RAINFOREST REGENERATION IN FRAGMENTED FOREST LANDSCAPES

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Abstract

Rainforests are severely threatened by agricultural expansion, frequently resulting in the fragmentation of formerly extensive tracts of continuous forest. The immediate and longer-term effects of fragmentation on tree regeneration, and on alpha- and beta-diversity, remain poorly understood. Forest area and isolation can drive changes in diversity, and may be key considerations for conserving forest biodiversity in human-modified landscapes. I studied trees, saplings, and seedlings (pre- and post-fragmentation recruits), in 14 forest fragments and 5 continuous forest sites in Sabah, Malaysian Borneo. Local alpha-diversity of seedlings was significantly lower in fragments than in undisturbed continuous forest, and lowest in the smallest fragments, potentially signalling an extinction debt. However, saplings showed no declines in alpha-diversity, suggesting that density dependent mortality and/or year-to-year variation in recruitment may compensate for reductions in seedling richness: low seedling diversity may not necessarily translate into low sapling diversity. Nonetheless, 57-64% of genera in small fragments occurred only as adult trees, with no seedlings present, indicating a recruitment failure of some genera. This contributed to greater distinctiveness (increased beta-diversity) of seedling communities in small fragments, which were diverging from trees in the same fragment, and from seedlings in other fragments. Divergence, which has not yet been observed in mature trees, may continue as seedling cohorts mature, causing fragment communities to follow different trajectories of change. Regeneration of 25 functionally-important dipterocarp species was reduced in fragments by almost half (comparing four fragments and four continuous forest sites), but some dipterocarps were still recruiting seedlings effectively in fragments. Collectively, the research shows that there may be some taxonomic impoverishment within fragments (reduced plot-scale alpha-diversity; possible losses from entire fragments), but that continued recruitment in fragments is resulting in increasingly divergent plant communities (increased beta-diversity). Hence, forest fragments continue to make a valuable contribution to landscape-scale diversity and warrant future protection.

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Author's declaration

I declare that the work presented in this thesis is my own. This work has not previously been presented for an award at this, or any other, University.

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All chapters are reproduced in full in this thesis, with minor formatting alterations. The text was written by myself with input from JKH and CDT. AJ helped with data collection and SB provided logistical support for fieldwork. JH and MJMS also contributed to revisions. The study was supervised by JKH, CDT, CM, JH, and MJMS.

CHAPTER 1

General introduction

Due to the widespread and pervasive influence of humanity on the planet it is becoming widely accepted that we have entered into a new geological epoch – the Anthropocene (e.g. Malhi et al. 2014). Even in the farthest reaches of remote tropical rainforests human impacts are increasingly in evidence, and in more accessible regions human development has transformed landscapes, turning vast areas of diverse continuous forest into agricultural monocultures (Gibbs et al. 2010). An increasing global human population needs more land and more resources, leaving progressively less space to nature. One of these resources is vegetable oil, and consequently the area of land under oil palm cultivation has steadily increased from 4.3 million ha in 1980 to 42.8 million ha in 2014 (FAO 2016), often at the expense of previously intact lowland tropical rainforest (Fitzherbert et al. 2008). Agricultural expansion of this kind tends to leave remnants of forest isolated within vast swathes of cropland, with varying impacts on the forest community therein (Fischer & Lindenmayer 2007).

Trees are a fundamental component of forests, determining physical microclimatic conditions as well as influencing important ecological processes, and tree species diversity is important for maintaining forest ecosystem function (Hooper et al. 2012). Tropical rainforests are some of the most diverse ecosystems on earth (LaManna et al. 2017), and play a vital role in climate regulation and carbon sequestration (Pan et al. 2011, Bonan 2008). Remnants of such forests are likely to represent unique combinations of tree species that in turn support unique combinations of numerous other taxa (e.g. Arroyo-Rodríguez et al. 2012, Williams-Linera et al. 2002). It is therefore important to understand whether or not these forest remnants will continue to be important reservoirs of biodiversity into the future, and thus worth conserving on this basis, potentially at the expense of other areas of forest if targets for the total area of forest protected in the region are met.

In this thesis, I examine how tree recruitment is impacted by forest fragmentation, and discuss how tree diversity in forest fragments may be affected in future as a result. This introductory chapter provides a background to the key questions that are interrogated later in the thesis, as well as highlighting important gaps in scientific knowledge in this field. First I discuss the exceptionally high diversity of tropical forest ecosystems and how ecological diversity is measured. I then discuss the threats to tropical forests in general, the threats to biodiversity posed by habitat fragmentation, and more specifically the impacts of forest fragmentation on trees. I next introduce the concept of biodiversity hotspots and describe the Sundaland biodiversity hotspot in Southeast Asia, which is formed of the archipelago of islands that include Borneo, where this study was conducted. I then discuss the impacts of forest loss and fragmentation on trees in the Dipterocarpaceae, a family of trees that dominates the study region. I next introduce the study region and present background information on the sites I surveyed, and finally provide an outline of the key aims and hypotheses addressed in each chapter of this thesis.

1.1 Why are tropical forests so diverse?

Ecological diversity can be difficult to define and quantify, partly due to the various resolutions and scales at which it can be measured. These range from genetic to ecosystem diversity, from local to global scales, and from the diversity present at a given location (alpha diversity) to the differences in the organisms present in different locations (beta diversity). Thus, genes, species, traits, and presence or absence in a quadrat (for some examples) can all be appropriate sampling units in different situations (Gotelli et al. 2013). It is also challenging to quantify diversity as it consists of two fundamental components: richness and relative abundance (Magurran 1988). Richness is the number of e.g. species in a specified area, and is arguably the simplest and most intuitive measure of alpha diversity. However, the relative abundance of species provides additional information on the dominance, rarity and evenness of the species present. Richness and abundance estimates can be used to compare the alpha diversity of spatially-defined units, and differences in the community composition of two such units can be measured as beta diversity (Magurran 2004). Many different metrics are available for quantifying beta diversity in order to examine differences in community composition (Tuomisto 2010). Measuring ecological diversity by choosing appropriate alpha and beta diversity metrics can provide a way of distinguishing and comparing ecosystems, habitats, and taxonomic groups.

There are an estimated 300,000 species of angiosperm (flowering plants) and a further 650 species of gymnosperm globally (Prance 2000). These species are not distributed evenly across the globe, and some regions have orders of magnitude more species than others. Among other things, the interaction of climatic history, higher speciation rates, and stronger negative density-dependent interactions between plant species and their natural enemies, have led to a disproportionate amount of global diversity being located in the tropics (LaManna et al. 2017, Mittelbach et al. 2007). Tropical rainforests represent some of the most species-rich ecosystems on earth, and Amazonia and Southeast Asia typically have upwards of 150 tree species per hectare (Phillips et al. 1994): on average six times more than an equivalent area of temperate forest (Novotny et al. 2006). Many hypotheses have been developed over the course of the last few centuries which attempt to explain how the latitudinal gradient in diversity, with low diversity towards the poles and high diversity at the equator, evolved in time and space. These hypotheses are not necessarily mutually exclusive, and can be broadly classified into those pertaining to genetic differentiation, environmental change, niche and/or habitat diversification, or biotic interaction (Figure 1.1, Brown 2014, Hill & Hill 2001). It is likely that the diversity gradient developed through a combination of interacting factors, and it is becoming increasingly possible to test certain key hypotheses as a result of advances in phylogetic tools and greater data availability.

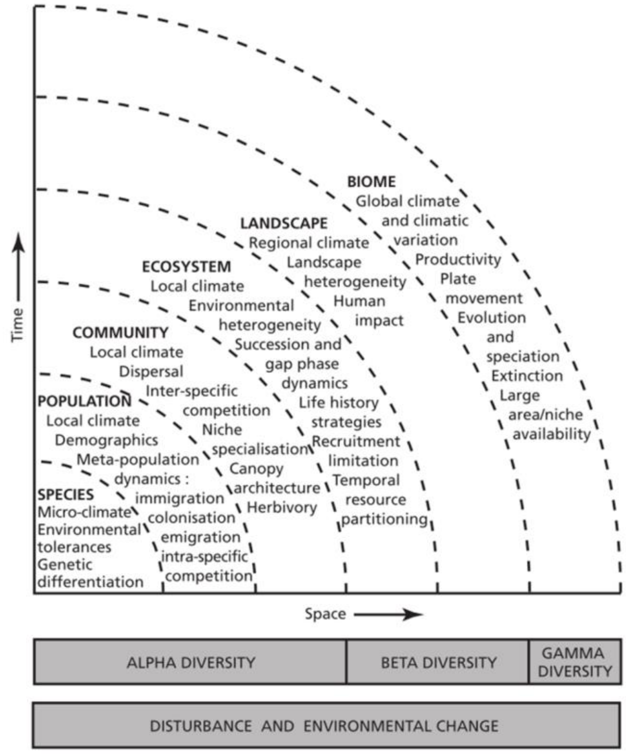

Figure 1.1. Multiple hypotheses have been developed to explain the latitudinal diversity gradient, which has arisen and is maintained through a combination of spatial and temporal processes (figure from Hill & Hill 2001, reprinted with kind permission from SAGE publishing).

One mechanism driving maintenance of plant diversity in tropical forests is the Janzen-Connell effect of negative density dependence, whereby (1) seedling survival increases with distance from the parent tree, and (2) common species at high population densities are likely to experience attacks from specialised natural enemies and thus have a lower survival rate than occasionally occurring rare species (Connell 1971, Janzen 1970). Because high conspecific density has a negative effect on seedling recruitment and survival, individuals of rare species are more likely to survive, maintaining high species diversity. Although this mechanism operates in both tropical and temperate regions, the strength of conspecific negative density dependence increases towards the equator (LaManna et al. 2017), possibly resulting from greater intraspecific competition for resources, or due to a higher frequency of specialized insects in the tropics (Forister et al. 2014).

This general pattern of declining diversity with distance from the equator is not exclusive to plants, and has been observed across many groups of macro-organisms. For many years it has been debated whether the tropics represent a “cradle” or a “museum” of diversity, i.e. the result of recent and rapid speciation, or gradual accumulation, preservation, and low extinction rates of species over time in the stable and favourable climate near the equator (Stebbins 1974). Relatively recent advances in phylogenetic tools have allowed this theory to be tested empirically on a range of taxa, and many studies now indicate the tropics to be both evolutionary cradles and museums of diversity (e.g. ants: Moreau & Bell 2013, leaf beetles: McKenna & Farrell 2006, and trees: Pennington et al. 2015). Palaeontological and phylogenetic data provide evidence for higher rates of origination and diversification in the tropics: as well as being more likely to originate in the tropics and persist there for longer, the majority of taxa found outside of the tropics belong to lineages that originated in the tropics and continue to persist there (Jablonski et al. 2006, Mittelbach et al. 2007).

It is thought that time and area have both played an important role in providing greater opportunity for diversification in the tropics: relative to the tropics, temperate zones have experienced greater climatic fluctuations through time and consist of relatively smaller areas of similar environment, restricting the potential for species to spread and diversify (Chown & Gaston 2000, Mittelbach et al. 2007). However, these diversity patterns that are nearly ubiquitous in macro-organisms are less well understood among micro-organisms, which may be subject to a different set of drivers. While some fungal groups are most diverse in the tropics, others show the reverse pattern (Peay et al. 2016), and soil bacterial diversity is unrelated to latitude and largely explained by soil pH (Fierer & Jackson 2006). It remains an on-going challenge to determine the relative importance of the many competing theories explaining the latitudinal diversity gradient in macro-organisms, but it is becoming increasingly possible to test them due to continuing advances in many fields of biology and biogeography, and the development of new analytical tools (Mittelbach et al. 2007). However, local and regional diversity is becoming increasingly dictated by human-mediated habitat disturbance and destruction, which can drastically reduce the number of species in an area, for example via the replacement of natural forest with agricultural land, or via non-sustainable use of ecosystems: for example intensive commercial logging or a high intensity of poaching.

Island biogeography theory (IBT, MacArthur & Wilson 1967) cites habitat area and isolation as the key drivers of species richness, acting together to shape population and community dynamics. It emphasises the importance of large areas of habitat, which contain more species and more individuals of each species, reducing the likelihood of extinction. It also emphasises the role of connectivity in enabling immigration and movement between habitat patches/islands, similarly reducing local extinction rates. These ideas have played an important role in our approach to nature conservation, as habitat destruction worldwide is resulting in increasingly fragmented (formerly continuous) natural ecosystems (Laurance & Bierregaard 1997, Laurance 2008, see section 1.2). IBT relates to how empty islands are colonised, rather than how established communities go extinct, and a greater loss of area is required for the extinction than for the arrival of a species (Rybicki & Hanski 2013, He & Hubbell 2011), however the relationship is broadly similar. As a result, habitat fragmentation is likely to be a key driver of the species richness of habitat remnants, and the impacts scale with the size of the habitat patch and its degree of isolation, so that the smallest, most isolated patches are expected to have the fewest species. Thus, IBT has helped to shape the SLOSS debate – whether a ‘single large’ reserve is better than ‘several small’ ones. The answer to this is more nuanced than a straight-forward species-area relationship and largely depends on the nestedness of the biota within the reserves: several small reserves may conserve more diversity than a single large one if they share few species (e.g. Arroyo-Rodriguez et al. 2009). It must also be taken into account that communities on an island surrounded by water are likely to experience greater isolation than communities within a forest patch of similar size and distance from other patches of nearby habitat. The permeability of the matrix of land surrounding a forest patch is also likely to vary substantially depending on the nature of the matrix (e.g. pasture land, urban land, plantation crop etc.; Fitzherbert et al. 2008), and on the forest species in question, which will vary widely in mobility and dispersal ability. Despite these caveats, IBT has provided a useful conceptual framework for understanding some of the effects of habitat fragmentation. The species-area relationship in human-modified landscapes has been widely studied and discovered across a range of taxa inhabiting patches of habitat (e.g. ants: Brühl et al. 2003, birds and insects: Hill et al. 2011, birds: Boscolo & Metzger 2011, bats: Struebig et al. 2008), but there remain gaps in the scientific literature. It is important to fill these gaps in order to be able to predict the severity of fragmentation effects on understudied taxa such as forest trees in Southeast Asia.

However, more factors than fragment area and isolation are important in determining patterns of species diversity in habitat fragments, and these factors are discussed in more depth in the next section.

1.2 Threats to tropical diversity and the impact of habitat fragmentation

Biodiversity has intrinsic value, as well as mechanistic and cultural value. It is increasingly recognised that loss of diversity has negative consequences for ecosystem function and resilience (Hooper et al. 2012). Although increasing tree diversity doesn't necessarily translate directly into higher carbon stocks (Sullivan et al. 2017), erosion of biodiversity may reduce the ability of ecosystems to maintain important functions such as carbon storage and nutrient cycling (Maestre et al. 2012). Forest degradation and conversion to agriculture are important anthropogenic threats to tropical diversity (Newbold et al. 2015), and simultaneously threaten ecosystem functioning and local economies reliant on use of forest resources (Hoekstra et al. 2005). Degredation commonly occurs as a result of commercial logging, which falls into three broad categories of transformation: selective logging, clear-felling where the land is retained as forestry, and clear-felling followed by conversion to other land uses (e.g. oil palm). Selective logging is the least destructive but alters forest structure and tree community composition by removing large individuals of commercially valuable timber species (Wilcove et al. 2013). The impacts on biodiversity and ecosystem function depend on the intensity of logging and number of rotations, which dictate the level of degradation of the forest that remains. In a pan-tropical meta-analysis, Burivakiva et al. (2014) found a significant relationship between increasing logging intensity and decreasing species richness of invertebrates, amphibians, and mammals, and that although the species richness of habitat generalist birds increased with logging intensity, forest specialist birds declined. However, selectively logged forest can retain a substantial proportion of the biodiversity of primary forest (e.g. twice-logged forest in Southeast Asia retained 75% of the bird and dung beetle species found in adjacent primary forest and there was no significant difference in the microclimates of understory microhabitats; Senior et al. 2018, Edwards et al. 2011), and so recovering selectively logged forest can act as an important buffer to areas of primary forest.

