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Reduced-impact logging and biodiversity conservation: a case study from Borneo

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Abstract. A key driver of rain forest degradation is rampant commercial logging. Reduced-impact logging (RIL) techniques dramatically reduce residual damage to vegetation and soils, and they enhance the long-term economic viability of timber operations when compared to conventionally managed logging enterprises. Consequently, the application of RIL is increasing across the tropics, yet our knowledge of the potential for RIL also to reduce the negative impacts of logging on biodiversity is minimal. We compare the impacts of RIL on birds, leaf-litter ants, and dung beetles during a second logging rotation in Sabah, Borneo, with the impacts of conventional logging (CL) as well as with primary (unlogged) forest. Our study took place 1–8 years after the cessation of logging. The species richness and composition of RIL vs. CL forests were very similar for each taxonomic group. Both RIL and CL differed significantly from unlogged forests in terms of bird and ant species composition (although both retained a large number of the species found in unlogged forests), whereas the composition of dung beetle communities did not differ significantly among forest types. Our results show little difference in biodiversity between RIL and CL over the short term. However, biodiversity benefits from RIL may accrue over longer time periods after the cessation of logging. We highlight a severe lack of studies investigating this possibility. Moreover, if RIL increases the economic value of selectively logged forests (e.g., via REDD+, a United Nations program: Reducing Emissions from Deforestation and Forest Degradation in Developing Countries), it could help prevent them from being converted to agricultural plantations, which results in a tremendous loss of biodiversity.

Key words: agricultural conversion; avifauna; degraded lands; oil palm; paper pulp; selective logging; Southeast Asia; sustainable forest management; tropical rain forest.

INTRODUCTION

A key driver of rain forest degradation is rampant commercial logging (Nepstad et al. 1999, Laporte et al. 2007, Asner et al. 2009). Destructive felling and log extraction techniques, liberal harvesting limits, and rapid rotations are causing massive disruption to the structure, carbon stores, and long-term timber yields of natural forests across huge areas of the tropics. Some 403 million hectares of tropical forest are officially designated for timber production (Blaser et al. 2011), while the rate of logging is about 20 times the rate of forest clearance (Asner et al. 2009). Consequently, timber companies are under increasing pressure to adopt logging practices that are less detrimental to forest structure and carbon storage, and that provide economically viable timber harvests over longer time frames (e.g., Putz et al. 2008, Blaser et al. 2011).

Such practices fall under the rubric of "reduced-impact logging" (RIL), which proponents argue can improve management of timber concessions to produce a win–win situation for timber companies and forest conservation. A variety of activities are grouped under the umbrella of RIL, including: (1) pre-felling inventories (Comprehensive Harvesting Plan) and vine cutting; (2) the use of crews trained in directional felling; (3) limits on the number and size of skid trails, logging roads, and stumping grounds (see Plate 1); (4) restrictions on the number, size, or types of trees that can be felled; and (5) post-felling closure operations to remove blockages in streams, and so forth (Pinard et al. 1995, Dykstra and Elias 2003). Although RIL techniques do not directly equate with the long-term economic viability

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of timber operations, their application does makes significant strides toward that goal.

RIL results in a sharp reduction of residual damage to the forest (Johns et al. 1996, Pinard and Putz 1996, Bertault and Sist 1997, Pereira et al. 2002). For instance, in Borneo, 41% of non-harvest trees were crushed by falling lumber and tractors under conventional logging (CL) regimes, but this residual damage was reduced to 17% with the application of RIL (Pinard and Putz 1996). Lower residual damage, often combined with lower initial harvests (e.g., Pinard and Putz 1996, Bertault and Sist 1997), in turn offers longer-term economic benefits via higher future timber yields (Boltz et al. 2001, Valle et al. 2007) and via the sale of spared carbon under REDD+, the United Nations program: Reducing Emissions from Deforestation and Forest Degradation in Developing Countries (Putz et al. 2008). Take-up of RIL is now increasing: it is a prerequisite for timber certification under the Forest Stewardship Council (FSC), which permits sale of timber at a price premium and which currently accounts for 5% of timber produced globally (FSC 2011). Some regions now permit only RIL (e.g., Sabah, Borneo since 1 April 2010).

The application of RIL could also have important implications for the long-term conservation of biodiversity within tropical rain forests. By improving long-term timber yields, RIL could protect logged rain forests from conversion to agriculture; conversion results in a tremendous loss of biodiversity (Cannon et al. 1998, Meijaard and Sheil 2007, Fitzherbert et al. 2008, Edwards et al. 2010) and is also a major contributor to anthropogenic carbon emissions (Danielsen et al. 2008). Furthermore, conventional logging shifts the composition of animal and insect species (Owiunji and Plumptre 1998, Hamer et al. 2003, Peters et al. 2006, Edwards et al. 2011) away from those found in primary forests, as populations of forest interior species decline (e.g., Sekercioglu 2002) while non-forest and edge-dwelling species increase (e.g., Hamer et al. 2003). The reduction in harvest volumes and residual tree mortality with RIL could alleviate these negative impacts of logging on biodiversity, which would be extremely valuable to conservation.

