TROPICAL FORESTS

Tropical forest clearance impacts biodiversity and function, whereas logging changes structure

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The impacts of degradation and deforestation on tropical forests are poorly understood, particularly at landscape scales. We present an extensive ecosystem analysis 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 spanning a broad suite of ecosystem properties: (i) structure and environment, (ii) species traits, (iii) biodiversity, and (iv) ecosystem functions. Responses were highly heterogeneous and often complex and nonlinear. Variables that were directly impacted by the physical process of timber extraction, such as soil structure, were sensitive to even moderate amounts of logging, whereas measures of biodiversity and ecosystem functioning were generally resilient to logging but more affected by conversion to oil palm plantation.

Tropical forests support biodiversity and provide ecosystem services, such as stocks and flows of carbon, nutrients, and water, 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 [4051 metric tons CO_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 logging and forest conversion in the tropics to other land uses, such as oil palm (the forest disturbance gradient), is limited (*10*–*12*). The logistical challenges of studying highly biodiverse tropical forest ecosystems means that there are few comprehensive assessments of the impacts on biodiversity and the multiple ecosystem functions and services that tropical forests provide across the full disturbance gradient at the landscape scale (*13*). In this study, we undertook a comprehensive assessment 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 and examine the points along that gradient where changes from old-growth forest conditions are most apparent.

We synthesized data from 82 metrics of ecosystem properties that collectively provide a comprehensive assessment of environmental and ecological conditions, capturing aspects of the forest structure and environment as well as measures of biodiversity and ecosystem functioning. Data were collected as part of a coordinated large-scale study in the Stability of Altered Forest Ecosystems (SAFE) Project (*14*) and associated sites of the Human Modified Tropical Forests (HMTF) program in the Malaysian state of Sabah, Borneo (Fig. 1a), where patterns of deforestation are representative of other regions in Southeast Asia (*15*). Study sites were located in areas of intact and disturbed lowland dipterocarp rainforest and oil palm plantations.

We used a replicated experimental design and standardized analyses (sample sizes ranging from 27 to 373,968 across the 82 variables; table S1) to quantify the impacts of selective logging and land-use change across different intensities of disturbance from (i) old-growth forest (OGF), through (ii) moderately logged (MLF) and (iii) highly logged (HLF) forest, to (iv) oil palm plantation (OP). To allow us to synthesize the effects of habitat change on the whole ecosystem, we focused on understanding the comprehensive impacts of changes rather than assessing specific drivers affecting each metric. Logged forest sites had an average of ~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) (*16*). 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 (*17*). Measurements with airborne light detection and ranging (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 (*18*).

Categorizing variables into ecological levels

The 82 response variables (tables S1 to S5) detail ecosystem properties sampled in OGF and one or more of the disturbed habitat categories. Each property was categorized into one of four ecological levels, building in complexity and distance from the direct impacts of logging (*17*). Although the assignment of responses to levels is partly subjective, 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 (structure and environment) 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 (tree traits) constituted the traits of the remaining tree community, reflecting the change in plant species composition caused by selective

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logging as well as subsequent colonization and growth of early successional species. Tree traits were grouped according to whether they contributed to structural stability and defense (structural traits), leaf photosynthetic potential and leaf longevity (photosynthesis traits), or foliar concentrations of key mineral nutrients (nutrient traits). Level 3 (biodiversity) quantified below- and above-ground multitrophic and functional biodiversity, from assemblages of soil microorganisms to consumers in higher trophic levels, 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 (functioning) corresponded to ecosystem functions, such as decomposition, which, within a given environment, are largely defined by the composition of communities described in levels 2 and 3.

To allow comparison of multiple responses on a common scale, we transformed the raw data when necessary to improve normality and then standardized all variables as *z*-scores (by mean-centering each variable by subtracting its mean value and dividing by its standard deviation) before analyzing them using linear mixed-effects models to assess effects across the disturbance gradient (the four disturbance categories: OGF, MLF, HLF, and OP) while taking account of the spatial hierarchical structure of our datasets (fig. S1). To provide a comprehensive assessment, where 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 (*19*): effort-standardized species richness (Hill number $q = 0$), Shannon diversity ($q = 1$), and Simpson's 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 focused on examining whether each variable changed from values recorded within OGF and where along the gradient the change occurred.

