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Original Article

Functional trait profiles and diversity of trees regenerating in disturbed tropical forests and agroforests in Indonesia



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ABSTRACT

A main question in restoration of degraded forests and forest landscapes recovering from logging and fire is what to expect from natural regeneration through surviving propagules in the soil or seed sources and associated dispersal agents from the surrounding landscape mosaic, as alternative to tree planting. Tree diversity in secondary forests may be high, but based on newcomer species of low wood density and long-distance, abiotic dispersal modes. We compiled and analyzed three pairs of case studies (totaling 815 plots and 11.8 ha) of secondary forests recovering from logging, fire and conversion to agroforest in Sumatra and Kalimantan (Indonesia) on mineral soils. Data on tree species diversity, wood density frequency distribution (indicative of successional status) and dispersal modes were compared with those of less disturbed comparator forests in the same landscapes. Relatively undisturbed lowland dipterocarp forest in Kalimantan had close to 200 species of trees (>10 cm diameter) at a 1-ha sample scale (and 450 at a 10-ha scale). After repeated fires a sample area of 2 ha was needed to reach the same species richness. Regulation-based logging had little impact on tree species richness. In rubber agroforest with low-intensity management beyond rubber planting, 50 tree species were found at a 1-ha scale and close to 100 species in 3 ha. The Kalimantan forest after repeated fires had a markedly higher fraction of low-wood-density trees (40%), but otherwise, all forests sampled were similar in overall wood density profiles. Selectively logged forest managed by a local community (village forest) and rubber agroforest in Sumatra contained larger fractions of heavy-wood-density trees. The majority of trees (50%–70%) had birds, bats and primates as dispersal agents in all sites. Selectively logged forests had higher fractions of autochorous species (15%) compared to other sites. Anemochorous (wind-dispersed) species, especially *Macaranga lowii*, were most common (20%) in lowland dipterocarp forest. Comparison between secondary forests and agroforests showed the influence of farmer selection regarding what is allowed to grow beyond the pole stage. Wood density and seed dispersal profiles can be used as degradation indicators of species assemblages across various disturbance levels and types, as they reflect the habitat quality of the surrounding landscape mosaics.

1. Background

Restoration, starting a new phase in a local forest transition curve (Dewi et al., 2017), can be the result of natural regeneration after fires, logging or after land abandonment when a human population urbanizes (Wang et al., 2011). It can also be actively pursued, with a specific restoration goal guiding the interventions (Stanturf et al., 2014), choosing between assisted natural regeneration (Shono et al., 2007) and tree planting (Elliott et al., 2013). Either way, landscape restoration consists of halting ongoing and reversing past degradation, aiming for increased functionality, not necessarily recovering past system states (Potts et al., 2016; Scholes et al., 2018; van Noordwijk et al., 2020a, b).

Abbreviations: DBH, Diameter (of tree stems) at Breast Height; MoEF, Ministry of Environment and Forestry in Indonesia.

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At landscape scale, desired functionality may consist of combinations of hillslope and watershed protection (Creed and van Noordwijk, 2018), local income and livelihoods (Orsi et al., 2011; van Noordwijk et al., 2014), biodiversity conservation (Chazdon, 2014), or recovery of timber stock for future logging (Lamb, 1998), with terrestrial carbon storage as a side effect (Cavanaugh et al., 2014; van Noordwijk et al., 2020a). Desired functional traits at species level depend on desired (agro)ecosystem functionality at community scale. For example, landscape-level hydrological functions will depend on the Leaf Area Index (and its phenology), the root system properties and the litter layer generated (Creed and van Noordwijk, 2018). Productivity may depend on growth rate, timber quality, fruit, resin, honey, or other non-timber forest products value generated. From a biodiversity perspective, invasiveness of the early-successional species commonly promoted indicates a threat of restoration to native flora and fauna (Kindt et al., 2021).

The tree species that regenerate depend on the availability of viable seedbanks and resprouting roots or stems remaining in the soil, or on the influx of seeds from a surrounding landscape mosaic (Chokkalingam et al., 2001). The type and spatial scale of preceding degradation may define the transport distances to be bridged in natural regeneration. Tree reproduction depends on flowering, pollination, seed dispersal, avoidance of seed predation, germination, seedling growth to reach sapling, pole and finally, reproductive tree stage. Whereas concerns in agricultural landscapes are mostly about impacts of agrochemicals on pollinators (Potts et al., 2016), concerns for forests in the literature relate to both the loss of pollinators and biological dispersal agents. A meta-analysis of 145 forest studies by Neuschulz et al. (2016) found that negative effects of forest disturbance on two early steps of plant regeneration (pollination and seed dispersal) were more than twice as strong as the effects on seed predation, recruitment and herbivory. The estimated effects for pollination were larger than (but not statistically distinguishable from) those on seed dispersal. According to the meta-analysis, large-seeded plants, typical for late-successional forest habitat, are more affected by disturbance than small-seeded plant species, according to this meta-analysis.

Variously described as the 'empty' forest (Redford, 1992; Sreekar et al., 2015) or the 'silent' forest (Rogers, 2011), impacts of hunting on tropical mammal and bird populations have been documented across the tropics (Benítez-López et al., 2017). Overhunting of harvest-sensitive frugivore bird species has been shown to threaten the diversity of tree regeneration in forests across the Brazilian Amazon (Peres et al., 2016). In their account of defaunation for a tropical tree community Harrison et al. (2013), saw strong evidence that over-hunting has engendered pervasive changes in tree population spatial structure and dynamics, leading to a consistent decline in local tree diversity over time. Ghazoul and Chazdon (2017) defined a critical threshold in forest degradation as the "state where the capacity for regeneration is greatly reduced or lost, recovery is arrested, core interactions and feedbacks are broken, and human intervention is required to initiate a trajectory of recovery". Loss of dispersal agents is such a critical point, where even if some mother seed trees remain in the landscape, natural regeneration will be greatly reduced in its tree diversity. As results for tropical forest regeneration depend on context (Elliott et al., 2013), we focus here on experience in one of the worlds' biodiversity hotspots, Indonesia, with forests threatened by logging and fire as major disturbances. Blackham et al. (2014) described the dramatic effect of widespread fire in Central Kalimantan on both existing peat swamp forests and their regeneration stages. Regrowth was dominated by a few abundant wind-dispersed tree species and tree species dispersed by small-to medium-sized birds. Relative to that situation, the mandated (but not commonly implemented) management of logging concessions was supposed to maintain both tree reproduction (by protecting 'mother trees' as seed source) and dispersal agents (by control of hunting).

Regeneration in secondary forests depends on the drivers of preceding degradation, the scale at which restoration is applied, the availability of pollinators, seed sources, and seed dispersal agents (Sayer et al., 2004; Neuschulz et al., 2016). Beyond the seedling stage, the types of management can influence the emerging vegetation (saplings, poles, trees) and its species composition. Post-logging or post-fire recovery, community forest management regimes, and conversion to agroforest can all, at least in part, rely on natural regeneration. However, it may differ in seed sources, dispersal agents, and opportunities for tree establishment, including fire frequency. As some ecosystems recover rapidly without human intervention land managers should first consider what the likely outcome of a passive restoration (natural regeneration) approach would be based on the natural ecosystem resilience, past land-use history, and the surrounding landscape matrix (Holl and Aide, 2011).

