The long-term response of avian communities to selective logging



Cain Agger



The University Of Sheffield.



Abstract

South East Asian biodiversity has found itself at a tipping-point, owing to the fact logging intensities in the area are the highest on Earth. The degraded forests that remain following multiple rounds of intensive logging are often perceived to be unable to support biodiversity, thus conversion of logged land to monoculture palm oil is rampant. However, this cannot be further from the truth as even repetitively logged forests are able to support biodiversity in the short-term. Therefore, there have been calls to conserve logged forests to provide suitable habitat for biodiversity to recover. This conservation potential hinges on the ability of selectively logged forests to retain biodiversity in the long-term. Using mist netting, the understorey avian community was sampled in primary and twice-logged forests in Sabah, Borneo. The last logging rotation in the study area occurred fifteen years prior, allowing the long-term response of the forests avian community to logging to be examined. Community composition recovers following logging, to the point it is analogous between forest types. Species retention also improves through time as community metrics show little difference between forest types and comparative analysis between short-term and long-term datasets demonstrates re-dispersal. The increasing similarity of species resource use between forest types also supports the ability of logged forests to recover. In addition, these analyses also highlight the important role of generalist and specialist avian species during recovery. The avian community does have the ability to persist and recover long-term following logging; overall biodiversity is likely to show the same pattern. Utilising these degraded forests for conservation and halting the proliferation of palm oil should therefore be a priority for policy-makers and conservationists.

1. Introduction

Tropical rainforests cover 13% of the Earth's terrestrial area, yet they lay claim to between one-half and two-thirds of the Earth's terrestrial biodiversity (Gardner et al, 2010; Pimm and Sugden, 1994). A plethora of anthropogenic-induced threats are damaging this diversity; however, logging is the most wide-spread human activity in the tropics (Edwards and Laurance, 2013). Over 400 million hectares of tropical rainforest lie in timber concessions designated for selective logging (Blaser et al, 2011). Nowhere else are these threats more pronounced than in South East Asia, where magnitudes of both biodiversity and rates of timber extraction exceed that of most other tropical forests (Sodhi et al, 2010; Sodhi et al, 2010).

South East Asia could lose three quarters of its original rainforest alongside 42% of its biodiversity by 2100 (Sodhi et al, 2010). Selective logging is the most common timber extraction system in South East Asia and represents a large proportion of the area's economy, with Indonesia, Malaysia and the Philippines together exporting more than 80% of all tropical timber during the late twentieth century (Wilcove et al, 2013; Berry et al, 2010). During selective logging, trees are designated for extraction based on several criteria, including size and species identity (Martin et al, 2015). Overall, this reduces the number of trees extracted per hectare while maintaining economic viability. However, in South East Asia's dipterocarp forests, at its most intensive levels 'selective' logging is misleading. Most large, marketable trees are removed using liberal logging criteria (Edwards et al, 2011), in turn modifying other direct impacts such as ground compaction and tree species recruitment (Martine et al, 2015). Depending on market value and demand, selective logging rounds are increasingly being repeated ~20 years later, creating a matrix of highly degraded forests logged at least twice (Edwards et al, 2011).

Selectively logged forests are pre-perceived to be degraded, making these forest vulnerable to further degradation through relogging, clear-felling and conversion to plantation and agricultural land (Srinivasan, Hines and Quader, 2015). Particularly in SE Asia selectively logged forests face further pressure from oil palm conversion; together Malaysia and Indonesia produce more than 80%

of all oil palm (Fitzherbert et al, 2008). Due to international pressure, the conversion of primary forests to oil palm has been restricted (Mccarthy and Cramb, 2009), making selectively logged forests increasingly vulnerable to conversion. These selectively logged forests may, however, contain conservation potential, depending on the consequences of selective logging for biodiversity.

The effects of selective logging on biodiversity arise as a result of shifts in forest structure and abiotic conditions, which in turn affect associated resource availabilities (Woodcock, Edwards and Halme, 2015). The manner biodiversity responds to these environmental changes is complex and incredibly variable. Nevertheless, recent evidence suggests that selectively logged forests are by far the most biologically similar anthropogenically degraded areas to primary forests, compared with agricultural and agro-forestry systems (Gibson et al, 2011). Previous studies undertaken throughout the tropics have demonstrated that selective logging has limited effects on diversity and species richness (Edwards et al, 2011). Selective logging has no impact on 85-100% of mammal and invertebrate species (Putz et al, 2012). Additionally, 75% of bird and dung beetle species persist in selectively logged forests and logging has no significant effect on globally imperilled bird species (Edwards et al, 2011). On the other hand, changes in community composition, species trophic levels and feeding guild representation are commonly reported (Edwards *et al.*, 2013; Woodcock *et al.*, 2013; Banks-Leite, Ewers and Metzger, 2010). Nonetheless, the consensus that selectively logged forests can retain most of their biological value has been developed.

