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Divergent tree seedling communities indicate different trajectories of change among rain forest remnants

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Abstract

Aim: To examine plant community composition within rain forest remnants, and whether communities in different fragments follow similar trajectories of change in composition. We investigate whether plant communities in rain forest fragments either diverge from, or become more similar to, plant communities in other fragments, in order to understand the biodiversity value of forest fragments.

Location: Rain forest fragments embedded within agricultural landscapes in Sabah, Malaysian Borneo.

Methods: We examined 14 forest fragments (39–120,000 ha) and five sites in continuous forest, and compared pre-isolation (trees >5 cm dbh) and post-isolation (seedlings <1 cm dbh) plant community composition. We used Chao-Sørensen dissimilarity metric to compute beta diversity between all pairwise combinations of sites, and then used Non-Metric Multidimensional Scaling to reduce 18 pairwise values per site to a single site value, which we used to test whether fragment area and/or isolation are associated with changes in plant communities. We compare analyses for trees and seedlings, and whether community changes arise from recruitment failure.

Results: Seedlings in fragments have diverged most from other communities, and divergence was greatest between seedling communities in small fragments, which have not only diverged more from tree communities in the same fragment, but also from seedling communities at other sites. This finding is partly associated with recruitment failure: the number of genera represented by both trees and seedlings is positively associated with site area.

Main conclusions: Seedling communities are diverging in forest remnants, associated primarily with reductions in fragment area, whilst tree communities have not diverged, possibly due to extinction debts. Divergence is likely to continue as seedling cohorts mature, resulting in communities in fragments following different trajectories of change. Individual plant communities in each fragment may become impoverished, but they can support different communities of plants and hence contribute to landscape-scale diversity.

KEYWORDS
beta diversity, Borneo, community composition, extinction debt, forest fragmentation, recruitment failure

1 | INTRODUCTION

Tropical forests represent some of the most species-rich ecosystems on the planet, and are under continuing pressure from habitat loss and fragmentation, driven by deforestation for agricultural expansion (Taubert et al., 2018). When continuous tracts of habitat are substantially reduced in area and fragmented, the remnants of habitat are often relatively small and isolated from one another (Haddad et al., 2015). How the local plant composition within forest fragments will change thereafter is far from clear, and could either converge to a common set of species, or diverge to represent distinct subsets of species. For example, some non-viable populations will die out completely from a given fragment, whereas other species may increase or colonise, particularly those associated with habitat edges and disturbance (Harper et al., 2005). Consequently, the spatial patterns of communities may change, with communities within fragments becoming increasingly similar if the same species always decline in fragments and another set of species always increase and colonise, homogenising to a more uniform but impoverished set of pioneer-type species (Pütz, Groeneveld, Alves, Metzger, & Huth, 2011; Rocha-Santos et al., 2016). Alternatively, plant communities may diverge as a function of both chance events (e.g. stochastic recruitment) and more deterministic species-specific variation in growth and survival in remnants due to differences in remnant characteristics (Arroyo-Rodríguez et al., 2015). In this scenario, fragments will contribute to landscape-scale heterogeneity, even if individual remnants are impoverished, because fragments will support species not found in other fragments. However, tree mortality and recruitment are more variable in fragments than in more undisturbed continuous forest (Laurance et al., 2007). The trajectory of tree community composition change in fragments is also hard to project due to the long generation times of trees and consequent slow turnover rates. Hence, the outcome of habitat loss and fragmentation for plant communities within fragments is difficult to predict. The scenario that plays out will have important implications for the long-term composition of remnant fragments, and their conservation value. In this study, we examine the effects of area and isolation of forest remnants on local plant community composition, and test whether plant communities in different fragments will become more homogeneous or more divergent.

The biotic and abiotic effects of fragment creation from formerly continuous tracts of forest include altered microclimate, loss of seed dispersers and pollinators and changing patterns of herbivory, which have impacts on plant communities within fragments (Lopez & Terborgh, 2007), with the greatest changes taking place in the smallest and most isolated forest fragments (Hill et al., 2011). Defaunation of forest fragments is increasingly reported (e.g. Canale, Peres, Guidorizzi, Gatto, & Kierulff, 2012), and is likely to affect trees with animal-dispersed seeds more than those that are abiotically dispersed (Harrison et al., 2013), leading to changes in community composition. However, it may be decades before these effects have an impact on tree communities, because individual trees can live for many years without reproducing, invoking an extinction debt (Kuussaari et al., 2009). Nonetheless, differences in seedling communities may begin to emerge sooner if the altered abiotic and biotic conditions in fragments begin to affect tree regeneration. Given that many forests now occur as fragments, it is important to understand the trajectory that plant communities in fragments may follow.

Lowland tropical rain forest on Borneo hosts extremely high levels of biodiversity (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Many trees in these dipterocarp-dominated forests reproduce during mast fruiting events associated with El Niño events (Appanah, 1993), and it is unclear whether recruitment of trees is disrupted in rain forest remnants, which were formed during rapid expansion of agricultural (oil palm) plantations in the 1980s (Yeong, Reynolds, & Hill, 2016). A previous study showed that local richness of seedlings is reduced in forest fragments in Borneo (Stride et al., 2018), but impacts on plant community composition are less clear yet critical for conserving plant biodiversity, given that so much of the remaining forest has been degraded or lost (Haddad et al., 2015; Reynolds, Payne, Sinun, Mosigil, & Walsh, 2011). Even though small forest fragments in lowland areas of Borneo have altered ecosystem functioning (Yeong et al., 2016) and support fewer species (Lucey et al., 2017), they are important refuges for species in agricultural landscapes that are dominated by oil palm (Prescott et al., 2016). Individual fragments may also be important for increasing landscape-level connectivity (Scriven, Hodgson, McClean, & Hill, 2015), contributing to the dynamics and persistence of metapopulations of species restricted to fragments (Ovaskainen & Hanski, 2003). Thus, it is crucial to understand factors affecting plant community composition within fragments, and their relationship to one another within the wider landscape.

