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Rehabilitation of Logged Rain Forests: Avifaunal Composition, Habitat Structure, and Implications for Biodiversity-Friendly REDD+

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ABSTRACT

The inclusion of carbon stock enhancements under the Reducing Emissions from Deforestation and Forest Degradation (REDD+) framework will likely drive a rapid increase in biosequestration projects that remove carbon from the atmosphere through rehabilitation of degraded primary rain forests. Such projects could also present an important opportunity to reverse losses of biodiversity from degraded rain forests, but concern has recently been expressed that management interventions to increase carbon stocks may conflict with biodiversity conservation. Focusing on a large-scale rain forest rehabilitation project in northern Borneo, we examine: (i) how intensive rehabilitation of selectively logged forests affected patterns of bird community composition and (ii) whether changes in vegetation structure explain observed shifts in avian guild structure and species composition. Bird composition differed between unlogged, naturally regenerating logged, and rehabilitated logged habitats, with the avifauna of rehabilitated forest more similar to that of naturally regenerating forest. Crucially, rehabilitation did not adversely affect either those species that declined after logging or those species that are IUCN Red Listed. Rehabilitation reduced the prevalence of vines and shrubs within regenerating forest, and across all habitats, the abundance and species richness of all birds and of obligate frugivores were positively related to vine prevalence. In contrast, the abundance and richness of frugivore–insectivore generalists and of salliers were negatively related to vines, suggesting that avifaunal responses to forest rehabilitation were attributable to liberation cutting of vines. Management intervention to increase carbon stocks had little adverse effect on avian biodiversity and we therefore argue that rain forest rehabilitation should play a strong role in future REDD+ agreements.

Key words: Asian biodiversity crisis; birds; clean development mechanism; habitat restoration; Kyoto protocol; REDD+; silviculture.

HABITAT LOSS AND DEGRADATION ARE THE MAJOR DRIVERS OF GLOBAL DECLINES IN BIODIVERSITY (Sala *et al.* 2000, Tilman *et al.* 2001, Sodhi *et al.* 2004, Jetz *et al.* 2007). An estimated 5.8 million ha of tropical rain forests were cleared and a further 2.3 million ha degraded each year between 1990 and 1997 (Achard *et al.* 2002), and 60 percent of the remaining forest is now classified as degraded primary forest or as secondary growth on abandoned land (International Tropical Timber Organization [ITTO] 2002). While degraded and secondary forests are depauperate in forest specialist species compared with undisturbed habitat, they nonetheless support surprisingly high levels of biodiversity (Barlow *et al.* 2002, Barlow & Peres 2004, Dunn 2004, Barlow *et al.* 2007, Dent & Wright 2009, Berry *et al.* 2010, Edwards *et al.* 2010b), making their protection an essential part of global conservation strategies (Daily 2001, Dunn 2004, Wright 2005). Yet the conversion of degraded forests to low-biodiversity plantations and other such habitats is ongoing and increasing in rate (Sodhi *et al.* 2004, Koh & Wilcove 2008).

Globally, deforestation results in emissions of 5.6–8.6 Gt of carbon annually, which is supplemented by emissions from forest degradation, and these combine to make the second largest source of atmospheric carbon emissions after the burning of fossil fuels (Glenday 2006, Metz *et al.* 2007). There is thus ample scope for conservationists to argue for the protection of degraded forests using funds aimed at reducing global climate change (Stickler *et al.* 2009, Venter *et al.* 2009, Harvey *et al.* 2010). These arguments typically focus on the Reducing Emissions from Deforestation and Forest Degradation (REDD+) initiatives. REDD+ will eventually permit industrialized nations to offset carbon emissions by funding avoided degradation and deforestation through the conservation, carbon stock enhancement, and sustainable management of forests within developing nations (Campbell 2009, United Nations Framework Convention on Climate Change [UNFCCC] 2009). Since there is already a vibrant carbon market, worth US$126 billion in 2008 (Capoor & Ambrosi 2009), it is likely that REDD+ activities will result in substantial financial investment for forest protection and recovery (Miles & Kapos 2008).

The inclusion of carbon stock enhancement under REDD+ offers the potential to rehabilitate millions of hectares of habitat already degraded through unsustainable logging or fire, while also representing a longer-term mechanism for preventing deforestation of rehabilitated lands as future landscape planning decisions are made. Under rain forest rehabilitation schemes, forest density and structure are modified by planting a variety of native tree saplings and by cutting climbers, which retard tree regeneration and growth (Putz *et al.* 2001). It is this management that accelerates rates of regeneration in degraded forest, removing saleable units of carbon from the atmosphere.