The conservation value of selectively logged forests hinges on their ability to retain biodiversity over the long-term. Currently there is a paucity of information regarding the ability of selectively logged forests to retain or improve their biodiversity levels over time and following repeated rotations of selective logging. If biodiversity within selectively logged forest declines over the long-term, it may underscore the importance of alternative cutting regimes, active forest restoration techniques and the importance of conserving more irreplaceable primary forest (Cerullo and Edwards, 2018). On the other hand, if logged forest can retain or increase their initial post-logging biodiversity value over time, this will highlight their importance for conservation and the need to halt their on-going conversion to palm oil. This ability to retain biodiversity long-term post-logging may spotlight selectively logged forests as surprisingly low-cost options for conserving high levels of biodiversity, thanks to the big drop in the standing value of timber following two logging rotations (Fischer et al, 2011).

Edwards et al (2011) played an integral role in advancing our view of biodiversity within selectively logged forests. By sampling the avian and dung beetle community in primary, one rotation and two rotation selectively logged, these biodiversity indicators demonstrated the ability of selectively logged forests to retain biodiversity. Sampling took place five years post-logging, therefore the findings were restricted to this relatively short period, meaning only short-term conclusions could be drawn. ~10 years have passed since the publication of this study, giving biodiversity ample time to respond to the biotic and abiotic changes selective logging promotes.

By mirroring the robust data collection methods and carrying out sampling in the same areas as Edwards et al (2011), identical short-term and long-term datasets can be produced. This repeat sampling will give an account of how biodiversity has recovered ~15 years after selective logging and allow conclusions to be drawn on the ability of selectively logged forests to retain biodiversity in the long-term. This inquiry is approach using three angles: 1) Evaluate differences in broad-scale community characteristics and assess the ability of selectively logged forests to retain species over time. 2) Determine the changes that occur to avian community composition and its potential for long-term recovery following selective logging. 3) Characterise changes in the manner that avian communities utilise resources over time as a result of selective logging. Additional data analysis to the Edwards et al (2011) study is conducted here so that the many facets of long-term biodiversity recovery can be teased apart. Second rotation selectively logged areas are sampled here as they represent the areas most degraded by selective logging. Understorey birds are used as an indicator taxa as they are the best and most detailed studied taxa in the tropics, can indicate biodiversity responses at the community level (Lawton et al, 1998), and are the most cost-effective taxa for biodiversity surveys (Gardner et al, 2008). In addition, a recent meta-analysis quoted birds as taxa most sensitive towards forest conversion (Gibson et al, 2011).

2. Methodology

2.1 Study site

All fieldwork was conducted on the island of Borneo. The study area lies within the contiguous one million-hectare Yayasan Sabah logging concession in Sabah, north-east Borneo (4° 58'N, 117° 48'E). This concession encompasses production forest within the 238, 000 ha Ulu Segama-Malua Forest Reserve (US-MFR) alongside protected primary forest within the 45,200 ha Danum Valley Conservation Area (DVCA). Primary forests within the Yayasan Sabah concession comprises of lowland dry dipterocarp forest. These forests are dominated by large dipterocarp trees (*Dipterocarpaceae*), which are valuable timber producing trees (Johns, 1996). Between 1976 and 1991, the US-MFR was selectively logged (Whitmore, 1984). All commercially valuable trees of more than 0.6m diameter at breast height (DBH) were felled, resulting in approximately 120m³ of timber extracted per hectare (Marsh et al, 1992). Roughly 141,000 ha of the US-MFR was then relogged between 2001 and 2007. During this second rotation, minimum cutting diameters were reduced to 0.4m DBH for commercially viable species. This second rotation resulted in an additional 15-72m³ of timber extracted per hectare (Yayasan Sabah 2009, unpublished data).

2.2 Avian sampling

Fieldwork has taken place from June to September annually since 2014 and concluded during the 2019 field season. The understory avian community was sampled in a capture-mark-recapture methodology using mist-netting techniques in twice-logged (treatment) and primary forests (control). Six plots – three in primary forest (DVCA) and three in twice-logged forest (US-MFR) – were sampled. Each plot was sampled three times during each field season. Plots within each forest type were situated at least 1km apart.

Each plot contained three parallel 250 m line transects, placed >200 m apart to ensure statistical independence (Hill & Hamer, 2004). Each 250 m transect comprised fifteen 12 m mist nets, leaving 70 m of extra space in the transect for tree fall and precipitous gullies. Mist nets were open from 06:00 to 12:00 for two consecutive days with the following day consisting of setting up nets within the next plot. During netting, each transect was ran by two workers, allowing each transect within a plot to be sampled simultaneously.

