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Research

The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants

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South East Asia is widely regarded as a centre of threatened biodiversity owing to extensive logging and forest conversion to agriculture. In particular, forests degraded by repeated rounds of intensive logging are viewed as having little conservation value and are afforded meagre protection from conversion to oil palm. Here, we determine the biological value of such heavily degraded forests by comparing leaf-litter ant communities in unlogged (natural) and twice-logged forests in Sabah, Borneo. We accounted for impacts of logging on habitat heterogeneity by comparing species richness and composition at four nested spatial scales, and examining how species richness was partitioned across the landscape in each habitat. We found that twice-logged forest had fewer species occurrences, lower species richness at small spatial scales and altered species composition compared with natural forests. However, over 80 per cent of species found in unlogged forest were detected within twice-logged forest. Moreover, greater species turnover among sites in twice-logged forest resulted in identical species richness between habitats at the largest spatial scale. While two intensive logging cycles have negative impacts on ant communities, these degraded forests clearly provide important habitat for numerous species and preventing their conversion to oil palm and other crops should be a conservation priority.

Keywords: selective logging; secondary forest; Sundaland; diversity partitioning; scale-dependence; habitat heterogeneity

1. INTRODUCTION

South East Asia is a global centre of threatened biodiversity [1,2] and experiences some of the highest rates of deforestation and timber extraction in the tropics [3,4]. Most of the remaining forest in the region is designated for selective logging [5], but intensive logging reduces future timber harvests [6] and forests degraded in this way are then highly susceptible to conversion to oil palm plantations. Oil palm expansion is now the principal driver of lowland deforestation in the region [7] but plantations support only a small fraction of the species found in rainforests [8–11]. South East Asian biodiversity is thus critically dependent on rainforest protection, hence the sustainable management of large expanses of production forests is increasingly considered integral to regional conservation strategies [12–14].

Selective logging involves harvesting large-diameter trees of commercially valuable species. Previous studies from South East Asia and elsewhere indicate that one round of such logging has limited effects on species richness across a wide range of taxa, leading to a developing consensus that logged forests retain much of their value for biodiversity [13,15,16]. Selective logging was originally envisaged to allow re-harvesting at intervals of up to 70 years [17]. However, throughout South East Asia, continued timber production is increasingly dependent upon a second round of logging [6] in which most large- and medium-diameter trees remaining after the first logging rotation may be harvested less

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than 20 years later [18]. Such a rapid second harvest increases the probability that an area will be classified as degraded and considered for conversion to oil palm [7,14]. Consequently, there is an urgent need to consider the biodiversity value of rainforest that has undergone a second rotation of logging [19,20].

Forests recovering from logging typically have fewer areas of dense shade, fewer open gaps and a less heterogeneous vegetation structure than unlogged forest [21–23]. At larger spatial scales, however, the volume of timber extracted and the damage caused to residual trees vary considerably [24]. Logged landscapes thus form a mosaic of patches affected by different intensities of disturbance, and this artificial heterogeneity may alter the relationship between species richness and spatial scale [25,26]. Species richness in a landscape (γ-diversity) is related to the species composition within areas of the landscape (α-diversity) and the difference in species composition between those areas (β-diversity; [27,28]). Impacts of logging on landscape-scale diversity could therefore result from changes in both α- and β-diversities. Accordingly, there is a need to consider how logging disturbance affects communities at multiple spatial scales [29], particularly as the effects of repeated intensive logging on habitat heterogeneity are unknown [30].

Forest degradation also affects individual species differently and distinguishing the biological attributes of vulnerable and resistant species is an important theme in conservation biology [31,32], particularly given the potential impact of systematic changes in species composition on ecosystem functioning [33]. Body size is an important determinant of the functional impact of a species, because it influences resource exploitation and correlates with several other ecological and life-history traits ([34,35] and references therein). However, while the role of body size in determining sensitivity to disturbance is well-recorded for vertebrate species [36], few studies have provided such information for invertebrates [37,38].

Here, we examine the effects of a second cycle of logging on terrestrial leaf-litter ants, which attain exceptional densities and species richness in rainforests [39] and play keystone roles in nutrient cycling [40,41], as predators [42] and as seed dispersers [43,44]. Despite their sensitivity to soil compaction [45], leaf-litter ants are only modestly affected by a single round of selective logging [13]. We compare species richness between unlogged and twice-logged forest at several spatial scales and use multiplicative partitioning [46–48] to compare the contribution of each scale to overall species richness in each type of forest. We then determine whether community composition differs between unlogged and twice-logged forests, and we examine whether the body sizes of species influence their responses to repeated logging.

