

Ant and termite communities in isolated and continuous forest fragments in Singapore

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Abstract

The conservation of tropical rainforest biodiversity is a pressing issue, due to the rapid rate of deforestation. Secondary forests may provide a useful alternative to old growth forests, as they often contain a substantial proportion of the original biodiversity. In this study, we investigate species richness, density and composition of ants and termites in six forest sites in Singapore, each differing in habitat isolation and land-use history. The six sites include an old growth forest, a selectively logged old growth forest, and four secondary forests: either located on abandoned agricultural lands or in abandoned villages, and either isolated or adjacent to old growth forests. We found that the old growth forest had significantly higher species density of ants and termites than any other site. Rarefaction curves showed that ant and termite species richness

were highest in the old growth forest followed by the selectively logged forest albeit these results were not significantly different from other sites. Ant species composition changed along a gradient of fragment isolation. Termite community composition in the old growth forest shared a higher proportion of species with the adjacent secondary forest, than with the selectively logged old growth forest, suggesting that the species pool of adjacent habitats is important for species re-colonisation of regenerating habitats. Our results suggest, albeit without replications, that secondary forests differ in conservation value and that disturbed habitats in continuous forest fragments recover more rapidly than isolated ones. Further, we emphasise the importance of old growth forest fragments within man-made ecosystems as sources of original biodiversity.

Keywords biodiversity, conservation biology, community ecology, Singapore, species richness

Introduction

Pristine tropical rainforests are some of the most diverse ecosystems on Earth (Basset et al. 2012), yet, they are subjected to increasing rates of deforestation worldwide (Hansen et al. 2009) due to exploitation of timber and crop-land conversions (e.g. Malhi et al. 2008; Reynolds et al. 2011; Mayaux et al. 2013). Abandonment of deforested land is common and at the beginning of the 21st century half of all tropical forests were degraded or secondary (ITTO 2002), increasing the interest for the conservation value of these ecosystems (Lamb et al. 2005; Chazdon 2008).

Different taxonomic groups vary in their response to land-use intensity and levels of perturbation (Lawton et al. 1998; Barlow et al. 2007), with invertebrates showing some resilience to selective logging in old growth forests (Vasconcelos et al. 2000; Jones et al. 2003; Widodo et al. 2004; Gunawardene et al. 2010; Putz et al. 2012). Secondary forests, on the other hand, have depauperate species communities, and the species diversity they host generally declines with land-use intensity while increasing with the age and size of the habitat (Eggleton 1996; Vasconcelos 1999; Bandeira and Vasconcelos 2002; Bandeira et al. 2003; Bowen et al. 2007; Silva et al. 2007; Chazdon et al. 2009; Dent and Wright 2009; Brühl and Eltz 2010). Additionally, the habitat surrounding secondary forests and habitat isolation have

been shown to affect the recovery of biological communities (Prugh et al. 2008) and generally affect species communities (De Souza and Brown 1994; Carvalho and Vasconcelos 1999; Davies 2002; Vasconcelos and Bruna 2012). As many species disappear with forest clearance, the isolation of a regenerating forest may be detrimental to the recovery of species communities. The presence and proximity of intact forests, particularly old growth forests, therefore enhances re-colonisation of disturbed habitats (Chadzon et al. 2009; Dent and Wright 2009). Although secondary forests and old growth forests often support different species assemblage structures (Gunawardene et al. 2010), adjacent forests may have many species in common (Eggleton et al. 1999) due to the colonisation of species from a joint species pool. Forests surrounding recovering areas may also act as stepping stones for other colonising species. Data suggest that, although old growth forests have the highest species diversity and should remain the primary focus of conservation (Gibson et al. 2011), secondary forests can host a substantial proportion of the original species diversity and are therefore worth conserving and rehabilitating (Chadzon et al. 2009).

Social insects are highly successful in many terrestrial ecosystems, and ants and termites play a particularly important role in tropical forests, where their abundance and biomass are high (Fittkau and Klinge 1973; Petersen and Luxton 1982; Eggleton et al. 1996 1999; Sanderson 1996; Ellwood and Foster 2004; Jouquet et al. 2011, 2016). Ant diversity and functional diversity are closely linked (Bihn et al. 2010) as ants occupy a range of trophic positions (Blüthgen et al. 2003) and are crucial in many ecosystem functions (Del Toro et al. 2012). For example, they are predators of insects (Hölldobler and Wilson 1990), may reduce pollinator visitation (Junker et al. 2007), and frequently develop symbiotic associations with many plant species (Heil and McKey 2003). Termites are key invertebrate decomposers of organic matter in the tropics (Holt and Lepage 2000; Sugimoto et al. 2000) where they feed on materials from wood to mineralised soil (Bourguignon et al. 2011). Together, ants and termites play a major role in ecosystem functioning and plant growth through bioturbation and nutrient cycling (Bardgett et al. 2005; Evans et al. 2011). Due to the key role that ants and termites play in ecosystem functioning, their response to disturbance is important for the rehabilitation of disturbed areas (Majer et al. 2007; Jouquet et al. 2014). Ant and termite communities have been shown to vary in their tolerance to disturbance with ant diversity increasing and termite diversity decreasing in degraded areas compared with old growth forests (Luke et al. 2014).