Upon capture, each bird was identified to the species level and rung with a uniquely numbered metal leg-ring. Vital rate measurements were taken, included age (determined via plumage, feather condition, breeding status and other factors where applicable); sex (plumage, brood patch, metric measurements); brood patch conditions (scored on brood patch age); body moult condition (scored on the presence or absence of body feather growth); and wing feather moult (reproduction of wing feather condition onto a bespoke wing diagram). The only metric measurement taken was weight. All procedures conformed to British Trust of Ornithology guidelines.

2.3 Data analysis

2.3.1 Species retention

The environmental changes that logging produces alters avian populations at their basal level, these changes were assessed through community metrics such as species abundance, rarefied species richness, species evenness and effective diversity. Species richness is sensitive to sample size, thus rarefied species richness was employed to standardise sampling efforts. An accompanying rarefied species accumulation curve was constructed using the vegan package v2.5-3 (Oksanen et al, 2019) in R v3.4.1 (R Core Team, 2017). Species evenness was calculated using the the Pielou eveness measurement (*J*) and the Shannon-Weiner Index (H') was used to calculate effective diversity.

To permit comparisons between the short-term and long-term datasets, the catch rate for each species in each dataset was calculated and then divided by the total number of netting hours in the relevant dataset. Percentage difference between datasets was then calculated for each forest type. Only data collected from primary and second rotation logged forest was analysed from the short-term dataset to keep the logging rotation consistent between datasets. All data points comprising of zero were eliminated from the percentage difference calculation. While this may put more statistical weight onto species that are caught more often, percentage differences cannot be calculated when none of a species is caught and the small sample size of rarely netted species means they have less statistical weight.

2.3.2 Community composition

To determine how the constitution of species differs between forest types, non-metric multi-dimensional scaling was performed. This allowed for the ordination of plots according to species compositional similarities, using the Bray-Curtis index. The compositional differences between forest types was then tested using an analysis of similarity (ANOSIM), again utilising the Bray-Curtis index. All community composition analysis was conducted using the vegan package v2.5-3 (Oksanen et al, 2019) in R v3.4.1 (R Core Team, 2017).

2.3.3 Resource ecology

To assess differences in resource use between the forest types, analysis on weight, feeding guild and foraging level were conducted. Weight, diet and foraging patterns can be used to infer the quantity, quality and type of resource use (Petchey et al, 2007). A welch's t-test was conducted on mean species weight between primary and logged forest. A mean weight was calculated for each species, each mean was then repeated until the quantity of means being analysed matched the number of its representative species. Chi-squared goodness of fit tests were then performed to compare the number of individuals within the five present feeding guilds in each forest type. Therefore, differential abundances in each feeding guild depending on forest type could be identified. By conducting both the weight and feeding guild analysis on the mean individual level rather than the species level, a more representative sample of the forest types community could be created, as the relative abundance of each species within the forest type was included in both analyses. Two proportion z tests were then conducted on the mean percentage of time species spent foraging within any of the seven foraging levels in each forest type. Comparisons between the time spent within each foraging level were made between each forest type. The proportional amount of time species spent within each foraging level and relevant feeding guilds were assigned using the eltonian trait matrix (Wilman et al, 2014).

3. Results

3.1 Species retention

Data derived from 5813 individual birds from 136 species was collected, with a further 1748 recapture record. Species abundance was significantly higher in logged forest than primary forest (χ^2 = 64.99, d.f. = 1, *p* = <0.001) (*Table 1*). In contrast, none of the differences in rarefied species richness, species evenness and effective diversity were significant (rarefied richness: χ^2 = 0.042, d.f. = 1, *p* = 0.84; Eveness: χ^2 = 0.0015, d.f. = 1, *p* = 0.96; Diversity: χ^2 = 0.56, d.f. = 1, *p* = 0.45) between forest types. The community within both forest types was sufficiently sampled as both forest types reached an asymptote in *Fig 1*. The difference in observed species richness between forest types in *Fig 1* is akin to the difference seen in rarefied species richness (*Table 1*), these differences are small and non-significant.

Fores Table 1. Summary of rarefied species richness, species abundance, species evenness (Pielou eveness J) and effective diversity (Shannon-Weiner Index H') for both forest types.

Primary	3430	28.04	0.85	41.74
Logged	4131	26.52	0.80	35.15



Figure 1. Observed species richness, constructed using rarefied species accumulation curves for both forest types.



