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

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Abstract: The impacts of degradation and deforestation on tropical forests are poorly understood, particularly at landscape scales. 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 82 variables categorized into four ecological 'levels': 1) structure and environment, 2) species traits, 3) biodiversity, and 4) ecosystem functions. Responses were highly heterogeneous. Variables that were directly impacted by the physical processes of timber extraction were sensitive to even moderate amounts of logging, whereas biodiversity and ecosystem functions proved 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 services, 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 for timber which can increase vulnerability to subsequent deforestation (*3–5*). In Southeast Asia, many forests have experienced multiple rounds of selective logging, with some 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 increased carbon emissions (4,051 $MtCO_2$ in the same countries over the same period (*8*)). Indeed, ~45% of Southeast Asian oil palm plantations have been established through direct clearing of forest (*9*).

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 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 at the landscape scale. Here, we undertake the most comprehensive assessment to date of how biodiversity, structure, and functioning of tropical forest ecosystems are altered across a disturbance gradient of increasing intensity of selective logging and conversion to oil palm plantation. We synthesize data from 82 metrics of ecosystem properties, collected as part of a coordinated large-scale study in the Stability of Altered Forest Ecosystems (SAFE) Project (*14*) and associated sites in the Malaysian state of Sabah, Borneo (Fig. 1a), where patterns of deforestation are representative of other regions of Southeast Asia

(*15*). Study sites were located in areas of intact and disturbed lowland dipterocarp rainforest and oil palm plantations.

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) old-growth forest (OGF), through (2) moderately logged (MLF) and (3) highly logged (HLF) forest, to (4) oil palm plantation (OP). To allow us to synthesize the effects of habitat change on the whole ecosystem for the first time, we focus on understanding the comprehensive impacts of changes, rather than assessing specific drivers affecting each metric. Logged forest sites had an average of ca. 113 m^3 ha^{-1} of timber harvested during 1978, with a second cycle of harvesting in the late 1990s to early 2000s, removing a further ~66 m^3 ha^{-1} in three rounds (HLF sites) or ~37 m^3 ha^{-1} in two rounds (MLF). Forests along the disturbance intensity gradient were characterized 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.

The 82 response variables (Tables S1-5) detail ecosystem properties sampled in OGF and one or more of the disturbed habitat categories. Each property was categorized into one of four levels, building in complexity and distance from the direct impacts of logging. Although the assignment of responses to levels were somewhat arbitrary, they provide a useful framework for summarizing the ecosystem effects of logging and conversion, as each higher level generally captures features of properties at 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 and oil palm cultivation. Level 2 constituted the individual traits of the remaining tree community reflecting the change in plant species composition caused by selective

logging, as well as subsequent colonization and growth of early successional species. Traits were grouped according to whether they contributed to structural stability and defence (structural), were related to leaf photosynthetic potential and leaf longevity (photosynthesis), or were related to concentrations of key mineral nutrients (nutrient). 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 levels 2 and 3.

To allow comparison of multiple responses on a single scale, we standardized all variables as z-scores (by mean-centering and dividing by their standard deviations) before analyzing them using linear mixed-effects models to assess effects across the disturbance gradient while taking account of the spatial hierarchical structure of our datasets. If possible, datasets were analyzed across multiple facets and spatial scales (Table S1). For example, we calculated three measures of the effective number of species for some biodiversity datasets (*16*), relating to species richness (Hill number $q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$). Similarly, we analyzed the species richness of some groups at the finest spatial grain at which those data were collected, but also aggregated data to coarser grain sizes. 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 judgment. We therefore focus on examining whether each variable changed from values recorded within OGF, and where along the gradient change occurred.

