
Marsh, Charles J. ; Turner, Edgar C. ; Blonder, Benjamin Wong ; Bongalov, Boris; Both, Sabine ; Cruz, Rudi S. ; Elias, Dafydd M.O. ; Hemprich-Bennett, David ; Jotan, Palasiah ; Kemp, Victoria ; Kritzler, Ully H.; Milne, Sol ; Milodowski, David T. ; Mitchell, Simon L. ; Pillco, Milenka Montoya ; Nunes, Matheus Henrique ; Riutta, Terhi ; Robinson, Samuel J.B. ; Slade, Eleanor M. ; Bernard, Henry; Burslem, David F.R.P. ; Chung, Arthur Y.C. ; Clare, Elizabeth L. ; Coomes, David A. ; Davies, Zoe G. ; Edwards, David P. ; Johnson, David ; Kratina, Pavel ; Malhi, Yadvinder ; Majalap, Noreen ; Nilus, Reuben; Ostle, Nicholas J. ; Rossiter, Stephen J. ; Struebig, Matthew J. ; Tobias, Joseph A. ; Williams, Mathew; Ewers, Robert M. ; Lewis, Owen T. ; Reynolds, Glen; Teh, Yit Arn ; Hector, Andy. 2025. **Tropical forest clearance impacts biodiversity and function, whereas logging changes structure**.

This is the author's version of the work. It is posted here in accordance with the terms of the AAAS author rights and Licence to Publish, under a Creative Commons Attribution Licence (CC BY). The definitive version was published in *Science* 387 (6730): 171-175, 9 Jan 2025, DOI: https://doi.org/10.1126/science.adf9856.

Title: Tropical forest clearance impacts biodiversity and function whereas logging changes structure

Authors: Charles J. Marsh[1, †, *], Edgar C. Turner[2], Benjamin Wong Blonder[3], Boris Bongalov[4], Sabine Both[5,11], Rudi S. Cruz[6], Dafydd M. O. Elias[7], David Hemprich-Bennett[1,8], Palasiah Jotan[9], Victoria Kemp[8], Ully H. Kritzler[10], Sol Milne[11], David T. Milodowski[12], Simon L. Mitchell[13], Milenka Montoya Pillco[14], Matheus Henrique Nunes[4,15], Terhi Riutta[16,17,18], Samuel J. B. Robinson[7,19], Eleanor M. Slade[1,20], Henry Bernard[21], David F. R. P. Burslem[11], Arthur Y. C. Chung[22], Elizabeth L. Clare[8,23], David A. Coomes[4], Zoe G. Davies[13], David P. Edwards[4,24], David Johnson[10], Pavel Kratina[8], Yadvinder Malhi[16], Noreen Majalap[22], Reuben Nilus[22], Nicholas J. Ostle[19], Stephen J. Rossiter[8], Matthew J. Struebig[13], Joseph A. Tobias[18], Mathew Williams[12], Robert M. Ewers[18], Owen T. Lewis[1], Glen Reynolds[25], Yit Arn Teh[26], Andy Hector[27,*]

Affiliations:

[1]Department of Biology, University of Oxford; Oxford, UK.

[2]University Museum of Zoology, University of Cambridge; Cambridge, UK.

[3]Department of Environmental Science, Policy, and Management, University of California Berkeley; Berkeley, CA, USA.

[4]Department of Plant Sciences and Conservation Research Institute, University of Cambridge; Cambridge, UK.

[5]School of Environmental and Rural Science, University of New England; Armidale, Australia.

[6]Escuela de Biología, Universidad Nacional San Antonio Abad del Cusco; Cuzco, Peru.

[7]UK Centre for Ecology & Hydrology; Lancaster Environment Centre, Lancaster, UK.

[8]School of Biological and Behavioural Sciences, Queen Mary University of London; London, UK.

[9]Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague; Czech Republic.

[10]Department of Earth and Environmental Sciences, University of Manchester; Manchester, UK.

[11]School of Biological Sciences, University of Aberdeen; Aberdeen, UK.

[12]School of GeoSciences and NCEO, University of Edinburgh; Edinburgh, UK.

[13]Durrell Institute for Conservation & Ecology, School of Anthropology and Conservation, University of Kent; Canterbury, UK.

[14]Institute of Biological and Environmental Sciences, University of Aberdeen; Aberdeen, UK.

[15] Department of Geographical Sciences, University of Maryland, College Park, MD, USA.

[16]Environmental Change Institute & Leverhulme Centre for Nature Recovery, School of Geography and the Environment, University of Oxford; Oxford, UK.

[17] UK Centre for Ecology and Hydrology, Wallingford, UK.

[18]Faculty of Natural Sciences, Imperial College; London, UK.

[19]Lancaster Environment Centre, Lancaster University; Lancaster, UK.

[20]Asian School of the Environment, Nanyang Technological University; Singapore.

[21]Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah; Kota Kinabalu, Sabah, Malaysia.

[22]Forest Research Centre, Sabah Forestry Department; Sandakan, Sabah, Malaysia.

[23]Department of Biology, York University; Toronto, ON, Canada.

[24] Centre for Global Wood Security, University of Cambridge, Cambridge, UK.

[25]Southeast Asia Rainforest Research Partnership; Lahad Datu, Sabah, Malaysia.

[26]School of Natural and Environmental Sciences, Newcastle University; Newcastle upon Tyne, UK.

[27]Department of Biology & Leverhulme Centre for Nature Recovery, University of Oxford; Oxford, UK.

[28]Centre for Nature-based Climate Solutions, National University of Singapore; Singapore.

*Corresponding authors: charlie.marsh@mailbox.com, andrew.hector@biology.ox.ac.uk.

† Current address: Department of Biological Sciences, National University of Singapore; Singapore.

Abstract: 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: 1) structure and environment, 2) species traits, 3) biodiversity, and 4) ecosystem functions. Responses were highly heterogeneous and often complex and non-linear. 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.

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

Main Text: [Main Text = 2598; Figure captions = 405; References: 46 refs in main text, 112 in total]

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 (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 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*). Here, we undertake 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 synthesize 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) programme 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 use 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: (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, 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) (*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 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 S1-5) 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 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 multi-trophic 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 if necessary to improve normality and then standardized all variables as z-scores (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 focus on examining whether each variable changed from values recorded within OGF, and where along the gradient 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 significant) (*17*). 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 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 ± 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 (first axis values from a PCA; 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 $p < 0.05$). 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, 2 out of 4 variables LRT $p < 0.05$; OP excluded = 0.087 ± 0.023, 3 out of 3 variables LRT $p < 0.05$) (*20*).