Strong but heterogeneous responses to disturbance across ecological levels

Overall, 60 of the 82 response variables showed statistically significant differences across the disturbance intensity gradient [likelihood ratio tests (LRT) against a null model with no disturbance factor; table S6]. This was far greater than the expected level of false positives (~4 out of 82 with a significance level of $P < 0.05$) in the absence of any effect of disturbance (Fig. 2, solid lines). This result was consistent when controlling for dataset identity through randomization (84.27% of variables were significant) (*17*). The proportion of significant results and the degree of variation explained by disturbance intensity [the mean marginal coefficient of determination (R^2) from linear mixed-effects models for group; table S6], varied with the ecological level of the response variable. Generally, the responses that showed the strongest effect of disturbance were those most directly affected by logging (*18*): level 1, environment and structure (mean marginal R^2 ± SE 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 four variables LRT $P < 0.05$), and level 2, aggregated tree traits [first axis values from a principal components analysis (PCA); OP excluded = 0.253 ± 0.029, all three 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 $P < 0.05$). Ecosystem functioning variables (level 4) showed weaker responses to disturbance intensity overall, with little change across the gradient for some variables (OP included = 0.081 ±0.021, two out of four variables LRT $P < 0.05$; OP excluded = 0.087 ± 0.023, three out of three variables LRT $P < 0.05$) (*20*).

There was high variability in the observed patterns of responses to the disturbance gradient (Fig. 2). Whereas some variables showed simple, monotonic responses (e.g., estimates of biomass carbon stocks decreased with disturbance, whereas 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 (*16*). Overall, different impacts of land-use change were heterogeneous, often nonlinear, and frequently not strongly correlated. Therefore, the impacts of logging and conversion defy simple interpretations, most likely owing to a mixture of complex interactions, feedbacks, and system redundancy.

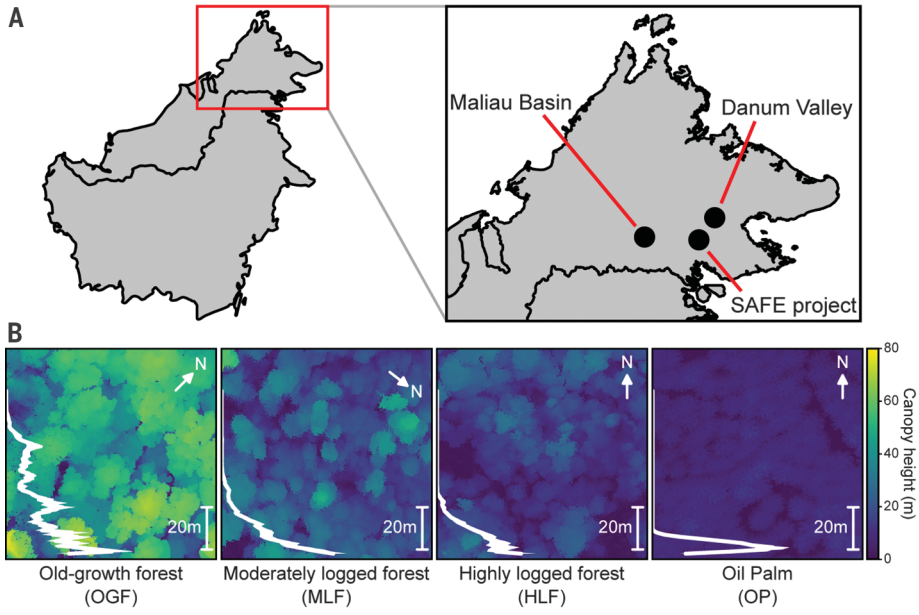

Fig. 1. Study sites and disturbance categories. (**A**) Location of the study sites in Sabah, Malaysian Borneo. (**B**) Canopy height profiles of the study systems for representative 1-ha plots (from left to right): OGF, MLF, HLF, and OP. Backgrounds show the maximum canopy height for each pixel, and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

Responses along the disturbance gradient

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. Variables showed a wide range of responses, but with some ecological levels responding in broadly similar ways. Structural and environmental components of the forest (level 1) were generally more sensitive to a moderate degree of logging (Fig. 3 and fig. S2). This was especially so for variables directly altered by the logging process itself, such as soil bulk density that was compacted by machinery (*21*) and above-ground carbon stock

