

Primary forests are irreplaceable for sustaining tropical biodiversity

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Human-driven land-use changes increasingly threaten biodiversity, particularly in tropical forests where both species diversity and human pressures on natural environments are high¹. The rapid conversion of tropical forests for agriculture, timber production and other uses has generated vast, human-dominated landscapes with potentially dire consequences for tropical biodiversity^{2–5}. Today, few truly undisturbed tropical forests exist, whereas those degraded by repeated logging and fires, as well as secondary and plantation forests, are rapidly expanding^{6,7}. Here we provide a global assessment of the impact of disturbance and land conversion on biodiversity in tropical forests using a meta-analysis of 138 studies. We analysed 2,220 pairwise comparisons of biodiversity values in primary forests (with little or no human disturbance) and disturbed forests. We found that biodiversity values were substantially lower in degraded forests, but that this varied considerably by geographic region, taxonomic group, ecological metric and disturbance type. Even after partly accounting for confounding colonization and succession effects due to the composition of surrounding habitats, isolation and time since disturbance, we find that most forms of forest degradation have an overwhelmingly detrimental effect on tropical biodiversity. Our results clearly indicate that when it comes to maintaining tropical biodiversity, there is no substitute for primary forests.

As the extent of primary forests is shrinking throughout the tropics, a growing body of work has quantified the biodiversity values of degraded tropical forests. The ecological responses following forest conversion vary markedly across taxonomic groups, human impact types, ecological metrics and geographic regions^{5,8–10}. Most studies, however, provide limited insight into the varied responses of tropical forest biota to human impacts because they are understandably restricted to particular disturbance types^{11,12}, taxa^{13,14} and geographic regions¹⁵. Therefore, their often contrasting conclusions might have clouded ongoing debates over the conservation value of modified forest ecosystems⁴. A comprehensive meta-analysis of the conservation value of human-modified tropical forests is therefore sorely lacking. Notably, such an assessment could provide a critical baseline for monitoring progress towards global conservation targets¹⁶, evaluate the biodiversity benefits of international carbon-trading initiatives to reduce emissions from deforestation and forest degradation^{17,18} (for example the United Nations REDD+ programme), and guide policy development through the integration of biodiversity data into the modelling of land-use change scenarios^{2,19,20}.

Here we conduct a global meta-analysis to measure the varied effects of land-use change and forest degradation on biodiversity in tropical

forests. From an exhaustive literature search, we identified 138 studies that reported measures of biodiversity from multiple sites in both primary and disturbed tropical forests (Methods). We necessarily assumed that all 'primary forests' referred to in our source literature are largely old-growth forests that have experienced little to no recent human disturbance, although we recognize that in reality few primary forests are likely to be genuinely pristine. Primary forests are starkly differentiated from disturbed sites, which encompass the full spectrum of degraded and converted forest types, including selectively logged forests, secondary forests and forests converted into various forms of agriculture. In total, these studies spanned 28 countries and 92 study landscapes (Fig. 1). To measure the effect size of human-driven land-use changes, we calculated the weighted average of the standardized difference (based on pooled variance measures) between mean biodiversity measurements in primary and disturbed sites²¹ (that is, Hedges' g^*). The effect size was positive when the biodiversity value of primary forest sites was greater than that of disturbed sites, implying that the measured disturbance had a detrimental impact on biodiversity. We used a resampling procedure based on 10,000 bootstrap samples (with replacement) to generate the median effect size and 95% confidence intervals.

Overall, human impacts reduced biodiversity in tropical forests, although the effect size varied by region, taxonomic group, metric and disturbance type (Fig. 2). The median effect size for all 2,220 pairwise comparisons from 138 studies was 0.51 (95% confidence interval, 0.44–0.58) (Supplementary Table 1). This changed little when we accounted for pseudoreplication from studies that reported multiple comparisons, using a resampling procedure in which one comparison per study was randomly drawn for 10,000 samples, yielding an overall effect size of 0.57 (0.35–0.79) (Supplementary Table 1). Our results are also robust to publication biases (Methods). The surrounding habitat might either ameliorate (if hospitable) or exacerbate (if hostile) the impact of forest disturbance on biodiversity²². Although data are lacking for a comprehensive analysis, to account partly for this effect we repeated our analysis using only those studies that had natural vegetation (that is, primary and selectively logged forests) as the surrounding habitat (70.1% of all pairwise comparisons). Using this subset, we detected no substantial change in either the direction or the magnitude of effect sizes for the full data set (0.58, 0.49–0.68), or for each of the variables described below (Supplementary Table 1).