The rehabilitation of forests to mitigate climate change also presents an important potential opportunity to reduce biodiversity losses resulting from forest degradation. Concern has, however, recently been expressed that overly vigorous management interventions to increase carbon stocks within degraded forests could be considered as 'plantation conversion by enrichment planting' and have adverse impacts on biodiversity (Putz & Redford 2009). It is therefore critical to identify whether vigorous rehabilitation, which offers the most potential in terms of carbon sequestration, is costly, neutral, or beneficial to biodiversity.

In a recent study, we found that intensive rehabilitation of heavily logged forest in Sabah, Malaysian Borneo resulted in the

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restoration of species richness and diversity of birds to levels found in unlogged forest, but with contrasting effects on different foraging guilds and with a reduction in overall abundance (Edwards *et al.* 2009). We suggested that this pattern may have resulted from differential responses of species in different guilds to changes in vegetation structure, but this hypothesis was not tested. Moreover no data were presented to indicate the effects of forest rehabilitation on how species composition changes or to indicate how groups that are of particular conservation concern—those that decline following logging and those that are Red Listed (Birdlife International 2009)—respond to rehabilitation.

Accordingly, here we examine how rehabilitation affected avifaunal composition, focusing on all birds and on the subset of species that are of particular conservation concern (herein termed imperiled birds). We then investigate the impact of rain forest rehabilitation on understory vegetation structure, and use these data to examine how changes to the vegetation affected the abundance and richness of all birds, of imperiled birds, and of those feeding and foraging guilds that are known to be most strongly affected by rehabilitation (Edwards *et al.* 2009). Only if our analyses indicate that rehabilitation has a largely neutral or a positive effect on biodiversity can rehabilitation of logged rain forest be considered a biodiversity-friendly method of biosequestration under REDD+.

METHODS

STUDY AREA.—We focus on the island of Borneo, which is a global hotspot of biodiversity and endemism (Myers *et al.* 2000, Corlett & Primack 2006). Bornean forests are dominated by large tree species of the family Dipterocarpaceae (Johns 1996), many of which are valuable as timber. Selective logging here has been extremely intensive (McMorrow & Talip 2001, Laurance 2007), with timber harvests of up to 175 m^3/ha (Pinard & Putz 1996) and with timber exports from Borneo alone exceeding the combined exports from Africa and Latin America (Cleary *et al.* 2007). Most remaining forest is reserved as production forest (Johns 1997) and has been selectively logged at least once (Edwards *et al.* 2010a, b).

Our study site is the Innoprise and Forest Absorbing CO_2 Emissions (FACE) Foundation Rainforest Rehabilitation Project (INFAPRO; Moura-Costa 1996), located in the 1 million ha Yayasan Sabah (YS) logging concession, Malaysian Borneo (see Edwards *et al.* 2009 for further details). This area was selectively logged in 1988–1989 following a modified uniform system, which seeks to transform uneven-aged and heterogeneous forest into a homogenous and even-aged forest that can then be re-logged when stands have sufficient residual trees of the right sizes. Under this system, commercial stems > 0.6 m diam were removed using tractor and high lead cable extraction techniques, resulting in *ca* 80–100 m^3 of timber extracted per ha (Whitmore 1984). Since 1993, INFAPRO has rehabilitated over 11,000 ha of selectively logged rain forest, with a further 14,000 ha designated for rehabilitation in the future (M. Snoep, pers. comm.). The INFAPRO area is surrounded by naturally regenerating rain forest in the Ulu Segama–Malua Forest Reserve and is situated near to the Danum Valley Conservation Area (DVCA) and Palum Tambun Watershed Reserve, which together comprise 45,200 ha of unlogged forest (Marsh & Greer 1992).

Rehabilitation management within INFAPRO was very vigorous and utilized a combination of enrichment planting and liberation cutting, with both treatments applied in all study locations (Moura-Costa 1996; see SOM for precise details of treatments applied by INFAPRO). Enrichment planting involved the planting of a mix of dipterocarp (95%) and wild fruit tree (5%) species at densities of up to ≈ 200 seedlings per ha along planting lines (see Table S1 for lists of seedling species and numbers planted). Liberation cutting involved the removal of all climbing vines and bamboos 6 mo before and 3 yr after enrichment planting, while noncommercial understory trees, shrubs, and gingers were cut along planting lines immediately before and 3 mo after enrichment planting.