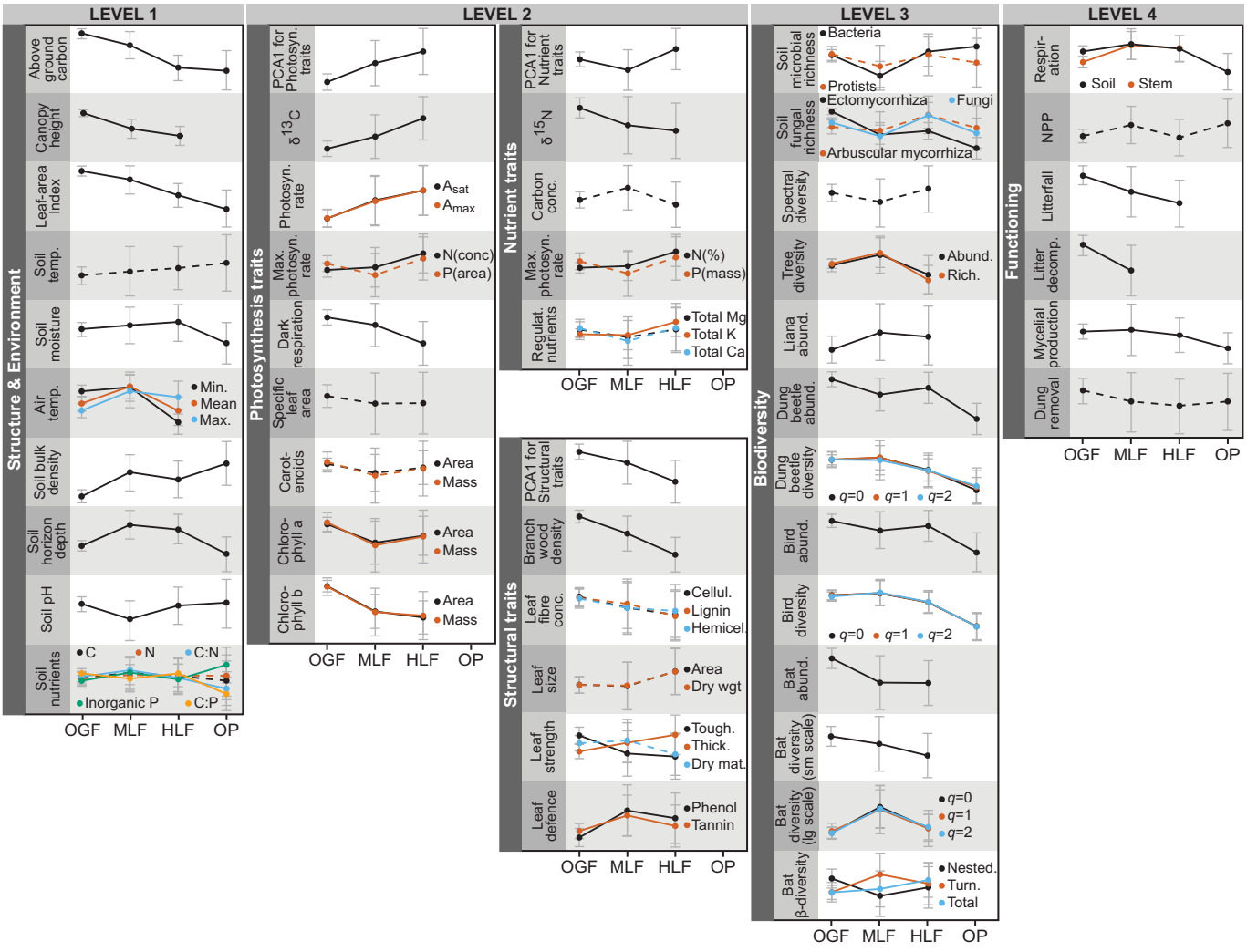

Fig. 2. Changes in different categories of the measured response variables across the disturbance gradient when OGF is moderately logged, highly logged, and converted to OP. Points show *z*-score standardized means (± 95% CI). Sample sizes range from 27 to 373,968 depending on the dataset. Line type indicates whether a model with disturbance was significantly different from a null model with no disturbance (solid lines = significant, $P < 0.05$; dashed lines = not significant). Tree traits (level 2) were analyzed individually as well as in combination through the first axis of a PCA.

that was reduced by timber removal (*22*–*24*). This indicates 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. Traits of the mature tree community (level 2) exhibit major changes consistent with the effects of selective logging (fig. S3) (*18*, *25*), which actively targets tree species with the most commercially desirable characteristics. Removing individuals of these species effectively reduces the incidence of traits such as structural features that aid longevity (*25*), while increasing the incidence of traits such as high photosynthetic rates and rapid growth (*22*), which are associated with species of low commercial value and early successional species that colonize open areas following logging.

