



## Differences in geographic distribution of ant species (Hymenoptera: Formicidae) between forests and rubber plantations: a case study in Xishuangbanna, China, and a global meta-analysis

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### Abstract

Rubber plantation is the most important commercial monoculture crop in northern Southeast Asia. Despite the large number of studies documenting the biological impacts of rubber plantations, most focus on changes in overall diversity, and little attention has been paid to other ecological aspects such as biogeographic affinities. Rubber cultivation, like other human-induced disturbances, non-randomly selects for species that can colonize altered environments or have generalized habitat requirements. Consequently, species in rubber plantations are expected to have broader geographic ranges than species in undisturbed habitats. To test this, we used an online database (antmaps.org) to compare the geographic distribution of ants in major habitat types (rainforest, limestone forest, and rubber plantation) in Xishuangbanna, Southwest China. Additionally, we conducted a meta-analysis of 24 other papers and compared the geographic distribution of ants in primary and secondary forests, and rubber plantations. Our results showed that rubber-plantation ants had, on average, wider geographic distributions, compared with rainforest and limestone-forest ants in Xishuangbanna. The same distributional pattern was observed from the global meta-analysis. Species that were characteristic of rubber plantations occupied wider geographic distributions than primary-forest ants, while secondary forest ants had intermediate geographic distributions. However, when only native ants were analyzed, geographic distributions did not vary among the three habitats. Our results show that forest conversion to monoculture rubber plantations replaces habitat specialist species with non-native generalists which have broader geographic distributions. This replacement by generalists results in homogenization of ants in disturbed habitats, which may alter ecosystem functions and services.

**Key words:** antmaps.org, biogeography, *Hevea brasiliensis*, Menglun, SE Asia, Yunnan.

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## Introduction

Rubber plantations are a major human-modified landscape feature in the tropics, covering ~ 9.9 million ha in 2012 (AHRENDTS & al. 2015, WARREN-THOMAS & al. 2015). The ever-increasing demand for natural rubber and the rise in rubber prices in the early 2000s has encouraged extensive cultivation of monoculture rubber across SE Asia and parts of Southwest China. This region (SE Asia and Southwest China), which corresponds to 84 percent of the global area for rubber planting, became the center of rubber cultivation (WARREN-THOMAS & al. 2018). This is alarming as the region coincides with four biodiversity hotspots (SODHI & al. 2010) and conversion of forests to rubber plantations has become the key biodiversity threat in northern SE Asia (WARREN-THOMAS & al. 2018).

Expansion of rubber plantations typically results in fragmentation of forests (XU & al. 2014), drastically turning diverse plant communities into homogenized communities (WARREN-THOMAS & al. 2015, BARNES & al. 2017). The understory of rubber plantations is generally kept devoid of plants, particularly in rows where rubber trees are planted (WARREN-THOMAS & al. 2015). In addition, frequent application of fertilizers, herbicides and pesticides (XU & al. 2014), and increased soil erosion (LI & al. 2007) in rubber plantations made it unsuitable for many organisms, massively reducing biodiversity compared to undisturbed forests (XU & al. 2014). Specifically, forest conversion to rubber plantations has caused declines in species richness of birds and mammals (PHOMMEXAY & al. 2011, LI & al. 2013) and litter and soil invertebrates (BENG & al. 2016, DRESCHER & al. 2016, BARNES & al. 2017). It also resulted in simplifications of assemblages of birds (NÁJERA & SIMONETTI 2010, LI & al. 2013), beetles (MENG & al. 2012) and ants (LIU & al. 2016).

Several studies have shown that disturbance (e.g., rubber cultivation) non-randomly selects for species that can colonize altered environments or have generalized habitat requirements (habitat generalists) (SMART & al. 2006, CLAVEL & al. 2011), leading to a shift from communities dominated by habitat specialists to communities dominated by habitat generalists (MARVIER & al. 2004). This has been shown in birds in fragmented landscapes

(DEVICTOR & al. 2008a, b) and butterflies in disturbed grasslands (KITAHAHA & al. 2000, BÖRSCHIG & al. 2013). Most of the ant species found in rubber plantations are indeed generalist species, which are also found in natural forests (ZHANG & al. 2013, THONGPHAK & KULSA 2014). This suggests that many species in rubber plantations have the ability to thrive in wider variety of habitat types (habitat generalization), which is often linked with species' colonizing ability (MARVIER & al. 2004, BÖRSCHIG & al. 2013).

One interesting aspect of habitat generalization is the breadth of the species geographic ranges (KATTAN 1992, GASTON 1996). Studies of butterflies have shown that species in relatively undisturbed habitats had narrower geographic ranges than species in disturbed habitats (KITAHAHA & al. 2000, BÖRSCHIG & al. 2013). Hence, human-modified systems are expected to be dominated by generalists with widespread distributions. This has been demonstrated using butterflies in Germany (BÖRSCHIG & al. 2013), however, it is yet to be tested on other organisms. In this study, we will use ants to investigate habitat association and biogeographic affinities at different spatial scales.