Despite the increasing interest in RIL operations, and the potential knock-on benefits for biodiversity conservation, the impacts of RIL are surprisingly poorly understood; our current knowledge base is insufficient to predict whether RIL has a critical role to play in global conservation efforts. A comprehensive review of the literature identified only 11 previous studies that examined the value of RIL for tropical forest biodiversity (Table 1). All of these studies compared the biodiversity of RIL with that of unlogged, primary forest. To date, however, only two studies have compared the biodiversity of RIL with that of both primary forest *and* of conventionally logged forest (Davis 2000, Foody and Cutler 2003; see Table 1). In a study of dung beetles in Sabah, Borneo, Davis (2000) suggested that RIL compared favorably with CL, because RIL had a higher species richness and contained more primary forest specialist species than CL. RIL, however, compared unfavorably with unlogged forest because the beetle community in RIL was more similar to that of the primary forest edge than the primary forest interior. In contrast, both RIL and CL did not appear to reduce the species richness of trees in Sabah compared to unlogged forests (Foody and Cutler 2003).

Moreover, no study has investigated the impacts of RIL during a second rotation of logging (Table 1), yet this is now a frequent application of RIL. In Southeast Asia (e.g., Malaysia and Indonesia), most of the remaining forest has already been logged once using conventional techniques and is slated to be logged again (e.g., Edwards et al. 2011), increasingly via RIL. In South America and Africa, widespread commercial logging of high-value timber (e.g., mahogany) has again relied mainly upon conventional techniques (Blaser et al. 2011). Because logging typically began later in these regions than in Southeast Asia, some areas of primary forests remain where a first logging rotation using RIL could now be applied. Nevertheless, a second rotation is likely to commence across large areas of conventionally once-logged forest as concessionaires "fish-down-the-value-chain" of timber (e.g., Ahrends et al. 2010). Thus, we believe the most important comparison is between the application of RIL and CL during a second logging rotation in forests that were conventionally logged during the first rotation. Here, we investigate the impacts of a second-logging rotation via RIL and CL, on birds, ants, and dung beetles in Sabah, Malaysian Borneo.

METHODS

Our study is based in the Yayasan Sabah (YS) logging concession in eastern Sabah, Malaysian Borneo. Within the YS concession is a 45 200-ha block of unlogged (primary) lowland dry dipterocarp rain forest in the Danum Valley Conservation Area and Palum Tambun Watershed Reserve; this area is dominated by valuable timber species of the Dipterocarpaceae (Fisher et al. 2011*a*). Contiguous with this primary forest is the 238 000-ha Ulu Segama-Malua Forest Reserve (US-MFR; again part of the YS concession), which was first logged between 1987 and 1991 using a modified uniform system in which all commercial stems >0.6 m diameter were removed (yielding an average of 113 m^3 of timber per hectare; Fisher et al. 2011*b*).

Most of the US-MFR was logged again between 2001 and 2007 using the modified uniform system, but with the minimum tree diameter reduced to >0.4 m (Fisher et al. 2011*a*). Re-logging resulted in a highly degraded forest devoid of emergent trees but abundant in pioneer trees, shrubs and vines, openings in the canopy, and logging roads and dumps (Ancrenaz et al. 2010). The majority of the second rotation was via conventional

Table 1. Studies examining the effect of reduced-impact logging (RIL) on tropical biodiversity.

Study	Location	Logging rotation studied	Timber cut (m^3/ha)	Years since logging	No. sites	Distance to control (km)	Taxa
a) With primary forest controls							
Azevedo-Ramos et al. (2006)	Amazon	first	19	0.5	3	NA	ants, arachnids, birds, mammals
Bicknell and Peres (2010)	Guyana	first	4	0.2–1.5	RIL = 3, UL = 3	4–8	vertebrates†
Castro-Arellano et al. (2009)	Amazon	first	18	2–3	RIL = 2, UL = 2	1–2	bats
Dias et al. (2010)	Amazon	first	15	1–8	RIL = 11, UL = 11	<2.5	fish
Felton et al. (2008)	Bolivia	first	20	1–4	RIL = 12, UL = 12	0–5	birds (PC)
Gerwing and Vidal (2002)	Amazon	first	37‡	6	1	NA	lianas
Presley et al. (2008)	Amazon	first	19	2	RIL = 2, UL = 2	1–2.3	bats
Webb and Peralta (1998)	Costa Rica	first	49	0–4	RIL = 4, UL = 4	<1	trees
Wunderle et al. (2006)	Amazon	first	19	2–4	RIL = 2, UL = 2	0	birds (MN)
b) With primary (UL) and conventionally logged (CL) forest controls							
Davis (2000)	Borneo	first	RIL = 104, CL = 154§	3–4	RIL = 1, UL = 2, CL = 1	>1	dung beetles
Foody and Cutler (2003)	Borneo	first	RIL = 104, CL = 154§	3–4	RIL = 1, UL = 2, CL = 1	2–4	trees
This study	Borneo	second	RIL = 16, CL = 47	1–8	RIL = 3, UL = 3, CL = 3	6–49	ants, birds (PC+MN), dung beetles

