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Comparative responses of termite functional and taxonomic diversity to land-use change

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Abstract. 1. While it is clear that land-use change significantly impacts the taxonomic dimension of soil biodiversity, how the functional dimension responds to land-use change is less well understood.

2. This study examined how the transformation of primary forests into rubber tree monocultures impacts individual termite species and how this change is reflected in termite taxonomic and functional α-diversity (within site) and β-diversity (among sites).

3. Overall, individual species responded strongly to land-use change, whereby only 11 of the 27 species found were able to tolerate both habitats. These differences caused a 27% reduction in termite taxonomic richness and reduced taxonomic β-diversity in rubber plantations compared with primary forests. The study also revealed that the forest conversion led to a shift in some termite species with smaller body size, shorter legs and smaller mandibular traits. Primary forests exhibited higher functional richness and functional β-diversity of termite species, indicating that functional traits of termite species in rubber plantations are more evenly distributed.

4. The present study suggests that forest conversion does not merely decrease taxonomic diversity of termites, but also exerts functional trait filtering within some termite species. The results affirm the need for biodiversity assessments that combine taxonomic and functional indicators when monitoring the impact of land-use change.

Key words. Beta diversity, body trait, land-use change, rubber plantation, termite assemblages, tropical primary forest.

Introduction

Land-use change is a major driving factor of biodiversity loss (Foley *et al.,* 2005). Rapid landscape changes occur throughout the tropics due to the spread of monoculture cash crops such as rubber or oil palm (Koh & Wilcove, 2008; Mann, 2009; Sodhi *et al.,* 2010). The conversion of natural forests to rubber plantations in general drastically decreases species diversity. Compared with natural forests, rubber plantations decreased the diversity of soil nematodes by 33% (Xiao *et al.*, 2014), the diversity of bird species by *c.* 34–56% (Sreekar *et al.*, 2015; Zhang *et al.*, 2017), anuran diversity by 38.9% (Behm *et al.*, 2013), spider diversity by 50–57.4% (Zheng *et al.*, 2015), and leaf litter ant diversity by 28% (Liu *et al.*, 2016). These dramatic changes stimulated our interest in the impact of such forest conversion on termite diversity and communities in tropical regions.

Termites are dominant members of the soil arthropod community in all tropical ecosystems, and their biomass may represent up to 95% of the total soil arthropod abundance (Eggleton *et al.*, 1998; Bignell & Eggleton, 2000). As ecosystem engineers, termites are responsible for large-scale bioturbation, soil aeration, and organic matter decomposition, altering physical,

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chemical, and biological properties of soils, which in turn affect plant growth and diversity (Garba *et al.*, 2011; Van der Plas *et al.*, 2013; Jouquet *et al.*, 2015). The decomposition of complex organic matter into nutrients available for plants is one of the most important ecosystem services termites provide to tropical forests, which leads to ecosystem stabilisation under global change (Obi & Ogunkunle, 2009; Bonachela *et al.*, 2015; Veldhuis *et al.*, 2017). Termites also increase net productivity of the system, and termite removal in crop fields leads to decreased quality and quantity of the harvest (Evans *et al.*, 2011). Understanding how land-use change affects termite assemblages is crucial for maintaining tropical ecosystem productivity and stability, especially under current global climate change.

The decline of species diversity is a common consequence of tropical forest conversion (Xiao *et al.*, 2014; Sreekar *et al.*, 2015; Liu *et al.*, 2016; Zhang *et al.*, 2017). However, many studies of land-use change impacts on soil biodiversity focus mostly on a simple taxonomic diversity index such as species richness or the Simpson diversity index (Vandewalle *et al.*, 2010). It remains unclear how functional diversity responds to land-use change, especially for termite assemblages. Functional diversity is a dimension of biodiversity that encompasses information on functional traits which is absent in taxonomic indices of species diversity (Moretti & Legg, 2009). Functional traits capture morphological, behavioural, and/or physiological characteristics of species that impact individual fitness and determine individual species' responses to environmental perturbations like land-use change (Moretti *et al.*, 2017). As a result, functional diversity and taxonomic diversity may not respond in the same way to land-use change.