Ants are one of the most commonly encountered terrestrial invertebrate groups and play important ecological roles in natural and man-made habitats (ANDERSEN 2019). They are primarily omnivores that occupy multiple trophic niches and interact with a wide range of organisms (BRÜHL & al. 2003, WIELGOSS & al. 2010). Ant assemblages tend to reflect the habitat conditions (BURBIDGE & al. 1992), such as plant cover, soil type and disturbance regimes (GOTELLI & ELLISON 2002). Ants are generally reported to react quickly to environmental changes (but their response patterns vary according to functional composition and biogeographic history, ANDERSEN 2019). Furthermore, their responses to environmental change are often congruent with response patterns of other taxa (BRÜHL & al. 2003). These characteristics make ants good bioindicators of environmental change (NAKAMURA & al. 2007, TIEDE & al. 2017, ANDERSEN 2019). Moreover, the taxonomy of ants is relatively well-known, and they are readily sampled (BUR-

BIDGE & al. 1992), making ants an ideal group to study the ecological impacts of rubber plantations. Lastly, the online ant database antmaps.org (JANICKI & al. 2016, GUÉNARD & al. 2017), which shows regions where ant species occur, makes it possible to compare geographic distributions of ant species.

Here, we present a case study that investigated the impacts of rubber plantations on the breadth of the species geographic ranges in Xishuangbanna, Southwest China, where rubber plantations had covered ~ 21% of total land area in 2018 (ZHANG & al. 2019). We hypothesized that rubber plantations are characterized by species with relatively wider geographic distributions compared with forest ants. We then used the results of the present and other studies to test whether the geographic distributions of ant species typically found in rubber plantations are larger than those of ant species found in forests.

## Materials and methods

**Ant surveys in Xishuangbanna:** Ant surveys were conducted in Xishuangbanna Tropical Botanical Garden (XTBG; 21° 55' N, 101° 15' E), Menglun, Mengla, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, Southwest China. Ant surveys were conducted in the dry season in November 2015 within a rubber-plantation monoculture and two types of forest habitat (tropical rainforest and limestone forest) typically found in this region. XTBG and surrounding areas lie around 600 m above sea level and experience a mean temperature of 21.4 °C (CAO & al. 2006). The mean annual rainfall is 1493 mm, 80 percent of which falls between May and October. The forests found in this region are now highly fragmented, and remnant forest patches are found on limestone-derived substrates or other, primarily alluvial substrates.

The rainforest and limestone forest sites where the survey was conducted had similar canopy closure while the rubber plantation was slightly more open, ~ 98% closure in both forests and ~ 90% in rubber plantation. Rubber trees in this region, however, defoliate in response to cold weather in January and February (LIN & al. 2018). Plant species richness is highest in rainforest, followed by limestone forest (PASION & al. 2018). Common trees found in the rainforests are *Milletia leptobotrya* and *Pittosporopsis kerrii* while common species in limestone vegetation include *Cleistanthus sumatranus*, *Lasiococca comberi* and *Celtis philippensis*. Understory vegetation is thicker (PASION & al. 2018) and the depth of humus layer and leaf litter is greater in the rainforest and limestone forest (average depth of 37 and 23 mm, respectively, measured at the study plots described below) than in the rubber plantations (10 mm).

For each habitat type, five replicate plots (10 m × 10 m) were established at least 50 m away from the habitat edges. To assure independence of leaf-litter samples, McGLYNN (2006) suggested a minimum distance of five meters between sampling plots. Following McGLYNN (2006) and MEZGER & PFEIFFER (2011), distances between plots were at least 25 m. Due to survey permit restrictions, ants were

sampled from one location (XTBG), and our plots were spatially aggregated to one area per habitat type.

Two methods (litter extraction and baiting) were employed to collect ants from each plot. Sampling was carried out during warm (> 20 °C) and sunny periods of the day between 1300 and 1700 h each day. For litter extraction, four 0.5 m × 0.5 m quadrats were selected within each plot. In placing the quadrats, areas with relatively uniform litter coverage were selected and any naturally disturbed areas with thick rain-washed litter deposits were avoided. Within each quadrat, litter and loose topsoil were collected by hand. Collected materials were then passed through a sifter (1 cm square mesh) to remove large materials. Samples were kept in cotton bags for no more than 3 to 4 hours and processed using Winkler bags for three days (OLSON 1991). All extracted material was kept in 95 percent ethanol.

For baiting, three types of baits were used, two carbohydrate (honey and lipid-based peanut butter) and one protein (water-based canned tuna), to attract ants on the ground and tree trunks. Within each replicate plot, nine trees were randomly selected with diameters ranging from 6 to 31 cm in rainforest, 5 to 60 cm in limestone forest and 19 to 28 cm in rubber plantation. As rubber trees had smooth bark, trees with relatively smooth bark were selected in the other two habitat types. This was done to eliminate the influence of bark roughness from our study and aimed to investigate the effects of habitat differences on arboreal ants. In each plot, 18 baits (six per type) were allocated such that each bait type was attached in exactly three trees, on the tree trunk and on the ground near the tree base. Baits were prepared by placing honey (1.0 g per trap), peanut butter (1.5 g) or canned tuna (3.0 g) on the center of a 9 cm-diameter filter paper. Tuna was wrapped in a polystyrene net (0.3 mm mesh) and attached to the filter paper with pins to prevent ants from taking the whole bait. Ground baits were set by placing the filter paper directly on the forest litter, approximately 1 m away from the tree base. Arboreal baits were set by attaching a folded filter paper (so that the baits did not fall) to the tree trunk at 1.3 m from the ground using metal wires. Each bait was visited every 30 min for two hours and any ants on the filter paper were collected and placed in a plastic tube with 95 percent ethanol.