Note: NA indicates that the study used before- and after-treatment censuses within a single location.
† Vertebrates were four mammal, one reptile, and 10 bird species (or groups of species).
‡ Extracted from Johns et al. (1996).
§ Extracted from Pinard and Putz (1996).

logging (see Plate 1), but in some areas reduced-impact logging (RIL) was applied. RIL included a Comprehensive Harvesting Plan (in which all trees were inventoried, geo-referenced, and graded as harvestable or not), a limit on the number of tractor extraction trails, directional felling by trained crews, and post-logging surveys before coupes were closed. As a result, the 25 076 ha under RIL had less timber removed (16.0 ± 2.6 m^3/ha, from 3.9 ± 0.6 logs/ha) than the 153 292 ha that was conventionally logged (CL; 46.6 ± 9.2 m^3/ha, from 12.9 ± 2.1 logs/ha) (extracted from data used in Fisher et al. [2011*a*]). Furthermore, of the 4217 skid trails permitted within the RIL area, only 3525 were opened (no records exist for the CL forest). Thus, the US-MFR offers an ideal opportunity to compare RIL with CL as part of the second logging rotation.

Sampling

Fieldwork was conducted from July to October 2007, May to August 2008, May to October 2009, and March to April 2011. We created three widely spaced sampling sites in each of the three forest types (unlogged, RIL, and CL), using a space-for-time substitution as an alternative to following land-use change over decades (Pickett 1989). Within a habitat, sites were located $\geq$3.8 km apart, and between habitats, sites were separated by 11.2–48.5 km. Distances ranged from 15.0 to 21.3 km between CL sites and the nearest primary forest edge, and from 5.7 to 12.7 km between RIL sites and primary forest. However, previous work has revealed no impact of distance from primary forest edge on metrics of biodiversity in these logged forests (Fisher et al. 2011*b*).

Our study taxa were sampled in each of these sites (total $n = 9$), with the exception of dung beetles, which were sampled in two sites per habitat ($n = 6$). Sampling took place 1–8 years after logging, during the relatively dry period of the year. Within each taxon, sampling was rotated between forest types to minimize any temporal effects. Birds, ants, and dung beetles are reliable indicators of patterns of biodiversity in other taxonomic groups (Howard et al. 1998, Schulze et al. 2004, Barlow et al. 2007), are the most cost-effective taxa to sample (Gardner et al. 2008), and provide key ecosystem functions such as predation, seed dispersal, and nutrient recycling (e.g., Nichols et al. 2008).

Avifauna.—We used two sampling techniques: point counts (2008, 2009, 2011) and mist nets (2007, 2008, and 2009). Studies in tropical forests have indicated that bird census points separated by >200 m can be considered to be statistically independent (see Hill and Hamer 2004).

Birds were sampled using unlimited-radius point counts (see Lees and Peres 2006, Edwards et al. 2010, 2011). At each site, 12 count stations were established at 250-m intervals (108 stations in total) along a line transect, and each station was visited for 15 min on three consecutive days between 05:45 and 10:30 hours. A single experienced observer (D. P. Edwards) noted all birds seen and heard during each sampling period (except Apodidae and Hirundinidae, which are difficult to detect and identify within a closed canopy). Unknown vocalizations were recorded using Edirol R-09HR (Roland Edirol, Hamamatsu, Shizuoka, Japan) and Sennheiser ME66 (Sennheiser, Wennebostel, Niedersachsen, Germany) equipment and subsequently were checked against known calls (from xeno-canto; *available online*).[7] Given that many tropical birds show high site fidelity, the final count for a particular species at a station was taken as the highest number of individuals recorded on any of the three visits (following Edwards et al. 2010, 2011). Because we used index counts, it is plausible that the detectability of some species differed between forest types, biasing our results by under- or overestimating the relative abundance of that species. However, in our densely forested and steep environment, meeting the three key assumptions of distance sampling, that (1) all individuals are detected at distance 0 m (our forest is ~75 m tall in places), (2) all individuals are detected before evasive movements are made, and (3) distances are measured accurately, is unlikely (Buckland 2006).

We used mist netting to survey the cryptic understory birds that can be under-sampled by point counts (Blake and Loiselle 2001). At each site, we erected 15 mist nets along two transects positioned 500–800 m apart; nets were opened from 06:00 to 12:00 hours on three consecutive days (4860 mist-net hours in total; for details, see Edwards et al. [2009]). Because the canopy of repeatedly logged forests is lower than in unlogged forests, canopy species are likely to forage lower and be more susceptible to capture in mist nets (Remsen and Good 1996). We therefore restricted our analysis to species that are not considered to be canopy specialists (Edwards et al. 2011).