Figure 2. Percentage differences in catch rates between the short-term and long-term datasets. The species represent each forest type are different because all data points comprising of zero were eliminated from the percentage different calculation. Species names are coded here to aid with plotting. The first letters from each word in a species name is combined with the first three letters of their family name. For example, APFLY represent the Asian Paradise Flycatche

Fig 2 shows that both forest types contain a wide range of different responses to the ~15 years between sampling and re-sampling. Species that increase their catch rate in one forest type generally show the opposite trend in the other forest type, suggesting species are recolonising and moving between forest types. Primary forest contains a high proportion of species that increase their catch rate. Logged forest is more balanced in the amount of change in catch rate, however it is also more extreme than primary forest with larger increases and decreases in catch rate. These differences between forest types indicate that more species are recolonising primary forest.

3.2 Community composition

The similarity between species assemblages in forest types was not significant (ANOSIM: r = 0.59, p = 0.2). Fig 3 presents a large clustering of species between the primary and logged forest polygons, meaning many species are unaffected or have recovered since logging occurred as they are equally as likely to be present in their forest type. The number of species present within each forest types

polygon is consistent between forest types too, meaning the number of species that prefer either forest type is consistent between primary and logged forest.



NMDS1

Figure 3. A NMDS showing the community composition change between primary and logged forest. Black outlined points represent a singular species and study plots are numbered and sorted by forest type. Representative coloured polygons are drawn within forest types for ease of interpretation. The Bray-Curtis dissimilarity calculation and three dimensions (k=3) were used to construct the NMDS.

3.3 Resource ecology

There is no significant difference in mean bird weight between primary (26.53g) and logged forest (26.70g)(Welch's t = 0.055, d.f. = 138.6, p = 0.96), suggesting species that reside in logged forest are at no resource availability disadvantage.

The proportion of individuals representing each feeding guild in each forest type remains relatively constant between primary and logged forest (*Fig 4*), with there being no significant difference in all feeding guilds (Invertebrate: $\chi 2 = 2.52$, d.f. = 1, p = 0.11; Seed: $\chi 2 = 2.77$, d.f. = 1, p = 0.095; FruiNect: $\chi 2 = 3.27$, d.f. = 1, p = 0.07; VertFishScav: $\chi 2 = 1.45$, d.f. = 1, p = 0.22) other than omnivory. Logged forest contains a significantly higher proportion of omnivorous individuals than primary forest ($\chi 2 = 118.48$, d.f. = 1, p = <0.001). Foraging level is also not affected by logging. Two proportion z tests showed no significant difference in the proportion of time birds spend within each foraging level in each forest type (Water below surf: $x^2 = 1.29 \cdot 10^{30}$, d.f. = 1, p = 1; Water around surf: $x^2 = 1.18 \cdot 10^{30}$, d.f. = 1, p = 1; Ground: $x^2 = 0.052$, d.f. = 1, p = 0.81; Understorey: $x^2 = 0.361$, d.f. = 1, p = 1; Aerial: $x^2 = 2.84 \cdot 10^{32}$, d.f. = 1, p = 1).





4. Discussion

This study currently represents the only investigation into the long-term responses of understorey avian communities to repeated selective logging in South East Asia. Selectively logging an area twice adds to and magnifies the damage that the first logging rotation caused (Edwards et al, 2011), and considering selective logging in Ulu Segama is as intense as selective logging can get, the results here may represent a 'worst case scenario'. Studies investigating the short-term effects of selective logging on a wide range of taxa have demonstrated the surprisingly low impact for biodiversity (Edwards et al, 2011; Berry et al, 2010; Edwards et al, 2009; Putz et al; 2012), the results of the present study support this pattern. Of all the community metrics assessed here, only species abundance was found to significantly differ between selectively logged and primary forest. Overall catch rates have decreased in logged forest and increased in primary forest thought time. Additionally, slight community compositional differences were detected between forest types though they were insignificant. The way species use and interact with resources in their environment also remains largely unchanged, however the number of omnivorous species increases in selectively logged forest.

Species abundance was roughly 20% higher in selectively logged forest than primary forest, while all other community metrics showed no change. During netting there were few species that were not present in both forest types and the species that were only present in one forest type were usually netted at low frequencies, meaning species retention may remain relatively high over time, just as it does in the short-term (Edwards et al, 2011). Consequently, few species completely disappear once selective logging occurs and most species retain the ability to utilise the altered forest mosaic (Lambert, 1992). The increase in species abundance in logged forest may be a direct response to the environmental changes produced by selective logging (Dranzoa, 1998). Selective logging modifies vegetation structure, producing an understorey interspersed with dense, low stands of fast-growing pioneer species (i.e. liana vines, climbers and bamboos)(Pinard, Howlett and Davidson, 1996). Thus, producing an increase in the heterogeneity of microclimatic conditions, alongside creating changes in a plethora of environmental conditions (Thiollay, 1997; Mason, 1996). For example, the increase of

some bulbul and flowerpecker species following selective logging is attributed to the spread of small-fruited shrubs in logged forest (Johns, 1996). Although succession would have pushed the plant community further towards its apex state over the ~15 years since logging, it is unlikely that the plant community would have reached equivalency with the apex community, meaning altered environmental conditions are still exerting an effect on the avian community.

