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Research

The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning

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Relatively, little is known about the relationship between biodiversity and ecosystem functioning in forests, especially in the tropics. We describe the Sabah Biodiversity Experiment: a large-scale, long-term field study on the island of Borneo. The project aims at understanding the relationship between tree species diversity and the functioning of lowland dipterocarp rainforest during restoration following selective logging. The experiment is planned to run for several decades (from seed to adult tree), so here we focus on introducing the project and its experimental design and on assessing initial conditions and the potential for restoration of the structure and functioning of the study system, the Malua Forest Reserve. We estimate residual impacts 22 years after selective logging by comparison with an appropriate neighbouring area of primary forest in Danum Valley of similar conditions. There was no difference in the alpha or beta species diversity of transect plots in the two forest types, probably owing to the selective nature of the logging and potential effects of competitive release. However, despite equal total stem density, forest structure differed as expected with a deficit of large trees and a surfeit of saplings in selectively logged areas. These impacts on structure have the potential to influence ecosystem functioning. In particular, above-ground biomass and carbon pools in selectively logged areas were only 60 per cent of those in the primary forest even after 22 years of recovery. Our results establish the initial conditions for the Sabah Biodiversity Experiment and confirm the potential to accelerate restoration by using enrichment planting of dipterocarps to overcome recruitment limitation. What role dipterocarp diversity plays in restoration only will become clear with long-term results.

Keywords: enrichment planting; species richness; ecosystem functioning; selectively logged forest; Dipterocarpaceae; Sabah Biodiversity Experiment

1. INTRODUCTION

'We have done the easy stuff, working experimentally with herbaceous communities, and have learned a great deal about the diversity/functioning/stability relationship. However, we now must move on to address those ecosystems that control a good portion of the carbon, nutrient and water balances of the earth—the forests'.
Harold Mooney [1, p. VI]

(a) *Biodiversity and the functioning and stability of ecosystems*

As well as being renowned for their biodiversity, tropical forests also provide multiple local, regional and global ecosystem services [2]. For example, at the global scale, they contribute to climate regulation, whereas at the regional scale they provide water-storage capacity and at the local scale they can support

pest regulation, pollination, seed dispersal and soil fertility [3]. However, both the biodiversity and functioning of tropical forest ecosystems are under threat from human activities including over-harvesting of selectively logged trees and forest habitat fragmentation through conversion to agriculture and other land-use changes.

Recent research [4–6] has established that loss of biodiversity can have negative impacts on the functioning and stability of ecosystems. Indeed, Darwin laid out the rationale for a link between biodiversity and ecosystem functioning during the formative years of evolution and ecology [7,8]. Darwin's *principle of divergence* proposed that the evolution of species into different, complementary niches leads to an ecological 'division of labour', such that an ecosystem with a diverse community of species functions more effectively in terms of resource capture and cycling, and higher levels of productivity [9]. Consequently, sudden loss of biodiversity can have a negative effect on functioning by leaving niches vacant or under-used [10].

Meta-analysis has shown that, all else being equal, more diverse communities do indeed lead to more complete resource capture and retention and to higher levels of productivity [4,11–13]. Because different sets of species influence different ecosystem processes, higher levels of biodiversity are required to support full ecosystem multi-functionality than to underpin any single process [14–16]. Diversity also increases stability whenever species in a mixed community differ in their response to perturbation and when diversity increases mean levels of an ecosystem process relative to the variability in that process [17,18]. Ecosystem functioning refers to all the transfers of energy and matter owing to biogeochemical processes (or ecosystem processes) even though (for practical reasons) much research to date has focused on biomass production.

(b) Does biodiversity loss impact ecosystem functioning in tropical forests?

Relatively little is known about the relationship between biodiversity and ecosystem functioning in forests, particularly in the tropics. Indeed, one of the most significant recent conceptual advances in tropical forest ecology (and in community ecology in general), the unified neutral theory of biodiversity and biogeography [19], appears to imply no link between diversity and functioning. In neutral theory, species are identical in terms of the small number of traits that play a role in community dynamics, namely birth and death rates and immigration and speciation rates. Species are therefore identical and interchangeable and populations follow the random walk of ecological drift. Because species are identical, they co-occur entirely owing to the so-called equalizing forces that slow time to extinction while density- or frequency-dependent stabilizing forces are absent [20]. The neutral theory is supported by its unexpected early success in recreating realistic community characteristics such as relative abundance distributions. Despite this success, the plausibility of key assumptions of the neutral theory has come under increasing question [21,22]. The debate has now

moved on to the relative strength of equalizing and stabilizing in ecological communities, with tropical forests as one system suggested to have relatively strong equalizing forces (species fitnesses are similar) and weak stabilizing forces. If this were the case, then it would appear to suggest only weak effects of biodiversity loss on functioning in forest ecosystems. On the other hand, simulation studies predict impacts of species loss on carbon storage under some extinction scenarios [23].

Most of the evidence for the relationship between diversity and ecosystem functioning comes from observational surveys in temperate and boreal forests [24–26], where it is difficult to separate the effects of diversity from other confounding environmental variables. For example, these natural gradients of diversity often include one species that is present along the entire gradient, confounding species diversity with species identity [24]. Inventory data suggest a positive [27,28] or null [29] relationship between tree diversity and biomass production. Tree diversity has been found to positively affect soil cation exchange capacity [30] and nutrient turnover [31], but also decomposer fauna at the local scale [32]. Forest soil communities show contrasting behaviour in the way species richness and overall density respond to tree diversity: true bugs (Hemiptera, Heteroptera) were primarily affected by tree diversity and heterogeneity [33,34] but herbivores [35] and predatory arthropods [36] were correlated more with tree species identity than with species richness.

Some studies in tropical forests have compared the functionality of monocultures and mixtures in plantations [37,38] with results showing that mixed species stands can sometimes outperform monocultures, but that whether or not this occurs depends on having complementary mixtures of species and not just species richness '*per se*'. Some species grew better [39] and had greater canopy development [40] in mixtures, others in monocultures. Overall, a review of monoculture and polyculture plantations found that mixed species stands tend to be more productive [41]. Apart from these reviews comparing mixed- and single-species plantations, the small literature chiefly comprises work from the Neotropics by Ewel and co-worker [42,43] on predicting complementary mixtures of species and a pioneering biodiversity experiment by Potvin and co-workers [44–46].