We examine tree and seedling communities in rain forest remnants that vary in terms of their size and degree of isolation, and are embedded within a matrix of agricultural land. We calculate beta diversity in rain forest remnants and continuous forest, and quantify beta diversity between sites (quantifying the distinctiveness of communities of trees and seedlings among our 19 sites), as well as beta diversity of trees and seedlings within sites (quantifying the divergence of seedling communities from tree communities at the same sites). We examine whether tree recruitment is affected in forest fragments, and test whether seedling communities in fragments either diverge from, or become more similar to, seedling communities in other sites. We anticipate that any changes in plant communities will be greatest in the smallest, most isolated forest fragments, since tree species in these fragments are expected to experience the greatest changes to

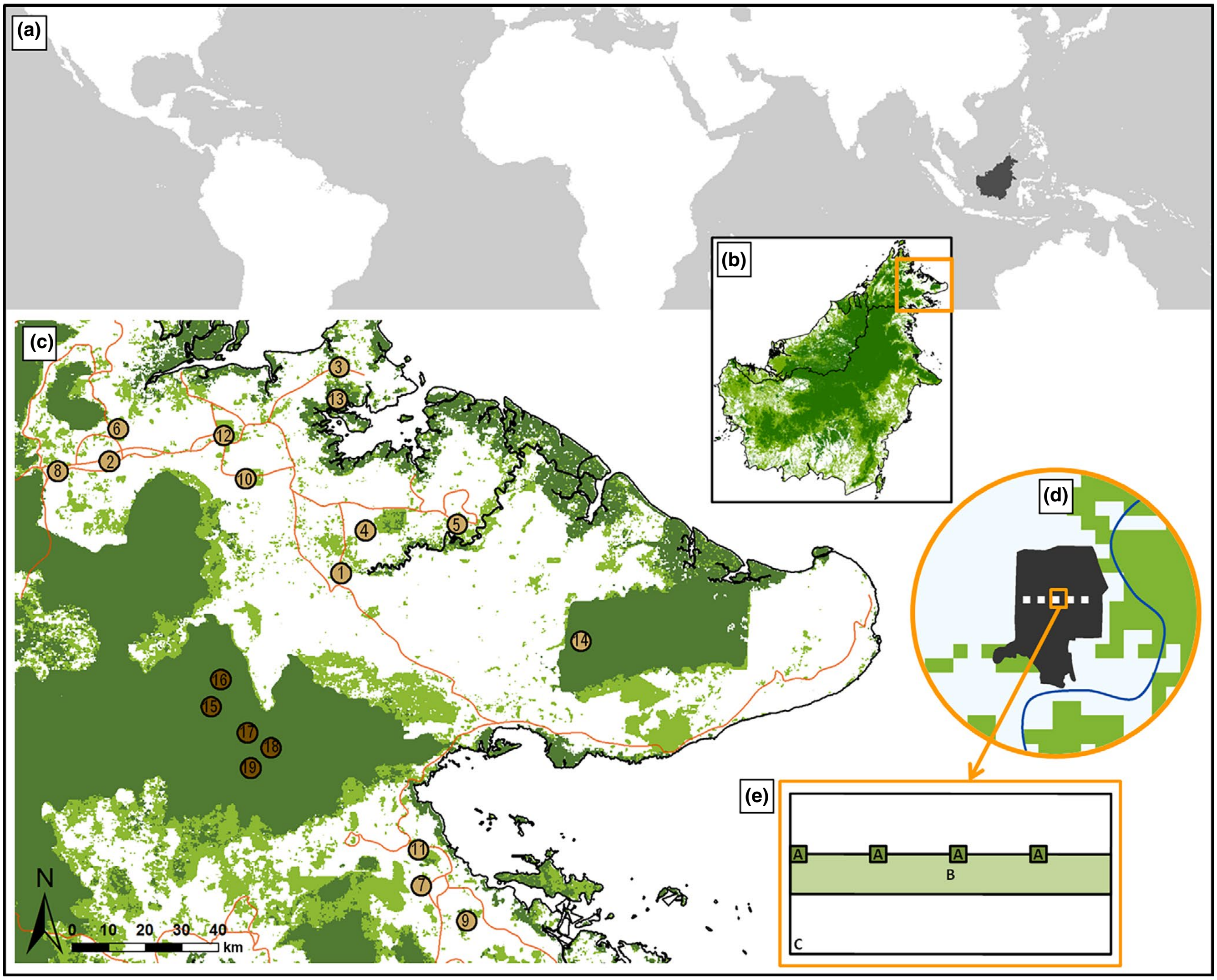

FIGURE 1 (a) World map showing Borneo. (b) Study area location on Borneo. (c) Sites are numbered in order of increasing size; dark green areas indicate forest; light green areas indicate regenerating or degraded forest; white areas indicate agricultural land predominantly covered by oil palm; sites 1–14 (light brown symbols) are forest fragment sites, sites 15–19 (dark brown symbols) are continuous forest sites. Forest cover data were obtained from (Miettinen et al., 2012). (d) A forest fragment. Within each site, five plots were arranged along a transect. (e) Nested sampling design (subplot area in brackets): A = seedling plots (four × (2 × 2 m)), B = trees 5–30 cm dbh (5 × 40 m), C = trees >30 cm dbh (20 × 40 m)

the physical environment, the highest levels of stochastic variation in population dynamics, the lowest levels of rescue effects from other fragments, and potentially the highest levels of human disturbance. First, we test (a) whether seedling communities in fragments are more distinct from communities in other sites, compared with patterns of seedling distinctiveness in continuous forest sites, and predict that any patterns seen in seedling communities will not be evident in tree communities, or far less so. We then test (b) whether seedling communities are diverging from tree communities within each site. We examine (c) whether patterns of divergence and distinctiveness of communities are associated with the size and isolation of sites. Finally, we test (d) whether changes in seedling community composition are driven by recruitment failure, and whether animal-dispersed genera are disproportionately affected. In this way, we assess whether each fragment will contribute to regional (landscape) diversity because there are different species in different fragments, or whether fragments will become increasingly similar, resulting in more homogenous plant communities and reduced regional diversity.

