Logging alters tropical forest structure, while conversion reduces biodiversity and functioning

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Abstract: Tropical forests are threatened by degradation and deforestation but the consequences for these ecosystems are poorly understood, particularly at the landscape scale. We present the most extensive ecosystem analysis to date of the impacts of logging and conversion of tropical forest to oil palm from a large-scale study in Borneo, synthesizing responses from 79 variables categorized into four hierarchical ecological 'levels': 1) structure and environment, 2) species traits, 3) biodiversity and 4) ecosystem functions. Variables at the lowest levels that were directly impacted by the physical processes of timber extraction, such as soil characteristics, were sensitive to even moderate amounts of logging, whereas biodiversity and ecosystem functions proved remarkably resilient to logging in many cases, but were more affected by conversion to oil palm plantation.

One-Sentence Summary: Logging tropical forest mostly impacts structure while biodiversity and functions are more vulnerable to habitat conversion

Main Text:

Tropical forests play key roles in supporting biodiversity and ecosystem service provision, but their structure and functioning are threatened by degradation and conversion to other land uses (*1*, *2*). A major cause of tropical forest degradation is selective logging which can make areas vulnerable to subsequent deforestation (*3–5*). In Southeast Asia, many forests have been subjected to multiple rounds of logging for timber, and then converted to oil palm plantations (*6*, *7*) resulting in large-scale forest losses (3.25 Mha in Malaysia and Indonesia between 2000 and 2011 (*8*)) and enhanced carbon emissions (4,051 $MtCO_2$ in the same countries over the same period (*8*)), with ~45% of Southeast Asian oil palm plantations being established on previously forested land (*9*).

However, knowledge of the full environmental impacts of deforestation and tropical land use change is limited (*10–12*). In particular, there are few comprehensive assessments of impacts on biodiversity and the multiple ecosystem functions and services that tropical forests provide, including stocks and flows of carbon, nutrients and water (*13*). The logistical challenges of studying the structure and functioning of hyper-diverse tropical forest ecosystems means that few studies have encompassed the full forest degradation gradient and simultaneously explored the wider impacts on both biodiversity and ecosystem functions present within tropical forests at the landscape scale.

Here, we undertake the most comprehensive assessment to date of how biodiversity, structure and functioning of these tropical forest ecosystems are altered across a gradient of

disturbance by an increasing intensity of selective logging and conversion of forest to oil palm plantation. We synthesize data from 79 metrics of ecosystem properties collected as part of a coordinated large-scale study. We use a replicated design and standardized analyses to quantify the impacts of selective logging and land-use change across different intensities of disturbance from: (1) undisturbed old-growth forest (OGF), through (2) moderately logged (MLF) and (3) highly logged (HLF) forest, to (4) oil palm plantation (OP). Our study sites are located in areas of intact and disturbed lowland dipterocarp rainforest and oil palm plantation in the Malaysian state of Sabah, Borneo (Fig. 1a). Forests along the disturbance intensity gradient were characterised by a decrease in basal area of mature trees, a more open canopy, fewer large trees and a higher proportion of pioneer tree species (see Methods for details). Measurements with airborne LiDAR showed a progressive reduction of canopy height and simplification of canopy structure from OGF to MLF and HLF (Fig. 1), culminating in a homogeneous, single low layer in oil palm plantations.

We quantified 79 response variables (Tables S1-4) detailing ecosystem properties sampled in OGF and one or more of the disturbed habitat categories. Each property was categorized into four levels according to an ecological hierarchy, building in complexity and distance from the direct impacts of logging, and where each higher level can be considered an emergent feature of lower levels. Level 1 comprised variables related to soil properties, microclimate and forest structure that are directly affected by the physical processes of timber extraction. Level 2 constituted the individual traits of the remaining tree community reflecting the change in plant species composition caused by selective logging. Level 3 quantified multi-trophic biodiversity, from assemblages of soil microorganisms to consumers in higher trophic orders, that strongly depend on the abiotic and structural conditions described in level 1, and the tree community

diversity and composition in level 2. Level 4 corresponded to ecosystem functions, which are largely defined by the composition of communities described in the lower levels.

