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Thresholds for adding degraded tropical forest to the conservation estate

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Abstract

Logged and disturbed forests are often viewed as degraded and depauperate environments - the poor cousins of primary forest. However, they are dynamic ecosystems [1] that provide refugia for large amounts of biodiversity [2,3], so we cannot afford to underestimate their conservation value [4]. Here, we present empirically defined thresholds for categorising the conservation value of logged forests, using one of the most comprehensive assessments of taxon responses to habitat degradation in any tropical forest environment. We analysed the impact of logging intensity on the individual occurrence patterns of 1,681 taxa belonging to 86 taxonomic orders and 126 functional groups in Sabah, Malaysia. Our results demonstrate the existence of two conservation-relevant thresholds. First, lightly logged forests (< 29 % biomass removal) retain significant conservation value and largely intact functional composition, and are therefore likely to recover their pre-logging values if allowed to undergo natural regeneration. Second, the most extreme impacts occur in heavily degraded forests with more than two-thirds (> 68 %) of their biomass removed, and are likely to require more expensive measures to recover their biodiversity value. Overall, our data confirm that primary forests are irreplaceable [5], but they also reinforce the message that logged forests retain significant conservation value that should not be overlooked.

Introduction

Habitat degradation has seemingly contradictory impacts on the biodiversity of tropical forests. Human disturbance of tropical forests has resulted in the same amount of biodiversity loss as outright deforestation [6], leading to a widespread view that logged, degraded and regenerating tropical rainforests are depauperate environments relative to primary forest [5]. However, logged forests are also more dynamic environments than primary forest [1], can have elevated habitat heterogeneity [7], support enhanced populations of many taxa [8] and provide refugia for a remarkable diversity of species [2,3]. Given this apparent paradox, it is not immediately apparent whether degraded forests should be considered as conservation assets or not. As logged forests increasingly dominate tropical landscapes [9,10], questions around their conservation protection should be a priority. The intensity of logging varies greatly within and among tropical regions [11,12], which further complicates the debate around the conservation of logged and degraded forests. Precedents exist of even heavily logged forest being afforded the strictest levels of conservation protection [13], but we lack clear evidence about whether this approach should be expanded.

Conservation actions globally can be largely categorised as being either proactive or reactive [14]. Proactive conservation targets areas of low vulnerability, where approaches such as protecting the habitat are expected to deliver positive outcomes for biodiversity. By contrast, reactive conservation targets areas of high threat, where immediate action is required to stave off biodiversity loss. Lightly logged forest might retain sufficient biodiversity and ecological value to justify formal conservation protection, should that be a socially equitable approach in the region of interest [15]. This proactive approach to conservation in largely intact ecosystems seeks primarily to prevent additional habitat degradation from taking place. However, more heavily degraded forests might also require costly reactive conservation interventions – such as remediation, restoration and long-term management [14] – to accompany the protection of the habitat. In this study, we quantify how badly damaged a forest can be before it transitions from a situation where proactive conservation approaches might need to be replaced with reactive approaches, identifying two ecological thresholds that can be used to guide conservation decisions of this nature.

Identifying thresholds requires the quantification of biodiversity responses to disturbances, such as logging in tropical forests [16], which appears deceptively simple. Hundreds, if not thousands, of individual empirical studies have tackled this question, but each is commonly limited to one or a small number of taxonomic groups such as plants [17], mammals [18], birds [19] or ants [20], which creates two challenges. First, responses to forest degradation are often taxon-specific [21,22], although there are some landscape-level thresholds in community responses that exhibit remarkable congruence [23]. Second, taxon-specific studies can easily exaggerate perceived impacts on ecological functions, because they are unable to capture compensation by functionally similar taxa in unrelated taxonomic groups [24,25]. Consequently, answers obtained from taxonomically limited studies can reflect the researchers' choice of study taxa more than the community-wide effects of degradation on biodiversity and ecosystem functioning. This confusion of taxon-specific responses and cross-taxon ecological redundancy means we have little synthetic understanding of where to target different forms of conservation action along gradients of habitat degradation.

Here, we surmount these challenges by summarising responses collated across 127 biodiversity surveys (Table S1). Each survey took place in a single year, and all were conducted during an 11-year period at the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysia [26,27]. This experimental landscape encompasses a continuous gradient in logging intensity that ranges from unlogged primary forest, through salvage-logged forest (where no limits were placed on the number or size of trees to be removed), to riparian forest in protected riverine buffer zones and forest converted into oil palm plantations. Along this gradient, the percentage of biomass removed varied from zero through to 99 %, which we use as a generalised metric of forest degradation. This metric implicitly combines the initial removal of woody biomass through logging and land clearance with the gradual recovery of biomass that may have occurred since the last disturbance event(s), meaning our metric of forest degradation reflects the present-day balance between these two opposing forces. From previous work at this site, we have shown that forest degradation causes changes to local environmental conditions, including the microclimate [28] and the functional composition of the tree community [29].

Together, the biodiversity surveys contain information on the occurrence patterns of 4,689 taxa (Fig. S1) and 126 functional and morphological groups (Methods; Table S2). Of these, 1,681 taxa and all 126 functional groups were observed ≥ 5 times and were able to be modelled individually. Of the 1,681 taxa we modelled, more than half (n = 946, 56 %) were detected in more than one survey (Fig. S2), and more than half (54 %) of individual surveys consisted of multiple site visits (repeated observations of the same sites within the survey year). The taxa were widely distributed across the tree of life (Fig. S1) and encompassed representatives from 86 taxonomic orders and 679 genera, including 590 plants (understorey and canopy, including grasses, herbs and woody trees), 88 mammals (including bats), 161 birds, 9 reptiles, 42 amphibians, 26 fish, and 635 invertebrates (including 263 beetles, 199 lepidopterans, 130 ants and 33 spiders). The taxa ranged in body size over eight orders of magnitude from the smallest Featherwing beetles in the family Ptiliidae (17 mg) to the Bornean elephant *Elephas maximus* (3.2 tonnes), encompassed 21 diet groups spread across six trophic levels, and represented 18 categories of movement mode, physiology, habitat use, sociality and conservation status (Methods; Table S2). Functional groups based on trophic levels and diet were agnostic to taxonomy, recognising for example that both spiders and birds have insect prey and can contribute to the same ecological function [25] (Methods).

We focus our analyses on two critical points in the responses of individual taxa to habitat degradation. We define a “change point” as the first point along the degradation gradient at which a taxon exhibits a discernible change in occurrence probability. We then define a “maximum rate point”, which represents the point along the forest degradation gradient where the rate of change in occurrence probability is the most rapid. Both change and maximum rate points were calculated from derivatives of fitted occurrence models (Methods; Fig. S3).

Forest degradation causes immediate ecological change

No level of forest degradation was too low to have an impact (Fig. 1A): the occurrence patterns of 24 % (n = 396) of taxa and 34 % (n = 41) of functional groups were impacted from the onset of biomass removal. While seemingly extreme, such intense sensitivity to small amounts of forest disturbance echoes earlier, global analyses showing that tropical taxa in intact habitats are heavily impacted by very small amounts of forest loss [30].

More taxa and functional groups were negatively (425 and 51 respectively) than positively (330 and 32) affected by forest degradation, so the mean occurrence level reduced slowly as forest degradation increased (Fig. 1B). Surprisingly, the 811 taxa that were present in unlogged forest (≤5 % biomass removal) were twice as likely to have positive (28 %, n = 228 taxa) than negative (14 %, n = 110) responses to forest degradation, which reinforces previous analyses showing how logged forests have higher ecosystem energy flows and higher species richness than primary forest [1]. However, we emphasise that those taxa and functional groups that directly benefit from logging – around one-fifth of the study taxa – do not necessarily mitigate losses in other taxa: any human caused change in the ecosystem, whether positive or negative for an individual taxon or functional group, is noteworthy and potentially concerning. Increased occurrence can be a positive outcome for a specific taxon, yet represent a negative outcome for the ecosystem if, for example, they are invasive species. Forest degradation at our study site has promoted the invasion of non-native rodents [31] and plants [32], which is a globally common pattern [33]. However, there are many native and endemic taxa that do benefit from forest degradation, including invertebrate, bird and mammal species [1,2,8,24] that can exploit the higher bottom-up provision of food resources in degraded forests including fruits [24] and more palatable foliage [1]. Our study site also has low hunting pressure when compared to other logged forests in the wider region [34,35], so may represent a more positive outcome than expected in comparably degraded forests with more hunting. Nonetheless, it is clear that if hunting is restricted, logged and degraded forests can provide significant biodiversity and ecological value [35].

Many taxa and functional groups had change points (Fig. 1C) at low levels of biomass removal, and a maximum rate of change (Fig. 1D) in only lightly degraded forest. Together, these two patterns reinforce the unique and irreplaceable value of unlogged forest habitat [5]. Low intensity logging of forests continued to impact additional taxa and functional groups until around 30 % of biomass had been removed (Fig. 1C), after which more severe logging exerted little additional influence on the occurrence patterns of taxa until approximately 80 % of biomass had been removed. Past this latter point, the act of removing the last remaining trees began to rapidly impact a new suite of taxa and functional groups (Fig. 1A).