All ants were extracted from leaf litter and baiting samples, and were identified to genera using FAYLE & al. (2014) and to species or morphospecies using EGUCHI & al. (2011, 2014), LIU & al. (2015), and websites including AntWeb 2018 and an online pictorial record of ants in Xishuangbanna (LIU 2014) (<https://congliu0514.wordpress.com/ants-in-xishuangbanna/>). As far as possible, also taxonomists were consulted who have worked in the area (see Acknowledgements) for confirmation of our identifications.

**Data analysis:** First sampling sufficiency and gamma diversity (i.e., total number of species within each habitat type) of litter ants from 20 samples (5 plots × 4 quadrats) per habitat type were investigated using coverage- and sample-based rarefaction curves (HSIEH & al. 2016). A cov-

erage-based rarefaction curve plots the collected number of individuals (or samples) against the sample coverage, which represents the proportion of the total number of individuals in the community represented by the sampled species. A sample-based rarefaction curve, on the other hand, estimates the number of species found in a given number of observed individuals (or samples). Instead of individual-based rarefaction curves, sampled-based curves were generated as ants are eusocial organisms and the number of individuals often simply reflects the proximity of the samples to ant colonies and does not necessarily reflect sampling intensity. For both rarefaction curves, extrapolation was conducted by doubling the number of samples, and 100-replicate bootstrapping was used to estimate 95% confidence interval. All rarefaction curves were generated using the iNEXT package (HSIEH & al. 2016) available in R statistical software (R CORE TEAM 2018).

To test whether ant geographic distribution varied among species from the three different habitat types, antmaps.org (JANICKI & al. 2016, GUÉNARD & al. 2017) was used, which, based on over 1,900,000 records, shows the number of regions where particular ant species are known to occur. Antmaps.org generally defines geographic regions by countries, but larger countries (e.g., Australia, Brazil, China, Canada, and U.S.A.) are subdivided into smaller political regions (states or provinces). Isolated oceanic islands were also counted as individual regions. The number of regions occupied by an ant species can be used as a proxy measure of the extent of its geographic distribution, and it was tested whether ant species in the rubber plantation tended to have broader geographic distributions than the other habitat types. Each species was treated as a replicate, and neither samples nor plots were used as statistical replicates. Species-based analysis was more conservative than sample-based analysis, as the latter may inflate the average number of regions if the same common species (which often have wider geographic distributions) were collected from multiple samples. ANOVA was used to test whether the number of regions occupied by ant species (log-transformed prior to analysis) varied among the three habitats. When ANOVA returned significant results ( $P < 0.05$ ), Tukey's HSD post-hoc tests were run to see which habitats differ in ant geographic distribution. ANOVAs were run on: all species (i.e., same species may be included in two or more habitat types); and species that were only found in one of the three habitat types (hereafter habitat specialists). Analyses using habitat specialists represented a very conservative approach, as only the species that occurred in one habitat type were used. Only samples assigned to species names were included (morphospecies and species with "cf." and "nr." were excluded) in the geographical distribution analyses (approximately 44% of all species). In addition, geographic distributions of ants from different microhabitats were compared to determine whether ground and arboreal ant assemblages would present different patterns of geographic distributions (Tab. S1, as digital supplementary material to this article, at the journal's web pages).

**Meta-analysis of geographic distributions of ant species:** Our current study was limited geographically (restricted to Xishuangbanna Tropical Botanical Garden) and taxonomically (with a large proportion of unidentified species). The above analysis of geographic distributions was therefore extended using existing literature (both published and unpublished) which investigated ant assemblages in rubber plantations and other forests in China and elsewhere. Google Scholar was used from the 1<sup>st</sup> to 15<sup>th</sup> of July 2018 to search for relevant papers using "ants" AND "rubber" AND "plantation" AND "disturbance". The query revealed approximately 1900 articles, but the detailed review of the papers was limited to the first 500 resulting papers as the remaining papers became irrelevant. The abstracts (and methods and supplementary materials, when necessary) of the papers were examined to determine whether the papers investigated ants in rubber plantations or other types of habitat. Only ant species that were found in rubber plantations and different types of "natural" forests, which were subdivided into primary and secondary forests, were used in the study (i.e., other habitat types were excluded from the analysis). Unlike our case study, limestone forests were not focused on as few studies were conducted on this habitat type. When relevant papers only investigated ants from rubber plantations without referring to reference habitats (i.e., natural forests), studies that investigated ants in natural forests in the same region were also sought. Only papers that explicitly mentioned or listed ant species found in specific habitat types (rubber plantations and / or forests; see Tab. S2) were selected. A Web of Science query was also made on 14 August 2018 using the words "ants" AND "rubber plantation" and "ants" AND "disturbance" under "Topic" (publication years: 1900 - 2018) but did not return any additional papers. As Chinese studies are often published in local journals not registered in worldwide online database, these were collated by manually searching indexes of the journal titles. The references of the selected papers were also scanned for other relevant papers. As some studies recorded the occurrences of ant species based on unstandardized observations, quantitative data (i.e., abundance and sample) were not used. From these papers, the names of described species and their occurrences in primary forests, secondary forests, or rubber plantation were extracted. All scientific names were verified and updated according to online ant databases (e.g., ANTWEB 2018, BOLTON 2018) prior to checking their geographic distribution.