To allow comparison of multiple responses, we standardized all variables as z-scores (by dividing by their standard deviations) before analyzing them using linear mixed-effects models to assess effects across the disturbance intensity gradient while taking account of the spatial hierarchical structure of our datasets. If possible, datasets were analysed across multiple facets and spatial scales. For example, we calculated three measures of the effective number of species for some biodiversity datasets (*14*), relating to species richness (Hill number $q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$). Although positive or negative responses for some variables have clear desirable or undesirable consequences, for others such as β-diversity, there is no obvious value judgement. We therefore focus on examining whether each variable changed from levels recorded within OGF, and where along the gradient change occurred.

Overall, 57 of the 79 response variables showed significant differences across the disturbance intensity gradient, far more than the expected level of false positives in the absence of any effect of disturbance (Figure 2, solid lines). The proportion of significant results and the degree of variation explained by disturbance intensity (the mean marginal R^2 from linear mixed-effects models for group), varied with level in the ecological hierarchy of the response variable. Generally, the responses that showed the strongest effect of disturbance intensity were those most directly affected by logging (*15*) — level 1, quantifying aspects of forest environment and structure (OP sampled = 0.210 ± 0.034 s.e., 9 out of 12 variables significant; OP excluded = 0.185 ± 0.075, all 3 variables significant) and level 2, aggregated tree traits (red backgrounds in Fig. 2; OP excluded = 0.253 ± 0.029, all 3 variables significant) (*15*). Biodiversity measures showed stronger responses to disturbance intensity in variables where oil palm was sampled than

those measured in forest habitats only (OP sampled = 0.232 ± 0.023, 11 out of 13 variables significant; OP excluded = 0.114 ± 0.025, 9 out of 10 variables significant). While they were affected, variables at the highest hierarchical level — ecosystem functioning — showed weaker responses to disturbance intensity, with little change across the gradient for some variables (OP sampled = 0.086 ± 0.028, 2 out of 3 variables significant; OP excluded = 0.079 ± 0.018, 3 out of 4 variables significant) (*16*).

While some variables showed simple, monotonic responses to disturbance intensity (e.g. estimates of biomass carbon stocks decreased, while frequency of photosynthetic traits associated with earlier successional species increased), other variables responded in a more complex manner (e.g. stem respiration increased in MLF but decreased to levels lower than in OGF in OP). Some patterns were also scale-dependent. For example, bat species richness decreased linearly across the disturbance intensity gradient at fine scales, but was highest in MLF at coarse scales, perhaps driven by an increase in community turnover and influxes of disturbance-adapted species in logged forest (*17*).

To investigate the relative robustness of the different variables to disturbance intensity, we used simple statistical contrasts to determine the point along the gradient where each variable was most affected. The variables showed a wide range of responses, but with some levels of ecological hierarchy responding in broadly similar ways (Fig. S1 shows the results for variables measured only in forest and not in OP). For example, at level 1, components of the forest structure and environment (Fig. 3, blue text labels) were generally more sensitive to a moderate degree of logging (the variables with the large green bars at the bottom of Fig. 3). This was especially the case for variables directly altered by the logging process itself, such as soil bulk density that was compacted by machinery (*18*), and above-ground carbon stock that was reduced

by active timber removal (*19–21*). In level 2, we also recorded major changes in the leaf area index and traits of the remaining mature tree community that were consistent with the effects of selective logging (*15*, *22*). As selective logging targets tree species with the most commercially desirable characteristics, it results in a higher proportion of early successional species (*19*) that invest in traits that increase photosynthetic ability and rapid growth, but a reduced proportion of species with structural traits that aid longevity (*22*).

By contrast, at level 3, biodiversity components (Fig. 3, dark red text labels) were mostly altered by the conversion of logged forest to oil palm (the variables with large blue bars at the top of Fig. 3b) (*6*, *10*, *23*). This was particularly true of taxonomic groups at higher trophic-levels, such as birds (*10*, *20*), where increased mobility and behavioral plasticity may buffer their sensitivity to change until conditions become drastically altered (*24*). The diversity of exothermic groups, such as dung beetles, which can be particularly responsive to changes in microclimate (*25*, *26*), showed a slightly increased sensitivity to the initial impacts of logging than endothermic taxa, such as birds and bats. The richness of microbes, such as soil microorganisms, showed the greatest sensitivity to logging, although there were both negative (ectomycorrhizal fungi (*27*, *28*)) and positive (bacteria (*29*, *30*)) responses to the disturbance intensity gradient. Finally, at the highest ecological level, ecosystem functions (Fig. 3, green text labels) showed the weakest and most variable patterns (marginal R^2 values shown by high transparency of bars in Fig. 3). For example, although dung beetle richness and abundance decreased significantly along the disturbance intensity gradient, dung removal levels were maintained even in oil palm plantations (*31*). Previous research at the study sites found that, while a taxonomic group that dominates a particular function might decline along the logging

gradient, different taxonomic groups may increase their contribution, such that ecosystem functions are maintained at similar levels along the gradient (*24*).