2. METHODS

(a) *Study area and logging history*

Our study area is one of the largest and most biologically important areas of forest in South East Asia [12]: the 1 million hectare Yayasan Sabah (YS) logging concession in northeast Borneo (4°58′ N, 117°48′ E). These lowland forests are numerically dominated by large trees of the family Dipterocarpaceae [17], which are valuable timber species [49]. The area is typical of the moist tropics and experiences relatively little monthly variation in climate with a mean annual rainfall of 2700 mm and temperature of 27°C [50].

The Ulu Segama-Malua Forest Reserve (US-MFR) comprises 238 000 ha of production forest within the YS concession. Timber extraction in the US-MFR during the first logging cycle (1976–1991) followed a modified uniform system, with all stems of greater than 60 cm diameter at breast height (d.b.h.) removed using tractors and high lead cables [17], resulting in very high extraction rates ($>160\ \mathrm{m^3\ ha^{-1}}$ in some cases [50]). The area is currently undergoing a second logging rotation after a very brief regeneration period of 15–25 years [18], in contrast to the 70 year cycle originally proposed for Sabah [17]. During the second rotation, 141 000 ha (approx. 60%) of the US-MFR was relogged from 2001 to 2007 using the same extraction methods as during the first logging cycle. However, the minimum diameter of trees removed was reduced to 40 cm d.b.h. and harvests reached levels of $72\ \mathrm{m^3\ ha^{-1}}$ [18]. The US-MFR is contiguous with the unlogged forests of the Danum Valley Conservation Area and Palum Tambun Watershed Reserve (45 200 ha), providing a rare opportunity for comparison between unlogged and repeatedly logged rainforests.

(b) *Sampling*

Fieldwork took place between May and September 2007–2009, corresponding with the drier season each year. Twelve sites separated by at least 1.5 km were established across the unlogged and twice-logged forests (six sites in each type of forest; figure 1), with each site comprising two 150 m line transects separated by 500–800 m. All sites were at least 500 m from the nearest boundary with a different type of forest (natural, once-logged or twice-logged) and all transects started a minimum of 50 m from the nearest logging track. Ants were sampled from seven census points spaced at 25 m intervals on alternate sides of each transect (84 points in each type of forest). Each sampling point was considered independent, because the foraging range of most leaf-litter ant species is no greater than 5 m [51]. There is little annual variation in ant communities in Bornean rainforests, even between climatically distinct El Niño and La Niña years [52], and the order in which transects were sampled was also rotated between forest types to minimize any temporal effects.

Leaf litter and loose topsoil were collected from four $0.25\ \mathrm{m^2}$ quadrats positioned 0.5 m from each census point. Material was sieved (mesh $= 1\ \mathrm{cm^2}$) to remove larger debris and combined into one sample per point. Samples were then emptied into mesh bags and hung inside mini-Winkler extractors in the shade for 4 days [53], after which minor workers were stored in 95 per cent alcohol, identified to genus using online keys [54] and pre-sorted to morphospecies based on external characteristics. Where possible, morphospecies were assigned species names using published keys, the Antbase online image