Functional trait-based approaches have already been reported for some soil invertebrates like ants, Collembola, and Isopoda, which provided a useful insight into how species respond to land-use changes (Liu *et al.*, 2016; Rigal *et al.*, 2018) and climate change (Dias *et al.*, 2013). Meanwhile, land-use changes also are considered to act as an important ecological filter that changes the functional traits of invertebrates. For example, the community average body size of 1000 insect species decreased with increasing land-use intensity (Simons *et al.*, 2016). Therefore, focusing on functional traits rather than on species identity alone could offer new insights into the assessment of soil arthropod responses to land-use change (Vandewalle *et al.*, 2010). Nevertheless, little is known about how termite functional traits respond to land-use change, especially the conversion of forest habitats to rubber plantations.

In this study, we compared the termite assemblages in primary forests and monoculture rubber plantations in Xishuangbanna, southern Yunnan, China. Xishuangbanna, located within the Indo-Burma biodiversity hotspot (Myers *et al.*, 2000), is experiencing rapid expansion of rubber plantations, such that by 2010 rubber plantations covered more than 20% of the land area (Qiu, 2009; Xu *et al.*, 2014). These land-use trends are set to continue and possibly even accelerate, which will lead to extensive loss of biodiversity (Hansen *et al.*, 2013). Here, we investigated the impact of this land-use change on termites by first identifying how individual species respond from both a taxonomic and a functional perspective. We then determined how these individual species' responses contribute to changes in taxonomic and functional diversity at both the site-level richness (α-diversity) and among-site turnover (β-diversity) scales. Finally, we contrasted overall taxonomic and functional community composition in rubber plantations and primary forest.

Materials and methods

Study site and sampling localities

This study was conducted in Xishuangbanna (21°56′N, 101°11′E), Yunnan, southwest China. Xishuangbanna has a warm, humid subtropical climate with a mean annual temperature of 21.5°C, and *c*. 1565 mm year^{-1} of precipitation, of which roughly 70% falls during the rainy season from June to October. The elevation range is 400–1460 m asl and the soil type is red Ultisol.

We selected three locations in Xishuangbanna that were at least 70 km apart to investigate termite assemblages: Jinghong (22°07′N, 100°39′E, 792–806 m asl), Menglun (21°55′N, 101°16′E, 577–594 m asl), and Mengla (22°37′N, 101°35′E, 711–737 m asl) (Fig. S1). At each location, we sampled termites in monoculture rubber plantation (*Hevea brasiliensis*) and primary forest, which were a maximum of 3 km apart. Primary forest sites were dominated by 50- to 70-year-old trees, and rubber plantations sites all had similarly aged rubber trees (15–20 years old) and management practices such as green manure, compost and biological pest management with no use of pesticides or other chemicals (for details, see Xiao *et al.*, 2014).

Termite sampling

Termite assemblages were sampled according to a standard protocol (Jones *et al.*, 2003). At each forest type, we randomly established three standardised belt transects (100 × 2 m) at least 100 m apart from each other, and more than 100 m from the biotope boundary to avoid edge effects. Each transect was divided into 20 contiguous sections (each 5 × 2 m) and in each section one person-hour was spent and all encountered termites were collected and preserved in 80% ethanol. In each section, searching focused on common termite microhabitats such as dead wood with a diameter of > 1 cm, tree trunks and buttress roots, carton galleries or runways, nests and mounds. In the centre of each section, we took five samples of surface soil cores (12 × 12 cm, 10 cm deep) and hand-sorted for termites. In total, our survey included two forest types (primary forest and rubber plantation) × three sites (Jinghong, Menglun, Mengla) × three standardised belt transects, producing a total of 18 transects. All transects were sampled in April and October 2016.

Identification and functional traits of termites

Termites were identified to species level according to Cai and Huang (1980). The collected termite specimens were deposited at Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna, Yunnan, China. Termites were assigned to feeding groups following Eggleton *et al.* (1997) and Donovan *et al.* (2001), and the details of termite species within feeding groups are listed in Table S1.