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

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 (Figs. 3, 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 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.

In contrast, biodiversity components (level 3) were mostly altered by the conversion of logged forest to oil palm (Figs. 3, 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 important for conservation and restoration perspectives, given their role in supporting canopy-dominant dipterocarps (*33*).

Finally, ecosystem functions (level 4; Figs. 3, S4) 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 (*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 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, while 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 so 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 plantation 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, while preserving areas of remaining old growth forests is important for conserving unique 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, multi-use landscapes (*45*, *46*). However, it is important to consider multiple facets of these tropical environments in order 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.

References and Notes: [46 references (112 in total)]

1. J. Alroy, Effects of habitat disturbance on tropical forest biodiversity. *PNAS* **114**, 6056–6061 (2017).
2. L. Gibson, T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, N. S. Sodhi, Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378–381 (2011).
3. A. C. Hughes, Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* **8**, e01624 (2017).
4. N. S. Sodhi, L. P. Koh, B. W. Brook, P. K. L. Ng, Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution* **19**, 654–660 (2004).
5. R. C. Estoque, M. Ooba, V. Avitabile, Y. Hijioka, R. DasGupta, T. Togawa, Y. Murayama, The future of Southeast Asia’s forests. *Nature Communications* **10**, 1829 (2019).
6. D. S. Wilcove, X. Giam, D. P. Edwards, B. Fisher, L. P. Koh, Navjot’s nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution* **28**, 531–540 (2013).
7. P. R. van Gardingen, M. J. McLeish, P. D. Phillips, D. Fadilah, G. Tyrie, I. Yasman, Financial and ecological analysis of management options for logged-over Dipterocarp forests in Indonesian Borneo. *Forest Ecology and Management* **183**, 1–29 (2003).
8. S. Henders, U. M. Persson, T. Kastner, Trading forests: land-use change and carbon emissions embodied in production and exports of forest-risk commodities. *Environmental Research Letters* **10**, 125012 (2015).
9. V. Vijay, S. L. Pimm, C. N. Jenkins, S. J. Smith, The impacts of oil palm on recent deforestation and biodiversity loss. *PLOS ONE* **11**, e0159668 (2016).

10. D. P. Edwards, A. Magrach, P. Woodcock, Y. Ji, N. T.-L. Lim, F. A. Edwards, T. H. Larsen, W. W. Hsu, S. Benedick, C. V. Khen, A. Y. C. Chung, G. Reynolds, B. Fisher, W. F. Laurance, D. S. Wilcove, K. C. Hamer, D. W. Yu, Selective-logging and oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications* **24**, 2029–2049 (2014).

11. E. Meijaard, T. M. Brooks, K. M. Carlson, E. M. Slade, J. Garcia-Ulloa, D. L. A. Gaveau, J. S. H. Lee, T. Santika, D. Juffe-Bignoli, M. J. Struebig, S. A. Wich, M. Ancrenaz, L. P. Koh, N. Zamira, J. F. Abrams, H. H. T. Prins, C. N. Sendashonga, D. Murdiyarso, P. R. Furumo, N. Macfarlane, R. Hoffmann, M. Persio, A. Descals, Z. Szantoi, D. Sheil, The environmental impacts of palm oil in context. *Nature Plants* **6**, 1418–1426 (2020).

12. J. Drescher, K. Rembold, K. Allen, P. Beckschäfer, D. Buchori, Y. Clough, H. Faust, A. M. Fauzi, D. Gunawan, D. Hertel, B. Irawan, I. N. S. Jaya, B. Klarner, C. Kleinn, A. Knohl, M. M. Kotowska, V. Krashevska, V. Krishna, C. Leuschner, W. Lorenz, A. Meijide, D. Melati, M. Nomura, C. Pérez-Cruzado, M. Qaim, I. Z. Siregar, S. Steinebach, A. Tjoa, T. Tscharntke, B. Wick, K. Wiegand, H. Kreft, S. Scheu, Ecological and socio-economic functions across tropical land use systems after rainforest conversion. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150275 (2016).

13. A. D. Barnes, M. Jochum, S. Mumme, N. F. Haneda, A. Farajallah, T. H. Widarto, U. Brose, Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications* **5**, 5351 (2014).

14. R. M. Ewers, R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon, E. C. Turner, A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3292–3302 (2011).

15. G. Reynolds, J. Payne, W. Sinun, G. Mosigil, R. P. D. Walsh, Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3168–3176 (2011).

16. M. J. Struebig, A. Turner, E. Giles, F. Lasmana, S. Tollington, H. Bernard, D. Bell, "Chapter Three - Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo" in *Advances in Ecological Research*, G. Woodward, E. J. O'Gorman, Eds. (Academic Press, 2013)vol. 48 of *Global Change in Multispecies Systems: Part 3*, pp. 183–224.

17. Materials, methods and further results are available as supplementary materials.

18. M. Pfeifer, L. Kor, R. Nilus, E. Turner, J. Cusack, I. Lysenko, M. Khoo, V. K. Chey, A. C. Chung, R. M. Ewers, Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote Sensing of Environment* **176**, 84–97 (2016).

19. A. Chao, N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, A. M. Ellison, Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* **84**, 45–67 (2014).

20. C. Dislich, A. C. Keyel, J. Salecker, Y. Kisel, K. M. Meyer, M. Auliya, A. D. Barnes, M. D. Corre, K. Darras, H. Faust, B. Hess, S. Klasen, A. Knohl, H. Kreft, A. Meijide, F. Nurdiansyah, F. Otten, G. Pe'er, S. Steinebach, S. Tarigan, M. H. Tölle, T. Tscharntke, K. Wiegand, A review of the ecosystem functions in oil palm plantations, using forests as a reference system. *Biological Reviews* **92**, 1539–1569 (2017).

21. D. Hattori, T. Kenzo, K. O. Irino, J. J. Kendawang, I. Ninomiya, K. Sakurai, Effects of soil compaction on the growth and mortality of planted dipterocarp seedlings in a logged-over tropical rainforest in Sarawak, Malaysia. *Forest Ecology and Management* **310**, 770–776 (2013).