We found that human impacts on biodiversity varied by region. Although our data set is highly comprehensive, it is still limited given the vast extent of tropical forests and the myriad ways in which

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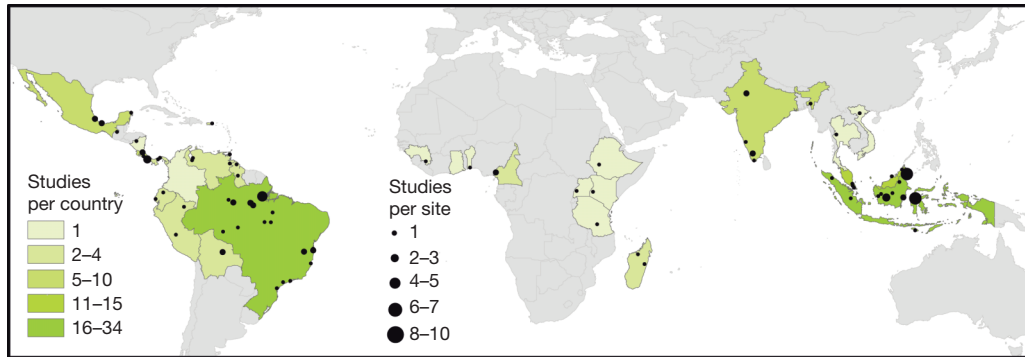


Figure 1 | Map of study sites by country and by study location. Country colour represents the number of studies per country ($n = 28$ total countries) and circle size represents the number of studies at each site ($n = 92$ total sites; only 82 sites with Global Positioning System coordinates are shown).

humans disturb them²³. Asia (52 studies) and South America (47) were the subjects of considerably more studies than were Central America (27) and Africa (12) (Fig. 1 and Supplementary Table 1). This regional bias implies that our findings might be more generalizable to Asia and South America than to other tropical regions. More critically, it highlights an urgent need for more research, particularly in Africa, which sustains the second largest contiguous tropical forest in the world⁵. Despite this important caveat, we found that Asia harbours the most sensitive biota, producing an effect size of 0.95 (0.83–1.08), which is substantially higher than that of the other three regions (Fig. 2a). This highlights the great toll human land-use changes are exacting in Asia, particularly in Southeast Asia, which most Asian studies (44 of 52) considered. Recent and widespread expansion of oil palm monoculture and exotic-tree plantations has greatly modified forest habitats in this region²⁴, but all forms of human impact were higher in Asia than

elsewhere (Fig. 3a), suggesting that this regional pattern holds regardless of disturbance type. Our results highlight the critical need to mitigate the particularly detrimental human impacts in Asia²⁵.

Most taxonomic groups we assessed were negatively affected by disturbance, with effect sizes greater than 0.5 (Fig. 2b and Supplementary Fig. 1b). However, mammals were less sensitive to the disturbances measured and, in some instances, actually benefited from human disturbance, with an effect size of -0.12 (-0.24 to -0.01). This disparity, largely due to higher mammal abundances in certain disturbance types (Fig. 3b and Supplementary Table 3), might arise because of mammals' high tolerance of degraded forests and forest edges²⁶, particularly among small mammals (-0.04 , -0.27 to 0.20) and bats (-0.24 , -0.42 to -0.06), which dominated most studies on mammals (Supplementary Table 1). At the other extreme, birds were the most sensitive group, with an effect size of 0.72 (0.52–0.93).