2 | METHODS

2.1 | Study sites

Plant community data were collected in 14 forest fragments and five "control" sites in continuous forest (a tract of forest of >1 million ha; Reynolds et al., 2011) in lowland (<500 m a.s.l.) dipterocarp rain forest in Sabah (Malaysian Borneo) during April–August 2015. Lowland Sabah comprises a fragmented mosaic of forest and agriculture, and all forest fragments were surrounded by mature oil palm plantations at the time of study. Three of the continuous forest sites were located within fully protected undisturbed primary forest (Danum Valley Conservation Area), and the other two sites within selectively twice-logged forest (Malua Forest Reserve), logged in the mid-1980s and 2005/6 (Figure 1; Reynolds et al., 2011). Sampling these five continuous forest sites therefore represented plant communities of closed-canopy forest typical of the region, to compare with forest fragments. The forest fragment sites were protected as "Virgin Jungle Reserves" (VJRs) in the 1950s for scientific research, and are managed by the Sabah Forestry Department. VJRs represent high-quality forest where logging is prohibited, although most have experienced low levels of disturbance from human encroachment, poaching and illegal felling (pers. obs., Sabah Forestry Department, 2005). The 14 forest fragments range in size from 39 to 120,000 ha (Figure 1, Table S1) and vary in their degree of isolation. Site 14 is much larger than all other forest fragments sampled, but nonetheless is isolated from continuous sites (Figure 1), is surrounded by non-forest habitat, and provides a useful additional site along the fragment size gradient. Fragment perimeter (and consequently fragment shape) was significantly correlated with fragment area (GLM: $p = < .001$, $R^2 = .62$; Table S1) and was therefore not included as an explanatory variable in analyses. All 19 sites were >2 km apart from their nearest neighbour.

2.2 | Floristic surveys of tree and seedling communities

In each of the 19 sites, a 1 km linear transect was established, comprising five plots placed at 160 m intervals (Figure 1), starting 100 m from the forest edge to avoid the main edge effects (Laurance, 2000; Ewers & Didham, 2006), and in forest fragments angled towards the fragment centre. However, in site #2 only three plots were possible owing to its small size and shape (44 ha; Table S1). Each plot was 20 × 40 m, and was sampled following a modified Gentry protocol, using a series of subplots to sample different size classes (Gentry, 1982; Figure 1). This nested design of subplots controlled for spatial aggregation of species and allowed us to sample lower density larger trees over a larger area, while the more densely occurring smaller trees and seedlings were sampled over a smaller area. Trees >5 cm dbh were divided into two size groups: those 5–30 cm dbh were sampled in one 5 × 40 m strip within each plot, whereas trees >30 cm dbh were enumerated in the full 20 × 40 m plot. Seedlings (non-climbing woody plants <1.5 m in height and <1 cm dbh) were enumerated in four 2 × 2 m subplots distributed evenly within each plot (Figure 1). We assume that seedlings have predominantly been recruited after the isolation of forest fragments in the 1990s (Table S1), the majority of recruiting during recent mast fruiting events (e.g. particularly strong global ENSO events took place in 1997/98 and 2015/16, resulting in mast flowering and fruiting; Connell & Green, 2000; Cpc.ncep.noaa.gov, 2018), while trees (>5 cm dbh) largely represent pre-isolation communities. For a detailed discussion on tree and seedling growth rates in fragments, see Stride et al. (2018), Text S6. Plot-level data were combined to compute the number of genera and abundance of individuals within each genus at each of the 19 sites. We used these data to compute the distinctiveness of tree and seedling communities among our 19 sites, as well as the divergence of seedling communities from tree communities at each site. Henceforth, we use "tree" and "seedling" as shorthand for tree and seedling community composition. Analyses were carried out with and without site #2 to ensure that sampling a smaller number of plots in site #2 did not affect our results. The results were qualitatively the same, and so we present analyses based on all 19 sites in the main text.

Where possible, plant identification was carried out in the field, and otherwise leaf samples and photographs were taken for identification by the botanist at Danum Valley Field Centre. All but six (0.06%) individuals were identified to genus level, and unidentified individuals were removed from the analysis. As in other studies, analyses were conducted at genus level due to the complexities of plant taxonomy and identification in highly diverse tropical rain forest (Stride et al., 2018).

2.3 | Measuring site area and isolation

We related patterns of distinctiveness and divergence of communities at each of the 19 sites to site area and isolation. We measured the area of forest fragments using R v. 3.2.2 (R Core Team, 2015) after tracing the outline of each fragment from satellite imagery (Google Earth Pro v.). Following standard protocol (e.g. Ewers et al., 2017), area was $\log_{10}$ transformed to reduce skew in the data. The isolation of each forest fragment was calculated by using forest land cover data (Miettinen, Shi, Tan, & Liew, 2012) at a grid cell resolution of 250 m to identify all forest patches within a 5 km radius of each forest fragment. The size of each forest patch and their distances from the site were used to calculate the isolation metric (McGarigal & Marks, 1995; Text S1). Each value was then subtracted from the maximum isolation value so that an isolation value of 0 indicates a highly connected site with high cover forest in the surrounding landscape, and increasing isolation values indicate decreasing amounts of forest cover in the landscape surrounding the site. We gave continuous forest sites a notional area of 1,000,000 ha (the area of the Yayasan Sabah Forest Reserve; Reynolds et al., 2011), and an isolation value of 0.