Leaf-litter ants.—Ants were sampled from seven census points spaced at 25-m intervals on alternate sides of each mist net transect in 2007–2009 (126 points in total; for details, see Woodcock et al. 2011). Each sampling point was considered independent, because the foraging range of most leaf-litter ant species is ≤ 5 m (Brühl et al. 2003), and all conspecific ants from a sampling point were considered to be from the same colony. Leaf litter and loose topsoil were collected from four 0.25-m^2 quadrats positioned 0.5 m from each census point. Material was sieved (1-cm^2 mesh) to remove larger debris and was combined into one sample per point. Samples were hung inside mini-Winkler extractors for four days, after which minor workers were extracted and identified to species or morphospecies based on personal reference collections of P. Woodcock, T. M. Fayle, and N. B. Tawatao. Voucher specimens of each species and morphospecies will be housed at the Forest Research Centre (FRC), Sandakan, Malaysia.

Dung beetles.—We used standardized pitfall traps baited with human dung (Larsen and Forsyth 2005) to sample dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in 2009 and 2011. At two sites within each forest category, we set five traps spaced at 100-m intervals centered on each mist net transect (60 traps in total; for details, see Edwards et al. 2011). Trap spacing should be sufficient for independence among traps (Larsen and Forsyth 2005). Traps were collected every 24 h for four days and were rebaited after two days. Species determinations were made using a reference collection (prepared by T. Larsen) deposited at the FRC.

Data analyses

Species richness and diversity partitioning.—Patterns of overall species richness were compared among forest types using sample-based rarefaction curves with 95% CI, constructed in EstimateS v. 8.2.0 (R. K. Colwell 2009). Species richness is highly sensitive to sample size, so accumulation curves were standardized by the total number of individuals (or ant colonies) sampled in each forest type (Gotelli and Colwell 2001). To estimate the probable species pool in each forest type and assess the completeness of our faunal surveys, we calculated the mean of five commonly used incidence-based species richness estimators (ICE, CHAO2, JACK1, JACK2, and BOOTSTRAP) using EstimateS v. 8.2. To control for any confounding effects of the spatial scale at which data were analyzed (Hill and Hamer 2004), we also compared species richness between forest types at the level of individual sample points (α-diversity), with a random factor of "site," using the lme function in the nlme package in R 2.11.1 (R Development Core Team 2010).

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). Our spatial arrangement of sites is similar across forest types, thus controlling for issues of greater spatial autocorrelation if some sites are more closely arranged. We partitioned species richness using a multiplicative framework in which $\gamma = \alpha \times \beta$ (Jost et al. 2010*a*, *b*). We assessed β-diversity at two spatial scales, such that overall γ-diversity within each forest was expressed as

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

where α_1 is species richness within sample points, β_1 is β-

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[7] http://www.xeno-canto.org/asia

PLATE 1. Re-logging of rain forest is prevalent in Southeast Asia. There is pressure for re-logging to be conducted using "reduced-impact logging" (RIL) techniques, which aim to reduce the amount of residual damage incurred by the forest. One key RIL method is decreasing the number of skid trails, logging roads, and stumping grounds that are cut into the forest. This image is of forest regeneration within a small stumping ground and logging road created during conventional re-logging of the Yayasan Sabah concession, Borneo, in 2001. Photo credit: D. P. Edwards.

diversity between sample points within sites, and β_2 is β-diversity between sites within each type of forest. We then assessed whether RIL influenced the turnover in species composition between sampling units, by comparing β-diversity at each spatial scale between unlogged, CL, and RIL forest.

Species composition.—In order to determine how patterns of species makeup differed among unlogged, RIL, and CL forests, we examined species abundance matrices using the R packages MASS (*available online*)[8] and Vegan (*available online*).[9] Occurrence data for each species were first converted into a proportion of the total number of occurrences (of all species) per site, thereby accounting for differences among sites in the total number of occurrences. Ordination of sites according to species similarity (Bray-Curtis index; Magurran 2004) was then achieved using nonmetric multidimensional scaling (MDS; Clarke and Warwick 2001) in MASS, and we tested for differences among forest types using a permutational multivariate analysis of variance with distance matrices (ADONIS) in Vegan.

The number of species from the unlogged forest species pool that were found in CL and RIL forests gives an indication of the conservation value of each type of forest. These measures are particularly valuable when sampling taxa in which the threat status of individual species is unknown (Barlow et al. 2010), as is the case for Bornean ants and dung beetles. However, rare species may, by chance, have been sampled only in one or another type of forest: Species rarely recorded in unlogged forest might not be reliant on primary habitat, whereas rarely recorded species in logged forest might not represent viable populations. Thus, we also sequentially removed species from the data set of each habitat with abundances of one individual (1), then two individuals (1+2), and then three individuals (1+2+3) to investigate how rarely sampled species affected assessments of the conservation value of our forest types.