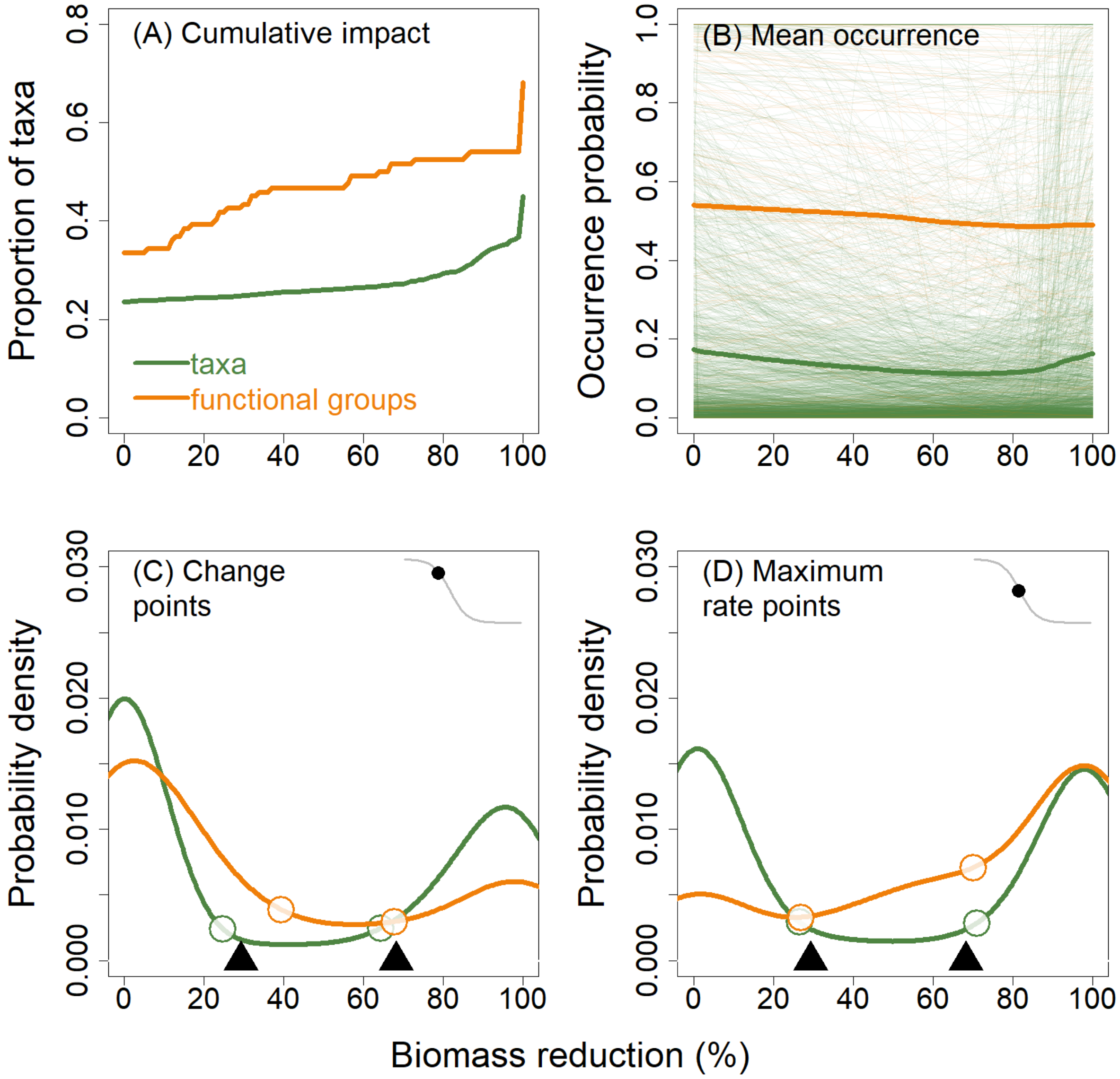

Figure 1: Summarised responses of 1,681 taxa and 126 functional groups to forest degradation. Forest degradation is represented as a percentage reduction in aboveground biomass density, where zero represents the median biomass density in unlogged forest. ***(A)*** *Cumulative distribution function of the proportion of taxa or functional groups that have passed a change point along the forest degradation gradient.* ***(B)*** *Mean occurrence probabilities along the forest degradation gradient. Thin lines show the fitted lines for all individual taxa and functional groups. Thick lines show the unweighted mean value of all fitted lines. Probability distribution functions show the spread of* ***(C)*** *change points and* ***(D)*** *maximum rates in occurrence for individual taxa and functional groups. Insets present a stylised representation of how change and maximum rate points are identified (see Fig. S3 for a more detailed explanation). Open circles represent locations at which the rate of accumulation of taxa accelerates, and are used to estimate thresholds (filled triangles) for conservation action*

(Methods). Peaks in the distributions represent points along the degradation gradient where the largest number of taxa or functional groups begin to be first impacted (C) or have their maximum rate of change in occurrence probability (D).

Ecological thresholds for proactive and reactive conservation

Our results indicate that forest that has lost less than 29 % of biomass (95 % bootstrapped confidence interval = 25-35 %; Methods) is likely to retain relatively high biodiversity and ecological value, and should be considered a viable addition to the proactively managed conservation estate (Fig. 1C, D). This value is similar to the more arbitrary definition of a high density forest in the widely used High Carbon Stock Approach [36], which sets a threshold at 150 $t.ha^{-1}$ of carbon regardless of pre-logging biomass (equivalent to 25 % biomass reduction at our study site). This threshold value represents the point at which changes in the occurrence patterns of many taxa have taken place (Fig. 1C), and where the number of functional groups experiencing maximum rates of change in occurrence begins to accelerate (Fig. 1D). However, most functional groups have had only relatively small changes in occurrence patterns at the 29 % threshold, implying the forest retains strong potential to recover through natural secondary successional processes if left alone, and means its conservation value can confidently be expected to increase through time without requiring direct, and often costly, management interventions.

Reactive conservation action may be best targeted in extremely degraded forests with around two-thirds of biomass loss (Fig. 1C, D; mean threshold of 68 %, 95 % bootstrapped confidence interval 60-83 %). Change points represent early signals of impending ecological changes, but those impending changes, and by association the largest ecological impacts, will only begin to fully manifest as taxa and functional groups reach their maximum rates of change in occurrence. The number of taxa and functional groups reaching maximum rates accelerated rapidly after 70 % biomass reduction (Fig. 1D). Even small improvements to the condition of the forest in this portion of the degradation gradient may be expected to have large impacts on the occurrence patterns of both individual taxa and functional groups, suggesting remedial action such as underplanting or liana cutting will likely be most effective if targeted here. We note, however, that our analysis examines the directed transition from unlogged to logged forest, and that our threshold is unlikely to mark the point at which taxa and functional groups recover to the same level following restoration of logged forest: a higher level of biomass restoration is likely required [37].

Vulnerability of taxonomic and functional groups to forest degradation

Forest degradation impacted taxa across the tree of life, but unevenly (Fig. 2A), emphasising how answers to critical conservation questions can be dependent on choices of study taxon. Of the 86 taxonomic orders in our analysis, 72 (81 %) included taxa whose occurrence patterns were significantly altered by habitat degradation, as were 83 (68 %) of the functional groups we analysed. We calculated the vulnerability of taxonomic and functional groups to habitat degradation as a product of probability of impact (the proportion of taxa within that group that were significantly impacted), and severity of impact (mean location of change points along the forest degradation gradient) (Methods). Both taxonomic and functional groups containing taxa that have a high probability of being impacted also tended to have a high severity of impact (Fig. 2, Pearson correlation, taxonomic groups: $r = 0.92$, df = 8, $p < 0.001$; functional groups: $r = 0.69$, df = 45, $p < 0.001$).

Across the major taxonomic groups, vertebrates were more vulnerable than invertebrates. Fish were the group with the highest proportion of taxa that were significantly impacted (77 %), and one of the most severely impacted groups, with many taxa heavily impacted by the early onset of logging [31]. Consequently, fish were also the most vulnerable taxonomic group to forest degradation, whereas ants and arachnids were the least vulnerable (Fig. 2A). Mammals also had high vulnerability to logging, which corroborates a previous pantropical analysis [11].

We found no significant differences in vulnerability among the different functional trait categories in the analysis (Fig. 2B, beta regression; $\chi^2_7 = 7.77$, $p = 0.35$). Rather, most categories of traits exhibited a range of vulnerability, reflecting the tremendous amount of variation of specific traits nested within those categories (Fig. 3A). For example, understorey birds had high vulnerability whereas arboreal mammals had low vulnerability, yet both functional groups represent traits related to the habitat strata they occupy and were therefore grouped together for this analysis.

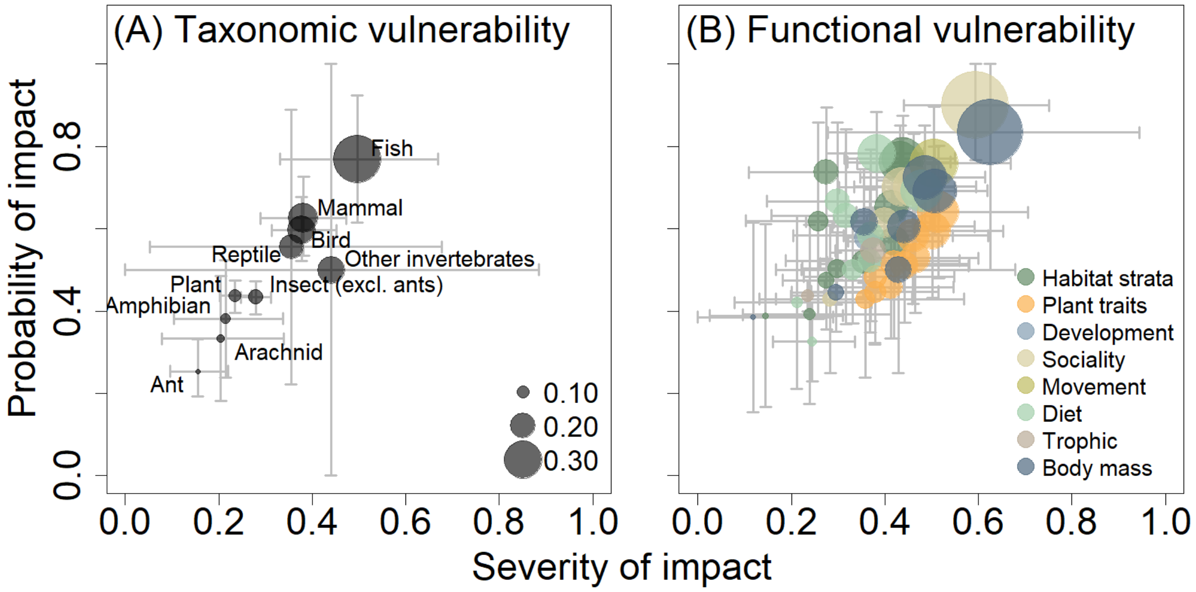

Figure 2. Vulnerability of ***(A)*** *taxonomic groups and* ***(B)*** *functional traits to habitat degradation. The magnitude of vulnerability is scaled by the size of the plotted points, and is the product of metrics representing the probability and severity of impact that habitat degradation has on taxa within the groups (Methods). Probability of impact is represented as the proportion of individual taxa within the group that had statistically significant changes in occurrence along the forest degradation gradient. Severity of impact is calculated as one minus the mean proportion of biomass reduction where individual taxa within the group have change points. Points are plotted at the mean values of probability and severity of impact per group, and lines represent the bootstrapped 95 % CI. Traits are grouped into categories for presentation (Methods; Table S2), and only functional traits containing ≥ 5 taxa are displayed. Functional groups are coloured according to broadly defined functional categories.*

System-wide turnover in the functional composition of degraded forest

Numerous functional traits are shared across multiple taxonomic groups, which should have led to occurrence patterns of functional groups that were largely robust to habitat degradation [24,25]. Yet instead, we found strong evidence of systemic changes to the functional composition of degraded tropical forest. Habitat degradation was associated with turnover from large to small taxa, specialist to generalist taxa, and from terrestrial to arboreal taxa (Fig. 3A). We found no general pattern with respect to trophic level, with no evidence that predators were more susceptible to habitat degradation than herbivores. The impacts of habitat degradation were felt by functional groups that generate the full breadth of ecological processes in tropical forest ecosystems (Fig. 3).

