Wood Density and Dispersal Modes of Trees Regenerating in Disturbed Forests and Agroforests in Indonesia

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Research

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Abstract

Natural regeneration depends on surviving propagules in the soil, seed sources from a surrounding landscape mosaic, and dispersal agents. We compiled and analyzed four sets of case studies varying in degree of disturbance, for secondary forests recovering from logging, fire, and conversion to agroforest in Sumatra or Kalimantan (Indonesia) on mineral and peat soils. Data on tree species diversity, wood density frequency distribution (indicative of successional status, databases with over 6000 species exist), and dispersal modes were compared with those for less disturbed comparator forests for the same landscapes. Undisturbed lowland dipterocarp forest in Kalimantan had close to 200 species of trees of more than 10 cm diameter at a 1 ha sample scale (and 450 at a 10-ha scale), regulation-based logging had little impact. Still, after the repeated fire a sample area of 2 ha was needed to reach the same species numbers. After forest conversion to low-management-intensity rubber agroforest, 50 tree species were found at a ha scale and close to 100 species in 3 ha. Peat swamp forest in Kalimantan and the Sumatra forest samples had close to 100 species in 1 to 2 ha. The Kalimantan forest after a repeated fire had a markedly higher fraction of low-wood-density trees (40%), but otherwise, all forests sampled were similar in overall wood density profiles. Logged-over forest managed by community (village forest) and rubber agroforest in Sumatra contained larger fractions of heavy-wood-density trees (including rubber). The majority of trees (50-70%) had birds, bats, and primates as dispersal agents in all sites. Logged-over forests on mineral soil had higher fractions of autochorous species (15%) compared to other sites. Anemochorous (wind-dispersed) species were most common (20%) in undisturbed lowland Dipterocarp forest and peat swamp forest recovering after logging and fire. 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 profile can be used as degradation indicators of species assemblages across various disturbance levels and types. They can also reflect the habitat quality of the surrounding forming restoration options.

1. Introduction

Restoration, crossing an inflection point in a forest transition curve (Dewi et al 2017), can be the result of natural regeneration during 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 (IPBES, 2018; van Noordwijk et al. 2020a,b). Desired functionality can be any combination of hillslope and watershed protection (Creed and van Noordwijk, 1998), 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 of all (Cavanaugh et al. 2014; van Noordwijk et al. 2020). Functional traits at species level desired to provide such functions at community scale depend on hydrological functions (including Leaf Area Index, root system, litter layer generated), productivity (growth rate, timber quality, fruit, resin, honey, or other non-timber forest products value generated), and from a biodiversity perspective, on the level of threat to native flora and fauna e.g. through invasiveness. 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). Regeneration depends on the dispersal ability of trees and the type and spatial scale of preceding degradation, that define the transport distances to be bridged in natural regeneration.

Dispersal ability of trees

Tree reproduction primarily depends on flowering, pollination, and seed dispersal. Whereas concerns in agricultural landscapes are mostly about impacts of agrochemicals on pollination (Potts et al. 2016), concerns for forests are mostly for the loss of biological dispersal agents. 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) and overhunting of harvest-sensitive frugivore bird species has been shown to threaten forests across the Brazilian Amazon (Peres et al., 2016). In their review 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 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 management of logging concessions was supposed to maintain both tree reproduction and dispersal agents.

Preceding degradation types

Regeneration in ‘secondary forests’ depends on the drivers of preceding degradation, the scale at which restoration is applied, the availability of seed sources, and seed dispersal agents (Sayer et al. 2004). 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, seed vectors, 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).

Recovery after logging as preceding degradation

Logging activities in Indonesia since the 1970s were handled by large companies with timber concession permits. 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), in practice logging intensities 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 & Kusters 2015).

Recovery after fire as preceding degradation

An increase in forest fire frequency in logged-over areas caused further forest cover loss, especially in years with a 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. 2019). 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 fire in drained peat swamp forest substantially changed community composition of tree species and species richness in Central Kalimantan (Tata and Pradjadinata 2013; Shiodera et al. (2016). After 15 years of natural regeneration and succession, the species composition started to converge on that of non-logged comparator forest (Tata & Pradjadinata 2013).

Forest rehabilitation efforts

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). After the catastrophic fires in 2015, the Government of Indonesia established a Peatland Restoration Agency that launched three strategies for restoring the peatland ecosystem: rewetting, replanting, and revitalization of livelihoods. Restoration of degraded peatlands is a high-cost initiative, which may require more than USD 2.3 million per ha (Hansson and Dargusch 2018); this is 400 times more than the Net Present Value estimated for logging (Sofiyuddin et al. 2012) that started the fire susceptibility, indicating that past logging decisions were not in the national economic interest. Lower-intensity management relying on natural regeneration (after rewetting in the case of drained peatlands) 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.

Agroforests

Agroforest management with selective retention of desirable trees by farmers and protection of saplings or poles that are considered to have utility values has been effective in the past when the surrounding forest matrix was still diverse. 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 the habitats they occupy (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 aim of this article is: (1) to compare tree diversity profiles in secondary forest ecosystems in Sumatra and Kalimantan after disturbance by logging, fire, and agroforest management, (2) to quantify wood density profiles and dispersal modes as tree functional traits of naturally regenerated tree populations 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.

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 GlobalTreeSearch (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/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 thousand different species of plants, of which 15 thousand species are endemic to this region. Borneo has higher endemicity than Sumatra, but similar levels of tree diversity in standard forest plots (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 2478 tree species in Indonesia (Figure 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

The data set we compiled from four landscapes in Kalimantan and Sumatra (Figure 2) each covered the least disturbed forest condition for which data are available and a forest that is 10-30 years into a natural regeneration process (Table 1).

The first two landscapes are both located in the lowland Dipterocarp forest domain in East Kalimantan, A1) Undisturbed forest in the Samboja Research Forest and A2) the same plots 28 years later after repeated fire events; B1) Undisturbed forest in Berau, B2) 15 year of natural regeneration after logging activities.

The third landscape is the peat swamp forest of Central Kalimantan, with two landscapes differing in disturbance intensity and history, with C1) a location with 20 years of recovery after logging but also with repeated fire history in Mangkok Resort of Sebangau National Park (SNP), and C2) a forest with 20 years of natural regeneration after logging in the Sebangau National Park at the Peat Forest Natural Laboratory (PFNL).