Additional impacts of commercial logging result from roads constructed for access to forest interiors, creating edges which alter the more stable interior environment of the forest and forming a barrier to movement of specialist forest-interior species (Benítez-López et al. 2010). Roads also open up access to forest interiors, facilitating deforestation (Barber et al. 2014) and defaunation via poaching (Laurance et al. 2009). In spite of this disturbance logged forests retain biodiversity value, but are vulnerable to clearance and conversion to agriculture due to their low timber values (McMorrow & Talip 2001). Agricultural expansion is a major threat to remaining primary and logged tropical forest worldwide (Gibbs et al. 2010). The increasing human population, increasing per capita consumption of meat, and increasing use of crop-based biofuels, have resulted in a large increase in the amount of agricultural land required globally, despite increasing yields. Cropland and pasture now occupies nearly 40% of terrestrial land area (Foley et al. 2005) and this area is projected to continue to increase (Laurance et al. 2014). Between 1980 and 2000 more than 83% of new agricultural land in the tropics came at the expense of disturbed or intact forest (Gibbs et al. 2010). Not only does conversion of a species-rich forest ecosystem to crop land result in landscape simplification and a reduction in species richness (Landis 2017), it disrupts a range of ecosystem functions provided by forested land, including water cycle regulation and carbon storage (Foley et al. 2005). Oil palm plantations, for example, only support around 15% of the species found in primary forest (Fitzherbert et al. 2018). The development of high-yielding cultivars has increased crop yields, but yield increases are also due to use of chemical fertilizer and pesticides, leading to water pollution and suppression of non-crop species, further reducing biodiversity in agricultural landscapes. Although certain low intensity systems, such as agro-forestry (Bhagwat et al. 2008), can sustain a moderate level of biodiversity, industrial-scale monocultures of soy, oil palm, rubber, or acacia are highly detrimental to most non-crop species (Gibson et al. 2011). Thus, not only are extensive tracts of natural habitat lost, but they are replaced by high-intensity cropland that can provide a considerable barrier to many forest species, preventing their movement across the landscape and isolating remaining areas of native habitat.

Forest loss as a result of agricultural expansion frequently creates forest fragments. Forest loss and fragmentation are amongst the greatest threats to global diversity, and are major causes of declining local diversity (Haddad et al. 2015, Hanski 2015), leading to local, regional, or total extinctions of species, especially those restricted in range (Brooks et al. 2002). The number of forest fragments globally is predicted to increase in tandem with a decrease in the average fragment area (Taubert et al. 2018). Species vary in terms of their vulnerability to habitat fragmentation, and certain traits, such as dispersal ability, fecundity, life history strategy, and generation time, may make them more or less vulnerable (Scriven et al. 2015, Ewers & Didham 2006). In addition, dispersal and re-colonisation patterns of habitat fragments are affected by the spatial configuration of the fragments across the landscape, and the suitability of the intervening matrix for species dependent on fragment habitat (Forman 1995). Thus, fragmentation effects can vary markedly depending on the taxa studied, the geographic location, the configuration of the landscape, and the nature of the land cover separating areas of similar habitat. Quantifying the number and relative abundances of species (or genera etc.) in samples of a given size facilitates comparisons of diversity in equivalent areas of forest that have undergone varying levels of human impact, for example, in forest fragments of different sizes. Such insights can inform conservation strategies, and are a focus of this study.

Figure 1.2. Clockwise from top left: a forest fragment surrounded by oil palm plantations; looking out over an oil palm plantation to a distant fragment of forest; palm fruits; structural simplification of environment inside an oil palm plantation relative to native forest (photo credit: G. Stride).

Habitat fragmentation and its impacts on trees

This thesis focuses on fragmentation effects on trees because they represent the key structural elements of forest fragments, and they carry out most of the photosynthesis upon which the rest of the ecosystem ultimately depends. Deforestation and habitat fragmentation have direct impacts on several aspects of tree diversity, as well as longer-term impacts that continue to manifest as a result of the physical and biological changes characterising habitat fragmentation. Either because areas within a concession are unplantable, or due to some form of protection, deforestation of previously forested land results in remnant patches of forest that are typically surrounded by agricultural land. The high tree species diversity of tropical rainforest is associated with low population densities, and many tree species have fewer than one reproductive individual per hectare (Primack & Hall 1992). Thus, forest fragmentation, which results in an immediate reduction in population size, may cause tree species to become isolated from external pollen sources by the intervening matrix. This can result in pollen limitation and reduced seedling recruitment or complete seedling recruitment failure (Aguilar et al. 2008).

Fragmentation of rainforest alters abiotic conditions by reducing forest area and increasing edge habitat, resulting in greater exposure to desiccation, higher wind speeds, higher light levels and temperatures, and greater variability in temperature (Laurance 2000). Edge effects may extend as far as 1.5 km into tropical forest (Chaplin-Kramer et al. 2015), though the most extreme are within 100 m of the edge (Laurance et al. 2002). As a result of forest fragmentation nearly 20% of the world's remaining forest is within 100 m of an edge (Haddad et al. 2015), and owing to the high edge to area ratio, fragmentation effects are generally more severe in smaller fragments (Haddad et al. 2015). Larger fragments tend to retain core areas more similar in forest structure and species composition to primary forest if they are not otherwise impacted by human activity such as logging or poaching (Rutledge 2003). Fragmentation frequently leads to changes in species richness (usually downwards) and species composition (in favour of disturbance-loving species) within a fragment (Rutledge 2003), although the trajectory of community composition change can be highly variable among fragments (Arroyo-Rodríguez et al. 2013). However, fragmentation impacts are variable across species with different generation times and dispersal abilities, and trees, which have very long generation times, may persist for many decades in a fragment without recruiting viable offspring. This creates an extinction debt that may continue for several centuries (Vellend et al. 2006, Tilman et al. 1994), meaning that the immediate detrimental impacts of fragmentation are often under-estimated. Extinction debts can, however, be detected by identifying whether trees are failing to recruit seedlings in forest fragments.

Another frequently reported consequence of forest fragmentation is defaunation due to poaching, as a result of increased access (Canale et al. 2012), and also due to limitation of movement of animals between patches (Kolb 2008). As a consequence, a number of key ecological process including pollination, seed dispersal, seed predation, and seedling herbivory, as well as decomposition and nutrient cycling, can be altered, with important consequences for plant diversity (Casante et al. 2002, Harrison et al. 2013). Seedling survival may also be reduced if seeds are not moved away from parent trees, due to increased density-dependent mortality (Wright 2002). Although the effects of defaunation tend to be detrimental to seedling recruitment and survival, reduced population sizes of pre-dispersal seed predators, herbivores and pathogens in fragments, may result in increased seed survival, seedling germination and seedling establishment (Granados et al. 2017). All of these altered processes may lead to long-term changes to the biological community, which are not necessarily evident immediately after fragmentation.

Certain life history characteristics may make species more or less vulnerable to the negative effects of fragmentation. Previous studies have shown that species with abiotic seed-dispersal mechanisms tend to be more prevalent in defaunated forests (Harrison et al. 2013), and wind-dispersed trees tend to be taller and have greater dispersal ability than animal-dispersed trees (Williams et al. 2016), and thus may be better adapted to persist in fragmented forest. The matrix of land surrounding forest fragments frequently consists of agricultural habitats that are inhospitable to forest species, rarely supporting forest trees outside of patches of forest, with a high mortality rate for seeds arriving into the agricultural area. Thus, immigration into isolated forest fragments is limited to species with high dispersal capacity (bird-dispersed or light-weight wind-dispersed seeds) able to arrive directly from areas of forest, and becomes increasingly uncommon as isolation increases (Cook et al. 2005, Yao et al. 1999). Isolated trees relying on animals for pollination and seed dispersal may experience declines in recruitment success.

Tree traits can often serve as useful proxies for other life history characteristics and can be used to assess species’ performance in response to forest fragmentation, giving insights into impacts on groups of species sharing the same trait. Wood specific gravity, henceforth referred to as wood density, is often used as a proxy for growth rate, and reflects wood quality and the partitioning of carbon inside a tree (Osunkoya et al. 2007). Along with light interception, it is a major determinant of tree growth rate, and these factors together explain a considerable proportion of variation in growth rate within a size class of tree in a given patch of forest (King et al. 2005). Species with a lower wood density tend to grow faster, and can respond rapidly to changes in the light environment, for example when a large tree is felled and gaps in the canopy open up. However, these species often have high mortality rates in low light. In contrast, tree species with higher wood density exhibit slower growth rates and reduced mortality due to greater investment in structural reinforcement. Seedlings of high wood density species have higher survival rates than low density tree species, but slower growth in the low light levels of the forest understory (Philipson et al. 2014, Walters and Reich 1996). At least initially, forest fragmentation and disturbance tend to create a higher light environment in the understory due to gap and edge creation, so it might be expected that pioneer-type low wood density species begin to proliferate in fragments, at the expense of shade-tolerant high wood density species. In this study we investigate whether wood density plays a role in the recruitment success of dipterocarps (trees in the Dipterocarpaceae family) in forest fragments.

Another trait that can provide insight into the effects of fragmentation on tree populations is flower size, which tends to correspond with pollination syndrome: in general smaller-bodied insects pollinate smaller-flowered tree species, whereas larger-flowered species are often pollinated by larger-bodied insects (Kettle et al. 2011). As a result mean pollen dispersal distance tends to increase with flower size, assuming larger-bodied insects are better dispersers (Breed et al. 2013). Low population density is common for tree species in tropical forests, and pollinators are adapted to the long distances between individual trees (Janzen 1971). This ability may in some way buffer the genetic effects of forest fragmentation if populations in neighbouring fragments are nonetheless united by the pollinators that travel between them (Kramer et al. 2008, Dick et al. 2003, White et al. 2002). However, a number of studies have found that the degree of inbreeding (measured as proportion of selfed seeds) tends to increase with decreasing population density of mature trees (e.g. Fukue et al. 2007, Naito et al. 2005, Ghazoul et al. 1998). In addition, species pollinated by small-bodied insects may be more susceptible to pollen limitation and selfing than those pollinated by more mobile, larger-bodied insects or birds (Breed et al. 2013). Such differences in the behaviour of pollinators and the impact of disturbance on pollinator populations, as well as the population density of tree species within fragments, may result in a range of responses to fragmentation in species with different flower sizes.

As a result of fragmentation, we might expect that any reduction in species richness seen in fragments may be the result of the loss of certain groups of species, according to their ecological traits, perhaps accompanied by the increased success of others. Due to the longevity of trees, the initial effects of fragmentation on species richness may not be immediately evident, but impacts are likely to manifest in generations recruited after fragmentation, due to changes in the recruitment success of different tree species and trait-types. Thus, studying post-fragmentation recruitment in forest fragments may reveal changes in both alpha and beta diversity of seedling and sapling communities, which may translate into longer-term changes in the composition of the tree community of the fragment. Homogenization of species diversity between forest fragments could occur as a result of the altered physical conditions (e.g. increased disturbance and a more open canopy) such that fragments become dominated by species sharing certain traits, for example, light-wooded pioneer species, or those with wind-dispersed pollen. Conversely, forest fragments may diverge in tree community composition if they follow different successional pathways due to differing biotic and abiotic conditions within fragments (Arroyo-Rodríguez et al. 2013). In addition, the stochastic nature of the sub-sample of the original community that each fragment represents mean that fragments are likely to have somewhat different starting points, from which their successional trajectory is also likely to differ. The extent to which fragmentation is driving subsequent homogenisation versus divergence is largely unknown.

These alternative pathways: homogenisation versus diversification of tree communities among fragments, warrant further study, as the former will result in overall reduction in landscape-scale species richness, while the latter will maintain or even enhance landscape-scale diversity, giving forest fragments an important role in the conservation of regional diversity. This issue is particularly important to understand in regions that are biodiversity hotspots. These regions are critical to global conservation as they represent a disproportionate proportion of the world’s biodiversity while simultaneously experiencing high levels of habitat destruction, resulting in a high risk of habitat fragmentation, reduced ecosystem function, and species extinctions (Mittermeier et al. 2011).

1.3 Biodiversity hotspots and threats to Southeast Asian rainforests

In 1988 Myers and colleagues began classifying especially vulnerable and species-rich regions of the world as biodiversity hotspots. These were areas containing extraordinary levels of plant endemism and highly-threatened habitat. In the ensuing decades more data have been gathered, and habitat destruction and degradation have led to large losses of tropical forests: between 1990 and 2010 there was a loss of 7.8 million ha of tropical forest per year (Achard et al. 2014). As a result, the 10 original biodiversity hotspots were extended to 25 by 2000 (Myers et al. 2000), 34 by 2005 (Mittermeier et al. 2005), and 35 by 2011 (Williams et al. 2011). Within these high priority hotspots, almost 87% of natural habitat is degraded or converted to another land use and only 3.4 million km^2 of intact vegetation remains (Mittermeier et al. 2011).

Owing to continuing deforestation and degradation of tropical forest, and high levels of endemism, many regions containing tropical rainforest qualify as biodiversity hotspots. The island of Borneo is part of the extensive island archipelago that forms the Sundaland hotspot in Southeast Asia (Figure 1.3). It is one of the most biodiverse regions of the world, where 60% of the 25,000 species of vascular plants are endemic (Mittermeier et al. 2011). Most of Malaysia and the western half of Indonesia fall within the hotspot. Malaysia and Indonesia are the largest oil palm producers globally, and oil palm *Elaeis guineensis* Jacq. plantations have replaced large areas of low-lying moist tropical forest. At least 1 million ha of forest in Malaysia and up to 3 million ha of forest in Indonesia were converted to oil palm plantations between 1990 and 2005, although these figures are uncertain and it is difficult to know if deforestation was driven by oil palm expansion, or whether planting followed forest that was cleared for another reason (Fitzherbert et al. 2008). In Malaysia, over 14% of the total land area is covered by oil palm agriculture and 73% of remaining forest is degraded, having been selectively logged at least twice for its valuable timber resource (FAO 2016, Reynolds et al. 2011). Based on extinctions across nine taxonomic groups in Singapore, Brook et al. (2003) estimated that the current rate of habitat destruction in Southeast Asia could result in the loss 13–42% of regional species populations over the course of the 21st century.