As was done for the Xishuangbanna study, each species was treated as a replicate to test whether the number of regions occupied by ant species (log-transformed prior to analysis) varied among the three habitats. Two sets of data were generated consisting of all species and habitat specialists. In addition, the same two sets of data were generated but using the data from the Old World only. This was done as most studies came from the Old World, and the small number of studies from the New World may present different patterns of geographic distributions of

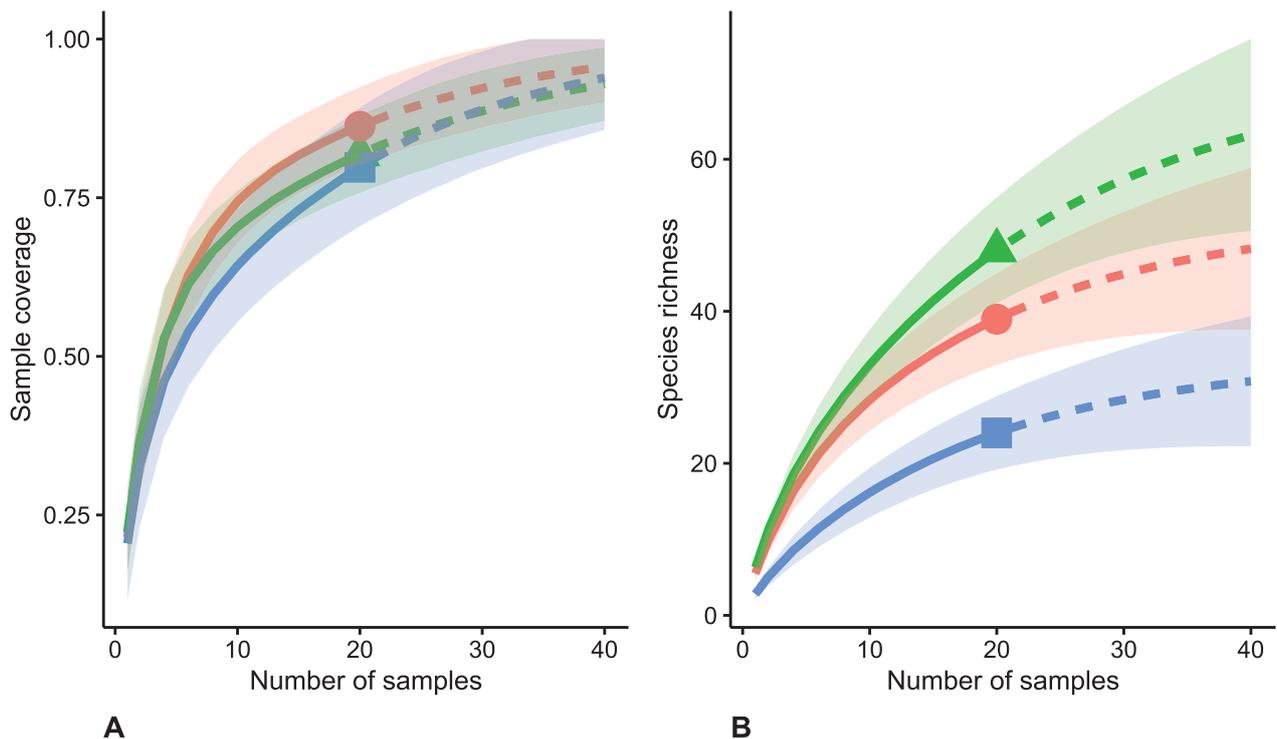


Fig. 1: Sample-based (A) and coverage-based (B) rarefaction curves using litter extraction samples from each habitat – rainforest (red, circle), limestone forest (green, triangle) and rubber plantation (blue, square) – from Xishuangbanna. Solid lines represent the rarefied values and dashed lines represent extrapolations up to a factor of two. Shaded areas represent 95% confidence interval.

ants. Further analyses excluding exotic species were conducted as exotic ant species are presumably common in disturbed habitats (i.e., rubber plantations). Ant species were classified as native and exotic based on the classifications available in antmaps.org. In total, eight datasets were constructed for the meta-analysis (all species vs. habitat specialists, all geographic areas vs. Old World only, all species vs. native species only).

As the number of ant species varied substantially among the three habitat types, analysis was also conducted based on the same number of species randomly drawn from the species pool of a given habitat type. This was done for all datasets (all species vs. habitat specialists, all geographic areas vs. Old World only, all vs. native species). For this analysis, ants from secondary forests were excluded, as their numbers were much smaller than those from the other habitat types, with less than 20 species found to be habitat specialists. The number of randomly drawn species was set to the smallest number observed between the primary forests and rubber plantations. Random selection of species and statistical analysis was repeated 1000 times, then the number of trials that returned significant *P* values was recorded. The probability of the trials that returned non-significant *P* values was calculated. If the probability of non-significant *P* values was less than 0.05, the geographic distributions of ants were deemed different among the corresponding habitat types.