The fourth landscape is in the lowland Dipterocarp forest of Bungo regency in Jambi province on Sumatra, D1) a village forest with a history of community-based forest management but still having oldgrowth forest elements, D2) rubber agroforest.

2.3 Plot-level data

An inventory of trees above 10 cm DBH (diameter 1.3 m above the ground) was conducted in all plots observed in Kalimantan. 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 (especially for Indonesia) 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}.

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 sensing imagery for the period shortly after the main documented disturbance (Figure 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 buffer of 40 km surrounding each plot. 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 (IFL) analyses were based on the following criteria: (1) minimum area of 50,000 has; (2) minimum IFL 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 IFL patch core areas are large enough to provide refuge for wide-ranging animal species. We then calculated the Euclidean distance from each plot to ‘primary forest’ patch, ‘any forest’ patch, and IFL. Table 2 presents the closest patches of ‘primary forest’, ‘any forest’, and IFL from each cluster of plots.

2.5 Data processing

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 by wind, (4) autochory by mechanical self-dispersed seeds, (5) hydrochory by water (Figure 3). Wood density and dispersal mode data were analyzed at the community level and compared between the data sets.

Correspondence Analysis (CA) 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). A bootstrapping procedure was used for assessing species accumulation curves with random starting positions but maintaining the spatial sequence of plots surveyed based on observed data on the species encountered in each plot 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 & 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).

3. Results

3.1 Species richness

3.1.1 Lowland Dipterocarp forest on mineral soils

As expected, the highest tree species richness (Figure 4) was found in the 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 (C). The original data set for 1981 was collected for 10.5-ha and included 555 tree species; 55 of these were Dipterocarps (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 undisturbed lowland forest of Berau (B1) was lower than that in Samboja. In 12 ha of primary lowland forest in Berau, 538 species (Sist & Saridan 1998) were found (with at least 10 cm DBH) with 182 tree species per ha on average (Sist & Saridan 1999). Species richness in natural regeneration after logging in Berau (B2) was not different from that in undisturbed condition; we found 173 species in a 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 resources provided by unlogged trees below 50 cm DBH were still available at close range.

Natural regeneration after logging by the local community (D1) and rubber agroforest managed by farmers (D2) in Jambi both contained a medium-level tree species richness (about 100 species in a ha) compared to undisturbed and disturbed forest in lowland forest East Kalimantan and peat swamp forest in Central Kalimantan. Rubber agroforest in Jambi (D2) still provided habitat for tree species richness similar to that of disturbed forest in the same area (D1). In both D1 and D2 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. Some forest timber species (including Dipterocarps) that naturally regenerated in the plot were maintained by the community, as well as tree species producing local fruits through selective weeding.

3.1.2 Peat swamp forests

Species richness in natural regeneration of peat swamp forest (C1 and C2), both in conditions disturbed by logging and fire was substantially lower than that in other ecosystems. In 20 years of regeneration after logging and forest fire in 1997/1998, the species richness in Mangkok resort (C1) recovered to about 90 species in 3 has area. This research site is in the rewetted area, influenced by canal blocking structures build in 2007. Limited species adapted to the wet condition which might affect species richness after rewetting. For a site close to C2, Mirmanto (2009), recorded 133 species of 2 ha in an undisturbed peat swamp forest. A natural regeneration site 20 years after logging in the Peat Forest Nature Laboratory (C2) had the lowest tree diversity, with about 80 species in 3 ha area. Our data set did not include undisturbed peat swamp forest as part of the comparison.

3.2 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 to 0.6 g cm^{-3} (Figure 5A). In the forests sampled after 15 years of natural regeneration post logging in Berau (B2) 20% of species were light wood density 0.3 to 0.4 g cm^{-3} (Figure 5B), 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 is rubber tree, 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 principle-component analysis (Figure 4) light wood density (0.3 – 0.4 g cm^{-3}) species were associated with natural regeneration of disturbed forests after repeated fires in lowland forests on mineral soils and very light wood density < 0.3 g cm^{-3} species were associated with disturbed forests after selective logged by the company in Berau (B2). Medium and heavy wood density trees were very common in forest ecosystems in Sumatra and Kalimantan, both in undisturbed and disturbed forests, as well as in rubber agroforests.

3.3 Dispersal modes

In all forest types, the sampled trees that depend on animals as dispersal agents were dominant. Natural regeneration of all forest types was dependent on animals as dispersal agents. More than 50% of species, both in undisturbed and disturbed forests were dispersed by forest canopy animals such as birds, bats and primates (Figure 7). More than 70% of the tree species in undisturbed of lowland forest in Samboja (A1) and in the disturbed peat swamp forest of Sebangau National Park (C1, C2) were dispersed by endo-zoochory, mostly associated with birds, bats and primates. Anemochorous species in Berau (B), both in undisturbed (21%; B1) and after logging (19%; B2), tended to be higher than that (about 10%) in other landscapes.

The correspondence analysis (Figure 6) suggested that endo-zoochory by birds, bats, and primates was closely associated with disturbed forest by logging and fire in the peatland of Sebangau. Natural regeneration after company logging of peatland in Sebangau (C1, C2), after community logging in Jambi (D1), and undisturbed forest in Samboja (A1) was also associated with this type of endo-zoochory. Natural regeneration after company logging in Berau (B2) was associated with anemochorous species, but undisturbed forest in the same landscape tended to be associated with autochorous species (B1; Figure 8).

4. Discussion

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 (Figure 9). 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.

Our analysis showed several differences at the community level between natural regeneration in undisturbed forests and in forests recovering from disturbances. Most of the differences were gradual (quantitative) rather than absolute (qualitative). 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.

4.1 Species richness

Variation of species richness had been noted in undisturbed lowland forest in East Kalimantan. Kartawinata (2010) summarized that lowland forest above 100 m above sea level contains high tree diversity on average 225 species in a ha, with Kalimantan the richest tree diversity island in Indonesia. Borneo had been seen as the center of diversity of Dipterocarps (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. Their autochory is likely to be part of such strategy (as seed predators couldn’t wait for food between masting years) – but it implies a low capacity to rapidly reclaim areas after disturbance and as such it is a late-successional strategy. Our data could also be seen in the light of an ongoing debate (Palmiotto et al. 2004) on the primary explanation for the high tree diversity of tropical forests: Niche-assembly (Ashton 1998) versus seed-dispersal limitations (Hubbell 2001). While soil-related niche diversity exists (Palmiotto et al. 2004), in the processes of natural regeneration, seed dispersal might well be the primary constraint.