SAMPLING.—Fieldwork was conducted from June to October 2007, May to September 2008, and May to July 2009, within DVCA and the Ulu Segama–Malua Forest Reserve (4°58′ N, 117°48′ E). Fifty-two transects were established across the forest matrix, comprising 18 transects in unlogged forest, 18 in logged forest that is naturally regenerating, and 16 in logged forest that has been rehabilitated (see also Edwards *et al.* 2009). Rehabilitated forests in the study areas were enrichment planted between 1993 and 1995 (≈ 6 yr after logging) and thus sampled ≈ 15 yr post management. Within a forest type, transects were located ≥ 500 m from the nearest neighboring transect, and between forest types, transects were located between 300 m and 24 km apart. We are confident that our transects were sufficiently far apart to ensure statistical independence of data because: (1) studies in tropical forests indicate that data from mist nets separated by > 200 m are statistically independent (Whitman *et al.* 1998, Pearman 2002, see Hill & Hamer 2004 for further discussion of this issue); and (2) in this study, only 19 of 3139 individuals (< 0.01%) were sampled on more than one transect.

AVIFAUNA.—We used a standardized mist netting protocol following Edwards *et al.* (2009). Each transect consisted of 15 mist nets (12 × 2.7 m; mesh size 25 mm), placed end-to-end in a straight line and opened between 0600 and 1200 h for three consecutive days (14,580 mist net hours in total). Each bird was marked with a metal leg ring that was individually numbered to prevent resampling of individuals. Mist netting was carried out during the drier season of the year (Walsh & Newberry 1999), but transects were nonetheless rotated between forest types to minimize any temporal effects.

VEGETATION.—To characterize the effect of rehabilitation on understory vegetation structure, we measured the following habitat variables from a point 3 m to the left-hand side of the center of the third, eighth, and 13th mist nets along each transect: circumference at breast height and distance to the two nearest saplings (dbh = 3–10 cm); number of tree and shrub seedlings (dbh < 3 cm, height > 1 m) within a 2 × 2 m quadrat centered around the sampling point; presence or absence of small (≤ 5 cm diam) and large (> 5 cm diam) lianas, and of nonwoody bamboo climbers within a vertical column extending to the canopy above the 2 × 2 m quadrat. Distances and sizes were measured with a tape measure.

Statistical analysis.—To determine how community composition was affected by rehabilitation, we investigated how patterns of species-abundance and species-composition differed among forest types using CAP v. 3.1 software (PISCES Conservation Ltd., Oxford, UK). This approach used species-abundance matrices, which were standardized as a percentage of birds within each site to account for differences among sites in total bird abundance (Table S1; see Edwards *et al.* 2009), together with presence–absence matrices. To test for differences among the different forest communities, we used an analysis of similarity (ANOSIM), which is a nonparametric permutations test analogous to an analysis of variance. In addition, we used a similarity percentage (SIMPER) test (Clarke & Warwick 2001) to quantify the degree of overall community difference and the influence that each bird species had in distinguishing between habitats.

To ascertain how susceptible individual species were to long-term impacts of selective logging, we compared the abundance of each species between unlogged and naturally regenerating forests using a generalized linear model (GLZ) with Poisson error and a log link in the R Stat 2.9.2 package (R Development Core Team 2008). Selecting only those 15 species that revealed a significant decline in abundance after logging (at the $P < 0.1$ level; Table S1), we then examined how forest rehabilitation affected the abundance of each species. Setting the significance threshold at $P < 0.05$ reduced the number of species to 12 (excluding *Napothera atrigularis*, *Trichixos pyrropygus*, *Cyornis superbus*) but had no qualitative effect on our results, and so only the former analyses are presented here. We also compared the richness and abundance of species on the Red List (Birdlife International 2009), which are typically restricted-range species that have undergone large population contractions as a result of forest conversion to agriculture. In both cases, counts were standardized as a percentage of the abundance and species richness of birds within a site, and analyzed using a GLZ with binomial error and a logit link.

Differences between forest types in understory vegetation structure were analyzed using: (i) general linear models (GLM) for averaged data, (ii) GLZ with Poisson error distributions and a log link for count data, and (iii) GLZ with binomial error distributions and a logit link for presence–absence data. To ordinate variation in vegetation structure among sites, vegetation variables that differed significantly between habitat types were then analyzed using principal components analysis (PCA; Hamer *et al.* 2003) in SPSS v. 14.0. We then used GLZs with Poisson error and a log link or with binomial error and a logit link, as appropriate, to examine the effects of variation in key components of vegetation structure on the abundance of individuals and species of all birds, of imperiled birds, and of those feeding and foraging guilds known to be most affected by rehabilitation (Edwards *et al.* 2009), *i.e.*, obligate frugivores, obligate insectivores, generalist frugivore–insectivores, and sallying foragers.

