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Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants.

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Abstract

Remnants of lowland rainforest remain following deforestation, but the longer-term effects of fragmentation remain poorly understood, partly due to the long generation times of trees. We study rainforest trees in three size classes: seedlings (<1 cm dbh), saplings (1-5 cm dbh) and trees (>5 cm), that broadly reflect pre- and post-fragmentation communities, and we examine the impacts of fragmentation on forest regeneration in Sabah, Malaysian Borneo. We found that seedling richness (measured as the number of genera per plot) in fragments was about 30 percent lower than in plots in undisturbed forest, and about 20 percent lower than in an extensive tract of selectively logged forest, providing evidence of recruitment declines in fragments. Seedling richness was lowest in small, isolated, and disturbed fragments, potentially signalling an extinction debt given that these fragmentation impacts were not observed in trees. Unlike seedlings, saplings showed no declines in richness in fragments, suggesting that density dependent mortality (where rare individuals have a higher survival rate) and/or year-to-year variation in which species are recruiting could potentially compensate for the reductions in seedling richness we observed. Longer-term studies are required to determine whether sporadic or failed recruitment in small fragments will eventually translate into reduced richness of mature trees, or whether the processes that currently retain high sapling richness will continue in fragments.

Keywords

Biodiversity; Borneo; extinction debt; forest fragments; habitat fragmentation; natural regeneration; oil palm landscape; tropical trees.

THE LONG-TERM EFFECTS OF HABITAT LOSS AND FRAGMENTATION on the floristic diversity of vegetation remnants remain uncertain, predominantly because plants often have long generation times. For example, the species richness of plants in temperate grassland and forest fragments has been found to reflect historic pre-fragmentation conditions rather than recent habitat availability (Krauss *et al.* 2010), implying century or longer extinction debts (Tilman *et al.* 1994; Kuussaari *et al.* 2009). These extinction debts may be compounded by similarly long colonisation lags (Diamond 1972), resulting in highly non-equilibrium communities in fragments. Thus, the effects of forest fragmentation and isolation on forest-dependent animal communities, which have been measured on time scales of years to decades (e.g. Fitzherbert *et al.* 2008; Hill *et al.* 2011), may just be the beginning of more fundamental changes in forest ecosystems, driven by the dynamics of long-lived and structurally important plant components of terrestrial ecosystems.

Habitat loss has particularly detrimental effects on highly diverse tropical forests, where the ecosystem biomass is primarily composed of (potentially) long-lived trees (Malhi *et al.* 2004). Deforestation in the tropics is driven primarily by agricultural expansion (Henders *et al.* 2015), linked to increasing demand for food from a growing human population (Koh & Wilcove 2008). Immediately following forest clearance of the surrounding land, some species will die out immediately in the remaining fragments, and other species will go extinct as a consequence of stochastic (meta) population dynamics (Laurance 2008). Systematic changes in community composition will also occur within fragments, given that species vary in their traits (Ewers & Didham 2006), and that reduced forest area and increased edge habitat alter the abiotic conditions (Laurance 2000), potentially leading to reduced species richness and an increased abundance of disturbance-loving species in fragments (Rutledge 2003). Fragment isolation is related to the amount of forest habitat within the landscape surrounding a forest fragment, and is the inverse of connectivity.

Increasing fragment isolation has the potential to disrupt biological processes such as pollination and seed dispersal, which could influence seedling recruitment (Aizen & Feinsinger 1994; Cordeiro & Howe 2001). These effects are generally most severe in small and isolated fragments (Haddad *et al.* 2015), but individual trees may persist for centuries without recruiting viable offspring, creating persistent extinction debts (Tilman *et al.* 1994; Vellend *et al.* 2006). Thus, the eventual impacts of fragmentation are likely to be under-estimated in short-term studies (Wearn *et al.* 2012), but differences in the species richness of pre- and post-fragmentation size classes of trees provide an initial assessment of emerging patterns of diversity change.

To assess the likelihood that fragmentation effects will result in recruitment failure and extinction debt we examine the genus richness of seedlings, saplings and mature trees in rainforest remnants. We evaluate whether tropical trees are continuing to recruit offspring within forest fragments that were probably formed about 20 years ago on Borneo, in the 1990s during rapid development of oil palm (*Elaeis guineensis* Jacq.) plantations. Southeast Asia is one of the most rapidly-changing landscapes globally and, on Borneo, oil palm plantations have replaced much of the original forest cover in lowland areas (Sodhi *et al.* 2010). Lowland tropical rainforest in Southeast Asia is dominated by a single family, the Dipterocarpaceae, which form the majority of the standing biomass (Curran *et al.* 1999). Throughout the aseasonal tropics, dipterocarps recruit seedlings almost exclusively via synchronised mast fruiting on an irregular supra-annual basis of two to 10 years (Appanah 1993), triggered by the droughts and low night time temperatures of El Niño Southern Oscillation (ENSO) events (Yasuda *et al.* 1999). The extent to which masting is disrupted by fragmentation is currently unknown, but given that fragments experience greater drought and higher temperatures than continuous tracts of forest (Ewers & Banks-Leite 2013), it seems likely that seed production and seedling survival will be affected. Understanding the impacts of rainforest fragmentation is critical for conserving biodiversity, given that so much of the remaining forest has been degraded by repeated logging (Reynolds *et al*. 2011), and fragmentation (Haddad *et al*. 2015). Moreover, isolated fragments of forest are increasingly important refuges for species in oil-palm dominated agricultural landscapes, making it important to understand factors affecting their long-term persistence.

We examine fragmentation effects by studying the consequences for plant communities within remaining rainforest patches following their insularisation. Our study landscape has undergone extensive deforestation, so that remaining patches of natural forest are surrounded by agricultural land. We enumerate plant richness within forest patches and examine changes in local (plot-scale) plant communities with respect to fragment size, shape and degree of isolation from other forest habitat. We compare genus richness of seedlings (<1 cm dbh and <1.5 m height), nearly all of which will have recruited after the forest fragments were isolated in the 1990s (Connell & Green, 2000), with the genus richness of forest trees. Trees that were already established at the time of fragmentation will predominantly fall into our tree (>5 cm dbh) size class category, although some fast-growing stems will have recruited since fragmentation. Thus, the tree size class provides us with an insight into pre-fragmentation communities, although there will have been some turnover. We also examine saplings (1 – 5 cm dbh), anticipating that this size class will comprise many post-fragmentation individuals, but also some pre-fragmentation individuals. We test the hypothesis that seedling recruitment is reduced within plots in forest fragments, compared with plots in continuous forest, and specifically that seedling and sapling genus richness is reduced in plots in small, isolated and more disturbed fragments. In this way, we assess the regeneration potential of forest fragments and whether there are extinction debts in tree communities.

METHODS

STUDY REGION AND SITES.—The study was carried out in Sabah (Malaysian Borneo) during April-August 2015, in lowland (< 500 m asl) dipterocarp rainforest. We compared plant communities in 14 forest fragments with 5 sites in an extensive tract of more continuous forest. The continuous forest sites were located within the Yayasan Sabah Forest Management Area (YSFMA, ~1,000,000-ha), three sites within fully-protected primary forest (Danum Valley Conservation Area), and two sites within twice-logged forest (Malua Forest Reserve), which was selectively logged in the mid-1980s (~120 m^3/ha timber extracted) and again in 2005/6 (~35m^3/ha timber extracted; Reynolds *et al.* 2011; Fig. S1).

The fragments of primary forest that we studied were protected as “Virgin Jungle Reserves” (VJRs) in the 1950s for scientific research, were formally gazetted in 1984 and are managed by the Sabah Forestry Department. These fragment VJRs make up ~1.2 percent of Sabah’s land area but represent nearly 20 percent of the reserve area in which logging is prohibited (McMorrow & Talip 2001). These fragment sites were not commercially logged prior to formation, but most have subsequently experienced low levels of disturbance from human encroachment (pers. obs.). The 14 fragments range in size from 40 to 120,000-ha (Fig. S1; Table S1), and were probably formed at least 20 years ago, during the rapid development of oil palm cultivation in the region in the 1990s (Reynolds *et al.* 2011). Sites were >2 km apart and fragments were surrounded by mature oil palm plantations at the time of study.

FLORISTIC SURVEYS.—A 1 km linear transect was set up at each of the 19 sites. Each transect comprised five plots spaced 160 m apart along the transect (Fig. S1), with the exception of site #2 (44-ha; Table S1), where only three plots were possible due to its small size. Transects in fragments started 100 m from the forest edge to avoid the main edge effects (Ewers & Didham 2006), and were angled towards the fragment centre. Each plot was 20 x 40 m, and was sampled following a modified Gentry protocol, using a series of subplots to sample different size classes (Gentry 1982; Fig. S1). Hence our approach was to sample with equal effort at each site (rather than in proportion to site area), and our analyses compare local (plot-scale) genus richness among sites.