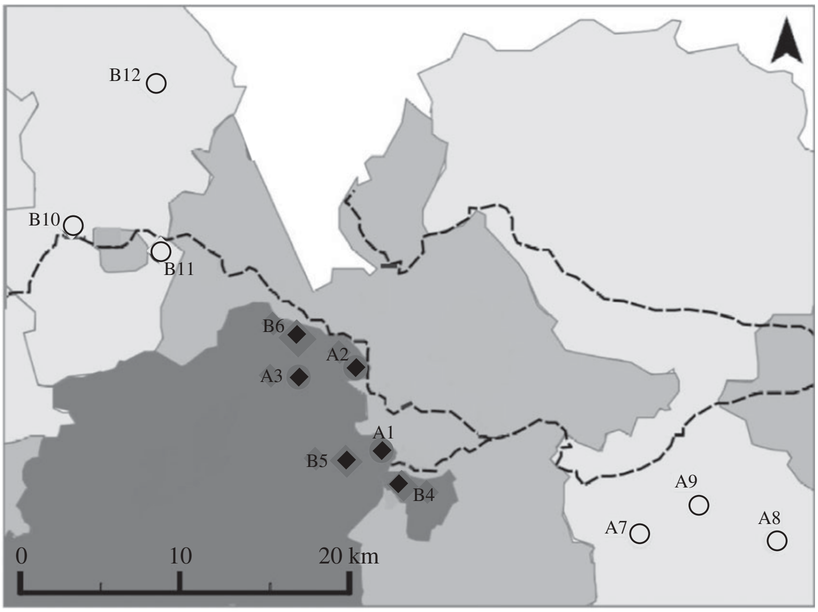

Figure 1. Map of study sites. Dark grey, unlogged forest; intermediate grey, once-logged forest; pale grey, twice-logged forest; white areas, oil palm plantations outside the Yayasan Sabah concession. Dashed lines are logging roads. Filled symbols are sampling sites in unlogged forest, open symbols in twice-logged forest. Sites are arranged into two groups (A and B), and within each group, the average pair-wise distances between sites in unlogged and twice-logged forests are approximately equal.

resource [55] and reference collections at the Natural History Museum (London) and Borneensis Collection (Universiti Malaysia Sabah). Voucher specimens of each species and morphospecies are housed at the Forest Research Centre, Sabah. The Winkler method is unreliable when the leaf litter and soil are damp, and so we did not sample for 2 days following any heavy rainfall [52].

We determined the dry mass of every species recorded on at least 12 occasions in unlogged forest (i.e. sampled at least once per transect on average). The mean mass of an individual was estimated from the total mass of at least five randomly selected minor workers weighed to the nearest 0.001 mg using a microbalance (Sartorius ME5, UK).

(c) *Data analysis*

(i) *Species richness and spatial scale*

The presence or absence of a species at each sampling point was recorded, giving a measure of species occurrence. Patterns of species richness were compared between forest types using sample-based rarefaction curves with 95% CI, constructed in EstimateS v. 8.0 (University of Connecticut, Storrs, CT, USA) [56]. Species richness is highly sensitive to sample size and even though sampling effort was standardized, differences in total occurrences among forest types could influence the number of species recorded. Consequently, accumulation curves were standardized by the number of ant occurrences in each forest [57].

To estimate the likely size of the species pool in each forest type and assess the completeness of our faunal surveys, we calculated the mean of six commonly used species richness estimators (ICE, CHAO2, JACK1, JACK2, MM Mean, Bootstrap) [51,58]. Within each forest, species richness was also determined at three scales (census point, transect and site) and we then used general linear models (GLMs) in SPSS v.16.0 to compare species richness between unlogged and twice-logged forests at each scale.

We also used diversity partitioning to assess the contributions of species richness within sampling units (α-diversity) and of differentiation in species composition between sampling units (β-diversity) to the overall species richness within each forest (γ-diversity). Following Jost *et al.* [48], we partitioned species richness using a multiplicative framework, in which $\gamma = \alpha \times \beta$. We assessed β-diversity at three spatial scales, such that overall γ-diversity within each forest was expressed as:

$$\gamma = \alpha_1 \times \beta_1 \times \beta_2 \times \beta_3,$$

where α_1 denotes species richness within census points, β_1, β-diversity between points within transects, β_2, β-diversity between transects within sites and β_3, β-diversity between sites within each type of forest. We then assessed whether logging influenced the turnover in species composition between sampling units, by comparing β-diversity at each spatial scale between unlogged and twice-logged forest. To gauge the effects of rare species on our conclusions, we also repeated this analysis with singletons and singletons + doubletons excluded from the data.

Logistical constraints meant that sampling sites in unlogged forest were, on average, closer together than those in logged forest. Consequently, a lower species turnover between sites (β_3) in unlogged forest could have been due to greater spatial autocorrelation among sites. Accordingly, we divided the sampling sites in unlogged and twice-logged forest into two groups (three sites per forest in each group) such that the spatial structure of unlogged and twice-logged forest sites was similar within each group (figure 1), and repeated our analyses for each dataset.