Logging activities resulted in the loss of natural forest cover from 118.5 Mha in 1990 to 91.0 Mha in 2015 (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 E Kalimantan. They found that some of the early established shrubs and trees were replaced by a group of species including *Macaranga*, which may persist for a longer period where it gets established early on.

Logging activities in the peat-swamp forest of Central Kalimantan did not significantly change tree species richness at sample plot level but indicated a difference in species composition compared to undisturbed forest (Schofield 2015). Another study reported regeneration in peat-swamp forests in Riau after reduced impact logging (RIL) practices (using rail for log transport rather than canals) and found that species richness in tree seedlings was higher than that of undisturbed forest. Logging created gaps that enabled the regeneration of species that were not present in an undisturbed peat-swamp forest (Mawazin and Subiakto 2013). A recent analysis by Mahayani et al. (2020) of phylogenetic diversity, community structure, and composition of the Berau forests showed rapid recovery a decade after logging and post logging silvicultural interventions.

4.2 Wood density

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 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 & Hastaniah 2000) or pre-existing seedlings at the gap formation are other factors affecting natural regeneration (Nifinluri et al. 1999).

Natural regeneration after repeated fires in mineral soil was associated with light wood density trees. Increasing disturbance severity affected the dominance of lower wood density (Slik et al. 2008). Pioneer species of *Macaranga gigantea* was the most dominant species after fires (Rahayu et al. 2017) and contributed to a low average of wood density (Slik et al. 2008). *Macaranga* is responsive to forest disturbance and its peak biomass was 6 – 11 years after disturbance (Fiala 1996). In Malaysia, *Macaranga gigantea* was absent in 20 years cleared forest, but it was found in a secondary forest 4 years after disturbance (Niiyama et al. 2003). In Samboja Research Forest *Macaranga gigantea* was still dominant in 13 years after the second fires (Rahayu et al. 2017). The seed of *Macaranga* genus remains dormant in the soil until there is a disturbance (Fiala 1996). It's grown from seed buried in the soil (Kiyono & Hastaniah 2000). The decrease of very-heavy wood-density species, such as *Eusideroxylon zwageri,* in natural regeneration after repeated fires occurred despite its capacity to regrow from damaged trees, stumps and roots. However, with repeated fire events the populations decline (van Nieuwstadt and Sheil 2004).

Wood density composition after 20 years of natural regeneration in peatland forest, after logging and fires remained the same with that in undisturbed forests on mineral soil, with high proportions of heavy wood density trees more than 50%. *Shorea balangeran* (0.83 g cm^{-3}), *Cratoxylum arborescens* (0.76 g cm^{-3}) and *Tetractomia tetandra* (0.76 g cm^{-3}) are the most dominant tree species in the natural regeneration after logging. *Shorea balangeran* has wide ecological amplitude from open area in dry land, deep peat, even in burnt forest with *Imperata* grassland (Daryono 2006; Omon 1999). While in natural regeneration after fire (and after logging), *Syzygium* sp. (0.72 g cm^{-3}), *Tetractomia tetandra* (0.76 g cm^{-3}) and *Elaeocarpus parvifolius* (0.55 g cm^{-3}) were dominant. Colonized pioneer species of *Eugenia cerina*, the same family as *Syzygium* sp. also occurred in burnt forest plots in Giam Siak, Riau, Sumatra (Gunawan et al. 2012). *Shorea balangeran* demonstrated the best survival and growth performance in peatland compared to three other native species, namely *Dyera poyphylla, Calophyllum bifflorum*, and *Callophyllum inophyllum* (Tata & Pradjadinata 2016) due to availability of pneumatophores (Page et al. 1999).

Tropical peat swamp forests (TPSF) are characterized in part by small-scale variations in topography ('hummocks' and 'hollows') that create distinct microhabitats and thus may contribute to niche diversification among TPSF tree species, although very few species are real hollow-specialists, and most tolerate the wet conditions as long as their stem base can remain above the water level most of the time (Freund et al. 2018). Measurements of stem-based methane emissions from tropical peat swamp forests (Pangala et al. 2013) suggest that air-filled porosity in their wood must be considerable, although the relationship between wood density and recorded methane emission was not very strong.

In a village forest logged by the local community in Jambi, natural regeneration contained a high proportion (up to 70%) of heavy wood density trees and 10% of very heavy wood density trees. A similar condition was encountered in rubber agroforests, where the proportion of heavy wood trees reach 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, Aporosa* (Werner 1997). Gillison et al. (2013) discussed plant functional types and traits as biodiversity indicators in landscape D with a different method: sampling a gradient of land cover types with forests such as D1 and jungle rubber plots such as D2 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.

4.3 Seed dispersal

Seed dispersal mode patterns of natural regeneration changed after repeated fires in Samboja. 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 Ballen (2006), which was based on the study in 1988. Similar changes in dispersal modes were found between an undisturbed forest and natural regeneration in a logged forest in Berau; similarly, changes in natural regeneration were identified in a Sebangau peat-swamp forest after logging and fire. The availability of remnant forests as a habitat of frugivore animals as dispersal agents in Berau and Sebangau sites was an important factor. Natural regeneration and residual stands in a village forest logged by the local community in Jambi demonstrated a similar pattern to the undisturbed Berau forest.

Component analysis (Figure 8) showed that tree species with endo-zoochorous dispersal were closely associated with natural regeneration in the peat-swamp forest after fire and logging. Trees with endo-zoochorous dispersal were also associated with natural regeneration after logging both by the community in mineral soil and by commercial companies in peat soil, 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 on mineral or peat soils.

The CA (Figure 8) has shown that tree species with autochorous dispersal are closely associated with undisturbed forest in Berau. In a ha plot, there were 19 tree species with autochory dispersal, including 13 *Shorea* species and six *Vatica* species. Those findings are in line with research conducted by Sist and Saridan (1998) that 61 Dipterocarps species were found in 12-ha area of undisturbed forest in Berau. Trees with anemochory type dispersal are closely associated with natural regeneration after repeated fires in Samboja forest. Samboja forest was dominated by the pioneer tree species *Macaranga gigantea*, an anemochory species, that developed well 10 years after a forest fire in 1997/1998. Trees with hydrochorous dispersal were limited to undisturbed and disturbed forests both on mineral and peat soils.

