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ORIGINAL PAPER

Enrichment planting to improve habitat quality and conservation value of tropical rainforest fragments

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Abstract Many areas of tropical rainforest have been fragmented and the habitat quality of fragments is often poor. For example, on Borneo, many forest fragments are highly degraded by repeated logging of Dipterocarpaceae trees prior to fragmentation, and we examined the viability of enrichment planting as a potential management tool to enhance the conservation value of these forest fragments. We planted seedlings of three dipterocarp species with contrasting light demands and tolerances (*Parashorea malaanonan* (light demander), *Dryobalanops lanceolata* (intermediate), *Hopea nervosa* (shade tolerant)) in eight forest fragment sites (3–3529 ha), and compared seedling performance with four sites in continuous forest. Eighteen months after planting, survival rates of seedlings were equally high in fragment sites (mean survival = 63 %), and in continuous forest sites (mean survival = 68 %). By contrast, seedling growth and herbivory rates were considerably higher in fragments (by 60 % for growth and 45 % for herbivory) associated with higher light environments in degraded forest fragments compared with continuous forest sites. Among the three study species, *H. nervosa* seedlings had the highest survival rates overall, and *P. malaanonan* seedlings generally grew fastest and suffered highest herbivory rates. There were no interactions between species performance and the effects of fragment

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site area, forest structure or soil characteristics of sites suggesting that the three species responded similarly to fragmentation effects. High survival of planted seedlings implies that enrichment planting would be a successful forest management strategy to improve forest quality, and hence conservation value, of fragments.

Keywords Forest fragmentation · Regeneration · Danum valley · Sabah · Malaysia · Oil palm

Introduction

Previously extensive areas of rainforest now persist as isolated fragments within agricultural and urban landscapes (Hill et al. 2011; Laurance et al. 2011). Forest fragmentation alters habitat quality as a consequence of increased edge effects, changes in vegetation structure (smaller fragments are often highly degraded and disturbed) and an altered microclimate (Ferreira and Laurance 1997; Didham and Lawton 1999). For example, fragmentation increases edge effects, which alter local microclimates and increase disturbance (e.g. windthrow of trees), and these effects are greater in smaller fragments (which have greater perimeter:area relationships). Fragmentation is also associated with reduced species richness of forest communities within fragments (e.g. Benitez-Malvido and Martinez-Ramos 2003; Lucey et al. 2014), thereby disrupting ecosystem processes such as nutrient cycling, forest regeneration and carbon storage within the fragments (Laurance et al. 2011; Magnago et al. 2015; Yeong et al. 2016). Small, low quality fragments typically have higher air temperatures, reduced humidity and drier soils (Ewers and Banks-Leite 2013) due to changes in canopy cover, light environments and edge effects (Didham and Lawton 1999). In this study we use the term 'quality' to refer to forest that has a structure characteristic of primary undisturbed forest, and the biotic and abiotic changes that occur following fragmentation reduce the habitat quality of fragments and number of species they support (e.g. Tawatao et al. 2014). Thus, the conservation value of forest fragments is associated with their size, as well as their habitat quality, which is determined primarily by the structure and composition of the tree species that they contain (Harrison and Bruna 1999; Dantas de Paula et al. 2015). Dipterocarp species are especially important in this context because they are key components of the forest canopy and essential in maintaining local conditions and habitats suitable for supporting forest-dependent animal and plant species and for improving the regeneration capacity of fragmented and disturbed sites. This, improving the habitat quality of fragments may help to maintain ecosystem functioning within fragments, thereby ensuring the long-term viability of forest fragments and enhancing their conservation value.

Rainforests on Borneo are dominated by trees from the Dipterocarpaceae family of trees (Bawa 1998; Ashton 2004), which are important timber trees as well as being important components of forest community and structural composition. This region is also, especially in low-lying areas, highly vulnerable to land-use change and extensive areas of rainforest have been heavily logged and subsequently converted to oil palm *Elaeis guineensis* plantations (Koh and Wilcove 2008). Many remaining areas of forest are highly degraded and fragmented (Reynolds et al. 2011), with natural forest remnants remaining as small patches scattered across plantation landscapes (Foster et al. 2011). Forest fragments in these landscapes may be retained if they contain 'High Conservation Values' (HCVs;

Senior et al. 2014) or occur in areas that are unsuitable for agriculture, e.g. too steep or flood prone to plant with oil palms (Foster et al. 2011). These forest patches have, in most cases, been repeatedly logged prior to fragmentation and large dipterocarps are present at much lower densities than in continuous forest, or even entirely absent (Yeong et al. 2016). There is potential to improve the vegetation structure of these fragmented sites through enrichment planting of dipterocarp seedlings, especially where natural recruitment of seedlings is inhibited by a lack of dipterocarps of fruiting size. The faunal species richness of highly-disturbed forest fragments is much lower than that of less-disturbed fragments, which are more similar to continuous forest (e.g. for ants, Tawatao et al. 2014). This implies that actions to accelerate forest regeneration and improve vegetation structure through enrichment planting of dipterocarp seedlings will increase species richness. This supports other studies highlighting the importance of habitat management for improving the effectiveness of Protected Areas (e.g. for vertebrates in Africa; Costelloe et al. 2015). Enrichment planting of dipterocarp seedlings has been used to restore continuous degraded tropical forests (Lamb et al. 2005; Stanturf et al. 2014), but the potential for its use in the rehabilitation of fragmented forest sites is not known.