The work by Ewel & co-worker involved only three species that were very different from one another. Their results emphasize the importance of species identity (traits) and community composition (interactions in mixture). Species mixtures were sometimes complementary but the balance with competitive interactions changed over time primarily driven by competition for light. Predicting the development of subsequent interactions from the initial combination of species' traits in a community was highlighted as the major challenge for designing utilitarian combinations of species, for use in agro-forestry for example.

In their biodiversity experiment in Panama, Potvin & co-workers planted six tree species in monocultures and mixtures, replicated over 24 plots. The first outcomes indicate a positive effect of biodiversity on productivity

owing to increased individual growth, but without any significant change in mortality rates [44,45]. Tree species richness was found to positively affect soil respiration [47], nutrient storage [48], and nitrogen and phosphorus pools [49], a result mainly explained by complementarity. Litter production and decomposition were primarily affected by species identity [50], although the lack of consideration for spatio-temporal heterogeneity might have influenced this finding.

Most recently, Ruiz-Jaen & Potvin [46] estimated above-ground carbon stocks in 124 subplots of 20×20 m of a 5 ha inventory plot in a 200 year-old tropical forest in Panama and used redundancy analysis to compare the influence of (i) tropical plant diversity (four functional groups given by the combinations of trees versus palms and understory versus canopy), (ii) the effects of five abiotic environmental parameters (topography and soil depth, bulk density, texture and colour), and (iii) spatial heterogeneity. Altogether, the three sources of variation accounted for 41 per cent of the variability in carbon storage, with plant functional group diversity accounting for the largest share of the variation at 20 per cent. The environmental variables and spatial heterogeneity, plus their two- and three-way interactions, accounted for the other half of the explained variation. These effects of biodiversity in a 200 year-old forest differ somewhat from those of the approximately 50 km apart plantation experiment described above and they also differ from the finding from the Barro Colorado Island 50 ha plot that there was no relationship between diversity and above-ground biomass [51]. The reasons for the differences in the results from these three studies all based in Panama are not clear but could include differences in the age of forests, rainfall or physical conditions.

(c) A new biodiversity experiment in the forests of Borneo

The Sabah Biodiversity Experiment (www.sabahbiodiversityexperiment.net) is part of an informal network of tree diversity experiments (www.TreeDivNet.ugent.be) including the BIOTREE (www.biotree.bgc-jena.mpg.de/deutsch/index.html) and BEF China (www.bef-china.de), where it is currently one of only two tropical studies and the sole study based in the palaeotropics [25]. The experiment differs in some important ways from any other biodiversity experiment conducted to date. Before introducing the experimental design and methodology, we highlight some of these key features. The Sabah Biodiversity Experiment is situated in mixed dipterocarp forest of South East Asia, which differs from those in Africa and Central America by being strongly dominated by a single family of trees, the Dipterocarpaceae [52]. Dipterocarp forests also often have higher canopies and higher above-ground biomass compared with the forests in other parts of the tropics [53]. The experiment is an attempt to transfer ideas and methods developed with model systems to a real-world setting. In particular, selectively logged forests in Sabah and the region are restored using enrichment planting. Enrichment planting is used for a number of reasons in different projects including timber production (e.g. the INNOPRISE corporation),

carbon storage (e.g. the INFAPRO project), and the restoration of biodiversity and the forest ecosystem structure (INIKEA). Enrichment planting in Sabah is usually performed by planting seedlings of dipterocarps (and a small number of other species) along cleared lines cut into the selectively logged forest vegetation. So, the aspect of diversity that is manipulated in the Sabah Biodiversity Experiment is that of the enrichment-planted seedlings, and these are placed into an existing matrix of vegetation left over from selective logging.

We introduce the Sabah Biodiversity Experiment in detail and present some initial results. As results will take time to emerge, we focus on documenting the initial conditions and the potential for forest restoration. While alpha and beta diversities of plant species in the selectively logged forest are not reduced, we document the expected changes in forest structure including a reduction of large trees and an increase in saplings. These changes in structure are associated with lower above-ground biomass and carbon stores.