We selected six morphological traits measured in all termite species that are relevant to resource use, foraging behaviour, and microhabitat preference (Eggleton, 2011): (i) head width – measured as maximum width of head, and as an indicator of overall body size; (ii) leg length – right hind femur length as a surrogate measurement of leg length which is related to foraging behaviour; (iii) Ra – distance between the apical tooth and first marginal tooth; (iv) R1 – distance between the first and second marginal tooth; (v) R2 – distance between the second marginal tooth and molar plate; and (vi) MP – extent of ridging on the molar plate. The mandibular traits (iii–vi) were measured on the right mandible (supplementary Fig. S2). The mandibles are used to grind and pound food sources such as plant material or soil, and variation in mandibular traits is associated with diet differences due to land-use change (Primanda *et al.*, 2005; Eggleton, 2011). Leg length and mandibular trait values were scaled relative to body size. Measurements were carried out only on the adult workers and there were 10 independent measurement sets for each species and land-use type, giving a total of 540 individual workers measured. In our study, although 11 termite species were observed in both primary forest and rubber monocluture, we selected the eight species to constrast morphological traits that varied between the two forest types We deleted the three termite species because their relative proportions of all termites were low (*Pericapritermes latignathus*, 0.75%; *Pericapritermes hepuensis*, 0.58%; *Odontotermes yunnanensis*, 0.56%) and the differences in frequency of occurrence per transect between primary forests and rubber plantations were not significant (*P. latignathus*, 9.06 ± 5.17 encounters vs. 7.00 ± 4.27; *P. hepuensis*, 8.94 ± 4.75 encounters vs. 6.50 ± 2.50; *O. yunnanensis*, 7.22 ± 1.53 encounters vs. 9.67 ± 6.03; mean ± SE).

Statistical analyses

We first determined how individual species traits varied between the two forest types, and we contrasted the traits of the eight most abundant termite species found in both primary forests and rubber plantations using a linear mixed MANOVA model where site and transect were treated as random effects. We present Bonferroni-corrected P-values.

To assess differences in diversity between both habitat types, we calculated taxonomic and functional richness (α-diversity) within sites and turnover (β-diversity) among sites. Taxonomic richness was calculated using the rarefied species richness in the R package INEXT (Hsieh *et al.*, 2016). Taxonomic β-diversity was calculated using the Sørensen index (β_{sor}) (Jost, 2007; Chao *et al.*, 2012), which reflects the dissimilarity in composition among pairs of sites within primary forests or rubber plantations. We used analysis of similarities (ANOSIM) with 999 permutations to test the significance of β_{sor} between primary forests and rubber plantations. Linear mixed models were used to compare the differences in termite taxonomic richness and β-diversity between the forest types and season (fixed effect) with site and transect as a random effect. We present Bonferroni-corrected P-values. These analyses were calculated using the R package BETAPART and VEGAN (Baselga, 2010; Oksanen *et al.*, 2019).

We assessed the functional diversity of termite communities using the 'functional richness' index based on the six morphological traits measured in all termite species. The functional richness index, the amount of functional trait space occupied by the species within a community, is one of major components of functional diversity (Villeger *et al.*, 2008). The six morphological traits of termites in the analysis were given equal weighting. Regarding functional β-diversity, we used a distance-based metric, the present/absent weight pairwise distance metric (D_{pw}) (Swenson, 2011; Swenson *et al.*, 2011). We chose D_{pw} because it reflects the overall dissimilarity between communities (Swenson *et al.*, 2011). These analyses were calculated using the R packages FD and PICANTE (Kembel *et al.*, 2010; Laliberte & Legendre, 2010).

Finally, we assessed the differences in termite taxonomic and functional community composition between the primary forests and rubber plantations using non-metric multidimensional scaling (NMDS) with Bray–Curtis distances. We used the community-weighted trait means calculated across all species and six functional traits to analyse functional community for each habitat type. A two-dimensional solution was selected because it consistently maintained a low stress (< 0.2) across multiple runs (Faith *et al.*, 1987). We again used ANOSIM with 999 permutations to test differences in termite composition between forest types.

Results

Species traits of termite responses to land-use change

A linear mixed MANOVA model showed that species' body size, leg size, and mandibular traits significantly responded to land-use change. Six out of the eight selected species found in both rubber plantations and primary forest exhibited significant differences in functional traits between the land-use types (Fig. 1). In total, 16 pairwise comparisons showed significant differences in body parameters, of which 15 were larger in primary forests than in rubber plantations (Fig. 1); the sole exception was distance between the apical tooth and first marginal tooth (Ra) in *P. tetraphilus* occurring in rubber plantations (Fig. 1).