Enrichment planting of dipterocarps has been commonly used in the rehabilitation of selectively-logged production forests in Southeast Asia (Ådjers et al. 1995; Hector et al. 2011), but has not previously been considered in rainforest fragments. Enrichment planting involves planting nursery-raised dipterocarp seedlings in degraded forests where natural regeneration of dipterocarps is limited due to low abundance, or absence, of mature reproductive trees (Wyatt-Smith 1963; Ådjers et al. 1995). Low natural seed production in degraded sites may also increase predation pressure on those few seeds that are produced, further reducing the occurrence of natural seedlings and natural forest regeneration. Previous studies have shown high growth and survival rates of dipterocarp seedlings planted in selectively-logged forests (Ådjers et al. 1995; Bebber et al. 2002a), due to increased light in more open-canopy logged forests (Tuomela et al. 1996). However, herbivory rates would also be expected to be higher in higher light environments due to increasing photosynthetic rates that increase plant nutrient content for insects (Strauss and Agrawal 1999), and increased insect abundance (Coley and Barone 1996; Basset et al. 2001), potentially affecting seedling survival (Eichhorn et al. 2010). Moreover, soil compaction at selectively logged sites may affect seedling establishment with compacted soils disrupting root development (Nussbaum et al. 1995; Pinard et al. 2000). Dipterocarps are classified according to their light requirements for growth, which correlates well with wood density (King et al. 2006; Gustafsson et al. 2016). Species with less dense wood are generally fast growers compared with medium and high density species (King et al. 2006). Most of the *Shorea* species (*Mutica* section) and *Parashorea* species are light-demanders which have lower wood density, while *Dryobalanops* species and *Dipterocarpus* species are intermediate (medium density), and the other *Shorea* species (*Shorea* section), *Hopea* species and *Vatica* species are shade-tolerant species (high density) (Newman et al. 1996, 1998; Brown et al. 1999; Ashton 2004). By studying species along a spectrum of light requirements we were able examine whether variation in canopy openness and hence light levels affected seedling growth and hence the suitability of these species for enrichment planting in fragments.

The main aim of this study was to investigate survival, growth and herbivory rates of experimentally-planted dipterocarp seedlings in rainforest fragments. We compared species with contrasting light requirements for growth; *Parashorea malaanonan* are light demanding, while *Dryobalanops* lanceolata are intermediate species, and *Hopea* nervosa are shade-tolerant species (Newman et al. 1996, 1998), which are commonly found across

the study sites (Ashton 2004). These three species were selected for study because we would expect seedling growth and survival of these species to differ in relation to the different light environments in forest fragments (Newman et al. 1996, 1998). We compared the performance of seedlings in forest fragment sites with performance in continuous forest sites to assess the effectiveness of enrichment planting in fragments. We tested the hypothesis that survival, growth and herbivory rates of experimentally-planted dipterocarp seedlings varied in relation to fragment area and forest habitat quality (as determined from measures of forest structure and soil characteristics at study sites).

Method

Study sites

The study was carried out in the Malaysian state of Sabah (Borneo; Fig. 1; Table 1). Sabah has a climate typical of the aseasonal tropics with mean annual temperatures of 27 °C and annual rainfall of 2800 mm (Walsh and Newbery 1999). A total of 12 sites were studied comprising eight forest fragment sites (3 ha to 3529 ha) and four sites within a large tract

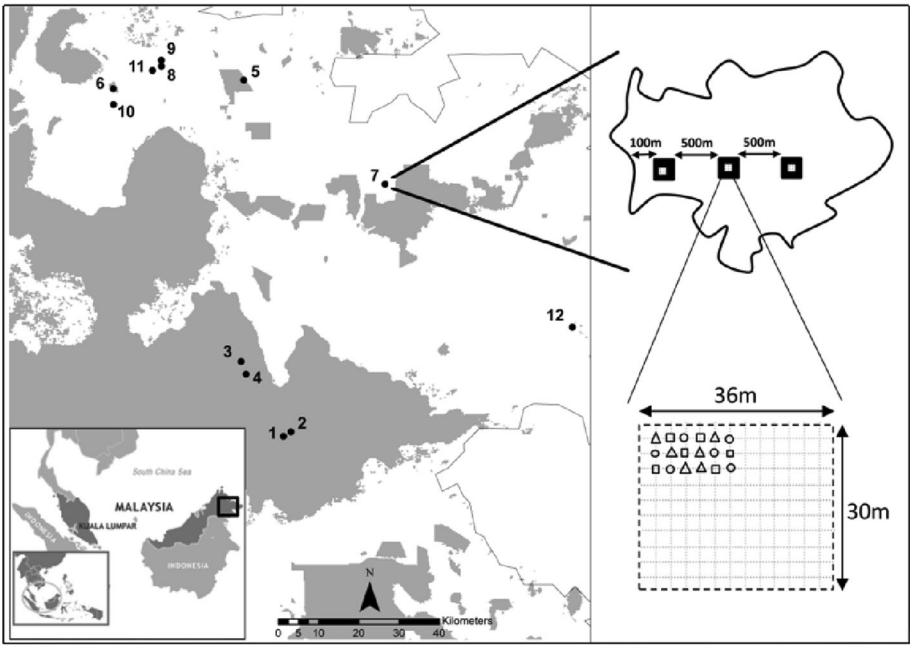


Fig. 1 Locations of study sites in Sabah, Malaysian Borneo. In the main panel, *grey shading* represents forest cover (undisturbed protected forest and selectively-logged production forest) and *black circles* show the locations of 12 study sites listed in Table 1. *White shading* represents non-forested areas, which are primarily oil palm plantations. *Right-hand panel* shows the experimental design for planting dipterocarp seedlings. One to three stations per site (depending on the area of the site) were placed 500 m apart along a transect and 100 m from forest edges. A total of 120 seedlings (40 seedlings per species) from three dipterocarp species (*P. malaanonan, D. lanceolata, H. nervosa*) were planted 3 m apart on a grid design at each station (species planted randomly; represented by *circles*, *triangles* and *squares*)