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 Management implications

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 undisturbed condition. Late succession species persistent in logged-over forest and newcomer pioneer species regenerated in disturbed area resulted in similar species richness to 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).

Not much is known regarding genetic diversity within a species in response to disturbance/ regeneration events. Ang et al. (2016) found that levels of genetic diversity of naturally regenerating seedlings of two Dipterocarp 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. *Dyera polyphylla* has anemochorous seed dispersal, which enables the seeds to disperse far beyond the pollination distance (Tata et al. 2018).

Beyond seed production and seed dispersal agents, other factors may limit the natural regeneration of native trees in disturbed forests. After the forest fires of 1982/3, 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).

Our results align with a recent analysis for the Amazonian forests (Hawes et al. 2020) that used 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 confirmed 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.

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. 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 put together included 41% fewer species than the undisturbed forests. The proportional loss varied among groups, with loss of tree species showing an intermediate responsiveness compared to various animal groups. Disturbed local communities are dominated by widespread species.

Returning to the central questions 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, 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 Figure 9 need to be connected (van Noordwijk, 2020).

Conclusions

Lowland forests in Kalimantan, both disturbed and undisturbed, contained high tree species richness. The tree species richness in mineral soils was higher than in peat soils. 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 was different from those in Samboja, 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) Community-scale wood density frequency and dispersal modes indicate forest disturbance history; 2) Kalimantan mineral-soil forests are richer in tree species than Sumatran or peat-swamp forests; 3) The majority of trees (50-70%) had birds, bats and primates as dispersal agents in all sites; 4) Forests recovering from repeated fires had a markedly increased fraction of low-wood-density trees; 5) Agroforest tree species richness shaped by past forested landscape mosaics may be non-reproducible.

Declarations

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.

Availability of data and material

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

Competing interests

The authors declare no competing interests.

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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 Noorwijk drafted the manuscript; Hesti Lestari Tata, Endri Martini provided inputs to the manuscript, Hani Nurroniah provided language editing and all co-authors read and approved the manuscript in its current form.

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Tables

Table 1. Tree observation data used in the analysis

Code	Location and background	Total sample, ha	Number of observed plots	Plot size (m)	Year of obser-vation	Source
A1	Undisturbed lowland mixed Dipterocarp forest in Samboja Research Forest, East Kalimantan,	1.8	180	10 x 10	1981	Kartawinata et al. (2008)
A2	Natural regeneration lowland Dipterocarp forest in Samboja, East Kalimantan 28 years after affected by repeated fires	1.8	180	10 x 10	2011	Rahayu et al. 2017
B1	Undisturbed lowland mixed Dipterocarp forest in Berau, East Kalimantan	1	100	10 x 10	2004	Rahayu et al. (2016)
B2	Natural regeneration forest 15 years after logging in Berau, East Kalimantan	1	100	10 x 10	2004	Rahayu et al. 2016
C1	Natural regeneration 20 years after logging and fire in peat-swamp forest of Mangkok resort of SNP, Central Kalimantan	2.7	270	10 x 10	2018	Unpublished
C2	Natural regeneration 20 years after logging in peat-swamp forest of SNP - PFNL, Palangkaraya, Central Kalimantan	2.7	270	10 x 10	2018	Unpublished
D1	Natural regeneration and residual trees after logging of a village forest that was managed by a community in Jambi, Sumatra	1.8	45	20 x 20	2012	ICRAF Database
D2	Rubber agroforest with low intensive management, selective weeding in Jambi, Sumatra	4.4	110	20 x 20	1998 - 2012	ICRAF database

Table 2. Nearest neighbor distances* for the sample plots to ‘any forest’ (including secondary and agroforest), to primary forest (pixel level) and intact forest landscape (minimum 20 ha of primary forest)

	To any forest	To primary forest	To intact forest landscape
	km	km	km
A2	6.2	10.0	11.4
B2	0.0	0.0	23.0
C1	0.0	>40	53.5
C2	0.0	>40	84.8
D1	0.0	4.9	19.0
D2	0.0	6.9	6.9