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[8] http://cran.r-project.org/web/packages/MASS/index.html

[9] http://CRAN.R-project.org/package=vegan

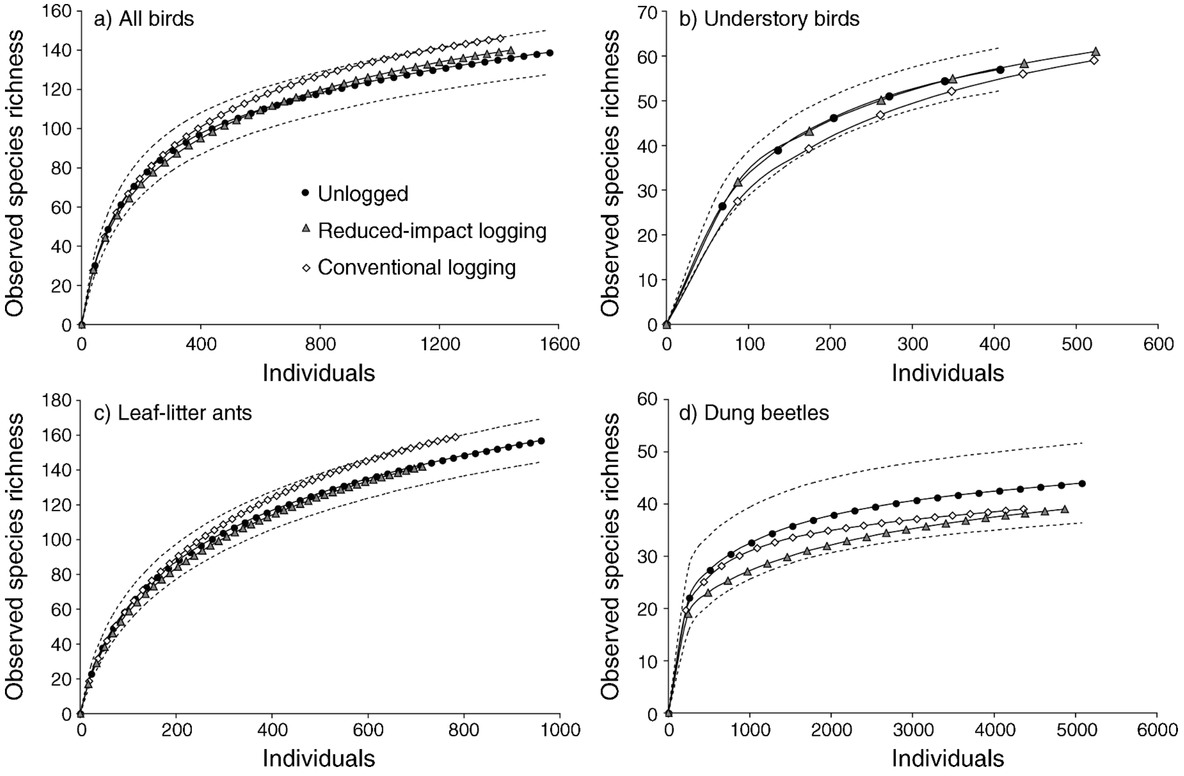

FIG. 1. Observed species richness (number of species), constructed using sample-based rarefaction curves for the three forest types, for (a) all birds, (b) understory birds, (c) leaf-litter ants, and (d) dung beetles. The *x*-axis is scaled to show the number of individuals, and scales differ between panels. Data are for unlogged forest (black circles, with dotted lines showing 95% CI), reduced-impact logged forest (gray triangles), and conventionally logged forest (white diamonds).

RESULTS

Species richness and diversity partitioning

We recorded 4414 individuals of 187 bird species with point counts (herein termed "all birds"), 1453 individuals of 82 bird species with mist netting (herein termed "understory birds"), 2455 colonies of 216 leaf-litter ant species, and 14 307 individuals of 48 dung beetle species. There was no difference in total species richness between unlogged, conventionally logged, and reduced-impact logged forests (Fig. 1, Table 2), with the exception of leaf-litter ants, which showed a decline in richness in RIL forest. Resampling the data with five estimators of species richness suggests that our observed patterns of species richness are reliable, indicating that each of our censuses exhibited >75% completeness (Table 2).

At the scale of individual sampling points, species richness differed between habitats for dung beetles (lme: $F_{2,52} = 6.0$, $P = 0.005$), with RIL ($P = 0.017$) and marginally CL ($P = 0.06$), having lower richness than in unlogged forest, but with no significant difference between RIL and CL ($P = 0.45$) (Table 2). All other sample-level measures of richness did not differ between forest types for each taxonomic group (all $P > 0.1$).

TABLE 2. Impacts of logging on select taxa in Sabah, Borneo, for unlogged forest (UL), conventionally logged forest (CL), and reduced-impact logged forest (RIL).