2.4 | Data analyses

2.4.1 | Computing distinctiveness and divergence of communities

We computed pairwise Chao-Sørensen abundance-based dissimilarities between trees and between seedlings across all our sites, between seedlings and trees within sites and for all pairwise combinations of trees and seedlings in all sites for the full plant community. The Chao-Sørensen index was the most appropriate dissimilarity metric to use because it reduces under-sampling bias by estimating the number of unseen rare species, and is therefore

TABLE 1 GLM metrics for tree distinctiveness, seedling distinctiveness and tree seedling divergence. Model set does not include any models for which a higher ranked (lower AIC), nested model exists. Significant variables are highlighted in bold

Response variable	Predictor variables	*df*	Estimate	AICc	Δ_i	Residual deviance	Adjusted R^2
Tree distinctiveness	Area + Isolation	16	−0.02 0.00	−42.89	0.00	0.08	.12
	Null	18	0.23	−42.11	0.78	0.10	.00
	Isolation	17	0.00	−42.09	0.80	0.09	.04
	Area	17	0.00	−40.25	2.64	0.10	.00
Seedling distinctiveness	**Area**	**17**	**−0.05**	**−31.50**	**0.00**	**0.15**	**.37**
	Null	18	0.33	−23.43	8.07	0.26	.00
Tree seedling divergence	**Area**	**17**	**−0.04**	**−38.35**	**0.00**	**0.19**	**.21**
	Null	18	0.29	−31.27	7.08	0.17	.00

Abbreviations: *df*, degrees of freedom; Δ_i, difference between AICc and lowest AICc value in model set.

useful when sampling communities that have high alpha diversity and a large fraction of rare species (Chao, Chazdon, Colwell, & Shen, 2004). To examine distinctiveness of trees and seedlings among sites, we used Non-metric Multidimensional Scaling (NMDS) ordination on each dissimilarity matrix (trees and seedlings separately), and then calculated the Euclidean distance of each site to the NMDS centroid (i.e. distance of the community at each site from the "average" community), for seedlings and trees. This reduced 18 pairwise comparisons per site to a single value for each cohort for each site. Divergence between seedlings and trees at each site was computed in a similar way: we used NMDS ordination of the dissimilarity matrix containing both trees and seedlings, and divergence between trees and seedlings within each site was calculated as the Euclidean distance in the ordination between tree and seedling cohorts at the same sites. This gave a single divergence value of trees from seedlings for each site. This approach provided three separate measures of beta diversity per site that quantified the variability in taxonomic composition among tree and seedling communities at different sites, as well as between seedling and tree communities at the same sites. These measures could be used to test for differences in beta diversity among sites varying in area and degree of isolation from other forest habitats (Anderson, Ellingsen, & McArdle, 2006).

To examine whether differences in patterns of distinctiveness and divergence in our study were due to geographical distance between sites, we conducted two Mantel tests regressing Chao-Sørensen abundance-based pairwise dissimilarities of trees and seedlings separately, against a matrix of geographical distances. Significance of the Mantel correlation statistic was determined by generating 999 random permutations of each matrix, and comparing these with the observed matrix.

2.4.2 | Divergence and distinctiveness in relation to site area and isolation

We used generalised linear models (GLMs) to test whether variation in tree seedling divergence (Euclidean distance between cohorts in NMDS ordination), and changes in tree and seedling distinctiveness among sites (distance-to-centroid in NMDS ordinations) were due to site area and isolation. Models were fitted with area and isolation separately and together in the same model, and the model fit was evaluated based on the relative AIC (Table 1). Values approaching zero indicate low divergence/distinctiveness, and those approaching one indicate high levels of divergence/distinctiveness.

2.4.3 | Variation in divergence and distinctiveness due to recruitment failure

We examined whether variation in distinctiveness and divergence was due primarily to recruitment failure of some tree genera, as opposed to the arrival of new genera, by partitioning genera at each site into three groups and calculating the number of genera in each: those present as trees and seedlings (representing successful recruitment), those present as trees but not seedlings (representing potential recruitment failure), and those present as seedlings but not trees (representing arrival of new genera). We then used Poisson GLMs to model these values in relation to site area and isolation separately and together in the same model, and the model fit was evaluated based on the relative AIC (Table 2). We also split genera into animal-dispersed and wind-dispersed groups and repeated this analysis in order to examine whether any changes in plant communities with fragments were greater among animal-dispersed genera due to the effects of defaunation.

In order to ensure that the results of these analyses were not skewed by the greater proximity of continuous forest sites to one another, compared with fragment sites, by the inclusion of selectively logged continuous forest sites, or by the inclusion of site 14 (the largest forest fragment) we repeated all analyses with (a) 14 fragment sites only, (b) all fragment sites and one continuous forest site (n = 15), (c) all fragment sites, one primary continuous forest site, and one selectively logged continuous forest site (n = 16), (d) all fragment sites and three primary continuous forest sites (n = 17) and (e) all sites except for site 14 (n = 18). Our results were qualitatively the same for all these analyses, and so we only report results for the full data set (n = 19). The results of the remaining analyses can be found in the Supplementary Online Material (Tables S3, S4 and S7). All analyses were performed using R packages vegan (Oksanen, et al., 2015) and CommEcol (Sanches Melo, 2017) in R v. 3.2.2 (R Core Team, 2015).

TABLE 2 GLM metrics of models relating number of genera occurring at each of the 19 sites which were present (a) as both trees and seedlings, (b) tree genera without seedlings and (c) seedling genera without trees. Model set does not include any models for which a higher ranked (lower AIC), nested model exists. Significant variables are highlighted in bold

Response variable	Predictor variables	*df*	Estimate	AICc	Δ_i	Residual deviance	Adjusted R^2
Trees and seedlings	**Area**	**17**	**0.10**	**103.65**	**0.00**	**10.60**	**.45**
	Null	18	2.89	110.10	6.45	19.05	.00
Trees only	Null	18	3.51	120.63	0.00	17.17	.00
	Area	17	−0.02	121.36	0.73	15.89	.07
	Isolation	17	0.00	121.87	1.24	16.70	.03
Seedlings only	Null	18	2.00	91.88	0.00	17.85	.00
	Isolation	17	0.00	93.77	1.89	17.59	.02
	Area	17	0.00	93.88	2.00	17.85	.00

Abbreviations: *df*, degrees of freedom; Δ_i, difference between AICc and lowest AICc value in model set.