* Distances to nearest sampling plot

Figures

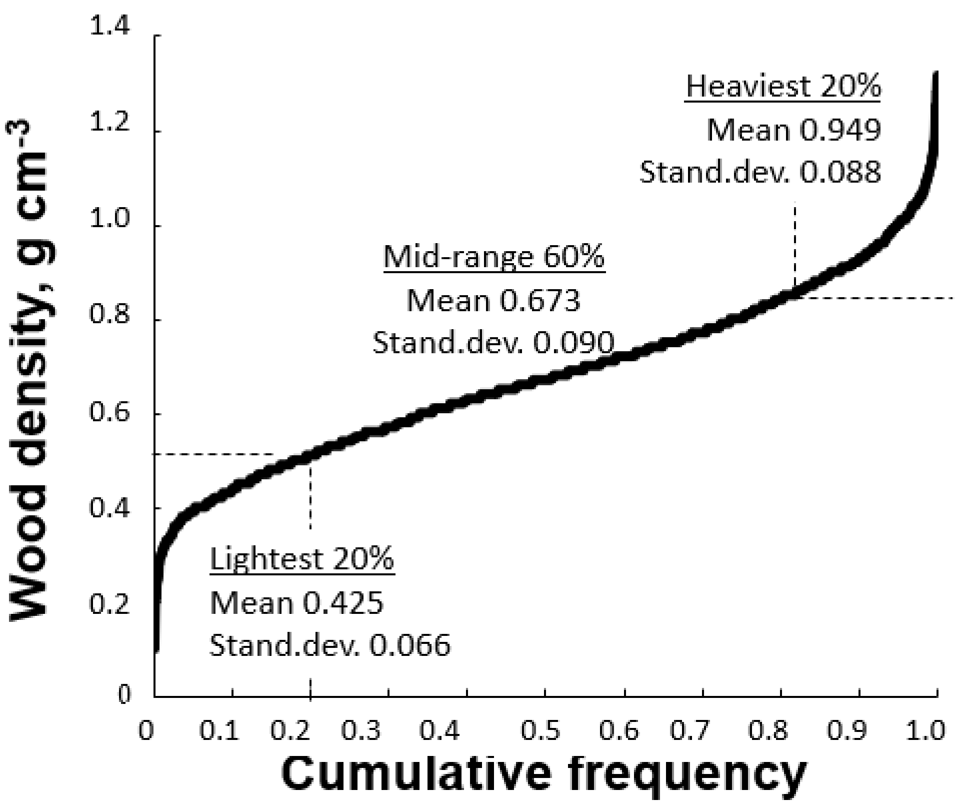

Figure 1

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

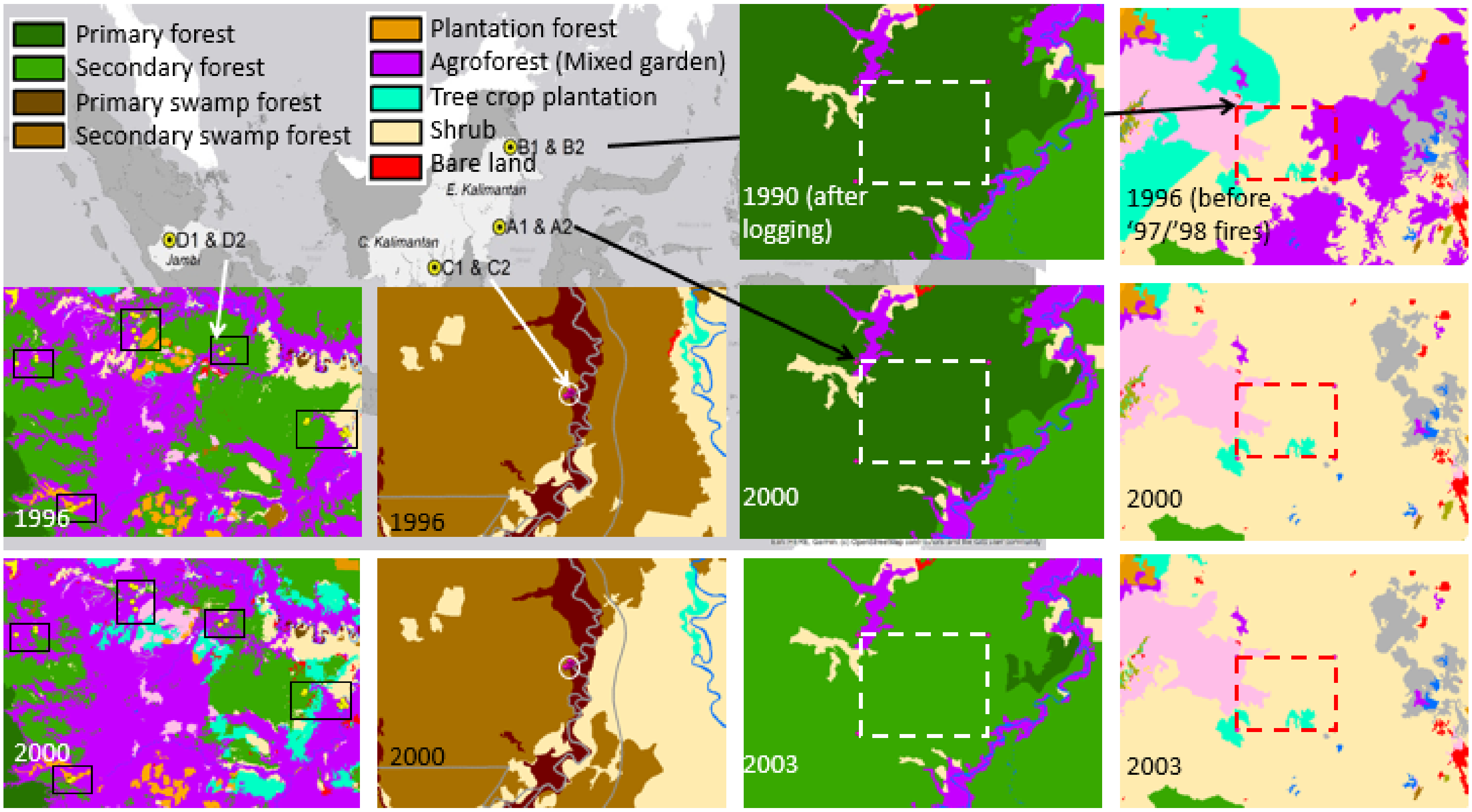

Figure 2

MAP of locations, with inserts of interpreted satellite imagery of the surrounding vegetation in the initial years of recovery Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 3

Classification for pollination and seed dispersal based on botanical descriptions (van Noordwijk et al. 2019)