Logging activities in Indonesia were handled by large companies with timber concession permits since the 1970s. While regulations prescribed selective logging and retention of mother seed trees for a 30-year logging cycle (e.g. restricting logging to trees above 50 or 60 cm stem diameter), logging intensities in practice exceeded the recovery potential of large forest areas. A change in regulations in 1998, allowed communities to be involved in forest extraction and in issuing permits for small-scale companies, with less control over forest management practices (Obidzinski and Kusters, 2015). An increase in forest fire frequency in selectively logged areas caused further forest cover loss, especially in years of long dry season (Adrianto et al., 2019). The recovery time of forests after selective logging indicated by aboveground carbon stock recovery is at least 26 years, but it can be longer depending on the intensity of logging intervention (Butarbutar et al., 2016). Twenty-eight years after repeated fire events, aboveground carbon stock in Samboja Research Forest, East Kalimantan reached 60% of its value before the fire (Rahayu et al., 2016). Sixteen years after large forest fires mosaic forest stands were dominated by pioneer species of light wood density species (Slik et al., 2002; Toma et al., 2016). While logging initially will reduce carbon stock more than biodiversity if done according to regulations, and maintaining seed sources (Meijaard et al., 2005; Clark and Covey, 2012; Sari et al., 2020), it may lead to a shift to a more 'pioneer' type forest, with wind-dispersed, lower-wood-density, fast-growing species more prominent than before logging occurred. Wood density across all known tree species is negatively correlated with growth rate, but also with mortality rate; it relates to mechanical properties of hydraulic conductance in the stem (Chave et al., 2009). Fire events may be survived by some of the largest, high wood density tree species, and can be based on both on-site propagules (including resprouting stumps) and a new seed influx from the surrounding forest (van Nieuwstadt and Sheil, 2004). Forest rehabilitation efforts were initiated in Indonesia since the 1950s, but they have not - proportional to the efforts - resulted in positive impacts on forest recovery (Nawir et al., 2007). Lower-intensity management relying on natural regeneration can potentially be an effective tool for large-scale forest and landscape restoration (Chazdon and Guariguata, 2016), but its success may depend on a 'seed rain' from surrounding landscape mosaics.

Agroforest management implies the selective retention of desirable trees by farmers and protection of saplings or poles that are considered to have utility values. This management style has been effective in the past when the surrounding forest matrix was still diverse (van Noordwijk et al., 2012). Its potential in more severely degraded landscapes with large scale tree plantations and tree crop monocultures is less clear (Scales and Marsden, 2008). In community-based forest management and agroforests, selective retention of trees resulting from natural regeneration plays a large role (Ordonez et al., 2014). Human seed dispersal (e.g. by eating local fruits in temporary dwellings in swiddens) likely contributed to the increased frequency of fruit trees, noted for both Peruvian Amazon and Borneo (Pinedo-Vasquez and Padoch, 1996) as well as documented for Sumatra (Tata et al., 2008a) and Sulawesi (Kessler et al., 2005). Primates are among the most important seed dispersers in their habitats (McConkey, 2018) and human impact on forests has started in this tradition, suggesting that there is no sharp delineation of the concept of 'natural regeneration' and its role in 'managed' landscape restoration. Its role in avoiding diversity loss at a landscape scale is, however, contested. Agroforestry systems operate in at least three orders

of magnitude of tree diversity (1–10, 10–100, 100–1000 tree species in the pool from which plot-level tree stands in agroforests or simpler agroforestry systems are recruited), with Indonesian agroforest in the highest category (van Noordwijk et al., 2019).

The objectives of this study were: (1) to compare tree diversity profiles in secondary forest ecosystems in Sumatra and Kalimantan after disturbance by logging, fire, and conversion to agroforest management (null-hypothesis: tree diversity profiles are independent of degradation-restoration history), (2) to quantify wood density profiles and dispersal modes as tree functional traits of naturally regenerated tree populations (null-hypothesis: frequencies of wood density and dispersal mode classes are independent of degradation-restoration history), and (3) to interpret the site and landscape-level data in terms of transport distances for tree dispersal and enabling conditions for regenerating tree diversity in managed restoration processes (hypothesis: site-specific diagnostic analysis can guide restoration planning).

2. Material and methods

2.1. Indonesian tree flora

One of the main challenges to biodiversity research is diversity itself. Even in extensive surveys a large fraction of species may only be encountered once or twice. Thus, it is hard to decide whether observations are signs of viable populations, occasional 'migrants' trying to settle with little chance of survival, or transient species that may disappear during the process of succession. Even for large-sized organisms like tropical trees, this may be the case. The gamma-diversity of the biogeographic species pool is huge in Southeast Asia. The global number of tree species currently known to science is 60,065 according to the Global Tree Search (Beech et al., 2017). This represents 20% of all angiosperm and gymnosperm plant species. For Indonesia, the database lists a total of 5,668 tree species, classified in 820 genera and 137 plant families. There are 338 monospecific tree genera (41%), and 25 monospecific tree families (18%). The species-richest tree families are Rubiaceae, Myrtaceae, Euphorbiaceae, Lauraceae, Dipterocarpaceae, Phyllanthaceae, Moraceae, Fabaceae (all with at least 200 species per family); the species-richest tree genera are *Syzygium*, *Ficus*, *Elaeocarpus*, *Shorea*, and *Diospyros* (all with at least 100 tree species per genus). *Shorea*, with wind-dispersed seeds, is the only non-animal dispersed genus in this list. The Sundaland floristic region, with Borneo and Sumatra (Laumonier et al., 2010) as main islands, holds about 28,000 different species of plants, of which about 15,000 species are endemic to this region. Borneo has higher endemicity than Sumatra, but similar levels of tree diversity in standard forest plots according to existing comparisons (MacKinnon et al., 1996).

Among the best-studied and most relevant functional aspects of tree diversity are wood density and fruit dispersal modes. While further strength and durability traits are relevant for wood technology, the simplest indicator is wood density (the air-dry weight per unit volume). Our current database (http://db.worldagroforestry.org/wd) contains data for 2,478 tree species in Indonesia (Fig. 1; Hairiah et al., 2011) with a mean density of 0.424 g·cm^{-3} for the lightest 20% of species, 0.673 g·cm^{-3} for the middle 60%, and 0.949 g·cm^{-3} for the top 20%. Where log transport is mostly by rivers, the latter group ('sinkers') require special attention, while the others ('floaters') are easy to handle. Commercial preference for species has shifted over time and lower wood density species have become more attractive with increased industrial processing for durable products, and extraction of fiber for pulp and paper factories.

2.2. Landscapes

Each of the datasets we compiled from three landscapes in Kalimantan and Sumatra (Fig. 2) covered a disturbed forest that is 10–30 years into a natural regeneration process and the least disturbed forest condition for which data are available (Table 1).

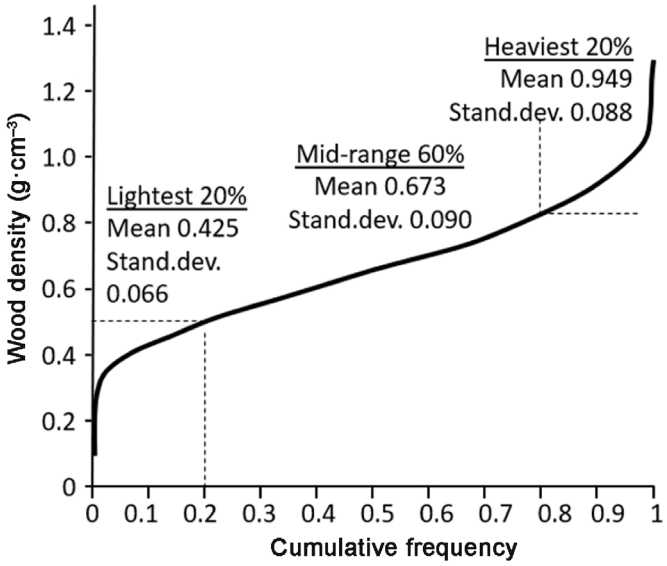


Fig. 1. Frequency distribution of the 2478 Indonesian tree species in the wood density database (van Noordwijk et al., 2019).