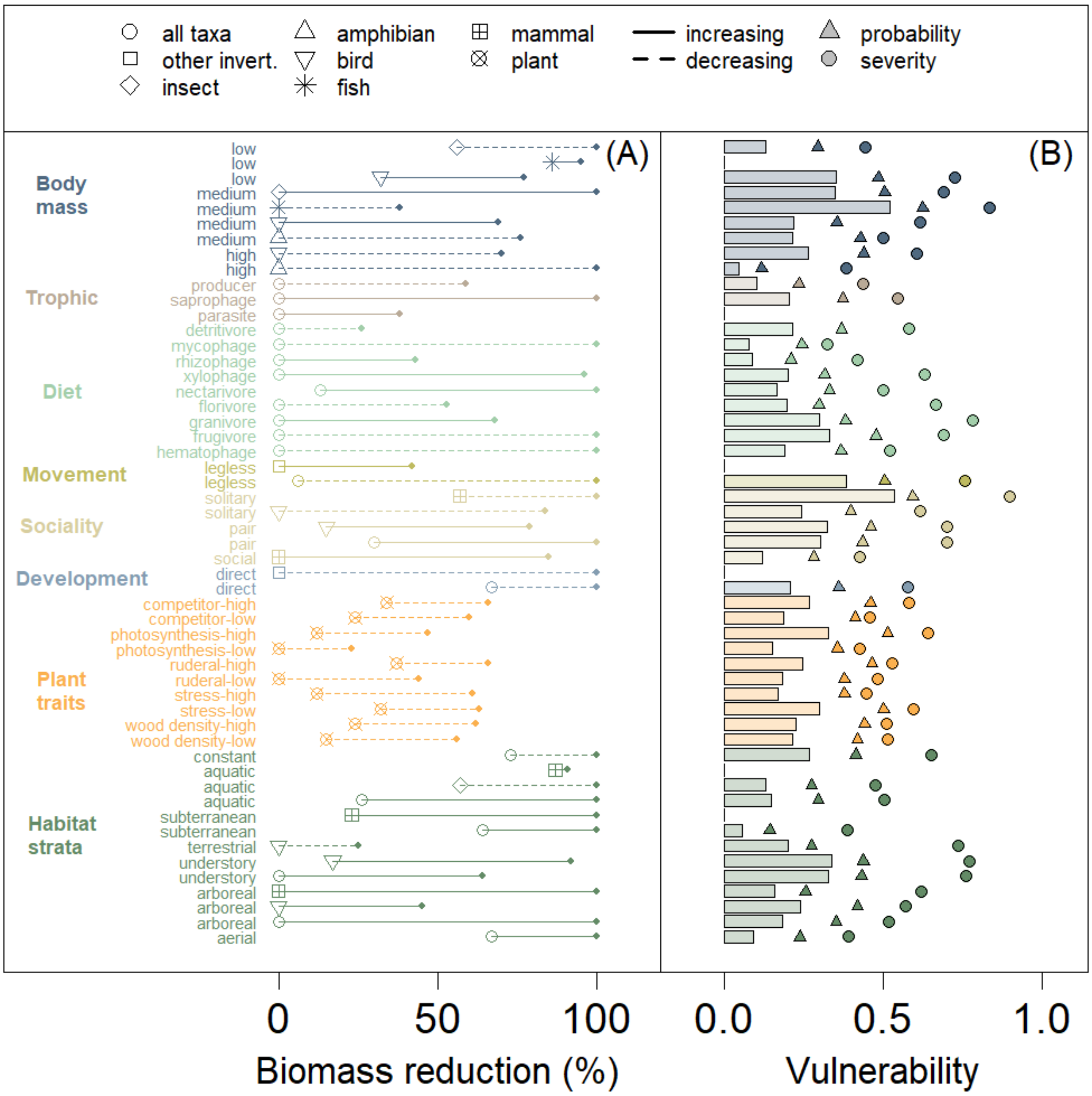

*Figure 3. Functional group responses to a forest degradation gradient, showing **(A)** critical thresholds and turnover, and **(B)** vulnerability, probability of impact and severity of impact, to biomass reduction. Analyses were conducted on the 126 functional groups described in Table S2, but here we present only functional groups that had statistically significant responses to forest degradation. All other groups not displayed had non-significant responses. In (A), lines represent a single functional group and connect the change point (symbol) to the maximum rate point (dot) for that group. Line type indicates whether the occurrence probability of that functional group is increasing (solid) or decreasing (dashed) along the forest degradation gradient, and symbols represent different taxa. The 'Other invert.' grouping contains non-insect invertebrates. In (B), vulnerability is shown in bars, with symbols representing the probability and severity of the impact that habitat degradation has on taxa within the groups. These metrics were calculated only for functional groups containing ≥ 5 taxa and*

are not shown for groups with fewer than this. In all panels, functional groups are coloured according to broadly defined functional categories.

All plant functional groups declined in occurrence as habitat degradation increased, with the most sensitive being those with low rates of photosynthetic activity measured in the field [29], including high timber value species in the Dipterocarpaceae. Pioneer tree species, including those with low wood density, might normally be expected to increase rather than decrease in response to logging disturbance [38]. However, very high amounts of biomass removal necessarily results in the extraction of a progressively higher proportion of standing trees [39], which inevitably includes species with low wood density. There was strong turnover in the body size of most animal taxa, with declines in large-bodied taxa like the Lowland litter frog *Leptobrachium abbotti* occurring across the entire degradation gradient, while small-bodied taxa like the cyprinid fish *Barbonymus balleroides* began to increase in the more heavily degraded forest. Habitat generalists that exploit multiple strata within the forest (such as termites in the genus *Microcerotermes*), and dietary generalists that consume many types of prey (omnivores like the bearded pig *Sus barbatus*), both increased in occurrence, whereas trophic specialists like the Rhinoceros hornbill *Buceros rhinoceros* declined. Turnover in specific dietary types was highly variable. The occurrence of fruit and flower feeders declined as habitat degradation progressed, while seed and nectar feeders increased. The occurrence of animals that feed on live wood and live roots also increased, while those that feed on dead plant material and fungus declined. Finally, there was considerable turnover in the ability of taxa to exploit the various forest strata as forest degradation progressed (Fig. 3). The occurrence of arboreal birds and mammals, including the Bornean orangutan *Pongo pygmaeus*, increased along the first half of the degradation gradient, after which mammals that have belowground prey like the Large treeshrew *Tupaia tana* began to increase. At the same time, the occurrence of terrestrial birds like the Argus pheasant *Argusianus argus* declined rapidly, followed by declines in the occurrence of aquatic invertebrates and mammals at high levels of forest degradation.

Rules of thumb for conservation planning

We found that focussing on the conservation of either individual taxa or functional groups resulted in remarkably congruent locations for ecological thresholds, providing clear, empirically justified rules of thumb about exactly where to target conservation action. Together, our data indicate that actions designed to proactively avoid ecological change should be targeted at different points in the forest degradation gradient than reactive action to reverse historic ecological change. Our data were collected from a single site, however, and taxon responses to habitat degradation can vary across geographical gradients [40,41] meaning the exact location of taxon-specific thresholds might similarly vary, so more studies of a similar nature will be required to strengthen confidence in the generality of our conclusions.

Forests that have lost less than 30 % of their biomass retain very high biodiversity and ecological value, and can make a significant contribution to the terrestrial and freshwater conservation estates. Proactive conservation decisions – actions designed to safeguard a habitat against further degradation – in these relatively lightly degraded forests could include adding them directly to the conservation estate by giving them protected area status [13], should that be a valid and equitable approach to conservation in the region [15]. Alternatively, depending on the local political and economic situation, maximum timber extraction rates could be set at levels that ensure the threshold is not passed, and might simultaneously consider protecting the three-dimensional structure of the forest, which also impacts the biodiversity value of logged forests [16]. However, we stress that 30 % biomass loss is not the same as 30 % biomass extraction, as the former includes the collateral damage to a forest from logging activity that can be more than triple the extracted biomass of harvested timber alone [42]. Biomass extraction rates should then be set at targets considerably lower than 30 % – perhaps as low as 10 % – although the use of Reduced Impact Logging techniques might facilitate higher commercial extraction rates.

Forest that have lost between 30 and 68 % of their biomass are likely to require a mix of conservation actions encompassing both proactive and reactive strategies, with reactive approaches increasing in importance as biomass loss progresses and ultimately passes the 68 % threshold. The conservation gains that could be obtained from reactive conservation and forest restoration efforts – specific actions designed to reverse the degradation of a habitat – are likely to be highest where tree biomass has been reduced by more than two-thirds (68 %). Assuming that the biodiversity and ecosystem functionality of a degraded forest will recover as forest biomass increases, then remedial action such as underplanting, liana cutting and invasive species control, are likely to have the greatest impact on occurrence patterns of both taxa and functional groups in these heavily degraded forests. Given such actions will accelerate the accumulation of carbon in degraded forests [43], funding for remedial actions might be raised through the sale of carbon credits [44].

There is no doubt, from our results and others [5], that primary forests are unique. Nonetheless, our data contribute to an emerging evidence base demonstrating that logged forests can and do retain significant biodiversity [2,3,8] and ecological [1] value. Moreover, the ecological and biodiversity differences that do exist between primary forests and lightly logged forests can be small [5,11,45]. These results demand that we stop devaluing degraded tropical forests for what they have lost, and rather appreciate them for the many values they retain. The future of conservation across the tropics is highly dependent on human modified habitats [4], and the way we choose to manage logged tropical forests will play a decisive role in stemming global biodiversity loss.

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Author contributions

RME designed the study, conducted the analyses and drafted the manuscript. CDLO, WDP, GR and CBL supported the data analysis, helped interpret the results and edited the manuscript. All other authors contributed field data and checked the manuscript.

Inclusion and ethics

All data used were collected in Malaysia. Non-Malaysian researchers conducting field work collaborated with local researchers throughout the research process. All local collaborators were invited to co-author this publication, as were all Malaysian research students involved in data collection.

Methods

All data manipulation, data analysis and construction of figures were conducted in the R v4.02 computing environment [46], using the packages ape [47], betareg [48], dplyr [49], lme4 [50], lmtest [51], lubridate [52], MASS [53], openxlsx [54], paletteer [55], pastecs [56], png [57], raster [58], reshape2 [59], rgdal [60], rgeos [61], safedata [62], scales [63], sf [64], spgwr [65], stringr [66] and strucchange [67].

Taxa records and functional groups

We summarize taxon responses from 8,130 combinations of surveys and taxa. We compiled biodiversity data from 52 published data sources (Table S1), from which we extracted presence-absence data following exactly the methods of Ewers *et al*. [68]. Previous analyses of multi-taxa biodiversity data have demonstrated that comparisons of presence-absence data among taxa are more robust than analyses of abundance data [23,69]. Moreover, abundance data were not available for all taxa, meaning presence-absence data is the highest-level data that allowed us to use exactly the same analysis method for all taxa. Data sources that sampled multiple years were split into separate, annual surveys, allowing us to more accurately align biodiversity observations with forest degradation measurements taken at different time points, and to account for year-to-year variation in taxon specific responses to the same ecological gradient [68]. Data sources that included multiple sampling methods were also split into separate, method specific surveys [68]. This process resulted in a total of 127 surveys being used for analysis.

Not all taxa in all surveys were identified to species or morphospecies level. We retained data on taxa identified to higher taxonomic levels because these could often be confidently placed into valid functional groups for analysis. Our data encompassed 4,691 taxa distributed widely across the terrestrial tree of life (Fig. S1), of which 1,777 were identified to species and a further 2,288 to morphospecies. We restricted our statistical analyses to 1,681 taxa that had ≥ 5 occurrences (Fig. S1), of which over half (n = 946) were observed in more than one survey (Fig. S2). Sensitivity analyses on these same data have demonstrated that a cut-off of 5 occurrences is appropriate to generate consistently reliable results [68].