3 | RESULTS

A total of 6,351 individuals, comprising 2,646 trees (>5 cm dbh) and 3,705 seedlings (<1 cm dbh and <1.5 m in height), were recorded at our 19 study sites (93 plots in total), belonging to 207 genera in 68 families. Lowland dipterocarp rain forest on Borneo contains an average of 103.0 ± 12.7 (mean ± *SE*) genera per 640 trees >9.8 cm dbh (Slik *et al.* 2003). An average of six random samples of 640 trees >9.8 cm dbh from our dataset contained 125.2 ± 2.4 genera, demonstrating that we captured a representative proportion of the diversity present. Combining trees and seedlings, we found that 22.2% (*n* = 46) of genera were only observed at a single site, 27.1% (*n* = 56) were represented by two or fewer individuals and 14.5% (*n* = 30) of genera were represented by a single individual. The two commonest plant families were Dipterocarpaceae (507 trees [19.2%], and 1687 seedlings [45.5%]) and Euphorbiaceae (297 trees [11.1%], and 491 seedlings [13.2%]).

Neither the pairwise dissimilarities of seedlings nor of trees were related to geographical distance between sites, implying that variation in community composition is not simply due to site proximity (Mantel test; trees: $r = .08$, $p = .22$; seedlings: $r = .08$, $p = .20$; $n = 171$ pairs, 19 sites, and 999 permutations for both tests). Pairwise dissimilarities of seedlings and of trees, and of site area and of site isolation, were also unrelated to the Euclidean distances between site means of the following variables (for collection methods see Stride et al., 2018): soil pH, canopy cover, temperature and photosynthetically active radiation (Mantel tests, Tables S5 and S6). This demonstrates that compositional differences were not associated with local environmental conditions (as measured), and nor were the site area and isolation metrics systematically related to underlying environments present at each site.

3.1 | Variation in divergence and distinctiveness, and the role of site area and isolation

Tree community distinctiveness did not vary significantly in relation to forest area or isolation (Figure 2a–c). In contrast, seedling communities in small forest fragments were most distinctive from other seedling communities (Figure 2d–f), and seedling divergence from adult trees was also greatest in small forest fragments (Figure 2g–i). Area outperformed isolation as the strongest predictor of seedling distinctiveness and tree seedling divergence in univariate and bivariate models (Table 1). However, models including both area and isolation were within 2 AIC points of the best (area only, Table 1) model. We conclude that increasing levels of tree seedling divergence and seedling distinctiveness are associated with decreasing fragment area, and weakly correlated with increasing isolation, but there is little variation in tree distinctiveness among sites.

Our results were similar regardless of whether we included all 19 sites, just fragments (i.e. excluding all five continuous sites), included only one or two of the continuous forest sites, excluded continuous logged forest sites, or excluded the largest fragment site (Tables 1 and 2, Tables S3 and S7). Thus, the relative spatial proximity of sites within the continuous forest, and inclusion of previously logged versus unlogged forest sites, did not affect our conclusions.

The distinctiveness of seedling communities that we find in small fragments could arise in two different ways, either by representing a predictable subset of genera (in which case they would diverge from large fragments and continuous forest, but not from one another), or by diverging from one another (each small fragment having a unique community). Comparisons of pairwise dissimilarities (*n* = 10 pairs in each group) revealed that differences between seedling communities for the five smallest forest fragments were the highest (A1: 40–307 ha, mean pairwise dissimilarity ± *SE* = 0.66 ± 0.09, Figure 3a, Table S2), still relatively high for the five medium forest fragments (A2: 419–2,473 ha, mean = 0.62 ± 0.06), but lower for the five largest forest fragments (A3: 2,473–123,000 ha, mean = 0.35 ± 0.07) and for pairwise comparisons among continuous forest sites (mean = 0.30 ± 0.07). Similarly, pairwise dissimilarities between seedling communities in the most isolated forest fragments (I1: 4.96–6.71, mean pairwise dissimilarity ± SE = 0.58 ± 0.07; I2: 4.04–4.57, mean = 0.68 ± 0.06, Figure 3c) were greater than those in less isolated forest fragments (I3: 2.76–4.04, mean = 0.49 ± 0.08) or continuous forest sites