A nested design was used to ensure adequate sampling of different tree size classes (seedlings, saplings, trees), because a larger sampling area was required for trees and we did not want to over-sample saplings and seedlings. Seedlings were defined as non-climbing woody plants <1.5 m in height and <1 cm dbh, and were measured and identified in four 2 m x 2 m sub- plots distributed evenly within each plot (Fig. S1). All seedlings are expected to have been recruited since fragmentation during mast fruiting events (e.g. 1997/98 and 2015/16 were particularly strong global ENSO events (Curran *et al*. 1999; Cpc.ncep.noaa.gov 2017). Saplings were defined as non-climbing woody plants 1–5 cm dbh, and they were enumerated and identified in four 5 m x 5 m subplots within each plot (Fig. S1). Trees >5 cm dbh were divided into two groups: those 5–30 cm dbh were sampled in one 5 m x 40 m strip within each plot, and trees >30 cm dbh were enumerated in the full 20 x 40 m plot (Fig. S1). It is difficult to estimate the age of individual trees due to high levels of inter- and intra-specific variation in growth rates, depending on life-history strategy and resource availability (especially light). Therefore we defined size classes to represent individuals that predominantly germinated prior to fragment formation (“trees”), after fragment formation (“seedlings”), and an intermediate group (“saplings”) which contains many individuals germinating after fragment formation, but also includes individuals germinating prior to fragmentation. Our analyses focus on comparing the genus richness of each size class (seedlings, sapling, trees) separately among sites. We also computed plot-level plant diversity using Simpson’s index (supplementary material), which confirmed that our results were not confounded by variation in stem density across sites (Fig. S4; Table S5), and so we only include analyses of genus richness in the main text. We also performed an individual stem-based rarefaction analysis of genus richness (see Text S1), by combining data from all plots at a site (excluding Site 2 with only three plots), which supported our overall conclusions, and again confirmed that our main findings were not affected by variation in stem density.

Plant identification was carried out in the field where possible and confirmed by the botanist at Danum Valley Field Centre, based on leaf samples and photographs taken in the field. All but six individuals were named to species or genus level, and unidentified individuals (representing 0.06% of stems) were removed from the analysis. We carry out all analyses at genus level given the complexities of plant identification. However, we also repeated our analyses at species level, and results were qualitatively the same (Fig. S2, Table S2) implying that finer resolution identification would not have altered our conclusions.

SITE AND PLOT CHARACTERISTICS.—In order to relate our findings on plant genus richness to attributes of the sites where data were collected, we recorded the following site characteristics. We measured fragment area and perimeter using ArcMap 10.0 and R v. 3.2.2, after tracing the outline of each fragment from Google Earth satellite imagery. Fragment shape was calculated from the area (m^2) and perimeter (m), where a value of 1 indicates a circular fragment, and values approaching a maximum of 5 indicate a highly convoluted shape (Arroyo-Rodríguez & Mandujano 2006; see Text S2 for equation). The connectivity (i.e. inverse of isolation) of each fragment was calculated from forest land cover data (Miettinen *et al*. 2012) at a grid cell resolution of 250 m to identify the size of, and distance to, all forest patches within a 5 km radius of each site (McGarigal & Marks 1995; for equation, see Text S3). A connectivity value of 0 for a fragment indicates an absence of patches of forest in the surrounding landscape, and increasing connectivity values indicate a greater total area of forest cover in the surrounding landscape. This metric represents the degree of isolation of a site by taking into account the amount of forest habitat within the buffer, and weights it by area and proximity. We tested the sensitivity of our findings to different buffer widths, using buffer distances of 1 – 10 km, representing a range of seed and pollinator dispersal distances (Table S6). However, our results were not affected by different buffer widths and so we only report data for connectivity values based on 5 km buffer in the main text.

In order to characterise the forest in each of the plots within each of the 19 sites (93 plots in total), we measured the following variables: temperature and light intensity (mean values (^{o}C and lux) from two Hobo® loggers placed 1.8 m from the ground within each plot, measured between 10am and 4pm over 2-3 days); photosynthetically active radiation (mean of four measurements taken within each seedling sub-plot (four sub-plots per plot) using a Skye Light Meter for Growers Limited); leaf litter depth (mean of four measurements using a steel ruler); canopy cover (taken in the centre of the plot using a densiometer). We also counted the number of lianas rooted within seedling sub-plots (Fig. S1). Many of these predictor variables were correlated with one another, and so we used principal components analysis (PCA) to reduce these six variables to a smaller number of independent factors, and the first principal component of this PCA was used in our analyses of seedling, sapling, and tree genus richness as an index of forest disturbance at sites.

DATA ANALYSES.—In order to test the hypothesis that tree recruitment is impaired in forest fragments compared with continuous forest sites, we first calculated the number of plant genera per plot, separately for seedlings, saplings and trees (Fig. 2), and compared genus richness in fragments, logged continuous forest, and primary continuous forest sites using one-way ANOVAs, followed by post-hoc Tukey HSD tests.

In order to test the hypothesis that seedling and sapling genus richness is lowest in small, isolated and most disturbed fragments, we carried out three general linear mixed effects models (GLMMs) to evaluate seedling, sapling and tree genus richness (response variable = number of genera per plot) in relation to four site attributes: size, shape, connectivity, and disturbance (PCA factor score; PC1). We gave sites in continuous forest a notional area of 800,000-ha (the area of the Yayasan Sabah Forest Reserve; Reynolds *et al.* 2011), and values of 1 for shape and 17,000,000 for connectivity so that these five sites could be included in our analyses. We carried out Poisson GLMMs with a log-link function, including 2-way interactions between the four predictor site attributes (with data analysed at plot-level; 93 data points), and site identity was included as a random effect to account for non-independence of plots within sites. Area was log10-transformed and connectivity was cube-root transformed to reduce skew in the data, and all four predictor variables were scaled to have a mean of 0 and variance of 1 prior to analysis, to aid comparison of their relative importance on genus richness. The top models were identified using an AIC approach (Burnham & Anderson 2002), where delta AICc <2 of the best model were included in the top models, and model averaging was then used to find the importance of each variable and determine their relative effect sizes: effect sizes whose confidence intervals (CIs) did not cross zero were assumed to be significant predictors of plant richness. All analyses were performed using the R package vegan (Oksanen *et al.* 2011) in R v. 3.2.2 (R Development Core Team 2015).

RESULTS

Across the 93 plots at 19 sites, we surveyed 9608 individual plants, representing 222 genera and 76 families. As is typical for this region, the Dipterocarpaceae family was dominant across all size classes, and 27 percent of all individuals were represented by this family. The most numerous genus was *Shorea* (Dipterocarpaceae), which formed 30 percent of individual seedlings, 4 percent of saplings, and 8 percent of trees. The frequency distributions of stem sizes across the three forest types were similar, although only primary forest contained individuals over 125 cm dbh (Fig. 1).

The first principal component (PC1), constructed from six variables describing site and plot characteristics, accounted for 32.5 percent of the overall variation, and increased with increasing light, temperature, and a more open canopy (Fig. S3A). Hence we conclude that PC1 is a measure of forest disturbance, and PC1 scores were negatively correlated with site area and connectivity (Fig. S3B), indicating that forest disturbance is greater in small and isolated forest fragments.

VARIATION IN PLANT GENUS RICHNESS AMONG STUDY SITES.—Seedling genus richness was much lower in plots in fragments compared with plots in primary and logged forest (one-way ANOVA of genus richness by forest type; $F_{(2,90)} = 8.55$, $p < 0.001$) , but there was no significant difference between seedling genus richness in primary and logged forest. Fragment seedling genus richness (N = 14 sites; mean = 7.3 genera per plot ± 0.3 SE) was 29 percent lower than in primary continuous forest (N = 3 sites, mean = 10.3 genera per plot ± 0.7 SE), and 20 percent lower than in logged continuous forest (N = 2 sites, mean = 9.1 genera per plot ± 1.2 SE; Fig. 2). However, there was little impact of fragmentation on genus richness of either saplings ($F_{(2,90)} = 2.36$, $p = 0.10$; fragments, mean richness = 16.9 genera per plot ± 0.7 SE; logged forest, mean = 20.5 ± 2.0; primary forest, mean = 15.9 genera per plot ± 1.0) or trees ($F_{(2,90)} = 0.82$, $p = 0.44$; fragments, mean = 16.8 genera per plot ± 0.5 SE; logged forest, mean = 18.6 genera per plot ± 1.6; primary forest, mean = 16.5 genera per plot ± 0.8). Thus we conclude that forest fragmentation reduces local seedling genus richness but has no impact on the genus richness of saplings or trees.

EFFECTS OF SITE CHARACTERISTICS ON PLANT RICHNESS.—Outputs from GLMMs revealed that seedling genus richness was positively associated with site area, and there was an indication that connectivity, and forest disturbance of sites were also important (Fig. 3). Site area was the most important variable in the best model (Table 1), and seedling genus richness was particularly low in small, isolated, highly disturbed sites. Our rarefaction analyses of seedling data found similar trends (Fig. S5, see Text S1 for further discussion). In contrast to data for seedlings, and even though we assumed that saplings were predominantly produced after fragmentation, there was no effect of site area (or any other predictor variable) on sapling genus richness. This result was robust to varying the stem diameter threshold for our sapling size class (Table S7), and to the removal of high wood density, slow-growing genera (> 0.75 g/cm^3; Table S8). Additionally, results were qualitatively similar when we split our data set according to the median wood density of all genera we encountered in our study (0.55 g/cm^3), indicating that differences in plant growth rates are not having major impacts on our designation of post- and pre-fragmentation individuals, or our overall findings (Table S9, see Text S6 for further discussion). We assumed that trees were representative of pre-fragmentation communities and as predicted, tree genus richness did not vary according to site area. Tree genus richness did however vary according to levels of forest disturbance at sites (PC1 score), indicating that sites with more open canopies, higher temperatures and higher light environments contained fewer tree genera.