Table 1 Summary data for survival, growth and herbivory rates of planted seedlings of three dipterocarp species *(P. malaanonan; D. lanceolata; H. nervosa;* 40 seedlings planted per species per station, 1–3 stations per site depending on site area)

Site	Area (ha)	# of stations	Survival (%)		Growth (mm year^{-1})		Herbivory (%)		Forest quality				Dipterocarp tree density (ha^{-1})		Dipterocarp tree richness (ha^{-1})		PAR (μmolm^{-2}s^{-1})	
									PCF1 score		PCS1 score							
			$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1	cont.	3	73.1	5.1	0.57	0.03	25.9	12.2	1.03	0.30	1.54	0.15	33.3	6.7	23.3	6.7	6.4	0.9
2	cont.	3	67.7	9.2	0.68	0.02	25.1	9.1	0.47	0.12	0.49	0.53	56.7	12.0	36.7	3.3	8.5	1.5
3*	cont.	3	65.0	10.3	1.35	0.04	36.5	13.5	0.42	0.52	0.90	0.33	46.7	8.8	36.7	8.8	20.2	5.9
4*	cont.	3	65.4	9.0	1.01	0.15	29.9	9.8	0.56	0.36	0.44	0.16	30.0	15.3	20.0	10.0	13.0	4.2
5	3529	3	71.5	3.1	1.36	0.17	40.4	13.0	1.03	0.15	−0.27	0.28	43.3	3.3	30.0	5.8	8.3	2.0
6	500	3	66.6	9.6	0.96	0.08	49.9	13.7	0.17	0.18	0.56	0.22	60.0	5.8	16.7	6.7	24.2	5.6
7	250	3	59.6	9.3	2.32	0.41	52.4	11.6	−1.10	0.09	−0.88	0.21	6.7	3.3	6.7	3.3	31.5	14.4
8*	120	3	69.7	4.7	3.13	0.46	38.4	11.1	−1.09	0.27	−1.10	0.35	10.0	5.8	10.0	5.8	42.5	11.9
9*	85	3	69.7	6.8	2.63	0.45	65.2	6.4	−0.63	0.65	−0.51	0.37	20.0	20.0	10.0	10.0	66.5	25.1
10	45	2	72.7	6.7	0.82	0.08	42.3	12.1	0.39	0.12	0.18	0.76	40.0	0.1	35.0	5.0	14.5	3.3
11*	12	2	61.4	4.0	3.62	0.83	54.5	7.0	−0.49	0.81	−0.99	0.48	30.0	30.0	20.0	20.0	44.9	16.7
12*	3	1	31.3	5.0	2.76	0.24	75.9	12.0	−2.35	–	−1.85	–	0.0	–	0.0	–	128.8	–

Data are also presented for site area, habitat quality (PCF1 (forest structure) and PCS1 (soil characteristics)), dipterocarp tree density and richness (>30 cm DBH), photosynthetic active radiation (PAR)

* Selectively-logged sites. Data are mean values (±SEs) per station. 'cont.' refers to four continuous forest study sites in the 800,000 ha Yayasan Sabah Forest Management Area (Reynolds et al. 2011)

of continuous forest (Yayasan Sabah Forest Management Area (~800,000 ha). The continuous forest sites were in undisturbed primary forest in the Danum Valley Conservation Area (two sites), and the Malua Forest Reserve that had been selectively logged twice in the mid-1980s and 2005/6 (two sites; Reynolds et al. 2011; Hector et al. 2011). All study sites comprised lowland dipterocarp forest below 300 m elevation (Reynolds et al. 2011). Soils in the region are sandy to clay-loam soils, derived from basic and intermediate igneous rocks, mudstone and sandstone (Marsh and Greer 1992). All study fragments were surrounded by mature fruiting oil palm plantations at the time of the study and forest fragments were probably formed in the 1990s during the rapid expansion of the oil palm industry in Sabah (Reynolds et al. 2011). Study fragments were formed from heavily-degraded forest that had been repeatedly logged prior to conversion to plantations (N = 4 sites), as well as from previously undisturbed forest ('Virgin Jungle Reserves'; Tawatao et al. 2014; N = 4 sites) and thus study sites spanned a gradient of forest habitat quality typical in the region, as well as a wide range of fragment sizes (from 3 to 3,529 ha; Table 1). At each of the 12 study sites, stations were established along a line transect at 500 m intervals (1–3 stations per transect depending on site area; total of 32 stations). All stations in fragments were located at least 100 m from edges to avoid major edge effects.