In this study, we investigate the composition of ant and termite communities in forest fragments with different land-use history and fragment isolation in order to evaluate the conservation value of secondary forests in Singapore. Specifically, we aim to investigate ant and termite species richness, density and assemblage structure in a primary and selectively logged old growth forest, as well as in four secondary forest patches that differ in land-use history (abandoned agriculture or village) and isolation (continuous forest patch or isolated patch surrounded by urban areas) in Singapore.

Methods

Study sites

Before the establishment of the Straits Settlement in the 19th Century (Corlett 1992) the majority of Singapore's land surface was covered by natural vegetation. In the subsequent 190 years, old growth forests have been reduced to a few small patches in Bukit Timah and around the Central Catchment (Corlett 1997), which today comprise old growth forests, selectively logged forests and secondary forests (Yee et al. 2011; Nature Society of Singapore 2013). Following the change in land-use policy in the 1970s, many villages and agricultural land were abandoned (Dale 1999) and today Singapore is made up of a mosaic of urban landscapes and forest fragments.

We sampled ants and termites in six sites (Fig. 1): old growth forest (OGF), selectively logged forest (SL), secondary forest situated on abandoned agricultural land in a continuous patch of forest in the MacRitchie nature reserve (SAC), secondary forest situated on land from an abandoned village in the MacRitchie nature reserve (SVC), secondary forest situated on land from an abandoned village in an isolated forest patch (SVI) and secondary forest situated on abandoned agriculture land in an isolated forest patch (SAI).

(i) OGF: Old growth hill dipterocarp forest with species composition characteristic of old growth forests including large old trees. The site was located in Bukit Timah Nature Reserve (N 01.357°, E 103.775°) and does not have a history of logging.

(ii) SL: Selectively logged forest adjacent to an unlogged old growth forest. It is believed that selective logging took place 100-150 years ago to provide fire wood for processing gambier in adjacent plantations (Nature Society of Singapore 2013). The plant species composition was that of an unlogged old growth forest but the site

lacked larger emergent trees present in old growth forests. The site was located near the MacRitchie Reservoir in the Central Catchment Nature Reserve (N 01.342°, E 103.829°).

(iii) SAC: Secondary forest on abandoned agricultural land. The forest site is located adjacent to an old growth forest and a golf course with low forest stature and absence of trees with a diameter greater than 20cm at breast height. Species composition was dominated by native secondary forest species with only a few seedlings common to old growth forests. The site was located in the MacRitchie Nature Reserve in the Central Catchment Nature Reserve (N 01.360°, E 103.814°).

(iv) SVC: Secondary forest regenerated on land from an abandoned village, and situated adjacent to an old growth forest. Forest stature matches that of a old growth forest, except that the large trees were species characteristic of villages in the region (e.g. fruit trees such as *Durio zibethinus*, *Artocarpus integer* and *Nephelium lappaceum*). The lower stratum was dominated by old growth forest species that probably dispersed from the nearby old growth forest. This forest was located in Bukit Timah Nature Reserve (N 1.345°, E 103.777°), at the foothills of the OGF site.

(v) SVI: Secondary forest regenerated on land from an abandoned village. The species composition was dominated by native secondary forest species with no species associated with old growth forests. The site was located in an isolated forest fragment surrounded by urban areas in the Clementi Woods 2.5km from the Bukit Timah Nature Reserve (N 01.331°, E 103.778°).

(vi) SAI: Secondary forest regenerated from abandoned agricultural land. Species composition was dominated by wind-dispersed species of trees and included many non-native species. The site was located in an isolated forest fragment surrounded by urban areas in Bukit Batok 1.75km from the Bukit Timah Nature Reserve (N 01.357°, E 103.747°).

Sampling methods

Sampling of both ants and termites was conducted using standardised sampling protocols. Surface foraging ants were collected using pitfall traps and Berlese funnels

across a 50m x 50m grid where the traps were located 10m apart. In total 25 pitfall traps (9cm diameter 15cm high) were used with 80% ethanol. The traps were located at ground level and protected from flooding using plastic plates supported by wooden sticks and secured at a height of 10cm. The pitfall traps were emptied after 48 hours.