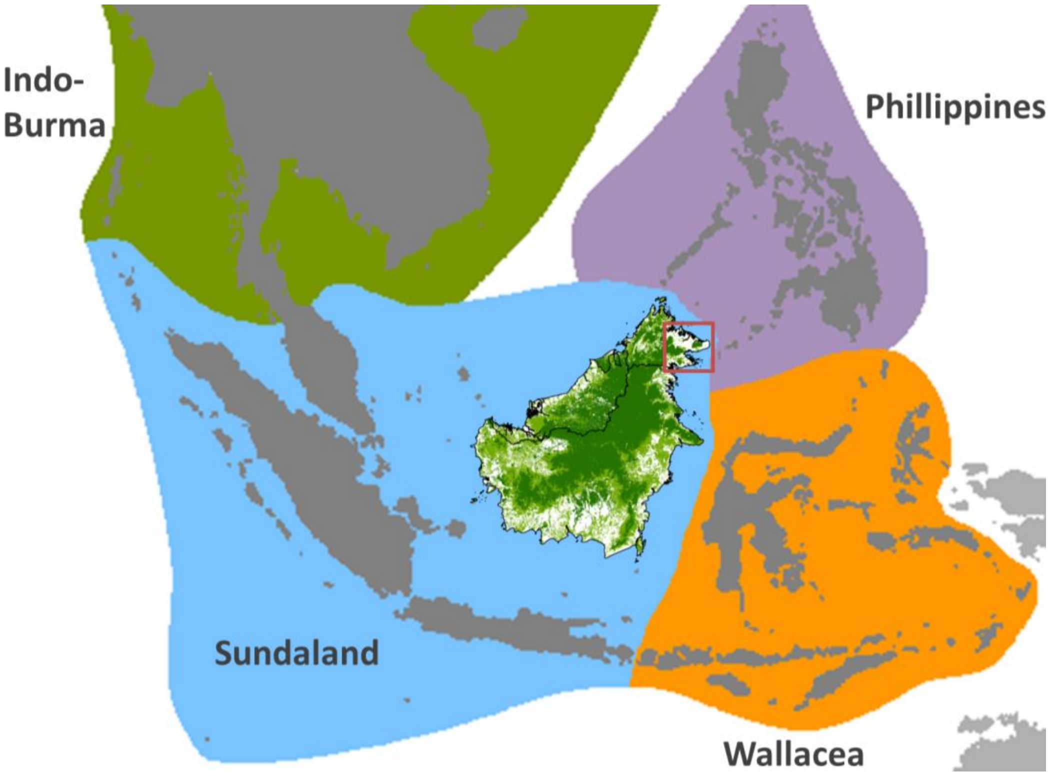

Figure 1.3. Map of Southeast Asian biodiversity hotspots (Myers et al. 2000). On Borneo dark green areas indicate forest, light green areas indicate regenerating or degraded forest, and white areas indicate agricultural land predominantly covered by oil palm (forest cover data were obtained from Miettinen et al. 2012). Red box indicates study area location on Borneo, where empirical data for chapters 2 – 4 were collected over two field seasons.

Changing climatic cues on Borneo

Borneo straddles the equator and experiences a typical wet equatorial climate. Eastern Sabah is broadly aseasonal, with minor annual variation in rainfall brought about by the Indo-Australian monsoon system. The months of November through to March are typically wetter, when the northeast monsoon influences the region, while the southwest monsoon from June to August tends to bring slightly drier conditions, and monthly mean rainfall ranges from 315 mm in January to 156 mm in April. Temperature records show that there is little variation from one month to the next: mean annual temperature is 26.9^{o}C ± 1.7^{o}C (Walsh et al. 2011, Marsh & Greer 1992). As a result, annual phenological cues are muted, and photoperiod is constant throughout the year due to the latitude. Instead many tree species flower and fruit synchronously on a supra-annual basis in response to climatic changes induced by El Niño Southern Oscillation (ENSO) events (Numata et al. 2013). These ENSO events occur irregularly on a roughly 3 – 7 year basis and vary in severity, bringing about changes in ocean and atmospheric currents that have global consequences. On Borneo, ENSO events translate to periods of high atmospheric pressure that cause a marked decrease in rainfall, and extreme droughts during stronger ENSO events. Each ENSO event typically lasts for around a year and a half but the incidence of drought varies throughout the Southeast Asian archipelago: in northern Borneo the most severe drought tends to occur during the months of February to mid-May during ENSO years (Walsh & Newbery 1999). Strong ENSO events have significant implications for forest structure: the droughts and low daytime temperatures are principal cues for the initiation of synchronised mass flowering of hundreds of plant species throughout the mixed dipterocarp forest on Borneo, but can also lead to significant defoliation and mortality of canopy trees due to drought (Williamson & Ickes 2002).

On Borneo, mean temperatures are predicted to rise between 0.9^{o}C and 3.2^{o}C by 2080, relative to mean temperatures between 1950 and 2000 (IPCC 2013, Fifth Assessment Report for RCP 2.6 and 8.5 respectively). Rising temperatures combined with increasing forest degradation and fragmentation on Borneo may also lead to increased incidence of fire (Cochrane & Laurance 2007). Future changes in patterns of precipitation are less clear and locally important global weather patterns such as ENSO may become more severe, and perhaps more frequent (Fasullo et al. 2018). As the majority of successful tree seedling recruitment of many tree species in the region occurs as a result of mass flowering events, changes in ENSO frequency and severity are likely to have important consequences for many tree species in this region of the tropics (Cai et al. 2014, Corlett & Lafrankie 1998). Thus, major changes to the composition of forest fragments may take place as a result of climatic change, especially because the most severe consequences of climate change on plant phenology are likely to affect populations in isolated fragments (Corlett & Lafrankie 1998), where the impacts of climate change and fragmentation may interact via the altered microclimates of forest edges and fragments.

Figure 1.4. Clockwise from top: lowland dipterocarp rainforest in the Danum Valley Conservation Area; roads into the forest create edges, but can be useful for moving about; a dipterocarp demonstrating why it's so appealing to loggers (photo credit: G. Stride).

Lowland dipterocarp forest in Southeast Asia

Lowland dipterocarp forest is amongst the most species-rich forest globally and is the most widespread forest type on the island of Borneo (Whitmore 1984). Combined with a high level of endemism (e.g. over 40% of tree species in Brunei Darussalam are endemic to Borneo, Ashton 2010), the severe loss of lowland forest over the past few decades has put many species at risk of extinction: currently just 50% of the forest remains where historically Borneo was almost completely forested (Gaveau et al. 2014). Much of the remaining intact forest is confined to montane regions in remote areas in the centre of the island, and the remainder of intact forest lies in small pockets in the lowlands, increasingly isolated from similar habitat by extensive oil palm plantations (Miettinen et al. 2011, Proctor et al. 2011). In Sabah, the northern state of Malaysian Borneo, many of the remaining forest fragments greater than 20 ha are protected as Virgin Jungle Reserves (VJRs), which vary in size, shape and degree of isolation. VJRs were originally designated in the 1950s in order to protect undisturbed areas of formerly continuous forest for scientific research and for the preservation of the country's natural heritage, in particular genetic diversity (Toh & Grace 2006). Although VJRs cover only 1.2% of Sabah's land area, they represent nearly 20% of the reserve area in which logging is prohibited (McMorrow & Talip 2001). As a result, VJRs continue to support high levels of mature tree species diversity, and thus may represent important reservoirs of species and genetic diversity outside of continuous forest. However, it is likely that the effects of fragmentation described above will have consequences for tree recruitment in VJRs, and, these impacts are largely unknown. It is important to understand whether trees in VJRs will continue to recruit seedlings, and if groups of trees sharing certain life history characteristics will increase or decline in abundance, as changing patterns of seedling recruitment will have implications for the success of VJRs at conserving the biodiversity of the region.

1.4 The importance of dipterocarps in Southeast Asian rainforests

Dipterocarps can form over 70% of canopy and emergent tree biomass in Southeast Asian lowland tropical rainforest, and are thus a significant taxon whose loss impacts the structure and ecological processes of the forest ecosystem (Ellison et al. 2005, Curran et al. 1999). However, species in this family share a number of characteristics that may make them particularly vulnerable to the effects of reduced population density through forest fragmentation, and to climate change. Many species have well developed self-incompatibility mechanisms, with low survivorship of selfed progeny (Ismail et al. 2014, Ashton 2003), and are often pollinated by small insects which may be unable to disperse between forest patches (Kettle et al. 2011). Dipterocarps themselves have low dispersal ability, with winged seeds that tend to disperse less than 100 m from the parent tree via gyration – and the majority fall within 10 m (Smith et al. 2015). The seeds are also highly recalcitrant and must germinate soon after reaching the forest floor, so secondary seed dispersal has little effect on the overall distances dispersed. Consequently, dipterocarps have very limited capacity to cross non-forest habitats in order to colonise new sites for forest regeneration (Kettle et al. 2011, Corlett 2009). Predominantly outcrossing species such as those in the Dipterocarpaceae retain deleterious recessive alleles in their populations, and therefore face a heightened risk of inbreeding depression when selfing does occur, for example in fragmented forest with a low population density (Naito et al. 2008). If fragments remain isolated for long periods of time, and if the population persists, inbreeding and selfing over multiple tree generations may reduce growth, disease resistance and reproductive output, as well as the capacity to adapt to changing environmental and climatic conditions (Lee et al. 2002, Ellstram & Elam 1993).

In general, closely related species tend to be similar in wood density, thus light-wood genera such as *Macaranga*, in the Euphorbiaceae family, which are well known pioneers, might be expected to perform well in fragments in comparison to heavier-wood genera such as *Dryobalanops*, in the Dipterocarpaceae (Chave et al. 2006, Suzuki 1999). However, even within genera there is often considerable variation in wood density. Although dipterocarps tend to be shade-tolerant canopy trees, the largest genus, *Shorea*, exhibits a range of wood densities from relatively low (e.g. *S. parvifolia*) to relatively high (e.g. *S. atrinervosa*), and wood density can vary quite considerably within species and individuals, depending on the location and age of the tree, and on the location on the tree from which the measurement is taken (Henry et al. 2010). In addition, despite being generally shade-tolerant canopy and emergent species, dipterocarps gain woody biomass more rapidly than many other trees (Banin et al. 2014). This property, together with their height and their dominance in Bornean forests, is part of the reason for the higher average above ground biomass of forests in Borneo relative to those in Amazonia (Slik et al. 2010).

Within the Dipterocarpaceae, flower size varies by an order of magnitude and is broadly linked to pollinator size and thus pollen dispersal capacity (Kettle et al. 2011). As a result, small-flowered species pollinated exclusively by small-bodied pollinators may be more vulnerable to elevated levels of selfing as a result of forest fragmentation than larger-flowered species pollinated by bees, moths or large scarabid beetles, which are not completely confined to forest habitats. These larger-bodied pollinators may be more able to move between forest fragments, and have greater capacity to move between individuals of low-density populations within fragments (Fukue et al. 2007). Lack of inter-fragment movement by pollinators effectively isolates populations within forest fragments, leading to pollen limitation and an increase in selfing, which has been shown to result in higher levels of flower abscission, reduced fruit set, and increased seed abortion (Fukue et al. 2007, Maycock et al. 2005), thereby reducing seedling recruitment success in this group. Higher levels of selfing and inbreeding depression have been observed in a number of small-flowered *Shorea* species pollinated by small-bodied pollinators when the population density is low (e.g. Fukue et al. 2007, Obayashi et al. 2002, Nagamitsu et al. 2001). However, larger flowers may not safe guard tree species against the effects of fragmentation, as several studies have demonstrated that even pollinators likely to be capable of moving between fragments may preferentially remain within a local patch and forage among nearby plants (Ismail et al. 2012, Rasmussen & Brødsgaard 1992). The giant honey bee is one of the largest and most mobile pollinators of dipterocarp flowers, capable of travelling distances of over 100 km, but the inferred mean pollen dispersal distance by this species is only about 207 m (Kettle et al. 2011).

Another characteristic of trees in this family is that the majority of successful seedling recruitment occurs following mass flowering events triggered by the drought and low day time temperatures of ENSO events (Numata et al. 2013). Fragments often experience elevated levels of drought and higher ambient temperature due to a more open canopy, which may disrupt the receipt of flowering cues. As well as this individual ENSO events are projected to change in frequency and strength, which may also alter the efficacy of cues (Fasullo et al. 2018). The consequences of forest fragmentation on dipterocarp recruitment are largely unknown. Owing to their important structural and ecological role in lowland forest throughout the region, as well as their significant contribution to the regional carbon sink, it is important to understand whether they will persist in fragments into the future.

1.5 Study location and site selection

Tree data was collected in lowland tropical rainforest sites in Sabah, Malaysian Borneo, during two field seasons (April – August 2015, and January – April 2017). This landscape has undergone recent and extensive deforestation: of the intact forest area estimated for Sabah in 1973 from LANDSAT satellite imagery, 39.5% was lost by 2010. Lowland rainforest (< 500 m.a.s.l.) was especially affected, and was reduced from 39,721 km^2 in 1973 to 18,978 km^2 in 2010, a 52.3% reduction in forest area. Of the remaing lowland forest, an estimated 11,634 km^2 (61.3%) was logged by 2010 (Gaveau et al. 2014), but despite this retains high conservation value and should be protected from further deforestation (Edwards et al. 2011). Less than a third of remaining intact forest in Sabah is formally protected (7.8% of Sabah’s land area; Bryan et al. 2013). The principal driver of forest loss during this time period was the spread of industrial oil palm plantations, with the period between deforestation and conversion to plantation frequently less than five years (Gaveau et al. 2016).

During the first field season I sampled trees, saplings, and seedlings in 19 sites (Figure 1.4, Table 1.1), including 14 forest fragments and five sites in continuous forest (two logged and three undisturbed). During the second season I sampled dipterocarp trees and seedlings in four forest fragments and four continuous forest sites: two logged and two undisturbed (Table 1.1). All sites were within the same major floristic region (Slik et al. 2003) below 400 m, and were comprised of mixed dipterocarp forest. Satellite imagery (Google Earth Pro 2015) was used to confirm that closed canopy forest was still present within areas designated as VJRs, and sites that were too degraded (i.e. not representative of the pre-fragmentation forest) were not sampled. Fragments were selected to represent a range of sizes, from 39 – 112,000 ha, and were completely surrounded by a matrix of open habitat and oil palm plantations at the time of sampling. Forest fragments were formed at least 20 years ago (Yeong et al. 2016), and most fragments were completely surrounded by established industrial oil palm plantations by 1995, indicating that deforestation occurred before this date (Table 1.1, Gaveau et al. 2014, Gaveau et al. 2016). The fragments sampled in this study were protected as Class VI reserves (Virgin Jungle Reserves, VJRs) in 1984 (CAIMS, 2005). This level of protection prohibits logging and poaching, and although both activities are evident in many fragments (pers. obs.), they represent relatively undisturbed closed canopy forest.

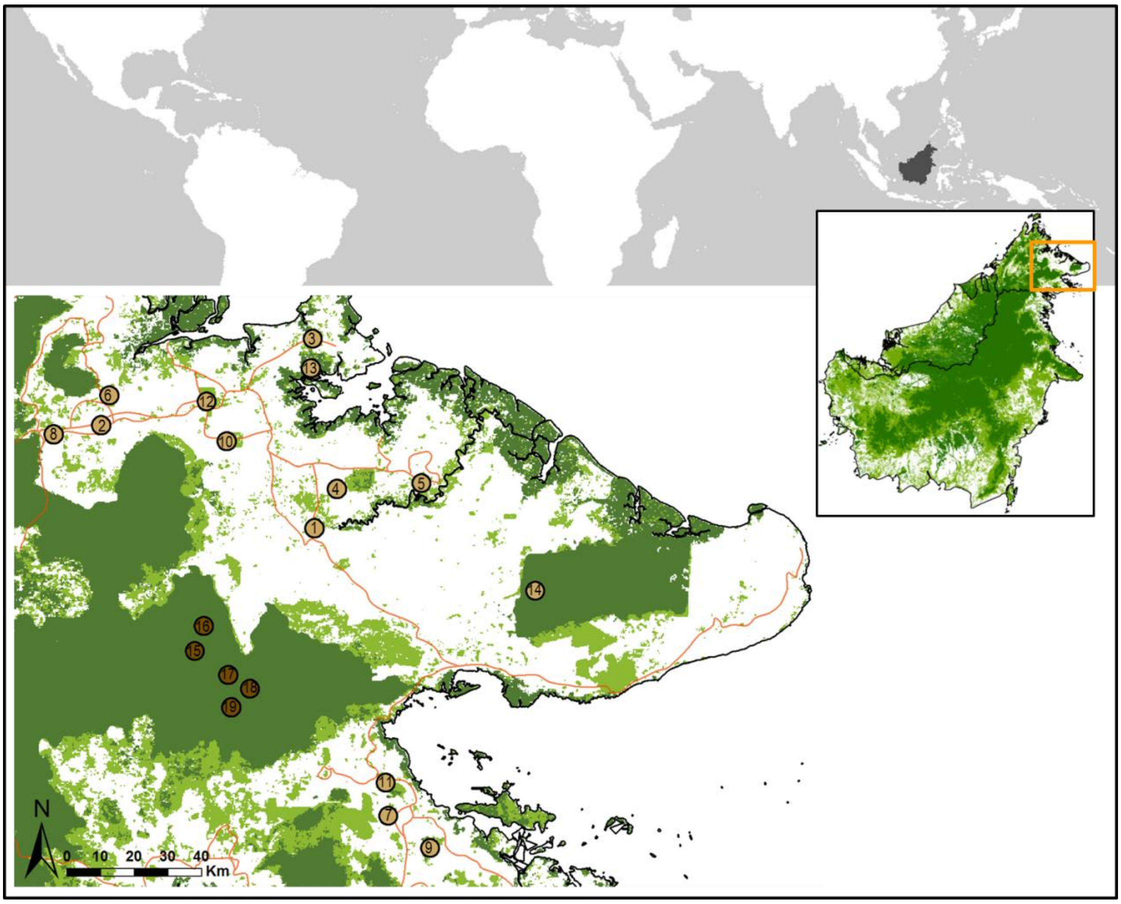

Figure 1.5. Study site location on Borneo. Inset shows forest cover on Borneo. Dark green areas represent closed canopy forest, light green areas represent degraded or regenerating forest, white areas represent predominantly agricultural land.