Measuring survival, growth and herbivory of planted seedlings

Seedlings from three dipterocarp species (*P. malaanonan, D. lanceolata, H. nervosa*) were acquired from nurseries of the Sabah Biodiversity Experiment (SBE, Hector et al. 2011) and the Innoprise-Forest Absorbing Carbon Emissions Foundation (FACE) Rainforest Rehabilitation Project (INFAPRO) within the Ulu-Segama Forest Reserve of the Yayasan Sabah Forest Management Area (Reynolds et al. 2011). All seedlings had been germinated from seeds collected locally and were about 1 year old at the time of planting. A total of 40 seedlings per species per station were planted within a 36 m × 30 m zone located at the centre of each station (grand total of 3840 seedlings planted across the 12 study sites, 32 stations and three dipterocarp species; Online Resource 1). Seedlings were planted 3 m apart on a grid design without fertilizer or watering, using similar techniques described in Hector et al. (2011). All the seedlings were planted between October and December 2010 when rainfall was typically high for the region (>250 mm per month, Online Resource 2). Seedlings were tagged with aluminium tags stamped with a unique code. Any seedlings that died within 2 months of being planted were replaced between January and February 2011 (to avoid over-estimating mortality as a direct result of planting), which is standard practice in other enrichment planting projects (Hector et al. 2011). We measured seedling survival, growth rates (seedling height; in mm, measured from the ground to the apical meristem) and herbivory rates (area of leaf damaged). In order to be able to measure leaf area damage over time, the top four leaves of each seedling (excluding flushing leaves that were not fully expanded) were marked on the underside of the leaf near the petiole with a paint marker (1 dot for the top leaf, 2 dots for the second leaves etc., following the method of Bagchi et al. 2010). Leaf area damage of these marked leaves was estimated by eye, to the nearest 5 %.

Survival of planted seedlings was assessed 18 months after planting during August to October 2012. We recorded the number of seedlings that had survived, seedling height and leaf area damage. Relative growth rates were estimated for each seedling based on height measurements, and were calculated as: growth rate per year = $[(\ln G_2 - \ln G_1)/(t_2 - t_1)] \times 12$, where G_1 and G_2 is seedling height (in mm year^{-1}) at time t_1 (planting date)

and t_2 (re-measurement date 18 months later). We also measured seedling growth rates based on stem diameter measurements, which are reported in supplementary online resource documents (Online Resources 3–7). Herbivory was estimated as: leaf area damage (%) = LA_1–LA_2 where LA_1 and LA_2 are the % of leaf area present at the first and second measurement 18 months later, and the difference computed per seedling as the mean of four leaves. Leaf area damage was recorded as 100 % if marked leaves were missing from the stem.

Assessing forest habitat quality at study sites

In order to quantify forest habitat quality at sites, we measured 15 variables related to vegetation, soil and environmental variables at each of the 32 study stations. These measurements and analyses have been described in detail elsewhere (Yeong et al. 2016) and so we will only briefly describe them here. We carried out two principal components analyses (PCAs), and variables were incorporated either into a PCA quantifying forest structure (9 variables) or a PCA quantifying soil characteristics (6 variables; Online Resource 8). To quantify forest structure we measured: distance and girth diameter at breast height (DBH) of two saplings (5–30 cm DBH) and two large trees (>30 cm DBH) nearest to the centre of the station in each of four quadrants (positioned along the main compass bearings) up to a distance of 30 m from the centre of the station (maximum 8 trees and 8 saplings per station), ground cover (estimated by eye within 10 m radius), canopy cover (densiometer measures), and temperature (Hobo® logger placed 1.8 m from the ground on a tree stem for 10 days during April–July 2011). We also measured dipterocarp tree density and richness (>30 cm DBH), leaf litter depth (using a steel ruler), and light intensity (photosynthetic active radiation (PAR), using a Skye Light Meter for Growers Limited). To quantify soil characteristics at each station we measured the following (from 25 cores per station, cores measuring 4 cm by 10 cm); soil moisture (% gravimetric soil moisture), soil pH (pH-meter in slurry of water and soil), soil nitrogen (N), carbon (C) and C:N ratio (using dry combustion C/N analyser), and soluble phosphorus (P, using wet digestion methods with hydrogen peroxide, lithium sulphate and sulphuric acid). Thus, data on dipterocarp and non-dipterocarp tree density, dipterocarp tree species richness, non-dipterocarp sapling density, canopy and ground cover, leaf litter depth, and PAR were incorporated into a PCA quantifying forest structure (PCF scores), and data on soil moisture, soil pH, total soil nitrogen and carbon, soluble phosphorus and C:N ratio were incorporated into another PCA quantifying soil characteristics (PCS scores; Online Resource 8; Yeong et al. 2016). All variables were normalised where necessary and standardised by subtracting the mean value and dividing by twice the standard deviation prior to incorporations into the PCAs (Grueber et al. 2011). The first PCF score (PCF1) for forest structure accounted for 42 % of the variation in the vegetation dataset and increased with (in order of importance) increasing dipterocarp tree density and richness, canopy cover, leaf litter depth, and decreasing PAR (Online Resource 8). The first PCS score (PCS1) for soil characteristics accounted for 34 % of the variation in the soil dataset and increased with (in order of importance) increasing soil moisture, soluble P, total C and decreasing soil pH. PCF1 and PCS1 scores were highest in continuous undisturbed forest sites and lowest in small fragments that had been repeatedly logged (Yeong et al. 2016) and thus we used PCF1 and PCS1 scores as our measures of forest habitat quality at sites.