Table 1. Number of ant occurrences and the observed and estimated species richness of ants at different spatial scales in unlogged and twice-logged rainforests in northern Borneo. Estimated species richness is the mean of six presence–absence estimators (see text for details). Means are ±1 s.e.

	unlogged	twice-logged	F	p
number of occurrences	1909	1495	—	—
observed number of species	196	196	—	—
estimated species pool	243.7	249.3	—	—
mean no. species per site	100 ± 2.4	87.7 ± 3.1	9.7	0.011
mean no. species per transect	71.7 ± 2.4	60.8 ± 2.4	10.1	0.004
mean no. species per metre square	22.7 ± 0.7	17.8 ± 0.7	25.5	<0.001

(ii) *Species composition and uniqueness*

To compare ant communities between unlogged and twice-logged forests, occurrence data for each species were first converted into a proportion of the total number of occurrences per site, thereby accounting for differences among sites in the total number of ant occurrences. Ordination of sites according to species similarity (Bray–Curtis index) [27] was then achieved using non-metric multi-dimensional scaling [59] in CAP v. 3.1 (PISCES Conservation Ltd, Oxford, UK). We then used an analysis of similarity (ANOSIM), which is a non-parametric permutations test, to test for significant differences in patterns of species occurrence between unlogged and logged forest. We conducted these analyses on the overall dataset with pair-wise comparisons for the two subsets of sites with similar spatial structure (see above).

The number of species unique to unlogged forest, and the number of species found in both unlogged and twice-logged forests give an indication of the conservation value of each type of forest. These measures are particularly valuable when sampling taxa for which the threat status of individual species is unknown [60], as is the case for Bornean ants. However, rare species may, by chance, have been sampled only in one or other type of forest. Thus, following Barlow *et al.* [60], we investigated how the number of species unique to unlogged forest changed with the sequential removal from the dataset of species from increasing occurrence classes up to six occurrences in total. For each reduced dataset, we then calculated the number of species unique to unlogged forest, expressed both as a percentage of the total number of species across both types of forest and of the total number of species in unlogged forest.

(iii) *Body size and sensitivity to disturbance*

We used GLMs to examine whether differences in species occurrence between unlogged and logged forest were related to body size. The limited phylogenetic information for South East Asian ant species precluded the use of phylogenetic contrasts or related statistical techniques [61] to control for phylogenetic non-independence. As an alternative, we included subfamily as a fixed effect in our analyses, following the study of Benedick *et al.* [38].

We also used GLMs with binomial error and a logit link to identify species that had significantly fewer occurrences in logged forest, and then to test whether or not the body masses of species that declined differed significantly from those of species that did not decline. These analyses were conducted for all species, and for the most common subfamilies (Myrmicinae and Pomerinae). Our dataset of species sampled on at least 12 occasions in unlogged forest contained 52 species from 24 genera and the average number of species per genus was similar for species with significantly fewer occurrences in logged forest (2.3) and those that did not decline significantly (1.6). Any phylogenetic non-independence at the level of genus was thus unlikely to have influenced our comparison between habitats. All analyses were conducted in SPSS v. 16.0.

3. RESULTS

(a) ***Species richness and spatial scale***

We sampled more than 40 000 ants comprising 3404 species occurrences and 229 species (electronic supplementary material, tables S1 and S2). Species richness estimators indicated that we sampled both communities effectively (table 1). There were 22 per cent fewer occurrences in twice-logged forest compared with unlogged forest and species richness in unlogged forest was significantly higher at the levels of census point, transect and site (table 1). However, the relative difference in species richness between forest types decreased with increasing spatial scale (table 1), and at the largest scale sampled there was no difference between unlogged and logged forest in the observed species richness or estimated species pool (table 1 and figure 2).

Multiplicative partitioning indicated that unlogged forest had higher α-diversity than logged forest, balanced to some extent by higher species turnover between sampling units at larger spatial scales in logged forest (table 2). This pattern was robust to the removal of singletons and doubletons, although γ-diversity tended to decline to a greater degree in logged forest when these occasional species were excluded, and when controlling for possible spatial autocorrelation (electronic supplementary material, table S3).