Continuous forest sites were located in the Danum Valley Conservation Area (unlogged sites) and Malua Forest Reserve (logged sites) within the Yayasan Sabah Forest Management Area, an area of roughly 1 million ha which contains almost two-thirds of the remaining primary forest in Sabah. Most of the remaining land is for commercial forestry (Reynolds et al., 2011). Danum Valley Conservation Area (DVCA) is classified as Class I Protection Forest Reserve, as represents 43,800 ha of primary forest that has never been logged. Protection Forest Reserves are designated to perform a number of functions, but primarily to safeguard the water supply, soil fertility and environmental quality of the region. In contrast, Malua Forest Reserve has been logged at least three times, most recently in 2007. Until then it was a Class II Commercial Forest Reserve, which generated revenue for the state through provision of timber and other forest products (McMorrow & Talip, 2001). It has now been set aside as part of a rehabilitation project known as Malua Bio-bank, which aims to restore forest structure and function under a programme of sustainable forest management, and upgraded to a Class I Protection Forest Reserve. Malua Forest Reserve is 33,969 ha in size, and despite its degraded state harbours many endangered species, augments the area of continuous forest in Sabah, and provides a buffer zone between the pristine forest of DVCA and the oil palm matrix that dominates the lowlands outside of the Yayasan Sabah management area. Owing to the repeated harvesting of mature trees, especially dipterocarps, the big-tree component within Malua Forest Reserve has been severely depleted, and the forest structure drastically altered. Sampling in logged as well as unlogged continuous forest sites enabled better representation the remaining lowland forest on Borneo, of which the majority (>60%; Gaveau et al. 2014) has been logged at varying degrees of intensity. Owing to the variation in degree of human disturbance of forest within fragments, sampling in both types of continuous forest provides a better baseline for comparison of the effects of fragmentation between continuous forest and forest fragments.

Sampling in forest fragments was conducted in Virgin Jungle Reserves (VJRs), which are managed by the Sabah Forestry Department. VJRs represent relatively undisturbed areas of formerly continuous forest where logging is prohibited, and were formally gazetted as Class VI Forest Reserves in 1984 when existing forest reserves were divided into seven classes designating use and level of protection (McMorrow & Talip 2001). VJRs were designated in order to provide undisturbed forest for scientific research and for preservation of the country’s natural heritage, in particular genetic diversity (Toh & Grace 2006). However, some illegal felling continues to this day in most VJRs, with large dipterocarps a particular target. Despite their official protection some VJRs have disappeared entirely or have been heavily degraded.

VJRs cover only 1.2% of Sabah’s land area and represent nearly 20% of the reserve area in which logging is prohibited (McMorrow & Talip 2001). Although historically Sabah was almost completely forested, by 1984 when VJRs were established only 63% of the state remained under natural forest cover. However, even during the late 1990s there remained extensive tracts of undisturbed forest that have since been degraded or deforested, so that only areas under some form of protection, or that represent land unsuitable for logging or conversion, remain today (Reynolds et al. 2011). Thus, the majority of VJRs have become increasingly isolated from similar habitat and continuous forest since their creation. The effect of fragmentation and isolation on each VJR is varied but is likely to have increased in severity over time.

Table 1.1. Summary information for study sites, providing information on location, forest type, and size of each site. FF = forest fragment; LF = twice-logged continuous forest; PF = primary continuous forest. Sites in bold were sampled in 2017 as well as 2015. Isolation based on presence of established industrial oil palm plantations (Gaveau et al. 2014, Gaveau et al. 2016).

Site #	Site name	Type	Latitude	Longitude	Area (ha)	Isolation complete (year)
1	Pin supu	FF	5.40	117.95	39.58	1995
2	Sapi A	FF	5.70	117.40	43.85	1995
3	**Labuk Rd**	**FF**	**5.89**	**117.93**	**121.5**	**1970s**
4	**Materis**	**FF**	**5.51**	**118.02**	**245.6**	**2000**
5	Keruak	FF	5.51	118.29	307.2	2000
6	**Sapi C**	**FF**	**5.72**	**117.41**	**419.2**	**1995**
7	Kunak	FF	4.66	118.15	512.3	1990
8	Ulu sapa payau	FF	5.66	117.27	694.7	1995
9	**Kalumpang**	**FF**	**4.58**	**118.26**	**2069**	**1990**
10	Luangmanis B	FF	5.65	117.73	2473	1995
11	Madai baturong	FF	4.74	118.13	3015	1990
12	Luangmanis A	FF	5.72	117.69	3228	1995
13	Sepilok	FF	5.86	117.94	6441	1970s
14	Tabin	FF	5.21	118.50	123000	2000
15	**Malua Forest Reserve A**	**LF**	**5.10**	**117.67**	**1000000**	
16	**Malua Forest Reserve B**	**LF**	**5.12**	**117.67**	**1000000**	
17	Borneo Rainforest Lodge	PF	5.03	117.75	1000000	
18	**West 15 (DVCA)**	**PF**	**4.97**	**117.79**	**1000000**	
19	**Tembaling (DVCA)**	**PF**	**4.95**	**117.81**	**1000000**	

Sampling in the largest forest fragment site (site 14) was conducted within an area designated as VJR within the Tabin Wildlife Reserve, which has a history of selective logging that officially continued until 1989. From 1984 it was protected as a Wildlife Reserve, for the conservation of resident populations of the Sumatran rhinoceros (*Dicerorhinus sumatransis harrisson*, now functionally extinct from Sabah) and the Asiatic elephant (*Elaphus maximus*), and is managed by the Sabah Wildlife Department (Nor et al. 1989). It is the largest remaining forest fragment in northeast Sabah, and is isolated from the peninsular of continuous forest that hosts the Yayasan Sabah management area by a distance of nearly 38 km. Due to its large size (112,000 ha) it is sometimes considered as continuous forest, but in this study it is classified as a fragment due to its complete isolation.

1.6 Thesis aims and rationale

The main aims of this thesis are to investigate the impact of forest fragmentation on current and future tree diversity and community composition of forest fragments. To do this, I compare size classes of trees representing individuals which were likely to have been recruited pre- and post-fragmentation in order to understand if some trees may be failing to recruit seedlings in small forest fragments. Forest fragments were formed at least 20 years ago and it is assumed that the majority of tree seedlings (<1 cm dbh and < 1.5 m in height) were recruited since fragment isolation, thus providing insight into fragmentation effects which are not yet apparent among the long-lived mature tree component of the forest. For this study I collected data in the fragmented lowland tropical rainforest landscape of Sabah, Malaysian Borneo, and compared alpha and beta components of tree diversity in continuous forest and forest fragments which varied in size, shape, and degree of isolation.

I compared the alpha diversity (measured as genus-level richness) of mature trees, saplings, and seedlings in 14 forest fragments and five sites in logged and unlogged continuous forest in order to examine whether there was a reduction in the alpha diversity of post-fragmentation recruits, and identify which characteristics of forest fragments might act as predictors of this pattern. I then investigated beta diversity among tree and seedling communities in the same set of 19 sites to understand whether fragments were diverging or homogenizing in composition. Finally, I compared seedling recruitment of 25 dipterocarp species in four forest fragments with recruitment in four sites in continuous forest, in order to investigate whether they were failing to recruit in fragments. In the general discussion, I synthesise this information and include further interpretation of the combined results. I then use this information to make some predictions as to the future of forest fragments in this landscape, and how they might compare to those in other tropical regions, as well as providing a set of recommendations for their future conservation.

The specific objectives of each data chapter are outlined below:

Chapter 2 – Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants

The first concern is that fragments may become depauperate in species, relative to continuous forest. Species-area relationships have been reported in many taxa in fragmented landscapes in temperate and tropical ecosystems, but data on trees in Southeast Asia are lacking. Furthermore, even in fragments that lose some species, the number of species in sample plots (i.e. per unit area) may still be high. In order to assess the regeneration potential of tropical forest fragments, and whether there might be extinction debts in tree communities, I grouped trees into pre- and post-fragmentation size classes. It was then possible to test the relationship between the taxonomic richness of each size class, and fragment characteristics varying in severity (i.e. area, degree of isolation, shape, and level of disturbance). I tested the hypotheses that

(1) Seedling and sapling (post-fragmentation size classes) richness is reduced within plots in forest fragments compared with plots in continuous forest.
(2) Seedling and sapling richness is negatively correlated with fragment area and isolation, and is most reduced in plots in small, isolated forest fragments.
(3) Tree (pre-fragmentation size class) richness is maintained at pre-fragmentation levels, equivalent to that found in continuous forest.

Chapter 3 – Divergent tree seedling communities indicate different trajectories of change among rainforest remnants

A reduced number of seedling genera were found in plots in forest fragments in chapter 2, implying some degree of seedling recruitment failure, but it was not clear whether it was the same or a different set of genera successfully recruiting seedlings in each forest fragment. In order to understand the contribution of forest fragments to landscape-scale diversity, and hence their importance as reservoirs of biodiversity, it is important to know whether rainforest fragmentation leads to homogenisation or diversification of plant communities among fragments. I tested

(1) Whether seedling communities are less (homogenization) or more (diversification) distinctive in forest fragments than in continuous forest, and whether tree communities lack similar trends

(2) Whether seedling communities are diverging from tree communities in the same site
(3) Whether patterns of divergence and distinctiveness of communities are associated with the size and isolation of sites
(4) Whether changes in seedling community composition are driven by recruitment failure, and whether animal-dispersed genera are disproportionately affected.

Chapter 4 – Forest fragmentation alters recruitment of tropical trees: a study of dipterocarps on Borneo

This chapter concentrates on dipterocarps because they form such an important component of the forest throughout the aseasonal lowland rainforest in Southeast Asia. Failure of dipterocarps to regenerate would therefore have major repercussions for forest community composition, and potentially for forest structure and ecosystem functioning, but data are lacking on the effects of fragmentation on dipterocarp seedling recruitment success. In Chapters 2 and 3 I study the alpha and beta diversity of the whole tree community, which indicated that some genera were failing to recruit seedlings. Here I study the recruitment effort of dipterocarp species in order to verify that conclusion, and to understand whether certain life history characteristics are able to buffer the deleterious effects of fragmentation. I tested the hypotheses that

(1) Dipterocarps in forest fragments are recruiting fewer seedlings relative to continuous forest or failing to recruit seedlings at all.
(2) Wood density and flower size, serving as proxies for growth rate and pollination syndrome, act as predictors of recruitment success in forest fragments.

CHAPTER 2

Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants.

2.1 Abstract

Remnants of lowland rainforest remain following deforestation, but the longer-term effects of fragmentation remain poorly understood, partly due to the long generation times of trees. We study rainforest trees in three size classes: seedlings (<1 cm dbh), saplings (1-5 cm dbh) and trees (>5 cm), that broadly reflect pre- and post-fragmentation communities, and we examine the impacts of fragmentation on forest regeneration in Sabah, Malaysian Borneo. We found that seedling richness (measured as the number of genera per plot) in fragments was about 30 percent lower than in plots in undisturbed forest, and about 20 percent lower than in an extensive tract of selectively logged forest, providing evidence of recruitment declines in fragments. Seedling richness was lowest in small, isolated, and disturbed fragments, potentially signalling an extinction debt given that these fragmentation impacts were not observed in trees. Unlike seedlings, saplings showed no declines in richness in fragments, suggesting that density dependent mortality (where rare individuals have a higher survival rate) and/or year-to-year variation in which species are recruiting could potentially compensate for the reductions in seedling richness we observed. Longer-term studies are required to determine whether sporadic or failed recruitment in small fragments will eventually translate into reduced richness of mature trees, or whether the processes that currently retain high sapling richness will continue in fragments.

Keywords: Biodiversity, Borneo, extinction debt, forest fragments, habitat fragmentation, natural regeneration, oil palm landscape, tropical trees.

2.2 Introduction

The long-term effects of habitat loss and fragmentation on the floristic diversity of vegetation remnants remain uncertain, predominantly because plants often have long generation times. For example, the species richness of plants in temperate grassland and forest fragments has been found to reflect historic pre-fragmentation conditions rather than recent habitat availability (Krauss et al. 2010), implying century or longer extinction debts (Tilman et al. 1994; Kuussaari et al. 2009). These extinction debts may be compounded by similarly long colonisation lags (Diamond 1972), resulting in highly non-equilibrium communities in fragments. Thus, the effects of forest fragmentation and isolation on forest-dependent animal communities, which have been measured on time scales of years to decades (e.g. Struebig et al. 2008; Hill et al. 2011), may just be the beginning of more fundamental changes in forest ecosystems, driven by the dynamics of long-lived and structurally important plant components of terrestrial ecosystems.

Habitat loss has particularly detrimental effects on highly diverse tropical forests, where the ecosystem biomass is primarily composed of (potentially) long-lived trees (Malhi et al. 2004). Deforestation in the tropics is driven primarily by agricultural expansion (Henders et al. 2015), linked to increasing demand for food from a growing human population (Koh & Wilcove 2008). Immediately following forest clearance of the surrounding land, some species will die out immediately in the remaining fragments, and other species will go extinct as a consequence of stochastic (meta) population dynamics (Laurance 2008). Systematic changes in community composition will also occur within fragments, given that species vary in their traits (Ewers & Didham 2006), and that reduced forest area and increased edge habitat alter the abiotic conditions (Laurance 2000), potentially leading to reduced species richness and an increased abundance of disturbance-loving species in fragments (Rutledge 2003). Fragment isolation is related to the amount of forest habitat within the landscape surrounding a forest fragment, and is the inverse of connectivity. Increasing fragment isolation has the potential to disrupt biological processes such as pollination and seed dispersal, which could influence seedling recruitment (Aizen & Feinsinger 1994; Cordeiro & Howe 2001). These effects are generally most severe in small and isolated fragments (Haddad et al. 2015; Benítez-Malvido & Martínez-Ramos 2003), but individual trees may persist for centuries without recruiting viable offspring, creating persistent extinction debts (Tilman et al. 1994; Vellend et al. 2006). Thus, the eventual impacts of fragmentation are likely to be under-estimated in short-term studies (Wearn et al. 2012), but differences in the species richness of pre- and post-fragmentation size classes of trees provide an initial assessment of emerging patterns of diversity change.