DISCUSSION

Forest fragmentation significantly reduced the local genus richness of tree seedlings. On average, only 4.2 seedling genera (± 0.97 SE) were found per 16 m^2 plot in the smallest fragment (39.6 ha), compared to 11.8 seedling genera (± 0.86) per plot in a primary forest site in continuous forest. The absence of any reduced genus richness in trees may be indicative of an extinction debt in small fragments, although our failure to find any reduction in sapling genus richness may suggest that there are compensatory processes in operation (see below).

NO EFFECTS OF FRAGMENTATION ON TREE GENUS RICHNESS.— Given the age of our fragments, we assume that our tree size class would have mostly germinated prior to fragmentation, and that the genus richness of these trees broadly represents the 'pre-isolation' condition of the forest. Although we did not detect direct effects of fragment size or isolation on our tree size class, we did find indirect effects because reduced genus richness was associated with disturbance, and fragments generally contained more disturbed forest; Fig. S3B). Hence trees were affected by local forest disturbance rather than by the direct effects of fragmentation in reducing site area and isolation.

REDUCED LOCAL GENUS RICHNESS OF SEEDLINGS IN FRAGMENTS.— The reduced number of seedling genera per plot in (small) forest fragments, compared to continuous forest, could arise from multiple processes relating both to the biological and physical conditions of the fragments. Forest fragments experience a change in physical (micro)climatic conditions associated with increased disturbance and edge effects, particularly through greater wind disturbance and elevated desiccation (Laurance 2004). This can alter the cues linked to the initiation of (sporadic) mass flowering (Curran *et al.* 1999) and may hamper the physiological ability of trees to support fruit development, the germination of seeds, and affect the establishment and survival of seedlings (Delissio & Primack 2003). Fragmentation may also lead to the loss of pollinators (Aizen & Feinsinger 1994) and change patterns of seed predation and dispersal (Cordeiro & Howe 2001). Self-incompatibility mechanisms in tropical trees may lead to reproductive failure among species with small numbers of individuals surviving per fragment (Ghazoul *et al.* 1998; Naito *et al.* 2008). Given that different species of trees will flower and fruit in response to different physical cues, and exhibit different interactions with specialised and generalist natural enemies, it is likely that a combination of processes may reduce the ‘post-isolation’ genus richness of seedlings in forest fragments. In addition, our rarefaction analyses, that account for differences in seedling stem density, also found a trend of decreasing numbers of seedling genera in smaller fragments, and so it seems likely that regeneration processes are being disrupted in fragments.

LONG-TERM VIABILITY OF FRAGMENTS AND CONFLICTING RESULTS FROM SAPLINGS.—As with seedlings, we expected a high proportion of saplings to have germinated subsequent to fragmentation, yet we did not find any effects of fragmentation on saplings, despite finding an effect on seedlings. Isolation of our Virgin Jungle Reserve sites probably occurred at least 20 years before our study. Certain shade tolerant species are able to persist in seedling banks in the forest understory for a number of years (Brown & Whitmore 1992), and it is likely that our sapling size class comprises a mixture of individuals that germinated both pre- and post-fragmentation (Delissio *et al*. 2002). Nonetheless, a portion of saplings will have recruited post-fragmentation, and hence we expected (but did not observe), some effects of fragmentation on sapling genus richness. There are a number of possible explanations for this disparity between seedlings and saplings, which could result from a combination of the following: 1) more sporadic recruitment of seedlings in small fragments than in continuous forest; 2) increased density-dependent survival of the rarest seedlings; and 3) delayed (lagged) impacts of fragmentation on seedling recruitment failure. For example, if different species are recruited in different years in fragments (more so than in continuous forest) owing to disruption of flowering or reduced pollination in fragments, then there will be lower richness in any single seedling size class. However, the sapling size classes in the same plots are likely to include a wider age range of individuals than seedlings, and hence represent the survivors from several seedling size classes. The impact of recruiting different species in different years could be further enhanced if density-dependent mortality of conspecifics takes place, whereby rare species have a higher survival rate (LaManna *et al*. 2017). Survival of low density species may be elevated in fragments if herbivores and pathogens specialising on rare species become extinct from small areas of forest (Arnold & Asquith 2002). If sporadic recruitment and density-dependent processes allow sapling genus richness to be maintained, then fragmentation may not necessarily have longer-term detrimental impacts on plant richness. However, high sapling genus richness may reflect time lags between fragmentation and reduced seedling recruitment, such that surveys immediately post-fragmentation would not have detected any changes in seedling genus richness. If the first two processes are operating, then local (plot scale) genus richness of saplings and mature trees may not inevitably decline over time in small fragments, despite the reduction in seedling genus richness at any one time. Nonetheless, even if local plot scale genus richness is maintained, some (mainly rare) species and genera are still likely to be lost from small fragments. These explanations for the findings we report deserve further research, given that they lead to quite different expectations about future diversity changes in forest fragments.

CONCLUSIONS.—Small, isolated and disturbed forest fragments have lower local seedling genus richness but similar levels of sapling and tree genus richness, compared with continuous forest. Whether fragmentation will lead to long-term reductions in the plant diversity of fragments is not yet clear, given that genus richness is apparently maintained in the sapling size class post-fragmentation. The longevity of trees extends the window for conservation action (Wearn *et al*. 2012), and episodic recruitment, density dependence and lagged effects of fragmentation may buy more time still. The fact that recruitment patterns differ between fragments and continuous forest sites implies that there will be divergence in the plant communities of these areas, but it is too early to conclude that fragments will have reduced diversity in the long term. Hence, local tree genus richness may be maintained in fragments, regional habitat specialists may only survive in small fragments if continuous forest no longer exists elsewhere, and small fragments may increasingly support unique biological communities. Thus, rainforest remnants may have inherent conservation value.

Author contributions

GS, JKH, and CDT conceived and designed the study; GS and AJ collected field data; GS led data analysis and wrote the first draft of the manuscript, with substantial contributions from JKH and CDT to all further revisions. SB, JH and MJMS also contributed to revisions. All authors gave final approval for publication.

Competing interests

The authors declare they have no competing interests.

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Data Availability: The data used in this study are archived at the Dryad Digital Repository (doi:10.5061/dryad.3jt6kh3).

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TABLES

TABLE 1. Top ranked GLMMs of factors affecting tree, sapling and seedling richness in 93 plots nested within 19 sites. Candidate models are ranked according to the Akaike's information criterion (AICc). Corresponding degrees of freedom (df), log-likelihood estimation (logLik), difference between AICc and lowest AICc value (Δ_i) in model set, Akaike weight (w_i: the probability that each model is the best approximating model), and marginal (R^2m) and conditional (R^2c) r-squared values are presented. Only models with $\Delta_i < 2$ were included in the averaged top models.

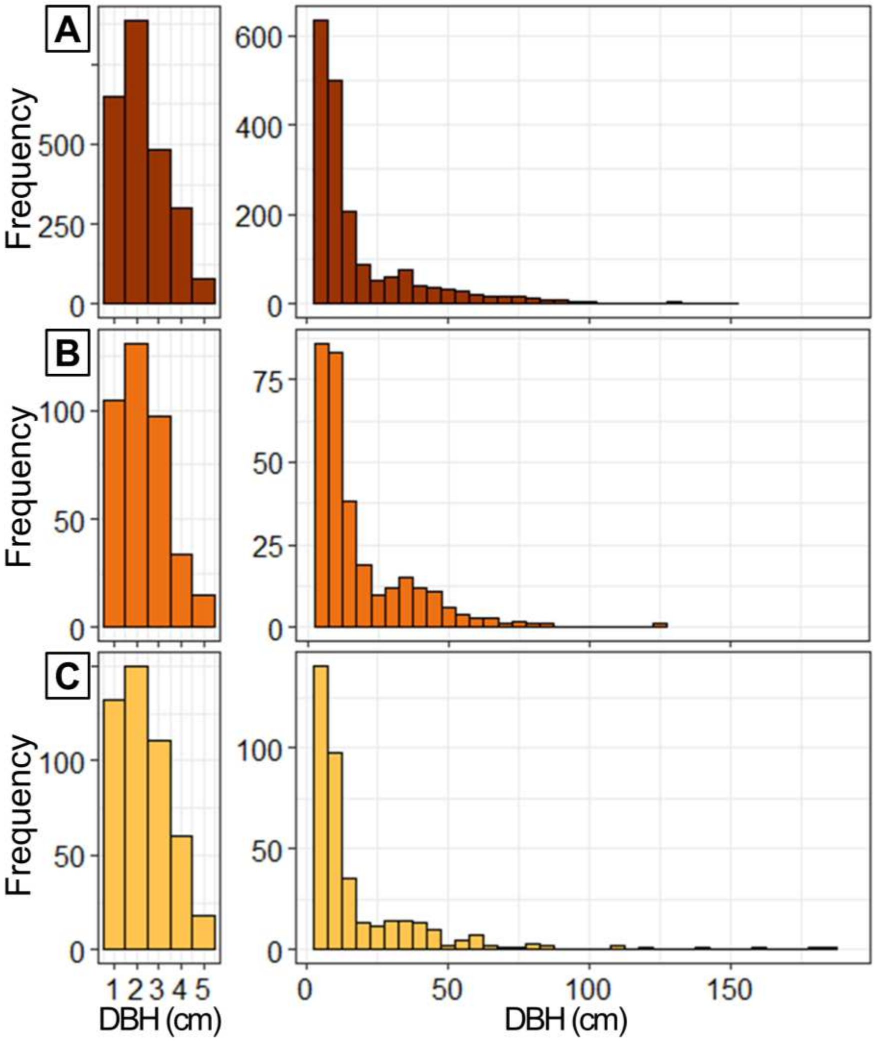
Response variable	**Candidate models**	**df**	**logLik**	**AICc**	**Δ_i**	**w_i**	**R^2m**	**R^2c**
Seedling richness	Area	3	-222.38	451	-	0.55	0.15	0.19
	Area + Connectivity	4	-222.11	452.7	1.65	0.24	0.16	0.19
	Area + Disturbance	4	-222.28	453	1.99	0.20	0.15	0.19
Sapling richness	-	2	-285.96	576	-	0.42	0	0.16
	Disturbance	3	-285.46	577.2	1.14	0.24	0.02	0.16
	Shape	3	-285.76	577.8	1.75	0.18	0.01	0.16
	Connectivity	3	-285.80	577.9	1.82	0.17	0.01	0.16
Tree richness	Disturbance	3	-265.77	537.8	-	0.51	0.05	0.10
	Disturbance + Shape	4	-265.26	539	1.17	0.28	0.07	0.10
	-	2	-267.70	539.5	1.72	0.21	0	0.10