2. METHODS
(a) Location

The Sabah Biodiversity Experiment is named after the Malaysian state that forms the northeastern tip of the island of Borneo (figure 1a). The region is relatively aseasonal with an annual rainfall of greater than 3000 mm. In 2000, a suitable experimental location was identified in the southern part of the Malua Forest Reserve (05°05'20″ N, 117°38'32″ E, 102 m a.s.l.)—a 35 000 ha area of selectively logged production forest (figure 1a inset). The Sabah Biodiversity Experiment Malua field camp is a satellite of the larger Danum Valley Field Centre that lies to the south (22.6 km air distance). The Malua Forest Reserve is part of a concession of 1 million ha that belongs to the publicly owned Yayasan Sabah (Sabah Foundation), whose purpose is to increase the welfare of the local people of Sabah by exploiting common natural resources, primarily timber [54]. Most of the area has been logged twice, once in the 1980s and once within the last 10 years, but an area of unlogged primary forest—the Danum Valley Conservation Area—was left at the heart of the concession. More specifically, the Malua Forest Reserve as a whole was selectively logged during the early 1980s and the area where the Sabah Biodiversity Experiment is now sited between 1984 and 1986. The area was re-logged in 2007 with the exception of the area used for the Sabah Biodiversity Experiment. The pre-logging timber volume was estimated as $193-221 \text{ m}^3 \text{ ha}^{-1}$ with dipterocarps comprising between 180 and $216 \text{ m}^3 \text{ ha}^{-1}$. These values are comparable with estimates of above-ground tree biomass at Danum Valley, supporting the comparability of the two sites (Yayasan Sabah, unpublished data; see §4). The soil of the area was classified as orthic acrisol, which is moderately acid (pH < 6), highly weathered and low in available nutrients, with a base saturation of 81 per cent (detailed protocols in the study of Majalap & Chu [55]). It has a marked increase of clay content with depth [56] and a low organic carbon content (topsoil: 1.2%, 1 m depth: 0.6% [57]). Bedrock consists of a mixture of mudstone and sandstone areas with other
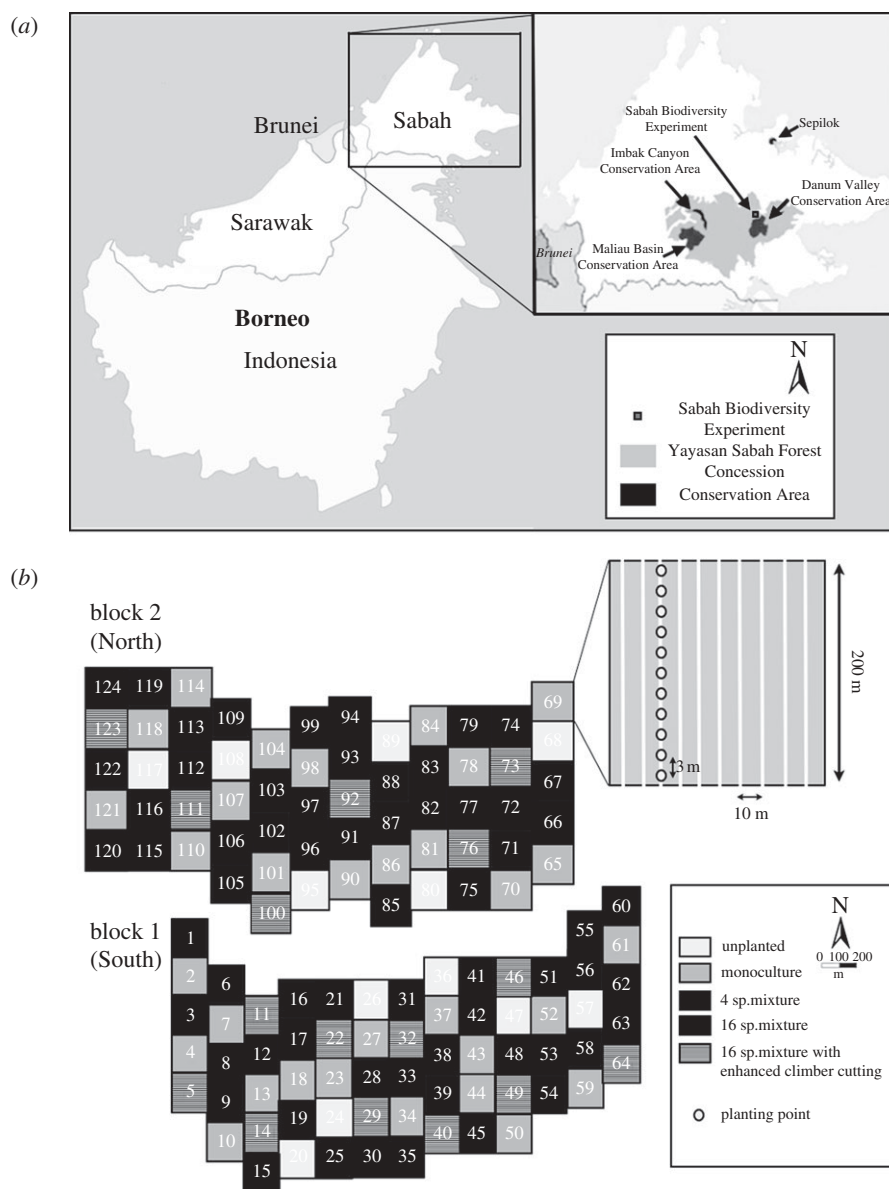
Figure 1. (a) Location of the Sabah Biodiversity Experiment within Borneo, Sabah and the local area (inset) showing some of the major areas of conserved forest. (b) Plan of the experimental site and enrichment-planting lines (inset).

miscellaneous rock types (Sabah Forestry Department 2010, unpublished data).

The most recent development relevant to the Sabah Biodiversity Experiment and the Malua Forest Reserve is the creation in 2008 of the Malua BioBank (www.maluabank.com), comprising 34 000 ha under a Conservation Management Plan that aims to 'improve wildlife habitat and promote ecosystem service functions including carbon sequestration and storage in above-ground biomass' in order to sell Biodiversity Conservation Certificates representing 100 m^2 of forest. The Sabah Biodiversity Experiment should therefore provide scientific information that could be used to guide and assess the management of the Malua BioBank.

(b) Experimental design

The Sabah Biodiversity Experiment is a field scale forest rehabilitation project and tree biodiversity experiment that covers 500 ha. Seedlings of 16 native

canopy tree species (Dipterocarpaceae; table 1) were enrichment planted along lines cut into the pre-existing selectively logged forest (figure 1b). The project comprises 124 4 ha plots (200 × 200 m) that follow a randomized block design. The core of the project is the set of 96 plots that form a gradient in the species richness of enrichment-planted dipterocarps, which includes enrichment planting with one of each of the 16 study species, 16 different four-species mixtures and all 16 species combined. Each diversity level comprises 32 plots divided equally between the two blocks so that each of the enrichment plantings using one or four species occurs once in each of the two blocks with 16 identical replicates of the full 16-species enrichment-planting mixture in each block. Responses in ecosystems properties and processes along this gradient of 96 plots enrichment planted with one, four or 16 species can be compared with those of 12 unplanted control plots (six in each block). The diversity gradient of 96 plots plus unplanted controls sum

Table 1. The 16 species of the Dipterocarpaceae family planted in the Sabah Biodiversity Experiment and their IUCN Red List status (downloaded on 20 November 2010 from www.iucnredlist.org).

genus	species	species authority	IUCN status
Shorea	*johorensis*	Foxw.	critically endangered
	gibbosa	Brandis.	critically endangered
	argentifolia	Sym.	endangered
	faguetiana	Heim.	endangered
	leprosula	Miq.	endangered
	macrophylla	Ashton	vulnerable
	macroptera	King	—
	ovalis	Korth.	—
	parvifolia	Dyer.	—
	beccariana	Bruck	not listed
Parashorea	*malaanonan*	(Blanco) Merr.	critically endangered
	tomentella	Meijer	not listed
Hopea	*sangal*	Korth.	critically endangered
	ferruginea	Parijs	critically endangered
Dryobalanops	*lanceolata*	Burck	endangered
Dipterocarpus	*conformis*	Slooten	—

to 108 plots divided equally between the two blocks. The final 16 plots form a sub-experiment to look at management treatments involving the frequency with which climbing plants (lianas) are removed during restoration. Standard enrichment-planting methods involve cutting of planting lines and of climbing species that would otherwise compete and damage the dipterocarp seedlings [58]. A recent suggestion to speed-up restoration of selectively logged dipterocarp forest is enhanced climber cutting, where the cutting occurs more widely in the intervening areas separating the planting lines that run in parallel at 10 m intervals. The final 16 plots will receive enhanced climber cutting for comparison with matched 16-species plots from the core diversity gradient. The initial plan was to have two identical blocks but for various logistical reasons (erosion of plots, neighbouring streams, etc.) the two blocks have different numbers of plots with 60 in the Northern block and 64 in the South and the replication of the enhanced climber-cutting plots is therefore unequal with six plots in the Northern block and 10 in the South.