To assess the likelihood that fragmentation effects will result in recruitment failure and extinction debt we examine the genus richness of seedlings, saplings and mature trees in rainforest remnants. We evaluate whether tropical trees are continuing to recruit offspring within forest fragments that were probably formed about 20 years ago on Borneo, in the 1990s during rapid development of oil palm (*Elaeis guineensis* Jacq.) plantations. Southeast Asia is one of the most rapidly-changing landscapes globally and, on Borneo, oil palm plantations have replaced much of the original forest cover in lowland areas (Sodhi et al. 2010). Lowland tropical rainforest in Southeast Asia is dominated by a single family, the Dipterocarpaceae, which form the majority of the standing biomass (Curran et al. 1999). Throughout the aseasonal tropics, dipterocarps recruit seedlings almost exclusively via synchronised mast fruiting on an irregular supra-annual basis of two to 10 years (Appanah 1993), triggered by the droughts and low night time temperatures of El Niño Southern Oscillation (ENSO) events (Yasuda et al. 1999). The extent to which masting is disrupted by fragmentation is currently unknown, but given that fragments experience greater drought and higher temperatures than continuous tracts of forest (Ewers & Banks-Leite 2013), it seems likely that seed production and seedling survival will be affected. Understanding the impacts of rainforest fragmentation is critical for conserving biodiversity, given that so much of the remaining forest has been degraded by repeated logging (Reynolds et al. 2011), and fragmentation (Haddad et al. 2015). Moreover, isolated fragments of forest are increasingly important refuges for species in oil-palm dominated agricultural landscapes, making it important to understand factors affecting their long-term persistence.

We examine fragmentation effects by studying the consequences for plant communities within remaining rainforest patches following their insularisation. Our study landscape has undergone extensive deforestation, so that remaining patches of natural forest are surrounded by agricultural land. We enumerate plant richness within forest patches and examine changes in local (plot-scale) plant communities with respect to fragment size, shape and degree of isolation from other forest habitat. We compare genus richness of seedlings (<1 cm dbh and <1.5 m height), nearly all of which will have recruited after the forest fragments were isolated in the 1990s (Connell & Green 2000), with the genus richness of forest trees. Trees that were already established at the time of fragmentation will predominantly fall into our tree (>5 cm dbh) size class category, although some fast-growing stems will have recruited since fragmentation. Thus, the tree size class provides us with an insight into pre-fragmentation communities, although there will have been some turnover. We also examine saplings (1 – 5 cm dbh), anticipating that this size class will comprise many post-fragmentation individuals, but also some pre-fragmentation individuals. We test the hypothesis that seedling recruitment is reduced within plots in forest fragments, compared with plots in continuous forest, and specifically that seedling and sapling genus richness is reduced in plots in small, isolated and more disturbed fragments. In this way, we assess the regeneration potential of forest fragments and whether there are extinction debts in tree communities.

2.3 Methods

Study region and sites

The study was carried out in Sabah (Malaysian Borneo) during April-August 2015, in lowland (< 500 m asl) dipterocarp rainforest. We compared plant communities in 14 forest fragments with 5 sites in an extensive tract of more continuous forest. The continuous forest sites were located within the Yayasan Sabah Forest Management Area (YSFMA, ~1,000,000-ha), three sites within fully-protected primary forest (Danum Valley Conservation Area), and two sites within twice-logged forest (Malua Forest Reserve), which was selectively logged in the mid-1980s (~120 m^3/ha timber extracted) and again in 2005/6 (~35m^3/ha timber extracted; Reynolds et al. 2011; Figure 2.1).

The fragments of primary forest that we studied were protected as “Virgin Jungle Reserves” (VJRs) in the 1950s for scientific research, were formally gazetted in 1984 and are managed by the Sabah Forestry Department. These fragment VJRs make up ~1.2 percent of Sabah’s land area but represent nearly 20 percent of the reserve area in which logging is prohibited (McMorrow & Talip 2001). These fragment sites were not commercially logged prior to formation, but most have subsequently experienced low levels of disturbance from human encroachment (pers. obs.). The 14 fragments range in size from 40 to 120,000-ha (Figure 2.1; Table 2.1), and were probably formed at least 20 years ago, during the rapid development of oil palm cultivation in the region in the 1990s (Reynolds et al. 2011). Sites were >2 km apart and fragments were surrounded by mature oil palm plantations at the time of study.

Floristic surveys

A 1 km linear transect was set up at each of the 19 sites. Each transect comprised five plots spaced 160 m apart along the transect (Figure 2.1), with the exception of site #2 (44-ha; Table 2.1), where only three plots were possible due to its small size. Transects in fragments started 100 m from the forest edge to avoid the main edge effects (Ewers & Didham 2006), and were angled towards the fragment centre. Each plot was 20 x 40 m, and was sampled following a modified Gentry protocol, using a series of subplots to sample different size classes (Gentry

1982; Figure 2.1). Hence our approach was to sample with equal effort at each site (rather than in proportion to site area), and our analyses compare local (plot-scale) genus richness among sites.

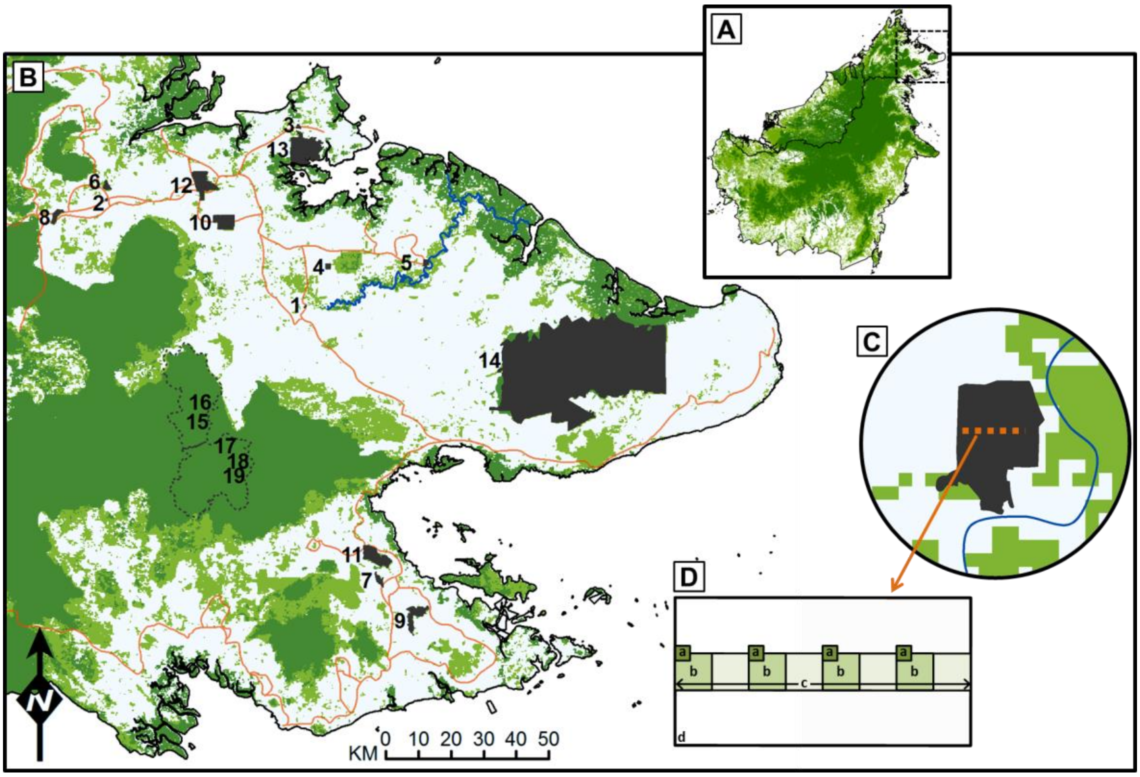

Figure 2.1. (A) Study area location on Borneo and (B) location of sites. Sites are numbered in order of increasing size; dark green areas indicate forest; light green areas indicate regenerating or degraded forest; white areas indicate agricultural land predominantly covered by oil palm; sites 15 – 19 within dotted areas are continuous forest sites. Forest cover data were obtained from Miettinen et al. 2010. (C) Five plots along a transect in a forest fragment site. (D) Nested sampling design (subplot area in brackets): a = seedling plots (4 x (2 x 2 m)), b = saplings 1-5 cm dbh (4 x (5 x 5 m)), c = trees 5 – 30 cm dbh (5 x 40 m), d = trees >30 cm dbh (20 x 40 m).

A nested design was used to ensure adequate sampling of different tree size classes (seedlings, saplings, trees), because a larger sampling area was required for trees and we did not want to over-sample saplings and seedlings. Seedlings were defined as non-climbing woody plants <1.5 m in height and <1 cm dbh, and were measured and identified in four 2 m x 2 m sub- plots distributed evenly within each plot (Figure 2.1). All seedlings are expected to have been recruited since fragmentation during mast fruiting events (e.g. 1997/98 and 2015/16 were particularly strong global ENSO events (Curran et al. 1999; Cpc.ncep.noaa.gov 2017). Saplings were defined as non-climbing woody plants 1–5 cm dbh, and they were enumerated and identified in four 5 m x 5 m subplots within each plot (Figure 2.1). Trees >5 cm dbh were divided into two groups: those 5–30 cm dbh were sampled in one 5 m x 40 m strip within each plot, and trees >30 cm dbh were enumerated in the full 20 x 40 m plot (Figure 2.1). It is difficult to estimate the age of individual trees due to high levels of inter- and intra-specific variation in growth rates, depending on life-history strategy and resource availability (especially light). Therefore we defined size classes to represent individuals that predominantly germinated prior to fragment formation ("trees"), after fragment formation ("seedlings"), and an intermediate group ("saplings") which contains many individuals germinating after fragment formation, but also includes individuals germinating prior to fragmentation. Our analyses focus on comparing the genus richness of each size class (seedlings, sapling, trees) separately among sites. We also computed plot-level plant diversity using Simpson's index (supplementary material), which confirmed that our results were not confounded by variation in stem density across sites (Figure S2.3; Table S2.4), and so we only include analyses of genus richness in the main text. We also performed an individual stem-based rarefaction analysis of genus richness (see Text S2.1), by combining data from all plots at a site (excluding Site 2 with only three plots), which supported our overall conclusions, and again confirmed that our main findings were not affected by variation in stem density.

Plant identification was carried out in the field where possible and confirmed by the botanist (Mike Bernadus) at Danum Valley Field Centre, based on leaf samples and photographs taken in the field. All but six individuals were named to species or genus level, and unidentified individuals (representing 0.06% of stems) were removed from the analysis. We carry out all analyses at genus level given the complexities of plant identification. However, we also repeated our analyses at species level, and results were qualitatively the same (Figure S2.1, Table S2.1) implying that finer resolution identification would not have altered our conclusions.

Site and plot characteristics

In order to relate our findings on plant genus richness to attributes of the sites where data were collected, we recorded the following site characteristics. We measured fragment area and perimeter using ArcMap 10.0 and R v. 3.2.2, after tracing the outline of each fragment from Google Earth satellite imagery. Fragment shape was calculated from the area (m^2) and perimeter (m), where a value of 1 indicates a circular fragment, and values approaching a maximum of 5 indicate a highly convoluted shape (Arroyo-Rodríguez & Mandujano 2006; see Text S2.2 for equation). The connectivity (i.e. inverse of isolation) of each fragment was calculated from forest land cover data (Miettinen et al. 2012) at a grid cell resolution of 250 m to identify the size of, and distance to, all forest patches within a 5 km radius of each site

(McGarigal & Marks 1995; for equation, see Text S2.3). A connectivity value of 0 for a fragment indicates an absence of patches of forest in the surrounding landscape, and increasing connectivity values indicate a greater total area of forest cover in the surrounding landscape. This metric represents the degree of isolation of a site by taking into account the amount of forest habitat within the buffer, and weights it by area and proximity. We tested the sensitivity of our findings to different buffer widths, using buffer distances of 1 – 10 km, representing a range of seed and pollinator dispersal distances (Table S2.5). However, our results were not affected by different buffer widths and so we only report data for connectivity values based on 5 km buffer in the main text.

In order to characterise the forest in each of the plots within each of the 19 sites (93 plots in total), we measured the following variables: temperature and light intensity (mean values (^{o}C and lux) from two Hobo® loggers placed 1.8 m from the ground within each plot, measured between 10am and 4pm over 2-3 days); photosynthetically active radiation (mean of four measurements taken within each seedling sub-plot (four sub-plots per plot) using a Skye Light Meter for Growers Limited); leaf litter depth (mean of four measurements using a steel ruler); canopy cover (taken in the centre of the plot using a densiometer). We also counted the number of lianas rooted within seedling sub-plots (Figure 2.1). Many of these predictor variables were correlated with one another, and so we used principal components analysis (PCA) to reduce these six variables to a smaller number of independent factors, and the first principal component of this PCA was used in our analyses of seedling, sapling, and tree genus richness as an index of forest disturbance at sites.

Table 2.1. Summary information for study sites, providing information on location, size, shape and connectivity of each site. FF = forest fragment; LF = twice-logged continuous forest; PF = primary continuous forest.

Site #	Site name	Type	Area (ha)[a]	Shape Index[b]	Connectivity[c]
1	Pin Supu	FF	39.58	1.37	2021014.2
2	Sapi A	FF	43.85	1.09	686479.5
3	Labuk Rd	FF	121.5	1.34	10652909.4
4	Materis	FF	245.6	1.19	14388115.8
5	Keruak	FF	307.2	1.43	1740.0
6	SapiC	FF	419.2	1.48	62003.4
7	Kunak	FF	512.3	1.80	3071774.1
8	USP	FF	694.7	1.52	558054.8

9	Kalumpang	FF	2069	2.30	248812.5
10	Luangmanis B	FF	2473	1.23	4936762.4
11	Madai	FF	3015	1.52	0.2
12	Luangmanis A	FF	3228	1.89	395896.2
13	Sepilok	FF	6441	2.21	373502.0
14	Tabin	FF	123000	1.82	11321427.8
15	Malua A	LF	1000000	1.00	17000000
16	Malua B	LF	1000000	1.00	17000000
17	BRL	PF	1000000	1.00	17000000
18	Danum	PF	1000000	1.00	17000000
19	Tembaling	PF	1000000	1.00	17000000

[a] Fragment area calculated using Google Earth imagery; continuous forest sites assigned a value of 800,000 ha, the area of the YSFMA.

[b] Shape index calculated as in Arroyo-Rodríguez et al. 2006 (see Text S2.1 for further details)

[c] Connectivity (5km buffer) calculated as in FRAGSTATS (McGarigal & Marks 1995; see Text S2.2 for further details)

Data analyses

In order to test the hypothesis that tree recruitment is impaired in forest fragments compared with continuous forest sites, we first calculated the number of plant genera per plot, separately for seedlings, saplings and trees (Figure 2.3), and compared genus richness in fragments, logged continuous forest, and primary continuous forest sites using one-way ANOVAs, followed by post-hoc Tukey HSD tests.