Litter foraging ants were collected from the leaf litter in 25 1m² quadrats across the grid. Ants were collected from the leaf litter using Berlese funnels with 100W light bulbs and extractions continued until the litter was dry. Ants were extracted in the lab.

Termites were collected following a modified version of the standardised sampling protocol described in Roisin and Leponce (2004). One 250m transect was located in each of the sites and split into 25 5m² quadrats (2.24m x 2.24m) that were located 10m apart. In each quadrat termites were actively searched for during 0.5 person-hours in a range of micro-habitats (e.g. mounds, arboreal nests, galleries, dead wood, trees, leaf litter, and soil to a 5cm depth) from the ground to 1.8m height.

Identification

All samples were grouped into morphospecies based on the morphology of workers (ants) and soldiers (termites). When possible, morphospecies were identified to species using keys and monographic revisions (Thapa 1982; Tho 1992; Bolton 1994; Bolton 2003; Hashimoto 2003). Samples of termite incipient colonies, comprising dealates and larvae only, were discarded as they did not represent established colonies.

Data analysis

Analyses for ants and termites were conducted separately, unless otherwise stated. Differences in species richness among sites were investigated using species rarefaction curves and confidence intervals (CIs) calculated with the Mao-Tau method implemented in EstimateS 9 (Colwell 2013). The rarefaction curves were scaled using occurrences (presence/absence data for species in traps (ants) and quadrats (termites)) as abscissa. The unique number of species recorded in each site (species only found in one site) was estimated and chi-square tests were conducted in order to examine potential significant differences among sites.

Species density was based on the presence/absence of species in each trap (ants) or quadrat (termites). Data on ant species that were collected from pitfall traps

and Berlese traps in the same sampling location were pooled due to the close proximity of the traps. The difference in ant and termite species density among sites was examined using a Kruskal-Wallis test and evaluated using the *kruskalmc* function in the *pgirmess* package, R (Giraudoux 2011). Parametric values and species density for termite feeding-groups were analysed using ANOVA followed by a *post hoc* test (TukeyHSD) in R (version 2.15.3). Termite species density of feeding-groups among sites was also compared using a simplified version of the feeding-group classification in Donovan et al. (2001). Feeding-groups I and II were grouped into wood-feeders, and feeding-groups III and IV were grouped into soil-feeders, as suggested by Bourguignon et al. (2011). The assignment of species to particular feeding-groups is consistent with previous studies (e.g. Jones and Prasetyo 2002; Jones et al. 2010).

Nonmetric multidimensional scaling (NMDS) analyses were conducted using Bray-Curtis distances to compare species composition among sites. NMDS analysis was preferred as it performs well when the dataset consists of null values due to the absence of species from some sites. NMDS only included species that were recorded four times or more. Significant differences in species composition among sites were tested with ANOSIM implemented in the software PAST 2.14 (Hammer et al. 2001). ANOSIM was implemented using species density data, Morisita distance and 9999 permutations. *P*-values were corrected with Bonferroni tests. Lastly, we examined the correlation between ant and termite community structures using a Mantel test, performed on the matrices generated by ANOSIM. The Mantel test was implemented using the Pearson method in R, with the function *mantel* in the *vegan* package (Oksanen et al. 2017).

Results

Ants

In this study, 105 ant species belonging to 40 genera were collected and identified from the six study sites (Table S1). The highest number of ant species was found in OGF (53 species) while the lowest number of species was found in SAI (29 species) (Fig. 2A). All 95% confidence intervals of the rarefaction curves overlapped (confidence intervals not showed).

Species density (\pm SE) of ants was the highest in OGF with 7.4 (\pm 0.36) species per trap and lowest in SAI with 3.9 (\pm 0.39) species per trap (Fig. 3A). The density of ant species differed significantly among sites (ANOVA, treatment *df* = 5, residual *df*

= 144, F-value = 8.03, p -value < 0.001), with OGF being significantly different from all secondary forests except for SAC, while species density in SAI was significantly lower than the density in all sites except for SVC and SVI (Fig. 3A). The number of unique species differed significantly between sites ($\chi^2 = 12.88$, $df = 5$, $p = 0.025$) and was by far the highest in OGF, including 18 species that were only found in that site. All other sites ranged between six and seven unique species (Fig. 3B). However, when taking species density and sampling effort into account, the difference in unique species between sites fell below the significance level ($\chi^2 = 5.52$, $df = 5$, $p = 0.356$).