(c) *Planting and replanting*
The seedlings required for the initial planting were collected throughout the neighbouring Ulu Segama and Malua forest reserves with the exception of *Hopea ferruginea* (INIKEA nursery at Lawasong) and *Dipterocarpus conformis* (Tawau Hill area collection). The ages of the seedlings varied but were predominantly from a single fruiting and seedlings were selected to be of as similar size as possible. The planting material was assembled at the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO) nursery in 2001, with the

first round of planting beginning in July 2002 with block one completed by December and block two completed in September 2003. Seedlings are planted on parallel lines 10 m apart with one seedling planted every 3 m (except where not possible due to rocks, streams, etc.). It is standard practice to have one round of replanting following a period to allow initial mortality to occur. Therefore, a second collection of seedlings was assembled at a purpose-built nursery in the Malua field camp from both local fruiting events and the INFAPRO nursery. Replanting began in January 2009, and the first block was completed in October 2010. Final seedling collections in December 2009 and August 2010 provided the final seedling stock for replanting of the second block, which is underway at the time of writing and planned for completion during 2011. The survival and growth of the enrichment-planting seedlings are being regularly monitored.

(d) *Diversity and composition*
Four identical transect plots of 10×250 m were established in the primary forest of Danum Valley Conservation Area and in the Sabah Biodiversity Experiment (surveying only the background vegetation between the planting lines). All trees greater than 10 cm diameter at breast height (d.b.h. at 130 cm) were identified by a local tree expert to genus level, or to species level where possible. In 1 ha, we identified 104 species in unlogged forest of Danum Valley and 107 species in selectively logged forest of the Sabah Biodiversity Experiment (electronic supplementary material, table S1). For comparison, an independent survey of the same area of selectively logged forest identified up to 180 species for a total area of 5.25 ha (Sabah Forestry Department 2010, unpublished data). Further details are available in the study of Saner [57]. Forest community composition was analysed with non-metric multidimensional scaling (NMDS) ordination to identify the effects of disturbance history on plant community assemblage. The proportion of each species in a transect plot and the Bray–Curtis dissimilarity function were used to calculate the distance matrix [59]. Alpha and beta diversities were calculated with Shannon's diversity index and Whittacker's measure of beta diversity, respectively [60]. This was implemented using the diversity function in the vegan package in R [61]. Values were calculated per transect plot within each forest type and means and standard errors were calculated from these values.

(e) *Structure and functioning*
Above-ground tree biomass was calculated for unlogged forest and for selectively logged forest based on d.b.h. measurements. Total stand basal area was calculated from d.b.h. and height and volume were predicted from d.b.h. using established allometric equations from Pinard [62]. Above-ground stem (trunk) biomass for individual trees was then calculated by multiplying volume with wood density. Total above-ground biomass was then calculated by multiplying above-ground stem biomass by the standard factor of 1.9 [63]. Carbon stocks were estimated only for the logged forest
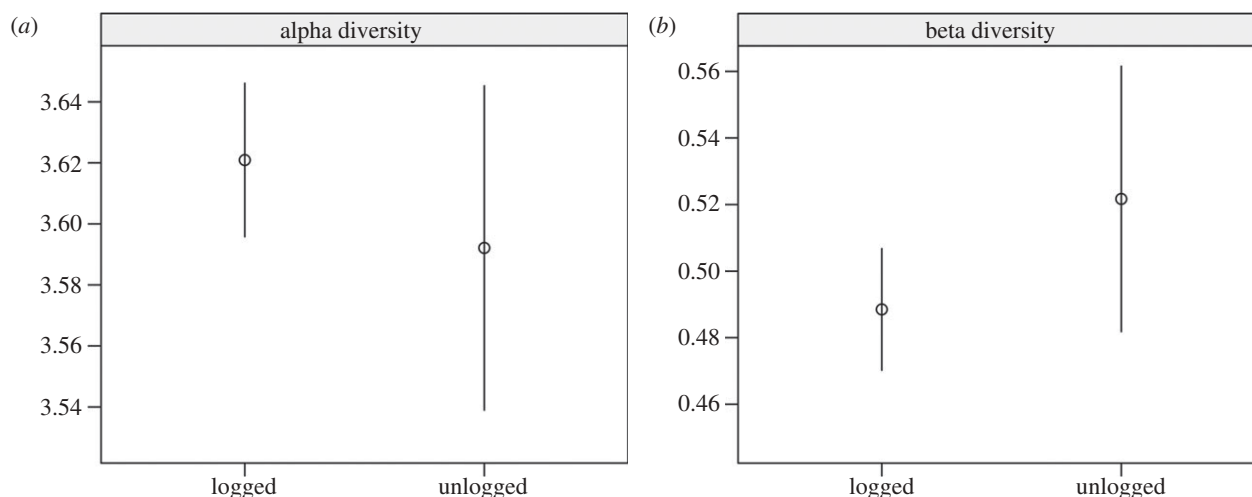
Figure 2. (*a*) Alpha and (*b*) beta diversities in selectively logged and unlogged forests (mean ± s.e.m.; *n* = 4). Shannon's diversity index estimates the number of species per transect lines within each forest type and Whittacker's beta diversity estimates the similarity/turnover in species between transect lines within each forest type.

following the standard assumption that half of above-ground biomass is carbon [63,64].

(f) Baseline carbon details

Apart from above-ground tree biomass, several other components of the baseline carbon estimation were estimated or measured along the transect plots of the selectively logged forest. Below-ground coarse roots were estimated from existing root shoot ratios (17% of above-ground tree biomass [65]). Dead standing trees were surveyed and their contribution to total carbon stocks was calculated based on d.b.h. measurements and a mean wood density of 500 kg m^{-3} [66]. Furthermore, litterfall traps (1 m^2, *n* = 40) were randomly allocated along the transect plots, and fine litterfall was collected every other week over one year (*n* = 25). At the same 40 sites, soil respiration rates were estimated using an infrared gas analyser CARBOCAP GMP343 (Vaisala, Finland) and a self-made chamber [67]. Over two months, nine measurements were performed (seven day-time (08.00–12.00) and two night-time (20.00–04.00) measurements) over 5 min intervals. Along the transect plots, quadrats (5 × 5 m, *n* = 24) were randomly selected and all saplings and seedlings were harvested. Subquadrats (0.5 × 0.5 m) were established within quadrats for collecting the standing litter, including leaf litter and woody debris. Within each subquadrat, vertical cores (100 cm^3) were taken from the top soil (0–5 cm) to determine fine root biomass (≥2 mm diameter). All collected samples were dried in a glasshouse (7 days, 60°C) prior to measurement. A carbon content of 50 per cent of total biomass was used for harvesting saplings, seedlings and fine root biomass and 42 per cent for fine litter fall, leaf litter and woody debris.