The first two landscapes are both located in the lowland dipterocarp forest domain in East Kalimantan, A1) Relatively undisturbed forest in the Samboja Research Forest and A2) the same plots 28 years later after repeated fire events; B1) Relatively undisturbed forest in Berau, B2) 15 year of natural regeneration after logging activities. The third landscape is in the lowland dipterocarp forest of Bungo regency in Jambi Province on Sumatra, C1) a village forest with a history of community-based forest management but still having old-growth forest elements, C2) rubber agroforest.

2.3. Plot-level data

An inventory of trees above 10 cm DBH (diameter at breast height, i.e. 1.3 m above the ground) was conducted in all plots; it was done by co-authors of this study, except for A1, B1 and B2 where we used existing data sources. Herbarium specimens were collected during the inventory to confirm species identification in the Herbarium Bogoriense, Cibinong, Bogor, Indonesia. The wood density of each tree was extracted from the wood density database developed by World Agroforestry that is available at http://db.worldagroforestry.org/wd. We classified wood density data in five classes (Indonesian Wood Construction Regulation, 1984): (1) very light: <0.3 g·cm^{-3}, (2) light: 0.3–0.4 g·cm^{-3}, (3) medium: 0.4–0.6 g·cm^{-3}, (4) heavy: 0.6–0.9 g·cm^{-3}, and (5) very heavy: >0.9 g·cm^{-3}. Con-generic data were used as estimates to fill gaps in the wood density database. Frequency distributions were weighted by the basal area encountered for each species.

Information on dispersal modes of each species was extracted from various resources (including flora descriptions of fruits) and categorized by five modes: (1) endo-zoochory, mostly by birds, bats, and primates, (2) epi-zoochory, mostly by ground mammals, (3) anemochory (wind dispersal), (4) autochory by mechanical self-dispersed seeds and gravity-dispersed seeds (barochory), (5) hydrochory by water (van Noordwijk et al., 2019).

2.4. Spatial analysis

The various types of disturbance differ in their spatial scale and hence in the travel distances involved for propagules from the nearest intact forest to reach the regenerating stand. Based on the coordinates of the various sample plots we searched land cover maps derived from remote

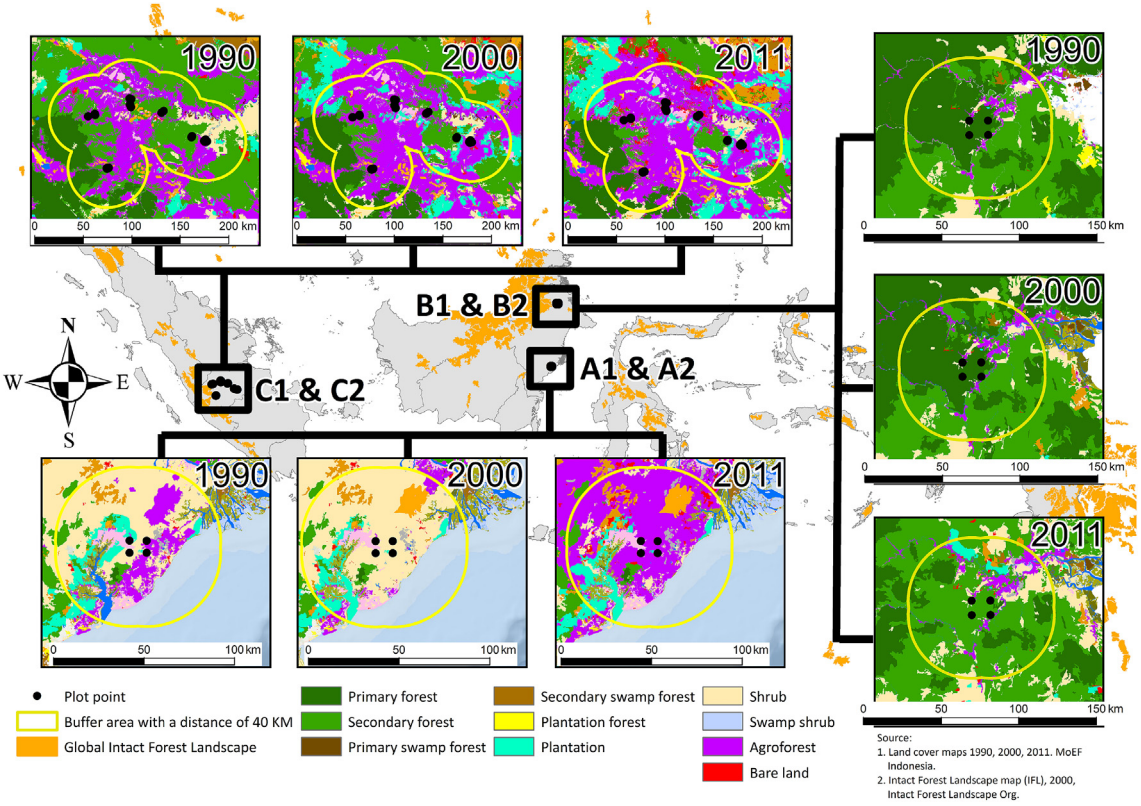


Fig. 2. Map of locations (inner rectangles), with inserts of interpreted satellite imagery of the surrounding (using a 40-km buffer) vegetation in the initial years of recovery; in relatively undisturbed forest (**A1**, **B1**), naturally regeneration after disturbances (**A2**, **B2**, **C1**) and rubber agroforests (**C2**).

Table 1
Forest plot inventory data used in the analysis.

Code	Forest condition	Location	Sampled area (ha)	Number of plots	Plot size (m)	Year of observation	Source
A1	Relatively undisturbed lowland mixed dipterocarp forest	Samboja Research Forest, East Kalimantan	1.8	180	10 × 10	1981	Kartawinata et al. (2008)
A2	Natural regeneration lowland dipterocarp forest in 28 years after impacts of repeated fires	Samboja Research Forest, East Kalimantan	1.8	180	10 × 10	2011	Rahayu et al. (2017)
B1	Relatively undisturbed lowland mixed dipterocarp forest	Berau, East Kalimantan	1	100	10 × 10	2004	Rahayu et al. (2016)
B2	Natural regeneration forest 15 years after logging	Berau, East Kalimantan	1	100	10 × 10	2004	Rahayu et al. (2016)
C1	Natural regeneration and residual trees after logging of a village forest managed by the local community	Jambi, Sumatra	1.8	45	20 × 20	2012	ICRAF Database, surveys by co-authors
C2	Rubber agroforest with low intensive management, selective weeding	Jambi, Sumatra	4.4	110	20 × 20	1998–2012	ICRAF database, surveys by co-authors

sensing imagery for the period shortly after the main documented disturbance (Fig. 2). Two sources of maps were used: (i) land cover maps produced by the Ministry of Environment and Forestry (MoEF) which are in the public domain; (ii) forest landscape global data of scale 1:1,000,000, downloaded from http://www.intactforests.org/. For each dataset, we created a spatial sampling window ('buffer') of 40 km surrounding each plot. Within that window we calculated the Euclidean distance from each plot to the nearest patch of 'any forest', 'primary forest' or 'intent forest landscape'. From the MoEF land cover map, we delineated 'primary forest' patches by delineating contiguous pixels identified as a primary forest with minimum areas of 20 ha. Other forests were included in the 'any forest' category. The global Intact Forest Landscape analyses were based on the following criteria: (1) minimum area of 50,000 ha; (2) minimum patch width of 10 km; and (3) minimum corridor/appendage width of 2 km (Potapov et al., 2008). The criteria were developed to ensure that Intact Forest Landscape core areas are large enough to provide refuge for wide-ranging animal species.