Two-dimension NMDS had a stress (loss function) of 0.18 which suggests the presence of a disturbance gradient, with OGF and SL at one end of the scatter plot and SVI and SAI on the other (Fig. 4A). Species composition significantly differed among sites (ANOSIM: global $R = 0.503$, $p < 0.001$) and all sites were significantly different from each other (Table 1).

Termites

In this study, 52 species of termites belonging to 22 genera were recorded in the six study sites (Table S2). OGF had the highest species richness among the sites with 29 species, which was significantly higher than in SAC (Fig. 2B). All other 95% confidence intervals of the rarefaction curves overlapped (confidence intervals not showed). SVI had the lowest species richness with eight species.

Termite species density (\pm SE) was significantly higher in OGF and SAC, with 3.3 (\pm 0.28) and 3.2 (\pm 0.19) species per quadrat, respectively, than in any other site except for SVC. The lowest termite species density was found in SVI with 0.9 (\pm 0.17) species per quadrat (Fig. 3A). The number of unique species significantly differed among sites ($\chi^2 = 13.16$, $df = 5$, $p = 0.022$). The highest number of unique species was found in OGF including 10 species that were only found in that site, followed by SVC with 6 unique species. There was little difference between the remaining sites where the unique species ranged from one in SVI to three in SL and SAC (Fig. 3B). However, when species density and sampling effort were considered in each site, the difference in unique species between sites fell below the significance level ($\chi^2 = 5.01$, $df = 5$, $p = 0.415$).

Species density of termite feeding-groups was significantly different between wood- and soil-feeding termites (ANOVA, $p < 0.001$), with wood-feeding termites having the highest species density (wood-feeders: 1.4 ± 0.08 species per quadrat; soil-

feeders: 0.8 ± 0.08 species per quadrat). Termite species density for feeding-groups varied significantly among sites (wood-feeders: ANOVA, $p < 0.001$, soil-feeders: ANOVA, $p = 0.007$) with the highest density of wood-feeding termites found in SAC ($2.4 (\pm 0.19)$ species per quadrat) and the lowest found in SVI ($0.2 (\pm 0.80)$ species per quadrat). The highest density of soil-feeding species was found in OGF ($1.6 (\pm 0.22)$ species per quadrat) and the lowest in SVI ($0.08 (\pm 0.06)$ species per quadrat) (Fig. 5).

Two-dimension NMDS had a stress (loss function) of 0.14 and revealed a gradient along the second axis starting with OGF and ending with SVI (Fig. 4B). SL was closer to OGF, followed by SVC and SAC, suggesting that the secondary forests located in the continuous forest fragments shared a large proportion of species with the old growth forest (Fig. 4B). Species composition significantly differed among sites (ANOSIM: global $R = 0.259$, $p < 0.001$) and all sites were significantly different from each other, apart from SL-SAC and SVI-SAI (Table 1).

Correlation between ant and termite communities

The Mantel test showed a significant correlation in ant-termite species composition among sites (Pearson $R = 0.747$, $p = 0.024$). Note that using the Spearman or the Kendall methods did not change the results.

Discussion

In this study, we examined ant and termite communities in six sites with different land-use histories and levels of isolation from forest habitats. The six sites were all substantially different and comprised a primary and a selectively logged old growth forest, as well as four secondary forest patches that differed in land-use history (abandoned agriculture or village) and isolation (continuous forest patch or isolated patch surrounded by urban areas). Consequently, all sites had distinct levels of land-use history and isolation without replication. The lack of replication was due to the time-consuming and intense nature of the sampling techniques and careful species identification. Nevertheless, our results provide an important contribution to the field though data on the effect of isolation and habitat connectivity as well as the value of secondary forests and the importance of old growth forests as a source of original biodiversity.

Our results show that OGF had the highest species richness, density and number of unique species of both ants and termites. However, the confidence intervals

of species rarefaction curves overlapped in all cases, except for in OGF and SAC, where termite species richness was significantly different. The large number of unique species in OGF was largely due to the high species density compared with other sites. The high species richness that was recorded in OGF was consistent with other studies of ants (e.g. Floren and Linsenmair 2005; Fayle et al. 2010; Leal et al. 2012), termites (e.g. Eggleton et al. 1996, 2002; Vasconcellos et al. 2010) and other organisms (e.g. Barlow et al. 2007). Studies have shown that termite species richness varies very little between old secondary and old growth forests (Eggleton et al. 1999). These data are consistent with the results in this study where SL had the second highest species richness. The high species richness may be due to the ability of ants and termites to re-colonise secondary forests within a 30 year time period, explaining the similarity between the selectively logged forest and the secondary forests in this study. However, while the age of a forest habitat is important, the levels of original degradation and residual vegetation also have a large impact on forest recovery (Chazdon 2008).