RESULTS

Patterns of species abundance and composition.—We recorded 3139 individuals of 98 species across the three forest types (Table S1). Overall species abundance distributions did not differ markedly between habitats, although the commonest species (little spiderhunter *Arachnothera longirostra*) comprised a much smaller proportion of the total in unlogged forest (Fig. 1). In addition, there were clear differences between unlogged forest and the other two habitats in the proportional abundances of individual species (Fig. 1; mean residual ± 1 SE: 0.7% ± 0.1 for naturally regenerating forest, and 0.8% ± 0.2 for rehabilitated forest).

As a result, patterns of species-abundance were significantly different among the forest types (ANOSIM: $R = 0.12$, $P = 0.001$), with pairwise comparisons indicating that patterns differed between each pair of habitats (unlogged vs. naturally regenerating: $R = 0.10$, $P = 0.015$; naturally regenerating vs. rehabilitated: $R = 0.12$, $P = 0.002$; unlogged vs. rehabilitated: $R = 0.17$, $P = 0.002$). Similarly, species-composition, as measured by presence–absence matrices, revealed variation among forest types (ANOSIM: $R = 0.08$, $P = 0.001$), with pairwise comparisons again indicating that patterns differed between all habitat pairs (unlogged vs. naturally regenerating: $R = 0.07$, $P = 0.025$; naturally regenerating vs. rehabilitated: $R = 0.07$, $P = 0.033$; unlogged vs. rehabilitated: $R = 0.11$, $P = 0.018$). Rehabilitated forests were thus marginally more similar to naturally regenerating forest than to unlogged forest in patterns of both species-abundance and species-composition, which was confirmed by the SIMPER analysis (average dissimilarity: species-abundance—unlogged vs. rehabilitated = 56% and naturally regenerating vs. rehabilitated = 52%; species-composition—unlogged vs. rehabilitated = 47% and naturally regenerating vs. rehabilitated = 45%).

Of the 98 species sampled, SIMPER analysis also revealed that ten species in each habitat pair accounted for over one third of the between-habitat dissimilarity in patterns of species abundance (Table 1; unlogged vs. naturally regenerating = 37%; unlogged vs. rehabilitated = 37%; naturally regenerating vs. rehabilitated = 40%), while ten species accounted for about a quarter of dissimilarity in

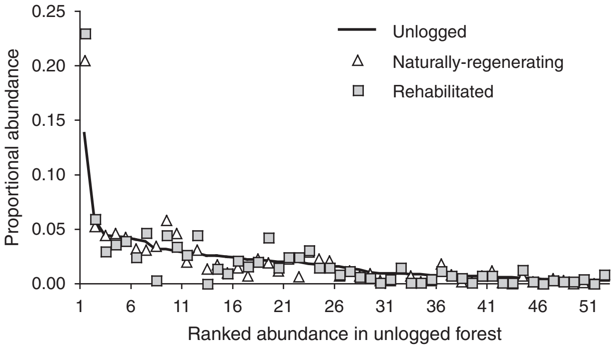

FIGURE 1. Ranked abundance of the 52 most abundant species (≥3 individuals) in unlogged forest, with abundance of the same species in naturally regenerating and in rehabilitated forest.

TABLE 1. *The ten bird species that made the highest contributions to differences in patterns of species-abundance and of species-composition among the three habitats. Mean % is the percentage abundance of each bird species (species-abundance) or the percentage presence of each bird species (species-composition). Dissimilarity* D *is a measure of the strength of the contribution that each species made toward the between habitat differences. Forest types: UL = unlogged; NR = naturally regenerating; R = rehabilitated. Species highlighted in bold are Red Listed (Birdlife International 2009).*