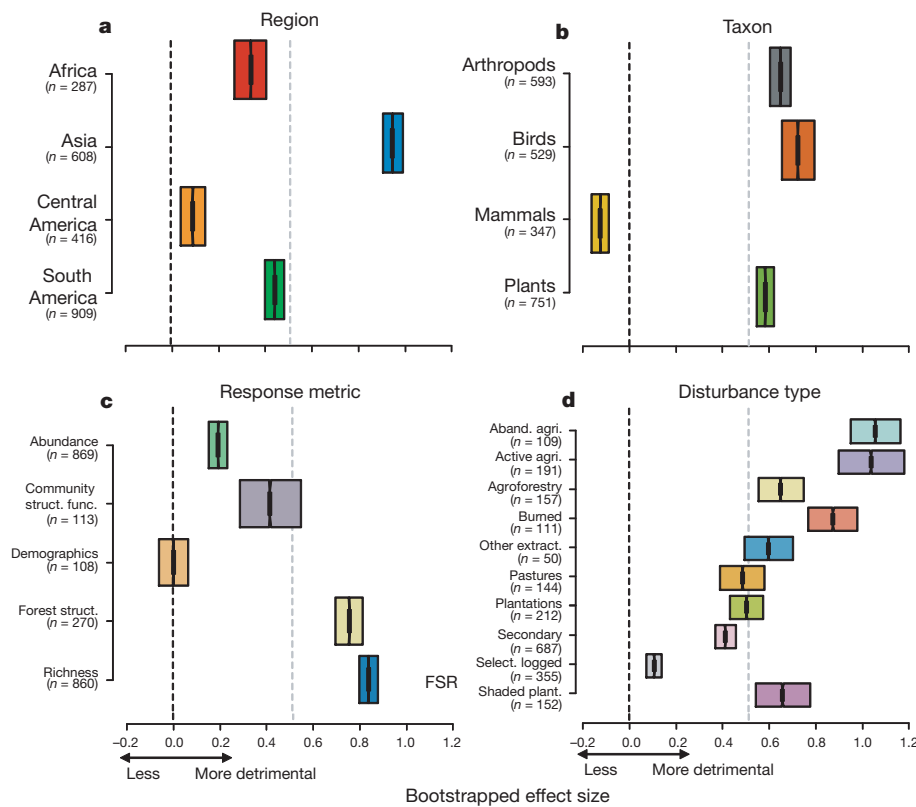


Figure 2 | Box plots of bootstrapped effect size. a, By region; b, by taxon; c, by response metric; d, by disturbance type (omitting clear-cut and disturbed/hunted owing to small sample sizes, that is, <50 comparisons). Plotted are median values and interquartile ranges of 10,000 resampled (with replacement) effect size calculations for each group. Widths of notches in box plots

approximate 95% confidence intervals. Median value for forest species richness (FSR) is plotted for comparison. The vertical black and grey dashed lines represent an effect size of zero and the median effect size for the entire data set, respectively. Sample size is shown in parentheses.

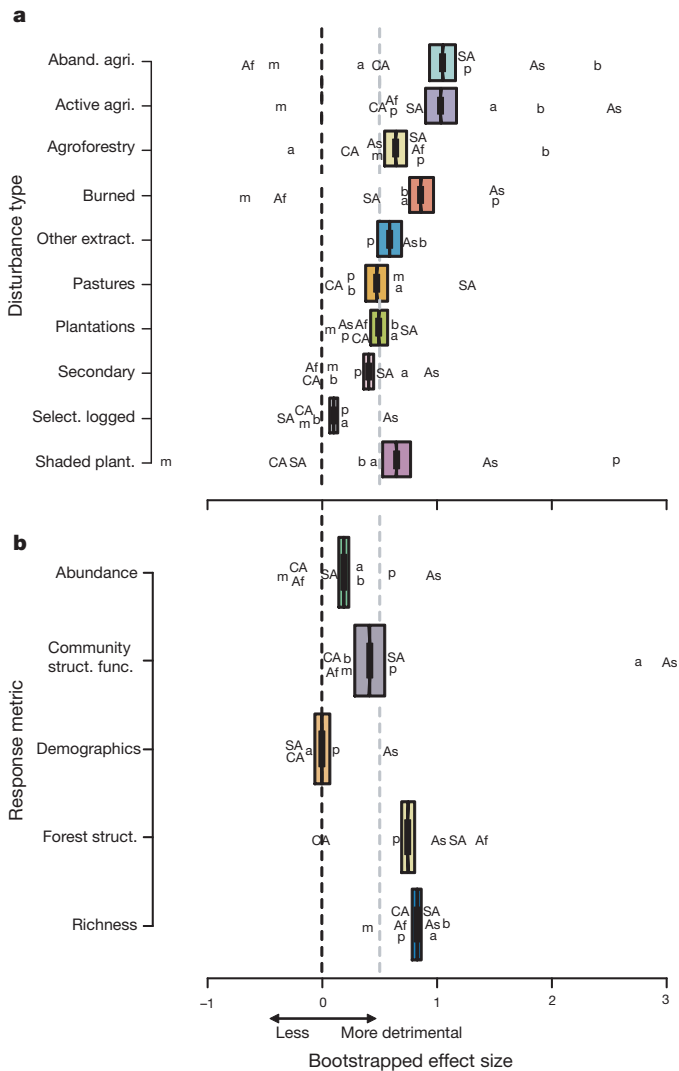


Figure 3 | Box plots of bootstrapped effect size. **a**, By disturbance type; **b**, by response metric, as in Fig. 2. Median effect size is also plotted as a function of region and taxon, with overlapping points stacked: Af, Africa; As, Asia; CA, Central America; SA, South America; a, arthropods; b, birds; m, mammals; p, plants. Vertical lines are as in Fig. 2.