Overall, 60 of the 82 response variables showed significant differences across the disturbance intensity gradient (Likelihood Ratio Tests (*LRT*) against a null model with no disturbance factor: $p < 0.05$; Table S6), far greater than the expected level of false positives (~4

out of 82 expected with a significance threshold of $p < 0.05$) 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; Table S6), varied with ecological level of the response variable. Generally, the responses that showed the strongest effect of disturbance were those most directly affected by logging (*17*) — level 1, quantifying aspects of forest environment and structure (mean marginal $R^2 \pm$ s.e. for datasets with OP included = 0.210 ± 0.034, 9 out of 12 variables LRT $p < 0.05$; OP excluded = 0.228 ± 0.068, all 4 variables LRT $p < 0.05$) and level 2, aggregated tree traits (red backgrounds in Fig. 2; OP excluded = 0.253 ± 0.029, all 3 variables LRT $p < 0.05$). Biodiversity measures, level 3, showed stronger responses to disturbance intensity in variables where oil palm was sampled than those measured in forest habitats only (OP included = 0.232 ± 0.023, 11 out of 13 variables LRT $p < 0.05$; OP excluded = 0.113 ± 0.021, 11 out of 12 variables LRT $p < 0.05$). While they were affected, ecosystem functioning variables showed weaker responses to disturbance intensity, with little change across the gradient for some variables (OP included = 0.081 ±0.021, 2 out of 4 variables LRT $p < 0.05$; OP excluded = 0.087 ± 0.023, 3 out of 3 variables LRT $p < 0.05$) (*18*).

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 (*19*). However, overall, different impacts of land-use

change were heterogeneous, often non-linear and frequently not strongly correlated. Therefore, due to complex interactions, feedbacks and system redundancy, the impacts of logging and conversion defy simple interpretations.

To investigate the relative robustness of the different variables to disturbance intensity, we used sequential statistical contrasts to determine the stage along the disturbance gradient at which each variable was most affected: the initial logging of old-growth forest, further rounds of logging, or conversion to oil palm. The variables showed a wide range of responses, but with some ecological levels responding in broadly similar ways. 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 (*20*), and above-ground carbon stock that was reduced by timber removal (*21–23*), indicating that impacts on variables at level 1 are likely due to the direct effects of the timber removal and the conversion process, even several decades after they have taken place. In level 2, we recorded major changes in the traits of the mature tree community that were consistent with the effects of selective logging (*17*, *24*). This is likely due to selective logging actively targeting tree species with the most commercially desirable characteristics, effectively reducing the incidence of traits such as structural features that aid longevity (*24*), while increasing the incidence of traits such as high photosynthetic rates and rapid growth (*21*), which are associated with species of low commercial value and early successional species that colonize open areas following logging.

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*, *25*). This was particularly true of taxonomic groups at higher trophic-

levels, such as birds (*10*, *22*), where increased mobility and behavioral plasticity may buffer their sensitivity to change until conditions become drastically altered (*26*). In highly disturbed oil palm plantations, the severe changes in plant food resources, reduced structural complexity, and shift to hotter, drier, and more variable microclimatic conditions, likely resulted in the reduced abundance and diversity of many taxa, and survival of only disturbance tolerant species (*27*). The diversity of ectothermic groups, such as dung beetles, which can be particularly responsive to changes in microclimate (*28*), showed a slightly increased sensitivity to the initial impacts of logging than endothermic taxa, such as birds and bats. The richness of soil microorganisms showed the greatest sensitivity to logging, although there were both negative (ectomycorrhizal fungi (*29*, *30*)) and positive (bacteria (*31*)) responses to disturbance. The impact on ectomycorrhizal fungi is likely to be particularly important from conservation and restoration perspectives, given their role in supporting canopy-dominant dipterocarps (*32*).

Finally, 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, Table S6). For example, rates of dung removal were maintained in oil palm plantations, even though dung beetle richness and abundance decreased significantly with disturbance (*33*), with a small number of disturbance-tolerant species increasing their contribution to dung removal in disturbed habitats (*34*). Such functional redundancy may confer greater resilience of ecosystem functions to disturbance ("the insurance hypothesis" or "portfolio effect"). For example, previous research at the study sites found that, while a taxonomic group that dominates litter decomposition and seed and invertebrate predation might decline along the logging gradient, different taxonomic groups increase their contribution, maintaining ecosystem functions at similar levels (*26*). The relative stability of ecosystem functions may also be related to the large spatial extent and

connectivity of the habitat blocks investigated, which can enhance the relationship between biodiversity and ecosystem functions and services (*35*).