By contrast, biodiversity components (level 3) were mostly altered by the conversion of logged forest to oil palm (Fig. 3 and fig. S4) (*6*, *10*, *26*). This was particularly true of taxonomic groups at higher trophic levels, such as birds (*10*, *23*), where increased mobility and behavioral plasticity may buffer their sensitivity to change until conditions become drastically altered (*27*). In the highly disturbed conditions of oil palm plantations, major changes in plant food resources, reduced structural complexity, and shifts to hotter, drier, and more variable microclimatic conditions likely resulted in the reduced abundance and diversity of many taxa and a community composed of disturbance-tolerant species (*28*). The diversity of ectothermic groups, such as dung beetles, which can be particularly responsive to changes in microclimate (*29*), showed a slightly increased sensitivity to the initial impacts of logging relative to 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 (*30*, *31*)] and positive [bacteria (*32*)] responses to disturbance. The impact on ectomycorrhizal fungi is likely to be particularly notable for conservation and restoration perspectives, given their role in supporting canopy-dominant dipterocarps (*33*).

Lastly, ecosystem functions (level 4; Fig. 3 and fig. S4) showed the weakest and most variable patterns (marginal R^2 values, shown by high transparency of bars in Fig. 3 and 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 (*34*), with a small number of disturbance-tolerant species increasing their contribution to dung removal in disturbed habitats (*35*). Such functional redundancy and compensation may confer greater resilience (here, the ability to both resist and recover from