Statistical analysis

We carried out two types of generalized linear mixed models (GLMMs) to examine seedling performance among sites. In all analyses, the three response variables we examined were the same and were; individual seedling measures of survival (i.e. seedling dead or alive), growth (seedling height), and herbivory. The first GLMMs (3 models) quantified the effect of fragmentation per se, and we included survival, growth and herbivory of seedlings at each station as dependent variables, forest type (continuous forest or fragment) and species identity (*P. malaanonan, D. lanceolata* or *H. nervosa*) as fixed factors, and 'station nested within site' as a random factor. To examine the effects of site area and forest habitat quality on seedlings, the second GLMMs (3 models) included survival, growth and herbivory of seedlings at each station as dependent variables, with site area, habitat quality (PCF1 and PCS1 scores) and species identity (*P. malaanonan, D. lanceolata* or *H. nervosa*) as fixed factors, and 'station nested within site' included as a random factor. To allow all sites to be analysed in these second GLMMs, we assumed that the four continuous study sites were from an area of forest of 800,000 ha (the area of the Yayasan Sabah Forest Management Area). We used the 'glmer' function with a binomial error distribution for analyses of seedling survival, and the 'lmer' function with gaussian error distribution for measures of herbivory and growth using the lme4 package for R 3.2.0 (R Core Team 2013). All models were checked for homogeneity of variances and normality of residuals (Faraway 2006; Warton and Hui 2011). Transformations were performed to correct non-normal residuals and non-homogenous variances as follows: $\log_{10}$ (leaf area damaged/1-leaf area damaged) and cube root transformation (growth). To allow direct comparison of the relative importance of each predictor variable for explaining

Table 2 Summary data comparing seedling survival, growth and herbivory rates (mean values ± SEs) of three dipterocarp species in continuous forest (N = 4 sites) and forest fragment sites (N = 8 sites)

Variables	Continuous forest		Forest fragments	
	$\bar{x}$	SE	$\bar{x}$	SE
Survival (%)				
PM	52.80	3.92	50.45	5.37
DL	69.19	1.95	66.08	4.96
HN	81.36	1.49	70.63	5.66
Growth (mm year^{-1})				
PM	2.434	0.516	7.827	1.488
DL	2.522	0.501	4.958	0.865
HN	2.720	0.557	5.915	0.927
Herbivory (% damage)				
PM	51.47	4.33	72.39	4.12
DL	19.89	1.21	47.68	5.15
HN	16.65	3.05	37.19	5.72

Data combining all three species are plotted in Fig. 2

Survival, growth or herbivory rates that differed significantly between continuous sites and fragment sites (i.e. 95 % CIs exclude zero values) are in bold. These findings were similar when the outlier small study site (site 12; 3 ha) was excluded

PM Parashorea malaanonan light demander, *DL Dryobalanops lanceolata* intermediate, *HN Hopea nervosa* shade tolerant species

changes in seedling survival, growth and herbivory, predictor variables were standardised by subtracting the mean value and dividing by twice the standard deviation (Grueber et al. 2011). Best-fitting models were identified using Akaike Information Criteria (AICc; Burnham and Anderson 2002) and model-averaging procedures were used if multiple models were equally good (i.e. ΔAICc <2).

Results

Compared with continuous forest sites, forest fragments generally had lower habitat quality (i.e. lower PCF1 and PCS1scores), corresponding to ~50 % reduction in the density of large dipterocarp trees and ~13 % higher light levels (PAR; Table 1). Sites with high PCF1 and PCS1 scores were generally in undisturbed continuous forest, and were characterized by having a high density and richness of dipterocarp trees, a closed canopy, deep leaf litter layer, cooler temperatures, lower light levels, higher soil moisture, lower soil pH and a higher concentrations of soil C and soluble P (Online Resource 8).

Survival rates of planted seedlings

Survival rates of planted seedlings were generally high across all study sites (mean survival of all species at all 12 sites = 66.5 %; range = 18.0–90.5 %; Table 2). Seedling survival rates in fragments (mean = 62.8 % ± 4.8) were not significantly different from survival rates in continuous forest (mean = 67.8 % ± 1.9; E = −0.17, CIs = −0.83 to 0.49; Fig. 2), even though very low survival rates were recorded in the smallest fragment (3 ha; mean survival of all three species = 31.3 % ± 5.0; Fig. 3). Survival rates of seedlings were not affected by site area (mean effect size = −0.054, CIs = −0.043 to 0.323, although this was close to significance; Fig. 3a), forest structure (PCF1 score; mean effect size = −0.177, CIs = −0.493 to 0.140; Fig. 3b) or soil characteristics (PCS1 score; mean effect size = −0.037, CIs = −0.377 to 0.302; Figs. 3c, 4). Thus, seedling survival rates were generally high amongst all study sites and were relatively insensitive to fragmentation and habitat degradation.

Growth and herbivory rates of planted seedlings

Seedling growth and herbivory rates were higher in fragments compared with continuous forest sites (growth rate effect size = −0.15, CIs = −0.23 to −0.05; herbivory effect

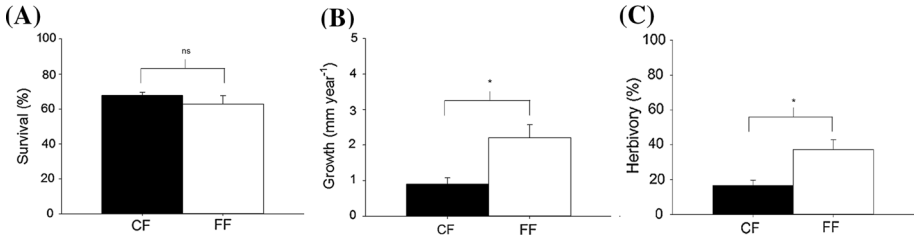


Fig. 2 Differences in seedling **a** survival, **b** growth and **c** herbivory rates between continuous forest sites (CF, N = 4 sites, *black bars*) and forest fragment sites (FF, N = 8 sites, *white bars*). Data are measurements from seedlings 18 months after planting. Mean values (±SE) are plotted (combining data for the three dipterocarp species), and *bars* with *asterisks* are significantly different at the 5 % level