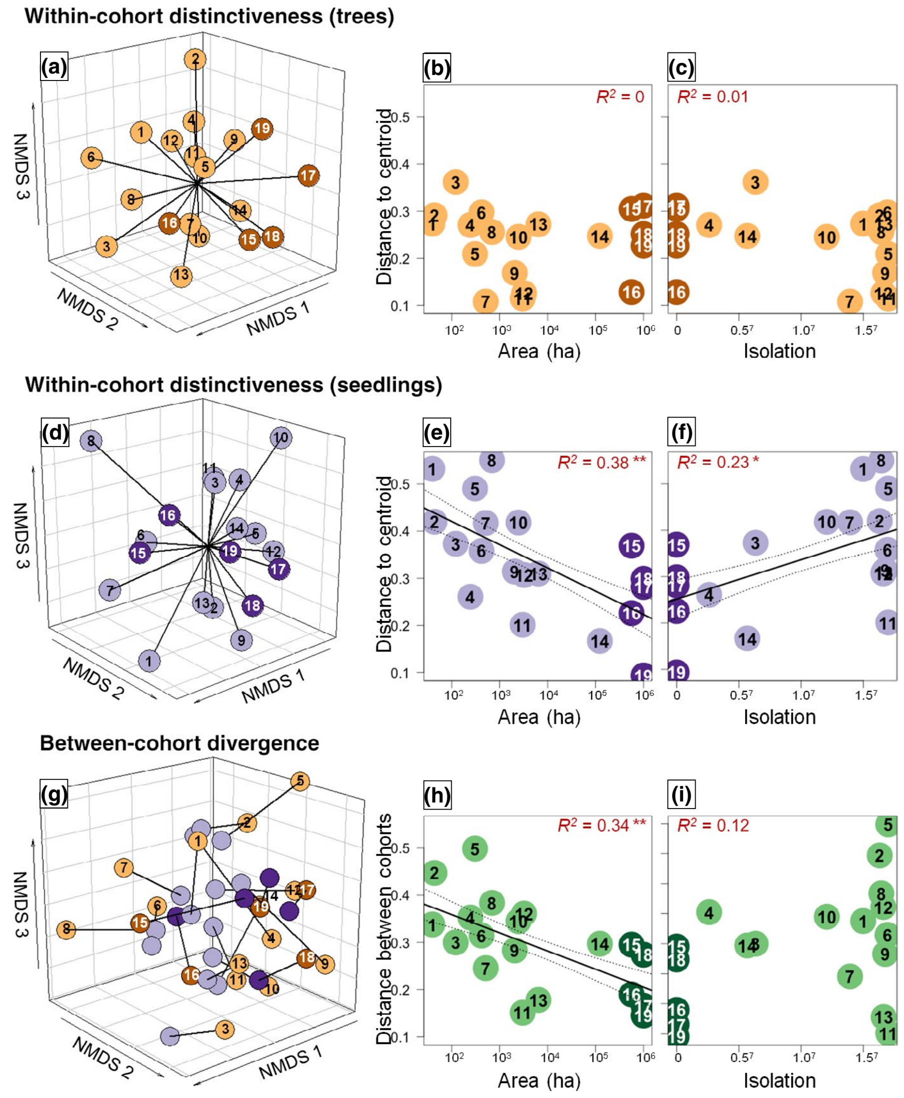

FIGURE 2 Divergence and distinctiveness of tree and seedling communities at sites in relation to site area and isolation. Panels a–c show within-cohort divergence of tree communities, panels d–f show within-cohort divergence of seedlings communities, and g–i show tree seedling divergence within sites. (a) and (d): three-dimensional NMDS ordinations showing the distinctiveness of trees (a) and seedlings (d) in relation to the average community (plot centroid). Numbers within circles refer to site numbers, lighter colours = fragment sites, darker colours = continuous forest sites. b–c: tree distinctiveness (distance-to-centroid) plotted against site area (b) and isolation (c). e–f: seedling distinctiveness (distance-to-centroid) plotted against site area (e) and isolation (f). G: three-dimensional NMDS ordination showing divergence between trees (brown circles) and seedlings (purple) at the same sites. Lines join tree and seedling values at the same sites. h–i: tree seedling divergence (Euclidean distance between cohorts in NMDS) in sites plotted against site area (h) and isolation (i). Fitted lines show significant relationships (solid line, $p < .05$; dashed line, $p < .1$) in univariate GLMs of distinctiveness or divergence against site area or isolation, and R^2 value is adjusted R^2

(mean = 0.30 ± 0.07). Hence, we conclude that seedling communities in the smallest, most isolated fragments are more different to one another than larger, less isolated fragments or continuous forest sites.

Increased distinctiveness of communities in small fragments means that the accumulation of genera (per individual plant sampled) is maintained, and might even be slightly increased, in small forest fragments, compared with continuous forest sites (Figure 3b,d). This indicates that higher dissimilarities among small fragments are not due simply to the systematic loss of genera.

3.2 | Role of recruitment failure

The number of plant genera occurring at each of our 19 sites that were present as both seedlings and trees increased with site area (Table 2, Figure 4a; n = 19 sites), indicating diminished recruitment in small fragments. By contrast, the number of genera presents only as trees but not as seedlings, or only as seedlings but not trees ("immigrants" at a plot scale) was not related to site area. Isolation was a poor predictor in comparison with area in all univariate models (Table 2). We conclude that reproductive failure of certain genera in

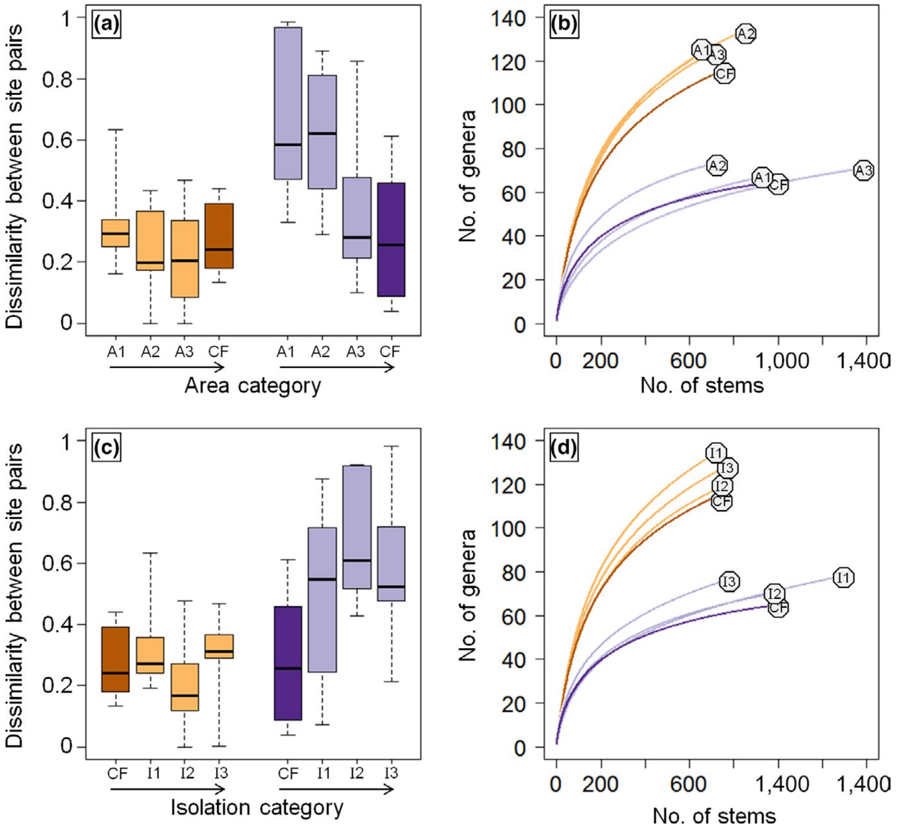

FIGURE 3 Chao-Sørensen dissimilarity of trees (brown bars) and seedlings (purple bars) between pairs of sites grouped by (a) area or (c) isolation, and observed genus richness, constructed using sample-based rarefaction curves for sites grouped by (b) area and (d) isolation. Lighter colours = fragment sites, darker colours = continuous forest sites. Site 10 was included in both intermediate groups so that each group contained five sites. A1 represents the smallest fragments, and I3 the most isolated fragments (see Table S2 for range of values of area and isolation represented by sites in each group). Boxplots show variation in dissimilarity values: boxplot horizontal lines represent medians, boxes indicate the 25th and 75th percentiles and the whiskers represent the range of values