22. T. Riutta, Y. Malhi, L. K. Kho, T. R. Marthews, W. Huaraca Huasco, M. Khoo, S. Tan, E. Turner, G. Reynolds, S. Both, D. F. R. P. Burslem, Y. A. Teh, C. S. Vairappan, N. Majalap, R. M. Ewers, Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology* **24**, 2913–2928 (2018).

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

24. M. Pfeifer, V. Lefebvre, E. Turner, J. Cusack, M. Khoo, V. K. Chey, M. Peni, R. M. Ewers, Deadwood biomass: an underestimated carbon stock in degraded tropical forests? *Environmental Research Letters* **10**, 044019 (2015).

25. S. Both, T. Riutta, C. E. T. Paine, D. M. O. Elias, R. S. Cruz, A. Jain, D. Johnson, U. H. Kritzler, M. Kuntz, N. Majalap-Lee, N. Mielke, M. X. Montoya Pillco, N. J. Ostle, Y. Arn Teh, Y. Malhi, D. F. R. P. Burslem, Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytologist* **221**, 1853–1865 (2019).

26. D. P. Edwards, T. H. Larsen, T. D. S. Docherty, F. A. Ansell, W. W. Hsu, M. A. Derhé, K. C. Hamer, D. S. Wilcove, Degraded lands worth protecting: the biological importance of Southeast Asia’s repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences* **278**, 82–90 (2011).

27. R. M. Ewers, M. J. W. Boyle, R. A. Gleave, N. S. Plowman, S. Benedick, H. Bernard, T. R. Bishop, E. Y. Bakhtiar, V. K. Chey, A. Y. C. Chung, R. G. Davies, D. P. Edwards, P. Eggleton, T. M. Fayle, S. R. Hardwick, R. Homathevi, R. L. Kitching, M. S. Khoo, S. H. Luke, J. J. March, R. Nilus, M. Pfeifer, S. V. Rao, A. C. Sharp, J. L. Snaddon, N. E. Stork, M. J. Struebig, O. R. Wearn, K. M. Yusah, E. C. Turner, Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications* **6**, 6836 (2015).

28. S. Savilaakso, C. Garcia, J. Garcia-Ulloa, J. Ghazoul, M. Groom, M. R. Guariguata, Y. Laumonier, R. Nasi, G. Petrokofsky, J. Snaddon, M. Zrust, Systematic review of effects on biodiversity from oil palm production. *Environmental Evidence* **3**, 4 (2014).

29. J. Williamson, E. Teh, T. Jucker, M. Brindle, E. Bush, A. Y. C. Chung, J. Parrett, O. T. Lewis, S. J. Rossiter, E. M. Slade, Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil palm–forest mosaic. *Functional Ecology* **36**, 1655–1667 (2022).

30. D. Kerfahi, B. M. Tripathi, J. Lee, D. P. Edwards, J. M. Adams, The impact of selective-logging and forest clearance for oil palm on fungal communities in Borneo. *PLOS ONE* **9**, e111525 (2014).

31. K. L. McGuire, H. D’Angelo, F. Q. Brearley, S. M. Gedallovich, N. Babar, N. Yang, C. M. Gillikin, R. Gradoville, C. Bateman, B. L. Turner, P. Mansor, J. W. Leff, N. Fierer, Responses of soil fungi to logging and oil palm agriculture in Southeast Asian tropical forests. *Microbial Ecology* **69**, 733–747 (2015).

32. L. Lee-Cruz, D. P. Edwards, B. M. Tripathi, J. M. Adams, Impact of logging and forest conversion to oil palm plantations on soil bacterial communities in Borneo. *Applied and Environmental Microbiology* (2013).

33. D. Johnson, X. Liu, D. F. R. P. Burslem, Symbiotic control of canopy dominance in subtropical and tropical forests. *Trends in Plant Science* **28**, 995–1003 (2023).

34. C. L. Gray, E. M. Slade, D. J. Mann, O. T. Lewis, Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecology and Evolution* **4**, 1049–1060 (2014).

35. E. M. Slade, D. J. Mann, O. T. Lewis, Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. *Biological Conservation* **144**, 166–174 (2011).

36. S. Yachi, M. Loreau, Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences* **96**, 1463–1468 (1999).

37. C. L. Lehman, D. Tilman, Biodiversity, stability, and productivity in competitive communities. *The American Naturalist* **156**, 534–552 (2000).

38. J. Qiu, B. J. Cardinale, Scaling up biodiversity–ecosystem function relationships across space and over time. *Ecology* **101**, e03166 (2020).

39. R. M. Ewers, C. D. L. Orme, W. D. Pearse, N. Zulkifli, G. Yvon-Durocher, K. M. Yusah, N. Yoh, D. C. J. Yeo, A. Wong, J. Williamson, C. L. Wilkinson, F. Wiederkehr, B. L. Webber, O. R. Wearn, L. Wai, M. Vollans, J. P. Twining, E. C. Turner, J. A. Tobias, J. Thorley, E. M. Telford, Y. A. Teh, H. H. Tan, T. Swinfield, M. Svátek, M. Struebig, N. Stork, J. Sleutel, E. M. Slade, A. Sharp, A. Shabrani, S. S. Sethi, D. J. I. Seaman, A. Sawang, G. B. Roxby, J. M. Rowcliffe, S. J. Rossiter, T. Riutta, H. Rahman, L. Qie, E. Psomas, A. Prairie, F. Poznansky, R. Pillay, L. Picinali, A. Pianzin, M. Pfeifer, J. M. Parrett, C. D. Noble, R. Nilus, N. Mustaffa, K. E. Mullin, S. Mitchell, A. R. Mckinlay, S. Maunsell, R. Matula, M. Massam, S. Martin, Y. Malhi, N. Majalap, C. S. Maclean, E. Mackintosh, S. H. Luke, O. T. Lewis, H. J. Layfield, I. Lane-Shaw, B. H. Kueh, P. Kratina, O. Konopik, R. Kitching, L. Kinneen, V. A. Kemp, P. Jotan, N. Jones, E. W. Jebrail, M. Hroneš, S. P. Heon, D. R. Hemprich-Bennett, J. K. Haysom, M. F. Harianja, J. Hardwick, N. Gregory, R. Gray, R. E. J. Gray, N. Granville, R. Gill, A. Fraser, W. A. Foster, H. Folkard-Tapp, R. J. Fletcher, A. H. Fikri, T. M. Fayle, A. Faruk, P. Eggleton, D. P. Edwards, R. Drinkwater, R. A. Dow, T. F. Döbert, R. K. Didham, K. J. M. Dickinson, N. J. Deere, T. de Lorm, M. M. Dawood, C. W. Davison, Z. G. Davies, R. G. Davies, M. Dančák, J. Cusack, E. L. Clare, A. Chung, V. K. Chey, P. M. Chapman, L. Cator, D. Carpenter, C. Carbone, K. Calloway, E. R. Bush, D. F. R. P. Burslem, K. D. Brown, S. J. Brooks, E. Brasington, H. Brant, M. J. W. Boyle, S. Both, J. Blackman, T. R. Bishop, J. E. Bicknell, H. Bernard, S. Basrur, M. V. L. Barclay, H. Barclay, G. Atton, M. Ancrenaz, D. C. Aldridge, O. Z. Daniel, G. Reynolds, C. Banks-Leite, Thresholds for adding degraded tropical forest to the conservation estate. *Nature* **631**, 808–813 (2024).