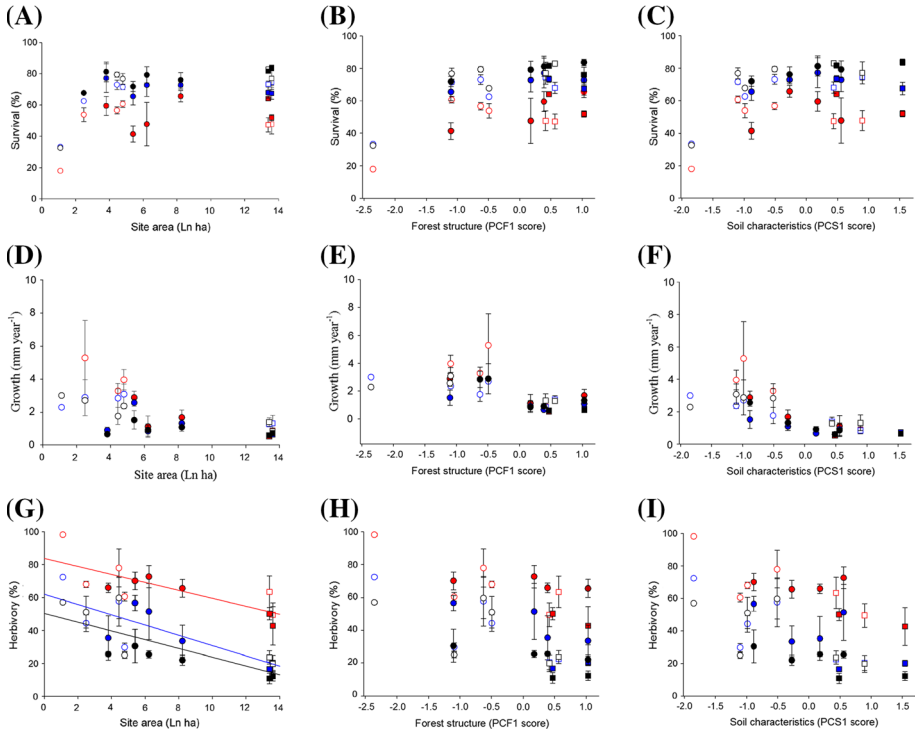
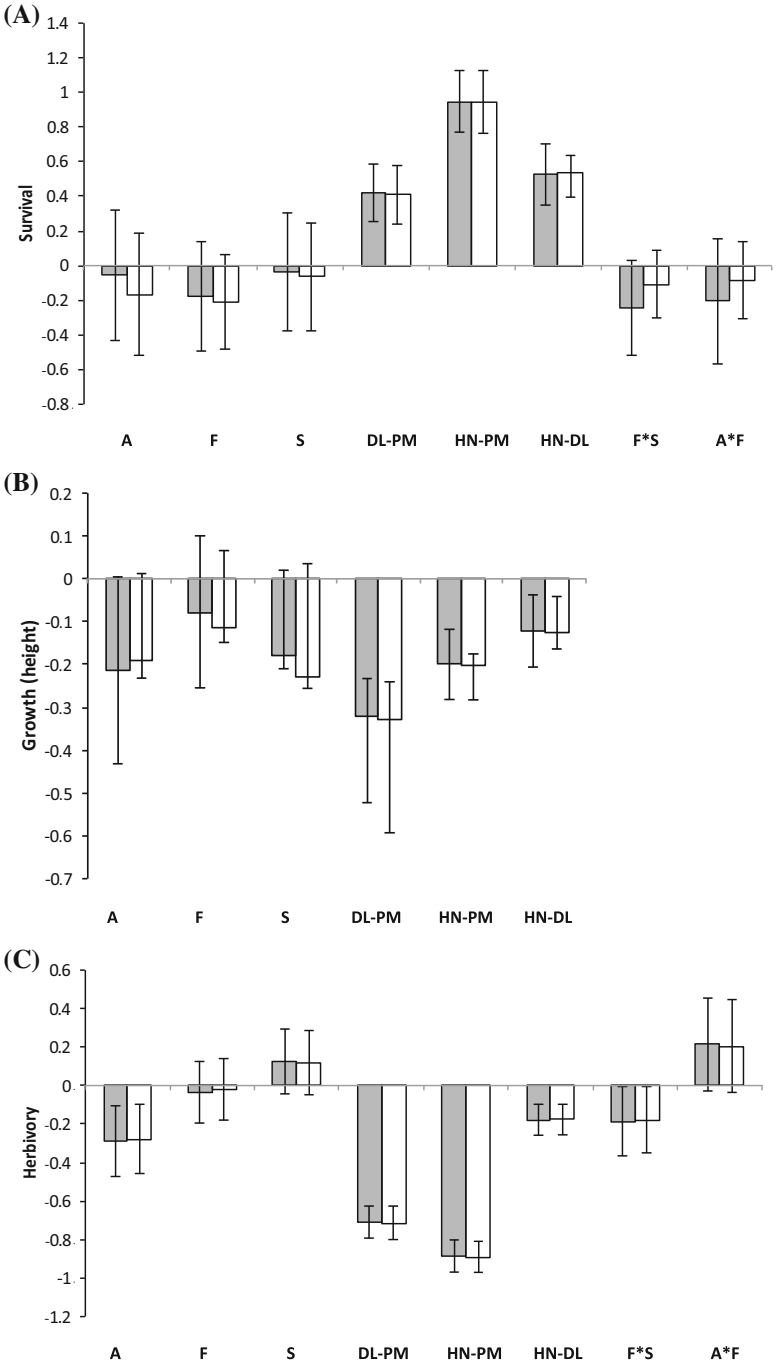