Termite community responses to land-use change

At the community level, termite diversity was also sensitive to land-use change, and across all metrics of diversity, termite diversity was higher in primary forests than in rubber plantations. Linear mixed models showed that forest type had a significant effect on termite taxonomic richness ($F = 29.07$, $P < 0.01$) and species β-diversity ($F = 35.1$, $P < 0.001$), but the season did not (Table S2). A total of 27 termite species from three families and 15 genera were recorded: 10 species were observed only in primary forests, six species only in rubber plantations, and 11 species in both (Table S1). Termite taxonomic rarefied richness was significantly higher in primary

Fig. 1. . The impact of forest conversion into rubber plantation on functional traits of termite worker species. We assessed the differences using a linear mixed MANOVA model. Data are expressed as means ± SE. $^{*}P < 0.05$; $^{**}P < 0.01$. The termite species are the eight most abundant termite species found in both primary forests and rubber plantations and the six morphological traits of termite include body size, leg length and the mandibular traits (Ra, R1, R2, MP). Ra, distance between the apical tooth and first marginal tooth on the right mandible of workers; R1, distance between the first and second marginal tooth on the right mandible of workers; R2, distance between the second marginal tooth and molar plate on the right mandible of workers; MP, extent of ridging on the molar plate on the right mandible of workers. [Colour figure can be viewed at wileyonlinelibrary.com].

forests (21.38 ± 0.83 species; mean ± SE) than in rubber plantations (15.53 ± 2.23), which indicated that conversion of forest into rubber plantations reduced the species richness of termites by 27.35% on average (Figs 2a, S3). For taxonomic β-diversity, our data showed that pairs of primary forest sites were more dissimilar than pairs of rubber plantation sites (ANOSIM: $R = 0.72$, $P < 0.001$) (Fig. 2c). The same trend occurred for termite functional diversity. Functional richness (101% higher) and functional β-diversity (D_{pw}) were significantly higher in primary forests than in rubber plantations ($t = 2.61$, $P = 0.014$; ANOSIM: $R = 0.21$, $P = 0.006$) (Fig. 2b,d).

Feeding group structure of termites varied with forest type (Fig. 3). Litter feeder termites were only found in primary forests, and there was a higher proportion of fungus-growing termites in primary forests than in rubber plantations (Fig. 3). By contrast, there was a higher proportion of wood-feeding termites in rubber plantations than in primary forests (Fig. 3).

The NMDS ordination indicated that there was a clear distinction in termite taxonomic composition between primary forests and rubber plantations ($R = 0.57$, $P < 0.001$) and the asymptotic stress was 0.14 (Fig. 4a). Similarly, termite functional composition was significantly different between the two forest types ($R = 0.40$, $P = 0.001$, stress = 0.17; Fig. 4b). Furthermore, we did not detect significant differences in termite taxonomic composition within the three survey sites in primary forest ($R = 0.09$, $P = 0.11$) or in rubber monoculture ($R = 0.14$, $P = 0.08$) (Fig. S4).

Discussion

Our study demonstrated a strong effect of the conversion of primary forest to monoculture rubber plantations on termite species, as 27.35% of the termite species we found were absent from rubber plantations. For the species that were able to tolerate both rubber plantations and primary forests, their traits were, on average, smaller in rubber plantations. Finally, these responses of individual species resulted in a sharp decline in termite taxonomic and functional diversity at both intra- (α) and inter-site (β) scales.

Forest conversion effects on individual species

Particular termite species revealed clear responses to land-use change in our study. While the majority of recorded species we collected were found in both primary forest and rubber plantations, their occurrences were significantly higher, on average, in the primary forest. This indicates the lower-quality habitat in rubber plantations associated with lower diversity and different community structure of termite species. On the other hand,