40. H. Barclay, C. L. Gray, S. H. Luke, A. Nainar, J. L. Snaddon, E. C. Turner, "RSPO manual on best management practices (BMPs) for the management and rehabilitation of riparian reserves" (Roundtable on Sustainable Palm Oil, 2017).

41. J. E. Bicknell, J. R. O'Hanley, P. R. Armsworth, E. M. Slade, N. J. Deere, S. L. Mitchell, D. Hemprich-Bennett, V. Kemp, S. J. Rossiter, O. T. Lewis, D. A. Coomes, A. L. Agama, G. Reynolds, M. J. Struebig, Z. G. Davies, Enhancing the ecological value of oil palm agriculture through set-asides. *Nature Sustainability* **6**, 513–525 (2023).

42. S. H. Luke, E. M. Slade, C. L. Gray, K. V. Annammala, J. Drewer, J. Williamson, A. L. Agama, M. Ationg, S. L. Mitchell, C. S. Vairappan, M. J. Struebig, Riparian buffers in tropical agriculture: Scientific support, effectiveness and directions for policy. *Journal of Applied Ecology* **56**, 85–92 (2019).

43. J. M. R. Benayas, A. C. Newton, A. Diaz, J. M. Bullock, Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* **325**, 1121–1124 (2009).

44. N. J. Deere, G. Guillera-Arroita, T. Swinfield, D. T. Milodowski, D. A. Coomes, H. Bernard, G. Reynolds, Z. G. Davies, M. J. Struebig, Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations. *Proceedings of the National Academy of Sciences* **117**, 26254–26262 (2020).

45. C. Y. Shimamoto, A. A. Padial, C. M. da Rosa, M. C. M. Marques, Restoration of ecosystem services in tropical forests: A global meta-analysis. *PLOS ONE* **13**, e0208523 (2018).

46. M. P. Barral, J. M. Rey Benayas, P. Meli, N. O. Maceira, Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: A global meta-analysis. *Agriculture, Ecosystems & Environment* **202**, 223–231 (2015).

47. C. J. Marsh, E. C. Turner, B. W. Blonder, B. Bongalov, S. Both, R. S. Cruz, D. M. O. Elias, D. Hemprich-Bennett, P. Jotan, V. Kemp, U. H. Kritzler, S. Milne, D. T. Milodowski, S. L. Mitchell, M. Montoya Pillco, M. H. Nunes, T. Riutta, S. J. B. Robinson, E. M. Slade, H. Henry, D. F. R. P. Burslem, A. Y. C. Chung, E. L. Clare, D. A. Coomes, Z. G. Davies, E. David P., D. Johnson, P. Kratina, Y. Malhi, N. Majalap, R. Nilus, N. J. Ostle, S. J. Rossiter, M. J. Struebig, J. A. Tobias, M. Williams, R. M. Ewers, O. T. Lewis, G. Reynolds, Y. A. Teh, A. Hector, Data analysis scripts for Marsh et al. 2024 "Logging alters tropical forest structure, while conversion to agriculture reduces biodiversity and functioning," Zenodo (2024); https://doi.org/10.5281/zenodo.13161799.

48. D. J. I. Seaman, M. Voigt, G. Bocedi, J. M. J. Travis, S. C. F. Palmer, M. Ancrenaz, S. Wich, E. Meijaard, H. Bernard, N. J. Deere, T. Humle, M. J. Struebig, Orangutan movement and population dynamics across human-modified landscapes: implications of policy and management. *Landscape Ecol* **36**, 2957–2975 (2021).

49. T. Riutta, R. M. Ewers, Y. Malhi, N. Majalap, K. L. Khoon, Total and partitioned soil respiration and below-ground carbon budget in SAFE intensive carbon plots, Zenodo (2021); https://doi.org/10.5281/zenodo.4542881.

50. C. J. Marsh, M. H. Nunes, B. Bongalov, T. Riutta, Craig. C. Brelsford, D. A. Coomes, Selected data sets for Marsh et al. 2024 "Logging alters tropical forest structure, while conversion to agriculture reduces biodiversity and functioning," (2024); https://doi.org/10.5281/zenodo.13329230.

51. D. M. O. Elias, N. P. McNamara, N. J. Ostle, N. Majalap-Lee, Soil properties across primary forest, logged forest and oil palm plantation in Sabah, Malaysia, NERC Environmental Information Data Centre (2018); https://doi.org/10.5285/7e046092-8405-41b8-9e38-67a844bb9e7d.

52. B. Blonder, S. Both, D. A. Coomes, D. Elias, T. Jucker, J. Kvasnica, N. Majalap, Y. S. Malhi, D. Milodowski, T. Riutta, M. Svátek, Extreme and highly heterogeneous microclimates in selectively logged tropical forests. *Frontiers in Forests and Global Change* **1**, 5 (2018).

53. S. Both, D. F. R. P. Burslem, T. Riutta, Y. Malhi, N. Majalap, Y. A. Teh, Community-weighted mean traits in old-growth and selectively logged forest, Zenodo (2019); https://doi.org/10.5281/zenodo.3247602.

54. D. Elias, S. Both, T. Goodall, S. Robinson, N. Majalap-Lee, R. Griffiths, N. Ostle, N. McNamara, Soil microbial communities from tropical forest and oil palm, Zenodo (2024); https://doi.org/10.5281/zenodo.13341608.

55. S. Both, D. F. R. P. Burslem, T. Riutta, Y. Malhi, N. Majalap, Y. A. Teh, Functional traits of tree species in old-growth and selectively logged forest, Zenodo (2019); https://doi.org/10.5281/zenodo.3247631.