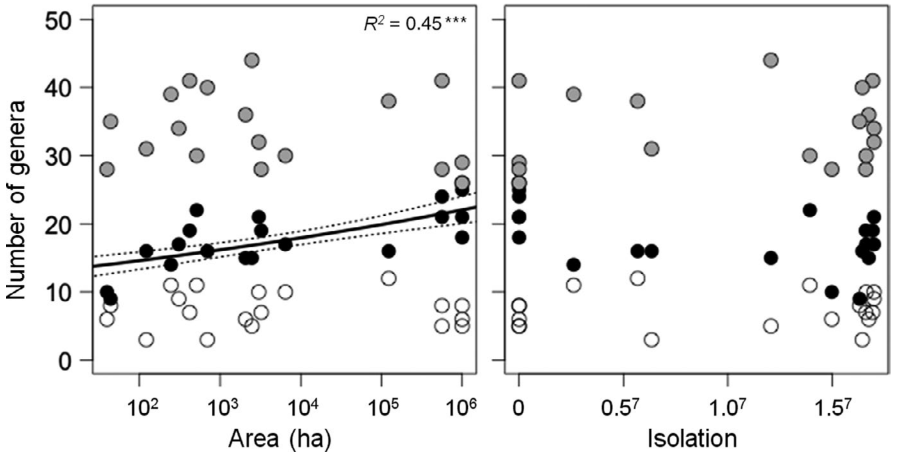

FIGURE 4 The number of genera occurring at each of the 19 sites that are present as trees and seedlings (black dots = recruitment success), trees without seedlings (grey dots = no evidence of recruitment in the study plots), and seedlings without trees (white dots = presumed immigration into the study plots), in relation to site area (left) and isolation (right). Fitted line shows significant relationship in full model of recruitment success versus area, and r^2 value is adjusted R^2

smaller forest fragments may be responsible for variation in seedling distinctiveness among sites. Results were qualitatively similar when we repeated the analyses on fragments only (Table 2), and on predominantly animal- and wind-dispersed genera separately (Figure S1). In the latter, the only difference of note was a greater number of abiotically dispersed genera present in sites as trees without seedlings, and we conclude that defaunation was not an important driver of the variation in seedling distinctiveness we observed.

4 | DISCUSSION

Our results demonstrate that tree recruitment varies considerably among fragments, with the greatest impacts observed in the smallest remaining fragments, and with a possible additional role for fragment isolation. We found that seedling communities in small forest fragments are diverging from those in continuous forest sites, from seedling communities in other forest fragments, and from tree communities in the same forest fragment. Further evidence that plant communities in small fragments are showing the greatest compositional turnover is indicated by a lower proportion of genera represented as both trees and seedlings. It is likely that small fragments will continue to have biodiversity value (through their heterogeneity across landscapes; e.g. Wintle et al., 2019), but each fragment will become decreasingly like the small part of a continuous forest that it once was. Although the identities of plant species within tropical communities vary considerably across tropical regions, the findings from our study that communities in different fragments are diverging from one another supports studies in the neotropics (Arroyo-Rodríguez et al., 2013; Ewers et al., 2017; Rocha-Santos et al., 2016), with no evidence for communities in fragments converging to the same subset of species (Laurance et al., 2007). Hence, our findings from Borneo are similar to neotropical studies even though studies are likely to differ in the relative importance of defaunation and loss of animal seed dispersers, given that Bornean forest canopies are dominated by wind-dispersed dipterocarp species (Harrison et al., 2013).

Before interpreting our results in detail, we should recognise that trees are long-lived organisms and mature individuals may persist for several centuries in forest fragments protected against logging and other human disturbance (so-called "living dead" trees by Janzen, 1986). However, disruption of physical and biological processes within fragments as a result of edge creation, reduced population sizes, and changes to the abundances and identities of pollinators, herbivores and seed dispersers, may result in reduced recruitment success or complete recruitment failure in some species, but potentially increased recruitment in others (e.g. Laurance et al., 2007). Tree longevity masks the long-term changes in plant communities within fragments, creating community composition lags that may take many decades to be fully realised (Kuussaari et al., 2009). Impacts are likely to manifest themselves much sooner in seedling communities representing the recruitment successes and failures of established trees. However, we should be cautious in our interpretation because tree and seedling community structures are not directly comparable: seedling and tree dynamics operate on different time scales (although they are obviously linked), and many biological processes and chance events determine an individual's survival between seedling and tree stage, so few seedlings ever become trees regardless of whether the site is a fragment or not (Lopez & Terborgh, 2007). Nevertheless, differences seen now in seedling communities are likely to be expressed in future tree communities, providing insight into the future composition and biodiversity value of forest fragments.

4.1 | The distinctiveness of seedling communities is increasing among small fragments

Seedling communities in small fragments are not diverging in parallel (Arroyo-Rodríguez et al., 2013; Ewers et al., 2017; Rocha-Santos et al., 2016), and differences in community composition among small fragments are even greater than those among medium or large fragments (Figure 3a, Table 1). Thus, increasingly distinctive plant communities appear to be generated in fragments, which collectively retain considerable diversity (even if each individual fragment has reduced richness: Stride et al., 2018); whereas we find no evidence that small and isolated fragments are following the same trajectory of change to become impoverished to a set of common taxa—and hence no evidence for homogenisation (Laurance et al., 2007). Far from homogenising to a common set of (potentially) disturbance-adapted genera, a different set of genera is recruiting seedlings in each fragment.

These patterns for seedlings are not seen amongst tree communities, which represent as close as we can get to the pre-isolation condition of the forest, and pairwise dissimilarity is not correlated with geographical distance (i.e. we are not observing the impacts of pre-existing environmental gradients). This suggests that the shifts in seedling composition we observe are likely to have been driven by the conditions in fragments rather than by pre-existing differences in community composition. The fact that relatively fewer tree genera are recruiting seedlings in the smallest fragments suggests that some genera are failing in some aspect of their reproduction in these sites, be that an ability to flower, fruit, produce viable seed, or for any germinating seedlings to survive (Bruna 2002; Cordeiro & Howe, 2001). The recruitment divergence we observe suggests that this is happening in different ways in different fragments.

