between habitat pairs. (AF = alluvial forest; LF = limestone forest; RP = rubber plantation).

The IndVal protocol found two species (*Oecophylla smaragdina* Fabricius and *T. melanocephalum*) with significant indicator values for the rubber plantation and no indicator species

associated with either the alluvial forest or the limestone forest (Table 3). As we found similar assemblage composition between the alluvial and limestone forests, we decided to

combine the two habitats and use them as a single group in the IndVal. Three species (*Tetramorium nipponense*, *Monomorium* sp. 2, and *Strumigenys* sp. 1) with significant indicator values ($P < 0.05$) resulted from the combined group

(Table 3). All five indicator species were found only within the habitat they indicated and had indicator values of more than 0.7, suggesting that they may be regarded as “strong” indicators of their particular habitats.

Table 3 Results of IndVal procedure of Dufrene and Legendre (1997) showing five indicator species with significant indicator values ($P < 0.05$) and their incidence frequency (i.e., number of plots where the species was sampled) in the forest (alluvial forest, AF, and limestone forest, LF) and rubber plantation habitats. Values in parentheses indicate species incidence frequency in the AF and LF plots, respectively.

Indicator species	Indicator value	Indicator for	Frequency in the habitats	
			Rubber plantation	Forests* (AF + LF)
<i>Oecophylla smaragdina</i>	0.80	Rubber plantation	4	0
<i>Tapinoma melanocephalum</i>	0.80	Rubber plantation	4	0
<i>Tetramorium nipponense</i>	1.00	Forest	0	10 (5 + 5)
<i>Monomorium</i> sp. 2	0.80	Forest	0	8 (4 + 4)
<i>Strumigenys</i> sp. 1	0.80	Forest	0	8 (5 + 3)

Discussion

Our results showed a significant reduction in species richness and changes in community composition in the rubber plantation compared with the forest habitats. These results are consistent with the previous findings on the effects of rainforest conversion to monoculture rubber plantations on ant diversity in Xishuangbanna (Liu et al. 2016) and elsewhere in tropical East Asia (Lee et al. 2020, Nazarreta et al. 2020). Denser vegetation in forests contributes to greater soil volume and litter thickness, positively correlated with ant species richness and diversity (Mezger & Pfeiffer 2011). The more complex environments in forests also promote resource utilization by more species and inhibit the dominance of abundant species, which otherwise would become numerically and competitively dominant in disturbed habitats like rubber plantations (Lassau & Hochuli 2004, Sarty et al. 2006).

Contrary to our expectation, the limestone forest had intermediate ant species richness between the alluvial forest and the rubber plantation. The limestone forest may have represented a structurally intermediate habitat between the alluvial forest and rubber plantation. Indeed, plant species richness, understory vegetation, and soil and litter layer thickness in the limestone forest were intermediate between alluvial forest and rubber plantation and may explain this finding. However, we found that limestone forest ant assemblage was similar only to the ant assemblage in the alluvial forest and was clearly different from that in the rubber plantation. The differences in aboveground biomass, plant species diversity, and the corresponding changes in structural complexity have driven the differences in assemblage compositions (Solar et al. 2016, Carvalho et al. 2020). Both the alluvial and limestone forests were more diverse in terms of flora (trees, understory vegetation, etc.). They had greater aboveground biomass, whereas the rubber plantation was poor in both aboveground biomass and plant diversity. Therefore, the forest habitats had more contributors to soil volume, litter thickness, and overall structural complexity, which inhibited dominance by a few taxa and the

simplification of the ant community. Soil properties in the rubber plantation may have also served as a factor as soil compaction was found to shift ant assemblage compositions (Schmidt et al. 2017, Rocha-Ortega & García-Martínez 2020).

Our results also showed that species turnover (species replacement by new species not found in other plots) drives beta-diversity patterns in the three habitats. It is possible that, at the scale of our sampling, both the alluvial and limestone forests present high habitat heterogeneity, which resulted in high species turnover in our plots. However, the same could not be said for the rubber plantation. Competition and the presence of different dominant species in the rubber plantation plots, which could have influenced their co-occurring species (Blüthgen & Fiedler 2004, McGlynn 2006), may explain the high turnover rates observed in the rubber plantation.