	Mean %				Mean %		
Species-abundance	*UL*	*NR*	*D*	Species-composition	*UL*	*NR*	*D*
Arachnothera longirostra	13	20	5.6	***Rhinomyias umbratilis***	**67**	**28**	**1.1**
Chalcophaps indica	3	3	1.8	***Alcippe brunneicauda***	**67**	**33**	**1.1**
Sasia abnormis	3	6	1.7	*Pycnonotus erythropthalmos*	28	61	1.1
Stachyris erythroptera	4	3	1.6	***Kenopia striata***	**56**	**28**	**1.0**
Malacocincla malaccensis	**6**	**5**	**1.6**	***Cyornis caerulatus***	**61**	**44**	**1.0**
Tricholestes criniger	3	4	1.5	*Copsychus malabaricus*	**44**	**56**	**1.0**
Trichastoma bicolor	4	4	1.5	***Malacopteron magnum***	**44**	**56**	**1.0**
Malacopteron magnum	**2**	**2**	**1.4**	*Malacopteron magnirostre*	61	50	1.0
Malacocincla sepiaria	3	2	1.4	*Chalcophaps indica*	56	67	1.0
Hypogramma hypogrammicum	4	4	1.4	***Macronous ptilosus***	**56**	**67**	**1.0**
	UL	*R*			*UL*	*R*	
Arachnothera longirostra	13	26	5.8	***Cyornis caerulatus***	**61**	**19**	**1.2**
Malacocincla malaccensis	**6**	**7**	**2.1**	***Alcippe brunneicauda***	**67**	**31**	**1.2**
Malacopteron cinereum	3	5	1.9	*Chalcophaps indica*	56	6	1.1
Trichastoma bicolor	4	3	1.8	***Macronous ptilosus***	**56**	**25**	**1.1**
Philentoma pyrhoptera	2	5	1.8	*Malacopteron magnirostre*	61	38	1.1
Stachyris erythroptera	4	5	1.7	***Rhinomyias umbratilis***	**67**	**44**	**1.1**
Malacocincla sepiaria	3	3	1.6	***Kenopia striata***	**56**	**38**	**1.1**
Sasia abnormis	3	5	1.5	*Pellorneum capistratum*	61	50	1.1
Tricholestes criniger	3	4	1.5	***Malacopteron magnum***	**44**	**50**	**1.1**
Alophoixus phaeocephalus	4	4	1.5	*Copsychus malabaricus*	44	44	1.0
	NR	*R*			*NR*	*R*	
Arachnothera longirostra	20	26	5.6	*Chalcophaps indica*	67	6	1.3
Malacocincla malaccensis	5	7	1.9	***Macronous ptilosus***	**67**	**25**	**1.2**
Tricholestes criniger	4	4	1.8	*Pycnonotus erythropthalmos*	61	31	1.2
Philentoma pyrhoptera	2	5	1.7	*Copsychus malabaricus*	56	44	1.1
Malacopteron cinereum	3	5	1.7	*Pellorneum capistratum*	78	50	1.1
Sasia abnormis	6	5	1.7	***Malacopteron magnum***	**56**	**50**	**1.1**
Trichastoma bicolor	4	3	1.7	*Malacopteron magnirostre*	50	38	1.1
Chalcophaps indica	0	0	1.6	*Malacocincla sepiaria*	72	56	1.1
Alophoixus phaeocephalus	4	4	1.5	***Rhinomyias umbratilis***	**28**	**44**	**1.0**
Hypogramma hypogrammicum	4	4	1.5	*Arachnothera affinis*	33	44	1.0

patterns of species composition (Table 1; unlogged vs. naturally regenerating = 23%; unlogged vs. rehabilitated = 24%; naturally regenerating vs. rehabilitated = 25%). Pivotally, both measures indicated that the key differences in patterns of abundance and composition between naturally regenerating and rehabilitated forest were primarily driven by species that are not considered to be of particular conservation concern (nonbold in Table 1). Focusing on species of conservation concern, the same six species were responsible for driving changes in composition between unlogged forest and both naturally regenerating and rehabilitated forest. Moreover, only one of these species (Fluffy-backed Tit-babbler *Macronous ptilosus*) revealed an opposing response, increasing following logging but decreasing after rehabilitation.

Fifteen species declined in abundance after logging (mean decline = 74.1% ± 0.04 SE; range = 46–100%; Table S1). However, neither the proportion of these species among species sampled (GLZ: $\chi^2 = 1.1$, $P = 0.3$) nor the proportional abundance of individuals belonging to these species ($\chi^2 = 3.1$, $P = 0.1$) differed significantly between naturally regenerating and rehabilitated forest (Fig. 2A). Hence both these measures remained lower in rehabilitated forest compared with unlogged forest (Fig. 2A; abundance, $\chi^2 = 34.3$, $P < 0.0001$; richness, $\chi^2 = 13.5$, $P = 0.0002$).