Thirteen random sites were selected across the Sabah Biodiversity Experiment for a soil organic carbon profile down to 1 m depth. Soil pits were excavated and soil cores were taken from layers of 0.1 m depth (*n* = 396). Carbon content was determined by the Walkley–Black method, a wet chemical analysis. For further details on any of these components of the baseline carbon estimation, see Saner [57].

(g) Species functional traits

Wood density was estimated with a random intercept linear mixed effects model using all the data on Dipterocarpaceae from www.worldagroforestrycentre.org and Burgess [68]. Site-specific estimates for a subset of species were also made following the water-displacement protocols of Chave *et al.* [69], which correlated strongly with the previously published data (data not shown). Seed volume was estimated using measurements from the literature (calculated as a spheroid based on mean nut length and width estimates obtained from Newman *et al.* [70,71]). Survival, a key demographic process, was estimated for each species as the proportion of the first round of enrichment-planted tree seedlings surviving after seven years. Further details can be found in the study of Dzulkifli [72].

3. RESULTS
(a) Diversity and composition
Logging had no effect on average alpha or beta diversities of transect plots within each forest type (figure 2). This was not an effect of differences in individual tree density (see below and tables 2 and 3). However, the NMDS multi-variate analysis suggests that logging had impacts on species composition, with Malua and Danum transect plots clustering on opposing sides of NMDS axis 1 (figure 3). The NMDS shows a large dissimilarity in species composition between unlogged and selectively logged forest transect plots as well as identifying only a handful (<25) of shared species.

(b) Structure
Logging had the expected impacts on forest structure, even 22 years after disturbance. The total stand basal area for unlogged forest was 29.9 ± 0.7 versus 25.0 ± 0.8 s.e.m. m^2 ha^{-1} for logged forest (tables 2 and 3). The relative contribution of dipterocarps to total basal area was approximately 60 per cent in unlogged forest when compared with about 30 per cent in logged forest. Trees greater than 90 cm d.b.h. were entirely

Table 2. Unlogged forest: overview of the nine most important tree families and the 10 most important species (>10 cm d.b.h.). BA, mean ($\pm$s.e.m.) basal area.

family	species	BA (m² ha⁻¹)	BA (%)	d.b.h. range (cm)	tree density (ha⁻¹)
Dipterocarpaceae		18.24 ($\pm$0.66)	61.0	10.1–170.3	87
	Shorea johorensis	9.09 ($\pm$0.67)	30.4	10.5–170.3	21
	Shorea parvifolia	6.22 ($\pm$0.09)	20.8	11.7–116.3	28
	Parashorea malaanonan	1.61 ($\pm$0.26)	5.4	10.6–67.2	12
	Hopea nervosa	0.99 ($\pm$0.11)	3.3	10.1–47.5	17
Meliaceae		1.91 ($\pm$0.11)	6.4	10.0–32.3	61
	Chisocheton sarawakensis	0.55 ($\pm$0.04)	1.8	10.0–30.0	17
	Aglaia elliptica	0.45 ($\pm$0.02)	1.5	10.1–31.8	15
	Aglaia macrocarpa	0.39 ($\pm$0.03)	1.3	11.4–31.0	10
Leguminosae		1.89 ($\pm$0.40)	6.3	10.0–144.8	6
	Koompassia excelsa	1.65 ($\pm$0.41)	5.6	144.8	1
Lauraceae		1.33 ($\pm$0.09)	4.4	10.0–45.6	44
Euphorbiaceae		1.13 ($\pm$0.08)	3.8	20.0–36.1	61
Myrtaceae		0.98 ($\pm$0.13)	3.3	10.7–57.1	19
	Syzygium fastigiatum	0.63 ($\pm$0.12)	2.1	14.1–57.1	5
Tiliaceae		0.76 ($\pm$0.08)	2.5	10.0–43.1	21
	Pentace laxiflora	0.65 ($\pm$0.08)	2.2	11.4–43.1	15
Fagaceae		0.62 ($\pm$0.06)	2.1	11.7–50.5	10
Burseraceae		0.38 ($\pm$0.03)	1.3	10.6–41.4	11
others		2.67 ($\pm$0.04)	8.9	10.0–52.0	99
total		29.91 ($\pm$0.66)	100	10.0–170.3	410

Table 3. Logged forest: overview of the nine most important tree families and the 10 most important species (>10 cm d.b.h.). BA, mean ($\pm$ s.e.m.) basal area.

family	species	BA (m² ha⁻¹)	BA (%)	d.b.h. range (cm)	tree density (ha⁻¹)
Dipterocarpaceae		6.88 ($\pm$0.17)	27.6	10.0–84.3	69
	Shorea johorensis	1.61 ($\pm$0.17)	6.4	13.8–84.3	7
	Shorea gibbosa	1.54 ($\pm$0.14)	6.2	10.6–72.5	13
	Dryobalanops lanceolata	0.86 ($\pm$0.08)	3.4	12.8–72.1	7
	Shorea fallax	0.67 ($\pm$0.17)	2.7	13.4–71.0	3
	Dipterocarpus caudiferus	0.59 ($\pm$0.10)	2.4	9.8–60.5	10
Euphorbiaceae		5.42 ($\pm$0.24)	21.7	10.0–64.0	107
	Macaranga pearsonii	2.75 ($\pm$0.21)	11.0	17.0–64.0	24
	Macaranga gigantea	1.29 ($\pm$0.05)	5.2	13.0–38.8	23
Rubiaceae		3.79 ($\pm$0.16)	15.2	10.0–48.0	74
	Neolamarckia cadamba	3.11 ($\pm$0.13)	12.4	10.2–48.0	33
Leguminosae		0.84 ($\pm$0.10)	3.4	10.3–72.8	14
Datiscaceae		0.79 ($\pm$0.16)	3.2	23.8–80.9	4
	Octomeles sumatrana	0.79 ($\pm$0.16)	3.2	23.8–80.9	4
Lauraceae		0.75 ($\pm$0.07)	3.0	11.1–59.8	12
Sonneratiaceae		0.71 ($\pm$0.14)	2.8	14.2–77.2	5
	Duabanga moluccana	0.71 ($\pm$0.14)	2.8	14.2–77.2	5
Sapindaceae		0.55 ($\pm$0.06)	2.2	16.5–51.2	8
Tiliaceae		0.54 ($\pm$0.07)	2.2	11.5–62.1	8
others		4.69 ($\pm$0.13)	18.8	10.0–59.1	116
total		24.96 ($\pm$0.83)	100	10.0–84.3	417

absent from the transects in the logged forest but present in matched transect plots in the primary forest of Danum Valley (figure 4a). Differences in total basal area were owing to tree size and not tree density which was similar in the two forest types: the unlogged forest had a total of 410 stems in the surveyed hectare (sum of the four transect plots) versus 417 in the hectare of logged forest. The frequency of the smallest measured trees (10–20 cm) was lower in the logged forest (figure 4a).