FIGURE LEGENDS

FIGURE 1. Overall frequency distribution of sapling (left) and tree (right) stem sizes in (A) forest fragments (brown bars, n = 68 plots), (B) logged forest (orange bars, n = 10 plots), and (C) primary forest (yellow bars, n = 15 plots) sites.

FIGURE 2. Effect of fragmentation on size class richness in primary, logged, and fragmented forest sites. Mean of standardised plant genus richness values (± SE) of size classes in plots located in primary continuous forest (yellow bars; n = 15), previously logged continuous forest (orange bars; n = 10), and forest fragments (brown bars; n = 68). ANOVA of plant richness by forest type: $p \leq 0.001$ = ***.

FIGURE 3. Effect of site characteristics on size class richness. A. Effect size of variables included in averaged models. Effect sizes whose 95% confidence intervals did not cross zero were assumed to be significant, and are shaded in grey. B. Impact of area, connectivity, fragment shape, and forest disturbance (principal component) on richness of trees, saplings, and seedlings. Brown symbols (fragments), orange symbols (logged forest) and yellow symbols (primary forest) show genus richness values of plots, and hollow circles are site means with standard error. Black line is fitted for variables where the slope was significantly different from zero in averaged top models; dotted line is fitted where variable was included in averaged top models but was not significant.


A
B
C
Frequency
Frequency
Frequency
0
250
500
600
400
200
0
100
50
0
75
50
25
0
100
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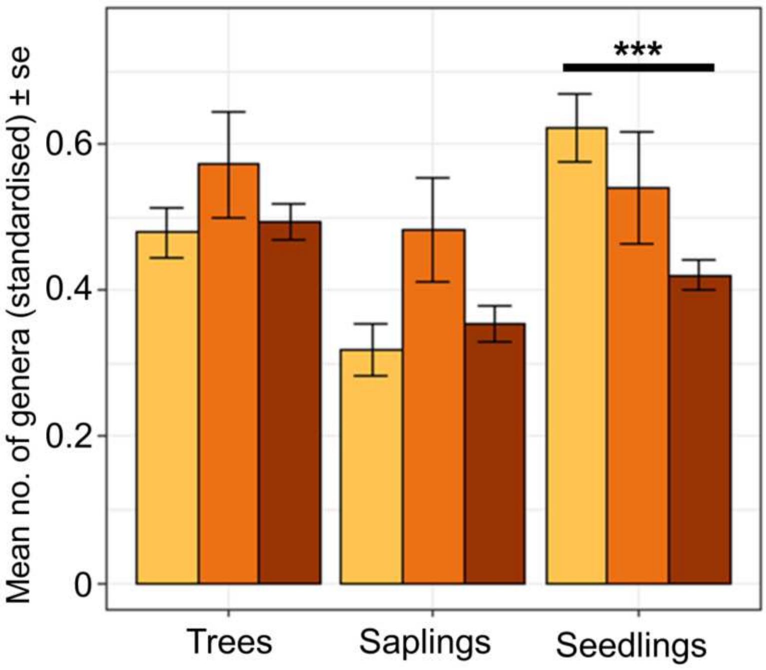
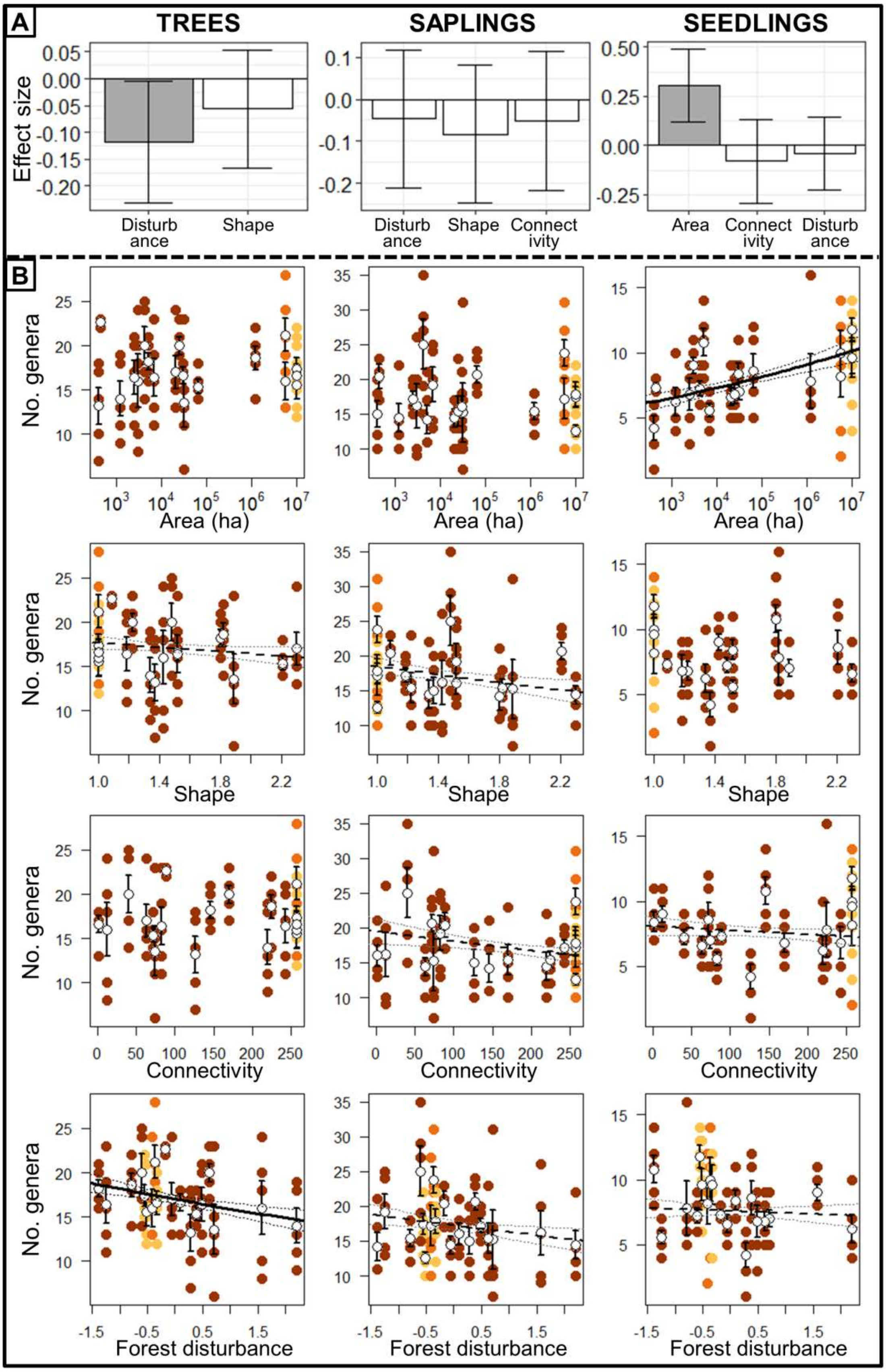
0
100
50
0
1 2 3 4 5
DBH (cm)
0
50
100
150
DBH (cm)

FIGURE 1.



Mean no. of genera (standardised) ± se
0.6
0.4
0.2
0
***
Trees
Saplings
Seedlings

FIGURE 2.



530

531 FIGURE 3.

Supporting Information

Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants.