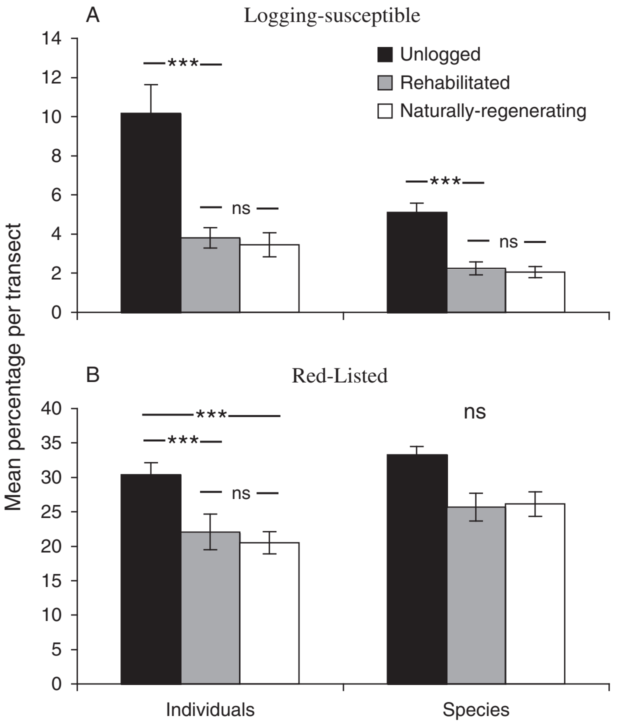

FIGURE 2. The prevalence of birds of conservation concern. (A) The mean percentage of all bird individuals and species per transect that are classified as logging-susceptible. (B) The mean percentage of all bird individuals and species per transect that are Red Listed. Error bars indicate ± 1 SE, and superscripts represent pairwise differences as follows: $^{ns}P \geq 0.07$; $^{***}P < 0.0001$.

Thirty-six Red-Listed species were recorded during the study. The proportional abundance of individuals belonging to these species differed between forest types (Fig. 2B; $\chi^2 = 29.7$, $P < 0.0001$). Pairwise comparisons revealed that proportional abundance was similar between naturally regenerating and rehabilitated forest, but was lower in both these forest types than in unlogged forest (Fig. 3B). However, the proportion of Red-Listed species among all species sampled did not differ significantly between the forest types (Fig. 2B; $\chi^2 = 5.2$, $P = 0.1$).

VEGETATION STRUCTURE AND AVIFAUNAL TRENDS.—The density of tree and shrub seedlings was reduced by 20 percent, and the prevalence of small and large lianas were more than 50 percent lower in rehabilitated forest than in unlogged or naturally regenerating forests (Table 2). These are all components of vegetation that are managed by liberation cutting. In contrast, the prevalence of climbing bamboos was between 2.5 and 3.5 times lower in unlogged than in logged forest (Table 2). Girths and distances to saplings did not differ among the three forest types ($P > 0.2$ in both cases).

PCA extracted two components of variation in vegetation structure (FAC1 and FAC2) that accounted for 37 percent and 25 percent of the variability in the data, respectively. The first factor (FAC1) primarily increased with the prevalence of small and large lianas, while FAC2 increased with higher densities of seedlings but lower prevalence of climbing bamboos (Table S2). FAC1 was significantly lower in rehabilitated forests than elsewhere (Table 1; KW: $\chi^2 = 22.9$, df = 2, $P < 0.001$) indicating that liberation cutting affects this component, whereas FAC2 differed significantly between unlogged and logged forest types (Table 1; $\chi^2 = 8.8$, df = 2, $P = 0.012$).

Focusing on the effect of liana prevalence (FAC1) on the bird community, there was a positive relationship with abundance (GLZ: $\chi^2 = 33.8$, $P < 0.0001$) and species richness ($\chi^2 = 5.0$, $P = 0.026$) of all birds (Fig. 3A), and with the proportional abundance ($\chi^2 = 25.1$, $P < 0.0001$) and richness ($\chi^2 = 5.7$, $P = 0.017$) of obligate frugivores (Fig. 3B). Conversely, there was a negative relationship with the proportional abundance ($\chi^2 = 49.0$, $P < 0.0001$) and richness ($\chi^2 = 10.4$, $P = 0.0013$) of fruit-insect feeding generalists (Fig. 3C), and with the proportional abundance of sallying foragers (Fig. 3D, $\chi^2 = 7.8$, $P = 0.005$). There was no effect of lianas on the species richness of salliers, or on the abundance or richness of insectivores (all $P > 0.2$). Finally, focusing on imperiled groups, there was no effect of liana prevalence on the proportional abundance or richness of IUCN Red-listed or logging susceptible species (all $P > 0.25$).