2.5. Data processing

Wood density and dispersal mode data were analyzed at the community level and compared between the data sets. A bootstrapping procedure (rarefaction) was used for assessing species accumulation curves with random starting positions for the resampling. This procedure, in contrast with fully random resampling of plots, maintains the spatial sequence of plots surveyed as this may contain relevant indicators of spatial heterogeneity within the plots. One hundred replication were used to obtain a standard deviation on each expected species number per sample intensity. The BiodiversityR package in R (Kindt and Coe, 2005) was used to generate species accumulation curves with the 'unconditioned' method (Colwell et al., 2012) whereby the standard deviation is estimated based on the diversity across plots with similar conditions (as part of gamma diversity). Two versions were derived from the primary calculations that use plots as unit, one with sampled area (as plot sizes differed between the surveys) and one with numbers of trees encountered

as the independent variable, as the two will differ when tree density is variable, and both provide relevant perspectives.

Two diversity indices were calculated: the Shannon-Wiener index ($H' = -\sum_{i=1}^{R}(\frac{n_i}{N})\ln(\frac{n_i}{N})$) and the Simpson index ($1 - D = 1 - \sum_{i=1}^{R}(\frac{n_i}{N})^2$), with n_i number of individuals per species i (out of the total, R) and N the grand total of individuals. The Simpson index indicates the probability that two randomly selected trees within a data set belong to the same species.

Correspondence Analysis routines in the SPSS software were used to explore patterns of similarity in the multidimensional space formed by forest ecosystems and functional traits of regenerated species (wood density and dispersal modes).

3. Results

3.1. Species richness

As expected, the highest tree species richness (Fig. 3) was found in the relatively undisturbed lowland dipterocarp forest on mineral soils in the comparison (A1, Samboja Research Forest). A total of 273 tree species was found in a 1.8-ha forest plot in 1981. The area included here was resampled after fires affected the forest (A2). The original data set for 1981 was collected for 10.5-ha and included 555 tree species; 55 of these were Dipterocarpaceae (Kartawinata et al., 2008; Kartawinata, 2010). Repeated forest fires in 1982/1983 and 1997/1998 affected the species richness significantly when resampled in 2011 (A2). Species richness of the same 1.8-ha area decreased to 181 species (Rahayu et al., 2017). Data for 1.65 ha sampled in 2003 showed 148 species (Simbolon, 2005), suggesting that species richness increased significantly during the 2003–2011 period. During these observations the dominant tree species in the plot changed from *Shorea laevis*, a late succession high-wood-density species in 1981 (Kartawinata et al., 2008) to *Mallotus paniculatus* in 2003 (Simbolon, 2005) and *Macaranga gigantea* in 2011 (Rahayu et al., 2017). Both *Mallotus paniculatus* and *Macaranga gigantea* are low-wood-density pioneer species.

Species richness in the relatively undisturbed lowland forest of Berau (B1) was lower than that in Samboja (A1). In 12 ha of primary lowland forest in Berau, 538 species (Sist and Saridan, 1998) were found (with at least 10 cm DBH) with 182 tree species per ha on average (Sist and Saridan, 1999). Species richness in natural regeneration after logging in Berau (B2) was not different from that in relatively undisturbed condition; we found 173 species in 1 ha. This result was based on a logging practice that actually (which is quite rare) followed the standard regulation, to only cut trees above 50 cm DBH. Seed sources provided by unlogged trees below 50-cm DBH were still available at close range.

Natural regeneration after logging by the local community (C1) and rubber agroforest managed by farmers (C2) in Jambi both contained a lower tree species richness (about 100 species in 1 ha) compared to relatively undisturbed and disturbed forest in lowland forest East Kalimantan. Rubber agroforest in Jambi (C2) still provided habitat for tree species richness similar to that of disturbed forest in the same area (C1). In both C1 and C2, forest management retained trees producing commercial fruits such as durian (*Durio zibethinus*), 'mata kucing' which is a local variety of longan (*Dimocarpus longan*), rambutan (*Nephelium lappaceum*), and some forest timber species. A number of forest timber species (including Dipterocarpaceae) that naturally regenerated in the plot were maintained by the community, as well as tree species producing local fruits through selective weeding. Differences between curves based on trees encountered (Fig. 3a) and area surveyed (Fig. 3b) were small.

Table 2
Observed number of species (NB sampled area was not the same between the studies) and diversity indices for the relatively undisturbed forest (A1 and A2), secondary forests (A2, B2 and C1) and rubber agroforest (C2); C2* represents diversity in all trees excluding rubber (*Hevea brasiliensis*).

	A1	A2	B1	B2	C1	C2	C2*
Observed species	248	189	174	168	92	104	103
Simpson (1–D)	0.99	0.95	0.99	0.98	0.95	0.62	0.97
Shannon-Wiener (H')	4.86	4.03	4.82	4.51	3.57	2.24	4.02

3.2. Diversity indices

The diversity indices (Table 2) confirmed the very high diversity of relatively undisturbed forest plots (A1 and B1) and relatively small reductions in the secondary forests (A2 and B2); diversity in the community-managed forest in Sumatra (C1) was lower than the four Kalimantan sites (A1–B2), especially as reflected in the Shannon-Wiener index. The Simpson indices (1–D) indicate that the chance of two randomly chosen trees to belong to the same species was 1%–5% in all datasets except for C2. For the rubber agroforest two version of the diversity indices were compared: one that includes the rubber trees, and one without. When rubber trees are ignored, tree diversity in C2 was higher than that in C1 and comparable to the A2 plots.

3.3. Wood density

In terms of wood density, only one data set stood out from the rest. The naturally regenerated forest 28 years after repeated fires in Samboja Research Forest (A2) was dominated (70%) by light to medium wood density trees, less 0.3–0.6 g·cm^{-3} (Fig. 4a). In the forests sampled after 15 years of natural regeneration post logging in Berau (B2) 20% of species

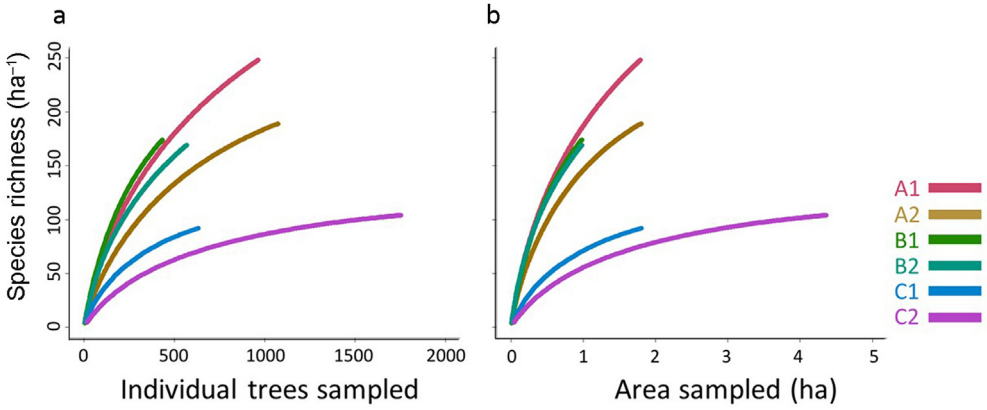


Fig. 3. Tree species richness in the six types of forests, in relation to the number of trees encountered (**a**) or area sampled (**b**), based on rarefaction analysis, in relatively undisturbed forest (**A1**, **B1**), naturally regeneration after disturbances (**A2**, **B2**, **C1**) and rubber agroforests (**C2**); compare Fig. S1 for 95% confidence intervals.

were light wood density 0.3–0.4 g·cm^{-3} (Fig. 4b), but otherwise, this forest followed the overall trend. Gaps created by selective logging of trees above 50-cm diameter had been occupied by pioneer species, but the overall forest was similar in wood density profile to data for other sites. As rubber (*Hevea brasiliensis*) has a wood density of 0.62 g·cm^{-3}, and 60% of trees in the rubber agroforestry systems in Jambi (C2) belongs to this species, its wood density profile shows relatively few trees on both the light and heavy side of the spectrum, with 20% of medium wood density trees.