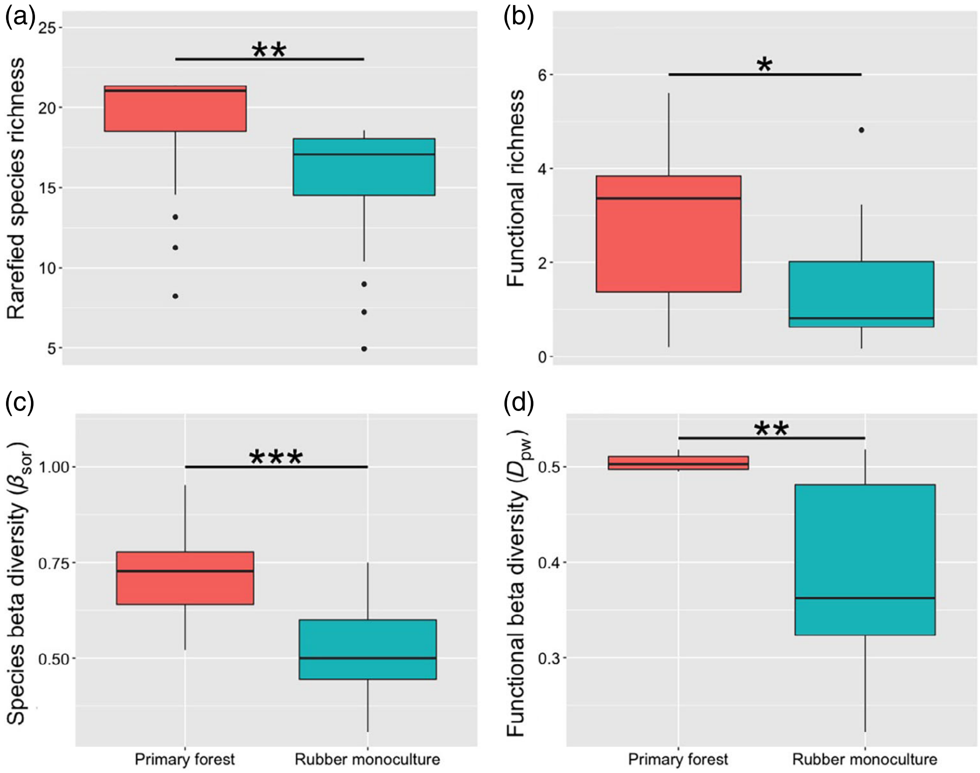

Fig. 2. The impact of forest conversion into rubber plantation on taxonomical and functional components of diversity indices. We assessed the differences in α-diversity using a linear mixed model and β-diversity using analysis of similarities (ANOSIM). (a) Taxonomic rarefied richness (α-diversity); (b) functional richness (α-diversity); (c) taxonomic β-diversity; (d) functional β-diversity (D_{pw}). Median values, 25th–75th percentiles of values (box) and min–max values (whiskers) excluding outliers are shown. *$P < 0.05$; **$P < 0.01$; *** $P < 0.001$. [Colour figure can be viewed at wileyonlinelibrary.com].

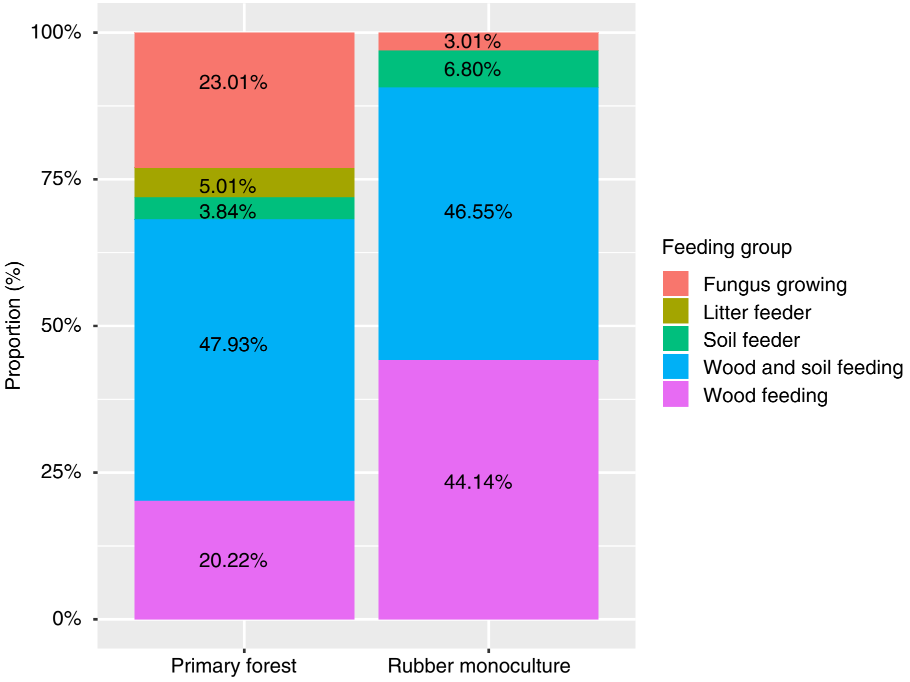

Fig. 3. Proportion of termites in each feeding group in primary forest and rubber monoculture. [Colour figure can be viewed at wileyonlinelibrary.com].