Differences between sites appeared to be related to the land-use history and location (continuous or isolated forest patches), although the lack of replication prevents us from drawing general conclusions. In this study, both ants and termites showed a general decline in species richness and density with disturbance and isolation which is consistent with studies that have examined the impact of isolation (De Souza and Brown 1994; Carvalho and Vasconcelos 1999; Davies 2002; Vasconcelos and Bruna 2012) and habitat disturbance (e.g. Eggleton 1996, Vasconcelos 1999; Bandeira and Vasconcellos 2002; Bandeira et al. 2003; Silva et al. 2007; Brühl and Eltz 2010) on ant and termite communities. Among the secondary forest sites, the abandoned villages had slightly lower species richness and density than the abandoned agricultural lands; however the differences were not significant.

In the secondary forests, a larger number of ant and termite species was recorded in the continuous forest fragments. Continuous forests are known to host a higher number of species than isolated fragments (Vasconcelos and Bruna 2012), while agro-forestry located adjacent to old growth forests have been shown to contain a large proportion of the original termite community (Ackerman et al. 2009). While the isolated sites and the continuous forest were less than 2.5km apart, termite alate imagoes, the founders of new colonies, are weak flyers (Nutting 1969), and generally do not disperse more than 0.5km, and exceptionally up to 1 km (Messenger and

Mullins 2005; Hu et al. 2007). Ant female alate imagoes, on the other hand, may disperse from a few meters up to twelve kilometres, depending on the species (Markin et al. 1971; Hölldobler and Wilson 1990; Tschinkel 2006). This explains the higher impact of fragment isolation on termites compared with ants. Alternatively, ant species are generally better adapted to perturbation than termites and able to maintain colonies in disturbed areas (see Gove et al. 2005) from where they can re-colonise isolated forest patches. The results in this study concur with Chadzon et al., (2009) and Dent and Wright (2009) where species recovery increased with reduced levels of disturbance and proximity to undisturbed forest.

Within the termite communities, wood-feeding termites did not show a strong species density pattern among sites with no significant difference between SAI and OGF (see feeding-group assignment in Table S2). Further, the highest species density of wood-feeding termites was recorded in one of the secondary forests (SAC). Among the soil-feeding termites the species density pattern was strong, although there was no significant difference among sites located in the same patch of continuous forest. OGF and SVC were located one kilometre apart and five kilometres away from SL and SAC, that were located no more than 2.5km apart. A road divided the forest and separated the OGF, SVC patch and the SL, SAC patch, possibly acting as a dispersal barrier for soil-feeding termites. Overall, our results concur with previous studies that have showed that soil-feeding termites are highly sensitive to disturbance and arid environments compared with wood-feeding termites (Wood et al. 1982; Eggleton et al. 2002; Davies et al. 2003; Jones et al. 2003).

Ant and termite species composition among sites were significantly correlated. This suggests that the two dominant groups of social insects in the tropics react in a similar fashion to environmental perturbation. Additionally, species composition significantly differed among all sites, except for the termite species composition in two paired sites (Table 1). The high species turnover among the relatively clustered sites in Singapore suggests that ants and termites are heterogeneously distributed. This may be particularly true in Singapore that is highly influenced by anthropogenic disturbance, as portrayed by the mosaic of forests and urban areas. Roads and urban areas may further prevent colonisation of forest patches by vulnerable species.

Secondary forests, arising from partial or complete forest clearance and abandonment, are now some of the dominant ecosystems in the tropics (ITTO 2002). In this study, we sampled ant and termite communities at the ground level which

means that our conclusions do not necessarily apply to arboreal ant communities. Deforestation could potentially be more damaging for arboreal ant communities than their ground-dwelling counterpart due to their dependence on suitable trees (Klimes et al. 2015). Although the results in this study must be carefully considered, due to the lack of replication of each site, we provide important insights into role of habitat isolation and disturbance for the recovery of ant and termite communities. Ant and termite communities may recover on land that has been left undisturbed, but the recovery is faster, and more complete, in areas with fewer barriers (water, roads, urban areas). Conservation efforts should therefore be directed towards keeping larger patches of forest, although, it is not advisable to remove smaller forest fragments as these may contain rare species. While old growth forests may be the main target for conservation (Gibson et al. 2011), secondary forests have clear conservation value (Gray et al. 2015), although studies are needed to set conservation priorities and determine the factors that positively affect secondary forest biodiversity.