	All birds			Understory birds			Leaf-litter ants			Dung beetles		
Measurement	UL	CL	RIL	UL	CL	RIL	UL	CL	RIL	UL	CL	RIL
N	1569	1405	1440	407	522	524	960	782	713	5076	4362	4869
S_{obs}	139	146	140	57	59	61	157	159	142	44	39	39
S_{est}	172	171	167	67	72	72	204	202	189	51	45	47
$S_{\mathrm{obs}}/S_{\mathrm{est}}$	0.81	0.85	0.84	0.85	0.82	0.84	0.77	0.79	0.75	0.86	0.87	0.84
S_{obs}/sample	30^{a} (1)	28^{a} (1)	28^{a} (1)	27^{a} (3)	28^{a} (3)	32^{a} (2)	23^{a} (1)	19^{a} (1)	17^{a} (1)	22^{a} (1)	20^{ab} (1)	19^{b} (1)

Notes: Measurements are: N, total abundance (number of individuals or number of ant colonies); S_{obs}, observed species richness; S_{est}, estimated species richness; $S_{\mathrm{obs}}/S_{\mathrm{est}}$, proportion of species detected; and S_{obs}/sample, mean species richness per sample point (with SE in parentheses). Within each taxon, for S_{obs}/sample (the only measurement tested), different superscript letters indicate significant differences at the $P < 0.05$ level.

TABLE 3. Diversity partitioning for all birds, understory birds, leaf-litter ants, and dung beetles in unlogged (UL), conventionally logged (CL), and reduced-impact logged (RIL) forest.

	All birds			Understory birds			Leaf-litter ants			Dung beetles		
Measurement	UL	CL	RIL	UL	CL	RIL	UL	CL	RIL	UL	CL	RIL
α_1	30.4	27.6	28.0	26.5	27.5	31.8	22.9	18.6	17.0	22.1	19.7	19.0
β_1	3.3	3.6	3.5	1.4	1.3	1.3	4.4	4.9	5.0	1.7	1.8	1.7
β_2	1.4	1.5	1.4	1.5	1.6	1.4	1.6	1.8	1.7	1.2	1.1	1.2
γ	139	146	140	57	59	61	157	159	142	44	39	39

Notes: Measurements are: α_1, average number of species per sample point; β_1, species turnover between sample points within sites; β_2, species turnover between sites in each forest; γ, total species richness within each forest. Note that $\gamma = \alpha_1 \times \beta_1 \times \beta_2$. Numbers are rounded to one decimal place.

Diversity partitioning of species richness revealed that the species turnover between sample points (β_1) of all birds and of leaf-litter ants was slightly higher in RIL and CL than in unlogged forest (Table 3). In contrast, β_1 did not differ between habitats for understory birds and dung beetles, while the species turnover between sites (β_2) did not differ between forests types for any taxonomic group (Table 3)

Species composition

Patterns of species composition differed significantly among the forest types for all birds (Fig. 2a; ADONIS: $r^2 = 0.41$, df = 2, $P = 0.005$), understory birds (Fig. 2b; $r^2 = 0.35$, df = 2, $P = 0.02$), and leaf-litter ants (Fig. 2c; $r^2 = 0.33$, df = 2, $P = 0.005$), but not for dung beetles (Fig. 2d; $r^2 = 0.3$, df = 2, $P = 0.69$). In the cases of all birds, understory birds, and leaf-litter ants, pairwise comparisons revealed that RIL and CL forests were significantly different from unlogged forests (all $P < 0.001$), whereas RIL and CL only differed for ants ($P < 0.001$). In the case of all birds and understory birds, the community composition in RIL appeared to be marginally closer to that in unlogged forest than was the case with CL compared to unlogged forest (Fig. 2a, b).

Both RIL and CL forests retained a large number of species found in unlogged forest (range 67–86% with "0" abundance classes removed; Fig. 3). In turn, the sequential removal of rarely recorded species from the