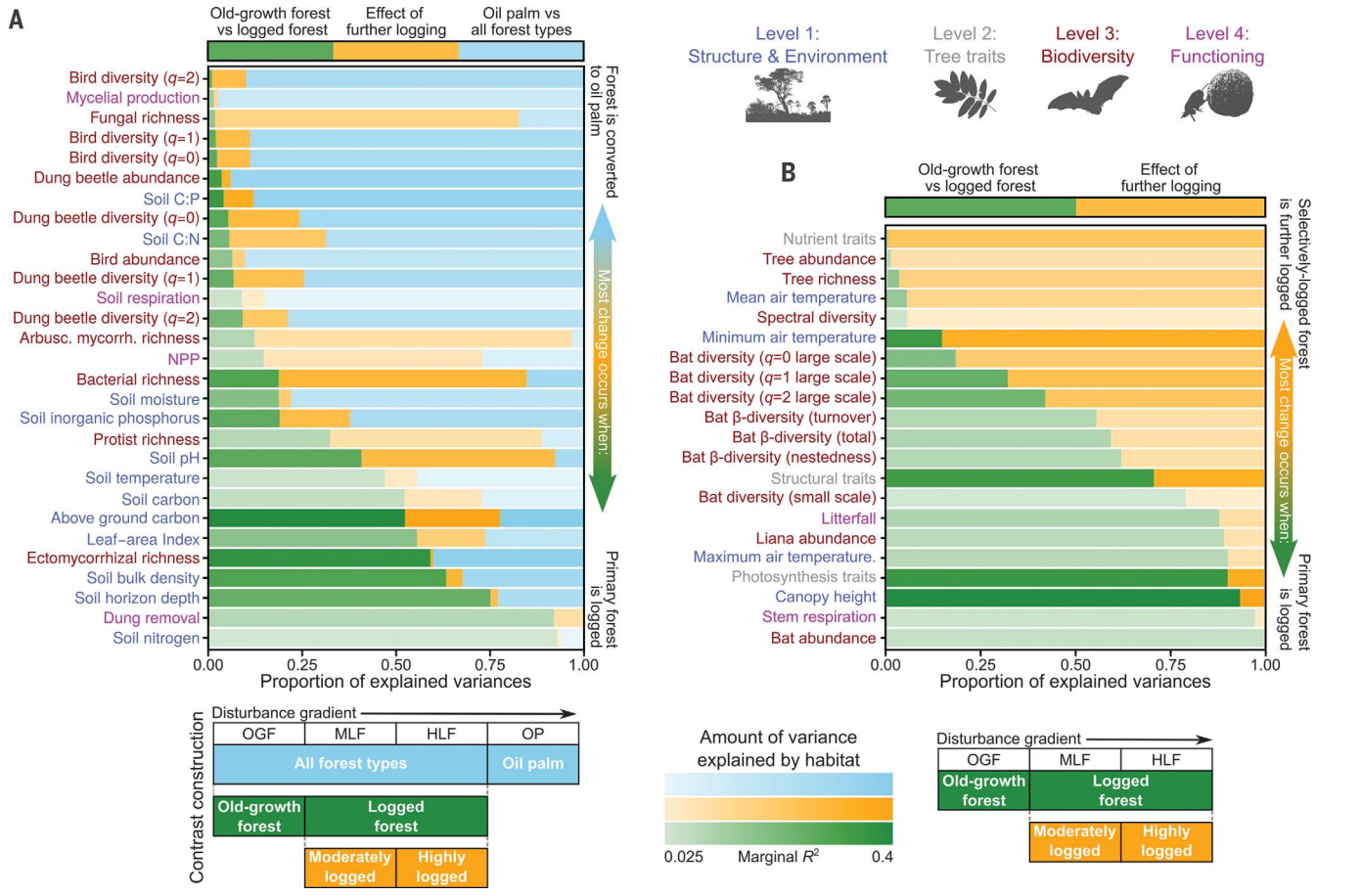

Fig. 3. Impacts of different degrees and types of disturbance when OGF is moderately logged, highly logged, and converted to OP. The overall effect of disturbance was partitioned into (**A**) three (for datasets that did sample in oil palm) or (**B**) two (for datasets that did not sample in oil palm) single degree of freedom contrasts that compare: (i) the effect of logging old-growth forest [OGF versus logged forest (MLF-HLF), green bars]; (ii) the effect of further logging (MLF versus HLF, orange bars); and (iii) the effect of converting forest to oil palm plantation [OP versus combined forest types (OG-MLF-HLF), blue bars]. Sample sizes range from 27 to 373,968 depending on the dataset. 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 tree traits (level 2, gray text), those related to biodiversity (level 3, dark red text), and those related to ecosystem functioning (level 4, purple 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).

change) of ecosystem functions to disturbance, through mechanisms such as the "insurance hypothesis" (*36*) or "portfolio effect" (*37*). Indeed, previous research at these study sites found that, whereas certain taxonomic groups that dominated litter decomposition and seed and invertebrate predation in old-growth forests declined along the logging gradient, different taxonomic groups compensated by increasing their contribution and, thus, maintained those ecosystem functions at similar levels (*27*). 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 (*38*).

Implications for tropical forest conservation

Our findings increase understanding of the ecosystem-wide impacts of habitat change in the tropics, with implications for land-use management and restoration. Although our large-scale study shares the standard limitations of the space-for-time approach to observational data, by adopting a unified framework that considers all measured variables, we reveal that selective logging and forest conversion to oil palm plantations have different environmental impacts and that these vary depending on which aspects of the ecosystem are considered. Even a single type of land use can have a range of impacts when the environment is assessed comprehensively to encompass its abiotic and biotic structure, biological diversity, and the multiple ecosystem functions and services that it provides. This emphasizes the importance of considering a broad range of ecological properties when making land management, conservation, and research decisions.

Our finding that factors associated with forest structure and environment (level 1) are highly sensitive to disturbance shows that even low-intensity logging will result in changes in these characteristics and highlights the importance of maintaining areas of intact, undisturbed forest. The large negative effects on biodiversity when forest is converted to oil palm are consistent with findings from other studies in the region (*23*, *26*) and confirm the value of disturbed forest for the maintenance of high overall biodiversity at the landscape scale (*39*). Therefore, although preserving areas of remaining old-growth forests is important for conserving distinct aspects of their biodiversity and functioning, protecting logged forest can also contribute to maintaining biodiversity and ecosystem functioning relative to landscapes with higher levels of conversion to agriculture. This validates an increasing focus within 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) (*40*)], where it can support both biodiversity (*41*) and ecosystem processes (*42*). 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 could affect nutrient cycling and predator control (*20*).

Understanding at which points on the deforestation gradient biodiversity and associated ecosystem functions are most affected is important for identifying priority habitats for conservation and restoration (*39*, *43*, *44*) and can aid decision making in these complex, multiuse landscapes (*45*, *46*). However, it is important to consider multiple facets of these tropical environments to avoid the risk of unintended consequences possible from more narrow assessments. This study provides an initial comprehensive synthesis and overview of the responses of a tropical forest ecosystem to degradation and deforestation. However, despite the breadth of ecosystem properties investigated, this study represents only a single area and ecosystem type: lowland tropical forest. Future research should establish whether these responses are consistent across other tropical landscapes and in relation to the wider range of land-use changes seen across the global tropics.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adf9856
Materials and Methods
Figs. S1 to S4
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MDAR Reproducibility Checklist

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