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Table 1. Differences in species composition between sites for ants (bold font) and termites (normal font). Values were obtained with ANOSIM and represent R-values that increase with site dissimilarity.

Termites/ Ants	OGF	SL	SAC	SVC	SVI	SAI
OGF	-	0.295*	0.408*	0.658*	0.561*	0.596*
SL	0.254*	-	0.397*	0.566*	0.486*	0.472*
SAC	0.260*	0.056	-	0.723*	0.638*	0.531*
SVC	0.436*	0.266*	0.473*	-	0.335*	0.513*
SVI	0.371*	0.154*	0.345*	0.139*	-	0.400*
SAI	0.407*	0.179*	0.340*	0.209*	0.035	-

* significant difference among the paired sites ($p < 0.01$).

Table S1. Ant occurrence in the six sampling sites: OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest fragment, SAI: secondary forest on abandoned agricultural land in isolated forest fragment.

Table S2. Termite occurrence in the six sampling sites: OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest fragment, SAI: secondary forest on abandoned agricultural land in isolated forest fragment. * indicate species for which identification is unsure. Feeding-groups were either: W, wood-feeders; or S, soil-feeders.

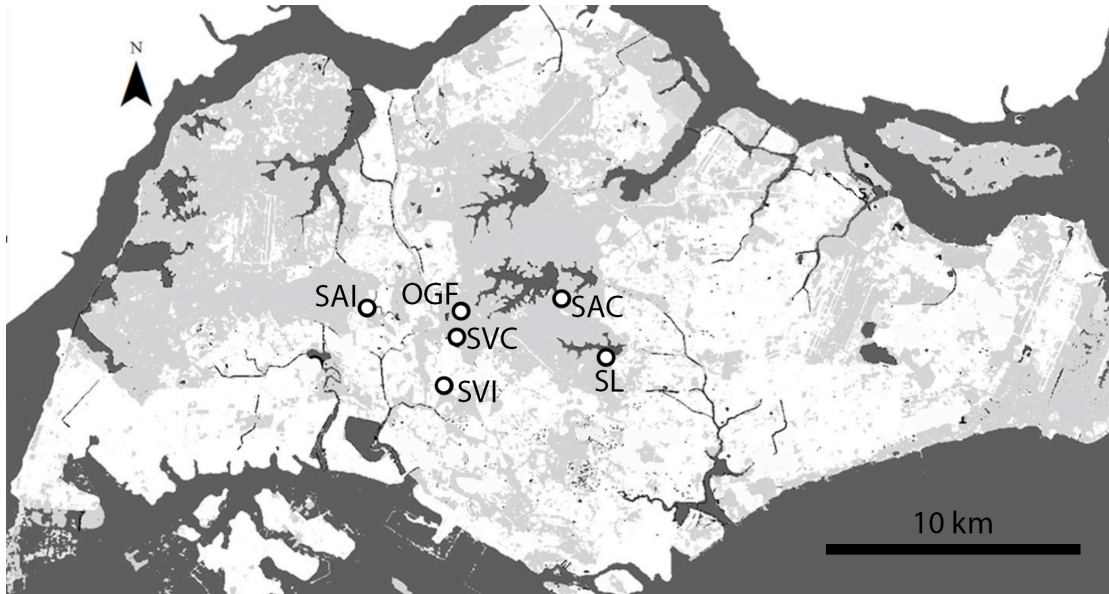


Fig. 1. Map of Singapore showing the location of each transect. Urban areas on the map are white, and parks and forests are grey (Zhang and Evans in press).