These results varied by disturbance type; birds constituted the group most sensitive to forest conversion into agriculture (active agriculture, abandoned agriculture and agroforestry systems), whereas plants constituted the group most sensitive to burned forests and shaded plantations (Fig. 3a and Supplementary Table 2). The effect size for arthropods (0.64, 0.52–0.78) when further differentiated into the three main taxonomic orders revealed some differences: Coleoptera was more sensitive to disturbance (1.01, 0.75–1.30) than were Hymenoptera (0.41, 0.11–0.69) and Lepidoptera (0.58, 0.28–0.89) (Supplementary Table 1). In general, our findings reflect a paucity of information about most of the world's tropical biota; more data are needed to understand the ecological mechanisms underlying the differing vulnerability of taxa to human disturbance²⁷.

The source literature we considered used various measures of biodiversity, which we broadly differentiated into five response metrics: abundance, community structure and function, demographics, forest structure, and richness (Methods, Fig. 2c and Supplementary Fig. 1a). Of these, abundance and richness were the most commonly reported metrics, together comprising over three-quarters of all pairwise comparisons. Richness (0.83, 0.72–0.95) was markedly more sensitive to human disturbance than abundance (0.19, 0.07–0.31) (Figs 2c and

3b and Supplementary Tables 2 and 3). This result accords with expectations, given observations of large increases in the abundance of generalist species following similarly large declines in richness in degraded tropical forests^{5,28}. Furthermore, our measure of richness was predictably conservative because it assessed both forest specialists and generalists; when restricted to forest specialists ($n = 70$ comparisons), the effect size for species richness increased to 1.16 (0.69–1.65) (Fig. 2c and Supplementary Table 1). Measures of forest species richness therefore could serve as a simple yet effective metric to assess the conservation value of tropical forests and the relative impacts of different patterns of human modification, particularly during the early stages of forest conversion when conservation actions are most urgently needed.

We identified 12 general forest disturbance or conversion classes, and all but one of those with adequate sample sizes had effect sizes greater than 0.4 (Supplementary Table 1). In general, agricultural land-use classes (abandoned and active agricultural sites) had a much greater impact than agroforestry systems and plantations (both shaded and unshaded) (Fig. 2d). As the single exception, selectively logged forests (largely those affected by a single cutting cycle) had a much smaller, yet still positive, effect size of 0.11 (0.01–0.20). This is consistent with previous studies showing that selectively logged forests retain a high richness of forest taxa¹². Although these findings suggest that logged forests could contribute to biodiversity conservation, there are several caveats that need consideration: (i) if logged forest sites are adjacent to primary forests, spill-over effects might exaggerate the species richness of logged forests²² (acting as sink habitats); (ii) the proximity of logged forests to primary forests might also result in species extinction debts that are repaid over lengthy periods of time, beyond the timescale of the short-term studies that comprise most of our data set (83.6% had a time since disturbance of ≤ 12 yr); (iii) repeated logging might further exacerbate these biodiversity impacts; and (iv) the networks of forest roads created by logging operations might facilitate human immigration to forest frontiers and trigger associated increases in fires and forest conversion²⁹. As selective logging continues to expand across the tropics³⁰, understanding its long-term impacts and interactions with other forms of disturbance such as fire and invasive species⁵ will become increasingly important for the conservation of tropical biodiversity.

In contrast with the relatively benign selectively logged forests, secondary forests of varying ages had an intermediate effect size of 0.41 (0.28–0.54). It has been suggested recently that secondary forests can be an effective complement to primary forests in supporting tropical biodiversity, and should therefore represent a priority for conservation¹¹. Although the wide variety of secondary forests measured vary markedly in biodiversity value depending on forest age and land-use history, our meta-analysis demonstrates that secondary forests invariably have much lower biodiversity values than do remnant areas of relatively undisturbed primary forest (Supplementary Table 2). Although regenerating degraded areas can greatly increase the long-term persistence of biodiversity in severely modified landscapes⁶, our findings suggest that protecting remaining primary forests and restoring selectively logged forests are likely to offer the greatest conservation benefits for tropical biota.