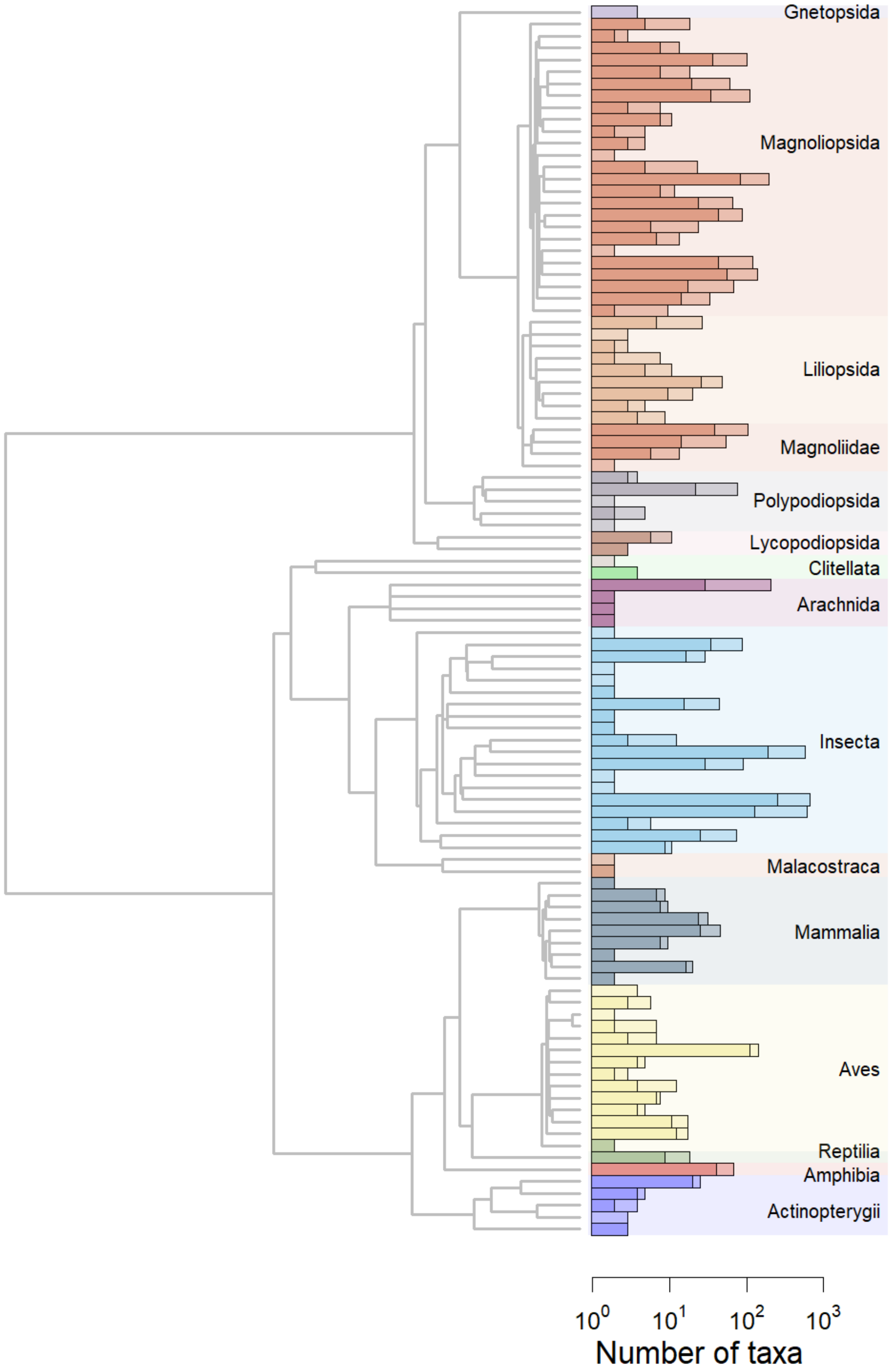

Fig. S1. Phylogenetic super-tree [54] *showing the 103 orders represented in the full set of biodiversity*

530 *surveys, of which 86 had at least one taxon with enough occurrence observations to be analysed. Bar length represents the number of taxa per order (light shading), and the number of taxa that were*

analysed (dark shading). Bars are presented on a $\log_{10}$-scale and are coloured according to taxonomic class.

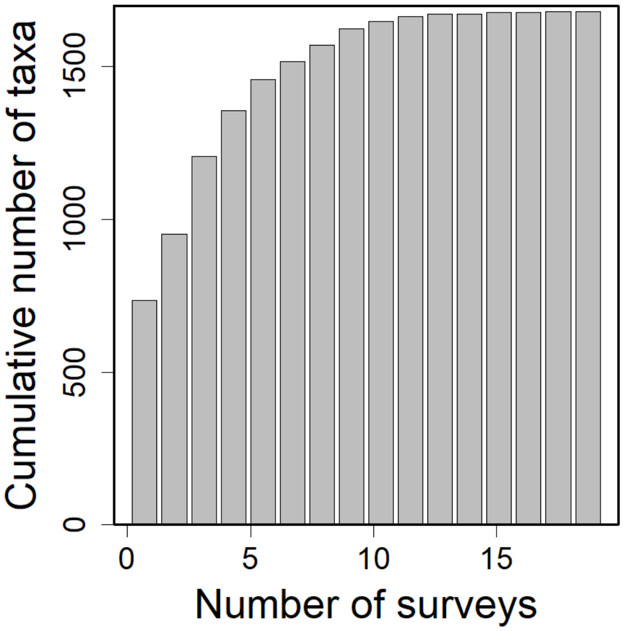

Fig. S2. Distribution of number of surveys per taxon for the 1,681 modelled taxa.

Taxonomic and functional groups: We aggregated taxa into high level taxonomic and functional groups to examine group-specific trends. First, we categorised taxa into 10 taxonomic groups for separate analysis (plants, arachnids, non-ant insects, ants, other invertebrates, mammals, birds, reptiles, amphibians and fish). Second, we compiled information on directly recorded morphological, functional and physiological traits for as many taxa as we could, which we used to allocate taxa into 126 functional groups (Table S2). In doing so, we relied heavily on previously published surveys [70-77], literature reviews and expert knowledge.

We included IUCN Red List status [78], which we collapsed into two categories: threatened (Critically Endangered, Endangered or Vulnerable) or not threatened (Least Concern, Lower Risk or Near Threatened). For plant taxa, we obtained data on wood density and photosynthesis rates [70], and used data on leaf area, leaf dry matter content and specific leaf area to estimate the strength of their association with each of three life history strategies: competitor; stress-tolerator; or ruderal (CSR) [79]. All four traits were continuous, which we categorised into two groupings for analysis (low and high according to whether trait values were below or above the median respectively).

For animal taxa, we compiled data on body mass for mammals [71], birds [80], fish [72] and beetles [73] from previously published surveys, estimated amphibian body mass from snout-venter length (SVL) measurements [81], and estimated ant body mass using a combination of morphometric data [59] and published scaling relationships [66]. Body mass was categorised into three groupings (low, medium and high) separately for each taxonomic group. Grouping boundaries were set by $\log_{10}$-transforming body mass and dividing taxa into three equal quantiles.

Animal taxa were assigned categories for physiology (endotherm or ectotherm), development (direct or indirect), sociality (solitary, pair, social or eusocial) and movement mode (winged, legged or legless). We used published records and expert knowledge to record non-mutually exclusive categories of forest strata use, classified as the strata where that taxon forages for food (subterranean, ground-dwelling, understorey, canopy-dwelling or aquatic), trophic level (saprophage, producer, herbivore, carnivore, parasite, parasitoid), and 21 diet categories (soil feeder, coprophage, necrophage, detritivore, saprophage, algivore, mycophage, rhizophage, folivore, florivore, nectarivore, palynivore, frugivore, granivore, xylophage, phloeophage, bacteriophage, invertivore, vertivore, piscivore, hematophage). For each of these last three functional traits, we counted the number of categories associated with each taxon, and categorised taxa as having either low or high generalism according to whether they fell above or below the median value for that trait.

Quantifying forest degradation

We followed the protocols described in Ewers et al. [68] to develop a quantitative metric of forest degradation. Briefly, data were collected at the SAFE Project [26] study site in Sabah, Malaysia. Taxa were sampled at sites that varied in the extent of historical disturbance from unlogged, old growth forest through to salvage logged forest and into deforested sites converted into oil palm plantations. We based our degradation metric on Aboveground Carbon Density (ACD, $Mg.ha^{-1}$) derived from airborne LiDAR data [82,83]. ACD values varied between 1 $Mg.ha^{-1}$ in cleared areas to a maximum of 273 $Mg.ha^{-1}$ in unlogged forest. For ease of interpretation, we converted ACD into a metric representing the percentage reduction in biomass relative to unlogged forest. We set the value of unlogged forest (0 % biomass removal) to be the median biomass density observed in unlogged forest (230 $Mg.ha^{-1}$). We chose to report values as a percentage as opposed to $Mg.ha^{-1}$ as it is more easily transferrable to other tropical forests where the maximum ACD may vary [84]. Forest degradation was quantified at two time points that approximately bracketed a salvage logging operation in the project area –

November 2014[82] and April 2016[83] – and taxa were analysed using the forest degradation values that were most closely matched in time to the date of the survey in which the taxon was observed.

The occurrence of a taxon at a given site is almost certainly a response to habitat conditions in a wider radius surrounding that site, so we calculated a spatial average to use as our predictor variable in analyses[33]. We selected all pixels within a radius of 250, 500, 1000, 2000 and 4000 m respectively around each sample site, allowing different taxa to respond to forest degradation at different spatial scales. Pixels within the buffer area were averaged, with pixels weighted using a Gaussian distance weighting to ensure that those located close to the sample site carried more weight than those located further away. The Gaussian distance weighting (W_g) was given by the equation:

$$W_g = e^{\left(-\left(\frac{d}{h}\right)\right)^2}$$

where d represents distance from the central sample site and h gives the bandwidth that was calculated as the maximum buffer distance divided by 100 (ref. [85]).

Quantifying and summarising taxa responses to forest quality

We focus our analyses on the response patterns of individual taxa or functional groups and not aggregated metrics such as species richness[86] or coarse, vote-counting comparisons of the number of positively *versus* negatively impacted taxa[87]. We take this approach because the turnover in the identity of taxa and functions are more sensitive measures of changes in biodiversity and ecosystem function. We focus instead on the locations of significant changes in response along the forest degradation gradient as opposed to the signs of those changes.

We test for two conservation-relevant patterns of change in the responses of individual taxa to forest degradation (Fig. S3): (1) change points: the point at which forest degradation first exerts a discernible impact on the occurrence pattern of a taxon or functional group[88]; and (2) maximum rate points: the point along the degradation gradient where the rate of change in occurrence is most rapid.

We use the aggregation of change points across taxa and functional groups along the forest degradation gradient to identify thresholds for prioritising proactive conservation, whereas the aggregation of maximum rate points indicates locations where relatively small changes in habitat quality can have the largest impact on the system. If the pattern by which biodiversity recovers from logging is the reverse of the pattern by which it is impacted by logging – i.e. if there is no hysteresis

[37] – then maximum rate points represent thresholds where reactive conservation actions, such as forest restoration, are likely to be most effective. This is because conservation actions that add small amounts of biomass to the forest are expected to result in the largest collective change in the occurrence patterns of the impacted taxa.

Occurrence models: We standardised all taxon observations to presence-absence data. To generate equivalent data for functional groups, within each survey we aggregated the presences of all taxa that belonged to a particular functional group. For each taxon and functional group, we then determined which survey(s) contained relevant data and combined all observations into a single dataframe for analysis. Only taxa or functional groups that had ≥ 5 occurrence records were analysed, and is the threshold value that results in repeated single-year surveys having the most consistent ecological results [68]. All individual taxa and functional groups were analysed independently of each other.

All models tested for an effect of percentage forest degradation on the probability of occurrence. Forest degradation was calculated at each of the five buffer sizes, and we selected the most appropriate spatial scale using Akaike Information Criterion (AIC) [53]. Statistical significance of the best model was determined with a log-likelihood ratio test comparing the best model to a null model. We tested for a main, linear effect of forest degradation only. This was because visual inspection and diagnostic plots of exploratory analyses containing a polynomial term failed to identify clear cases of taxa that had peaks in occurrence at intermediate levels of biomass removal.