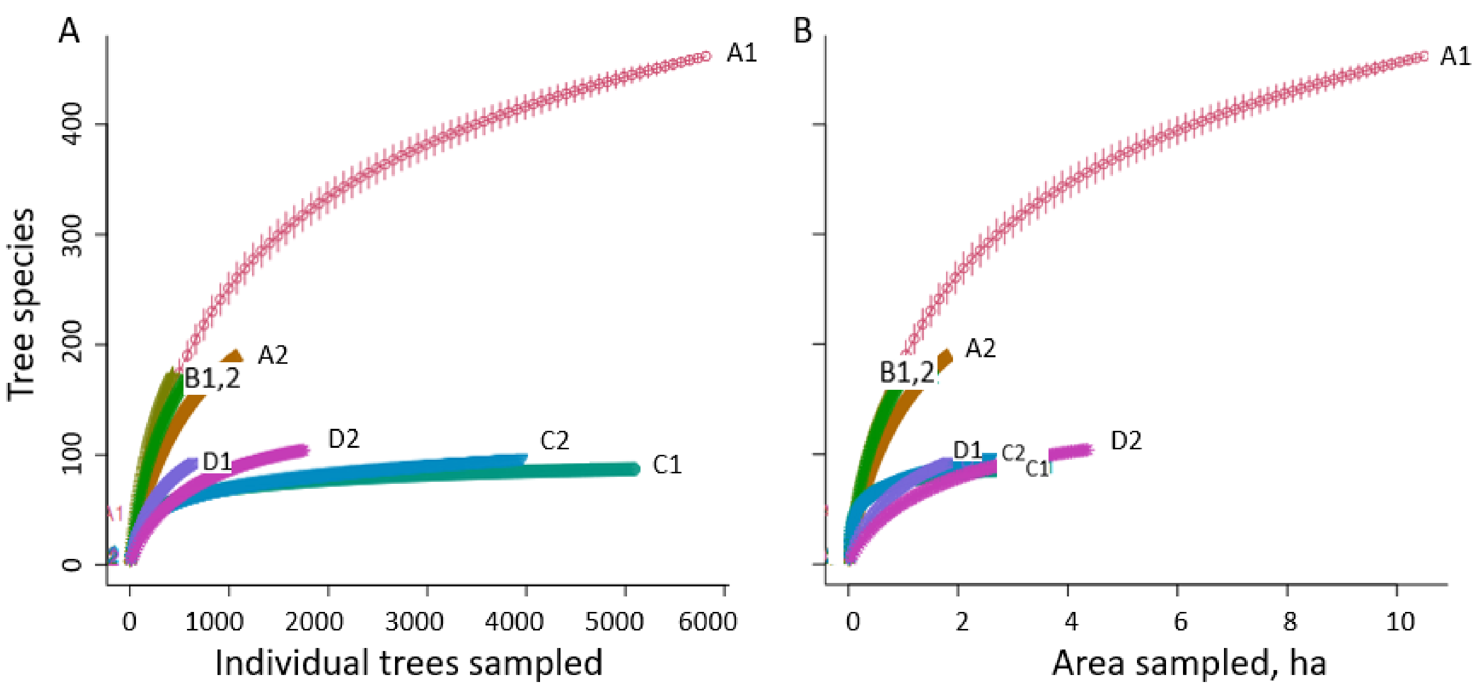

Figure 4

Tree species richness in the eight types of (secondary) forests, in relation to the number of trees encountered (A) or area sampled (B), based on rarefaction analysis

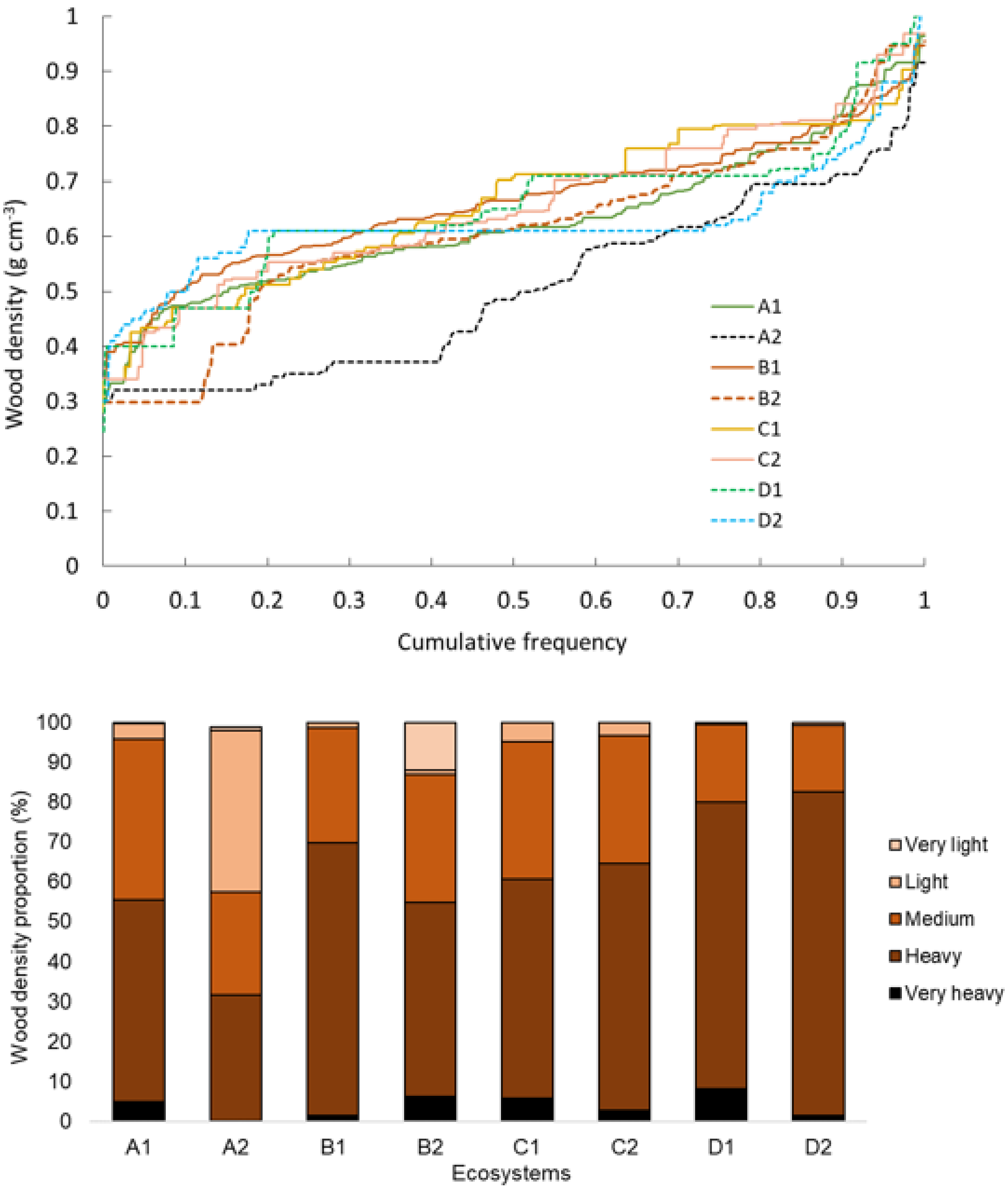

Figure 5

5A. Wood density profile based on cumulative basal area in undisturbed forest, naturally regeneration after disturbance and rubber agroforest 5B. Wood density proportion in undisturbed forest, naturally regeneration after disturbances and rubber agroforests