**Additional meta-analysis using SCI-listed journals and ground ants:** Additional analyses were run

using only data from (1) papers published in journals indexed in Science Citation Index (SCI); and (2) papers which conducted ground sampling only. (1) was done as all papers found from SCI were taxonomically rigorous, in that they either included a qualified taxonomist as a co-author or clearly stated that taxonomic identification was assisted by a qualified taxonomist. (2) was done as ants from different microhabitats (epigeaic, hypogaeic, and arboreal) may present different patterns of ant geographic distribution. Only ground ants were selected because most of the papers compiled collected ants from the ground strata. Unfortunately, it was not possible to separate hypogaeic from epigeaic ants, as the studies found did not distinguish between them. Analyses for arboreal ants were not performed as the studies on arboreal ants were very limited. In total, 16 additional datasets were made (all species vs. habitat specialists, all geographic areas vs. Old World areas, all species vs. native species for the SCI papers and ground ants only analyses; see Tab. S3). All analyses were conducted using R statistical software (R CORE TEAM 2018).

## Results

**Local ant surveys:** We collected a total of 19,072 ant individuals, from 89 species and 35 genera, from litter extraction and baiting in the three habitats within XTBG (see Tab. S4 for full species list). The highest number of ants was collected from the rubber plantation (10,453), followed by rainforest and limestone forest (6127 and

Tab. 1: Comparisons of the mean number of regions occupied by ants from the three habitat types at XTBG. Mean number of occupied regions are shown for two classes of ants: all species and habitat specialist species only. Superscript letters indicate results of Tukey's post-hoc test when ANOVA results returned significant  $P$  values (in bold). Total number of ant species are enclosed in parentheses.

Dataset	Mean number of regions occupied by ants			ANOVA results ( $P$ value)
	Rainforest	Limestone forest	Rubber plantation	
All species	14.9 (28 spp.) <sup>a</sup>	20.3 (19 spp.) <sup>ab</sup>	52.7 (12 spp.) <sup>b</sup>	<b>0.033</b>
Habitat specialists	14.2 (13 spp.)	39.0 (4 spp.)	70.9 (7 spp.)	0.062

Tab. 2: Comparisons of the mean number of regions occupied by ants from different habitat types at two geographic scales: Global (New and Old World combined) and Old World region only. Mean number of occupied regions are shown for two classes of ants: all species and habitat specialist species only. Additional datasets (natives only) were generated by exclusion of exotic ants (as classified in antmaps.org). Superscript letters indicate results of Tukey's post-hoc test when ANOVA results returned significant  $P$  values (in bold). \* denotes that comparison was made between only the primary-forest and rubber-plantation ants due to relatively low number of species in secondary forests. Total numbers of ant species are shown enclosed in parentheses.

Dataset	Mean number of regions occupied by ants			ANOVA results ( $P$ value)	
	Primary forest	Secondary forest	Rubber plantation	Normal analysis	Subsampling*
<b>Global scale (25 studies)</b>					
All species	20.0 (231 spp.) <sup>a</sup>	24.6 (106 spp.) <sup>ab</sup>	29.9 (180 spp.) <sup>b</sup>	<b>0.008</b>	<b>0.002</b>
Habitat specialists	14.5 (112 spp.) <sup>a</sup>	19.5 (19 spp.) <sup>ab</sup>	30.9 (82 spp.) <sup>b</sup>	<b>0.003</b>	<b>0.001</b>
All species (natives only)	12.9 (203 spp.)	14.8 (88 spp.)	15.8 (134 spp.)	0.337	0.983
Habitat specialists (natives only)	13.0 (108 spp.)	18.9 (18 spp.)	17.3 (61 spp.)	0.449	0.969
<b>Old World only (22 studies)</b>					
All species	18.9 (191 spp.) <sup>a</sup>	21.9 (95 spp.) <sup>ab</sup>	27.6 (150 spp.) <sup>b</sup>	<b>0.015</b>	<b>0.008</b>
Habitat specialists	12.6 (77 spp.) <sup>a</sup>	9.8 (13 spp.) <sup>a</sup>	27.8 (56 spp.) <sup>b</sup>	<b>0.002</b>	<b>0.039</b>
All species (natives only)	11.3 (166 spp.)	12.2 (79 spp.)	12.8 (112 spp.)	0.144	0.959
Habitat specialists (natives only)	10.3 (73 spp.)	8.0 (12 spp.)	11.0 (41 spp.)	0.322	0.934

2492, respectively). The rainforest was most species rich with 62 species, followed by limestone forest with 49 and rubber plantation with 37. Coverage-based rarefaction curves indicate that the litter samples represented around 80 percent sample completeness for all habitat types, with extrapolating to twice the sample size yielding around 90 percent sample coverage (Fig. 1A). Sample-based rarefaction curves showed that expected species richness (i.e., gamma diversity) was lower in rubber plantation than rainforest and limestone forest (Fig. 1B). Confidence intervals between rainforest and limestone forest overlapped. In addition, extrapolation showed some increase in species richness estimates, but relative differences among the habitats did not change (Fig. 1B).

A total of 39 species (44% of the total number of species collected), 28 from rainforest (45%), 19 from limestone forest (39%) and 12 from rubber plantation (32%), were identified to described species and were used to test whether rubber-plantation ants had broader geographic distributions than ants from other habitat types (Tab. 1; see Tab. S5 for a full list of species with corresponding

number of regions occupied). Thirteen species were sampled only from rainforest (i.e., habitat specialists) while four and seven were found only within limestone forest and rubber plantation, respectively. Rubber-plantation ants had the widest distribution range (mean = 52.7 regions), followed by limestone forest ants (mean = 20.3 regions) and rainforest ants (mean = 14.9 regions;  $F_{(2,56)} = 3.63$ ,  $P = 0.033$ ; Fig. 2A). The same trend was observed when analysis was conducted using only habitat specialist species, however, the differences were not significant ( $F_{(2,21)} = 3.18$ ,  $P = 0.062$ ; Fig. 2A).