If a given taxon or functional group was present in more than one survey, we first used a binomial generalised linear mixed model (GLMM) including a random intercept term for survey identity. If GLMMs failed to converge, or if the taxon or functional group was present in only a single survey, we used binomial generalised linear models (GLM). We were able to fit GLMMs to 798 out of the 946 taxa that were observed in multiple studies (84 % of fitted models) and 72 functional groups (59 %). The main reason by which GLMMs failed to converge was because taxa or functional groups observed in multiple datasets weren't necessarily observed equally in all datasets, and low numbers of observations in one or more surveys can limit the ability of a GLMM to estimate survey-specific random effects.

We opted not to use modelling methods that directly control for detectability, as such models routinely failed to converge in preliminary analyses. This problem is often encountered for analyses of tropical biodiversity where many species are rare and have low detection probabilities [89]. We note, however, that detectability models of species occupancy patterns along ecological gradients do not differ greatly from models that ignore detection probability [89], so we do not expect our choice of approach will notably influence our key results.

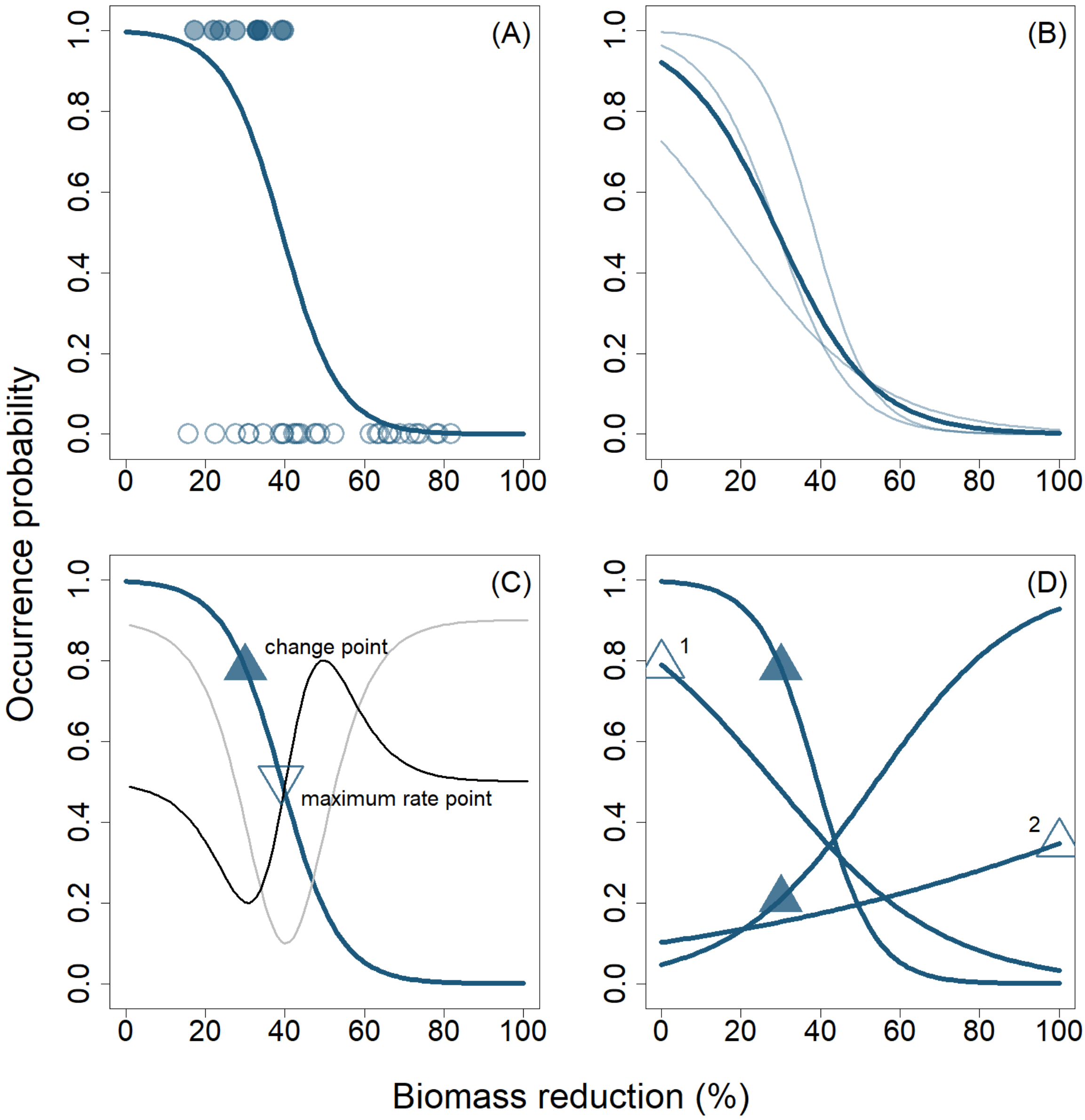

Figure S3: Visualisation of the data analysis process. ***(A)*** *For a given taxon in a given survey, we modelled taxon occurrence using presence (filled circles) and absence (open circles) data collected from individual surveys. Fitted occurrence probabilities were predicted across the forest degradation gradient. Forest degradation is represented as a percentage reduction in aboveground biomass, where zero represents the median biomass in unlogged forest.* ***(B)*** *Some taxa were observed in multiple surveys (represented by semi-transparent lines, here fitted as survey-specific linear models), each of which could have a different occurrence pattern [68]. In these cases, we used a mixed effect* *model to combine observations across all datasets, generating a single model of that taxon's occurrence pattern that was used to determine turning and maximum rate points (thick line).* ***(C)*** *The second derivative (black line; y-axis values not shown) of the fitted curve (thick blue line) was used to detect change points (filled triangle), which signify the point at which forest degradation first exerts a discernible impact on taxon occurrence* [88]*. Similarly, the first derivative (grey line; y-axis values not shown) was used to detect the point along the forest degradation gradient where the rate of change in occurrence of that taxon was the greatest (open triangle).* ***(D)*** *The approach used in panel (C) was applied to all taxa and functional groups. Two rules were used to record change points that fell outside of the survey's forest degradation range (open triangles): if the change point occurred below or above the range of feasible values it was truncated to 0 % or 100 % respectively (labelled 1 and 2 on the figure).*

Maximum rate points: We used the first derivatives of fitted models to find the point along the forest degradation gradient where the predicted rate of change in occurrence is most rapid [88], which we termed the 'maximum rate point' (Fig. S3C). This point was numerically estimated by identifying the point at which the predicted occurrence pattern from the binomial GLM had the highest absolute slope (as represented by the root of the second derivative), and corresponds to the point along the habitat degradation gradient where the probability of occurrence is 50 %. We used absolute slope as occurrence patterns may either increase or decrease along the forest degradation gradient, resulting in positive or negative slopes respectively.

Change points: We used the second derivatives of fitted models to find change points of the fitted binomial models (Fig. S3C, D), which represent the point along the forest degradation gradient where the rate of change in occurrence is itself changing the fastest [88]. As with the maximum rate points, these were numerically estimated by identifying the point at which the first derivative of the binomial GLM had the highest absolute slope (as represented by the root of the third derivative).

Binomial GLMs with significant slopes have a change point on either side of the maximum rate point, and we focussed our analyses on the point at the higher value of forest quality (lowest amount of biomass reduction in Fig. S3). These represent the change points at which taxa first begin to respond to reductions in forest quality. Change points are undefined for models with no significant slope.

Taxonomic bias in results: While the taxa we examined were diverse and are widely distributed across the tree of life (Fig. S1), they are not evenly distributed across the tree of life. If the different taxa exhibit consistent variation in the pattern of their responses, this taxonomic bias might impact our overall conclusions. To test for this, we modelled both maximum rate points and change points as a function of taxonomic group, and used log-likelihood ratio tests to compare both models against a null model. There was no significant effect in either case (change points: $\chi^2_{(-9)} = 2.79$, $P = 0.97$; maximum rate points: $\chi^2_{(-9)} = 9.78$, $P = 0.37$), indicating taxonomic bias in our dataset is unlikely to influence the interpretation of our results.

Temporal bias in results: Environmental conditions might influence the outcome of ecological studies [90]. If the surveys we analyse here are unequally distributed through time, and taxon responses to habitat degradation are time-dependent, then temporal autocorrelation might influence our conclusions. In a separate analysis of the same data used in this study, we have quantified this effect and demonstrated it is not a concern [68]. We examined whether taxon-specific occurrence patterns across the habitat degradation gradient varied among surveys and years. We found that while occurrence patterns do vary among surveys, there was no consistent signal of survey year on those patterns. Specifically, the number of years between two surveys had no significant impact on the probability of two surveys reporting statistically indistinguishable response patterns.

Long-term shifts in the composition of forest communities might mean the biodiversity patterns we associate with primary forest in our data are themselves depauperate relative to historical patterns [91]. Similarly, the complex logging history of our study site with repeated, but unequally distributed, rounds of logging means many sites have been through multiple stages of degradation separated by partial recovery [92,93]. Our data are not sufficient to quantify historical patterns of occupancy nor the impact of time lags on trajectories of occupancy, so we are unable to directly test for these effects. Nonetheless, long term declines and local extinction of megafauna like the Sumatran rhino *Dicerorhinus sumatrensis harrissoni* [94] make it likely that a shifting baseline is a valid concern at our study site. However, we have no way of knowing whether the rates of biodiversity change from the processes that might generate baseline shifts will be the same or different in primary and logged forest. Consequently, we can only emphasise that our analyses are based on a space-for-time substitution, which makes the implicit assumption that the effects of habitat degradation we quantify are additional to, and do not interact with, any other processes contributing to long-term biodiversity change.

Identifying thresholds: We fitted density curves to model the distribution of taxa and functional group change points along the forest degradation gradient. Density curves were fitted using the kernel density estimation function with default settings in the 'stats' package [46]. Estimates were extracted, and we used breakpoint regression on the fitted density distributions to identify the number and location of thresholds in aggregated biodiversity and functional group responses to forest degradation.

Thresholds differ from the analysis of individual change points in that it is based on the aggregation of all change points. Where change point analysis identified locations where the occurrence pattern of an individual taxon changes, the thresholds identified here represent locations where there is a change in the accumulated responses of the 1,681 taxa. Two classes of thresholds are possible: breakpoints signalling either an increase or decrease in the rate of accumulation of impacted taxa or functional groups. These acceleration points signify locations where the situation becomes *worse*, in that the rate at which the number of impacted taxa or functional groups begins to increase (or the rate of decline begins to slow down) as forest degradation increases.

We repeated this approach using the distribution of maximum rate points for both taxa and functional groups. In all cases, the breakpoint regression identified an optimal model containing two acceleration breakpoints. We set the threshold for proactive and reactive conservation to be based on the first and last acceleration points respectively. For each type of conservation, there were four proactive and four reactive thresholds estimated; one each for taxa change points, taxa maximum rate points, functional group change points and functional group maximum rate points. To obtain an aggregate threshold for proactive and reactive conservation, we used the mean of these four values.

We used bootstrapping to estimate a 95 % confidence interval around these means by resampling the fitted models 100 times and estimating the 2.5 and 97.5 % quantiles around the threshold estimates.