(b) ***Species composition and uniqueness***

The relative abundances of species shifted following logging, with the five most common species in unlogged forest accounting for a greater proportion of occurrences in logged forest, but with many intermediate and rarer species declining in relative incidence (figure 3). This was reflected in significant

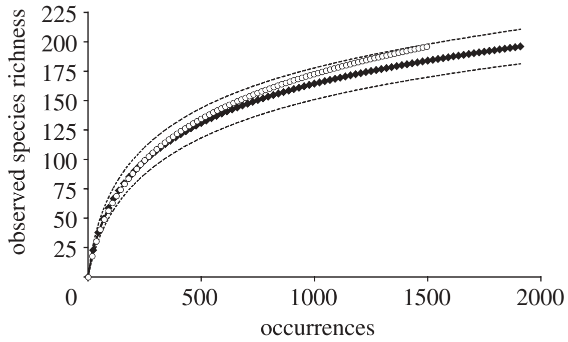

Figure 2. Species accumulation curves for leaf-litter ants in unlogged and twice-logged forests, with 95% CI shown for unlogged forest (dotted lines). Filled diamonds, unlogged; open circles, twice-logged.

Table 2. Multiplicative partitioning of species richness in unlogged and twice-logged forests. α_1, average number of species per census point; β_1, species turnover between census points within transects; β_2, turnover between transects within sites; β_3, turnover between sites in each forest; and γ, total species richness within each forest; $\gamma = \alpha_1 \times \beta_1 \times \beta_2 \times \beta_3$.

	unlogged	twice-logged
α_1	22.73	17.80
β_1	3.15	3.42
β_2	1.40	1.44
β_3	1.96	2.24
γ	196	196

differences between habitats in the patterns of species composition (figure 4; ANOSIM, $r = 0.34$, $p = 0.001$). Pair-wise comparisons of unlogged and logged forest communities within each of the two groups of sites that had similar spatial structure (figure 1) gave qualitatively identical results (figure 4; group A, $r = 0.48$; group B, $r = 0.30$, both $p < 0.05$). Repeatedly logged sites also displayed greater heterogeneity in composition, with communities at some sites similar to those in unlogged forest, but others very different (figure 4).

We found that 15 per cent (35 species) of the total species pool was unique to unlogged forest, rising to 17 per cent when expressed as a proportion of the total number of species sampled in unlogged forest (figure 5). Singletons and doubletons accounted for 27 per cent and 9 per cent, respectively, of species in unlogged forest, and 30 per cent and 13 per cent, respectively, of species in logged forest. When singletons and singletons + doubletons were sequentially removed from both habitats, 22 per cent and 30 per cent, respectively, of the species found in unlogged forest were detected only in that habitat. Removal of higher occurrence classes then had only a negligible effect on the proportion of species unique to unlogged forest (figure 5).

(c) *Body size and sensitivity to disturbance*

We sampled 52 species on at least 12 occasions (i.e. at least once per transect on average) in unlogged forest. Of these, 25 species had significantly fewer occurrences in logged forest, 26 species did not differ in occurrences between habitats and one species had more occurrences in logged forest (electronic supplementary material, table S1). All species that declined significantly were still present in logged forest, but their combined total number of occurrences was halved (from 709 to 346).

Among the 52 species that were censused reliably ($n \geq 12$) in unlogged forest, there was no relationship between body mass and change in occurrence ($p > 0.2$). Similarly, the body mass of species that declined significantly did not differ from that of species that increased or showed no change in the number of occurrences (all species, $p > 0.1$; Ponerinae, $p > 0.5$). However, within the Myrmicinae, species that declined were significantly lighter than species that did not decline ($\chi^2 = 4.5$, $p = 0.034$).

4. DISCUSSION

Repeatedly logged rainforest retained similar species richness to unlogged forest (table 1), with more than 80 per cent of the ant species sampled in unlogged forest also detected after two intensive logging cycles. This contrasts markedly with the oil palm plantations that are rapidly replacing logged forests across Malaysia and Indonesia [7], and that support as few as 5–13 per cent of the leaf-litter ant species found in unlogged forest [10,62]. Nonetheless, the proportion of the species found in unlogged forest that were also detected in repeatedly logged forest was approximately 10 per cent lower than estimated in comparisons between unlogged and once-logged forests (shared species: ants = 95%; multiple taxa = 92%; [13]). Coupled with significant reductions in species richness at smaller spatial scales and a 20 per cent decrease in species occurrences (table 1), these data suggest that intensive relogging after only a short period of regeneration has a stronger adverse effect on biodiversity than a single round of logging [13,15,18].