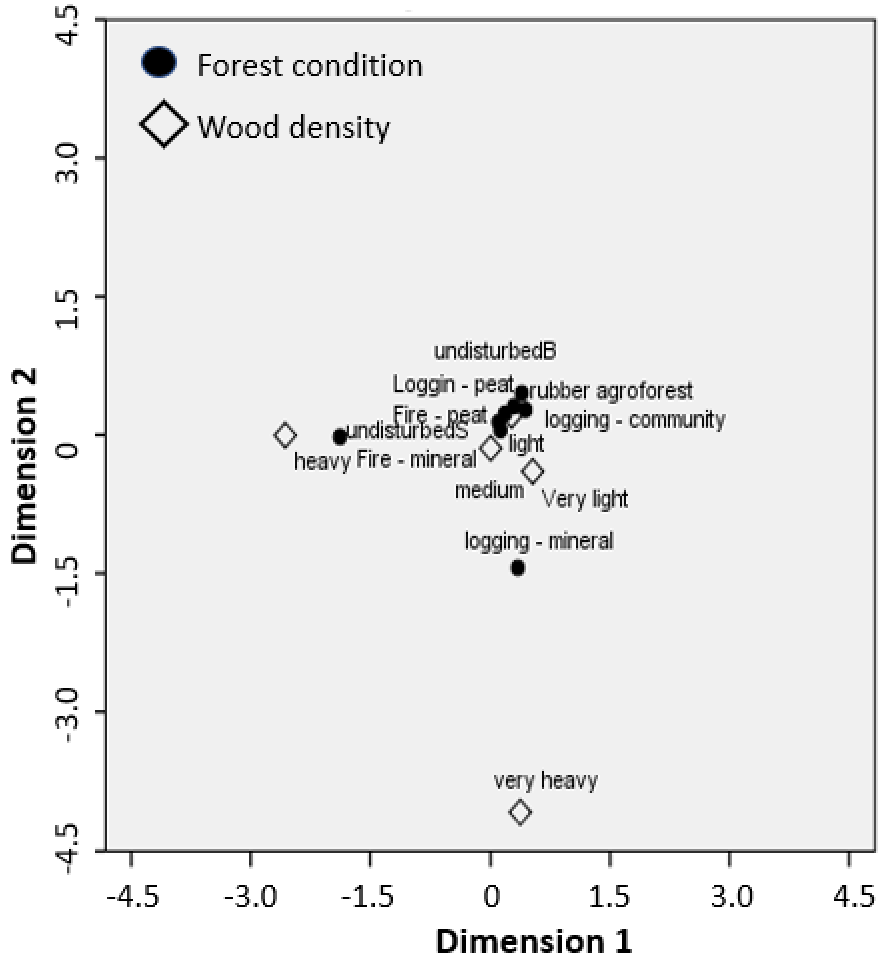

Figure 6

Correspondence analysis (with symmetrical normalisation) of wood density profiles of tree species in undisturbed forest, naturally regeneration after disturbances and rubber agroforest

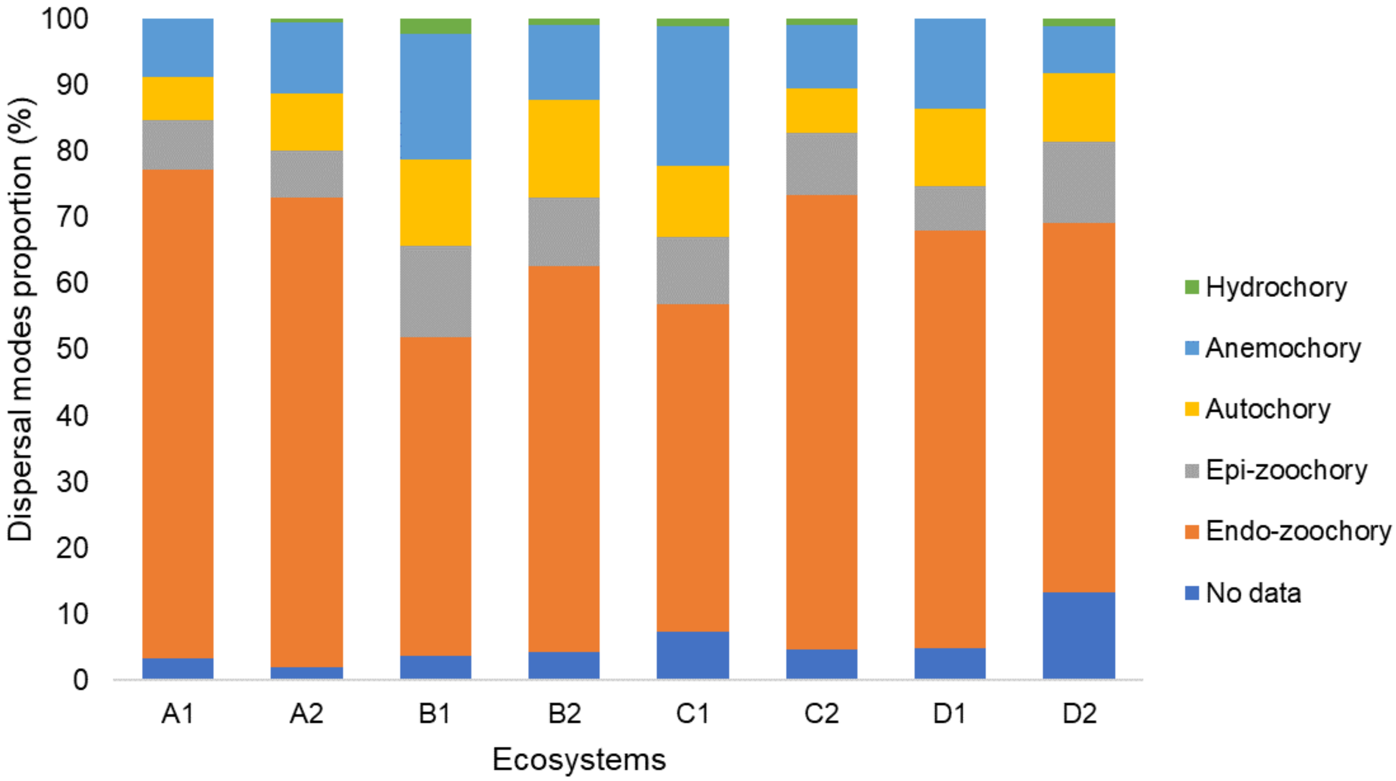

Figure 7

Dispersal modes proportion in undisturbed forests, naturally regeneration after disturbances and rubber agroforests