In order to test the hypothesis that seedling and sapling genus richness is lowest in small, isolated and most disturbed fragments, we carried out three general linear mixed effects models (GLMMs) to evaluate seedling, sapling and tree genus richness (response variable = number of genera per plot) in relation to four site attributes: size, shape, connectivity, and disturbance (PCA factor score; PC1). We gave sites in continuous forest a notional area of 800,000-ha (the area of the Yayasan Sabah Forest Reserve; Reynolds et al. 2011), and values of 1 for shape and 17,000,000 for connectivity so that these five sites could be included in our analyses. We carried out Poisson GLMMs with a log-link function, including 2-way interactions between the four predictor site attributes (with data analysed at plot-level; 93 data points), and site identity was included as a random effect to account for non-independence of plots within sites. Area was $\log_{10}$-transformed and connectivity was cube-root transformed to reduce skew in the data, and all four predictor variables were scaled to have a mean of 0 and variance of 1 prior to analysis, to aid comparison of their relative importance on genus richness. The top models were identified using an AIC approach (Burnham & Anderson 2002), where delta AICc <2 of the best model were included in the top models, and model averaging was then used to find the importance of each variable and determine their relative effect sizes: effect sizes whose confidence intervals (CIs) did not cross zero were assumed to be significant predictors of plant richness. All analyses were performed using the R package vegan (Oksanen *et al*. 2011) in R v. 3.2.2 (R Development Core Team 2015).

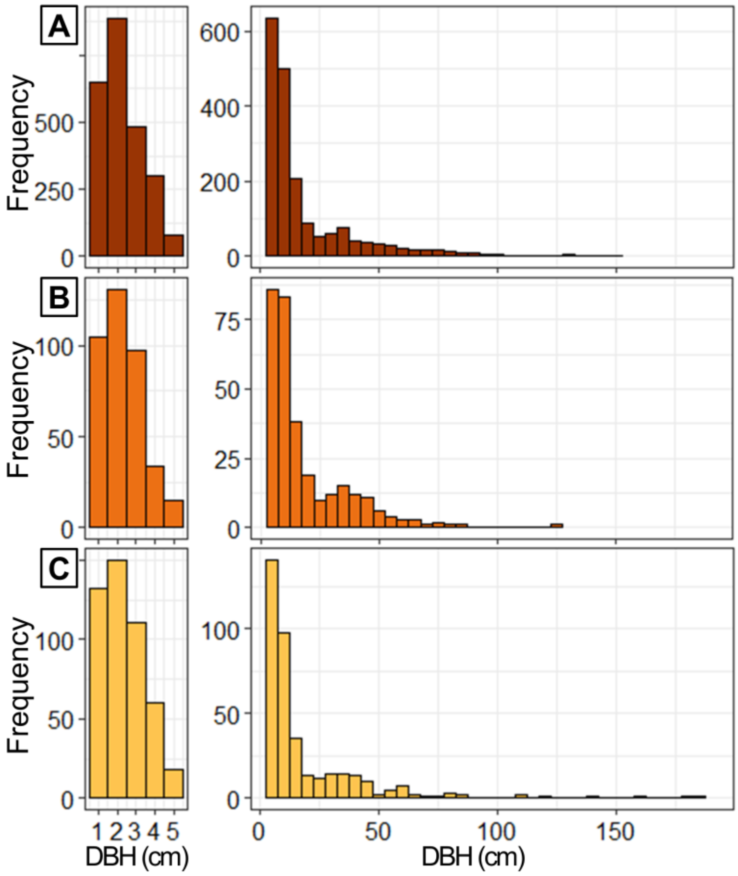

Figure 2.2. Overall frequency distribution of sapling (left) and tree (right) stem sizes in (A) forest fragments (brown bars, n = 68 plots), (B) logged forest (orange bars, n = 10 plots), and (C) primary forest (yellow bars, n = 15 plots) sites.

2.4 Results

Across the 93 plots at 19 sites, we surveyed 9608 individual plants, representing 222 genera and 76 families. As is typical for this region, the Dipterocarpaceae family was dominant across all size classes, and 27 percent of all individuals were represented by this family. The most numerous genus was *Shorea* (Dipterocarpaceae), which formed 30 percent of individual seedlings, 4 percent of saplings, and 8 percent of trees. The frequency distributions of stem sizes across the three forest types were similar, although only primary forest contained individuals over 125 cm dbh (Figure 2.2).

The first principal component (PC1), constructed from six variables describing site and plot characteristics, accounted for 32.5 percent of the overall variation, and increased with increasing light, temperature, and a more open canopy (Figure S2.2A). Hence we conclude that PC1 is a measure of forest disturbance, and PC1 scores were negatively correlated with site area and connectivity (Figure S2.2B), indicating that forest disturbance is greater in small and isolated forest fragments.

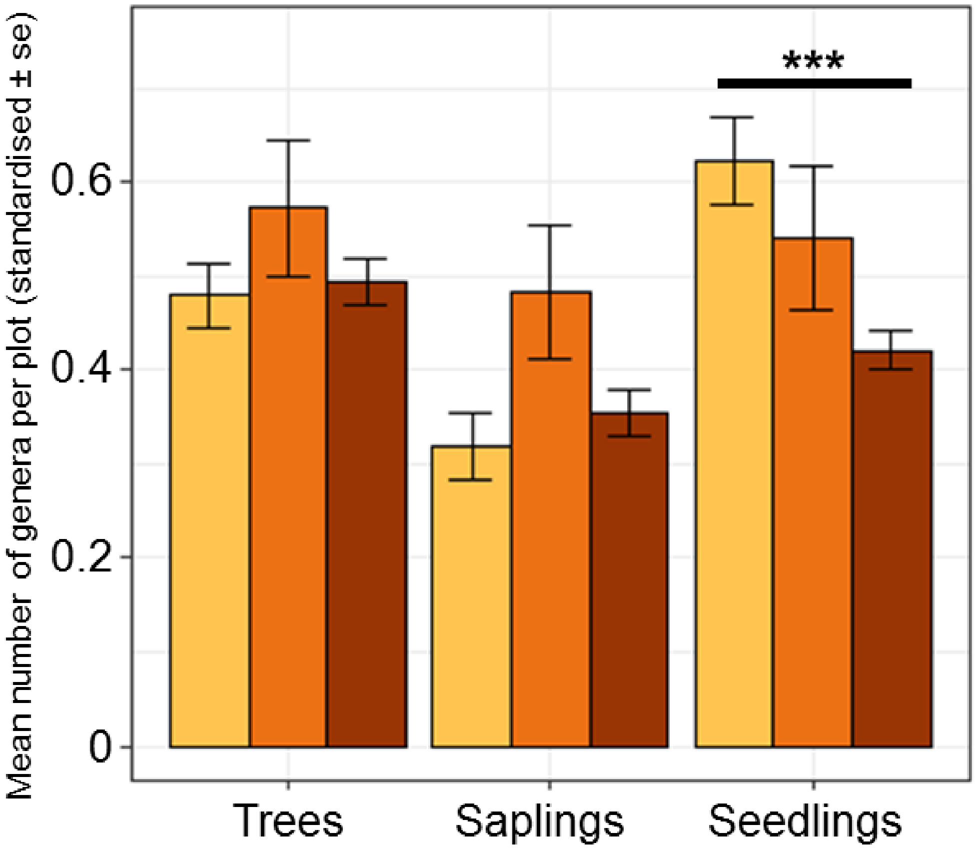

Figure 2.3. Effect of fragmentation on size class richness in primary, logged, and fragmented forest sites. Mean of standardised plant genus richness values (± SE) of size classes in plots located in primary continuous forest (yellow bars; n = 15), previously logged continuous forest (orange bars; n = 10), and forest fragments (brown bars; n = 68). ANOVA of plant richness by forest type: $p \leq 0.001$ = ***.

Variation in plant genus richness among study sites

Seedling genus richness was much lower in plots in fragments compared with plots in primary and logged forest (one-way ANOVA of genus richness by forest type; $F_{(2,90)} = 8.55$, $p < 0.001$) , but there was no significant difference between seedling genus richness in primary and logged forest. Fragment seedling genus richness (N = 14 sites; mean = 7.3 genera per plot ± 0.3 SE) was 29 percent lower than in primary continuous forest (N = 3 sites, mean = 10.3 genera per plot ± 0.7 SE), and 20 percent lower than in logged continuous forest (N = 2 sites, mean = 9.1 genera per plot ± 1.2 SE; Figure 2.3). However, there was little impact of fragmentation on genus richness of either saplings ($F_{(2,90)} = 2.36$, p = 0.10; fragments, mean richness = 16.9 genera per plot ± 0.7 SE; logged forest, mean = 20.5 ± 2.0; primary forest, mean = 15.9 genera per plot ± 1.0) or trees ($F_{(2,90)} = 0.82$, p = 0.44; fragments, mean = 16.8 genera per plot ± 0.5 SE; logged forest, mean = 18.6 genera per plot ± 1.6; primary forest, mean = 16.5 genera per plot ± 0.8). Thus we conclude that forest fragmentation reduces local seedling genus richness but has no impact on the genus richness of saplings or trees.

Effects of site characteristics on plant richness

Outputs from GLMMs revealed that seedling genus richness was positively associated with site area, and there was an indication that connectivity, and forest disturbance of sites were also important (Figure 2.4). Site area was the most important variable in the best model (Table 2.2), and seedling genus richness was particularly low in small, isolated, highly disturbed sites. Our rarefaction analyses of seedling data found similar trends (Figure S2.4, see Text S2.1 for further discussion). In contrast to data for seedlings, and even though we assumed that saplings were predominantly produced after fragmentation, there was no effect of site area (or any other predictor variable) on sapling genus richness. This result was robust to varying the stem diameter threshold for our sapling size class (Table S2.6), and to the removal of high wood density, slow-growing genera (> 0.75 g/cm^3; Table S2.7). Additionally, results were qualitatively similar when we split our data set according to the median wood density of all genera we encountered in our study (0.55 g/cm^3), indicating that differences in plant growth rates are not having major impacts on our designation of post- and pre-fragmentation individuals, or our overall findings (Table S2.8, see Text S2.4 for further discussion). We assumed that trees were representative of pre-fragmentation communities and as predicted, tree genus richness did not vary according to site area. Tree genus richness did however vary according to levels of forest disturbance at sites (PC1 score), indicating that sites with more open canopies, higher temperatures and higher light environments contained fewer tree genera.

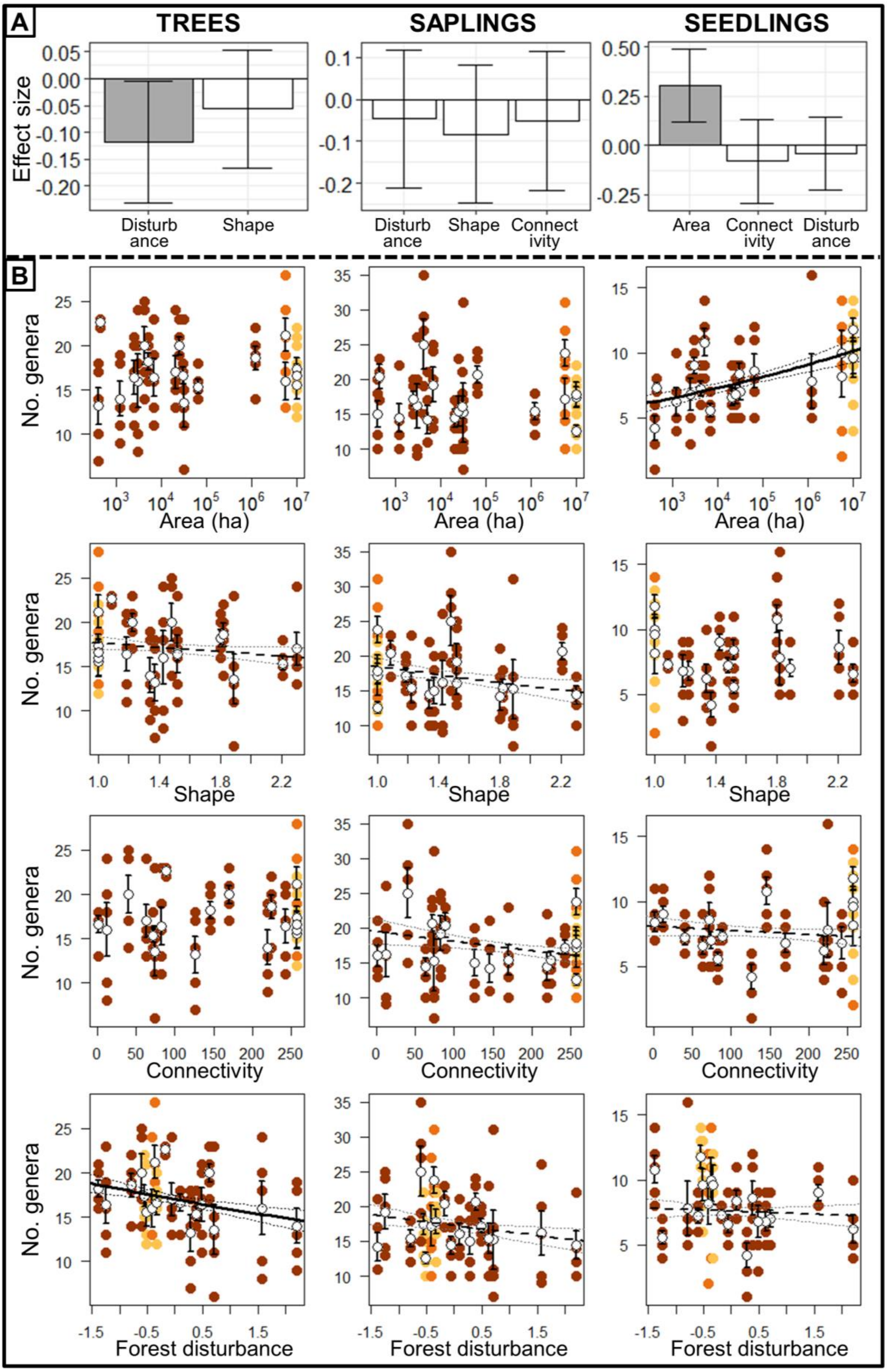
A
TREES
SAPLINGS
SEEDLINGS
Effect size
Disturb ance
Shape
Disturb ance
Shape
Connect ivity
Area
Connect ivity
Disturb ance
B
No. genera
Area (ha)
Shape
Connectivity
Forest disturbance

Figure 2.4.

Figure 2.4. Effect of site characteristics on size class richness. A. Effect size of variables included in averaged models. Effect sizes whose 95% confidence intervals did not cross zero were assumed to be significant, and are shaded in grey. B. Impact of area, connectivity, fragment shape, and forest disturbance (principal component) on richness of trees, saplings, and seedlings. Brown symbols (fragments), orange symbols (logged forest) and yellow symbols (primary forest) show genus richness values of plots, and hollow circles are site means with standard error. Black line is fitted for variables where the slope was significantly different from zero in averaged top models; dotted line is fitted where variable was included in averaged top models but was not significant.

Table 2.2. Top ranked GLMMs of factors affecting tree, sapling and seedling richness in 93 plots nested within 19 sites. Candidate models are ranked according to the Akaike's information criterion (AICc). Corresponding degrees of freedom (df), log-likelihood estimation (logLik), difference between AICc and lowest AICc value (Δ_i) in model set, Akaike weight (w_i: the probability that each model is the best approximating model), and marginal (R^2m) and conditional (R^2c) r-squared values are presented. Only models with $\Delta_i < 2$ were included in the averaged top models.

Response variable	**Candidate models**	**df**	**logLik**	**AICc**	**Δ_i**	**w_i**	**R^2m**	**R^2c**
Seedling richness	Area	3	-222.38	451	-	0.55	0.15	0.19
	Area + Connectivity	4	-222.11	452.7	1.65	0.24	0.16	0.19
	Area + Disturbance	4	-222.28	453	1.99	0.20	0.15	0.19
Sapling richness	-	2	-285.96	576	-	0.42	0	0.16
	Disturbance	3	-285.46	577.2	1.14	0.24	0.02	0.16
	Shape	3	-285.76	577.8	1.75	0.18	0.01	0.16
	Connectivity	3	-285.80	577.9	1.82	0.17	0.01	0.16
Tree richness	Disturbance	3	-265.77	537.8	-	0.51	0.05	0.10
	Disturbance + Shape	4	-265.26	539	1.17	0.28	0.07	0.10
	-	2	-267.70	539.5	1.72	0.21	0	0.10

2.5 Discussion

Forest fragmentation significantly reduced the local genus richness of tree seedlings. On average, only 4.2 seedling genera (± 0.97 SE) were found per 16 m^2 plot in the smallest fragment (39.6 ha), compared to 11.8 seedling genera (± 0.86) per plot in a primary forest site in continuous forest. The absence of any reduced genus richness in trees may be indicative of an extinction debt in small fragments, although our failure to find any reduction in sapling genus richness may suggest that there are compensatory processes in operation (see below).