56. E. M. Slade, E. Bush, D. J. Mann, Arthur. Y. C. Chung, Dung beetle community and dung removal data 2011, Zenodo (2019); https://doi.org/10.5281/zenodo.3247492.

57. E. M. Slade, S. Milne, D. J. Mann, Arthur. Y. C. Chung, J. Parrett, Dung beetle community and dung removal data 2015, Zenodo (2019); https://doi.org/10.5281/zenodo.3247494.

58. S. L. Mitchell, D. P. Edwards, H. Bernard, D. Coomes, T. Jucker, Z. G. Davies, M. J. Struebig, Data from: Riparian reserves help protect forest bird communities in oil palm dominated landscapes, version 1, Dryad (2019); https://doi.org/10.5061/DRYAD.KN251R8.

59. D. Hemprich-Bennett, V. Kemp, J. Blackman, H. Bernard, O. Lewis, M. Struebig, S. Rossiter, E. Clare, Impacts of rainforest degradation on the diets of the insectivorous bats of Sabah, Zenodo (2019); https://doi.org/10.5281/zenodo.3247465.

60. T. Riutta, R. M. Ewers, Y. Malhi, N. Majalap, M. Mills, Stem respiration in SAFE intensive GEM carbon plots, Zenodo (2024); https://doi.org/10.5281/zenodo.12799889.

61. S. Both, D. Johnson, D. Elias, N. Ostle, N. Majalap, Leaf litter decomposition in old-growth and selectively logged forest, Zenodo (2019); https://doi.org/10.5281/zenodo.3247639.

62. S. J. B. Robinson, D. Elias, D. Johnson, S. Both, T. Riutta, T. Goodall, N. Majalap, N. P. McNamara, R. Griffiths, N. Ostle, Mycelial soil fungal communty attributes and mycelial production across a forest disturbance gradient, Zenodo (2024); https://doi.org/10.5281/zenodo.13122107.

63. A. Baselga, Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* **8**, 799–808 (2017).

64. A. Baselga, Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143 (2010).

65. R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing (2023); https://www.R-project.org/.

66. A. Baselga, C. D. L. Orme, S. Villeger, J. De Bartoli, F. Leprieur, M. Logez, S. Martinez-Santalla, R. Martin-Devasa, C. Gomez-Rodriguez, R. M. Crujeiras, betapart: partitioning beta diversity into turnover and nestedness components, version 1.6 (2023); https://CRAN.R-project.org/package=betapart.

67. C. O. Wilke, cowplot: streamlined plot theme and plot annotations for “ggplot2,” version 1.1.3 (2024); https://CRAN.R-project.org/package=cowplot.

68. R. J. Hijmans, S. Phillips, J. Leathwick, dismo: species distribution modeling, version 1.3-14 (2023); https://CRAN.R-project.org/package=dismo.

69. H. Wickham, R. Francois, L. Henry, K. Müller, D. Vaughan, dplyr: a grammar of data manipulation, version 1.1.4 (2023); https://CRAN.R-project.org/package=dplyr.

70. W. Chang, extrafont: tools for using fonts, version 0.19 (2023); https://CRAN.R-project.org/package=extrafont.

71. H. Wickham, *Ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag, New York, 2016; https://ggplot2.tidyverse.org).

72. B. Auguie, gridExtra: miscellaneous functions for “grid” graphics, version 2.3 (2017); https://CRAN.R-project.org/package=gridExtra.

73. H. Wickham, T. L. Pedersen, gtable: arrange “grobs” in tables, version 0.3.5 (2024); https://CRAN.R-project.org/package=gtable.

74. T. C. Hsieh, K. H. Ma, A. Chao, iNEXT: iNterpolation and EXTrapolation for species diversity, version 3.0.1; http://chao.stat.nthu.edu.tw/wordpress/software-download/.

75. D. Sarkar, *Lattice: Multivariate Data Visualization with R* (Springer, New York, 2008; http://lmdvr.r-forge.r-project.org).

76. D. Bates, M. Machler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48 (2015).

77. S. Milton Bache, H. Wickham, magrittr: a forward-pipe operator for R, version 2.0.3 (2022); https://CRAN.R-project.org/package=magrittr.

78. K. Bartoń, MuMIn: multi-model inference, version 1.48.4 (2024); https://CRAN.R-project.org/package=MuMIn.

79. J. C. Nash, On best practice optimization methods in R. *Journal of Statistical Software* **60**, 1–14.

80. J. C. Nash, R. Varadhan, Unifying optimization algorithms to aid software system users: optimx for R. *Journal of Statistical Software* **43**, 1–14 (2011).

81. H. Wickham, J. Hester, J. Bryan, readr: read rectangular text data, version 2.1.5 (2024); https://CRAN.R-project.org/package=readr.

82. R. Bivand, C. Rundel, rgeos: interface to geometry engine - open source ('GEOS'), version 0.6-4 (2023); https://CRAN.R-project.org/package=rgeos.

83. J. J. Allaire, Y. Xie, C. Dervieux, J. McPherson, J. Luraschi, K. Ushey, A. Atkins, H. Wickham, J. Cheng, W. Chang, R. Iannone, rmarkdown: dynamic documents for R, version 2.27 (2024); https://github.com/rstudio/rmarkdown.

84. E. J. Pebesma, R. Bivand, Classes and methods for spatial data in R. *R News* **5**, 9–13 (2005).

85. R. Bivand, E. J. Pebesma, V. Gomez-Rubio, *Applied Spatial Data Analysis with R* (Springer, New York, ed. 2, 2013; https://asdar-book.org/).

86. H. Wickham, D. Vaughan, M. Girlich, tidyr: tidy messy data, version 1.3.1 (2024); https://CRAN.R-project.org/package=tidyr.

87. R. J. Hijmans, terra: spatial data analysis, version 1.7-78 (2024); https://CRAN.R-project.org/package=terra.

88. J. Oksanen, G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D. J. McGlinn, M.-H. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C. J. F. Ter Braak, J. Weedon, vegan: community ecology package, version 2.6-6.1 (2024); https://CRAN.R-project.org/package=vegan.

89. R. L. Wasserstein, A. L. Schirm, N. A. Lazar, Moving to a World Beyond "$p < 0.05$." *The American Statistician* **73**, 1–19 (2019).