The environmental changes generating abundance shifts may also be responsible for changes in community composition. The ANOSIM analysis conducted on community composition showed no significant difference between forest types. This may be due to the large amount of species able to colonise both forest types, as shown by the NMDS analysis and similar species the richness between forest types. Edwards et al (2011) uncovered a significant difference in community composition between forest types whereas in this resample there was no significant difference between forest types. This suggests there has been recovery during the ~10 years since the community was last sampled and that recovery is on track to reconstruct primary forest community compositions. The NMDS analysis also demonstrated there is a moderate change in community composition between forest types because of the relative similarity in the number of species that strongly prefer either forest type. This small shift in community composition may be present because full recovery is yet to occur, meaning primary and selectively logged forests are still disparate. In turn, this may be controlled by the habitat preferences of specialist and generalist species (Burivalova, Şekercioğlu and Koh, 2014; Banks-Leite, Ewers and Metzger, 2010). Given that Borneo's rainforests are the oldest on earth, the avian community is highly adapted and specialised (Cleary et al, 2007). Carrara et al (2015) demonstrated that the diversity of forest specialist species is positively correlated with canopy and primary forest cover. Because of specialist species reliance on the environmental conditions and resource availabilities of primary forests, degradation can produce rapid population declines. Oppositely, generalists can rapidly take advantage of the environmental conditions produced by selective logging (Thinh, Doherty and Huyvaert, 2012). Generalists can use various habitat types in the landscape matrix, (Devictor, Julliard and Jiguet, 2008). Therefore, their high level of plasticity in habitat choice allows generalists to take advantage of the reduced competition and vacant niches produced as specialists vacate (Carrara et al, 2015). The similarity in effective diversity between forest types reported here also supports the idea of turnover between specialist and generalist species.

This turnover is emphasized in the species catch rate comparative analysis. The results of this analysis are contrary to expectations. Catch rates show an overall decreasing trend in logged forest compared to the mostly increasing catch rate in primary forest. The interplay between generalist and specialist species is altered as forest succession occurs, underscoring the large role generalist and specialist species have in shaping their community. Generalist species may be re-dispersing into primary forest as succession makes the selectively logged habitat less heterogeneous and therefore less suitable for generalists (Honkanen et al, 2009). There is no benefit to staying in selectively logged forest as a generalist, however, there may be benefit in re-disperse into primary forests to take advantage of the reduced competition produced by the already low concentration of generalists in primary forest. Generalist species that originally dispersed into logged forests gained benefits from the altered habitat, but now this benefit is diminishing there is no strict advantage to remaining in logged forest. The wider range of difference in catch rate in logged forest compared to primary suggests that specialists are also re-dispersing into logged forest as it becomes more suitable, though this may be at smaller concentrations than generalists. Species re-dispersal is compounded by the almost identical level of species evenness between the forest types found in this study. The effect of resource availability throughout forest succession underpins this turnover between forest types, therefore effects on the way the community forages for and utilises resources may be occurring.

There was no significant difference in mean weight or preferred foraging level between forest types. The absence of weight reductions even though logged forests contain inferior quality resources may stem from the turnover in specialist species for generalists, as generalists can utilise a wider range of resources to supplement their diet. There is evidence from few species that logging affects foraging level, for example species of fantail Rhipidura shift their foraging level higher in response to logging (Driscoll and Kikkawa, 1989), however there is little evidence that the phenomena applies to most species (Lambert, 1992). The feeding guild abundance analysis showed that there are significantly more omnivorous species in selectively logged forest than in primary forest. This increase may be generated by the proliferation of generalist species in logged forest, who are often flexible with their dietary requirements (Terraube, Guixe and Arroy, 2014). The increased heterogeneity in resource availabilities produced by selective logging promotes omnivory, so species can best use the resources available in their habitat (Bonilla et al, 2012). Studies investigating the short-term effects of logging have developed the consensus that insectivorous species should decrease in abundance post-logging, as insect populations are impacted by the increase in canopy gaps and decrease in understorey moisture (Aleixo, 1999; Banks-Leite, Ewers and Metzger, 2010; Hamer et al, 2015; Srinivasan, 2013; Korthals, 1990). In addition, it has been established that frugivorous and nectivorous species should increase their abundances in selectively logged forest in response to the increase in fruiting and flowering understorey plants (Burivalova, Sekercioğlu and Koh, 2014; Banks-Leite, Ewers and Metzger, 2010). Our data undermines this consensus, supporting the idea that the avian community has been able to respond to forest succession over the ~15 years post logging and regain roughly similar levels of insectivorous, frugivorous and nectivorous species to primary forest.