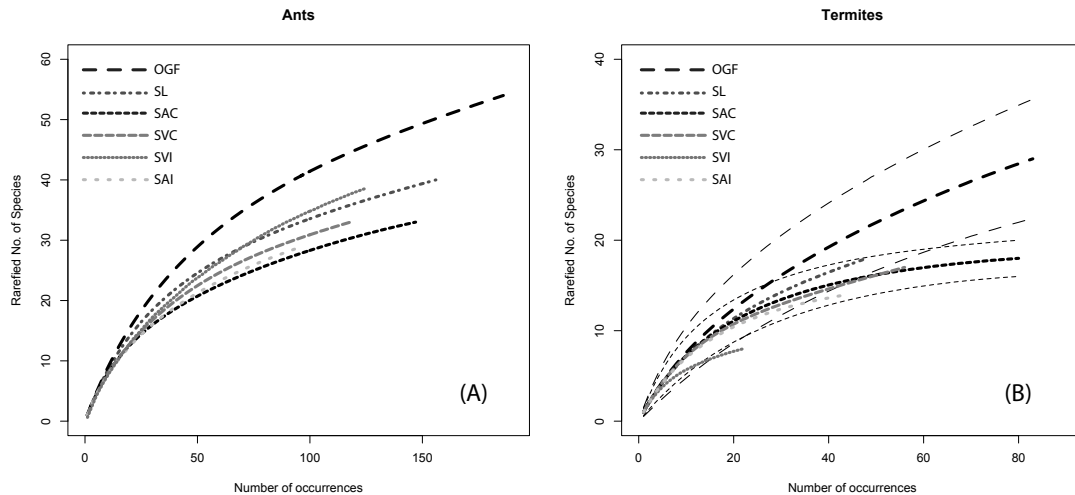


Fig. 2. Rarefaction curves calculated with Mao-Tau method for (A) ant and (B) termite assemblages. OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest fragment, SAI: secondary forest on abandoned agricultural land in isolated forest fragment. 95 % confidence interval calculated with Mao-Tau method (Colwell et al. 2004), showed in light stroke, indicated that SAC and OGF were significantly different for termites. Other comparisons did not significantly differ and confidence intervals are not shown. The three curves represented for termites of SAC and OGF are the rarefaction curves and the 95% confidence intervals.

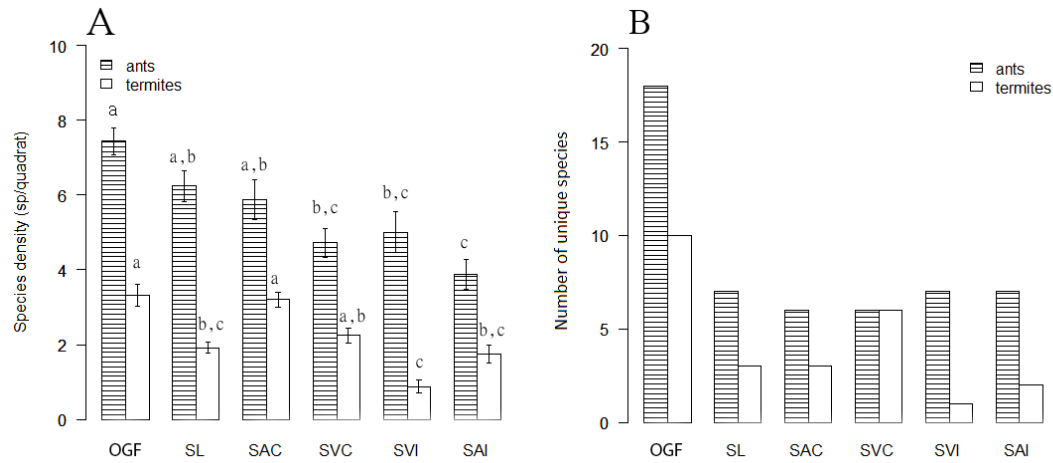


Fig. 3. (A) Species density, measured as the number of species per trap (ants) and quadrat (termites), and (B) number of unique species, species only found in one site, for ant and termites. OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest fragment, SAI: secondary forest on abandoned agricultural land in isolated forest fragment. Different letters indicate significant differences ($p < 0.05$).