90. G. N. Wilkinson, C. E. Rogers, Symbolic description of factorial models for analysis of variance. *Journal of the Royal Statistical Society. Series C (Applied Statistics)* **22**, 392–399 (1973).

91. A. Gelman, J. Hill, M. Yajima, Why We (Usually) Don't Have to Worry About Multiple Comparisons. *Journal of Research on Educational Effectiveness* **5**, 189–211 (2012).

92. T. R. Marthews, T. Riutta, I. Oliveras Menor, R. Urrutia, S. Moore, D. J. Metcalfe, Y. S. Malhi, O. L. Phillips, W. Huaraca Huasco, M. del C. Ruiz Jaén, C. Girardin, N. Butt, R. Cain, and colleagues from the R. and G. networks, Measuring tropical forest carbon allocation and cycling: A RAINFOR-GEM field manual for intensive census plots (v3.0) (2014).

93. J. Chave, C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira, J.-P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riéra, T. Yamakura, Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**, 87–99 (2005).

94. A. R. Martin, S. C. Thomas, A Reassessment of carbon content in tropical trees. *PLOS ONE* **6**, e23533 (2011).

95. D. T. Milodowski, D. A. Coomes, T. Swinfield, T. Jucker, T. Riutta, Y. Malhi, M. Svátek, J. Kvasnica, D. F. R. P. Burslem, R. M. Ewers, Y. A. Teh, M. Williams, The impact of logging on vertical canopy structure across a gradient of tropical forest degradation intensity in Borneo. *Journal of Applied Ecology* **58**, 1764–1775 (2021).

96. S. C. Stark, V. Leitold, J. L. Wu, M. O. Hunter, C. V. de Castilho, F. R. C. Costa, S. M. McMahon, G. G. Parker, M. T. Shimabukuro, M. A. Lefsky, M. Keller, L. F. Alves, J. Schietti, Y. E. Shimabukuro, D. O. Brandão, T. K. Woodcock, N. Higuchi, P. B. de Camargo, R. C. de Oliveira, S. R. Saleska, Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. *Ecology Letters* **15**, 1406–1414 (2012).

97. P. Schleppi, M. Conedera, I. Sedivy, A. Thimonier, Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agricultural and Forest Meteorology* **144**, 236–242 (2007).

98. A. Thimonier, I. Sedivy, P. Schleppi, Estimating leaf area index in different types of mature forest stands in Switzerland: a comparison of methods. *European Journal of Forest Research* **129**, 543–562 (2010).

99. J. M. Chen, J. Cihlar, Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *IEEE Transactions on Geoscience and Remote Sensing* **33**, 777–787 (1995).

100. J. J. Kozich, S. L. Westcott, N. T. Baxter, S. K. Highlander, P. D. Schloss, Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. *Applied and Environmental Microbiology* **79**, 5112–5120 (2013).

101. A. J. Baldwin, J. A. Moss, J. D. Pakulski, P. Catala, F. Joux, W. H. Jeffrey, Microbial diversity in a Pacific Ocean transect from the Arctic to Antarctic circles. *Aquatic Microbial Ecology* **41**, 91–102 (2005).

102. K. Ihrmark, I. T. M. Bödeker, K. Cruz-Martinez, H. Friberg, A. Kubartova, J. Schenck, Y. Strid, J. Stenlid, M. Brandström-Durling, K. E. Clemmensen, B. D. Lindahl, New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology* **82**, 666–677 (2012).

103. B. J. Callahan, P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, S. P. Holmes, DADA2: High resolution sample inference from Illumina amplicon data. *Nature methods* **13**, 581–583 (2016).

104. N. H. Nguyen, Z. Song, S. T. Bates, S. Branco, L. Tedersoo, J. Menke, J. S. Schilling, P. G. Kennedy, FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* **20**, 241–248 (2016).

105. A. K. Schweiger, J. Cavender-Bares, P. A. Townsend, S. E. Hobbie, M. D. Madritch, R. Wang, D. Tilman, J. A. Gamon, Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nature Ecology & Evolution* **2**, 976–982 (2018).

106. T. C. Hsieh, K. H. Ma, A. Chao, iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456 (2016).

107. D. R. Hemprich-Bennett, V. A. Kemp, J. Blackman, M. J. Struebig, O. T. Lewis, S. J. Rossiter, E. L. Clare, Altered structure of bat–prey interaction networks in logged tropical forests revealed by metabarcoding. *Molecular Ecology* **30**, 5844–5857 (2021).

108. K. A. Wilson, E. Meijaard, S. Drummond, H. S. Grantham, L. Boitani, G. Catullo, L. Christie, R. Dennis, I. Dutton, A. Falcucci, L. Maiorano, H. P. Possingham, C. Rondinini, W. R. Turner, O. Venter, M. Watts, Conserving biodiversity in production landscapes. *Ecological Applications* **20**, 1721–1732 (2010).

109. A. Baselga, C. D. L. Orme, betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**, 808–812 (2012).

110. T. Riutta, L. K. Kho, Y. A. Teh, R. Ewers, N. Majalap, Y. Malhi, Major and persistent shifts in below-ground carbon dynamics and soil respiration following logging in tropical forests. *Global Change Biology* **27**, 2225–2240 (2021).

111. S. Both, D. M. O. Elias, U. H. Kritzler, N. J. Ostle, D. Johnson, Land use not litter quality is a stronger driver of decomposition in hyperdiverse tropical forest. *Ecology and Evolution* **7**, 9307–9318 (2017).

112. S. J. B. Robinson, D. Elias, D. Johnson, S. Both, T. Riutta, T. Goodall, N. Majalap, N. P. McNamara, R. Griffiths, N. Ostle, Soil fungal community characteristics and mycelial production across a disturbance gradient in lowland dipterocarp rainforest in Borneo. *Frontiers in Forests and Global Change* **3** (2020).

Acknowledgments: We thank Sabah Forestry Department, Sabah Foundation and Universiti Malaysia Sabah. We thank Dan Lunn of Oxford University Statistical Consultancy for advice. We are grateful to the South East Asia Rainforest Research Partnership (SEARRP) for logistical support, and Dr Chey Vun Khen for his support and advice in the initial SAFE Project set-up. Fieldwork was supported by Rasizul Bin Sahamin, Joshua Blackman, Genevieve Durocher, Ryan Gray, Walter Huaraca Huasco, Unding Jami, Rostin Jantan, Alexander Karolus, Raina Manber, Toby Marthews and SEARRP staff, including Amir, Anis, Austin, David, Didy, Dino, Lizzie, Johnny, Kiki, Loly, Mudin, Noy and Zul. We thank Yayasan Sabah, Maliau Basin Management Committee, Danum Valley Management Committee, the State Secretary, Sabah Chief Minister's Departments, the Malaysian Economic Planning Unit and the Sabah Biodiversity Council for permission to conduct research.