Fig. 3 Relationships between dipterocarp seedling survival **a–c**, growth **d–f** and herbivory rates **g–i** of *P. malaanonan* (*red*), *D. lanceolata* (*blue*) and *H. nervosa* (*black*) seedlings 18 months after planting in relation to study site area (ln ha), forest structure (PCF1 score) and soil characteristics (PCS1 score). Data are mean survival, growth and herbivory rates (±SEs) in forest fragments (*circles*) and 'continuous' 800,000 ha forest sites (*squares*) that were unlogged (*solid symbols*) or selectively logged (*hollow symbols*). *Solid lines* are plotted for significant relationships. (Color figure online)

size = −0.81, CIs = −1.21 to −0.41; Fig. 2). Herbivory rates were negatively related to site area (mean effect size = −0.29, CIs = −0.47 to −0.11; Fig. 3) and an interaction between forest structure and soil characteristics (mean effect size = −0.188, CIs = −0.368 to −0.009) suggested that herbivory rates were particularly high in small sites with the poorest quality forest structure and soils. However, seedling growth rates were not related to site area (mean effect size = −0.213, CIs = −0.432 to 0.005), nor to forest structure (mean effect size = −0.08, CIs = −0.255 to 0.099) or soil characteristics (mean effect size = −0.179, CIs = −0.38 to 0.02; Figs. 3, 4). These results were qualitatively similar if the smallest site (site 12; 3 ha) was excluded from analyses (Online Resource 9; Fig. 4), showing that this very small site did not have a disproportionate effect on findings. Measures of seedling growth rates according to stem diameter measures showed similar trends to fragmentation as the measures of seedling height, but effects were often not significant (Online Resources 3–7).

Differences among species

Among the three study species, *H. nervosa* (shade-tolerant) seedlings had highest survival rates (mean = 70.6 % ± 5.7), compared with *D. lanceolata* (intermediate, 66.1 % ± 5.0)


(A)
Survival
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
A
F
S
DL-PM
HN-PM
HN-DL
F*S
A*F
(B)
Growth (height)
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
A
F
S
DL-PM
HN-PM
HN-DL
(C)
Herbivory
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
A
F
S
DL-PM
HN-PM
HN-DL
F*S
A*F

◀**Fig. 4** Effect sizes of predictor variables based on model averaging of best-fitting models from GLMMs analysing the effects of study site area, forest structure and soil characteristics (N = 12 study sites) on **a** survival, **b** growth and (**c**) herbivory rates of dipterocarp seedlings 18 months after planting. *Error bars* show model-averaged 95 % confidence intervals (CIs). *A* site area, *F* forest structure (from PCF1 score), *S* soil characteristics (from PCS1 score), *asterisks* indicates an interaction effect, *HN Hopea nervosa*, *PM Parashorea malaanonan, DL Dryobalanops lanceolata. Grey bars* are analyses of all 12 study sites, *white bars* are equivalent analyses excluding the outlier smallest site 12 (3 ha)

and *P. malaanonan* (light demander, 50.5 % ± 5.4; Fig. 3). Growth and herbivory rates of *P. malaanonan* (mean growth rate = 2.13 mm year^{-1} ± 0.44, mean herbivory = 65.42 % ± 4.21) were higher than *D. lanceolata* (growth = 1.46 mm year^{-1} ± 0.24, herbivory = 38.41 % ± 5.20) and *H. nervosa* (growth = 1.71 mm year^{-1} ± 0.27, herbivory = 30.26 % ± 4.78; Fig. 3). There was no interaction between species identity and site area, forest structure or soil characteristics suggesting that all three seedling species responded to fragmentation and habitat degradation in a similar way.

Discussion

Survival and growth of dipterocarp seedlings

Survival rates of planted dipterocarp seedlings were generally high in all sites (overall mean survival = 65 %), and were not sensitive to fragmentation effects or related to forest habitat quality (as measured by forest structure and soil characteristics). Survival rates were comparable to other studies on Borneo by Ådjers et al. (1995) and Romell et al. (2008). The exception was the smallest (3 ha) site which had much lower seedling survival (31 % compared with 70 % in fully protected continuous forest sites), primarily because of a large number of trees and branches falling onto seedlings due to high wind turbulence from edge effects (YKL pers. obs.). Similar effects of physical damage from litter fall have been reported in Brazilian forest fragments (Scariot 2000; Portela and Santos 2009). Rainfall during the period of planting (October–December 2010) was typically high and so seedlings were unlikely to have experienced drought conditions during planting, which can increase mortality (Bebber et al. 2002b), and reduced soil moisture in fragments was not sufficient to affect seedling survival. Severe droughts in the study region are associated with ENSO events (Walsh and Newbery 1999), which can lead to increased dipterocarp mortality (Woods 1989) and increased insect herbivore damage (Bebber et al. 2002b; McDowell et al. 2008). The importance of avoiding enrichment planting during droughts has been recognized (Hector et al. 2011).