We tested the relative importance of the above-mentioned ecological correlates in explaining the effect size. We used an information-theoretic approach to evaluate the performance of a candidate set of generalized linear models (Methods). After controlling for pseudo-replication from studies, the most parsimonious model in predicting the impact of anthropogenic forest disturbance on effect size was the null model (selected in 37.3% of 10,000 iterations), with the models 'Region' (23.1%) and 'Response metric' (14.4%) ranked second and third, respectively (Supplementary Table 5). This result also holds for a data set that includes only studies with natural vegetation as the surrounding habitat ($n = 1,557$), as well as for a smaller subset of data with information on time since disturbance and mean isolation

distance ($n = 630$; accounting for variation in colonization and succession effects²²) (Supplementary Fig. 2 and Supplementary Table 5). Our analysis of generalized linear models showed that the observed detrimental disturbance effects are essentially universal and that correlates such as region, taxonomic group, disturbance type and ecological measure have little impact on the effect size.

Our meta-analysis provides a global assessment of the relative conservation value of a broad range of human-modified tropical forests. Our results demonstrate that forest conversion and degradation consistently and greatly reduce biodiversity in tropical forest landscapes. As an exception, selective logging of forests has a much lower detrimental effect on measured biodiversity responses, implying that ecological restoration of such areas could help to alleviate threats to tropical biodiversity. Overall, however, we conclude that primary forests are irreplaceable for sustaining tropical biodiversity. Consequently, we strongly urge their protection by enhancing of enforcement in existing protected areas, expanding the current network of reserves and curbing international demand for forest commodities obtained at the expense of primary forests. Improving mechanisms for delivering and sustaining the social, financial and technical support necessary to achieve such goals continues to present one of the greatest challenges to tropical biodiversity conservation in the twenty-first century.

METHODS SUMMARY

Using Web of Science and BIOSIS, we searched for all relevant research articles published between 1975 and October 2010 that (i) included measures of biodiversity at multiple sites in both primary and disturbed tropical forests, (ii) indicated that the primary forests had little or no human disturbance and (iii) reported variance measures for biodiversity responses. From these studies, we compiled the biodiversity measures reported in both primary and disturbed forest sites and classified these measures using four variables: geographic region, taxonomic group, ecological response metric and disturbance type. For each paired biodiversity measure, we calculated the bias-corrected Hedges' g^* , the difference between primary and disturbed group means standardized by the pooled standard deviation. We then calculated the average effect size using the random-effects model, where effect sizes of individual comparisons are weighted by the inverse of within-study variance plus between-study variance²¹. We repeated this procedure after resampling the effect size calculations using 10,000 bootstrap samples (with replacement), from which we generated 95% confidence intervals. We calculated the effect size for the entire data set, for each subgroup of the four variables (region, taxon, response metric and disturbance type) and for each of the six two-level combinations of the four variables (for example disturbance type \times region). We repeated the above calculations for a subset of the data set with natural surrounding habitat, to account for the influence of this habitat. We also tested the effect sizes for possible publication bias. Following ref. 15, we performed an information-theoretic evaluation of a candidate set of generalized linear models to examine the influence of a set of proposed factors on the ecological responses tabulated. The generalized linear models related the Hedges' g^* effect size to the categorical predictor variables region, taxonomic group, metric and disturbance type in the 15 possible variable combinations.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Data. We searched for all relevant research articles published between 1975 and October 2010 using Web of Science and BIOSIS with the search query (TS = [(bird* OR mammal* OR reptile* OR amphibia* OR arthropod* OR plants* OR lepidoptera* OR hymenoptera* OR arachnid* OR coleoptera* OR diptera* OR homoptera* OR isoptera*) AND (clear-cutting* OR log* OR deforestation* OR fire* OR agriculture conversion* OR disturbance* OR degradation* OR secondary forest* OR plantation* OR fragment*)]). From this list, we reviewed articles and retained those studies that (i) included measures of biodiversity at multiple sites in both primary and disturbed tropical forests, (ii) indicated that the primary forests had little or no human disturbance and (iii) reported variance measures for biodiversity responses. We defined primary forests as primary or old-growth forests that have never been clear-felled and have been impacted by little or no known recent human disturbance.