It is clear that over the ~15 years since selective logging occurred on our study site, some degree of community recovery has occurred. Lambert (1992) concluded that time elapsed since logging is an important determinant of community composition. Banks-Leite, Ewers and Metzger (2010) supported this conclusion by showing there is a clear recovery towards the primary forest community composition as the forest cycles through its succession following one rotation of selective logging. The difference between the Edwards et al (2011) sample and the present re-sample further highlights recovery in the study site as community compositions resemble those of primary more in the long-term dataset. Furthermore, the catch rate analysis supports re-dispersal between forest types, suggesting recovery as species track favourable conditions as forest succession is occurring. Other studies have reported a general trend of increasing species richness with increasing vegetation maturity (Blake and Loiselle, 1991; Urban and Smith 1989), which was observed here as species richness's are very similar between forest types. Dunn (2004) noted that the recovery of avian community composition and species richness occurs on separate time scales in selectively logged forests. Our results support this conclusion as community composition remained disparate between forest types, whereas the small difference in species richness was insignificant. Once fully recovered both richness and community composition should reflect those of primary forest. The presence of community recovery during the ~15 years post-logging in the present study is further strengthened given the differential rates of recovery observed in community composition and species richness. Thus, the avian community has not entered an extinction debt and has the potential to recover following selective logging.

4.1 Conservation implications

The impacts of selective logging on biodiversity and the reduction in concession value following logging do not linearly scale. After two rotations of selective logging biodiversity can persist and recover long-term, whereas the standing value of timber drops by 81% following two rotations of selective logging (Fischer et al, 2011). This discrepancy in cost vs benefit can be exploited for a

cost-effective method to enact conservation purchases. As the majority of South East Asia's forests are unlikely to escape at least one logging rotation (Edwards et al, 2010) there is huge potential for conservation purchases, which can be strategically targeted to serve conservation aims. Considering 16% of selectively logged forests are deforested within one year following logging (Asner et al, 2006), expansion of the protected area network and increasing its connectivity should be a priority. Protected areas can prevent government-sanctioned deforestation and further conversion to large-scale agricultural plantations (Gaveau et al, 2012), while simultaneously reducing deleterious edge effects and ensuring larger, more viable populations of forest-dwelling species (Fischer et al, 2011).

Post-logging silvicultural practices and forest rehabilitation methods designed to augment forest regeneration have the potential to aid biodiversity recovery in purchased areas (Putz et al, 2012). Rehabilitated forests have significantly higher species richness and diversities than naturally regenerating forests (Edwards et al, 2009) and have no adverse effect on species that decline following logging or species on the IUCN red list (Ansell, Edwards and Hamer, 2010). During regeneration logged forests sequest five times more carbon than a comparative primary forest (Berry et al, 2010), therefore creating carbon-biodiversity co-benefits. These co-benefits create potential for cashflow through carbon payments from the UN's Reduced Emissions from Deforestation and Degradation programme (REDD+). These funds can be used to purchase more degraded land and further expand the protected area network where carbon benefits exist, creating a feedback loop of payments useful for protecting more areas where carbon-biodiversity co-benefit exist.

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Bibliography

Aleixo, A. (1999). Effects of Selective Logging on a Bird Community in the Brazilian Atlantic Forest. *The Condor*, 101(3), pp.537-548.

Ansell, F., Edwards, D. and Hamer, K. (2010). Rehabilitation of Logged Rain Forests: Avifaunal Composition, Habitat Structure, and Implications for Biodiversity-Friendly REDD+. *Biotropica*, 43(4), pp.504-511.

Ansell, F., Edwards, D. and Hamer, K. (2010). Rehabilitation of Logged Rain Forests: Avifaunal Composition, Habitat Structure, and Implications for Biodiversity-Friendly REDD+. *Biotropica*, 43(4), pp.504-511.

Asner, G., Broadbent, E., Oliveira, P., Keller, M., Knapp, D. and Silva, J. (2006). Condition and fate of logged forests in the Brazilian Amazon. *Proceedings of the National Academy of Sciences*, 103(34), pp.12947-12950.

Asner, G., Rudel, T., Aide, T., Defries, R. and Emerson, R. (2009). A Contemporary Assessment of Change in Humid Tropical Forests. *Conservation Biology*, 23(6), pp.1386-1395.