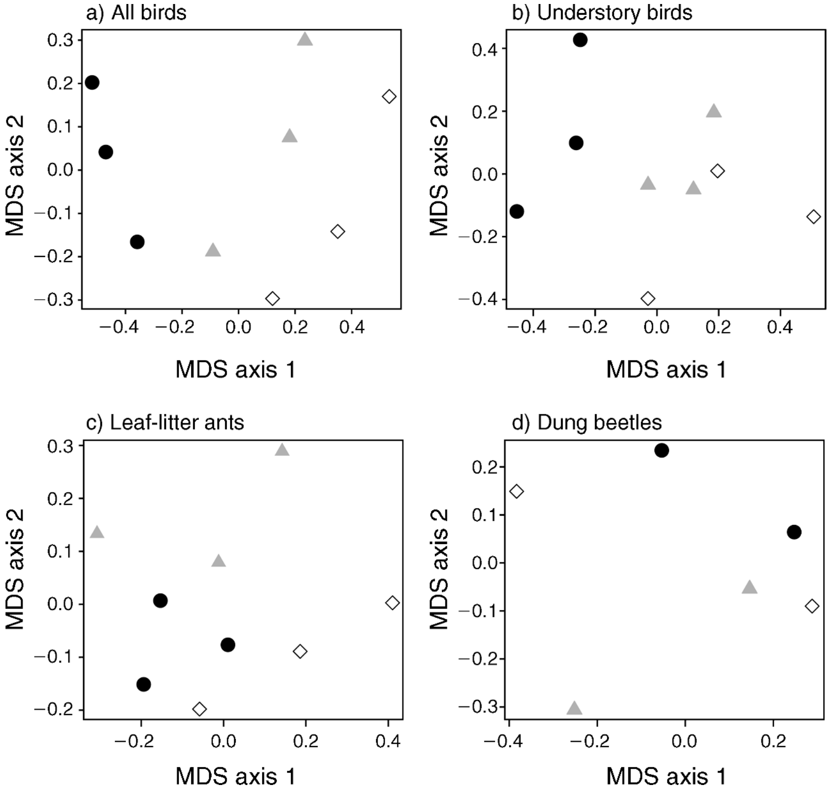

FIG. 2. Nonmetric multidimensional scaling (MDS) ordination of community structure among unlogged (black circles), reduced-impact logged (gray triangles), and conventionally logged (white diamonds) forests for (a) all birds (stress = 4.5), (b) understory birds (stress = 11.2), (c) leaf-litter ants (stress = 9.8), and (d) dung beetles (stress = 1.0).

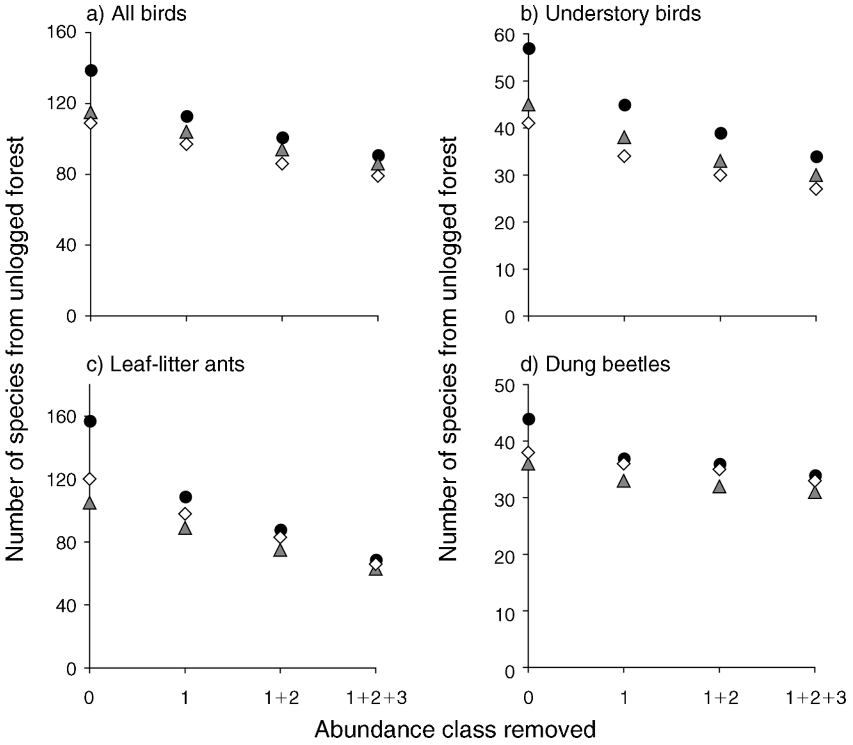

FIG. 3. Richness of unlogged forest species (black circles) within reduced-impact logged (gray triangles) and conventionally logged (white diamonds) forests, following the sequential removal from the data of increasing abundance classes. From the data set of each habitat, species with abundances of one individual (1), then two individuals (1+2), and then three individuals (1+2+3) were removed. This reveals how rarely sampled species affected assessments of the conservation value of our forest types.

data set up to three individuals (or ant colonies) indicated that both RIL and CL forests retained an increasing percentage of unlogged forest species (range 80–97%; Fig. 3). There was, however, no consistent pattern between RIL and CL, with RIL retaining a higher number of bird species, but a lower number of ant and dung beetle species than CL (Fig. 3).

DISCUSSION

The application of reduced-impact logging (RIL) techniques dramatically reduces the residual damage incurred by forests during logging (e.g., Pinard and Putz 1996). Yet the potential for RIL to also reduce the negative effects of logging on biodiversity is very poorly understood (Table 1). Focusing on birds, dung beetles, and leaf-litter ants, we found little evidence that a second round of logging using RIL had a significantly different impact on biodiversity in the near-term compared with conventional logging (CL) techniques. Both forms of logging shifted the composition of species compared to unlogged forests (Fig. 2) and both forms resulted in forests that retained high species richness (Table 2, Figs. 1 and 3). Our results again show that all forms of logging are harmful to some species, but that logged forests nevertheless retain very high levels of biodiversity (Table 1; see Cannon et al. 1998, Owiunji and Plumptre 1998, Sekercioglu 2002, Peters et al. 2006, Berry et al. 2010, Edwards et al. 2011).