Funding:

Data were collected and analyzed as part of the BALI (Biodiversity And Land-use Impacts on tropical ecosystem function) and LOMBOK (Land-use Options for Maintaining BiOdiversity & eKosystem functions) projects within the Human-modified Tropical Forests Programme funded by NERC (NE/K016377/1, NE/K016261/1, NE/K016148/1, NE/K016407/1).

Collection of dung beetle data was also supported by a British Ecological Society Small Ecological Project Grant, No.: 3256/4035, and the Varley-Gradwell Travelling Fellowship in Insect Ecology to EMS.

Collection of bird data was supported by NERC (NE/I028068/1) to JAT.

Collection of bat data was supported by a Bat Conservation International Student Research Scholarship to DHB.

TR acknowledges support from the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement No 865403).

Carbon cycle work was also supported by European Research Council Advanced Investigator Grant, GEM-TRAIT (321131) to YM.

The work of the Leverhulme Centre for Nature Recovery is made possible thanks to the generous support of the Leverhulme Trust.

The SAFE Project is funded by the Sime Darby Foundation and RME by the NOMIS Foundation.

Author contributions: Paper conceived, and initial draft prepared by CJM, ECT, AH. CJM performed all analyses. All authors contributed to further drafts and provided final approval.

Data collection and processing was carried out by BWB, BB, SB, RSC, DMOE, DPE, DH-B, PJ, VK, UKH, SM, DTM, SLM, MMP, MHN, TR, SJBR, EMS. Principal investigators of individual projects were HB, DFRPB, AYCC, ELC, DAC, ZGD, DPE, DJ, PK, YM, NM, RN, NJO, SJR, MJS, JAT and MW. The BALI and LOMBOK projects were planned by the project teams led by PIs YAT and OTL, and the SAFE Project established and led by GR and RME.

Competing interests: The authors declare no competing interests.

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://zenodo.org/records/13161799 (*47*). The DOIs for archived versions of the raw data for all datasets are listed in the methods and Tables S2-5.

Supplementary Materials:

Materials and Methods

Figs. S1 to S4

Tables S1 to S6

References (48-112)

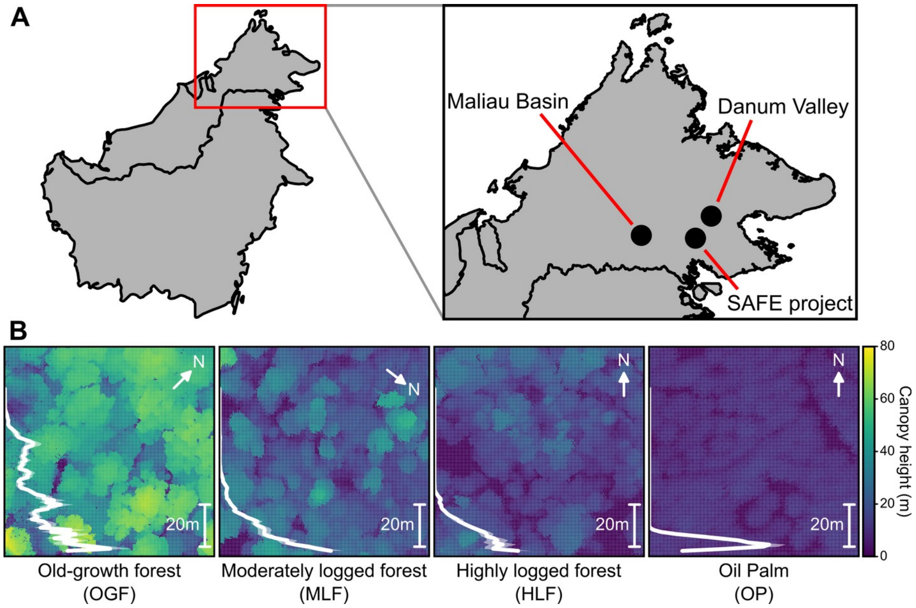

Fig. 1. Study sites and disturbance categories. (**A**) Location of the study sites in Sabah, Malaysian Borneo. (**B**) Canopy height profiles of the study systems for representative 1 ha plots (from left to right): old-growth forest (OGF), moderately logged forest (MLF), highly logged forest (HLF),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