In our study, forest fragments had lower canopy cover than continuous forest sites due to ~50 % reduction in the density of mature dipterocarp trees (Table 1). In association with this reduction in canopy cover, the understorey in forest fragments experienced higher light environments and our ground-based measure of PAR increased by ~13 % compared with continuous forest sites (Table 1). However, these changes in the light environment were not related to seedling survival. Previous studies have also shown high survival of planted dipterocarp seedlings in highly degraded sites (Sakai et al. 2014) although other studies have shown that high light availability reduces survival of dipterocarp seedlings (Brown and Whitmore 1992; Ashton 1995). Our results also contrast with other fragmentation studies showing reduced survival of tree seedlings in forest fragments due to increased temperature and reduced humidity (Benitez-Malvido 1998). Given that our study

sites spanned a wide range of sizes and levels of habitat quality, we conclude that seedling survival was relatively robust to these habitat changes, at least up to 18 months after planting. Further surveys are required to examine if seedling survival rates remain similarly high among sites over time.

Growth and herbivory of dipterocarp seedlings

Dipterocarp seedlings grew about 60 % faster in forest fragments than in continuous forest sites and growth rates were negatively related to site area. These findings were robust to any potential biases from the outlying smallest (3 ha) site, because results were qualitatively the same if this site was removed from the analyses. Forest fragments tended to have higher photosynthetic active radiation (PAR) levels due to fewer mature trees in fragments and hence reduced canopy cover (Laurance et al. 2011), which would be expected to result in increased plant photosynthetic rates and hence faster growth (Brown and Whitmore 1992; Zipperlen and Press 1996; Philipson et al. 2014), as seen in our study. Other studies on dipterocarp species have also shown that seedling growth increased with increasing canopy openness (Tuomela et al. 1996; Philipson et al. 2014), and light demanding species often outperform shade-tolerant species in high light environments (Gustafsson et al. 2016). The availability of soil nutrients is also important for the growth of seedlings in tropical rainforests (Nussbaum et al. 1995; Palmiotto et al. 2004), but soil nutrients (particularly C and P) were higher in undisturbed continuous forest and so we conclude that light was the primary factor enhancing seedling growth rates in fragments.

Herbivory rates of seedlings were lowest in continuous forest sites (Fig. 2) and increased with decreasing site area (Fig. 4), such that herbivory rates in fragments were approximately twice that of continuous forest sites. As with our measures of seedling growth, we assume that increased herbivory rates were probably related to higher light environments in forest fragments. Higher rates of photosynthesis are expected to increase plant nutrient content and reduce defensive phenolic compounds and tannins, and hence result in more palatable plant tissues for herbivores in high light environments (Coley and Barone 1996; Eichhorn et al. 2007). In addition, higher herbivory rates could be due to increased insect abundance in higher light environments (Coley and Barone 1996; Basset et al. 2001), and/or decreased abundance of herbivore predators in fragments (e.g. Rao et al. 2001; Terborgh et al. 2001).

High growth rates of seedlings were associated with high herbivory rates (Table 1), an observation that is consistent with the compensatory continuum hypothesis and limiting resource model whereby plants increase growth to compensate for herbivory damage in resource-rich (i.e. high light) environments (Wise and Abrahamson 2005). In addition, a common response to herbivory is for plants to increase photosynthesis and growth rates (Strauss and Agrawal 1999). Thus high rates of herbivory in high light environments might be expected to result in increased plant growth rates in forest fragments. This contrasts with other studies that have found that herbivory reduced dipterocarp seedling growth, although these effects were most evident in deeply-shaded sites (Paine et al. 2012).

Fragmentation reduced the density and diversity of naturally-occurring dipterocarps, potentially altering the effects of herbivory among seedlings (Janzen-Connell effect; Bagchi et al. 2011). For example, Massey et al. (2006) found that the rate of herbivory damage was higher in single-species versus mixed stands of dipterocarp seedlings. Even though in this study, the diversity and density of planted seedlings was the same among sites, local differences in natural seedling and dipterocarp tree diversity may affect the local distribution of herbivores, contributing to differences in the herbivory rates we observed.

Species differences in survival, growth and herbivory

There were differences in growth, survival and herbivory among the three study species that were related to species-specific light requirements for growth, but all three species responded in a similar way to forest fragmentation, without any interaction effects. Thus, herbivory rates of *P. malaanonan* (light-demanding species) seedlings were highest at all sites, most likely due to higher leaf nitrogen content, lower leaf defences, reduced leaf toughness and low lignin in light-demanding species (Coley and Barone 1996; Eichhorn et al. 2007). A light-demanding species such as *P. malaanonan* would be expected to have higher growth rates, as noted in Zipperlen and Press (1996), due to higher rates of photosynthesis in light-demanding species. Our results also support findings of other studies showing high survival of shade-tolerant species (i.e. *H. nervosa*; Whitmore and Brown 1996).

Rehabilitation of degraded forest fragments

We conclude that high survival of seedlings planted in forest fragments implies that restoration of these fragments by enrichment planting to improve the conservation value of fragments would be a feasible proposition. There were some differences among the three study species in their survival rates, but rehabilitation planting to increase tree diversity (and thus the animal species dependent on high plant diversity; Novotny et al. 2002), will require a range of species to be planted. Our findings provide evidence that enrichment planting is a viable option in degraded rainforest sites, and we suggest that enrichment planting should be a feature of forest and plantation management plans if the conservation value of these areas is to be maintained. If replanting is associated with concomitant enhancement of conservation values and ecosystem services (e.g. above ground carbon stocks), this provides further support for replanting programmes to be incorporated into plantation and forest management plans (Magnago et al. 2015).

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Author contribution All authors conceived and designed the experiments and wrote the manuscript. YKL performed the experiments, carried out the fieldwork, and analyzed the data.

Compliance with ethical standards

Conflicts of interest All authors declare that they have no conflicts of interests.

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