When we separated the species into different microhabitats, we found contrasting results. Arboreal ants from rubber plantations had wider geographic distributions than forest ants, regardless of using all species ( $F_{(2,8)} = 9.828$ ,  $P = 0.007$ ) or habitat specialist species only ( $F_{(2,6)} = 21.7$ ,  $P = 0.002$ ; Tab. S1). On the other hand, ground ants from the three habitats presented similar, but non-significant differences in geographic distribution regardless of using all species ( $F_{(2,51)} = 1.57$ ,  $P = 0.218$ ) or habitat specialist species ( $F_{(2,19)} = 2.334$ ,  $P = 0.124$ ; Tab. S1).

### Meta-analysis of geographic distribution of ant species:

We found a total of 24 relevant papers that investigated ants in rubber plantations and / or natural forests (primary or secondary forests, see Tab. S2). A total of 340 described species were used in the analysis, 231 from primary forests, 106 from secondary forests and 180 from rubber plantations (Tab. 2; see Tab. S6 for a full list of species with corresponding number of regions occupied). Primary-forest species had significantly smaller geographic distribution (mean = 20.0 regions), rubber plantation species had the largest (mean = 29.9 regions), whereas secondary-forest species were intermediate (mean = 24.6 regions;  $F_{(2,514)} = 4.891$ ,  $P = 0.008$ ; Fig. 2B). The results of subsampling 180 species showed significant differences in geographic distribution between primary forests and rubber plantations ( $P = 0.002$ ). The number of ant species became smaller when only habitat specialist species were included in the analysis (112 species in primary forests, 19 in secondary forests, and 82 in rubber plantations; Tab. 2). Species restricted to primary forests had the smallest range, followed by the secondary-forest specialists and rubber-plantation specialists ( $F_{(2,210)} = 5.80$ ,  $P = 0.003$ ; Fig. 2B). The results of subsampling 82 species returned significant differences in ant distributions ( $P = 0.001$ ).

For the Old World region data set, a total of 267 species were documented, 191 in primary forests, 95 in secondary forests and 150 in rubber plantations (Tab. 2). We found that species from primary forests appear to have smaller geographic distributions (mean = 18.9 regions) than species from secondary forests (mean = 21.9 regions) and rubber plantations (mean = 27.6 regions;  $F_{(2,433)} = 4.28$ ,  $P = 0.015$ ; Fig. 2C). The results of subsampling 150 species showed significant differences in geographic distribution between primary forests and rubber plantations ( $P = 0.008$ ). When we analyzed only habitat specialist species, primary forests still housed the highest number of species (77 species) followed by rubber plantations (56 species) and secondary forests (13 species; Tab. 2). Habitat specialist species from primary and secondary forests had significantly narrower geographic distributions (mean = 12.6 and 9.8 regions, respectively) than from rubber plantations (mean = 27.8 regions;  $F_{(2,143)} = 6.30$ ,  $P = 0.002$ ; Fig. 2C). Subsampling 56 species showed that primary-forest ants have significantly smaller geographic distributions than rubber-plantation ants ( $P < 0.039$ ).

When we only used native ant species for the global analysis (as classified in antmaps.org), we found similar geographic distributions of ant species among primary forests (mean = 12.9 regions), secondary forests (mean = 14.8 regions), and rubber plantations (mean = 15.8 regions;  $F_{(2,422)} = 1.09$ ,  $P = 0.337$ ; Fig. 2D). Geographic distributions of native habitat specialist ants were also similar among the three habitats (mean 13.0, 18.9, and 17.3 regions for primary-forest, secondary-forest, and rubber-plantation habitat specialists, respectively;  $F_{(2,184)} = 0.81$ ,  $P = 0.449$ ; Fig. 2D). The same results were obtained for the native ants from the Old World region dataset. Geographic