210 Our findings increase understanding of the ecosystem-wide impacts of habitat change in the tropics, with implications for land-use management and restoration. In particular, different land-uses — in this case selective logging *vs* conversion to oil palm plantation — have different environmental impacts. Additionally, even a single type of land use can have divergent impacts when the environment is assessed comprehensively to encompass its abiotic and biotic structure, 215 biological diversity, and the multiple ecosystem functions and services that it provides. We therefore stress the importance of considering a broad range of ecological properties when making land-management, conservation, and research decisions. Factors associated with level 1 are highly sensitive to disturbance, so even low intensity logging will result in changes in these characteristics, highlighting the importance of maintaining intact, undisturbed forest. By contrast, 220 if the aim is to maintain high biodiversity, then disturbed forest can still be valuable, consistent with findings from other studies in the region (*22*, *25*), whereas the negative effects on biodiversity are much larger when forest is converted to oil palm. Therefore, while conserving remaining old growth forests is important, protecting degraded logged forest may also contribute to maintaining biodiversity and ecosystem functioning. This validates an increasing focus within 225 tropical agricultural systems of maintaining forest in sensitive areas within plantations, such as steep slopes and river margins (e.g., as highlighted by the Roundtable on Sustainable Palm Oil (RSPO) (*36*)), where it can support biodiversity (*37*) and ecosystem processes (*38*). The reduction in some taxa, such as birds and ectomycorrhizal fungi, and some ecosystem functions, such as mycelial production, within oil palm also has implications for crop management, and 230 could affect nutrient cycling and predator control.

Understanding at which points in the deforestation pathway biodiversity and associated ecosystem functions are most affected represents an important starting point for identifying priority habitats for restoration (*39*, *40*)). This can aid decision-making on when to implement restoration, to halt and reverse global biodiversity declines, and to support ecosystem service provision in complex, multi-use tropical landscapes (*41*, *42*)), but requires multiple facets of an ecosystem to be considered to avoid unintended consequences. This study provides a detailed synthesis of the responses of a tropical forest ecosystem to degradation and deforestation that is unprecedented in its breadth. Responses were complex, with some, such as different aspects of vertebrate diversity, showing consistent patterns along the gradient, and others, such as ecosystem functions, showing heterogeneous responses. As this study represents only a single location and ecosystem, future research should establish whether responses are consistent across ecosystems, or if certain components show high heterogeneity between ecosystems, indicating unpredictability in how ecosystems respond to land-use change.

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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 82 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 S4

Tables S1 to S6

References (43-74)

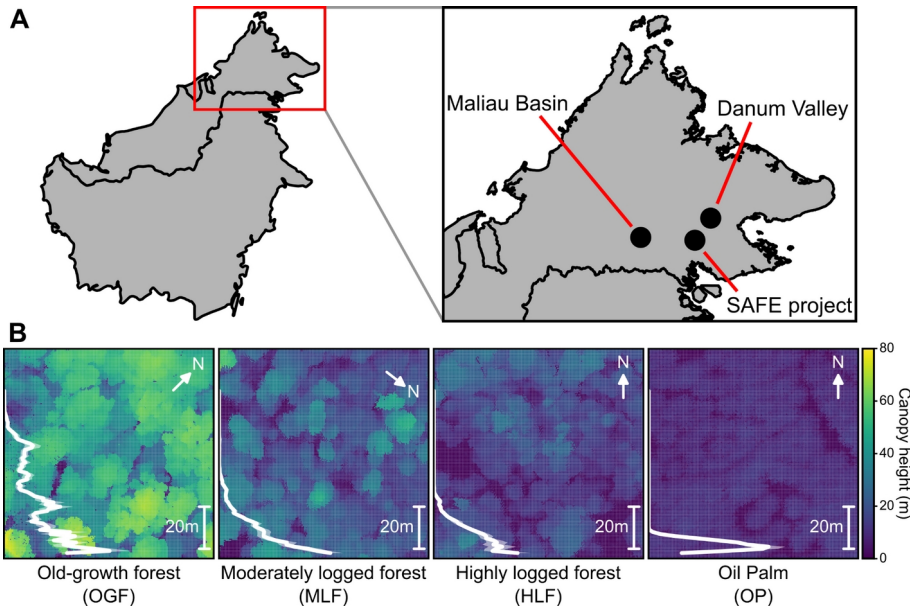

Fig. 1. Study sites and disturbance categories. (**A**) Location of the study sites in Sabah, Malaysian Borneo. (**B**) Canopy height profiles of the study systems for representative 1 ha plots (from left to right): old-growth forest (OGF), moderately logged forest (MLF), highly logged forest (HLF), 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.