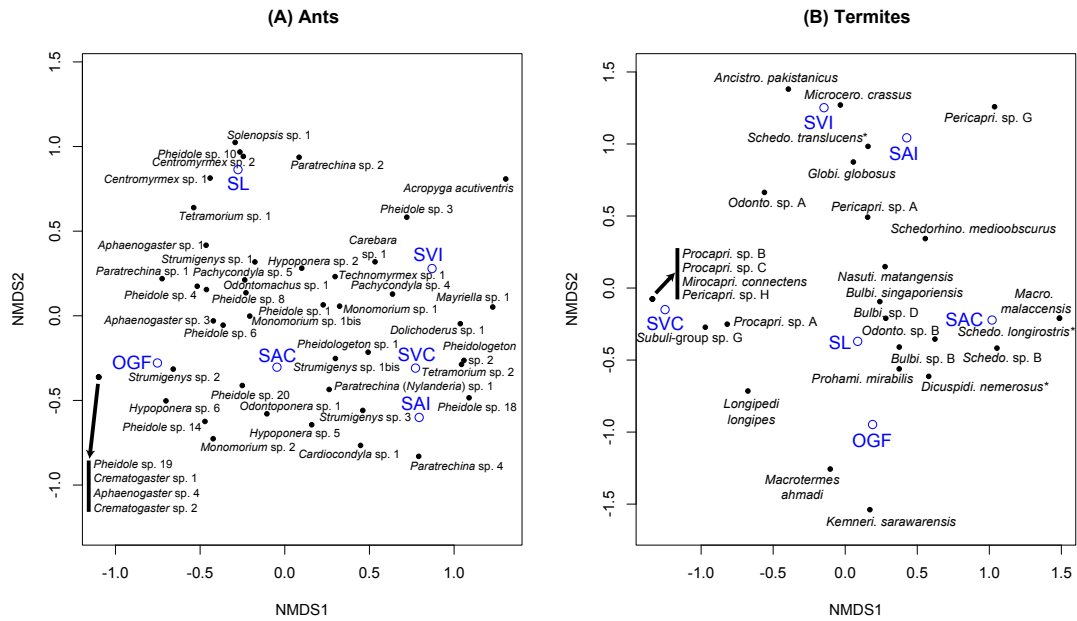


Fig. 4. Non-metric multidimensional scaling of (A) ant and (B) termite assemblages computed on species density data for each site. OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest, SAI: secondary forest on abandoned agricultural land in isolated forest fragment. Black points represent ant and termite species. * indicate species for which identification is uncertain.

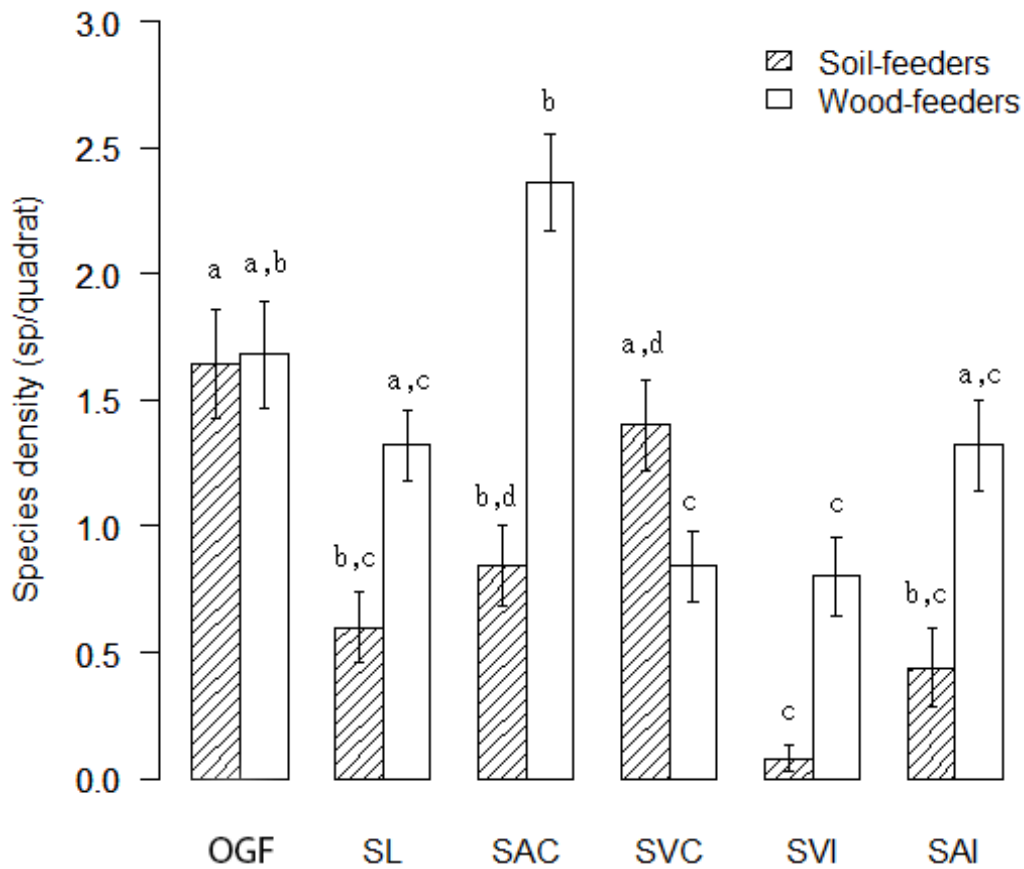


Fig. 5. Species density \pm SE (species per quadrat) of termite feeding-groups (soil- and wood-feeders) among sites. OGF: old growth forest; SL: selectively logged forest; SAC: secondary forest on abandoned agricultural land in continuous forest patch, SVC: secondary forest on abandoned village land in continuous forest fragment, SVI: secondary forest on abandoned village land in isolated forest fragment, SAI: secondary forest on abandoned agricultural land in isolated forest fragment. Different letters indicate significant differences ($p < 0.05$).