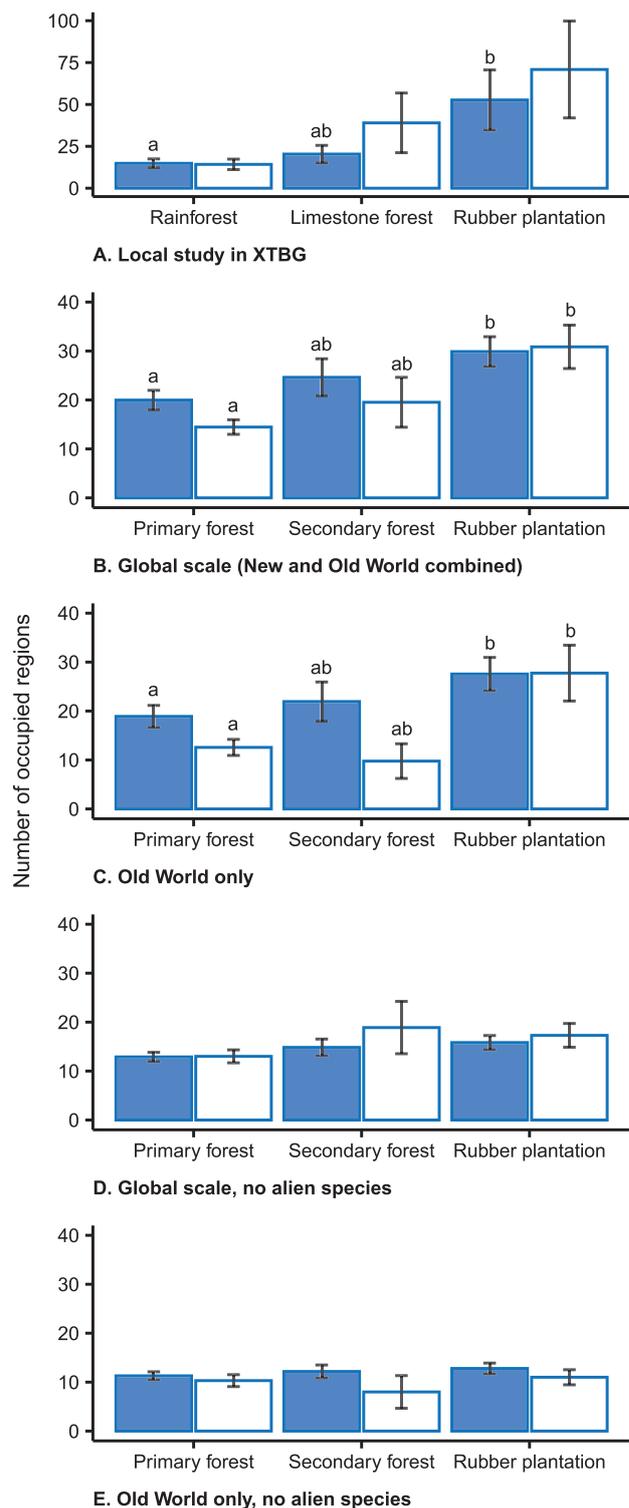


Fig. 2: Geographic distribution of species found in different habitats at different scales: A, from a local study in XTBG; B, from studies from a global scale (both the New and Old World regions); C, from studies conducted in the Old World only; D, global dataset without exotic species; and E, Old World dataset without exotic species. Solid bars represent all species (shared plus restricted) and open bars represent species found in only one habitat type. Different letters atop error bars signify statistical differences between habitat types, based on ANOVA results. Error bars without letters suggest non-statistical differences.

distributions were similar among the three habitats regardless of using all species (mean range of 11.3 regions for primary-forest ants, 12.2 regions for secondary-forest ants, and 12.8 regions for rubber-plantation ants) or only habitat specialist species (mean range of 10.3 regions for primary-forest ants, 8.0 regions for secondary-forest ants, and 11.0 regions for rubber-plantation ants; Fig. 2E). None of the statistical tests returned significant results (Tab. 2).

**Additional meta-analyses using SCI-listed journals and ground ants:** Analysis using only the data from papers published in SCI-listed journals generally showed the same results as those from all papers. Ants in rubber plantations had wider geographic distributions than forest ants (Tab. S3). Analysis using only ground ants also showed the same results as when using all ants. Subsampling the same number of species from rubber plantations and primary forests also revealed the same significant results, with the exception of data which included only native species. More detailed results are presented in the Supplementary Results.

## Discussion

Our case study and the meta-analysis showed consistent patterns with wider geographic distributions of ants in rubber plantations than natural habitats, suggesting that forest conversion to rubber plantations facilitates colonization by generalist ants with wider geographic distributions. This conforms with other studies which found broader distribution ranges of plants (AIDE & al. 2000), birds (SREEKAR & al. 2016), and lepidopterans (BÖRSCHIG & al. 2013) in disturbed versus relatively undisturbed habitats.

The shift from communities dominated by habitat specialists to communities dominated by generalists results from direct and indirect effects of disturbance (ANDERSEN 2019, SANTOANDRÉ & al. 2019). Like any cultivation practice, plantation establishment involves clearing of existing native vegetation and tilling of soil, which would directly remove most of the native forest species (SINCLAIR & NEW 2004). The indirect effects mostly include changes in microclimate, resource (food and habitat) availability, and interspecific interactions (ANDERSEN 2019, SANTOANDRÉ & al. 2019). Due to their specific habitat requirements, habitat specialists are usually more vulnerable to extinction from habitat alteration. Meanwhile, generalists, being able to thrive even in suboptimal environments, are usually less affected. Subsequent planting of the crop and formation of vegetation cover will create new niches for ants, but these niches are likely to be occupied first by generalist species with better dispersal abilities, thus replacing native species (MARVIER & al. 2004, SINCLAIR & NEW 2004, DEKONINCK & al. 2008). Consequently, the loss of habitat specialists releases generalists from competition pressure, which further enables generalists to proliferate in disturbed habitats (MARVIER & al. 2004, BÜCHI & VUILLEUMIER 2014).

Interestingly, native ant species across the different habitat types had similar geographic distributions which suggests that exotic and introduced ants found in these habitats comprise the differences in the species geographic

distributions. Specifically, within group comparisons showed a consistent significant decrease in the geographic distribution of rubber-plantation species from datasets including exotics to those without exotics (see Tab. S7). This indicates that the exotic ants in rubber plantations are the primary drivers of the differences in geographic distributions among all habitats. This is not surprising as rubber plantations often harbour much simplified assemblages, including exotic and invasive species (HOSOISHI & al. 2013, LIU & al. 2016), which typically possess larger geographic ranges.