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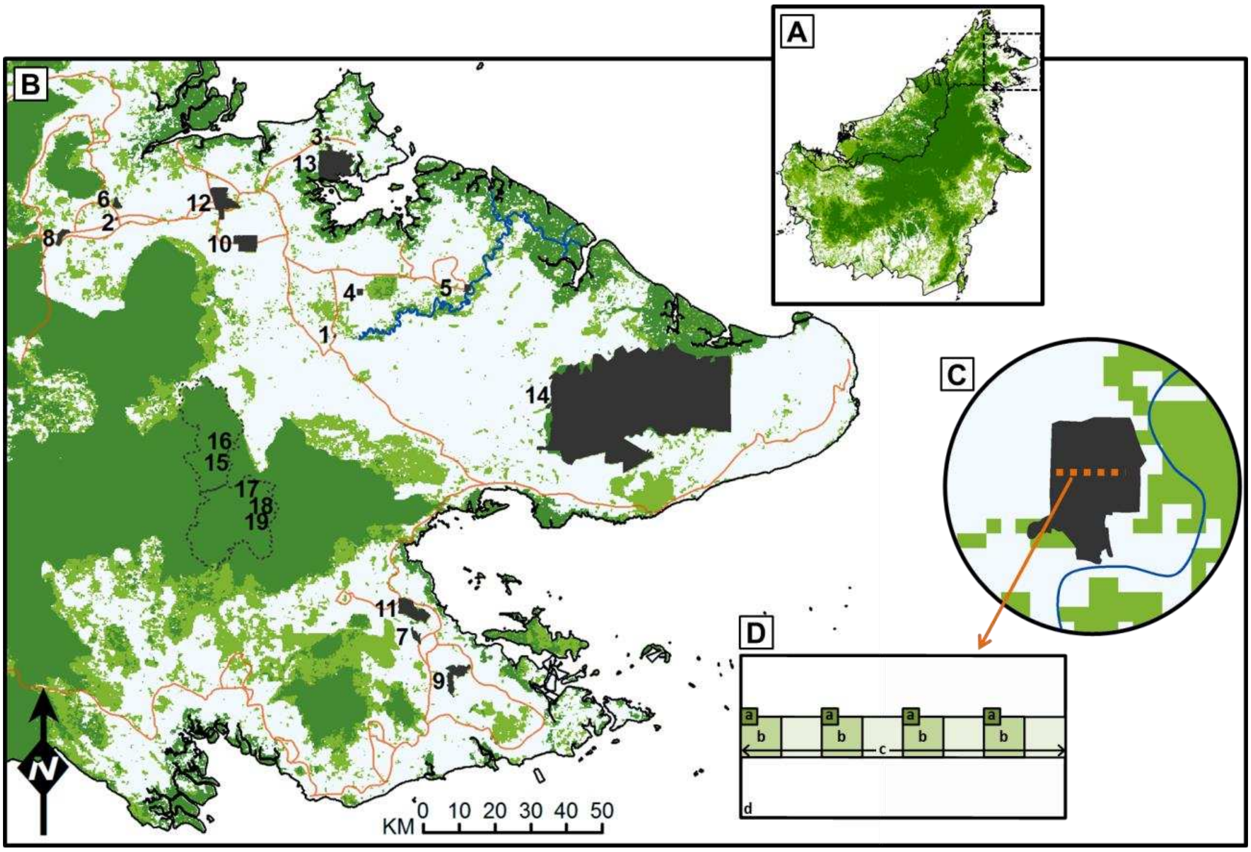


Figure S1. (A) Study area location on Borneo and (B) location of sites. Sites are numbered in order of increasing size; dark green areas indicate forest; light green areas indicate regenerating or degraded forest; white areas indicate agricultural land predominantly covered by oil palm; sites 15 – 19 within dotted areas are continuous forest sites. Forest cover data were obtained from Miettinen *et al*., 2010. (C) Five plots along a transect in a forest fragment site. (D) Nested sampling design (subplot area in brackets): a = seedling plots (4 x (2 x 2 m)), b = saplings 1-5 cm dbh (4 x (5 x 5 m)), c = trees 5 – 30 cm dbh (5 x 40 m), d = trees >30 cm dbh (20 x 40 m).

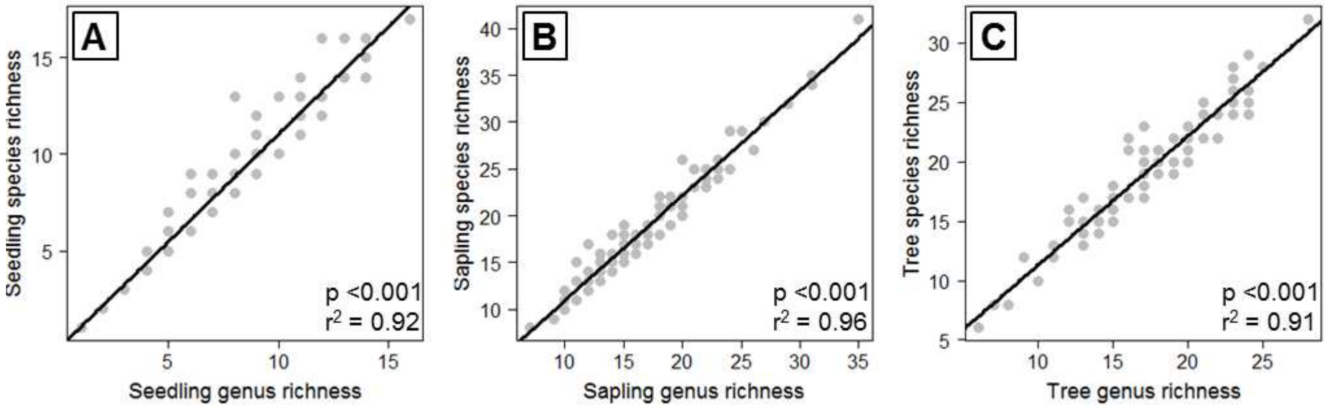
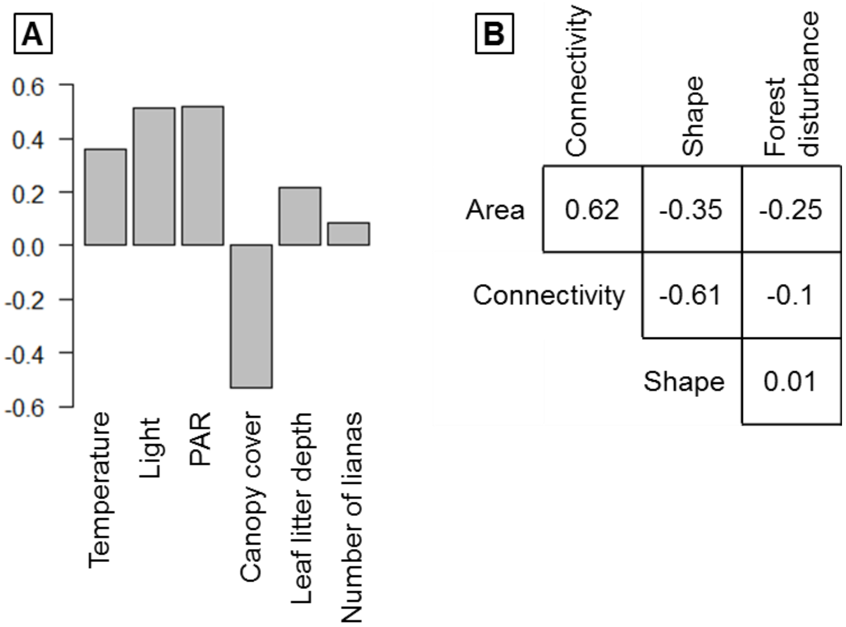


Figure S2. Correlation between number of species and number of genera of (A) seedlings, (B) saplings, and (C) trees identified in each plot (n = 93 plots). Black line is fitted using generalized linear regression, and R^2 value is adjusted R^2.



	Connectivity	Shape	Forest disturbance
Area	0.62	-0.35	-0.25
Connectivity		-0.61	-0.1
Shape			0.01

Figure S3. A) Variable scores in the first axis of a Principal Components Analysis characterising forest disturbance, accounting for 32.5% of the variation (among plots) in the data. Scores increased with higher light and PAR, higher temperature, and lower canopy cover, which we interpreted as being indicative of a higher level of disturbance. **B)** Matrix of Pearson correlation coefficients calculated between key variables, with 95% confidence intervals: positive correlations are indicated in blue, negative correlations in red. Non-significant correlations indicated by red cross.