In the correspondence analysis (Fig. 5) the six sites B1 (Berau), C1 and C2 (Jambi) were most closely associated, as they have very similar frequency distributions in wood density classes. The Samboja site A2 was most strongly associated with 'heavy' wood, as that may include tree species that survived the preceding fire events.

3.4. Dispersal modes

Natural regeneration of all forest types was dependent on animals as dispersal agents. More than 50% of species, in any of the forests, were dispersed by forest canopy animals such as birds, bats and primates (Fig. 6). More than 70% of the tree species in relatively undisturbed of lowland forest in Samboja (A1) were dispersed by endo-zoochory, mostly associated with birds, bats and primates. Anemochorous species in Berau (B), both in relatively undisturbed (21%; B1) and after logging (19%; B2), especially *Macaranga lowii*, tended to be more common than in other landscapes (about 10%).

The correspondence analysis (Fig. 7) suggested that endo-zoochory by birds, bats, and primates was closely associated with natural regeneration after community logging in Jambi (C1), and relatively undisturbed forest in Samboja (A1). The forest in Samboja recovering from fire (A2) was positioned halfway between endo-zoochory and autochory, indicating a greater proportion of trees with large, autochorous seeds. Both of the Berau (B) plots had a stronger presence of anemochorous trees. The rubber agroforests in Jambi (C2) differed in position from the other plots. The relative positioning of the sites differed from that for wood density (Fig. 5).

Table 3 presents the closest patches of 'primary forest', 'any forest', and intact forest landscapes from each cluster of plots. The largest distance (6.2 km) to 'any' forest was found in the Samboja (A2) site recovering from fire, with at least some of the plots in Berau (B) and Jambi (C) adjacent to forests that were not affected by the main disturbance events. For Berau some of the adjacent forest patched were considered to be primary forest, while the distance to the nearest primary forest was 10 km for the regenerating forests in Samboja and 4.9–6.9 km in Jambi. In contrast, the distances to the nearest intact forest landscape

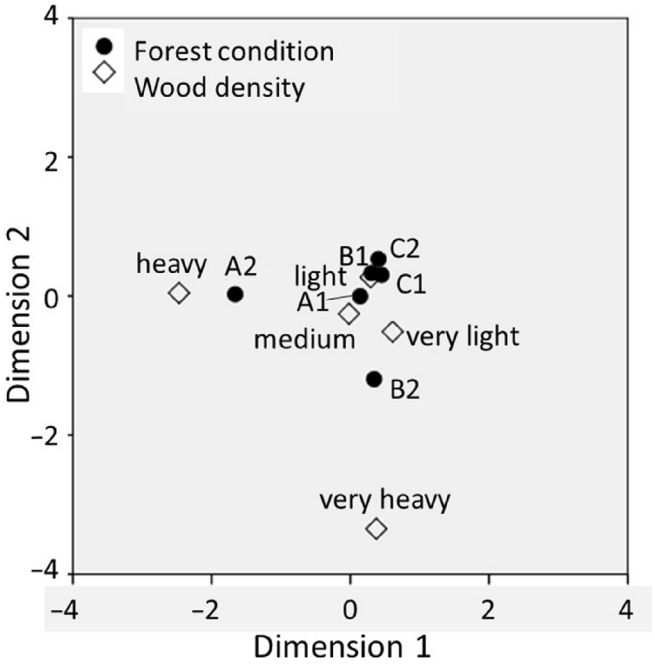


Fig. 5. Correspondence analysis (with symmetrical normalisation) of wood density profiles of tree species in relatively undisturbed forest, naturally regeneration after disturbances and rubber agroforest; dimensions 1 and 2 accounted for 68% and 23% of total variation, respectively.

was smallest in Jambi (6.9 km) and largest in Berau. Thus, the three ways of expressing the dispersal distances involved for regenerating trees gave a very different ranking of the A, B and C landscapes.

4. Discussion

4.1. Species richness

Confidence intervals for the tree diversity profiles for secondary forest ecosystems in Sumatra and Kalimantan after disturbance by logging, fire, and agroforest management did not overlap with those for less disturbed sites for the Samboja (A1) and Jambi (C1) sites (Fig. S1), leading us to reject the null-hypothesis that tree diversity profiles are independent of degradation-restoration history, but not for the Berau site (B1 and B2) where two logging intensities were compared.

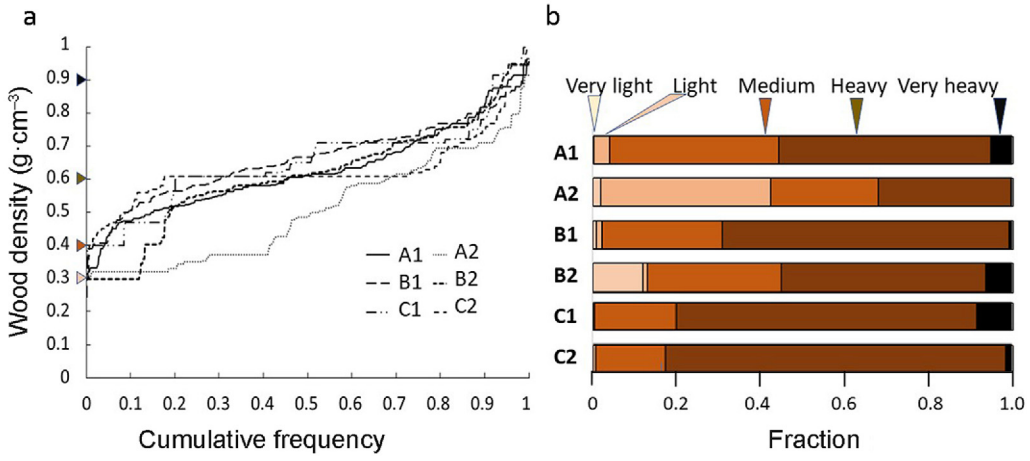


Fig. 4. a) Wood density profile based on cumulative basal area in relatively undisturbed forest, naturally regeneration after disturbance and rubber agroforest; **b)** wood density proportions in relatively undisturbed forest (**A1**, **B1**), naturally regeneration after disturbances (**A2**, **B2**, **C1**) and rubber agroforests (**C2**).

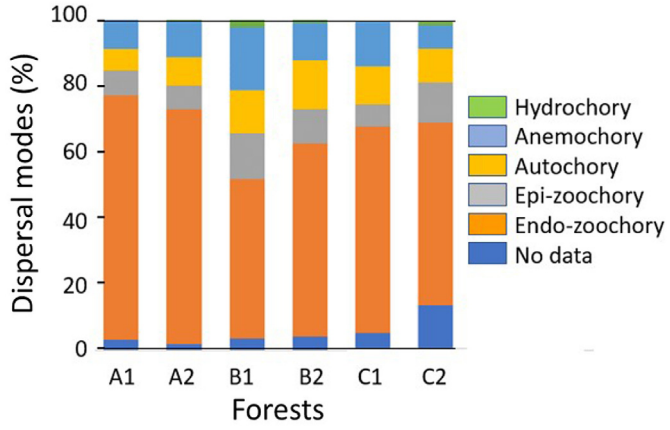


Fig. 6. Dispersal modes proportion in relatively undisturbed forest (**A1**, **B1**), naturally regeneration after disturbances (**A2**, **B2**, **C1**) and rubber agroforests (**C2**).