DISCUSSION

Forests degraded by poor logging practices are widespread within tropical landscapes, but these lands are at highest risk of conversion to agriculture, with 2.8 million ha of forest in Southeast Asia alone converted annually to oil palm between 2000 and 2005 (Koh & Wilcove 2008, Edwards *et al.* 2010a). Consequently, an urgent conservation priority is to identify novel sources of funding to protect these forests, leading to suggestions that carbon credits under

TABLE 2. *Differences in vegetation structure between the forest types. FAC1 and FAC2 are principal component scores from a principal components analysis of vegetation structure. Means ± 1 SE are given and superscripts represent pairwise differences at the* $P < 0.05$ *level.*

Vegetation measure	Unlogged	Naturally regenerating	Rehabilitated	χ^2	P
Tree seedling density/4 m^2	5.5 ± 0.7^a	4.8 ± 0.9^a	4 ± 0.8^b	11.5	0.003
Large lianas (% presence)	61^a	61^a	9^b	38.6	< 0.0001
Small lianas (% presence)	85.2^a	94.4^a	44.4^b	31.1	< 0.0001
Climbing bamboo (% presence)	9.3^b	37^a	22.2^a	12.4	0.002
FAC1	0.25 ± 0.2	0.62 ± 0.2	− 0.97 ± 0.2	22.9	< 0.001
FAC2	0.56 ± 0.2	− 0.26 ± 0.2	− 0.34 ± 0.3	8.8	0.012

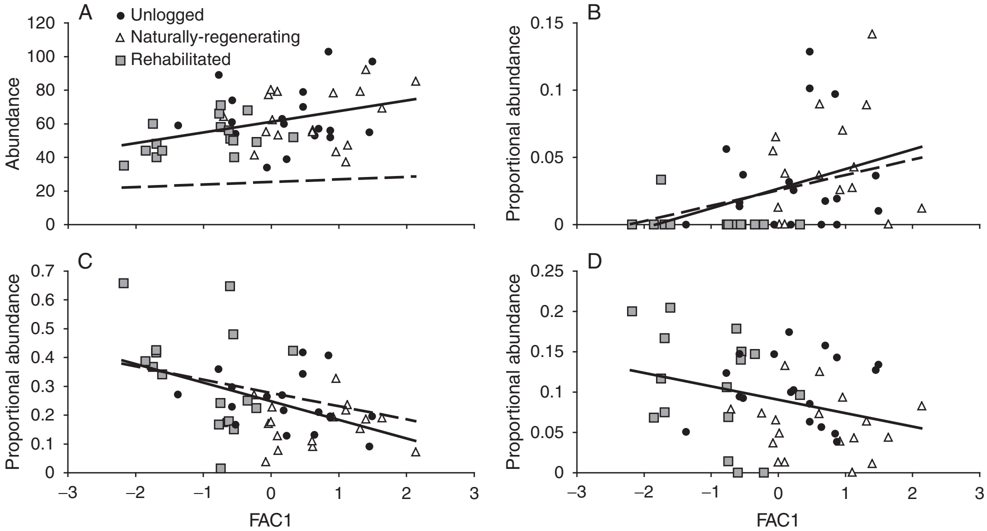

FIGURE 3. The effect of variation in liana prevalence (FAC1 from a principal components analysis) on the abundance of individuals and species of birds. See Methods for details of calculating FAC1. Solid lines and symbols represent the values for individuals, and dashed lines significant relationships for species richness. (A) All birds, (B) obligate frugivore guild, (C) generalist frugivore–insectivore guild, and (D) sallying guild.

the REDD+ initiative could give additional value to degraded lands (Venter *et al.* 2009, Harvey *et al.* 2010). In this study we investigated whether rehabilitation of logged rain forest, which will be funded under REDD+, represents a biodiversity-friendly mechanism of carbon sequestration that could be used to help stem the loss of tropical biodiversity.

Our results indicate that rehabilitation altered patterns of species-abundance and of species-composition of understory birds such that rehabilitated forests support a unique avifaunal community. However, this community was most similar to that of naturally regenerating forest and, crucially, there was no significant difference in the species richness or abundance of birds of conservation concern within rehabilitated forest compared with naturally regenerating forest (Fig. 2). Hence, rehabilitation does not represent a net cost to those species that are of particular conservation concern.

Rehabilitation of selectively logged forest substantially altered vegetation structure at the understory level. In particular, liberation cutting resulted in fewer tree and shrub seedlings and lianas, creating a relatively open understory. Climbing bamboos increased greatly in abundance post-logging but were no less abundant in rehabilitated forest than in naturally regenerating forest (Table 2) suggesting that in contrast to effects on seedlings and lianas, liberation cutting was not effective in suppressing the long-term growth of bamboo.