Influence of stem density on genus richness

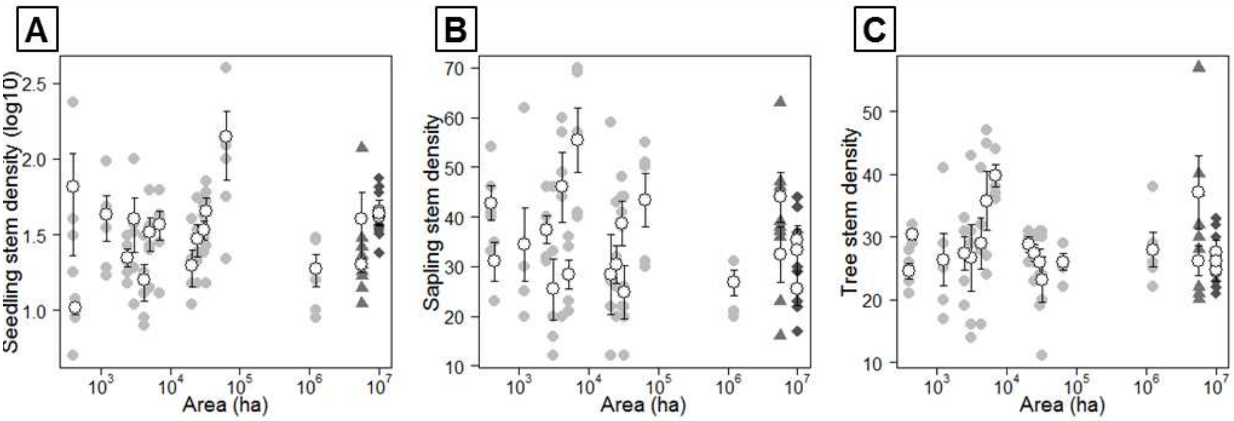


Figure S4. Variation in stem density of (A) seedling, (B) sapling, and (C) tree size classes with site area. Light grey circle (fragments), darker grey triangles (logged forest) and dark grey diamond (primary forest) show number of stems per plot, and black symbols are site means with standard error. There was no significant relationships between stem density and either area, connectivity, or shape (univariate GLMMs).

Text S1 Rarefaction analysis

Our sampling strategy and main findings pertain to analysis of plot-level local richness. We carried out several analyses to explore whether variation in stem density might affect our findings about fragmentation effects. Given that we only found significant effects of site characteristics for seedlings, we only carried out rarefaction analyses for seedling data. However, there were too few stems per plot for a meaningful rarefaction analysis (< 10 stems per plot in many plots), and so we carried out rarefaction analysis at site-level. We combined plot-level data within each site and removed Site #2 (Sapi A; which only had three plots), rarefied each sample to 50 stems, and regressed these values against each predictor variable. We show trend lines for area, connectivity, and disturbance, as these variables were important in top models of seedling genus richness. Although no univariate regressions were significant, the same trends that were seen in the analysis in the main text were evident (Figure S5). These findings support our results in the main text (Figures 2 and 3) that seedling genus richness was lower in smaller and more disturbed forest fragments.

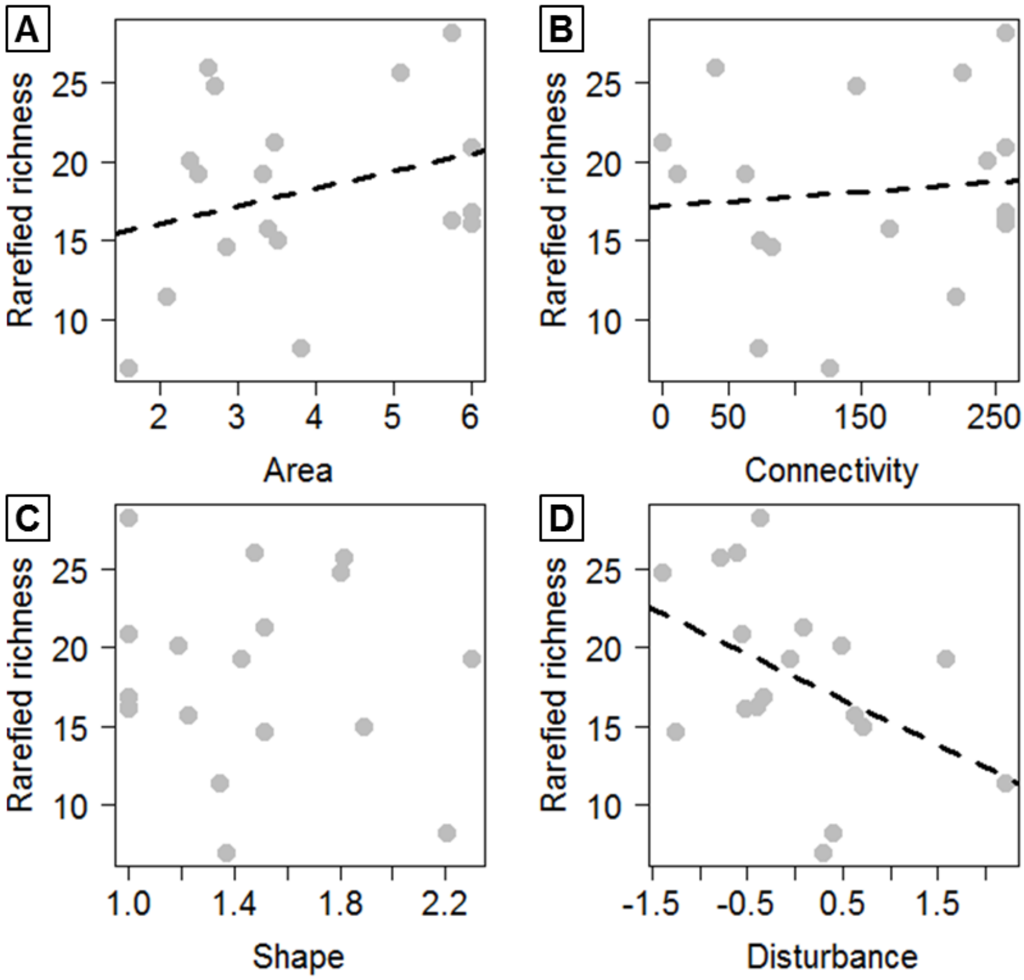


Figure S5. Rarefied seedling genus richness plotted against site characteristic predictor variables: (A) area (log10 ha), (B) connectivity, (C) shape, and (D) disturbance. Fitted lines are shown where the relationship was important in top models of seedling genus richness in the main text.

Text S2. Equation used to calculate the shape index of each site.

$$= p_{ij} / 2\sqrt{a_{ij}}\,\pi$$

a_{ij} = area (m^2) of $patch_{ij}$
p_{ij} = perimeter (m) of $patch_{ij}$

Shape = 1 when the patch is circular, and approaches a maximum of 5 when perimeter is very convoluted (Forman & Godron, 1986).

Text S3. Equation used to calculate the connectivity of each site.

$$= \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^{2}}$$

a_{ijs} = Area (m^2) of $patch_{ijs}$ within specified neighbourhood (m)* of $patch_{ij}$
h_{ijs} = Edge-to-edge distance between $patch_{ijs}$ and focal $patch_{ij}$

Connectivity = 0 when there are no neighbouring patches of forest within specified neighbourhood*, and increases as forest patches become closer, larger and less fragmented.

*1 – 10 km

Table S1. Summary information for study sites, providing information on location, size, shape and connectivity of each site. FF = forest fragment; LF = twice-logged continuous forest; PF = primary continuous forest.

Site #	Site name	Type	Area (ha)[a]	Shape Index[b]	Connectivity[c]	Latitude	Longitude
1	Pin Supu	FF	39.58	1.37	2021014.2	5.40	117.95
2	Sapi A	FF	43.85	1.09	686479.5	5.70	117.40
3	Labuk Rd	FF	121.5	1.34	10652909.4	5.89	117.93
4	Materis	FF	245.6	1.19	14388115.8	5.51	118.02
5	Keruak	FF	307.2	1.43	1740.0	5.51	118.29
6	SapiC	FF	419.2	1.48	62003.4	5.72	117.41
7	Kunak	FF	512.3	1.80	3071774.1	4.66	118.15
8	USP	FF	694.7	1.52	558054.8	5.66	117.27
9	Kalumpang	FF	2069	2.30	248812.5	4.58	118.26
10	Luangmanis B	FF	2473	1.23	4936762.4	5.65	117.73
11	Madai	FF	3015	1.52	0.2	4.74	118.13
12	Luangmanis A	FF	3228	1.89	395896.2	5.72	117.69
13	Sepilok	FF	6441	2.21	373502.0	5.86	117.94
14	Tabin	FF	123000	1.82	11321427.8	5.21	118.50
15	Malua A	LF	1000000	1.00	17000000	5.10	117.67
16	Malua B	LF	1000000	1.00	17000000	5.12	117.67
17	BRL	PF	1000000	1.00	17000000	5.03	117.75
18	Danum	PF	1000000	1.00	17000000	4.97	117.79
19	Tembaling	PF	1000000	1.00	17000000	4.95	117.81

[a] Fragment area calculated using Google Earth imagery; continuous forest sites assigned a value of 800,000 ha, the area of the YSFMA.