For each study, we recorded the biodiversity measures in both primary and disturbed forest sites. For those studies that reported results in figures only, we extracted results using DATATHIEF (<http://www.datathief.org>). The full data set is available in the online version of the paper. For each comparison, we recorded the region (Africa, Asia, Central America (including Mexico), South America) and broad taxonomic group (arthropods, birds, mammals, plants). Although arthropods span diverse groups with potentially differing responses to human impacts⁸, our sample included predominantly insects (Coleoptera, 29.2%; Hymenoptera, 22.9%; Lepidoptera, 22.6%) and we therefore treated it as a single group but reported differences between the three major insect orders represented. Mammals also comprised different groups, and we differentiated between bats (51.0%), large mammals (2.6%), primates (3.7%), small mammals (28.2%) and a miscellaneous group (14.4%).

We classified the biodiversity measure into five response metrics: abundance (for example density, capture frequency, occupancy estimates and biomass); community structure and function (for example abundance of different guilds (generalists, herb specialists and so on), proportion of trait states and individual weight); demographics (for example density of different age classes (adults/ juveniles/saplings/seedlings), fruit/flower production and genetic measures); forest structure (for example canopy height/cover/openness, basal area, litter depth, diameter at breast height and other physical structural measurements, and density of trees of a given diameter at breast height); and richness (for example observed/estimated/rarefied richness, species density and genera/family richness). We omitted diversity indices ($n = 151$; for example Fisher's alpha, Shannon–Wiener, Simpson's and Margalef's) because they were usually secondary (derived) measures of abundance and/or richness and are not straightforward to interpret.

We recorded the disturbance type as specified by the authors of the source literature, which formed twelve distinct groups: abandoned agriculture, active agriculture, agroforestry, burned forests, clear-cut forests, disturbed/hunted forests, other extracted forests, pastures, plantations, secondary forests, selectively logged forests and shaded plantations. To avoid an inadequate treatment of forest fragmentation, which is an important topic, we necessarily excluded data on forest fragments. However, we recognize that remnant forest fragments, particularly large ones, in heavily human-modified ecosystems might be critical for biodiversity persistence.

In addition, and where available, we collected data on patch size, surrounding habitat type, isolation distance and time since disturbance^{15,22}. We categorized the predominant surrounding habitat of disturbed forests into five broad groups: natural vegetation (that is, primary and selectively logged forests), agriculture, disturbed forests, pastures and tree plantations. Using maps and/or geo-referenced locations from the source literature, we calculated isolation distance as the mean distance between disturbed sites and the nearest primary forest site to account for colonization effects for a smaller set of the data. We measured time since disturbance as the amount of time that had elapsed between the most recent form of disturbance and the time of study, as indicated by the authors of the source literature, to account for post-disturbance and time-lag effects. We excluded patch size or area information from our analysis largely as a result of ambiguity and extremely low sample size (22.6% of the comparisons provided this information for disturbed sites). We have already acknowledged the potential confounding effects of area in detail elsewhere¹⁵.

Meta-analysis. For each comparison, we calculated Hedges' g , the difference between primary and disturbed group means standardized using the pooled standard deviation of the two groups²¹, defined as:

$$g = \frac{x_{\text{primary}} - x_{\text{disturbed}}}{SD_{\text{pooled}}}$$

where

$$SD_{\text{pooled}} = \sqrt{\frac{(n_{\text{primary}} - 1)SD_{\text{primary}}^2 + (n_{\text{disturbed}} - 1)SD_{\text{disturbed}}^2}{n_{\text{primary}} + n_{\text{disturbed}} - 2}}$$

Because Hedges' g is a biased estimator of population effect size, we used the conversion factor J to compute a bias-corrected metric, g^* (ref. 21), defined as $g^* = Jg$, where

$$J = 1 - \frac{3}{4(n_{\text{primary}} + n_{\text{disturbed}} - 2) - 1}$$

We then calculated the average effect size using the random-effects model, where effect sizes of individual comparisons are weighted by the inverse of within-study variance plus between-study variance²¹. For individual comparisons, we defined the effect size as positive for comparisons where the biodiversity value was higher in primary forest (such that a positive effect size indicates a more detrimental impact by the disturbance type). For a small subset of comparisons where the expected value would be lower in primary forest ($n = 180$, 8.1% of all pairwise comparisons; for example measures of saplings/seedlings/juveniles, early/mid-successional species, non-forest/open-forest species, common/generalist/visitor species, trees of diameter at breast height < 10 cm, dead/new trees and mortality/recruitment rates), we defined the effect size as negative for comparisons where the biodiversity value was higher in primary forest. As our results might be affected by the selection of comparisons with an opposite expectation of the direction of the effect, we repeated the procedure after omitting those comparisons. This led to an effect size of 0.45 (0.38–0.52), within the error of the effect size for the full data set, suggesting that our expectation did not affect the results (Supplementary Table 1).