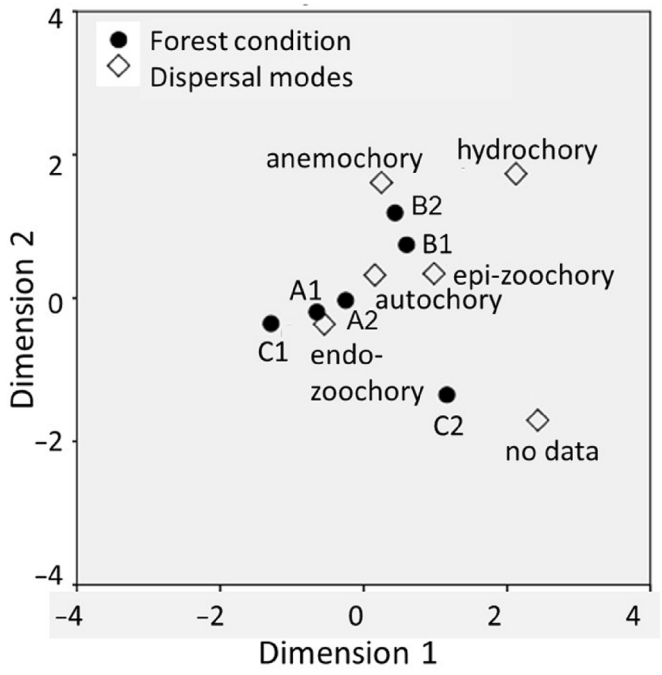


Fig. 7. Correspondence analysis of dispersal modes of species in relatively undisturbed forest, naturally regeneration after disturbance and rubber agroforest; dimensions 1 and 2 accounted for 44% and 42% of total variation, respectively.

Table 3
Distances (km) from sampling plots to the nearest forest of three types: 'any forest' (including secondary and agroforest), primary forest patches (regardless of size) and intact forest landscape (minimum 20 ha of primary forest); results reflect the situation at the time samples were recorded.

Code	Location	To any forest	To primary forest	To intact forest landscape
A1	Samboja Research Forest,	0	0	0
A2	East Kalimantan	6.2	10.0	11.4
B1	Berau, East Kalimantan	0	0	0
B2		0.0	0.0	23.0
C1	Jambi, Sumatra	0.0	4.9	19.0
C2		0.0	6.9	6.9

Biogeographic variation in species richness in relatively undisturbed lowland forest have been extensively studies in Southeast Asia. Kartawinata (2010) summarized data for relatively undisturbed lowland forest in East Kalimantan with on average 225 tree species in 1 ha. Kalimantan, the Indonesian part of the island of Borneo, has the highest recorded tree diversity in Indonesia. Borneo is seen as the center of diversity of Dipterocarpaceae (Maury-Lechon and Curtet, 1998), with their strategy of 'masting', e.g. large time intervals between years of high seed production, an adaptation to escape from seed predation. As specialized seed dispersers cannot bridge the time between masting years, autochory (heavy seeds) or anemochory (light seeds) has likely to be part of such strategy. Heavy-seeded autochory, as found in Dipterocarpaceae, is a late-successional trait that helps seedlings in establishing into dense vegetation, but it implies a low capacity to rapidly reclaim areas after disturbance.

Our data can also be seen in the light of an ongoing debate (Palmiotto et al., 2004) contrasting directional niche-assembly (Ashton, 1998) concepts with random-walk, seed-dispersal limitations (Hubbell, 2001) as primary explanation for the high tree diversity of tropical forests. While soil-related niche diversity exists in lowland tropical forests (Palmiotto et al., 2004), seed dispersal might well be the primary constraint in the processes of natural regeneration.

Although logging, if done carefully, does not lead to deforestation (FAO, 2015), selective logging in practice still leads to a significant reduction in tree species diversity per surface area, especially if it becomes associated with fire (Slik et al., 2002; Toma et al., 2016). In a logged forest in peninsular Malaysia, Johns (1989) documented domination by wind-dispersed pioneers such as *Macaranga* spp., *Mallotus* spp. and *Trema orientalis*, all of which were rare in an adjacent unlogged forest. In another study with a modest extraction intensity tree species richness was similar between unlogged and logged forest, while liana species richness was higher in logged forest (Cleary, 2017). Hiratsuka et al. (2006) followed vegetation dynamics from 2000 to 2003 of plots recovering from the 1998 fires in East Kalimantan. They found that some of the shrubs and trees that established early on were replaced by a group of species including *Macaranga*, which may persist for a longer period where it gets established. A recent analysis by Mahayani et al. (2020) of phylogenetic diversity, community structure, and composition of the Berau forests (B) showed rapid recovery of those properties a decade after logging and post logging silvicultural interventions.

Ecological textbooks suggest that disturbed local communities are commonly dominated by widespread species. In a meta-analysis of 875 tropical forest datasets that relate the degree of habitat disturbance in landscapes to the relative loss of species, Alroy (2017) found that all the disturbed habitats combined included 41% fewer species than the relatively undisturbed forests. The proportional loss varied among groups, with loss of tree species showing an intermediate responsiveness compared to various animal groups. Relative to those data, the degrees of disturbance were low in all three of our sites and diversity remained high.

4.2. Wood density

The wood density profiles of naturally regenerated tree populations (Fig. 4) were similar to that for the Indonesian tree flora as a whole (Fig. 1). The largest deviation from the pattern for relatively undisturbed forest was found after fire in the A2 site, followed by the effects of logging at the B2 site.

Natural regeneration after repeated fires in A2 was associated with trees of low wood density. Increasing severity of disturbance affected the dominance of trees of low wood density in the study by Slik et al. (2008). The pioneer species *Macaranga gigantea* dominated after fires in Samboja (Rahayu et al., 2017) and contributed to a low average wood density (Slik et al., 2008). *Macaranga* is responsive to forest disturbance and its peak biomass was recorded 6–11 years after disturbance (Fiala, 1996). In Malaysia, *Macaranga gigantea* was absent in forest with 20 years of recovery after clear-felling, but it was found in a secondary forest 4 years

after disturbance (Niiyama et al., 2003). In the Samboja Research Forest *Macaranga gigantea* was still dominant in 13 years after the second fires (Rahayu et al., 2017). The seed of *Macaranga* genus can remain dormant in the soil until there is a disturbance (Fiala, 1996; Kiyono and Hastaniah, 2000). Species with very-heavy wood, such as *Eusideroxylon zwageri*, decreased in natural regeneration after repeated fires despite the capacity of such trees to regrow from damaged trees, stumps and roots. Although single fire events may increase the relative presence of such species, with repeated fire events the populations of these species decline (van Nieuwstadt and Sheil, 2004).

Natural regeneration after logging forests on mineral soil had a significant effect on the wood density profiles. Populations of trees with very heavy wood remain the same in relatively undisturbed forest, while populations of trees with very light wood increased 15 years after logging. After logging the sunlight reaches the forest floor, which stimulates tree regeneration (Nifinluri et al., 1999), particularly of light-demanding pioneer species (Slik et al., 2008). Availability of seed sources (Kiyono and Hastaniah, 2000) or pre-existing seedlings at the gap formation are other factors affecting natural regeneration (Nifinluri et al., 1999).

In a village forest logged by the local community in Jambi (C), natural regeneration contained a high proportion (up to 70%) of trees with high and 10% of very high wood-density. A similar condition was encountered in rubber agroforests, where the proportion of trees with heavy wood reached up to 80%. Management practices applied in rubber agroforests and village forests, for instance, regular weeding, affected the growth of pioneer species that commonly have very light to light wood density, such as *Macaranga*, *Ficus*, and *Aporosa* (Werner, 1997). Gillison et al. (2013) discussed plant functional types and traits as biodiversity indicators in landscape C with a different method: sampling a gradient of land cover types with forests such as C1 and jungle rubber plots such as C2 as part of a wider range of land covers, and sampling various groups of fauna as well as flora. Different fauna groups were found to correlate with various aspects of vegetation, including litter layer and the ratio of botanical species and plant functional types.