Our findings increase understanding of ecosystem impacts of habitat change in the tropics. Lower-level properties, such as forest structure and tree traits, were the most affected during the transition from old-growth to logged forest, probably because these factors are directly affected by disturbance and timber removal. In contrast, biodiversity properties, such as species richness and abundance, were relatively robust to initial rounds of logging, with diversity of higher trophic-level taxa and ecosystem functions the most resilient. This is likely to be related to a number of factors including effects at the species, community and landscape scales (*32*). The relative stability of ecosystem functions may also be related to the large spatial scale of this study, which can enhance the relationship between biodiversity on ecosystem functions and services (*33*). At the community and species-level, it is likely that multiple species contributing to the same ecosystem functions resulted in a degree of functional redundancy that confers greater resilience of ecosystem functions to disturbance ("the insurance hypothesis" or "portfolio effect"). This can especially be the case where species are ecologically different such that response traits are diverse (*34*), response and effects traits of species are not correlated (*35*) and species networks are dominated by generalized interactions (*32*). In some cases, such as with abundant and disturbance-tolerant dung beetles, it is also likely that density compensation may have occurred, with highly-abundant species increasing their number and contribution to ecosystem functioning in disturbed habitats in response to declines in other species (*36*).

Our results also have implications for land use management and restoration in the tropics. First, different types of land use — in this case selective logging *vs* conversion to oil palm plantation — have different environmental impacts. Second, even a single type of land use can

have divergent impacts when the environment is assessed comprehensively to encompass both its biological diversity and the multiple ecosystem functions and services that it provides. In nearly all cases, we found that that the initial rounds of logging had more widespread impacts than further increases in logging intensity (i.e. logging of OGF to MLF had greater effects than intensification from MLF to HLF). This result is likely explained by the relatively greater initial loss of habitat structure that occurs when forest is selectively logged, with consequences for species interactions and microclimate. However, the cumulative effects of ongoing degradation and conversion caused oil palm plantations to have the lowest levels of biodiversity. These results highlight the value of maintaining forest habitat in the region (*20*) and the relative robustness of ecosystem processes to multiple rounds of disturbance (*23*).

Understanding the points across disturbance intensity gradients at which biodiversity and associated ecosystem functions are most affected represents an important starting point for identifying potential 'tipping points' and priority habitats for conservation and restoration (*37*, *38*). Such understanding is needed urgently to halt and reverse global biodiversity declines (*39*), and to support ecosystem service provision in complex, multi-use tropical landscapes (*40, 41*).

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Data and materials availability: Markdown documents containing R code and their outputs for the exploration of data, analysis and presentation of results for all 79 variables used in the study, along with the processed z-score standardised data, are available at https://github.com/charliem2003/BALI_synthesis. The raw data, with associated DOIs, for individual datasets are archived for public access at https://www.zenodo.org/communities/safe/.

Supplementary Materials:

Materials and Methods

Figs. S1 to S5

Tables S1 to S4

References (42-72)