[b] Shape index calculated as in Arroyo-Rodriguez et al., 2006 (see Text S1 for further details)

[c] Connectivity (5km buffer) calculated as in FRAGSTATS (McGarigal & Marks, 1995; see Text S2 for further details)

Table S2. Model-averaged coefficients of variables used to predict species richness of seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors

(SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling species richness	Intercept	2.15	0.04	2.07	2.23	
	Area	**0.38**	**0.09**	**0.20**	**0.57**	**1.00**
	Connectivity	-0.06	0.11	-0.28	0.15	0.29
Sapling species richness	Intercept	2.93	0.04	2.85	3.02	
	Disturbance	-0.11	0.09	-0.28	0.06	0.30
	Shape	-0.05	0.09	-0.23	0.12	0.16
	Connectivity	-0.04	0.09	-0.21	0.14	0.15
Tree species richness	Intercept	2.94	0.03	2.88	2.99	
	Disturbance	**-0.13**	**0.06**	**-0.25**	**-0.02**	**1.00**
	Shape	-0.10	0.06	-0.22	0.02	0.70
	Disturbance:Shape	-0.19	0.19	-0.55	0.18	0.16
	Connectivity	-0.06	0.07	-0.20	0.07	0.14
	Area	-0.05	0.06	-0.17	0.08	0.12

Table S3. Mean number of species, genera, and families in each size class, and total number of stems, with standard errors (SE), per site (average of 3 – 5 plots per site). Sites are arranged in order of increasing area (Table S1).

Site #	**Size Class**	**Species (±SE)**	**Genera (±SE)**	**Families (±SE)**	**Abundance (±SE)**
1	Seedlings	4.2 (0.97)	4.2 (0.97)	3.8 (0.86)	66 (42.91)
2	Seedlings	8.33 (0.67)	7.33 (0.33)	6.67 (0.33)	10.33 (0.88)
3	Seedlings	7 (0.84)	6.2 (1.07)	5.2 (0.80)	43 (14.40)
4	Seedlings	6.8 (1.20)	6.8 (1.20)	6 (1.14)	22.4 (2.93)
5	Seedlings	9.4 (0.51)	9 (0.63)	7.2 (0.20)	40 (15.72)
6	Seedlings	7.4 (0.75)	7.2 (0.58)	6.4 (0.40)	15.8 (4.19)
7	Seedlings	11.4 (1.03)	10.8 (1.07)	10 (1.14)	32.8 (8.10)
8	Seedlings	6.4 (0.93)	5.6 (0.51)	4.8 (0.20)	37.2 (8.14)
9	Seedlings	6.8 (0.73)	6.6 (0.68)	5.2 (0.73)	19.8 (5.44)
10	Seedlings	7.4 (0.87)	6.8 (0.73)	6 (0.63)	29.8 (7.01)
11	Seedlings	9 (0.71)	8.4 (0.75)	7.6 (0.40)	34 (4.93)
12	Seedlings	7.6 (0.87)	7 (0.63)	6.4 (0.68)	45.2 (10.46)
13	Seedlings	9.4 (1.25)	8.6 (1.29)	6.2 (1.24)	139.8 (67.09)
14	Seedlings	8 (2.28)	7.8 (2.08)	6.4 (1.03)	18.8 (4.53)
15	Seedlings	9.2 (1.93)	8.2 (1.66)	6.4 (1.21)	40 (19.75)

16	Seedlings	11.2 (1.98)	10 (1.70)	7.8 (1.16)	20 (2.12)
17	Seedlings	12.8 (1.02)	11.8 (0.86)	9.6 (0.75)	41.8 (5.12)
18	Seedlings	12.8 (1.11)	9.6 (1.21)	8.2 (1.20)	44.8 (8.39)
19	Seedlings	11.6 (1.83)	9.6 (1.50)	7.6 1.21)	43.6 (5.84)
1	Saplings	16.4 (2.38)	15 (1.84)	12.4 (1.47)	42.8 (3.48)
2	Saplings	22.67 (2.85)	20.33 (1.76)	16 (2.08)	31 (4.00)
3	Saplings	15.2 (2.18)	14.4 (2.04)	11.2 (1.20)	34.4 (7.34)
4	Saplings	19.2 (0.97)	17.2 (0.97)	13.4 (0.60)	37.4 (2.75)
5	Saplings	16.8 (3.38)	16.2 (3.17)	12.4 (2.16)	25.4 (6.24)
6	Saplings	28 (4.37)	25 (3.58)	18.6 (1.86)	46 (7.09)
7	Saplings	15.8 (2.06)	14.2 (2.06)	11.6 (1.44)	28.4 (2.94)
8	Saplings	21.2 (2.65)	19.2 (2.48)	14.6 (1.78)	55.4 (6.50)
9	Saplings	15.2 (1.50)	14.4 (1.33)	11.2 (1.50)	28.4 (8.03)
10	Saplings	17 (2.17)	15.4 (2.16)	11.8 (2.03)	30.4 (3.80)
11	Saplings	17.8 (1.77)	16 (1.52)	12.8 (0.73)	38.6 (4.47)
12	Saplings	16.8 (4.60)	15.2 (4.27)	11.6 (2.80)	24.8 (5.31)
13	Saplings	23.2 (1.88)	20.6 (1.21)	16 (1.10)	43.4 (5.33)
14	Saplings	17.8 (0.86)	15.4 (1.17)	12.2 (1.39)	26.8 (2.58)
15	Saplings	18.4 (3.26)	17.2 (2.92)	12.8 (1.88)	32.4 (5.64)
16	Saplings	26.4 (2.25)	23.8 (1.88)	18 (1.34)	44 (5.07)
17	Saplings	19.6 (1.81)	17.4 (1.47)	13.2 (1.24)	35.4 (2.82)
18	Saplings	13.6 (1.03)	12.6 (0.81)	9.4 (0.51)	25.4 (3.30)
19	Saplings	20.2 (2.15)	17.8 (1.74)	12.2 (1.39)	33.4 (4.27)
1	Trees	14.6 (2.48)	13.2 (2.08)	10.6 (1.69)	24.6 (1.21)
2	Trees	26 (1.15)	22.67 (0.33)	16 (0.58)	30.33 (0.88)
3	Trees	15.6 (2.06)	14 (1.95)	11.8 (1.59)	26.4 (4.19)
4	Trees	18.8 (2.22)	16.4 (1.94)	13 (0.71)	27.4 (2.71)
5	Trees	17.8 (3.94)	16 (3.03)	11.8 (2.37)	26.6 (5.32)
6	Trees	22.2 (2.42)	20 (2.07)	15.6 (1.21)	29 (4.02)
7	Trees	20.2 (1.24)	18.2 (0.97)	14 (0.45)	35.8 (4.62)
8	Trees	18.6 (2.62)	16.4 (2.14)	13.4 (1.81)	39.8 (1.74)
9	Trees	19 (1.55)	17 (1.87)	12.6 (1.72)	28.8 (1.16)
10	Trees	20.8 (1.24)	20 (1.00)	14 (0.84)	27.4 (1.33)
11	Trees	18.4 (1.17)	16.6 (0.93)	13.8 (0.66)	26 (2.17)
12	Trees	14.4 (2.91)	13.6 (2.79)	10.2 (2.06)	23.2 (3.65)
13	Trees	16.6 (1.21)	15.4 (0.75)	11.4 (0.87)	26 (1.34)
14	Trees	20 (1.30)	18.6 (1.33)	14.2 (0.97)	28 (2.74)
15	Trees	17.2 (2.08)	16 (2.14)	11.6 (1.69)	26.2 (2.42)
16	Trees	24 (2.17)	21.2 (1.85)	15.2 (0.97)	37.2 (5.84)
17	Trees	19.8 (0.92)	17.4 (1.21)	12.6 (0.93)	27.6 (1.86)
18	Trees	18.2 (1.77)	15.6 (1.60)	12.4 (0.93)	24.8 (1.88)
19	Trees	19.4 (1.08)	16.6 (1.33)	13.8 (1.07)	26.2 (1.59)

Text S4 Influence of soil nutrients on size class richness

We measured the following soil characteristics: soil pH (pH-meter in slurry of water and soil), soil nitrogen, carbon and C:N ratio (using dry combustion C/N analyser), and soil phosphorus (using acid-digestion method described in Grimshaw, 1989). Soil characteristics were measured from four soil cores per plot, that were bulked for each plot prior to analysis at the Forest Research Centre, Sepilok. The soil data were included initially in our analyses, but were not found to be important in predicting diversity differences among plots and sites, and hence they were excluded from the subsequent analyses.

Table S4. Mean site values with standard errors (SE) for soil nutrient data collected in each site. Sites are arranged in order of increasing area.