The use of RIL during a second round of logging in Southeast Asia does not appear to provide any major benefits to biodiversity when compared with CL, at least in the short term. This supports one of the two previous comparisons of RIL vs. CL from a first logging rotation, which showed that RIL retained a similar species richness of trees to those of unlogged forest and CL (Foody and Cutler 2003), but it contrasts with the other previous comparison, which showed that a first cut using RIL retained species richness and compositions of dung beetles more similar to those of unlogged forest than did CL (Davis 2000). One potential reason for the difference between our study and that of Davis (2000) is that the timber yields during the first logging rotation are so much higher than during the second rotation (e.g., in this study area, first rotation yields from CL are 113 m^3/ha, whereas second rotation yields from RIL are 16.0 m^3/ha and from CL are 46.6 m^3/ha [Fisher et al. 2011*b*]). It is therefore possible that the short-term benefits of RIL to biodiversity may be limited to cases involving the first round of logging of primary forests.

However, there could be as yet undetected benefits of RIL during the second rotation. (1) We focused on forests that were harvested using CL techniques during the first rotation, which has been the globally dominant form of logging of primary forest (Blaser et al. 2011). However, if the first rotation had also been conducted with RIL (e.g., as now often happens in Brazil), then there might have been clearer benefits in the second rotation. (2) The benefits might be more apparent on other continents, where the first rotation via CL typically causes less damage because timber yields are so much lower than in Southeast Asia (Putz et al. 2001). (3) We focused on birds, ants, and dung beetles, but the benefits of RIL could vary between taxonomic groups. Although the groups we chose are considered reasonable indicators of general patterns across taxa (Howard et al. 1998, Schulze et al. 2004, Barlow et al. 2007, Berry et al. 2010), they are not perfect surrogates; land managers and researchers should bear this in mind and strive to consider the impacts on an array of different taxa. In particular, although our taxa are not hunted or collected, groups that do suffer exploitation (e.g., mammals and orchids) could benefit from poorer access in RIL forest with fewer logging tracks and the closure of roads post-logging.

We also emphasize that we do not know how the biodiversity in RIL will respond over longer periods of time. The successional trajectory might be similar between RIL and CL forest, and biodiversity will recover in both forests with time (e.g., Dunn 2004). It is also possible that RIL will accelerate the return of closed-canopy forest, as it does when incorporated into the first rotation (Boltz et al. 2001, Valle et al. 2007), which would benefit species associated with mature forests. Finally, if two rounds of CL result in a loss of forest structure with time (e.g., tree death due to residual damage, extensive growth of vines, or fire; Pinard and Putz 1996, Laurance 2000, Cochrane and Laurance 2002), then there is likely to be an eventual crash in the numbers of forest-dwelling species. If the use of RIL prevents such further degradation of forest structure, then it would be highly beneficial to biodiversity. Understanding the potential for such longer-term benefits remains a vital question, because over 20% of the remaining tropical rain forests were being logged between 2000 and 2005 (Asner et al. 2009), mostly via CL, and because the application of a second logging rotation is becoming more frequent as unlogged forests designated for production are exhausted (Ahrends et al. 2010, Edwards et al. 2011).

Our work highlights an alarming lack of knowledge about the biodiversity implications of RIL. There is an urgent need for more studies spanning a greater range of taxonomic groups and regions (e.g., Africa and Australasia; Table 1), and spanning both the first and the second logging rotations. These studies need two vital components: appropriate controls and a long temporal component. On the control side, there are only three studies that compare the impacts of RIL on biodiversity using both unlogged and CL forest controls (this study, Davis 2000, Foody and Cutler 2003). All other studies solely relied upon unlogged forest controls, which could result in a number of misleading conclusions about the potential value of RIL for biodiversity (Table 1).

On the temporal side, all studies looked at the impacts of RIL within 10 years of timber extraction, and most did so within four years of extraction. Because forest regeneration, faunal recovery, and future timber rotations occur on timescales measured in decades, this is a critical gap in the knowledge. We advocate more studies in areas logged >10 years ago, as well as repeat censuses over longer time frames.

Although there is good evidence for both carbon and timber-stand recovery benefits of RIL compared to conventional logging operations, our results indicate that, from a biodiversity perspective, there is little difference between RIL and CL in the second rotation. However, there might well be undetected future benefits in terms of forest recovery or for different taxonomic groups. Furthermore, there is at least one way in which RIL can contribute substantially to biodiversity protection. If RIL increases the economic value of selectively logged forests (e.g., through carbon payments, higher long-term yields, and timber certification) and thereby prevents such lands from being converted to agricultural plantations, then it is performing an exceedingly valuable service for biodiversity. This is because numerous studies have demonstrated that large tracts of logged forests retain far more forest-dependent species than do agricultural plantations (Barlow et al. 2007, Steffan-Dewenter et al. 2007, Fitzherbert et al. 2008, Edwards et al. 2010). The defense of forests (logged and unlogged) from conversion to croplands is one of the most critical issues facing conservation biologists; if RIL can assist in this task, then the investment of conservation resources—both financial and political—in promoting RIL is amply justified.

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