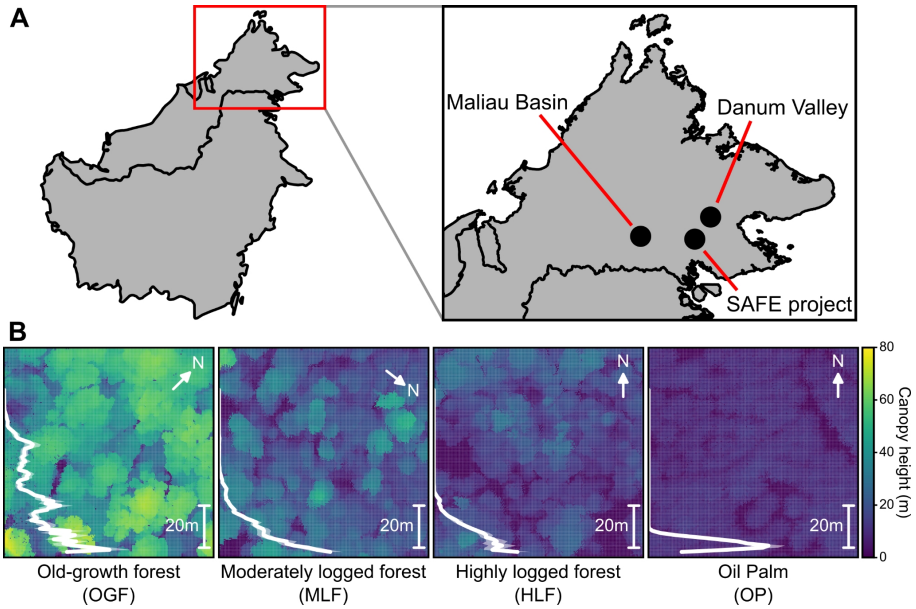

Fig. 1. Study sites and disturbance categories. (**A**) Location of the study sites in Sabah, Malaysian Borneo. (**B**) Canopy height profiles of the study systems for representative 1 ha plots (from left to right): old-growth forest (OGF), moderately logged forest (MLF), highly logged forest (HLF), and oil palm plantation (OP). Backgrounds show the maximum canopy height for each pixel, and inset graphs show the plant area density (mean ± 95% C.I.) of the vertical forest structure estimated through LiDAR.