Site #	pH (±SE)	Total P (±SE)	Total N (±SE)	Total C (±SE)	C:N ratio (±SE)
1	4.31 (0.11)	88.61 (6.53)	0.08 (0.02)	1.39 (0.00)	20.28 (4.19)
2	3.72 (0.09)	126.33 (10.68)	0.10 (0.02)	2.03 (0.26)	23.11 (4.33)
3	4.63 (0.20)	188.34 (19.83)	0.13 (0.03)	1.43 (0.22)	11.81 (1.31)
4	4.64 (0.15)	208.18 (13.47)	0.10 (0.02)	1.40 (0.17)	14.93 (0.88)
5	6.26 (0.45)	281.50 (25.48)	0.32 (0.07)	3.95 (0.98)	12.58 (1.11)
6	4.13 (0.04)	49.03 (8.95)	0.05 (0.01)	1.16 (0.09)	27.95 (6.16)
7	4.84 (0.32)	54.12 (11.04)	0.14 (0.02)	1.93 (0.25)	14.28 (1.37)
8	4.00 (0.16)	75.68 (19.54)	0.13 (0.01)	2.88 (0.62)	22.11 (4.49)
9	5.27 (0.23)	71.63 (4.65)	0.05 (0.00)	1.26 (0.07)	23.56 (1.01)
10	3.94 (0.05)	66.82 (10.28)	0.05 (0.01)	1.34 (0.15)	29.96 (3.13)
11	4.37 (0.08)	280.51 (11.70)	0.21 (0.02)	1.76 (0.14)	8.42 (0.79)
12	5.26 (0.41)	208.31 (35.81)	0.13 (0.01)	1.62 (0.14)	12.11 (0.44)
13	4.00 (0.05)	84.18 (22.16)	0.07 (0.02)	1.30 (0.12)	23.70 (6.24)
14	4.80 (0.14)	348.93 (41.68)	0.15 (0.01)	1.56 (0.16)	10.11 (0.29)
15	3.81 (0.08)	137.99 (7.11)	0.10 (0.02)	1.60 (0.19)	17.85 (2.33)
16	3.88 (0.18)	174.97 (9.39)	0.16 (0.02)	2.08 (0.21)	14.00 (1.56)
17	4.33 (0.13)	316.90 (73.58)	0.13 (0.03)	1.78 (0.13)	15.69 (2.28)
18	3.80 (0.09)	254.11 (23.84)	0.14 (0.03)	1.86 (0.18)	15.25 (2.41)
19	4.63 (0.28)	192.06 (32.32)	0.08 (0.02)	1.33 (0.20)	18.26 (3.27)

Table S5. Reciprocal Simpson diversity. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	Predictor	β	SE	Lower CI	Upper CI	RI
Seedling Simpson diversity	Intercept	0.29	0.04	0.22	0.36	
	Area	0.04	0.09	-0.13	0.21	0.46
	Connectivity	-0.03	0.06	-0.15	0.08	0.47
	Area:Connectivity	**-0.37**	**0.16**	**-0.69**	**-0.05**	**0.33**
	Disturbance	0.08	0.05	-0.02	0.17	0.55
	Shape	0.03	0.07	-0.10	0.17	0.27
	Connectivity:Disturbance	0.16	0.10	-0.02	0.35	0.19
Saplings Simpson diversity	Intercept	0.10	0.01	0.09	0.11	
	Connectivity	0.01	0.01	-0.02	0.03	0.21
	Disturbance	0.01	0.01	-0.02	0.03	0.24
Trees Simpson diversity	Intercept	0.09	0.00	0.08	0.09	
	Shape	0.01	0.01	-0.01	0.03	0.38
	Disturbance	**0.00**	**0.00**	**0.00**	**0.01**	**0.17**

Text S5 Influence of changing buffer size for calculation of connectivity metric

Altering the buffer width from 1 to 10 km, had little or no effect on the outcome of the model. Variables were standardised before being included in the GLMM and this meant there was little variation in values of connectivity, regardless of buffer size.

Table S6. Influence of change buffer size for calculation of connectivity metric.

Buffer size (km)	Response variable	Predictor	β	SE	Lower CI	Upper CI
1	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89

	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
2	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
3	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
4	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
5	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05

6	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
7	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
8	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
9	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
10	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49

	Connectivity	-0.08	0.11	-0.29	0.14
	Disturbance	-0.04	0.09	-0.23	0.14
Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
	Disturbance	-0.08	0.08	-0.25	0.08
	Shape	-0.05	0.08	-0.22	0.11
	Connectivity	-0.05	0.08	-0.21	0.12
Tree genera richness	Intercept	2.83	0.03	2.77	2.89
	Disturbance	-0.12	0.06	-0.23	0.00
	Shape	-0.06	0.06	-0.17	0.05

Table S7. Influence of changing size class upper/lower bounds on sapling and tree size classes. Model-averaged coefficients of variables used to predict genus richness of seedling (< 1cm dbh), sapling (1 – 2.5 cm dbh), and tree (>10 cm dbh) size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness	Intercept	2.06	0.04	1.98	2.15	
	Area	0.31	0.09	0.12	0.49	**1.00**
	Connectivity	-0.08	0.11	-0.29	0.13	0.24
	Disturbance	-0.04	0.09	-0.23	0.14	0.20
Sapling genera richness	Intercept	2.44	0.05	2.33	2.54	
	Disturbance	-0.10	0.11	-0.31	0.11	0.27
	Connectivity	-0.06	0.11	-0.27	0.15	0.21
Tree genera richness	Intercept	2.23	0.03	2.17	2.30	
	Disturbance	-0.19	0.07	-0.34	-0.05	**1.00**
	Area	-0.03	0.07	-0.18	0.11	0.27

Text S6. Wood density as a proxy for growth-rate of genera

In order to test the robustness of our results to the removal of slow-growing genera, we used wood density as a proxy for growth rate (Slik, 2005). We obtained wood density on dry weight (g/cm^3) data from The Global Wood Density database (Chave & al., 2009). We then removed high wood-density (>0.75 g/cm^3), slow-growing genera and repeated our analyses, but found no qualitative difference in our results (i.e. lower richness of seedlings in fragments, but no effects of fragmentation on saplings or trees). These analyses support our assumption that size is a reasonable proxy for pre- and post-fragmentation individuals.

We also carried out our analyses of fragmentation effects separately for high and low wood density groups, and we split our data set according to the median wood density of all genera we encountered in our study (0.55 g/cm3). We found significantly fewer low wood density tree genera present in plots in primary forest than in logged or fragmented forest (ANOVA of tree richness by forest type; high wood density: F(2,90) = 2.57, p = 0.08; low wood density: F(2,90) = 4.55, p = 0.01), however findings from our ANOVA analyses of tree, sapling and seedling richness were qualitatively similar to our original analysis i.e. both low and high wood density seedlings have lower richness in fragments (ANOVA of seedling richness by forest type; high wood density: F(2,90) = 5.60, p = 0.005; low wood density: F(2,90) = 4.60, p = 0.01; ANOVA of sapling richness by forest type high wood density: F(2,90) = 2.87, p = 0.06; low wood density: F(2,90) = 0.23, p = 0.80). Our findings from our GLMMs with respect to examining site characteristics important for richness were also qualitatively similar for the low and high wood density groups. As previously, there was no effect of site area on either high or low wood density sapling richness and so we conclude that differences in plant growth rates are not having major impacts on our designation of post- and pre-fragmentation individuals, or our overall findings.

Table S8. Influence of removal of high wood-density (>0.75 g/cm^3), slow-growing genera on size classes. Model-averaged coefficients of variables used to predict genus-level richness of seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness	Intercept	2.00	0.04	1.92	2.08	
	Area	0.28	0.09	0.10	0.46	**1.00**
	Connectivity	-0.06	0.09	-0.24	0.13	0.21
	Disturbance	-0.05	0.11	-0.27	0.16	0.22
Sapling genera richness	Intercept	2.76	0.04	2.68	2.84	
	Disturbance	-0.07	0.08	-0.23	0.09	0.21
	Connectivity	-0.06	0.08	-0.21	0.10	0.19
	Shape	-0.04	0.08	-0.20	0.12	0.17
Tree genera richness	Intercept	2.76	0.03	2.70	2.82	
	Disturbance	-0.13	0.06	-0.24	-0.01	**0.80**
	Shape	-0.05	0.06	-0.17	0.06	0.27

Table S9. Model-averaged coefficients of variables used to predict genus-level richness of low and high wood-density seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness (low wood density)	Intercept	1.16	0.06	1.04	1.27	
	Area	**0.30**	**0.12**	**0.06**	**0.53**	**1.00**
	Shape	-0.07	0.13	-0.33	0.18	0.28
Sapling genera richness (low	Intercept	1.85	0.05	1.75	1.96	
	Connectivity	-0.21	0.14	-0.48	0.06	0.44

wood density)	Shape	-0.20	0.14	-0.46	0.07	0.54
	Area	-0.13	0.11	-0.35	0.09	0.22
	Disturbance	-0.07	0.10	-0.27	0.13	0.09
Tree genera richness (low wood density)	Intercept	1.89	0.04	1.81	1.98	
	Area	-0.14	0.09	-0.32	0.04	0.41
	Connectivity	-0.09	0.09	-0.27	0.08	0.17
	Disturbance	-0.07	0.09	-0.25	0.11	0.13
	Shape	0.06	0.09	-0.11	0.24	0.13
Seedling genera richness (high wood density)	Intercept	1.54	0.06	1.41	1.66	
	Area	**0.31**	**0.14**	**0.04**	**0.59**	**1.00**
	Connectivity	-0.11	0.16	-0.43	0.20	0.20
	Disturbance	-0.07	0.14	-0.34	0.20	0.17
	Shape	0.06	0.13	-0.20	0.32	0.17
Sapling genera richness (high wood density)	Intercept	2.36	0.05	2.27	2.45	
	Disturbance	-0.11	0.09	-0.30	0.07	0.31
	Area	0.09	0.09	-0.10	0.27	0.24
Tree genera richness (high wood density)	Intercept	2.33	0.03	2.26	2.39	
	Disturbance	**-0.18**	**0.07**	**-0.32**	**-0.05**	**1.00**
	Shape	**-0.13**	**0.07**	**-0.27**	**0.00**	**0.72**

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