We calculated the effect size for the entire data set, for each subgroup of the four variables (region, taxon, response metric and disturbance type) and for each of the six two-level combinations of the four variables (for example disturbance type \times region) (Fig. 3, Supplementary Fig. 1 and Supplementary Tables 2–4). For all combinations, we repeated this procedure after resampling the random-model effect size calculations using 10,000 bootstrap samples (with replacement), from which we generated 95% confidence intervals³¹. To address potential spatial and temporal autocorrelation from studies that included several comparisons (for example multiple measurements of the same taxa, measurements of multiple taxa and measurements of multiple disturbance types), we repeated this procedure after resampling one comparison per study, again using 10,000 bootstrap samples (Supplementary Table 1). However, some autocorrelation (largely only spatial) remains because several studies were situated in the same site (Fig. 1), although it is probably not as pronounced as above. To account for the potential influence of the surrounding habitat, we repeated the above calculations for a subset of the data set with natural surrounding habitat (70.1% of data) (Supplementary Table 1).

We tested for publication bias using two methods to assess whether our calculated effect sizes were affected by the possible absence of studies not published owing to a failure to detect differences²¹. First, we visually examined a funnel plot of effect size plotted against standard error to assess the symmetry of study precision around effect size (Supplementary Fig. 3). The relatively symmetrical funnel plot suggests there is no relationship between effect size and study size, and that those studies with small (or negative) effect sizes do not have a lower probability of being published. Second, we sorted the data set by precision, from comparisons with small standard errors to those with large standard errors, and examined the change in cumulative effect size with the addition of the most imprecise studies (Supplementary Fig. 4). Although the addition of the most imprecise third of comparisons (those with the largest standard errors) does cause the cumulative effect size to increase, the effect size remains positive and does not overlap with zero at any point after the first 163 comparisons. We conclude that the impact of publication bias in our study is slight²¹.

Generalized linear models. Following ref. 15, we performed an information-theoretic evaluation of a candidate set of generalized linear models (GLMs) to examine the influence of a set of hypothesized factors on the ecological responses tabulated. The GLM related the Hedges' g^* effect size to the categorical predictor variables region, taxonomic group, metric and disturbance type in the 15 possible variable combinations (Supplementary Table 5). We also evaluated the null (intercept-only) model, in which only a mean effect size is estimated (that is, no correlates). As with the meta-analysis, we accounted for pseudoreplication by selecting a random subset of the full data set, such that only one observation from each study was fitted using GLMs, and repeating the fitting procedure a total of 10,000 times. Model comparisons and subsequent inference (using relative weights of evidence) were based on the small-sample-size-corrected Akaike's information criterion (AIC_c ; ref. 32), whereby a measure of Kullback–Leibler information loss (a fundamental conceptual measure of the relative distance of a given model from full reality, assumed to be represented in the model set) is derived and used as an objective basis for ranking the bias-corrected likelihood of models in an a-priori candidate set (thereby yielding an implicit estimate of model parsimony). The highest-ranked models according to AIC_c are those that

explain the most substantial proportion of variance in the data yet exclude unnecessary parameters that cannot be justified for inference on the basis of the data³³. For the randomized GLM fits, we calculated the proportion of times each model was selected as the top-ranked model (π_i), on the basis of AIC_c . We used the per cent deviance explained to represent the structural goodness of fit of each model, with the 95% confidence interval of the per cent deviance explained estimated as the 2.5 and 97.5 percentiles of the 10,000 sample fits. We repeated the above analysis using only data with natural surrounding habitat, and using isolation distance and time since disturbance as additional predictor variables, thus increasing the possible variable combinations to 64 (including the null

model) (Supplementary Table 5). All statistical analyses and figures were made using the program R, version 2.11.1 (ref. 34).

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