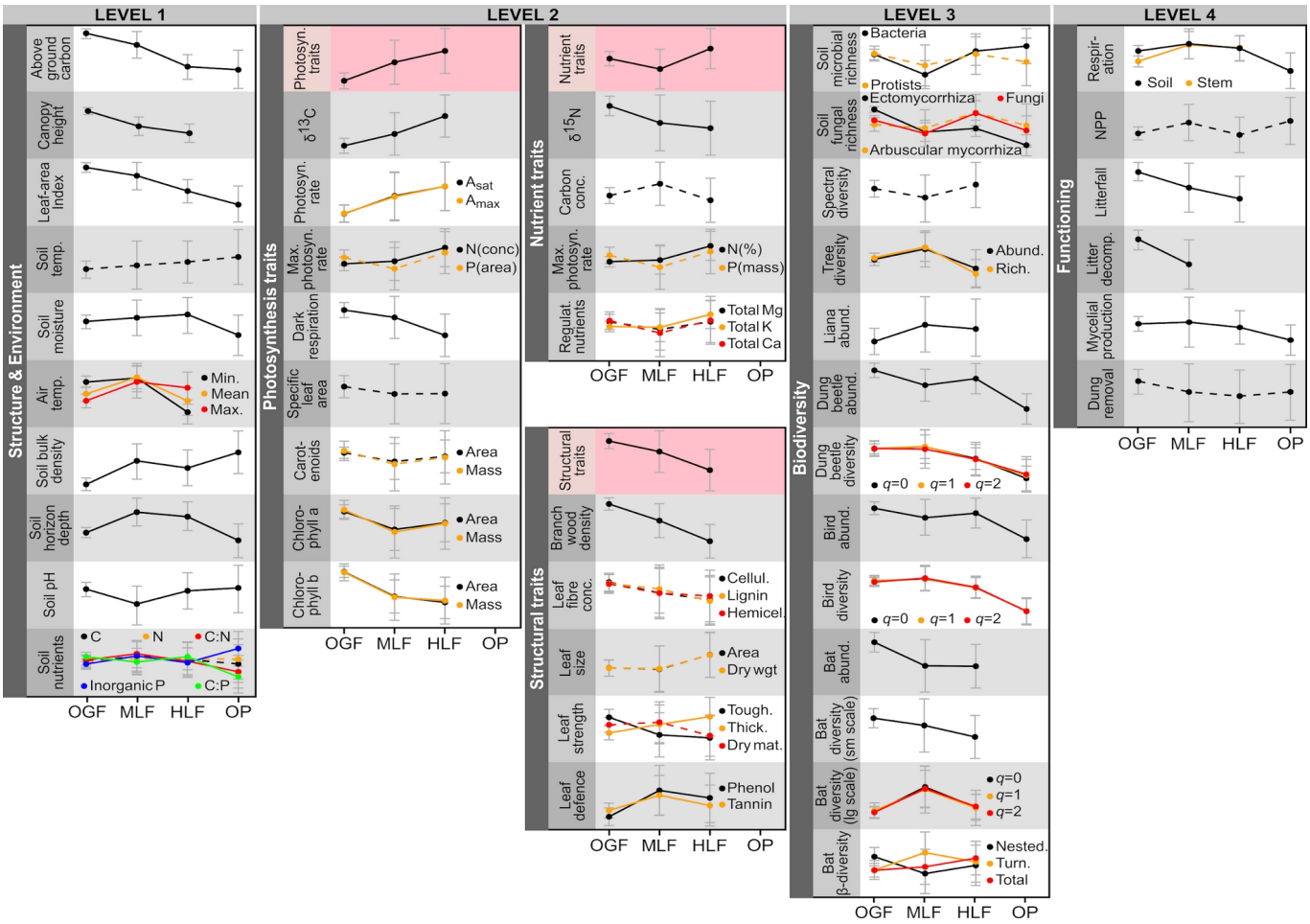

Fig. 2. Changes in different categories of the measured response variables across the disturbance gradient when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). Points show z-score standardized means (± 95% C.I.). Line type indicates whether 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 (level 2) were analyzed individually (Fig. S3) as well as in combination via the first axis of a PCA (red backgrounds).