These trajectories of change are likely to be driven by a combination of factors that alter the complex web of ecological processes that occur in forest interior environments, and which are changed in forest fragments. Physical differences in fragment size, age, amount of edge and the structure of the surrounding matrix, together influence the penetration of edge effects and the level of disturbance experienced within the fragment (Ewers & Banks-Leite, 2013; Laurance et al., 2007). Edge creation can alter forest microclimate, structure and composition, and these impacts can penetrate at least 2 km into the forest, with the most significant effects found within 100 m of the forest edge (Broadbent et al., 2008). Reduced soil moisture in fragments can reduce chances of seedling establishment and survival, and different species have different levels of drought tolerance (Delissio & Primack, 2003; O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014). Thus, a combination of demographic (e.g. increased stochasticity in small populations) and environmental effects is likely to affect the success and failure of individual species (Ovaskainen & Meerson, 2010). In addition, dispersal of both pollen and seeds will normally be limited between isolated patches of forest, and is likely to alter the reproductive success of tree populations over multiple generations (Cordeiro & Howe, 2001), although certain wind-pollinated and/or wind-dispersed species may avoid these negative consequences (Corlett, 2009). Many species, including dipterocarps, are predominantly outcrossing and retain deleterious recessive alleles in their populations; they face a heightened risk of inbreeding depression, and hence a reduced capacity to regenerate, if selfing is increased in small and isolated forest fragments (Naito et al., 2008). These factors will combine to create unique conditions in each forest fragment, impeding recruitment of those genera that are ill-adapted to the new conditions, while facilitating the success of others.

4.2 | Increasing divergence of communities within fragments

We conclude that seedling communities are diverging from tree communities in the same sites, and that seedling-tree divergence is greatest in the smallest forest fragments. This is consistent with the patterns of distinctiveness that we have just described (seedling but not tree community distinctiveness is elevated in the smallest forest fragments), but it is important to consider seedling divergence separately to distinctiveness because it confirms that the seedling community divergence we observed has arisen through changes (both failures and successes) in recruitment in different locations. The compositional change (from trees to seedlings, leading to the distinctiveness of seedling communities in different sites across landscapes) is driven partly by the recruitment failure of existing tree genera within plots (fewer genera are recruiting in small and isolated fragments) and partly by immigration, presumably mainly from adult trees located elsewhere in sites. If one just considers recruitment success (which may influence the trajectory of the future community), a greater proportion of genera of seedlings that we observed in the plots inside small fragments come from parent trees that must be growing outside the plots, whereas the reverse is true for plots in continuous forest (Figure 4a). If this relative increase in immigrant recruitment eventually translates into adult tree composition, it implies a much higher future turnover of the generic composition of trees per plot (i.e. at a scale of 0.08 ha) in small fragments than in continuous forest.

The difference between the origin of seedlings in small fragments compared with continuous forest arises because the recruitment success of standing trees was lowered in small fragments, but the immigration of new genera (not present as adult trees in the plots), remained similar across all sizes of fragments and in continuous forest (mean number of "parentless" seedling genera in five smallest forest fragments = 7.4 ± 1.4 *SE*, compared with 6.4 ± 0.7 in continuous forest sites; Figure 4a). This implies that current seed dispersal rates within fragments are not necessarily lower than in continuous forest sites. This result is somewhat surprising because defaunation is frequently reported in small fragments (Canale et al., 2012), disrupting seed dispersal and limiting movement of seeds away from parent trees (Harrison et al., 2013); thus we might expect there to be a reduced input of seedling genera into plots in smaller fragments from surrounding trees, and for the input of predominantly animal-dispersed genera to be even further reduced. Similarly, we might expect a relatively greater input of abiotically dispersed genera in smaller fragments. However, we did not find clear differences in the seedling recruitment successes and failures of animal and abiotically dispersed genera that would correspond to the defaunation of fragments (Figure S1). Hence we conclude that it is the reduced rate of recruitment of seedlings to parent trees within the plots in small fragments that is driving the observed patterns of increased divergence, not differences in immigration into the plots. Overall, our results support the hypothesis that recruitment differences are driving divergence between small fragments and continuous forest, and are responsible for the diversification of seedling communities across landscapes containing forest fragments.

4.3 | The landscape perspective

Given the divergence of seedling communities across forest fragments, our results could be a consequence of heterogeneity in altered physical, biological and human forces acting in different combinations and strengths in different locations. We conclude that surviving forest fragments still (for the time being) contain a mixture of forest trees broadly representative of pre-isolation communities, that tree recruitment is continuing within forest fragments as well as within continuous forest, and that recruitment has already generated divergence among the seedling communities in different locations; so there is potential for each forest fragment to embark on a different future successional trajectory. As such, although each individual small fragment may support an impoverished subset of species per plot (Stride et al., 2018), a diverging ensemble of forest fragments has the potential to support a considerable diversity of species. Each fragment can potentially support some species and genera that are not found in fragments elsewhere in the landscape, such that the fragments collectively support an equivalent number of genera (for a given number of stems) as would be found in continuous forest (Figure 3b,d), as proposed by the "dominance of beta diversity hypothesis" (Tscharntke et al., 2012). Hence, heterogeneous networks of small habitat fragments may have the capacity to make a major contribution to the persistence of biodiversity in otherwise intensively managed agricultural tropical landscapes (also see Arroyo-Rodríguez et al., 2013; Sfair, Arroyo-Rodríguez, Santos, & Tabarelli, 2016).

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COMPETING INTERESTS

The authors declare they have no competing interests.

DATA AVAILABILITY STATEMENT

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

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BIOSKETCH

Gail Stride conducted this work as part of her PhD at the University of York. Her research investigates the effects of forest fragmentation on tropical tree diversity, in particular the impacts on seedling recruitment and the implications for the long-term viability of forest fragments.

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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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