Vulnerability of taxonomic and functional categories to forest degradation: We combined two metrics to estimate the relative vulnerability of taxonomic and functional groups to forest degradation: (1) probability of impact, defined as the proportion of taxa within that group that exhibited a change point; and (2) severity of impact, defined as the mean location of change points among taxa within that group. Specifically, probability of impact (PI) is calculated as:

$$PI = \frac{\sum_{t=1}^{N} I_t}{N}$$

where N represents the number of taxa within that taxonomic category, I_t is a binary outcome representing whether taxon t is significantly impacted by forest degradation, calculated as:

$$I_t = \begin{cases} 1, & if\ p_t < 0.05 \\ 0, & if\ p_t \geq 0.05 \end{cases}$$

and p_t is the p-value from the analysis of taxon t's occurrence pattern in response to forest degradation. Taxonomic categories with large numbers of impacted taxa have high probability of impact values. Correlation analyses demonstrated that there was no impact of sample size (the number of taxa per group) on probability of impact for either taxonomic groups (r = -0.21, df = 8, p = 0.56) or for functional groups (r = -0.11, df = 45, p = 0.45).

Severity of impact (SI) is calculated as:

$$SI = 1 - \frac{\sum_{t=1}^{N} CP_t}{N \times 100}$$

where CP_t is the change point of taxon t's response pattern to forest degradation (Fig. S3C), and scales such that categories containing many taxa that tend to be impacted after the removal of small amounts of biomass have high severity of impact values. The change point for taxa that are not impacted by forest degradation ($p_t > 0.05$) is undefined, but excluding them from the severity of impact calculation would skew severity estimates: categories with large numbers of unimpacted taxa would retain the severity value calculated from the small number of impacted taxa. We therefore assigned unimpacted taxa a change point of 100 prior to calculating severity. This value indicates the taxon is not impacted until 100 % of biomass has been removed, and represents the least sensitive, real world change point value.

Both probability of impact and severity of impact are bounded at zero and one, and we combined them into a single metric of vulnerability (V) calculated as

$$V = PI \times SI$$

which is also bounded at zero and one. Taxonomic categories containing a high proportion of taxa that are impacted by low amounts of biodiversity loss have high vulnerability values. By contrast, categories in which a low proportion of taxa are impacted, and the taxa that are impacted only experience change points after the removal of large amounts of forest biomass, have the lowest vulnerability values.

To summarise functional vulnerability, we categorised functional groups into 10 higher level categories: Red List status, Habitat strata, Physiology, Development, Sociality, Movement, Diet, Trophic, Body mass and Plant traits (for all plant-specific functional groups). Within each category, we treated the individual functional groups as replicates, allowing us to calculate the probability of impact, severity of impact, and vulnerability of broadly categorised functional responses.

References

1 Malhi, Y. *et al.* Logged tropical forests have amplified and diverse ecosystem energetics. *Nature* **612**, 707-713 (2022).

2 Edwards, D. P. *et al.* Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proc. Roy. Soc. Lon. B* (2010).

3 Chazdon, R. L. *et al.* The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **23**, 1406-1417 (2009).

4 Gardner, T. A. *et al.* Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* **12**, 561-582 (2009).

5 Gibson, L. *et al.* Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378-381 (2011).

6 Barlow, J. *et al.* Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**, 144-147 (2016).

7 Ferraz, A. *et al.* Carbon storage potential in degraded forests of Kalimantan, Indonesia. *Environ. Res. Lett.* **13**, 095001 (2018).

8 Wearn, O. R. *et al.* Estimating animal density for a community of species using information obtained only from camera-traps. *Methods Ecol Evol* **13**, 2248-2261 (2022).

9 Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R. & Emerson, R. A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* **23**, 1386-1395 (2009).

10 Malhi, Y., Gardner, T. A., Goldsmith, G. R., Silman, M. R. & Zelazowski, P. Tropical forests in the anthropocene. *Annual Reviews in Environmental Resources* **39**, 125-159 (2014).

11 Burivalova, Z., Şekercioğlu, Ç. H. & Koh, L. P. Thresholds of logging intensity to maintain tropical forest biodiversity. *Curr. Biol.* **24**, 1893-1898 (2014).

12 Martin, P. A., Newton, A. C., Pfeifer, M., Khoo, M. & Bullock, J. M. Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *For. Ecol. Man.* **356**, 224-233 (2015).

13 Reynolds, G., Payne, J., Sinun, W., Mosigil, G. & Walsh, R. P. D. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. *Philos. Trans. R. Soc. B-Biol. Sci.* **366**, 3168-3176 (2011).

14 Brooks, T. M. *et al.* Global biodiversity conservation priorities. *Science* **313**, 58-61 (2006).

15 Schultz, B. *et al.* Recognizing the equity implications of restoration priority maps. *Environ. Res. Lett.* **17**, 114019 (2022).

16 Deere, N. J. *et al.* Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 26254-26262 (2020).

17 Costa, F. R. C. & Magnusson, W. E. Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a central Amazonian forest. *Biotropica* **35**, 103-114 (2003).

18 Brodie, J. F. *et al.* Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conserv. Biol.* **29**, 110-121 (2015).

19 Barlow, J., Mestre, L. A. M., Gardner, T. A. & Peres, C. A. The value of primary, secondary and plantation forests for Amazonian birds. *Biol. Conserv.* **136**, 212-231 (2007).

20 Widodo, E. S., Naito, T., Mohamed, M. & Hashimoto, Y. Effects of selective logging on the arboreal ants of a Bornean rainforest. *Entomological Science* **7**, 341-349 (2004).

21 Barlow, J. *et al.* Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 18555-18560 (2007).

22 Lawton, J. H. *et al.* Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**, 72-76 (1998).

23 Banks-Leite, C. *et al.* Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* **345**, 1041-1045 (2014).

24 Ewers, R. M. *et al.* Logging cuts the functional importance of invertebrates in tropical rainforest. *Nat. Comm.* **6**, 6836 (2015).

25 Harrison, M. L. K. & Banks-Leite, C. Edge effects on trophic cascades in tropical rainforests. *Conserv. Biol.* **34**, 977-987 (2020).

26 Ewers, R. M. *et al.* A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Phil. Trans. Roy. Soc. B* **366**, 3292-3302 (2011).

27 Haddad, N. M. *et al.* Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).

28 Hardwick, S. R. *et al.* The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. *Agri. For. Meteorol.* **201**, 187-195 (2015).

29 Both, S. *et al.* Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytol.* **221**, 1853-1865 (2019).

30 Betts, M. G. *et al.* Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**, 441-444 (2017).

31 Cusack, J. J., Wearn, O. R., Bernard, H. & Ewers, R. M. Influence of microhabitat structure and disturbance on detection of native and non-native murids in logged and unlogged forests of northern Borneo. *Journal of Tropical Ecology* **31**, 25-35 (2015).

32 Döbert, T. F., Webber, B. L., Sugau, J. B., Dickinson, K. J. M. & Didham, R. K. Logging, exotic plant invasions, and native plant reassembly in a lowland tropical rain forest. *Biotropica* **50**, 254-265 (2018).

33 Pfeifer, M. *et al.* Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187-191 (2017).

34 Wearn, O. R. *et al.* Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multi-species modelling approach. *Biol. Conserv.* **212**, 162-171 (2017).

35 Deere, N. J. *et al.* Implications of zero-deforestation commitments: forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes. *Conserv. Lett.* **13**, e12701 (2020).

36 Rosoman, G., Sheun, S. S., Opal, C., Anderson, P. & Trapshah, R. The HCS Approach Toolkit Version 2.0. (HCS Approach Steering Group, Singapore, 2017).

37 Staal, A. *et al.* Hysteresis of tropical forests in the 21st century. *Nat. Comm.* **11**, 4978 (2020).

38 Carreño-Rocabado, G. *et al.* Effects of disturbance intensity on species and functional diversity in a tropical forest. *J. Ecol.* **100**, 1453-1463 (2012).

39 Pfeifer, M. *et al.* Deadwood biomass: an underestimated carbon stock in degraded tropical forests? *Environ. Res. Lett.* **10**, 044019 (2015).

40 Williams, J. J. & Newbold, T. Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. *Divers. Dist.* (2021).

41 Orme, C. D. L. *et al.* Distance to range edge determines sensitivity to deforestation. *Nat. Ecol. Evol.* **3**, 886-891 (2019).

42 Pinard, M. A. & Putz, F. E. Retaining forest biomass by reducing logging damage. *Biotropica* **28**, 278-295 (1996).

43 Philipson, C. D. *et al.* Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science* **369**, 838-841 (2020).

44 van Oosterzee, P., Liu, H. & Preece, N. D. Cost benefits of forest restoration in a tropical grazing landscape: Thiaki rainforest restoration project. *Glob. Environ. Change* **63**, 102105 (2020).

45 Newbold, T. *et al.* Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45-50 (2015).

46 R Development Core Team. *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing, 2021).

47 Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526-528 (2019).

48 Cribari-Neto, F. & Zeileis, A. Beta regression in R. *Journal of Statistical Software* **34** (2010).

49 Wickham, H., Francois, R., Henry, L. & Muller, K. dplyr: A grammar of data manipulation (2021).

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

51 Zeileis, A. & Hothorn, T. Diagnostic checking in regression relationships. *R News* **2**, 7-10 (2002).

52 Grolemund, G. & Wickham, H. Dates and times made easy with lubridate. *Journal of Statistical Software* **40**, 1-25 (2011).

53 Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S. Fourth Edition*. (Springer, 2002).

54 Schauberger, P. & Walker, A. openxlsx: Read, Write and Edit xlsx Files (2021).

55 Hvitfeldt, E. paletteer: Comprehensive collection of color palettes (2021).

56 Grosjean, P. & Ibanez, F. pastecs: Package for Analysis of Space-Time Ecological Series (2018).

57 Urbanek, S. png: Read and Write PNG Images (2013).

58 Hijmans, R. J. raster: Geographic Data Analaysis and Modeling (2021).

59 Wickham, H. Reshaping data with the reshape Package. *Journal of Statistical Software* **21**, 1-20 (2007).

60 Bivand, R., Keitt, T. & Rowlingson, B. rgdal: Bindings for the 'Geospatial' Data Abstraction Library (2021).

61 Bivand, R. & Rundel, C. rgeos: Interface to Geometry Engine - Open Source ('GEOS') (2020).

62 Aldersley, A. & Orme, C. D. L. *safedata: Interface to Data from the SAFE Project*, <https://imperialcollegelondon.github.io/safedata/> (2019).

63 Wickham, H. & Seidel, D. P. scales: Scale functions for visualization (2020).

64 Pebesma, E. Simple features for R: standardized support for spatial vector data. *The R Journal* **10**, 439-446 (2018).

65 Bivand, R. & Yu, D. spgwr: Geographically Weighted Regression (2020).

66 Wickham, H. stringr: Simple, consistent wrappers for common string operations (2019).

67 Zeileis, A., Leisch, F., Hornik, K. & Kleiber, C. strucchange: an R package for testing for structural change in linear regression models. *Journal of Statistical Software* **7**, 1-38 (2002).

68 Ewers, R. M. *et al.* Variable responses of individual species to tropical forest degradation. *bioRxiv*, 2024.2002.2009.576668 (2024).

69 Banks-Leite, C., Larrosa, C., Carrasco, L. R., Tambosi, L. R. & Milner-Gulland, E. J. The suggestion that landscapes should contain 40% of forest cover lacks evidence and is problematic. *Ecol. Lett.* **24**, 1112-1113 (2021).

70 Both, S. *et al.* Functional traits of tree species in old-growth and selectively logged forest. (2019). 10.5281/ZENODO.3247631

71 Jones, K. E. *et al.* PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648-2648 (2009).

72 Wilkinson, C. & Ewers, R. M. Fish functional diversity traits. (2018). 10.5281/ZENODO.1237719

73 Vigus, H. Coleoptera functional and morphological traits. (2020). 10.5281/ZENODO.3908249

74 Bishop, T. & Ewers, R. Abundance and morphometrics of ant genera. (2018). 10.5281/ZENODO.1198839

75 Inger, R. F., Stuebing, R. B., Grafe, T. U. & Dehling, J. M. *A Field Guide to the Frogs of Borneo*. (Natural History Publications Borneo, 2017).