(c) Ecosystem functioning: carbon stocks

Because approximately 65 per cent (155 $\pm$ 10.3 s.e.m. Mg ha⁻¹) of the total carbon of tropical lowland dipterocarp forest occurs in above-ground biomass, logging can have large impacts on the carbon stocks of these ecosystems by removing the larger species with denser wood. Estimates from our data of above-ground tree biomass of the selectively logged forest were only 272.1 Mg ha⁻¹ (95% CI: 225.6–318.6) compared to 468.6 Mg ha⁻¹ (261.6–675.7) in the
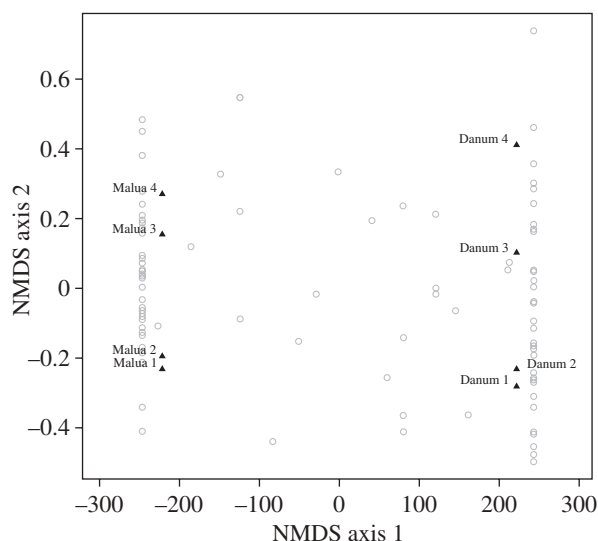
Figure 3. Differences in species composition of transects (solid triangles) and in individual species occurrence (open circles) in the Sabah Biodiversity Experiment area of the selectively logged forest of the Malua Forest Reserve (Malua 1–4) and the primary forest of Danum Valley Conservation Area (Danum 1–4) as shown by the first two axes from a multi-variate NMDS analysis.

primary forest of Danum Valley (figure 4*b*). As around 50 per cent of wood is assumed to be carbon [63], this leads to estimates of carbon stored of 136 Mg C ha^{-1} ($\pm$ 7.3 s.e.m.) in the selectively logged forest compared with 234.3 Mg C ha^{-1} ($\pm$ 32.5 s.e.m.) in the primary forest of Danum Valley (figure 5). Based on these estimates, the total area of 500 ha for the Sabah Biodiversity Experiment has an initial pre-enrichment planting total organic carbon content of 118.6 Gg C $\pm$ 4.2 (s.d.).

(d) *Species differences*

Preliminary inspection of our data on the traits of dipterocarps suggests substantial species differences. Wood density varies from 440 to 736 kg m^{-3} (figure 6*a*). For context, Borneo Ironwood or Belian (*Eusideroxylon zwageri* Teijsm. & Binnend.) has an air-dry density of 1000–1105 kg m^{-3}, while early successional *Macaranga* species have a wood density ranging from 270 to 590 kg m^{-3} (at 15% moisture content). Seed size also varied widely across three orders of magnitude from 0.028 to 28 cm^{-3}. Finally, survival of the enrichment-planted seedlings had a median value around 40 per cent but varied from approximately 10 to 60% (figure 6*c*).

4. DISCUSSION

Overall, the results of our comparison of the selectively logged lowland dipterocarp forest of the Malua Forest Reserve with the nearby primary forest of Danum Valley support the expectation that logging has chronic impacts on forest composition, structure and functioning, at least for the first 22 years since harvesting.

One exception was that the alpha and beta diversities of the transect plots in the selectively logged

forest were not reduced (figure 2) [73]. This was not a function of differences in tree stem and trunk density, which was very similar in the two forest types. Rather, this is probably partly because, by definition, selective logging removes a restricted range of species (here mainly dipterocarps) [74]. Selective logging may also have beneficial effects on the diversity of the pioneers and other non-harvested species through disturbance and release from competition with the large dipterocarp individuals that have been extracted [75]. Multi-variate analysis of the composition of the unlogged and selectively logged forest transect plots supports this explanation with apparent clustering of plots from the two forest types (figure 3), and while pioneer species were present in the selectively logged forest they were not detected in the samples from the unlogged forest.

These differences in composition had both structural and functional consequences 22 years after logging. As expected from its nature, selective logging reduced the frequency of large trees. Indeed, no trees greater than 90 cm d.b.h. were found in transect plots in the selectively logged forests, whereas trees up to twice this diameter were present in the samples from the primary forest of Danum Valley (figure 4*a*). It is important to point out that some larger trees do persist in the selectively logged forest because fewer species were selected for logging in the 1980s than in more recent times (e.g. the legume *Koompassia excelsa* (Becc.) Taub. is sometimes now logged for timber for parquet while previously the silica-rich wood was considered too brittle for any commercial use) and even individuals of desirable species sometimes occurred in inaccessible areas such as on steep slopes. However, it should be noted that the comparisons made here reflect the impact of one instance of selective logging only. Current logging methods include the use of helicopters that enable some of the remaining larger trees in inaccessible spots to be harvested. Comparison of Danum Valley with twice-logged areas of the Malua Forest Reserve would almost certainly reveal larger differences between the two areas and the estimates provided here are conservative in the sense that they consider the effects of only one round of selective logging when most areas have now undergone at least two rounds.

Through the use of bulldozers, dragging of logs on cables, establishment of log landings and so on, logging also damages and kills many seedlings [76] and exert a large impact on rooting and compaction in forest soils [76]. In addition to the reduced number of fruiting mother trees, and subsequent reduction in seedling recruitment, this probably explains the reduced levels of trees with current measurements in the smallest 10–20 cm d.b.h. size class. In contrast, measurements of d.b.h. in the range of approximately 20–80 cm were sometimes slightly above those in unlogged forest, perhaps reflecting reduced competition for seedlings that survived logging and benefited from the removal of larger individuals.