We included secondary forests in the meta-analysis for comparison. The mean distributional range of secondary-forest ants was intermediate as most species were not habitat specialists and found in primary forests and / or rubber plantations (e.g., BICKEL & WATANASIT 2005; RESENDE & al. 2011; LIU & al. 2015). These species from secondary forests were also typically found in other human-modified landscapes in general (e.g., plantation and urban landscapes; see NEWBOLD & al. 2015). While secondary forests harbour primary-forest ant species, they may also act as potential source of generalist species which may readily colonize disturbed habitats nearby.

Unlike the meta-analysis, our case study included a limestone forest, as natural forests in Xishuangbanna are typically found either on limestone or alluvial substrate. Although gamma diversity (total species richness) of the limestone forest was similar to that of rainforest, geographic distributions of ants were slightly lower. As limestone substrates provide higher soil pH, bedrocks with fissures and holes and shallow soil profiles with lower soil moisture retention (FU & al. 2016), species composition of plants and, consequently, herbivorous insects are known to be different between limestone forests and rainforests (CLEMENTS & al. 2006, KITCHING & al. 2015). Although limestone forests are known to harbour many endemic species (CLEMENTS & al. 2006), we found the lowest number of species unique to this habitat (only 11 as opposed to 24 and 14 species from the rainforest and rubber plantation, respectively), and many species found in limestone forests were also found in the rainforest and / or rubber plantation. For ant assemblages, limestone forests somewhat present habitat conditions similar to those of secondary forests, probably because many tree species in the limestone forests are deciduous and the canopy becomes more open during the dry seasons (CAO & ZHANG 1997).

Data published in non-SCI listed, local journals (grey literature) might be considered as “dubious”. We therefore conducted additional analyses based on the papers published in only SCI-listed journals in order to ensure taxonomic credibility of the data used in the meta-analysis. We feel, however, that these grey literature, at least from China, were conducted properly with species identifications generally verified by local taxonomists. In fact, we found highly consistent results regardless of the data used.

Ant assemblages sampled through different methods and at different microhabitats could potentially present different patterns of ant geographic distributions. Unfor-

tunately, we could not incorporate sampling methods as many of the studies we used in the meta-analysis did not specify the methods from which ant species were sampled. As for microhabitats, we found contrasting results in our case study: Arboreal ants in rubber plantations had wider geographic distributions than rainforest ants, whereas ground ants showed no differences. Our meta-analysis, however, showed wider geographic distributions of ground ants from rubber plantations. Meta-analysis using arboreal ants was not possible as the number of studies that sampled from the arboreal strata were limited. It would also be inappropriate to assign microhabitats to species based on the ID, as many arboreal ants forage actively near or on the ground and vice versa (HASHIMOTO & al. 2010). It would be interesting to look at arboreal assemblages as our case study found differences in geographic distributions despite having much fewer described species. Future research building up on this study could investigate potentially differing patterns among assemblages sampled through different techniques and at different microhabitats and spatial scales.

The measure of the size of geographic distribution used in our study is the number of regions that each species occupied. It is important to note that this measure is highly dependent on political boundaries, which may present a different pattern than the true distribution range of the ant species. Another key limitation is the assumption that the data (e.g., the identification of the species upon which it is based) in antmaps.org is correct. Our study assumes that we know the full distribution of the ant species, which is not the case (DUNN & al. 2009). For example, many species which were shown to occur in Yunnan, China, and say, Thailand are most likely present in Laos, Myanmar and Vietnam where many ant species are yet to be documented. A more comprehensive inventory of ants in understudied regions is needed to determine the full distribution range of these ant species and to understand the true patterns of ant geographic distributions between disturbed and non-disturbed habitats.

Identification of ants and other non-charismatic insects is a challenging task for ecological studies. Our case study was no exception – only 44% of the total ant species were identified to described species. This is a large proportion of the information to lose. In addition, this loss of information may be non-random, and the results may have suffered from taxonomic bias. That is, endemic species found in natural habitats are likely to be undescribed, whereas common and widely distributed species found in disturbed habitats (i.e., rubber plantations) are likely to be described (ESSL & al. 2013). We therefore expected that the proportion of the identified species would be the highest in the rubber plantations, potentially inflating their geographic distributions. In our case study, however, we found slightly higher proportions of identified species in the rainforest (45% or 28 of 62 species identified) and limestone forest (39% or 19 of 49) than rubber plantation (32% or 12 of 37). Similarly, one of the studies conducted in Xishuangbanna (LIU & al. 2016) found similar propor-

tions of identified species between rainforests (69% or 112 of 162 species identified) and rubber plantations (71% or 60 of 84). We therefore believe that our results are more unbiased than initially expected.

From a conservation perspective, we demonstrated that conversion of forests to rubber plantations leads to colonization by generalist ants with broader geographic distributions. This may be linked to biotic homogenization of disturbed habitats through the loss of native specialist species (SMART & al. 2006). Biotic homogenization could affect ecosystem functioning and productivity and may cause deterioration of ecosystem goods and services (CLAVEL & al. 2011). This is particularly alarming for the biodiversity of SE Asia (including Xishuangbanna), where large forested areas are converted to monoculture plantations (WARREN-THOMAS & al. 2015, DRESCHER & al. 2016). Future studies could include ants found in different types of modified habitats common in other parts of SE Asia such as oil palm, other monocultural tree plantations and urban areas.

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