Lohbeck et al. (2013) found that in dry forests in Mexico, succession starts with medium wood density tree species, with low wood density species coming into the vegetation when the pioneers have created a more favourable microclimate. All the sites considered here were 'humid' and had low wood density associated with pioneers after disturbance.

4.3. Seed dispersal

Seed dispersal mode patterns of natural regeneration changed after repeated fires in Samboja (A). Trees with frugivores (endo-zoochory) dispersal type decreased by 10%, but trees with epi-zoochory and autochory dispersal slightly increased. Decreasing bird species after fires affected the regeneration of tree species dispersed by bird zoochory. Bird species richness in Samboja Research Forest decreased significantly from 140 species in 1988 to 44 species in 2015 (Atmoko et al., 2015). Decreasing avifauna diversity in a burnt secondary forest was also reported by Slik and van Balen (2006), which was based on the study in 1988. The availability of remnant forests as a habitat of frugivore animals as dispersal agents in Berau was an important factor in B2. Natural regeneration and residual stands in a village forest logged by the local community in Jambi (C1) demonstrated a similar pattern to the relatively undisturbed Berau forest (B1).

Correspondence analysis (Fig. 7) showed that tree species with endo-zoochorous dispersal were associated with natural regeneration after logging both by the community, as well as after fires on mineral soil. The presence of forest canopy animals such as birds, bats, and primates is very important as a dispersal agent for forest regeneration after disturbance by logging and fires. The correspondence analysis (Fig. 7) also showed that tree species with autochorous dispersal are closely associated with relatively undisturbed forest in Berau (B1). Those findings are in line with research conducted by Sist and Saridan (1998) that 61 Dipterocarpaceae species were found in 12-ha area of relatively undisturbed forest in Berau. Trees with anemochorous dispersal are closely associated with natural regeneration after repeated fires in Samboja forest (A). Samboja forest was dominated by the pioneer tree species *Macaranga gigantea*, an anemochorous species, that developed well 10 years after a forest fire in 1997/1998. Trees with hydrochorous dispersal were limited to relatively undisturbed and disturbed forests.

Ganesh and Davidar (2001) reported for the Western Ghats in India that bird-dispersed species were the most common (59% of the tree population), followed by mammal-dispersed species (26%) with primates less important than bats and civets in seed dispersal. They found that many bird-dispersed species occurred at low density, but the total density of bird-dispersed species compares with that of mammal and mechanically dispersed species. Our presence/absence data for zoochorous trees may only reveal a small part of the longer-term tree population impacts, that include spatial distribution as element of extinction risk (Caughlin et al., 2015). Further analysis by fruit size might reveal more specific effects, as Corlett (2017) noted that larger-seeded fruits are consumed by progressively fewer dispersers, with the largest depending on only a few species of mammals and birds which are highly vulnerable to hunting, fragmentation, and habitat loss.

4.4. Distance effects and management implications

In line with our third objective, interpretation of site and landscape-level data in terms of transport distances for tree dispersal (Table 2) and enabling conditions for regenerating tree diversity in managed restoration processes can assist in a site-specific diagnostic analysis and related restoration planning. The three distances in Table 3 indicate opportunities in the period after disturbance for dispersal from mother trees that existed in 'any forest', 'primary forest' or 'intact forest' landscapes. The difference between the latter two indicators was largest in the logged Berau landscape (B2) that had patches of primary forest retained, but was more than 20 km from the nearest intact forest landscape. Effective dispersal distances for trees of more than 1 km are probably rare, but small probabilities at the tail of the statistical distribution may well be relevant for the re-establishment of tree species after disturbance. Out of 7 dispersal classes proposed by Vittoz and Engler (2007) on the basis of European data, human dispersal covered the largest distances. Among the non-human dispersal agents, the largest distances (99% of seeds within a distance of 1.5 km, and 50% within 400 m) are expected for endozoochory for seeds eaten by birds and large vertebrates and epizoochory for seeds carried externally by large mammals. For an understory frugivore bird in tropical Australia seed dispersal distances up to 100 m were similar to reported pollen dispersal distances (Westcott and Graham, 2000). Takeuchi et al. (2004) documented a five-fold difference in dispersal distances for three Dipterocarpaceae in Peninsular Malaysia, with the highest observed seed dispersal distance about 500 m. Interspecific variation among 41 tropical tree species in primary seed dispersal was described in a tropical forest on Barro Colorado Island, Panama from 19 years of data for 188 seed traps on a 50-ha plot in which all adult trees were censused every 5 years (Muller-Landau et al., 2008). For most species mean dispersal distances were less than 100 m. Among 31 animal-dispersed species, 20% of interspecific variation in dispersal distances was explained by seed mass (a negative effect) and tree height (a positive effect). The study found that there was wide variation in seed dispersal distances among species sharing the same mode of seed dispersal and that seed dispersal mode did not explain significant variation in seed dispersal distances. It did, however, explain significant variation in clumping with animal-dispersed species showing higher clumping of seed deposition. Our data showed very little evidence of clumping in the tree stage, as evidenced by the Simpson index. Estimated dispersal distances per generation are also relevant for studies of climate change adaptation and range for various plant–vector combinations from <10 m, for species dispersed by ants or mechanical means, to >10 km for some species dispersed by wind (tiny seeds), water, fruit pigeons, large fruit bats (tiny seeds), elephants, rhinoceroses, and people (Corlett,

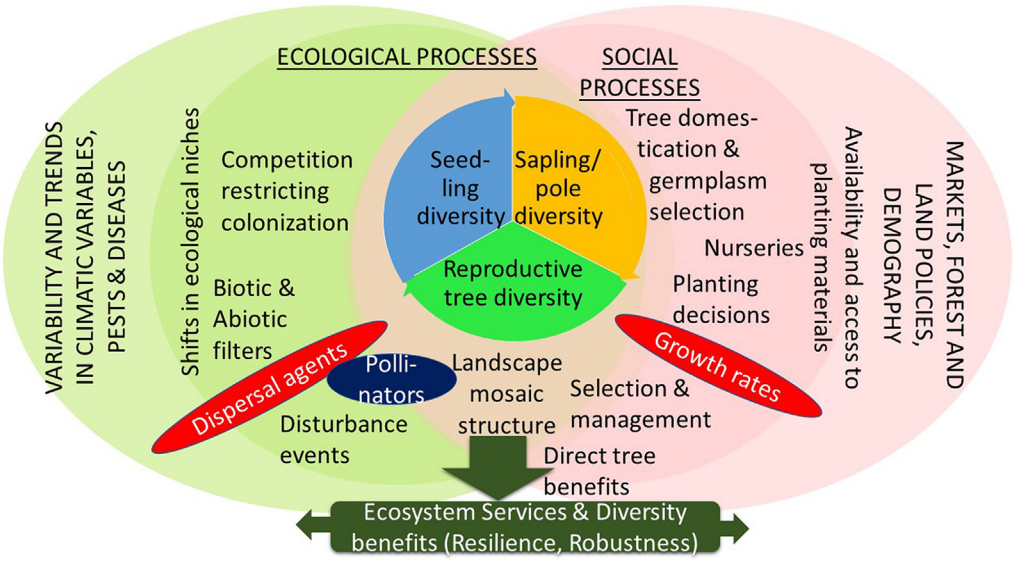


Fig. 8. The place of dispersal agents and tree growth rates (with wood density as proxy) in the social-ecological system approach to forest degradation and restoration (modified from van Noordwijk et al., 2019).

2009). According to Corlett's review for Southeast Asia, most plant species probably have maximum dispersal distances in the 100–1,000 m range, but the widespread, canopy-dominant Dipterocarpaceae and Fagaceae are normally dispersed <100 m. Large fruit bats and fruit pigeons are particularly important for long-distance dispersal in fragmented landscapes and should be protected from hunting.