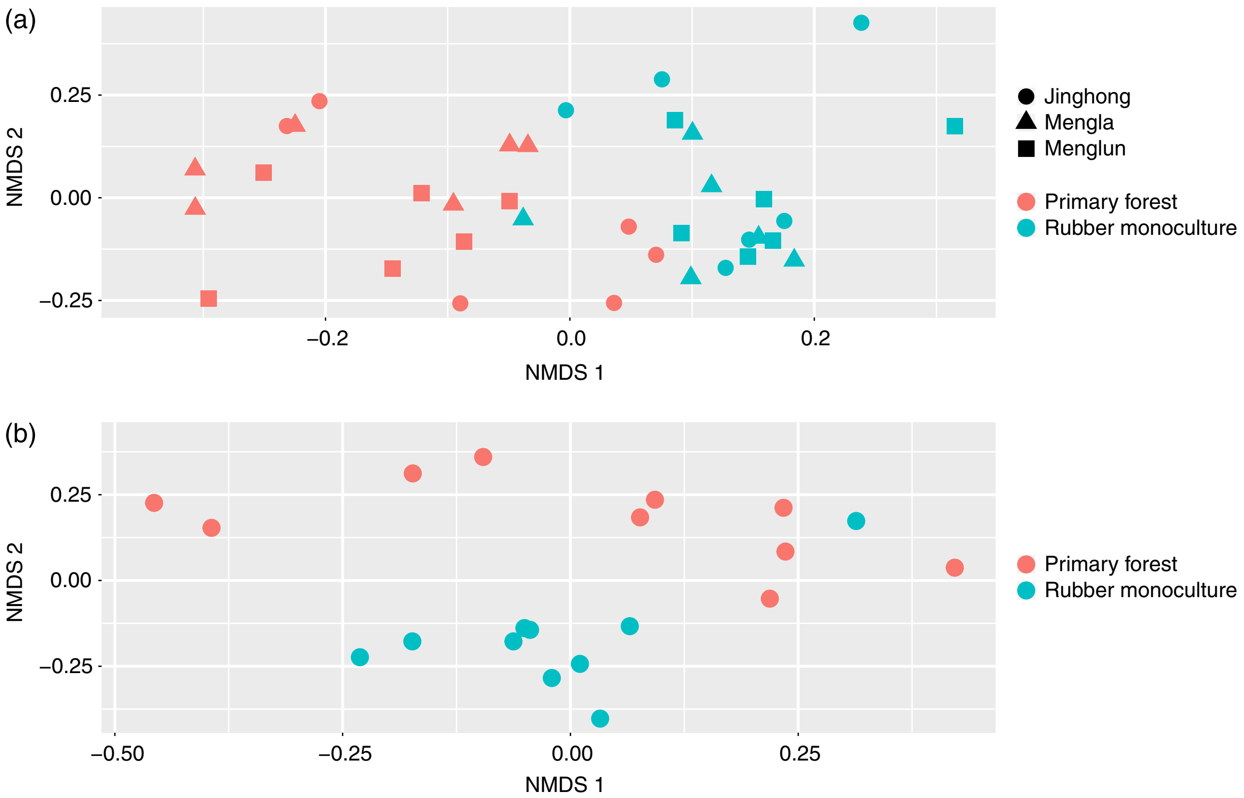

Fig. 4. . Non-metric multidimensional scaling ordinations of termite assemblage compositions (a) and body traits (b) in primary forests and rubber plantations. [Colour figure can be viewed at wileyonlinelibrary.com].

six species were only found in rubber plantations. On average, these six species had larger body size and leg length, which usually indicate higher mobility and longer life span (Simons *et al.*, 2016), which would provide an advantage over small species under high land-use intensity. Therefore, we expect that these are probably disturbance-tolerant species that are more competitive in disturbed habitats, such as rubber plantations.