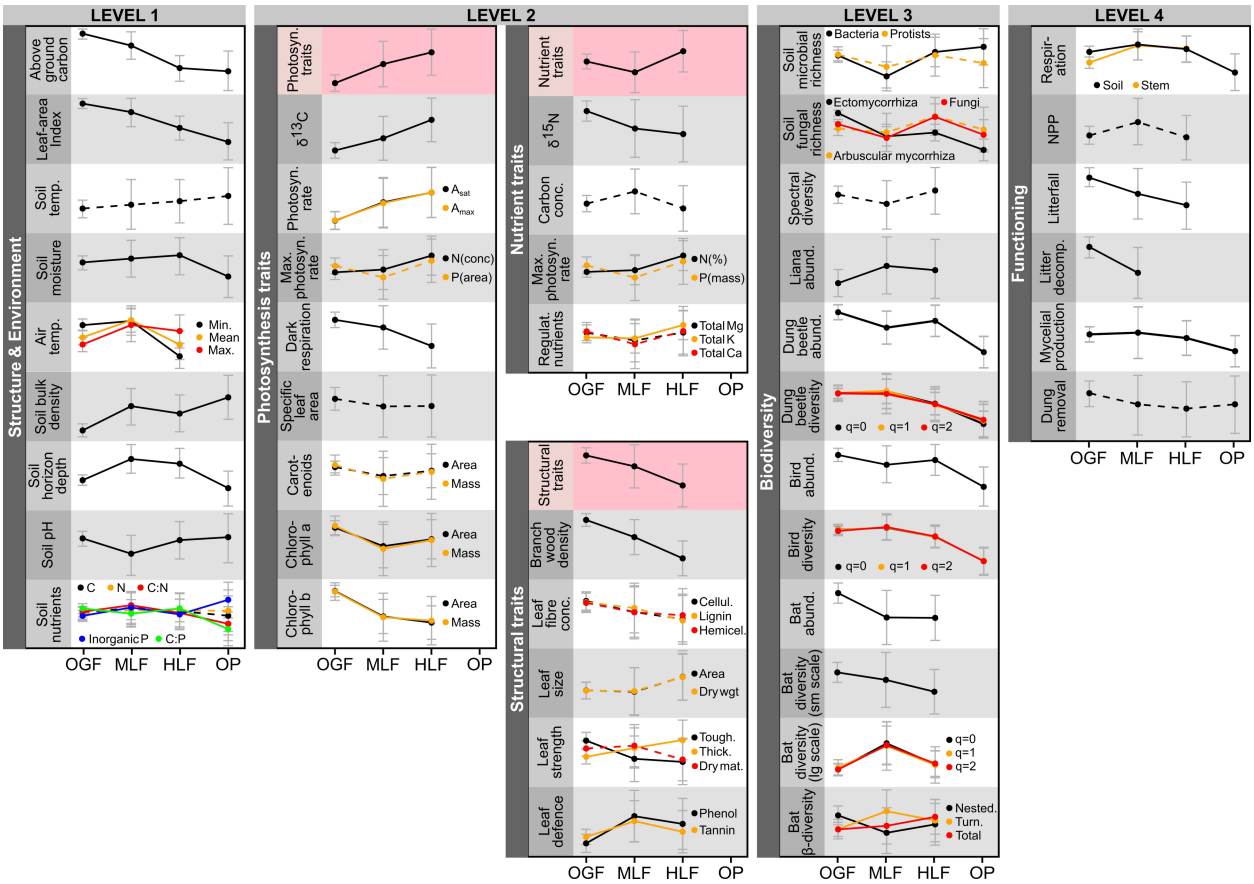

Fig. 2. Changes in different categories of the measured response variables across the disturbance gradient when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). Points show z-score standardized means (± 95% C.I.). Line type indicates whether a model with disturbance was significantly different from a null model with no disturbance (solid lines = significant, $p < 0.05$; dashed lines = non-significant). Tree traits were analyzed individually (Fig. S4) as well as in combination via the first axis of a PCA (red backgrounds).

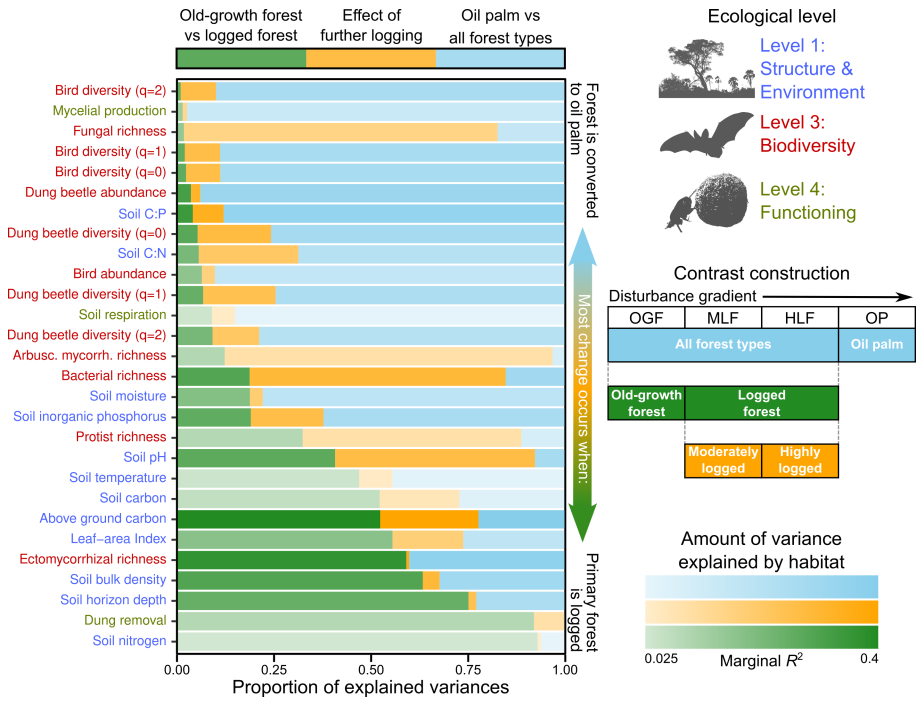

Fig. 3. Impacts of different degrees and types of disturbance when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). The overall effect of disturbance was partitioned into three single degree of freedom contrasts that compare: 1) the effect of logging old-growth forest (old-growth *vs* logged forest: OGF *vs* MLF-HLF; green bars); 2) further logging of moderately logged forest (MLF *vs* HLF; orange bars); and 3) converting forest to oil palm plantation (oil palm *vs* the combined forest types: OP *vs* OG-MLF-HLF; blue bars). The transparency for each variable is inversely related to its explanatory power (the marginal R^2 from the linear mixed-effects model). Response variables are categorized into ecological hierarchies: those related to the forest structure and environment (level 1; blue text); those related to biodiversity (level 3; dark red text); and those related to ecosystem functioning (level 4; dark green text), and are ordered by the size of the effect of logging OGF (variables at the bottom are mostly affected when OGF is logged, whereas those at the top are mostly affected when forest is converted to oil palm). Results of contrasts for

datasets that did not sample oil palm plantations, which includes all variables for level 2 (tree traits), are shown in Fig. S1 of the supplementary material.