The composition of bird communities within tropical forests is strongly influenced by the structure of the understory (Barlow & Peres 2004). In our study, the prevalence of lianas was positively related to the abundance and richness of all birds and of obligate frugivores (Figs. 3A and B) but negatively related to fruit-insect feeding generalists and salliers (Figs. 3C and D). FAC1 was also lower in rehabilitated forest than elsewhere (Table 1), providing strong evidence that the observed effects of forest rehabilitation on avian abundance and species composition were directly attributable to impacts of liberation cutting management on vegetation structure. These effects probably arose because understory frugivores typically feed on small fleshy fruits produced by vines and shrubs, while salliers favor undisturbed forest (Thiollay 1992), which has a more open understory (Hamer *et al.* 2003). Finally, it is plausible that in response to a lack of fruit but a more open understory, generalists have shifted from a more fruit-based to a more insect-based diet.

Evidence that liberation cutting drives declines in the abundance of all birds and frugivores (Figs. 3A and B) provides some support for the notion that rehabilitation management should incorporate breaks in the application of liberation cutting treatments in order to retain dense vine tangle and shrub microhabitats (Edwards *et al.* 2009). Such a strategy might seek to mimic the gap density and sizes found in undisturbed forest, and this would almost certainly increase the presence of vines within the landscape, with possible additional benefits for diversity and species composition in relation to gaps (Schemske & Brokaw 1981, Levey 1988, Schnitzer & Carson 2001). A break in treatment would, however, come at a reduction in the rate of tree recovery and carbon sequestration, which might impact on the cost-effectiveness of this treatment under REDD+.

This study confirms that even very vigorous rehabilitation of logged forests enables the high biological value of naturally regenerating rain forests (Dent & Wright 2009, Berry *et al.* 2010) to persist (see also Edwards *et al.* 2009). Research into the effects of forest rehabilitation on other taxa is thus now vital for a fuller understanding of the consequences of this biosequestration technique for biodiversity, although it is likely that the trends revealed by birds, which are reasonable indicators of general patterns across taxa (Howard *et al.* 1998, Barlow *et al.* 2007, Berry *et al.* 2010), will follow for other groups. Furthermore, it is also highly likely that less vigorous rehabilitation of degraded forest would similarly not harm biodiversity.

The size of the benefit from rehabilitation, in terms of carbon sequestration and biodiversity protection or recovery, will also vary with the intensity of habitat disturbance (Kobayashi 2007). Timber yields from many selectively logged forests are much lower than those in our study area, with harvests of $< 20\,\mathrm{m}^3$/ha in large areas of the Neotropics. In such areas, benefits of rehabilitation will be questionable because there is a limited amount of carbon that can be restored and given the desire for cost-effectiveness in terms of the level of benefit obtained per unit cost (Losos 2001). Conversely, even greater benefits might arise in areas that have experienced higher timber extraction rates than our study sites (*e.g.*, Pinard & Putz 1996), have undergone a second rotation of logging with associated additional residual damage (*e.g.*, Edwards *et al.* 2010b), have burned in forest fires, or have undergone regeneration of secondary forest on abandoned farmland. Such benefits have yet to be quantified, but one possibility is that focusing forest rehabilitation at the edges of unlogged (or better quality) forests will reduce edge-effects and degradation of remaining forest, while allowing recolonization of wildlife into the rehabilitated areas. Additionally, rehabilitation might enhance canopy cover such that degraded or secondary forests would continue to qualify for carbon credits even if a more stringent definition of forest, which elevates the current 10–30 percent canopy cover threshold, is imposed under future REDD+ agreements (Sasaki & Putz 2009).

Because most biological measures indicate that rehabilitated forest retains or even improves the high biological value of logged-over rain forests (this study and Edwards *et al.* 2009), we conclude that even vigorous rain forest rehabilitation represents a biodiversity-friendly biosequestration mechanism. Given the global abundance of degraded and secondary forests (ITTO 2002), and that these lands represent a critical component of the global conservation effort (Dent & Wright 2009), we argue that rain forest rehabilitation should play a strong role in the future REDD+ agreement and should warrant the use of significant carbon market funds for carbon protection and enhancement. Nevertheless, because we do not find a strongly positive benefit of rain forest rehabilitation for biodiversity, this argument should not be confused with promoting rehabilitation projects, in forest that has been logged with a similar or lower intensity, using conservation funds for biodiversity protection.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

METHODS. *Rehabilitation protocol within INFAPRO.*

TABLE S1. *Dipterocarp and fruit tree species planted within INFAPRO.*

TABLE S2. *Species list with abundances for each forest type.*

TABLE S3. *Contribution of variables to the PCA of understory vegetation structure.*

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