We estimate the total carbon stored in the selectively logged forest to be 237.2 Mg C ha^{-1} ($\pm$ 8.4 s.d.) with approximately two-thirds above and one-third below ground. The total can be divided into
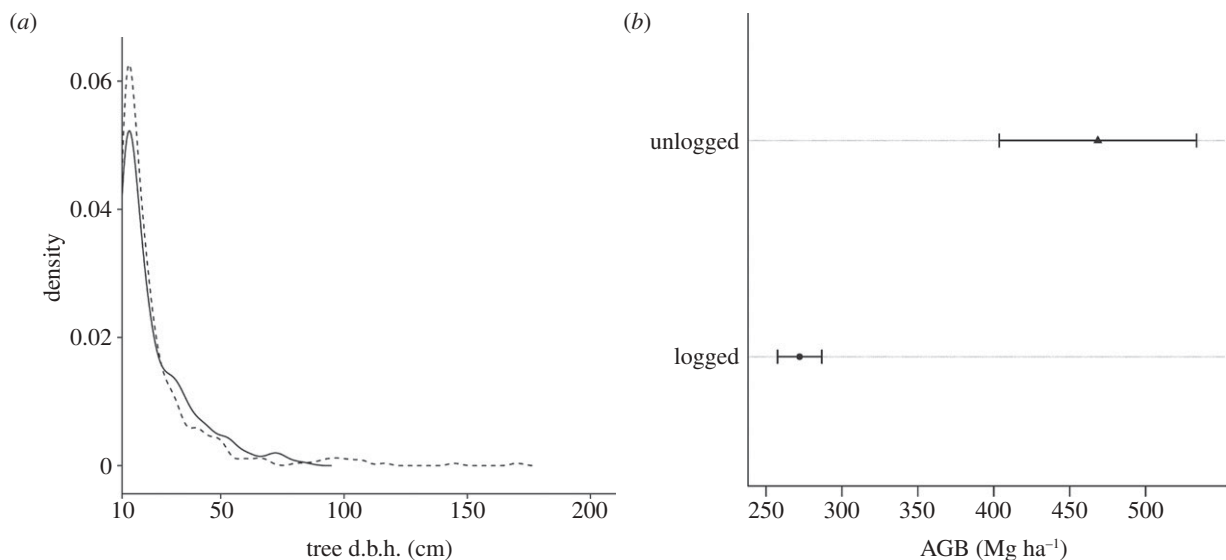
Figure 4. (*a*) Kernel density estimation (probability) of stand size distribution in logged (solid line) and unlogged (dotted line) forests. d.b.h. was measured ≥10 cm only. Note the increased density of mid-sized trees (30–80 cm) in selectively logged forest and the higher density of small (<20 cm) and large (>90 cm) trees in unlogged forests. (*b*) Estimates of total above-ground tree biomass (AGB; ±1 s.e.m.) for the background selectively logged forest of the Sabah Biodiversity Experiment (Malua Forest Reserve) and the primary unlogged forest of Danum Valley.

the following six major carbon pools by percentage (figure 5): above-ground tree (57%) and non-tree biomass (2%), below-ground roots (10%), forest floor litter (<1%), deadwood (6%) and soil (25%). Our results suggest that selective logging of dipterocarps has resulted in the above-ground biomass and carbon pools of the Malua lowland dipterocarp rainforest being depressed by approximately 40 per cent even 22 years after logging. However, indicators of nutrient and carbon turnover rates (dead standing wood, fine roots and litterfall) in the logged forest were not distinguishable from those observed in the neighbouring primary forest of the Danum Valley Conservation Area. This substantial reduction in carbon stocks 22 years after selective logging suggests that restoration and management practices that increase dipterocarp recruitment and basal area in logged dipterocarp forest do have the potential to increase carbon storage during this century by accelerating the return to pre-logging levels [58]. Based on our estimates from the Sabah Biodiversity Experiment (500 ha), enrichment planting in the Malua Forest Reserve (35 000 ha) and in the entire logged concession (1 million ha) has the potential to increase the amount of carbon stored by around 77 t C ha^{-1} in addition to having other potential associated benefits to biodiversity and other ecosystem processes and services. Although we cannot distinguish site from management effects, a survey of unlogged forest at Danum Valley and of the pre-logged forest of the Sabah Biodiversity Experiment completed in 1983 showed that estimated overall volume (unlogged: 178–230 m^3 ha^{-1}, logged: 193–221 m^3 ha^{-1}) and estimated dipterocarp volume (unlogged: 149–225 m^3 ha^{-1}, logged: 180–216 m^3 ha^{-1}) was comparable at both sites before logging in 1986 (Yayasan Sabah Forest Management Plan 1984–2032, unpublished data). We therefore assume that the effect of logging is real and approximately

as indicated. For comparison, we also report three studies that independently confirm the effect of logging on approximately 20 years old forest: the study of Berry *et al.* [77] reported a reduction of −99.0 Mg C ha^{-1} (with 95% CI of −162.5 to −35.5), Pinard & Putz [78] −186.5 Mg C ha^{-1} (with 95% CI of −261.7 to −111.3) and Tangki & Chappell [79] −334.7 Mg C ha^{-1} (with 95% CI of −512.4 to −157.0).