Dispersal agents and tree growth rates determine two important steps in the life cycle of trees in a social-ecological understanding of forest degradation and regeneration/restoration (Fig. 8). While we focused on the ecological and tree biological aspects of natural regeneration, with wood density as a proxy variable, our data were collected in real-world social-ecological systems rather than designed ecological experiments and thus include selective retention and possible harvests.

Our analysis showed several differences at the community level between natural regeneration in relatively undisturbed forests and in forests recovering from disturbances. Most of the differences were gradual and rather subtle. Tree diversity was still high with around one hundred species of trees of more than 10 cm diameter species per ha. Probably only a small part of natural regeneration depends on surviving propagules in the soil, with root suckers' part of the post-fire vegetation (van Nieuwstadt and Sheil, 2004). Autochorous (self-dispersed) trees occurred in all study sites. Where trees in the regenerating forests were still diverse; their occurrences probably mainly depend on frugivorous forest canopy animals as dispersal agents of endo-zoochorous seeds.

Our data showed that species richness was not the best indicator of forest disturbances due to logging activity and fires, because species richness in natural regeneration after disturbances could be similar with relatively undisturbed condition. Late succession species persistent in selectively logged forest and newcomer pioneer species regenerated in disturbed area resulted in similar species richness to relatively undisturbed forest, or even higher. Management practices significantly affected to species richness (Werner, 1997), depending on the level of management activities. More intensive management practiced in the systems negatively impacted to species richness (Rasnovi, 2006; Tata et al., 2008a).

Beyond seed production and seed dispersal agents, other factors may limit the natural regeneration of native trees in disturbed forests, including absence of pollinators (Neuschulz et al., 2016). After the forest fires of 1982/1983, there was a widely perceived urge to replant forests, preferably with late-successional species from the local flora, as there was little confidence in natural regeneration capacity and an absence of the type of data we now have in hands. The establishment of dipterocarp trees (especially in the genus *Shorea*), however, was found to be difficult and a lack of ectomycorrhizal partners in the soil was held responsible. Nursery inoculation techniques were established and widely disseminated (Smits, 1983). Tata et al. (2010), however, found that inoculation of *Shorea* seedlings was not necessary (and gave only a small positive effect) in rubber agroforests in Jambi. Whether the difference between Kalimantan and Sumatra in this contrast is indicative of Sumatran vs. Bornean *Shorea* species, or whether other factors are involved is yet to be ascertained in follow-up research. The main constraint to dipterocarp trees in rubber agroforests still is in the policy domain: as farmers fear to be caught for illegal logging if they harvest native tree species, they rather remove them in an early stage (Tata et al., 2008; 2009).

As a limitation to the current study, not much is known regarding genetic diversity within a species in response to disturbance/regeneration events. Genetic diversity is a concern for forest management, especially where limited 'founder populations' restrict subsequent adaptation to changing conditions. Ang et al. (2016) found that levels of genetic diversity of naturally regenerating seedlings of two Dipterocarpaceae species in a Bornean rainforest were statistically indistinguishable among unlogged, once logged and repeatedly logged forest areas. Where active tree planting is pursued, instead of relying on natural regeneration, genetic diversity may well be reduced, depending on species and seed selection procedures. Tree planting and reforestation practitioners often overlook both species and genetic diversity when implementing programs (Roshetko et al., 2018). In the case of *Dyera polyphylla*, a native peat-swamp tree species, however, the planted populations in Jambi and Central Kalimantan have no genetic diversity reduction compared with the wild population, and it has relatively low variation among the population. *D. polyphylla* has anemochorous seed dispersal, which enables the seeds to disperse far beyond the pollination distance (Tata et al., 2018).

Our results can be compared to a recent analysis for the Amazonian forests (Hawes et al., 2020) that compiled trait information (focusing on dispersal mode and seed size) for 846 tree species encountered in two study regions with regenerating secondary forests and primary forests disturbed by burning and selective logging. Their data showed that disturbance reduced tree diversity and increased the proportion of lower wood density and small-seeded tree species in study plots. It increased

the proportion of stems with seeds that are ingested by animals and reduced those dispersed by other mechanisms (e.g. wind). Older secondary forests had functionally similar plant communities to the most heavily disturbed primary forests. Mean seed size and wood density per plot were positively correlated for plant species with seeds ingested by animals. A similar relationship between seed size and wood density remains to be tested for Indonesian forests, with the dominance of Dipterocarpaceae possibly modifying the overall pattern.

Returning to the central restoration question of thresholds where the regeneration of diverse tropical forests is still feasible by reliance on natural processes, rather than 'tree planting', our data suggest that all study cases were in the 'natural regeneration' domain. This may have been implied by the selection of study sites on mineral soils, while the study of Blackham et al. (2014) referred to a case where peat swamp forest regeneration is retarded. Availability in the surrounding landscape mosaic of areas that still serve as habitat for forest canopy animals such as birds, bats, and primates is obviously an important factor, operating above the plot scale of our current data sets, to support natural regeneration in disturbed areas. It is all a matter of scale, relating the level of disturbance with the dispersal agents that can support regeneration. To fully understand threats and opportunities the social and ecological sides of Fig. 8 need to be connected (van Noordwijk, 2020).

5. Conclusions

Lowland forests in Kalimantan, both disturbed and relatively undisturbed, contained high tree species richness. Forest and agroforest management practices significantly affected tree species richness and composition. Selective weeding in rubber agroforests maintained valuable tree species. Abiding by logging regulations and following sustainable management practices in village forests contributed to maintaining tree species diversity. Functional traits of wood density and dispersal modes identified that tree species composition in the lowland forest of Berau (B) was different from those in Samboja (A), even though both forests were located in mineral soils of East Kalimantan. Repeated forest fires and logging activities in mineral soils significantly affected tree species composition. Light-wood species dominated the early stage of regeneration in natural forests after fires, but very-heavy-wood species were found in the post-logging forest on mineral soils. Tree species with endo-zoochorous dispersal represented more than half of the natural regeneration in disturbed forest. Availability of remnant forest in the surrounding areas as the habitat of forest canopy animals such as birds, bats, and primates appeared to be an important factor in support of natural regeneration in disturbed areas.

Our main conclusions are:

1) Intensity of past logging in Kalimantan did not affect tree species richness, fires did;
2) Community-scale wood density and dispersal mode frequency reflected forest disturbance history;
3) Forests recovering from repeated fires had a markedly increased fraction of low-wood-density trees;
4) The majority of trees (50%–70%) had birds, bats and primates as dispersal agents in all sites;
5) Agroforest tree species richness shaped by past forested landscape mosaics may not be replicable in the current landscape.

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Availability of data and materials

Upon publication, data will be made available via the ICRAF's data repository, following existing institutional policies.

Authors' contributions

Subekti Rahayu, Hesti Lestari Tata and Meine van Noordwijk conceived the manuscript; Subekti Rahayu provided the unpublished field data; Saida Rasnovi provided the dispersal modes database; Sonya Dewi and Muhammad Nugraha provided the spatial data analysis; Subekti Rahayu, Sidiq Pambudi, Dikdik Permadi and Roeland Kind provided the statistical data analysis; Subekti Rahayu and Meine van Noordwijk drafted the manuscript; Hesti Lestari Tata, Endri Martini and Hani Nurroniah provided inputs to the manuscript, and all co-authors read and approved the manuscript in its current form.

Ethics approval and consent to participate

All (agro)forest right-holders approved of data collection for the purpose of ecological research.

Consent for publication

Publication is approved by the relevant authorities in our respective institutions, in line with existing policies.

Competing interests

The authors declare no competing interests.

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Appendix A. Supplementary data

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