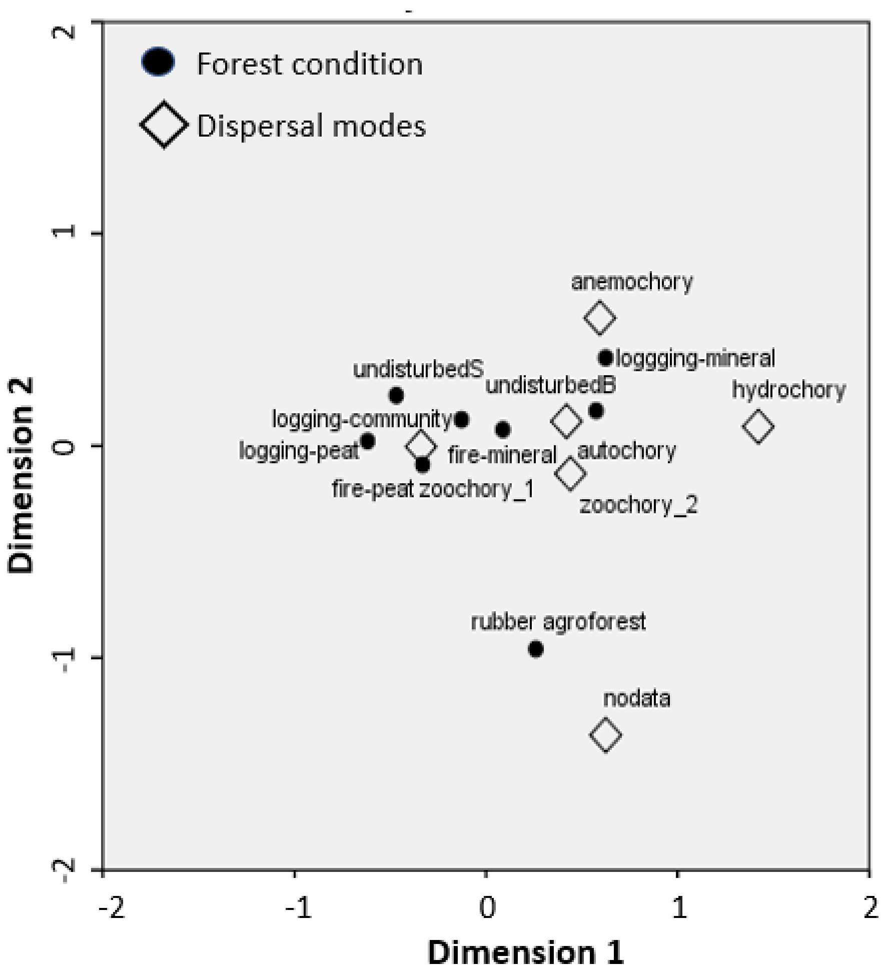

Figure 8

Correspondence analysis of dispersal modes of species in undisturbed forest, naturally regeneration after disturbance and rubber agroforest

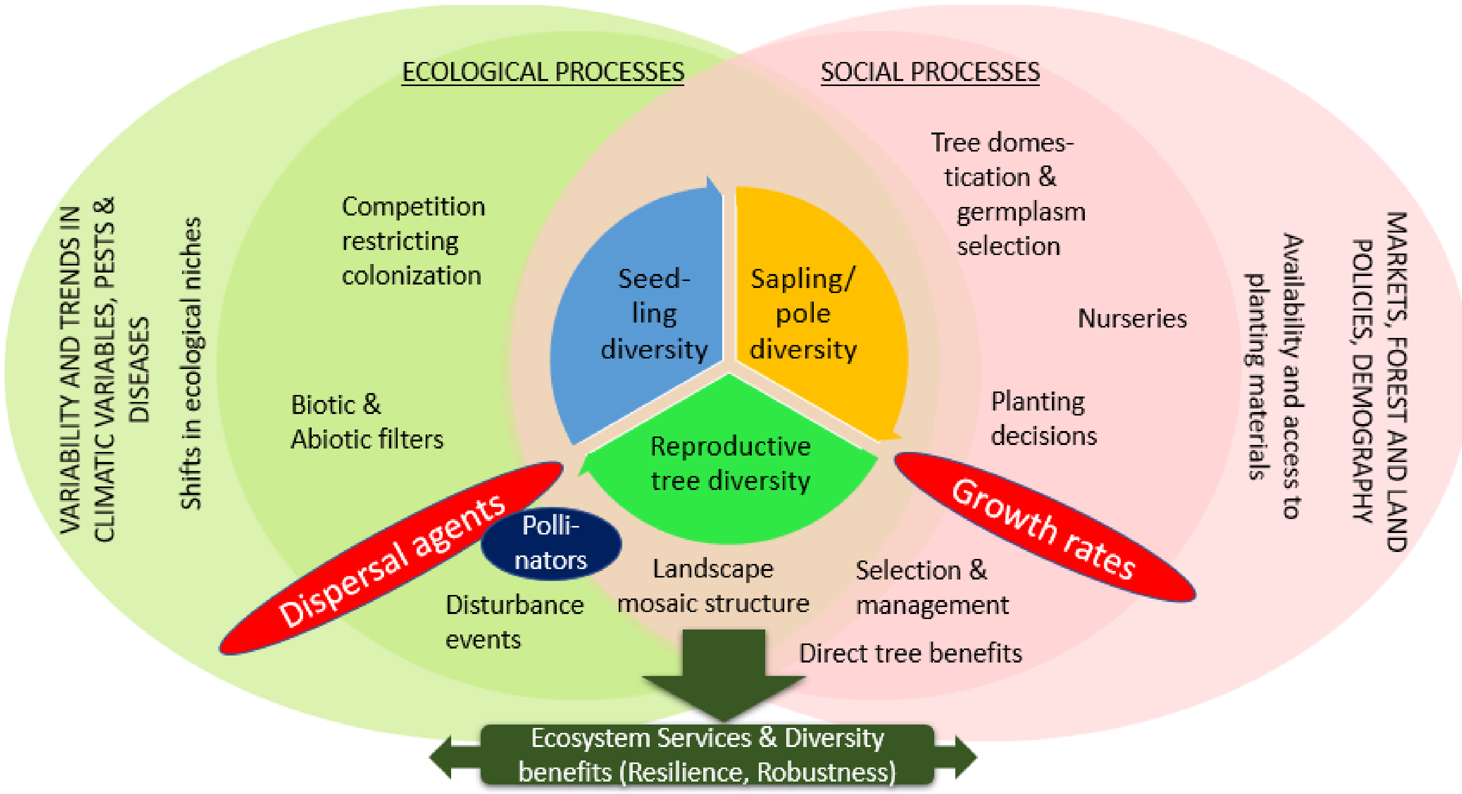

Figure 9

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)