Although it is too early to assess the effects of dipterocarp diversity on ecosystem functioning in our experiment, the range of values for the probable functionally relevant traits (figure 6) is consistent with the type of species differences that lead to complementarity [80]. Increasing diversity may therefore be valuable in dipterocarp replanting and restoration schemes [81]. One mechanism by which diversity could enhance forest functioning is a simple spatial insurance effect [17]. Enrichment restoration has traditionally used a small number of species—typically those surviving in nurseries from the last major reproductive event (dipterocarps typically reproduce synchronously and irregularly [82])—and involved planting them in monoculture (or low-diversity combinations) in selectively logged forests. In the long term, this risks enriching forest with a small number of species, setting up a self-reinforcing cycle as these species are over-represented in the next round of reproduction and replanting. So long as no species can survive under all conditions, replanting with one species will result in recruitment failure in unfavourable areas. If density is low enough, this will result in recruitment failure by late-successional species (with higher wood density) and increase the area of forest dominated by pioneer species (with lower wood density). Planting areas with more speciose mixtures with a greater diversity of traits should reduce the risk of this type of recruitment failure
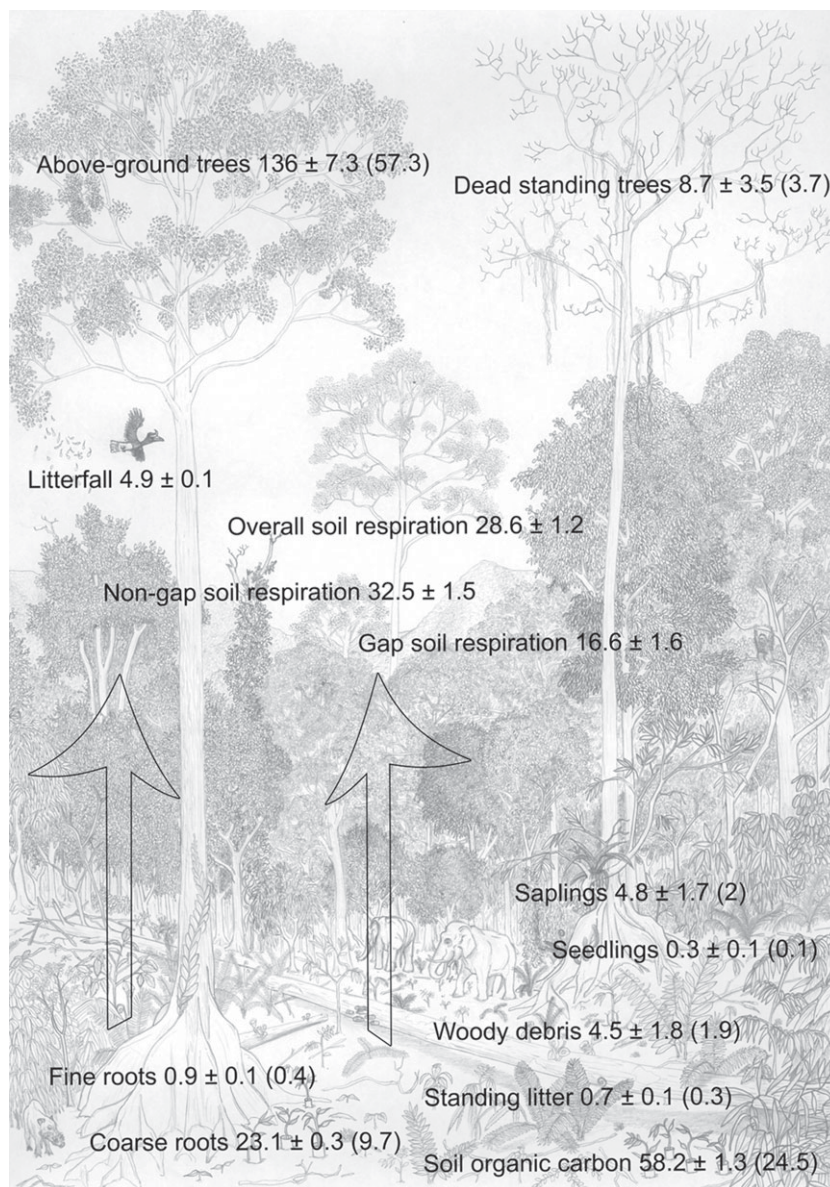
Figure 5. Overview of the baseline carbon budget for the selectively logged forest of the Sabah Biodiversity Experiment. Values are means $\pm$ s.e.m. Mg C ha^{-1} (with the per cent contribution to total organic C stocks given in parentheses). Litterfall and soil respiration rates are reported as Mg C ha^{-1} yr^{-1}.

through a spatial insurance effect. Thus, more diverse mixtures should spread risk and increase the chance of having the right species in the right place at the right time.

Selective logging directly and immediately reduces above-ground tree biomass carbon pools in our system by reducing total tree basal area [83,84]. It may have a long-term effect if its selective nature leads to a reduction in average wood density by increasing the abundance of early- relative to late-successional species as discussed above. Restoration and management practices for selectively logged forest that influence recruitment so as to increase total basal area and average wood density therefore have the potential to increase above-ground carbon storage during this century by accelerating the return to pre-logging levels. All else being equal, successful recruitment by species with higher than average wood density will result in greater carbon storage. However, all else may not be equal: enrichment-planting

schemes focusing on species with high wood density (presuming a choice including such species is available) could reduce above-ground carbon if wood density trade-offs against other species traits such as growth or recruitment rate. In the long term, enrichment planting could have other feedbacks on forest structure and function via changes in recruitment conditions (light levels, etc.). Understanding the relationship between recruitment, growth rates and relevant functional traits (wood density, etc.) [85] is therefore key to predicting and managing the long-term effects of selective logging and enrichment planting on the structure of the forest and on the services that it provides. Predicting which species provide the most complementary community of species therefore remains a key challenge [43]—especially when multiple forest ecosystem functions are considered. We hope the Sabah Biodiversity Experiment will contribute towards achieving this goal for lowland dipterocarp forests.
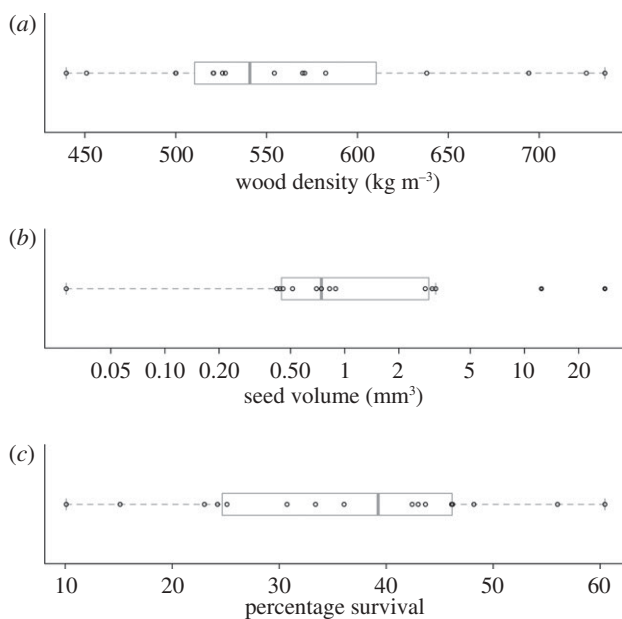
(a)

(b)

(c)

Figure 6. Variation in key functional traits ((*a*) wood density; (*b*) seed volume) and a demographic process ((*c*) percentage survival) of the dipterocarp species used for enrichment planting in the Sabah Biodiversity Experiment. Percentage survival is mean values from the first measure of first planting of the southern block.

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