No effects of fragmentation on tree genus richness

Given the age of our fragments, we assume that our tree size class would have mostly germinated prior to fragmentation, and that the genus richness of these trees broadly represents the 'pre-isolation' condition of the forest. Although we did not detect direct effects of fragment size or isolation on our tree size class, we did find indirect effects because reduced genus richness was associated with disturbance, and fragments generally contained more disturbed forest; Figure S2.2B). Hence trees were affected by local forest disturbance rather than by the direct effects of fragmentation in reducing site area and isolation.

Reduced local genus richness of seedlings in fragments

The reduced number of seedling genera per plot in (small) forest fragments, compared to continuous forest, could arise from multiple processes relating both to the biological and physical conditions of the fragments. Forest fragments experience a change in physical (micro)climatic conditions associated with increased disturbance and edge effects, particularly through greater wind disturbance and elevated desiccation (Laurance 2004). This can alter the cues linked to the initiation of (sporadic) mass flowering (Curran et al. 1999) and may hamper the physiological ability of trees to support fruit development, the germination of seeds, and affect the establishment and survival of seedlings (Delissio & Primack 2003). Fragmentation may also lead to the loss of pollinators (Aizen & Feinsinger 1994) and change patterns of seed predation and dispersal (Cordeiro & Howe 2001, Terborgh et al. 2001). Self-incompatibility mechanisms in tropical trees may lead to reproductive failure among species with small numbers of individuals surviving per fragment (Ghazoul et al. 1998; Naito et al. 2008). Given that different species of trees will flower and fruit in response to different physical cues, and exhibit different interactions with specialised and generalist natural enemies, it is likely that a combination of processes may reduce the 'post-isolation' genus richness of seedlings in forest fragments. In addition, our rarefaction analyses, that account for differences in seedling stem density, also found a trend of decreasing numbers of seedling genera in smaller fragments, and so it seems likely that regeneration processes are being disrupted in fragments.

Long-term viability of fragments and conflicting results from saplings

As with seedlings, we expected a high proportion of saplings to have germinated subsequent to fragmentation, yet we did not find any effects of fragmentation on saplings, despite finding an effect on seedlings. Isolation of our Virgin Jungle Reserve sites probably occurred at least 20 years before our study. Certain shade tolerant species are able to persist in seedling banks in the forest understory for a number of years (Wright et al. 2003, Brown & Whitmore 1992), and it is likely that our sapling size class comprises a mixture of individuals that germinated both pre- and post-fragmentation (Delissio et al. 2002). Nonetheless, a portion of saplings will have recruited post-fragmentation, and hence we expected (but did not observe), some effects of fragmentation on sapling genus richness. There are a number of possible explanations for this disparity between seedlings and saplings, which could result from a combination of the following: 1) more sporadic recruitment of seedlings in small fragments than in continuous forest; 2) increased density-dependent survival of the rarest seedlings; and 3) delayed (lagged) impacts of fragmentation on seedling recruitment failure. For example, if different species are recruited in different years in fragments (more so than in continuous forest) owing to disruption of flowering or reduced pollination in fragments, then there will be lower richness in any single seedling size class. However, the sapling size classes in the same plots are likely to include a wider age range of individuals than seedlings, and hence represent the survivors from several seedling size classes. The impact of recruiting different species in different years could be further enhanced if density-dependent mortality of conspecifics takes place, whereby rare species have a higher survival rate (LaManna et al. 2017). Survival of low density species may be elevated in fragments if herbivores and pathogens specialising on rare species become extinct from small areas of forest (Arnold & Asquith 2002). If sporadic recruitment and density-dependent processes allow sapling genus richness to be maintained, then fragmentation may not necessarily have longer-term detrimental impacts on plant richness. However, high sapling genus richness may reflect time lags between fragmentation and reduced seedling recruitment, such that surveys immediately post-fragmentation would not have detected any changes in seedling genus richness. If the first two processes are operating, then local (plot scale) genus richness of saplings and mature trees may not inevitably decline over time in small fragments, despite the reduction in seedling genus richness at any one time. Nonetheless, even if local plot scale genus richness is maintained, some (mainly rare) species and genera are still likely to be lost from small fragments. These explanations for the findings we report deserve further research, given that they lead to quite different expectations about future diversity changes in forest fragments.

2.6 Conclusions

Small, isolated and disturbed forest fragments have lower local seedling genus richness but similar levels of sapling and tree genus richness, compared with continuous forest. Whether fragmentation will lead to long-term reductions in the plant diversity of fragments is not yet clear, given that genus richness is apparently maintained in the sapling size class post-fragmentation. The longevity of trees extends the window for conservation action (Wearn et al. 2012), and episodic recruitment, density dependence and lagged effects of fragmentation may buy more time still. The fact that recruitment patterns differ between fragments and continuous forest sites implies that there will be divergence in the plant communities of these areas, but it is too early to conclude that fragments will have reduced diversity in the long term. Hence, local tree genus richness may be maintained in fragments, regional habitat specialists may only survive in small fragments if continuous forest no longer exists elsewhere, and small fragments may increasingly support unique biological communities. Thus, rainforest remnants may have inherent conservation value.

2.7 Author contributions and acknowledgements

GS, JKH, and CDT conceived and designed the study; GS and AJ collected field data; GS led data analysis and wrote the first draft of the manuscript, with substantial contributions from JKH and CDT to all further revisions. SB, JH and MJMS also contributed to revisions. All authors gave final approval for publication. The authors declare they have no competing interests.

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

CHAPTER 3

Divergent tree seedling communities indicate different trajectories of change among rainforest remnants

3.1 Abstract

Aim: To examine plant community composition within rainforest remnants, and whether communities in different fragments follow similar trajectories of change in composition. We investigate whether rainforest fragmentation leads to homogenisation or diversification of plant communities, in order to understand the biodiversity value of forest fragments.

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

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

Results: Seedlings in fragments have diverged most from other communities, and divergence is greatest between seedling communities in small fragments, which have not only diverged more from tree communities in the same fragment, but also from seedling communities at other sites. This finding is partly associated with recruitment failure: 57-64% of the genera in small fragments occurred only as adult trees, and not as seedlings, contrasting with 46-52% of genera in continuous forest.

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

Keywords: Beta diversity, Borneo, community composition, extinction debt, forest fragmentation, recruitment failure

3.2 Introduction

When continuous tracts of habitat are substantially reduced in area, the remnants of habitat are relatively small and often isolated from one another (Haddad et al. 2015). How the plant composition of these fragments will change thereafter is far from clear. For example, some non-viable populations will die out completely from a given fragment, whereas other species may increase or colonise, particularly those associated with habitat edges and disturbance (Harper et al. 2005). In addition, the spatial patterns of communities may change, with fragment communities becoming increasingly similar if the same species always decline in fragments and another set of species always increase and colonise, homogenising to a more uniform but impoverished set of pioneer-type species (Rocha-Santos et al. 2016, Pütz et al. 2011). Alternatively, plant communities may diverge as a function of both chance events (e.g. stochastic recruitment) and more deterministic species-specific variation in growth and survival in remnants due to differences in remnant characteristics (Arroyo-Rodriguez et al. 2015). In this scenario, fragments will contribute to landscape-scale heterogeneity, even if individual remnants are impoverished, because fragments will support species not found in other fragments. However, tree mortality and recruitment are more variable in fragments than in more undisturbed continuous forest (Laurance et al. 2007), and due to the long generation times of trees and consequent slow turnover rates, the trajectory of tree community composition change in fragments is difficult to study. Hence, the outcome of fragmentation for plant communities is difficult to predict. The scenario that plays out will have important implications for the long-term composition of remnant fragments, and their conservation value for maintaining landscape-scale biodiversity. In this study, we examine the effects of fragmentation on plant community composition in forest remnants that vary in size and isolation, to test whether fragmentation will result in homogenisation or divergence of plant communities within remaining remnants.

Tropical forests represent some of the most species-rich ecosystems on the planet, and are under continuing pressure from habitat loss and fragmentation, driven by deforestation for agricultural expansion (Taubert et al. 2018). The biotic and abiotic effects of fragmentation include altered microclimate, loss of seed dispersers and pollinators, and changing patterns of herbivory, which have impacts on plant communities (Lopez & Terborgh 2007, Terborgh et al. 2001), with the greatest changes taking place in the smallest and most isolated forest fragments (Hill et al. 2011). Defaunation of forest fragments is increasingly reported (e.g. Canale et al. 2012), and is likely to affect trees with animal-dispersed seeds more than those which are abiotically dispersed (Harrison et al. 2013). However, it may be decades before these effects have an impact on tree communities, due to the longevity of individual trees that can live for years without reproducing, invoking an extinction debt (Kuussaari et al. 2009). Nonetheless, differences in seedling communities may begin to emerge sooner following fragmentation, as altered abiotic and biotic conditions in fragments disrupt processes vital for successful tree regeneration. Given that forest fragmentation is such a widespread phenomenon, it is important to understand the trajectory that plant communities in fragments may follow.

To assess how fragmentation may affect plant communities, we examine the community composition of seedlings and mature trees in rainforest remnants formed on Borneo in the 1980s during rapid development of oil palm (*Elaeis guineensis* Jacq.) plantations (Yeong et al. 2016). Lowland tropical rainforest on Borneo hosts extremely high levels of biodiversity (Myers et al. 2000). Many trees in these dipterocarp-dominated forests on Borneo reproduce during mast fruiting events associated with El Niño events (Appanah 1993), and it is unclear whether recruitment of trees is disrupted in fragments. Previous studies have shown that local richness of seedlings is reduced in fragments (MacArthur & Wilson 1967; Stride et al. 2018), but impacts on plant community composition are less clear yet critical for conserving plant biodiversity, given that so much of the remaining forest has been degraded or lost (Reynolds et al. 2011; Haddad et al. 2015). Even though small forest fragments have altered ecosystem functioning (Yeong et al. 2016) and support fewer species (Lucey et al. 2017), they are important refuges for species in agricultural landscapes that are dominated by oil-palm (Prescott et al. 2016). Individual fragments may also be important for increasing landscape-level connectivity (Scriven et al. 2015), contributing to the dynamics and persistence of metapopulations of species restricted to fragments (Ovaskainen & Hanski 2003). Thus, it is crucial to understand factors affecting plant community composition within fragments, and the importance of fragments within the wider landscape.

We study beta diversity in rainforest remnants and continuous forest, as recorded in 2015, between sites (quantifying the distinctiveness of communities of trees and seedlings among sites), as well as beta diversity of trees and seedlings within sites (quantifying the divergence of seedling communities from tree communities). Slow-growing, shade-tolerant dipterocarp seedlings were monitored over a period of eight years, and even the slowest-growing surviving individuals were more than 1 cm in diameter after this time period (Philipson et al. 2014), thus we can be confident in our assumption that seedlings (<1 cm dbh) were predominantly recruited after the forest fragments were isolated, while trees (>5 cm dbh) largely represent pre-fragmentation communities (Connell & Green 2000). We examine whether tree recruitment is affected by forest fragmentation, and test whether seedling communities in fragments either diverge from, or become more similar to, seedling communities in other sites. We anticipate that any fragmentation effects will be greatest in the smallest, most isolated forest fragments. First we test (1) whether seedling communities are more distinctive in forest fragments than in continuous forest, and predict that the same is not true for tree communities in the same set of sites. We then test (2) whether seedling communities are diverging from tree communities in the same site. We examine (3) whether patterns of divergence and distinctiveness of communities are associated with the size and isolation of sites. Finally, we test (4) whether changes in seedling community composition are driven by recruitment failure, and whether animal-dispersed genera are disproportionately affected. In this way, we assess whether fragments will contribute to landscape-scale diversity, and hence be reserves of biodiversity in future, or whether fragments will become increasingly similar, resulting in more homogenous plant communities in these fragmented landscapes.

3.3 Methods

Study sites

Plant community data were collected in 14 forest fragments and five ‘control’ sites in continuous forest (a tract of forest of > 1 million ha; Reynolds et al. 2011) in lowland (< 500 m a.s.l.) dipterocarp rainforest in Sabah (Malaysian Borneo) during April-August 2015. Lowland Sabah comprises a fragmented mosaic of forest and agriculture, and all forest fragments were surrounded by mature oil palm plantations at the time of study. Three of the continuous forest sites were located within fully-protected undisturbed primary forest (Danum Valley Conservation Area), and the other two sites within selectively twice-logged forest (Malua Forest Reserve), logged in the mid-1980s and 2005/6 (Figure 3.1; Reynolds et al. 2011). Sampling these five continuous forest sites therefore represented plant communities of closed canopy forest typical of the region, to compare with forest fragments. The forest fragment sites were protected as “Virgin Jungle Reserves” (VJRs) in the 1950s for scientific research, and are managed by the Sabah Forestry Department. VJRs represent high-quality forest where logging is prohibited, although most have experienced low levels of disturbance from human encroachment, poaching and illegal felling (pers. obs., Sabah Forestry Department 2005). The 14 forest fragments range in size from 40 to 120,000 ha (Figure 3.1, Table S3.1) and vary in their degree of isolation. All 19 sites were >2 km apart.

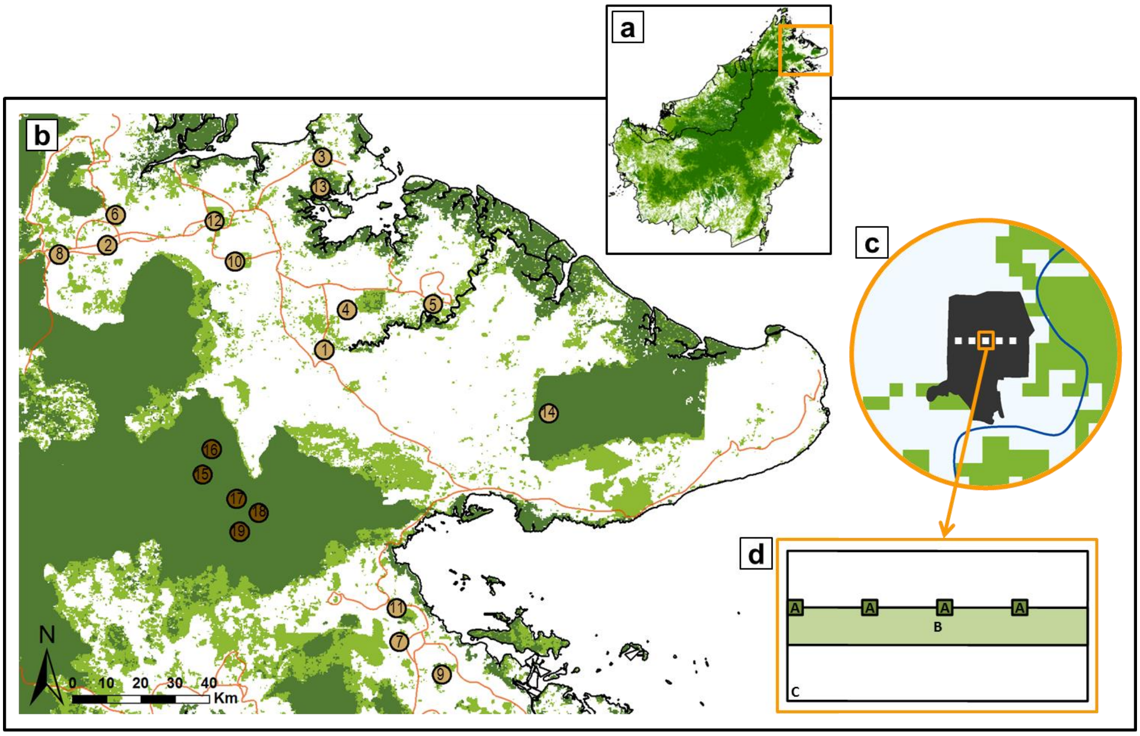

Figure 3.1. (a) Study area location on Borneo. (b) Sites are numbered in order of increasing size; dark green areas indicate forest; light green areas indicate regenerating or degraded forest; white areas indicate agricultural land predominantly covered by oil palm; sites 1 – 14 (light brown symbols) are forest fragment sites, sites 15 – 19 (dark brown symbols) are continuous forest sites. Forest cover data were obtained from (Miettinen et al. 2012). (c) A forest fragment. Within each site, five plots were arranged along a transect. (d) Nested sampling design (subplot area in brackets): A = seedling plots (four x (2 x 2 m)), B = trees 5 – 30 cm dbh (5 x 40 m), C = trees >30 cm dbh (20 x 40 m).