76 Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C. & Davies, R. G. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiv. Conserv.* **23**, 2817-2832 (2014).

77 Tobias, J. A. *et al.* AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581-597 (2022).

78 IUCN. The IUCN Red List of Threatened Species. (2021).

79 Pierce, S. *et al.* A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Func. Ecol.* **31**, 444-457 (2017).

80 Tobias, J. AVONET: a global database of bird traits. *Ecol. Lett.* (in press).

81 Santini, L., Benítez-López, A., Ficetola, G. F. & Huijbregts, M. A. J. Length–mass allometries in amphibians. *Integrative Zoology* **13**, 36-45 (2018).

82 Jucker, T. *et al.* Topography shapes the structure, composition and function of tropical forest landscapes. *Ecol. Lett.* **21**, 989-1000 (2018).

83 Jucker, T. *et al.* Estimating aboveground carbon density and its uncertainty in Borneo's structurally complex tropical forests using airborne laser scanning. *Biogeosciences* **15**, 3811-3830 (2018).

84 Asner, G. P. *et al.* Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. *Biol. Conserv.* **217**, 289-310 (2018).

85 Brunsdon, C., Fotheringham, A. S. & Charlton, M. E. Geographically weighted regression: a method for exploring spatial nonstationarity. *Geographical Analysis* **28**, 281-298 (1996).

86 Banks-Leite, C., Ewers, R. M. & Metzger, J. P. Unravelling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology* **93**, 2560-2569 (2012).

87 Fletcher, R. J. *et al.* Is habitat fragmentation good for biodiversity? *Biol. Conserv.* **226**, 9-15 (2018).

88 Ewers, R. M. & Didham, R. K. Continuous response functions for quantifying the strength of edge effects. *J. Appl. Ecol.* **43**, 527-536 (2006).

89 Banks-Leite, C. *et al.* Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. *J. Appl. Ecol.* **51**, 849-859 (2014).

90 Powers, S. M. & Hampton, S. E. Open science, reproducibility, and transparency in ecology. *Ecol. Appl.* **29**, e01822 (2019).

91 Stouffer, P. C. *et al.* Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. *Ecol. Lett.* **24**, 186-195 (2021).

92 Riutta, T. *et al.* Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biol.* **24**, 2913-2928 (2018).

93 Struebig, M. *et al.* Quantifying the biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from Borneo. *Adv. Ecol. Res.* **48**, 183-224 (2013).

94 Kretzschmar, P. *et al.* The catastrophic decline of the Sumatran rhino (Dicerorhinus sumatrensis harrissoni) in Sabah: Historic exploitation, reduced female reproductive performance and population viability. *Global Ecology and Conservation* **6**, 257-275 (2016).

95 Bernard, H., Hee, K. B. & Wong, A. Importance of riparian reserves and other forest fragments for small mammal diversity in disturbed and converted forest landscapes. (2020). 10.5281/ZENODO.3908128

96 Brant, H., Mumford, J., Ewers, R. & Benedick, S. Mosquito Data At Safe 2012-2014. (2018). 10.5281/ZENODO.1198846

97 Carpenter, D. *et al.* The Maliau Quantitative Inventory. (2021). 10.5281/zenodo.5562260

98 Chapman, P. M. & Davison, C. Small mammals at forest-oil palm edges raw datasets. (2019). 10.5281/ZENODO.2579792

99 Deere, N. J. Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations. (2020). 10.5281/zenodo.4010757

100 Döbert, T., Webber, B. L., Sugau, J. B., Dickinson, K. J. M. & Didham, R. K. Landuse change and species invasion. (2019). 10.5281/ZENODO.2536270

101 Drinkwater, R., Drinkwater, R., Swinfield, T. & Deere, N. J. Occurrence of blood feeding terrestrial leeches in a degraded forest ecosystem. (2019). 10.5281/ZENODO.3476542

102 Ewers, R. M. & Gray, R. The importance of vertebrates in regulating insect herbivory pressure along a gradient of logging intensity in Sabah, Borneo. (2020). 10.5281/ZENODO.3975973

103 Faruk, A. Leaf Litter Amphibian Communities. (2018). 10.5281/ZENODO.1303010

104 Fayle, T. M., Yusah, K. M., Ewers, R. M. & Boyle, M. J. W. How does forest conversion and fragmentation affect ant communities and the ecosystem processes that they mediate? (2020). 10.5281/ZENODO.3876227

105 Fraser, A. *et al.* Amphibian survey of riparian buffer zones at SAFE Project, Borneo. (2020). 10.5281/ZENODO.3973551

106 Fraser, A., Bernard, H., Mackintosh, E., Ewers, R. M. & Banks-Leite, C. Effects of habitat modification on a tritrophic cascade in a lowland tropical rainforest. (2020). 10.5281/ZENODO.3981222

107 Gray, R., Gill, R. & Ewers, R. The Role Of Competition In Structuring Ant Community Composition Across A Tropical Forest Disturbance Gradient. (2018). 10.5281/ZENODO.1198302

108 Gray, R., Slade, E., Chung, A. & Lewis, O. Riparian_Invertebrate_Movement_Data_SAFE. (2019). 10.5281/ZENODO.3475406

109 Gregory, N., Ewers, R. M., Cator, L. & Chung, A. Vectorial capacity of *Aedes albopictus* across an environmental gradient. (2020). 10.5281/zenodo.3994260

110 Hardwick, J. *et al.* The effects of habitat modification on the distribution and feeding ecology of Orthoptera 2015. (2020). 10.5281/zenodo.4275386

111 Hemprich-Bennett, D. *et al.* Impacts of rainforest degradation on the diets of the insectivorous bats of Sabah. (2019). 10.5281/ZENODO.3247465

112 Wearn, O. R., Carbone, C., Rowcliffe, J. M., Bernard, H. & Ewers, R. M. Grain-dependent responses of mammalian diversity to land use and the implications for conservation set-aside. *Ecol. Appl.* **26**, 1409-1420 (2016).

113 Heon, S., Chapman, P. M., Wearn, O. R., Berhard, H. & Ewers, R. M. Core SAFE project small mammal trapping data. (2020). 10.5281/ZENODO.3955050

114 Heon, S., Chapman, P., Bernard, H. & Ewers, R. M. Do Logging Roads Impede Small Mammal Movement In Borneo'S Tropical Rainforests? (2018). 10.5281/ZENODO.1304117

115 Jebrail, E. W., Dahwood, M., Fikri, A. H. & Yahya, B. The effects of progressive land use changes on the distribution, abundance and behavior of vector mosquitoes in Sabah, Malaysia. (2019). 10.5281/ZENODO.3475408

116 Kendall, A. & Ewers, R. M. The Effect Of Forest Modification On Ectoparasite Density And Diversity. (2018). 10.5281/ZENODO.1237736

117 Konopik, O. Functional diversity of amphibian assemblages along a disturbance gradient. (2018). 10.5281/ZENODO.1995439

118 Lane Shaw, I. & Ewers, R. M. Microclimate Change, Forest Disturbance And Twig-Dwelling Ants. (2018). 10.5281/ZENODO.1237732

119 Layfield, H. Otter Qpcr Data At Safe. (2018). 10.5281/ZENODO.1198475

120 Luke, S. H. *et al.* Freshwater invertebrates - diversity and function of stream macroinvertebrates: Effects of habitat conversion and strategies for conservation. (2021). 10.5281/zenodo.5710509

121 Luke, S. Ant And Termite Assemblages Along A Tropical Forest Disturbance Gradient In Sabah, Malaysia: A Study Of Co-Variation And Trophic Interactions. (2018). 10.5281/ZENODO.1198833

122 Mackintosh, E., Fraser, A., Banks-Leite, C., Ewers, R. M. & Chung, A. Effect of vertebrate exclusion on ecosystem functioning. (2021). 10.5281/zenodo.4630980

123 Maunsell, S. *et al.* Variation in arthropod responses to tropical landscape transformation: moths 2014. (2020). 10.5281/zenodo.4247169

124 Maunsell, S. *et al.* Variation in arthropod responses to tropical landscape transformation: spiders 2015. (2020). 10.5281/zenodo.4139684

125 Mitchell, S. L. *et al.* Spatial replication and habitat context matters for assessments of tropical biodiversity using acoustic indices. *Ecol. Indic.* **119**, 106717 (2020).

126 Mullin, K. *et al.* Bat activity in riparian reserves in forest and oil palm plantations. (2020). 10.5281/ZENODO.3971012

127 Noble, C. Impacts of habitat disturbance on population health of Bornean frogs. (2019). 10.5281/ZENODO.3485086

128 Pianzin, A., Wong, A., Bernard, H. & Struebig, M. Investigating the distribution and occupancy of otter species across human-modified landscapes in Sabah, Malaysia. (2020). 10.5281/zenodo.3897377

129 Pillay, R., Fletcher, R. J., Sieving, K. E., Udell, B. J. & Bernard, H. Bioacoustic monitoring reveals shifts in breeding songbird populations and singing behaviour with selective logging in tropical forests. (2019). 10.5281/ZENODO.3366104

130 Psomas, E. Myrmecophilous Pselaphine Beetles In Tropical Forests. (2018). 10.5281/ZENODO.1400562

131 Qie, L., Telford, E., Nilus, R. & Ewers, R. Increased importance of terrestrial vertebrate seed dispersal in tropical logged forests. (2020). 10.5281/ZENODO.3901735

132 Qie, L., Telford, E., Massam, M. & Ewers, R. Impact Of El Nino Drought On Seedling Dynamics. (2018). 10.5281/ZENODO.1400564

133 Sawang, A., Sharp, A., Chung, A., Ewers, R. & Barclay, M. Core - invert biomass + ordinal sort. (2019). 10.5281/zenodo.3354067

134 Seaman, D., Struebig, M., Bernard, H., Ancrenaz, M. & Ewers, R. M. The effect of tropical forest modification on primate population density and diversity. (2021). 10.5281/zenodo.5109892

135 Sethi, S. *et al.* Avifaunal and Herpetofaunal point counts with recorded acoustic data. (2020). 10.5281/ZENODO.3742834

136 Shapiro, D. & Ewers, R. M. Investigating Temperature Tolerance In Mosquito Disease Vectors Across A Land-Use Gradient. (2018). 10.5281/ZENODO.1237720

137 Sharp, A., Barclay, M., Chung, A. & Ewers, R. Beetle Diversity. (2018). 10.5281/ZENODO.1323504

138 Slade, E. M., Bush, E., Mann, D. J. & Chung, A. Y. C. Dung beetle community and dung removal data 2011. (2019). 10.5281/ZENODO.3247492

139 Slade, E. M., Chung, A. Y. C. & Parrett, J. Dung beetle community data 2018. (2020). 10.5281/ZENODO.3832076

140 Slade, E. M., Milne, S., Mann, D. J., Chung, A. Y. C. & Parrett, J. Dung beetle community and dung removal data 2015. (2019). 10.5281/ZENODO.3247494

141 Slade, E. M., Milne, S., Chung, A. Y. C., Williamson, J. & Parrett, J. Dung beetle community and dung removal data 2015. (2020). 10.5281/ZENODO.3906118

142 Slade, E. M., Williamson, J., Chung, A. Y. C., Parrett, J. & Heroin, H. Dung beetle community 2017/18. (2020). 10.5281/ZENODO.3906441

143 Turner, E. C. *et al.* Tree census data from the SAFE Project 2011-12. (2021). 10.5281/ZENODO.5729342

144 Twining, J. & Ewers, R. M. Terrestrial Scavenger Trapping Data. (2018). 10.5281/ZENODO.1237731

145 Vollans, M., Cator, L., Ewers, R. M. & Chung, A. Investigating the impact of human settlements upon the availability of larval habitats and Aedes albopictus population. (2020). 10.5281/ZENODO.3929764

146 Wilkinson, C. *et al.* All Fish catch data at the SAFE project 2011-2017. (2020). 10.5281/ZENODO.3982665

147 Williamson, J. Movement Patterns Of Invertebrates In Tropical Rainforest. (2018). 10.5281/ZENODO.1487595

Table S1. List of data sources compiled for analysis. For each data source, we present the surname of the first author and a survey citation; a weblink to a data publication or, if that is unavailable, then a weblink to a published paper presenting the data; the types of taxa included; the number of taxa; the number of sampling methods used; the number of sampling periods; and the final number of surveys we extracted from that data source.