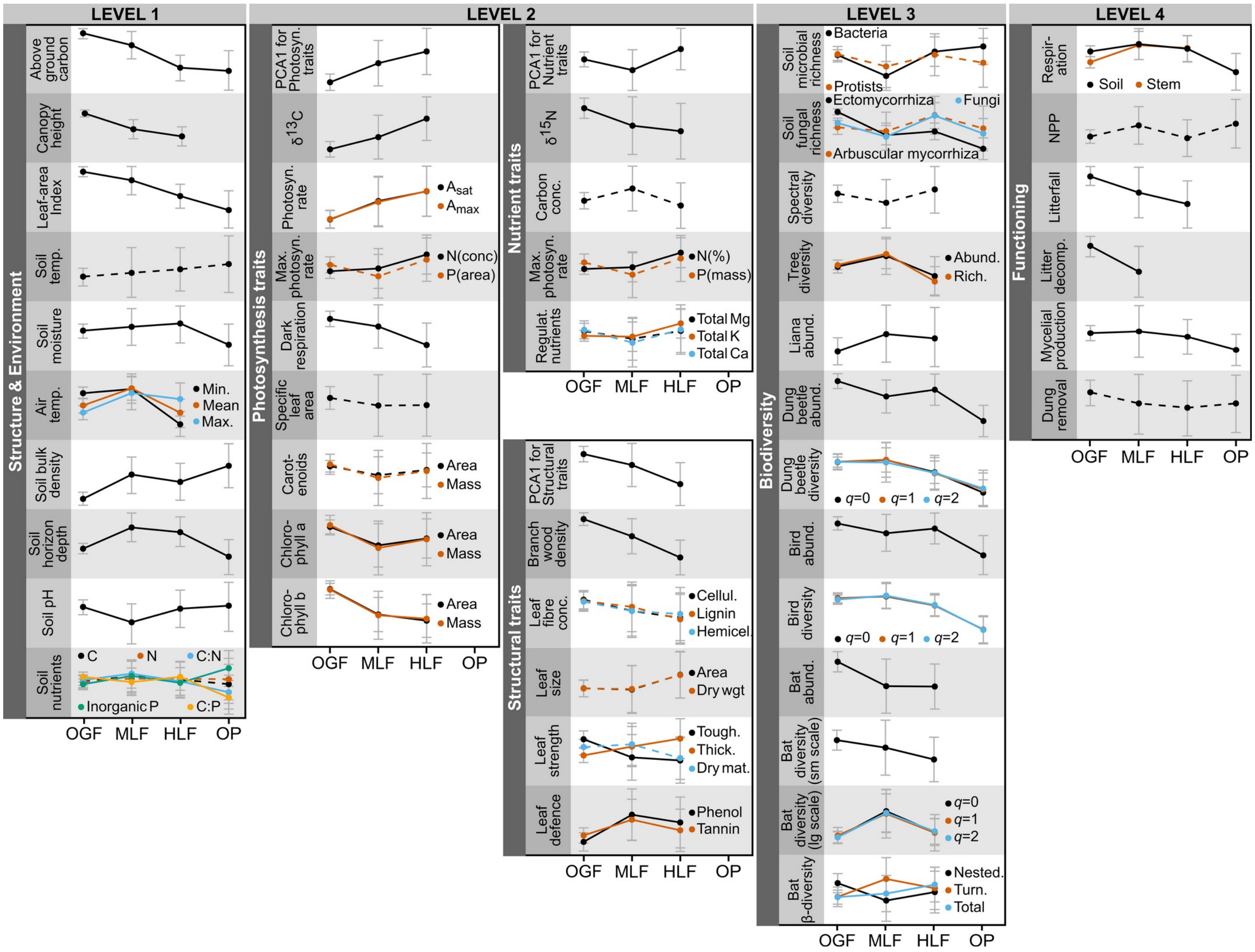

Fig. 2. Changes in different categories of the measured response variables across the disturbance gradient when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). Points show z-score standardized means (± 95% C.I.). Sample sizes ranged from 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 = 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).

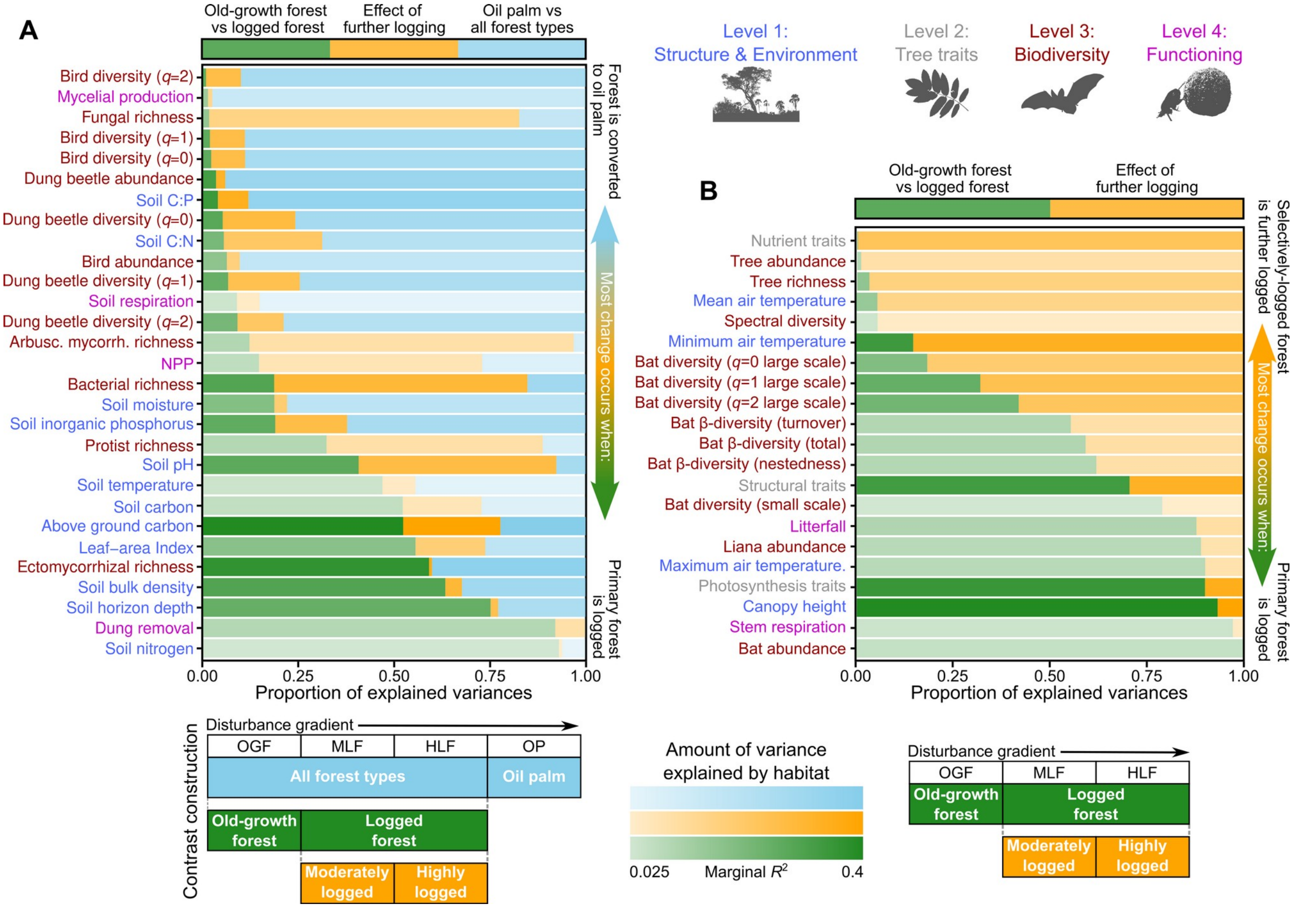

Fig. 3. Impacts of different degrees and types of disturbance when old-growth forest (OGF) is moderately logged (MLF), highly logged (HLF) and converted to oil palm plantation (OP). The overall effect of disturbance was partitioned into a) three (for datasets that did sample in oil palm), or b) two (for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