Banks-Leite, C., Ewers, R. and Metzger, J. (2010). Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos*, 119(6), pp.918-926.

Berry, N., Phillips, O., Lewis, S., Hill, J., Edwards, D., Tawatao, N., Ahmad, N., Magintan, D., Khen, C., Maryati, M., Ong, R. and Hamer, K. (2010). The high value of logged tropical forests: lessons from northern Borneo. *Biodiversity and Conservation*, 19(4), pp.985-997.

Blake, G, J., and Loiselle, A, B. (1991). Variation in Resource Abundance Affects Capture Rates of Birds in Three Lowland Habitats in Costa Rica. *The Auk*, 108(1), pp.114-130

Blaser, J., Poore, D., Chandrasekaran, C., Hirakuri, S., Sarre, A., Johnson, S., Rubin, H., and Sobra, F, M. (2006). Status of Tropical Forest Management 2005. Summary Report. *International Forestry Review*, 8(3), pp. 372-374

Burivalova, Z., Şekercioğlu, Ç. and Koh, L. (2014). Thresholds of Logging Intensity to Maintain Tropical Forest Biodiversity. *Current Biology*, 24(16), pp.1893-1898

Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J., Schondube, J., de Freitas, S. and Fahrig, L. (2015). Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological Conservation*, 184, pp.117-126.

Cerullo, G. and Edwards, D. (2018). Actively restoring resilience in selectively logged tropical forests. *Journal of Applied Ecology*, 56(1), pp.107-118.

Cleary, D., Boyle, T., Setyawati, T., Anggraeni, C., Loon, E. and Menken, S. (2007). bird species and traits associated with logged and unlogged forest in Borneo. *Ecological Applications*, 17(4), pp.1184-1197.

Devictor, V., Julliard, R. and Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, 117(4), pp.507-514.

Dranzoa, C. (1998). The avifauna 23 years after logging in Kibale National park, Uganda. *Biodiversity and Conservation*, 7, pp.777-797

Driscoll, P, V., and Kikkawa, J. (1989). Bird Species Diversity of Lowland Tropical Rainforests of New Guinea and Northern Australia. *Vertebrates in Complex Tropical systems*, 69(1), pp. 123-152

Dunn, R, R. (2004). Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, 18(1), pp.302-309

Edwards, D., Larsen, T., Docherty, T., Ansell, F., Hsu, W., Derhé, M., Hamer, K. and Wilcove, D. (2010). Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), pp.82-90.

Edwards, P, D. and Laurance, F, W. Biodiversity Despite Selective Logging. Science, 339(6120), pp. 646-647

Fisher, B., Edwards, D., Larsen, T., Ansell, F., Hsu, W., Roberts, C. and Wilcove, D. (2011). Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. *Conservation Letters*, 4(6), pp.443-450.

Fisher, B., Edwards, D., Larsen, T., Ansell, F., Hsu, W., Roberts, C. and Wilcove, D. (2011). Cost-effective conservation: calculating biodiversity and logging trade-offs in Southeast Asia. *Conservation Letters*, 4(6), pp.443-450.

Fitzherbert, E., Struebig, M., Morel, A., Danielsen, F., Bruhl, C., Donald, P. and Phalan, B. (2008). How will oil palm expansion affect biodiversity?. *Trends in Ecology & Evolution*, 23(10), pp.538-545.

Gardner, T., Barlow, J., Araujo, I., Ávila-Pires, T., Bonaldo, A., Costa, J., Esposito, M., Ferreira, L., Hawes, J., Hernandez, M., Hoogmoed, M., Leite, R., Lo-Man-Hung, N., Malcolm, J., Martins, M., Mestre, L., Miranda-Santos, R., Overal, W., Parry, L., Peters, S., Ribeiro-Junior, M., Da Silva, M., Da Silva Motta, C. and Peres, C. (2008). The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, 11(2), pp.139-150.

Gardner, T., Barlow, J., Sodhi, N. and Peres, C. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation*, 143(10), pp.2293-2300.

Gaveau, D., Curran, L., Paoli, G., Carlson, K., Wells, P., Besse-Rimba, A., Ratnasari, D. and Leader-Williams, N. (2012). Examining protected area effectiveness in Sumatra: importance of regulations governing unprotected lands. *Conservation Letters*, pp. 147-148

Hamer, K., Newton, R., Edwards, F., Benedick, S., Bottrell, S. and Edwards, D. (2015). Impacts of selective logging on insectivorous birds in Borneo: The importance of trophic position, body size and foraging height. *Biological Conservation*, 188, pp.82-88.

Hill, J.K., & Hamer, K.C. (2004). Determining impacts of habitat modification on diversity of tropical forest fauna: The importance of spatial scale. *Journal of Applied Ecology*. 41, pp.744–754.