First author	Link	Taxon type(s)	No. taxa	No. sampling methods	No. sample periods	No. surveys
Bernard [95]	https://zenodo.org/record/3908128	mammal	23	1	1	1
Bishop [74]	https://zenodo.org/record/1198839	invertebrate	299	1	1	1
Both [70]	https://zenodo.org/record/3247631	plant	262	1	1	1
Brant [96]	https://zenodo.org/record/1198846	invertebrate	43	2	2	3
Carpenter [97]	https://zenodo.org/record/5562260	invertebrate	106	6	1	6
Chapman [98]	https://zenodo.org/record/2579792	mammal	12	1	1	1
Deere [99]	https://zenodo.org/record/4010757	mammal	28	1	3	3
Döbert [100]	https://zenodo.org/record/2536270	plant	1,235	1	1	1
Drinkwater [101]	https://zenodo.org/record/3476542	invertebrate	2	1	2	2
Ewers [102]	https://zenodo.org/record/3975973	invertebrate	17	1	1	1
Faruk [103]	https://zenodo.org/record/1303010	amphibian	2	1	1	1
Fayle [104]	https://zenodo.org/record/3876227	invertebrate	271	1	1	1
Fraser [105]	https://zenodo.org/record/3973551	amphibian	22	1	1	1
Fraser [106]	https://zenodo.org/record/3981222	bird	82	1	1	1
Gray [107]	https://zenodo.org/record/1198302	invertebrate	56	1	1	1
Gray [108]	https://zenodo.org/record/3475406	invertebrate	11	1	1	2
Gregory [109]	https://zenodo.org/record/3994260	invertebrate	1	1	1	1
Hardwick [110]	https://zenodo.org/record/4275386	invertebrate	90	1	1	1
Hemprich-Bennett [111]	https://zenodo.org/record/3247465	mammal	47	1	3	3
Heon [112]	https://doi.org/10.1890/15-1363	mammal; bird; reptile	62	1	6	6
Heon [113]	https://zenodo.org/record/3955050	mammal; reptile; bird	35	1	7	7
Heon [114]	https://zenodo.org/record/1304117	mammal	8	1	1	1
Jebrail [115]	https://zenodo.org/record/3475408	invertebrate	7	1	1	1
Kendall [116]	https://zenodo.org/record/1237736	invertebrate	1	1	1	1
Konopik [117]	https://zenodo.org/record/1995439	amphibian	29	1	3	3
Lane Shaw [118]	https://zenodo.org/record/1237732	invertebrate	21	1	1	1
Layfield [119]	https://zenodo.org/record/1198475	mammal	1	1	1	1
Luke [120]	https://zenodo.org/record/5710509	invertebrate	191	3	2	6
Luke [121]	https://zenodo.org/record/1198833	invertebrate	27	2	1	2
Mackintosh [122]	https://zenodo.org/record/4630980	invertebrate	17	1	1	1
Maunsell [123]	https://zenodo.org/record/4247169	invertebrate	599	1	1	1

Maunsell [124]	https://zenodo.org/record/4139685	invertebrate	216	1	1	1
Mitchell [125]	https://doi.org/10.1016/j.ecolind.2020.106717	bird	135	1	5	5
Mullin [126]	https://zenodo.org/record/3971012	mammal	7	1	2	3
Noble [127]	https://zenodo.org/record/3485086	amphibian	11	1	1	1
Pianzin [128]	https://zenodo.org/record/3897377	mammal	2	1	1	1
Pillay [129]	https://zenodo.org/record/3366104	bird	7	1	2	2
Psomas [130]	https://zenodo.org/record/1400562	invertebrate	42	1	1	1
Qie [131]	https://zenodo.org/record/3901735	mammal; bird; reptile; invertebrate	54	1	1	1
Qie [132]	https://zenodo.org/record/1400564	plant	312	1	3	3
Sawang [133]	https://zenodo.org/record/3354068	invertebrate	8	1	2	2
Seaman [134]	https://zenodo.org/record/5109892	mammal	1	1	1	1
Sethi [135]	https://zenodo.org/record/3997172	bird; amphibian	290	1	2	3
Shapiro [136]	https://zenodo.org/record/1237720	invertebrate	10	1	1	1
Sharp [137]	https://zenodo.org/record/1323504	invertebrate	594	1	2	11
Slade [138-140]	https://zenodo.org/record/3247492 https://zenodo.org/record/3247494 https://zenodo.org/record/3832076	invertebrate	83	1	3	3
Slade [141,142]	https://zenodo.org/record/3906118 https://zenodo.org/record/3906441	invertebrate	72	1	2	2
Turner [143]	https://zenodo.org/record/5729342	plant	123	1	10	10
Twining [144]	https://zenodo.org/record/1237731	reptile; mammal	6	1	1	1
Vollans [145]	https://zenodo.org/record/3929764	invertebrate	2	1	1	1
Wilkinson [146]	https://zenodo.org/record/4072959	fish	36	3	5	10
Williamson [147]	https://zenodo.org/record/1487595	invertebrate	15	1	1	1

Table S2. List of functional groups used in analyses. Groups are a combination of up to four factors: (1) Category – used to aggregate functional groups into sets of related functions; (2) Taxon – used to separate functional groups by taxonomic identity; (3) Attributes – specific morphology, behaviour, life history strategy or conservation status; and (4) Level – used to separate attributes by categories of increasing value.

Category	Taxon[a]	Attributes	Level
Body mass	insect		low
Body mass	insect		medium
Body mass	insect		high
Body mass	ant		low
Body mass	ant		medium
Body mass	ant		high
Body mass	mammal		low
Body mass	mammal		medium
Body mass	mammal		high
Body mass	bird		low
Body mass	bird		medium
Body mass	bird		high
Body mass	amphibian		low
Body mass	amphibian		medium
Body mass	amphibian		high
Body mass	fish		low
Body mass	fish		medium
Body mass	fish		high
Trophic	all taxa	parasitoid	
Trophic	all taxa	parasite	
Trophic	all taxa	carnivore	
Trophic	all taxa	herbivore	
Trophic	all taxa	saprophage	
Trophic	all taxa	producer	
Trophic	all taxa	generalism	low
Trophic	all taxa	generalism	high[c]
Diet	all taxa	hematophage	
Diet	all taxa	piscivore	
Diet	all taxa	vertivore	
Diet	all taxa	invertivore	
Diet	all taxa	bacteriophage	
Diet	all taxa	frugivore	
Diet	all taxa	granivore	
Diet	all taxa	florivore	
Diet	all taxa	nectarivore	
Diet	all taxa	palynivore	
Diet	all taxa	folivore	
Diet	all taxa	phloeophage	
Diet	all taxa	xylophage	

Diet	all taxa	rhizophage	
Diet	all taxa	algivore	
Diet	all taxa	mycophage	
Diet	all taxa	saprophage	
Diet	all taxa	coprophage	
Diet	all taxa	necrophage	
Diet	all taxa	detritivore	
Diet	all taxa	saproxylic	
Diet	all taxa	soilphage	
Diet	all taxa	generalism	low[b]
Diet	all taxa	generalism	high[c]
Movement	invertebrate	legged	
Movement	invertebrate	legless	
Movement	insect	winged	
Movement	insect	legged	
Movement	mammal	winged	
Movement	mammal	legged	
Movement	reptile	legged	
Movement	reptile	legless	
Movement	all taxa	winged	
Movement	all taxa	legged	
Movement	all taxa	legless	
Sociality	insect	eusocial	
Sociality	insect	social	
Sociality	insect	solitary	
Sociality	mammal	social	
Sociality	mammal	pair	
Sociality	mammal	solitary	
Sociality	bird	pair	
Sociality	bird	solitary	
Sociality	amphibian	social	
Sociality	amphibian	solitary	
Sociality	all taxa	eusocial	
Sociality	all taxa	social	
Sociality	all taxa	pair	
Sociality	all taxa	solitary	
Development	invertebrate	direct	
Development	invertebrate	indirect	
Development	insect	direct	
Development	insect	indirect	
Development	all taxa	direct	
Development	all taxa	indirect	
Physiology	all taxa	endotherm	
Physiology	all taxa	ectotherm	
Habitat strata[d]	insect	arboreal	
Habitat strata	insect	understorey	
Habitat strata	insect	terrestrial	
Habitat strata	insect	subterranean	

Habitat strata	insect	aquatic	
Habitat strata	mammal	aerial	
Habitat strata	mammal	arboreal	
Habitat strata	mammal	understorey	
Habitat strata	mammal	terrestrial	
Habitat strata	mammal	subterranean	
Habitat strata	mammal	aquatic	
Habitat strata	bird	aerial	
Habitat strata	bird	arboreal	
Habitat strata	bird	understorey	
Habitat strata	bird	terrestrial	
Habitat strata	bird	aquatic	
Habitat strata	reptile	arboreal	
Habitat strata	reptile	terrestrial	
Habitat strata	reptile	subterranean	
Habitat strata	reptile	aquatic	
Habitat strata	amphibian	arboreal	
Habitat strata	amphibian	terrestrial	
Habitat strata	amphibian	subterranean	
Habitat strata	amphibian	aquatic	
Habitat strata	all taxa	aerial	
Habitat strata	all taxa	arboreal	
Habitat strata	all taxa	understorey	
Habitat strata	all taxa	terrestrial	
Habitat strata	all taxa	subterranean	
Habitat strata	all taxa	aquatic	
Habitat strata	all taxa	constant	
Habitat strata	all taxa	variable	
Habitat strata	all taxa	generalism	low[b]
Habitat strata	all taxa	generalism	high
Plant	plant	wood density	low
Plant	plant	wood density	high
Plant	plant	photosynthesis	low
Plant	plant	photosynthesis	high
Plant	plant	competitor	low
Plant	plant	competitor	high
Plant	plant	stress	low
Plant	plant	stress	high
Plant	plant	ruderal	low
Plant	plant	ruderal	high
Red List status	all taxa	threatened	
Red List status	all taxa	not threatened	

[a] Taxonomic groups for invertebrates have a partially nested structure. The group ‘invertebrate’ contains all invertebrate taxa except those belonging to class Insecta and class Arachnida. The group ‘insect’ contains all insect taxa (class Insecta) except ants (family Formicidae).

[b] Low generalism is equivalent to high specialism

[c] *High trophic and diet generalism is equivalent to high omnivory*

[d] *Habitat strata are defined as the forest layers where a taxon forages for food*