The indicator species characteristic of the habitats further strengthened the PERMANOVA results (Table 2). The indicator species for rubber plantation (*Oecophylla smaragdina* and *Tapinoma melanocephalum*) are known generalists with widespread distributions (Wetterer 2009, 2017) and were among the most abundant species from the rubber plantation in our study. *Oecophylla smaragdina* is arboreal, forages in both canopy and ground strata, and is very aggressive towards other insects, while *T. melanocephalum* is a widespread tramp species that can use virtually anything for its nests (Wetterer 2009, 2017). This suggests that the rubber plantation assemblage is characterized by numerically dominant and aggressive generalist ants, generally absent in forest habitats. We did not find indicator species for each forest habitat, indicating the absence of characteristic species from each of the two habitats. However, we found three indicator species associated with the two forest habitats, which suggests that the alluvial and limestone forests shared the same set of species and that none of the ant species are characteristic of neither alluvial nor limestone forests.

Our study also highlights the conservation value of limestone forests in Xishuangbanna. Limestone forests in the region have properly documented flora (e.g., Cao & Zhang 1997, Tang et al. 2011, Pasion et al. 2018). Still, its fauna has

been relatively understudied (e.g., Kitching et al. 2015, Dayananda et al. 2016). Despite the relatively poor flora and harsher environments, we showed that the limestone forest has comparative ant diversity and similar assemblage to the alluvial forest. Although limestone and alluvial forests are subjected to habitat conversion and other human disturbances (Li et al. 2007), plantations are generally established on more fertile alluvial soils (Liu & Slik 2014). Limestone forests could then serve as source pools for native forest ant species when most forests on other soil types in the region have already been disturbed and modified. A future goal in the study region would be to assess the presence of different indicator species for each forest habitat and a more extensive study scale, as limestone forests are known to harbor many endemic species (Clements et al. 2006).

If compared to a previous study in Xishuangbanna (Liu et al. 2016), our study sampled about 48% of the number of species they sampled (89 versus 186 species) despite collecting roughly the same number of ant individuals (~20,000 ant individuals). This large discrepancy can be explained by the scope of the sampling and the sampling techniques used in the studies. Liu et al. (2016) sampled from 11 rubber plantation sites and 24 forest sites, whereas our sampling was limited to the habitats within XTBG hence, the huge difference in the number of species sampled. Liu et al. (2016) collected ants using only the litter extraction method, whereas we supplemented litter extraction with baiting. We collected 1518 ant individuals by litter extraction (7.9% of the total number of individuals), corresponding to 68 of the 89 species we sampled. Most of the ants were collected by baits (92% of the total) for an additional 21 species sampled (23.6%). Although the sorting time has significantly increased, we obtained a fuller inventory of species, particularly in the rubber plantation (10 of the 37 species sampled by baiting), by supplementing litter extraction with baiting. Moreover, arboreal baiting collected additional species that were not collected by Liu et al. (2016), and we suggest sampling ants from little studied arboreal habitats in the future.

Overall, our results support the idea that environmental filtering becomes the primary driver of local assemblage formation in anthropogenic habitats, such as rubber plantations (Liu et al. 2016, Santoandré et al. 2019), where the environment (both the abiotic characteristics and biotic interactions) in anthropogenic habitats acts as an ecological filter that results in the selective loss of some species and the selective establishment of certain species (typically functionally more similar) that are better adapted to the novel rubber plantation habitat (Mori et al. 2018). Our study also showed the importance of looking at changes in alpha and beta diversities and species identities when investigating how habitat modification affects diversity. The fate of biodiversity in rubber-producing regions is still unknown. The current trends in rubber prices have left many producers, especially smallholders, looking for alternative income sources (Zhang et al. 2019). Some rubber plantations have been converted into 'green' rubber systems or other cash crops, but, likely, some will just be left abandoned, and how biodiversity will be affected in these abandoned and converted rubber plantations is still unknown. Future studies in the region could investigate what happens to ant diversity in these abandoned or converted rubber plantations. Given that plant diversity

will remain relatively poor, it is also interesting to investigate whether the original ant community (before forest conversion to rubber plantations) could re-establish in abandoned rubber plantations.

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+ Supplementary material Table S1 (available online)