Honkanen, M., Roberge, J., Rajasärkkä, A. and Mönkkönen, M. (2009). Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography*, 19(1), pp.61-71.

Johns, A.G. (1996) Bird population persistence in Sabahan logging concessions. Biological Conservation, 75, pp.3-10.

Korthals, G, W. (1990). A description of the litter dwelling arthropod fauna in a primary and a secondary rain forest in North-east Borneo. Unpublished report. Amsterdam: Free University.

Lambert, F, R. (1992). The consequences of selective logging for Bornean lowland forest birds. *Philosophical Transactions of the Royal Society B*, 355, pp.443-457

Lawton, J.H., Bignell, D, E., Bloemers, G, F., Eggleton, P., Hammond, P, M., Hodda, M, Holt, R, D., Larsen, T, B., Mawdsley, N, A., Stork, D., Srivastava, S, D. and Watt, A, D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*. 391, pp.72-76.

Marsh C. W., Greer A. G. 1992Forest land-use in Sabah, Malaysia—an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B*, 335,pp. 331–339

Martin, P., Newton, A., Pfeifer, M., Khoo, M. and Bullock, J. (2015). Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *Forest Ecology and Management*, 356, pp.224-233.

Mason, D. (1996). Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting. *Biotropica*, 28, pp.296-309

MCCARTHY, J. and CRAMB, R. (2009). Policy narratives, landholder engagement, and oil palm expansion on the Malaysian and Indonesian frontiers. *Geographical Journal*, 175(2), pp.112-123.

Oksanen, F, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Peter, R., Minchin, R, B., Simpson, L, G., Solymos, P., Stevens H, M. Szoecs, E., and Wagner, H. (2018). vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan

Petchey, O., Evans, K., Fishburn, I. and Gaston, K. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76(5), pp.977-985.

Pimm, S. and Sugden, A. (1994). Tropical Diversity and Global Change. Science, 263(5149), pp.933-934.

Pinard, M., Howlett, B. and Davidson, D. (1996). Site Conditions Limit Pioneer Tree Recruitment After Logging of Dipterocarp Forests in Sabah, Malaysia. *Biotropica*, 28(1), p.2.

Pineda-Diez de Bonilla, E., León-Cortés, J. and Rangel-Salazar, J. (2012). Diversity of bird feeding guilds in relation to habitat heterogeneity and land-use cover in a human-modified landscape in southern Mexico. *Journal of Tropical Ecology*, 28(4), pp.369-376.

Putz, F., Zuidema, P., Synnott, T., Peña-Claros, M., Pinard, M., Sheil, D., Vanclay, J., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J. and Zagt, R. (2012). Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters*, 5(4), pp.296-303.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Sodhi, N, S., Koh, L, P., Brook, B, W. and Ng, P, K. (2004). Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution*, 19(12), pp. 654-660.

Sodhi, N., Koh, L., Clements, R., Wanger, T., Hill, J., Hamer, K., Clough, Y., Tscharntke, T., Posa, M. and Lee, T. (2010). Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation*, 143(10), pp.2375-2384.

Sodhi, N., Posa, M., Lee, T., Bickford, D., Koh, L. and Brook, B. (2009). The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation*, 19(2), pp.317-328.

Srinivasan, U. (2013). A slippery slope: logging alters mass-abundance scaling in ecological communities. *Journal of Applied Ecology*, 50(4), pp.920-928.

Srinivasan, U., Hines, J. and Quader, S. (2015). Demographic superiority with increased logging in tropical understorey insectivorous birds. *Journal of Applied Ecology*, 52(5), pp.1374-1380.

Terraube, J., Guixé, D. and Arroyo, B. (2014). Diet composition and foraging success in generalist predators: Are specialist individuals better foragers?. *Basic and Applied Ecology*, 15(7), pp.616-624.

Thinh, V., Doherty, P. and Huyvaert, K. (2012). Effects of different logging schemes on bird communities in tropical forests: A simulation study. *Ecological Modelling*, 243, pp.95-100.

Thiollay, J, M. (1997). Disturbance, selective logging and bird diversity: a Neotropical forest study. *Biodiversity & Conservation*, 6(8), pp.1155-1173

Urban, L, D., and Smith, M, T. (1989). Microhabitat Pattern and the Structure of Forest Bird Communities. *The American Naturalist*, 133(6), pp. 811-829

Whitmore T. C. (1984). Tropical rain forests of the Far East, 2nd edn.Oxford, UK: Clarendon Press

Wilcove, D., Giam, X., Edwards, D., Fisher, B. and Koh, L. (2013). Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, 28(9), pp.531-540.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. and Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(7), pp.2027-2027.