Our data show that the morphological traits of some termite species were larger in primary forests than in rubber plantations. This pattern may be attributed to the following: first, a previous study carried out in the same site showed that the conversion of natural forests to rubber monocultures leads to a significant reduction in the quantity and quality of leaf litter, dead wood, and soil organic matter by decreasing plant diversity (Xiao *et al.*, 2014) and reducing the resource base of termites has been proposed as one of the important factors in changing termite body size (Liu *et al.*, 2016). Second, termite morphological traits (especially mandibular traits) may also be influenced by changes in the physical structure of the habitat (e.g. bulk density, soil aggregation, and soil moisture), because mandibular traits of termite workers are related to resource use and foraging behaviour, such as soil feeding, subterranean tunnelling and mound building (Eggleton, 2011). Higher bulk density and lower moisture in rubber plantations combined with more macroaggregate soil fractions could make the soil particles too hard for termite workers to bite (Chen *et al.*, 2017), and thus explain our observed differences in mandibular traits. Different species may have different sensitivities to environmental disturbance, which probably explains why the other termite species and other functional traits did not change significantly following forest conversion (Flynn *et al.*, 2009; Mayfield *et al.*, 2010).

Forest conversion effects on termite taxonomic diversity

On average, the taxonomic richness of termites in rubber plantations was about two-fold lower than in primary forests. This reduction in diversity is probably due to lower availability of food resources and altered physical structure of the habitat following forest conversion. Overall, our findings are consistent with previous work from other regions, which found that land-use change decreased termite diversity (Eggleton *et al.*, 2002; Jones *et al.*, 2003; Vasconcellos *et al.*, 2010; Luke *et al.*, 2014).

We also found significantly greater β-diversity of termite species in forest sites than in rubber plantations. The conversion of natural forests to rubber plantations reduces the variety and abundance of suitable termite microhabitats such as dead logs, humus around the bases of big trees, and rotting tree stumps (Eggleton *et al.*, 2002; Jones *et al.*, 2003). This may lead to environmental homogenisation of rubber plantations, which probably explains why lower β-diversity of termite species was found at rubber plantations. This conclusion is consistent with previous work showing reduced β-diversity of ant species in rubber plantations, resulting in spatial homogeneity of ant communities (Liu *et al.*, 2016).

Forest conversion effects on termite functional diversity

We found higher functional richness and functional β-diversity of termite species in forest sites than in rubber monoculture, indicating that functional traits of termite species in rubber plantations are more evenly distributed than those in primary forests. Our results are in line with a previous study showing that rubber plantations decreased the functional α- and β-diversity of ant species (Liu *et al.*, 2016). The differences in diversity between the two forest types are probably due to microhabitat differences (Jones *et al.*, 2003). Heterogeneous primary forests have greater structural complexity and variety of resources than do rubber plantations, as well as more varied microclimates and microhabitats, which allows for the coexistence of more functional traits and species in the community. By contrast, rubber plantations may filter for a restricted set of functional strategies due to the uniform environmental conditions, leading to functional homogenisation where termite species fulfil similar functional roles (Olden & Rooney, 2006; Rigal *et al.*, 2018). Our results provide additional evidence that uniform habitat constraints operate as filters, allowing only species with similar traits to assemble (Puttker *et al.*, 2015).

Conclusions

To the best of our knowledge, the present study is one of few studies that formally assesses the impact of land-use change on the functional trait structure of termite assemblages. In summary, our study revealed that the conversion from primary forests to rubber plantations resulted in the decline of termite taxonomic and functional diversity, and also changed the functional traits of some termite species. Moreover, our study suggests that functional traits have important potential as indicators of biodiversity responses to land-use changes.

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Author contributions

SL, XL and XY designed the experiment. SL and XL conducted the experiments, analysed the data and wrote the manuscript. All authors reviewed and commented on the manuscript.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Termite feeding group definitions, following Eggleton *et al.* (1997) and Donovan *et al.* (2001).

Table S2. Summary of the linear mixed models used to test for the effects of forest type, season and their interaction on the termite taxonomic richness.

Fig. S1. The three study sites (Jinghong, Menglun, Mengla) in Xishuangbanna, Yunnan province, China.

Fig. S2. The detailed morphological traits of termite worker.

Fig. S3. Rarefaction curves for termite species richness in primary forest and rubber monoculture.

Fig. S4. Non-metric multidimensional scaling (NMDS) ordinations of termite assemblage compositions among three survey sites in primary forests (a) and rubber monoculture (b).

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