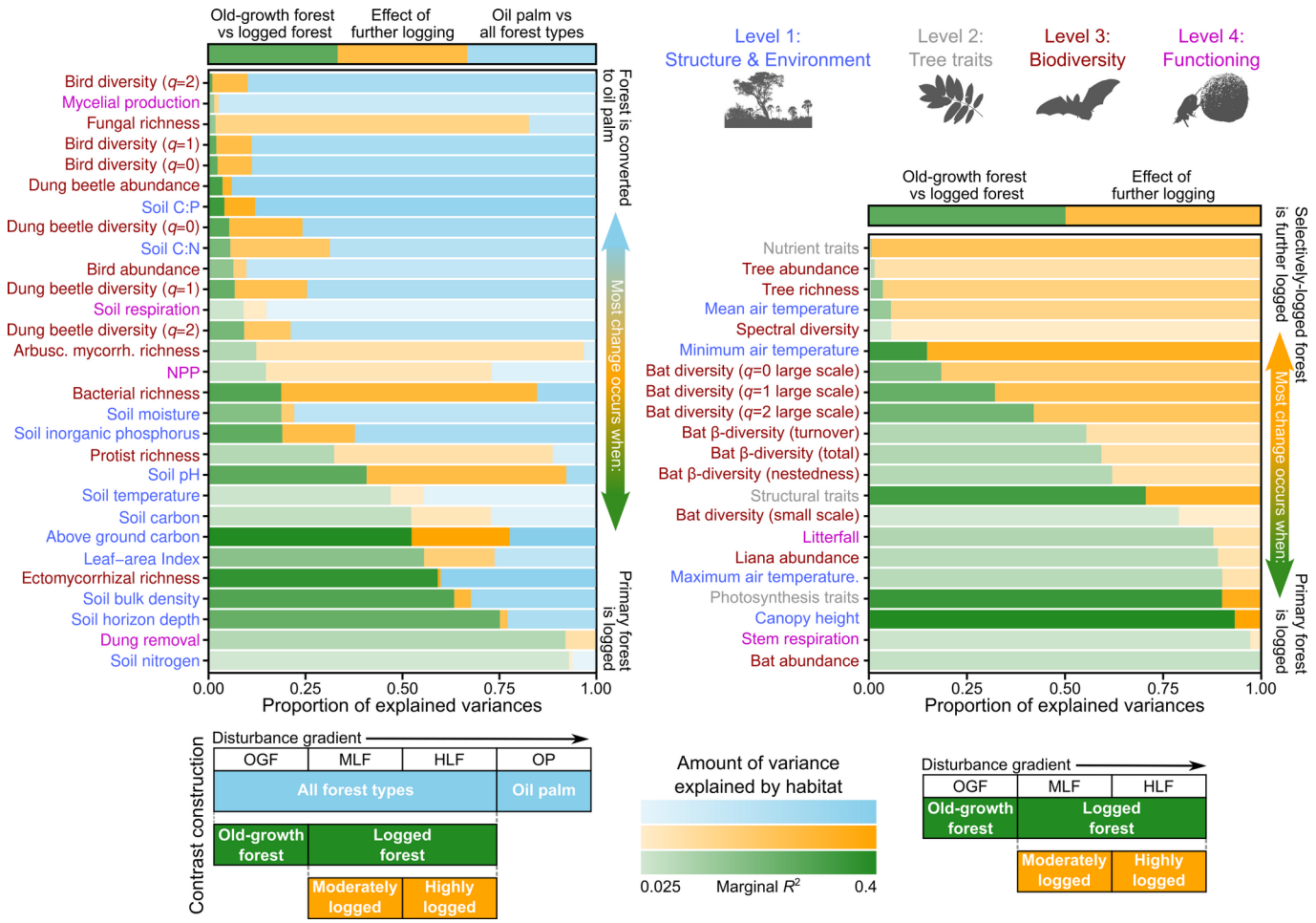

Fig. 3. Impacts of different degrees and types of disturbance when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). The overall effect of disturbance was partitioned into two (for datasets that did not sample in oil palm; right panel) or three (for datasets that did sample in oil palm; left panel) 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 levels: 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).