Terrestrial arthropods are sensitive to soil compaction and changes in microclimate associated with anthropogenic disturbance [45,52,63]. It is therefore probable that a second intensive logging rotation has increased the proportion of forest unsuitable for typical rainforest ants, leading to substantial reductions in ant populations (table 1 and electronic supplementary material, table S1). Importantly, these declines are apparently offset by areas within the logged forest matrix that have similar species composition to unlogged forest and that are presumably less heavily disturbed (figure 4). As with once-logged forest [26], large tracts of twice-logged habitat may therefore represent a heterogeneous matrix and encompass regions that vary considerably in their degree of disturbance. Our analysis of diversity partitioning also supports the argument that lower α-diversity in logged forest is counterbalanced by higher β-diversity at larger spatial scales (table 2; [26]). These results highlight the importance of considering each component of species richness at multiple spatial scales when comparing habitats [28–30]. The differences in α- and β-diversities between unlogged and twice-logged

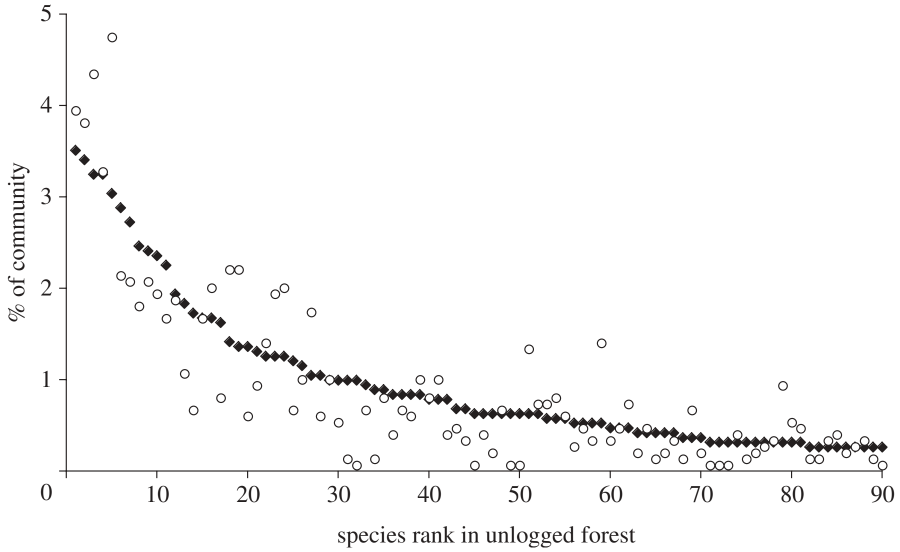

Figure 3. Percentage of leaf-litter ant species occurrences in unlogged and twice-logged forests comprising the 90 most commonly sampled species in unlogged forest. Filled diamonds, unlogged; open circles, twice-logged.

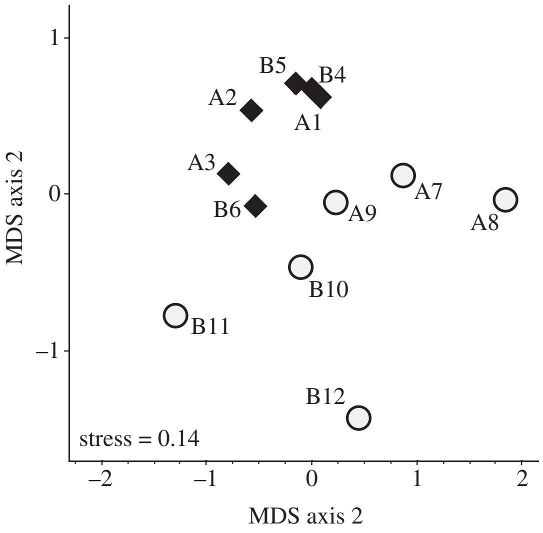

Figure 4. Multi-dimensional scaling (MDS) plots for sites in unlogged and twice-logged forests, based on the proportion of the total number of occurrences of leaf-litter ant species at each site. Sites closer together have more similar ant assemblages. Sites are arranged into two groups (A and B) as described in figure 1. Filled diamonds, unlogged; filled circles, twice-logged.

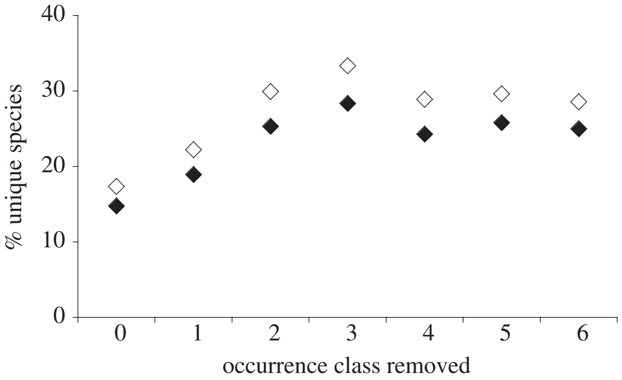

Figure 5. The percentage of leaf-litter ant species unique to unlogged forest following sequential removal from the data of increasing occurrence classes. Uniqueness is expressed as proportions of the entire species pool (filled diamonds) and of the species recorded in unlogged forest (open diamonds).

forests also suggest that habitat fragmentation might affect each forest type differently, indicating that a larger fragment of twice-logged forest may be necessary to support the same number of species found in a fragment of unlogged forest.

The proportion of species unique to unlogged forest increased considerably when singletons and doubletons were excluded from the data and when species not found in unlogged forest were discounted (figure 5). This supports the suggestion that such occasional species need to be properly and transparently accounted for when assessing biodiversity uniqueness [60]. While some of these infrequently sampled species might represent viable populations of inherently rare species, many are likely to be species that are censused unreliably by Winkler traps (e.g. singletons of multiple *Camponotus* spp., which are probably arboreal), are non-forest dwellers (e.g. *Anoplolepis gracilipes* in twice-logged forest), or are not viable populations. The upper estimate of approximately 30 per cent of unlogged forest species unique to that habitat (figure 5) could therefore be a more realistic assessment of the impact of repeated logging on conservation value. Nonetheless, in the regional context of increasing use of land for oil palm plantations, both unlogged and twice-logged forests are exceptionally biodiverse [8,9].

Almost half the species encountered commonly in unlogged forest were significantly less abundant in twice-logged forest. Such declines have the potential to exert secondary effects on ecosystem functioning, particularly if species loss is biased with respect to ecologically important characters [64]. Across the ant community, body size did not determine responses to disturbance. This contrasts with patterns in vertebrates [36] and suggests that logging may have limited impacts on functional effects that are correlated with ant body size. However, in one subfamily—the

Myrmicinae—species that declined were significantly lighter. This may be a consequence of altered microclimate, as smaller ant species tend to be more sensitive to hotter, drier conditions [65] such as those found in degraded forests [52]. As the Myrmicinae are important seed dispersal agents [44,66], the loss of small species could lead to shifts in plant community structure.

The only previous published study (Edwards *et al.* [18]) to investigate the effects of multiple logging rotations on biodiversity in South East Asia found that many of the species of birds and dung beetles recorded in unlogged forest declined in the wake of a second round of logging. Together with the results of the current study, these data suggest that such declines are likely to have occurred across a broad range of taxa. Given predictions that most of Borneo's forest outside of protected areas will soon have been logged at least once [22], and consequently that continued timber production will depend upon repeated logging of these areas [6], there is now a pressing need for long-term investigations of biodiversity recovery and potential extinction time-lags in repeatedly logged forest. We also suggest that urgent consideration should be given to alternative approaches to periodic logging that may prove less detrimental to biodiversity [67,68]. In particular, given the significant biodiversity costs and other possible long-term problems linked to increased risk of fires, heightened tree mortality and reduced capacity for regeneration owing to smothering with bamboo and lianas [69,70], a strong case can be made against allowing early re-entry into once-logged forests.

Despite these negative impacts, it is clear that a high proportion of the leaf-litter ant (table 1), bird and dung beetle faunas [18], and presumably other taxa [13,71], do persist in forests that have undergone a recent second round of logging and are now highly degraded in structure. Any coherent approach to South East Asian conservation should therefore recognize that even heavily degraded forests retain high biodiversity value [14]. The ability of many species to persist in such forests, presumably in patches of relatively undamaged vegetation, reduces their risk of extinction and indicates that twice-logged forests can provide important habitat at the meta-population level. Moreover, these degraded forests have far higher species richness than oil palm [9], but face ongoing and large-scale conversion to plantations. Preventing production forests from being converted to oil palm and other crops should therefore be an urgent priority of policy makers and conservationists in South East Asia.

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