Floristic surveys of tree and seedling communities

In each of the 19 sites, a 1 km linear transect was established, comprising five plots placed at 160 m intervals (Figure 3.1), starting 100 m from the forest edge to avoid the main edge effects (Laurance 2000; Ewers & Didham 2005), and in forest fragments angled towards the fragment centre. However, in site #2 only three plots were possible owing to its small size and shape (44 ha; Table S3.1). Each plot was 20 x 40 m, and was sampled following a modified Gentry protocol, using a series of subplots to sample different size classes (Gentry 1982; Figure 3.1). This nested design of subplots controlled for spatial aggregation of species and allowed us to sample lower density larger trees over a larger area, while the more densely occurring smaller trees and seedlings were sampled over a smaller area. Trees >5 cm dbh were divided into two size groups: those 5–30 cm dbh were sampled in one 5 m x 40 m strip within each plot, whereas trees >30 cm dbh were enumerated in the full 20 x 40 m plot. Seedlings (non-climbing woody plants <1.5 m in height and <1 cm dbh) were enumerated in four 2 m x 2 m sub-plots distributed evenly within each plot (Figure 3.1). We assume that seedlings have been recruited after forest fragmentation took place in the 1980s, the majority during recent mast fruiting events (e.g. a particularly strong global ENSO event took place in 2015/16; Cpc.ncep.noaa.gov. 2018). Plot-level data were combined to compute the number of genera and abundance of individuals within each genus at each of the 19 sites. We used these data to compute the distinctiveness of tree and seedling communities among our 19 sites, as well as the divergence of seedling communities from tree communities at each site. Henceforth we use “tree” and “seedling” as shorthand for tree and seedling community composition. Analyses were carried out with and without site #2 to ensure that sampling a smaller number of plots in site #2 did not affect our results. The results were qualitatively the same, and so we present analyses based on all 19 sites in the main text.

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

Measuring site area and isolation

We related patterns of distinctiveness and divergence of communities at each of the 19 sites to site area and isolation. We measured the area of forest fragments using R v. 3.2.2 (R Core Team 2015) after tracing the outline of each fragment from satellite imagery (Google Earth Pro 2015). Area was $\log_{10}$ transformed to reduce skew in the data. The isolation of each forest fragment was calculated by using forest land cover data (Miettinen et al. 2012) at a grid cell resolution of 250 m to identify all forest patches within a 5 km radius of each forest fragment. The size of each forest patch and their distances from the site were used to calculate the isolation metric (McGarigal et al. 1995; Text S3.1). Isolation was cube root transformed to reduce skew in the data and then subtracted from the maximum value so that an isolation value of 0 indicates a highly connected site with high cover forest in the surrounding landscape, and increasing isolation values indicate decreasing amounts of forest cover in the surrounding landscape. We gave continuous forest sites a notional area of 1,000,000 ha (the area of the Yayasan Sabah Forest Reserve; Reynolds et al. 2011), and an isolation value of 0.

Data analyses

Computing distinctiveness and divergence of communities

We computed pairwise Chao-Sørensen abundance-based dissimilarities between trees and between seedlings across all our sites, and for all pairwise combinations in all sites for the full plant community to calculate dissimilarities between seedlings and trees within sites. To examine distinctiveness of trees and seedlings among sites, we used Non-metric Multidimensional Scaling (NMDS) ordination on each dissimilarity matrix, and then calculated the distance of each site to the NMDS centroid (i.e. distance from the “average” community) to reduce 18 pairwise comparisons to a single value per cohort, per site. Divergence between seedlings and trees at each site was computed in a similar way: we used NMDS on a single dissimilarity matrix containing both cohorts, and tree-seedling divergence in each site was then calculated as the Euclidean distance in the ordination between tree and seedling cohorts in the same site.

To examine whether differences in patterns of distinctiveness and divergence in our study were due to geographical distance between sites, we conducted two Mantel tests regressing Chao-Sørensen abundance-based pairwise dissimilarities of trees and seedlings separately, against a matrix of geographical distances. Significance of the Mantel correlation statistic was determined by generating 10,000 random permutations of each matrix, and comparing these with the observed matrix.

Divergence and distinctiveness in relation to site area and isolation

We used generalised linear models (GLMs) to test whether variation in tree-seedling divergence (Euclidean distance between cohorts in NMDS ordination), and changes in tree and seedling distinctiveness among sites (distance-to-centroid in NMDS ordinations) were due to site area and isolation. Models were fitted with area and isolation separately and together in the same model, and the model fit was evaluated based on the relative AIC (Table 3.1). Values approaching zero indicate low divergence/distinctiveness, and those approaching one indicate high levels of divergence/distinctiveness.

Variation in divergence and distinctiveness due to recruitment failure

We examined whether variation in distinctiveness and divergence were due primarily to recruitment failure of some tree genera, as opposed to the arrival of new genera by partitioning genera at each site into three groups, and calculating the proportion of genera in each: those present as trees and seedlings (percentage of all genera present in the site, representing successful recruitment), those present as trees but not seedlings (percentage of tree genera present without seedlings in the same genus, representing recruitment failure), and those present as seedlings but not trees (percentage of seedling genera present without trees, representing arrival of new genera). We then used beta regression models to model these values in relation to site area and isolation. Beta regression models are suitable when the response variable is bounded at zero and one (Cribari-Neto & Zeileis 2010). We also split genera into animal-dispersed and wind-dispersed groups and repeated this analysis in order to examine whether fragmentation effects were greater among animal-dispersed genera due to the effects of defaunation. Data were not available to further partition animal-dispersed genera by diaspore size.

All analyses were performed using R packages vegan (Oksanen *et al.* 2015), betareg (Cribari-Neto & Zeileis 2010), and CommEcol (Sanches Melo 2017) in R v. 3.2.2 (R Core Team 2015).

3.4 Results

A total of 6,351 individuals, comprising 2,646 trees (> 5 cm dbh) and 3,705 seedlings (< 1 cm dbh and < 1.5 m in height), were recorded at our 19 study sites (93 plots in total); belonging to 207 genera in 68 families. Combining trees and seedlings, we found that 22.2% (n = 46) of genera occurred at only a single site, 27.1% (n = 56) were represented by two or fewer individuals, and 14.5% (n = 30) of genera were represented by a single individual. Hence, the Chao-Sørensen index was the most appropriate dissimilarity metric to use because it reduces under-sampling bias by estimating the number of unseen rare species, and is therefore useful when sampling communities that have high alpha diversity and a large fraction of rare species (Chao *et al.* 2004). The two commonest plant families were Dipterocarpaceae (507 trees [19.2%], and 1687 seedlings [45.5%]) and Euphorbiaceae (297 trees [11.1%], and 491 seedlings [13.2%]).

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

Tree community distinctiveness did not vary significantly in relation to forest area or isolation (Figure 3.2a – c). In contrast, seedling communities in small forest fragments were most distinctive from other seedling communities (Figure 3.2d – f), and seedling divergence from adult trees was also greatest in small forest fragments (Figure 3.2g – i). Area outperformed isolation as the strongest predictor of seedling distinctiveness and tree-seedling divergence in univariate and bivariate models (Table 3.1). However, models including both area and isolation were within 2 AIC points of the best (area only, Table 3.1) model. We conclude that increasing levels of tree-seedling divergence and seedling distinctiveness are associated with decreasing fragment area, and weakly correlated with increasing isolation, but there is little variation in tree distinctiveness among sites.

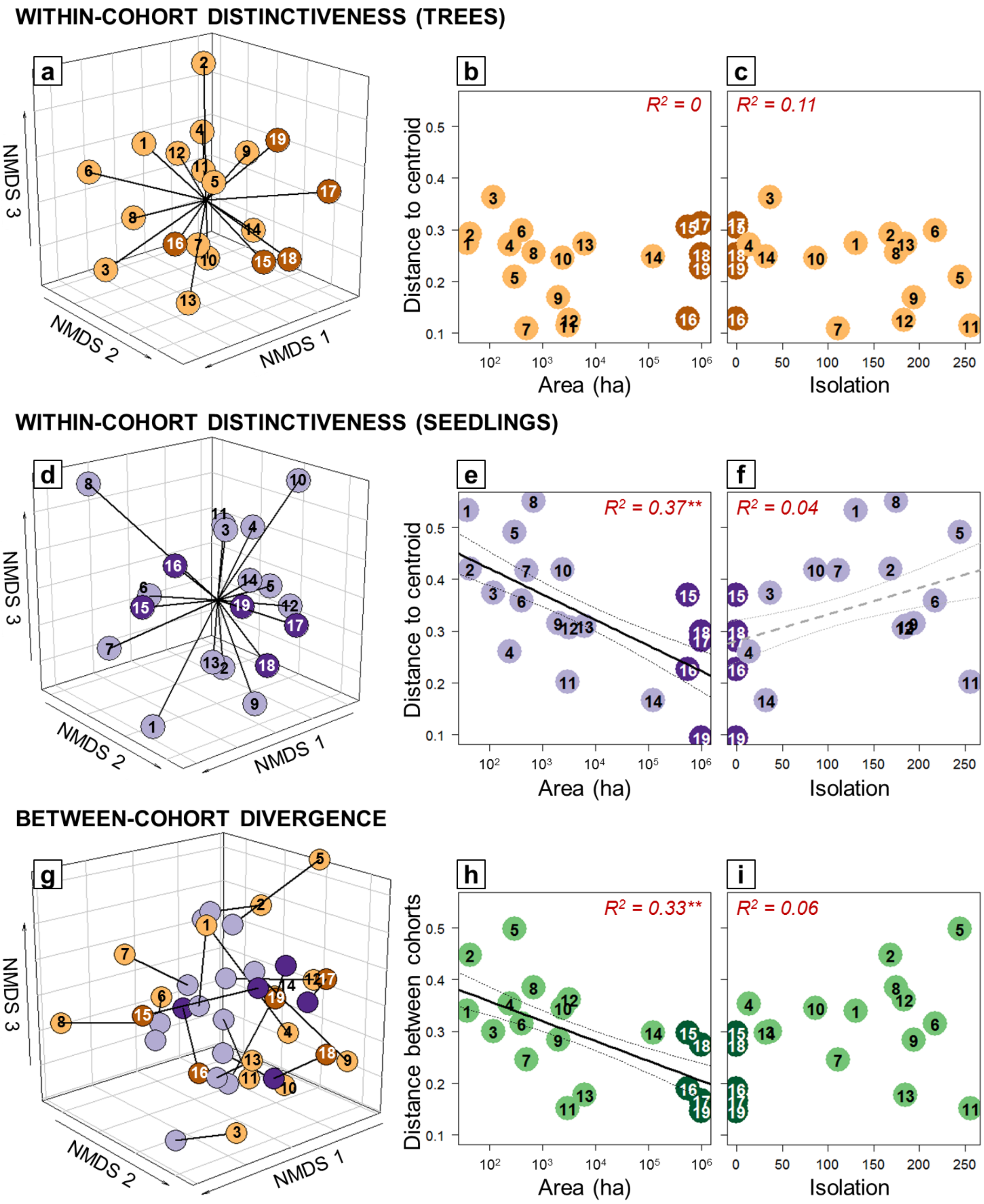

Figure 3.2. Divergence and distinctiveness of tree and seedling communities at sites in relation to site area and isolation. Panels a – c show within-cohort divergence of tree communities, panels d – f show within-cohort divergence of seedlings communities, and g – i show tree-

seedling divergence within sites. (a) and (d): three-dimensional NMDS ordinations showing the distinctiveness of trees (a) and seedlings (d) in relation to the average community (plot centroid). Numbers within circles refer to site numbers, lighter colours = fragment sites, darker colours = continuous forest sites. b – c: tree distinctiveness (distance to centroid) plotted against site area (b) and isolation (c). e – f: seedling distinctiveness (distance to centroid) plotted against site area (e) and isolation (f). g: three-dimensional NMDS ordination showing divergence between trees (brown circles) and seedlings (purple) at the same sites. Lines join tree and seedling values at the same sites. h – i: Tree-seedling divergence (Euclidean distance between cohorts in NMDS) in sites plotted against site area (h) and isolation (i). Fitted lines shows significant relationships (solid line, $p < 0.05$; dashed line, $p < 0.1$) in univariate GLMs of distinctiveness or divergence against site area or isolation, and R^2 value is adjusted R^2.

The distinctiveness of seedling communities that we find in small fragments could arise in two different ways, either by representing a predictable subset of genera (in which case they would diverge from large fragments and continuous forest, but not from one another), or by diverging from one another (each small fragment having a unique community). Comparisons of pairwise dissimilarities (n = 10 pairs in each group) revealed that differences between seedling communities for the five smallest forest fragments were the highest (A1: 40 – 307 ha, mean pairwise dissimilarity ± se = 0.66 ± 0.09, Figure 3.3a, Table S3.2), still relatively high for the five medium forest fragments (A2: 419 – 2473 ha, mean = 0.62 ± 0.06), but lower for the five largest forest fragments (A3: 2473 – 123,000 ha, mean = 0.35 ± 0.07) and for pairwise comparisons among continuous forest sites (mean = 0.30 ± 0.07). Similarly, pairwise dissimilarities between seedling communities in the most isolated forest fragments (I1: 4.96 – 6.71, mean pairwise dissimilarity ± se = 0.58 ± 0.07; I2: 4.04 – 4.57, mean = 0.68 ± 0.06, Figure 3.3c) were greater than those in less isolated forest fragments (I3: 2.76 – 4.04, mean = 0.49 ± 0.08) or continuous forest sites (mean = 0.30 ± 0.07). Hence we conclude that seedling communities in the smallest, most isolated fragments are more different to one another than larger, less isolated fragments or continuous forest sites.

Increased distinctiveness of communities in small fragments means that the accumulation of genera (per individual plant sampled) is maintained, and might even be slightly increased, in small forest fragments, compared to continuous forest sites (Figure 3.3b, d). This indicates that higher dissimilarities among small fragments are not due simply to the systematic loss of genera.

Neither the pairwise dissimilarities of seedlings nor of trees was related to geographical distance between sites, implying that variation in community composition is not simply due to site proximity (Mantel test; trees: r = 0.08, p = 0.22; seedlings: r = 0.08, p = 0.20; n = 171 pairs, 19 sites, and 999 permutations for both tests).

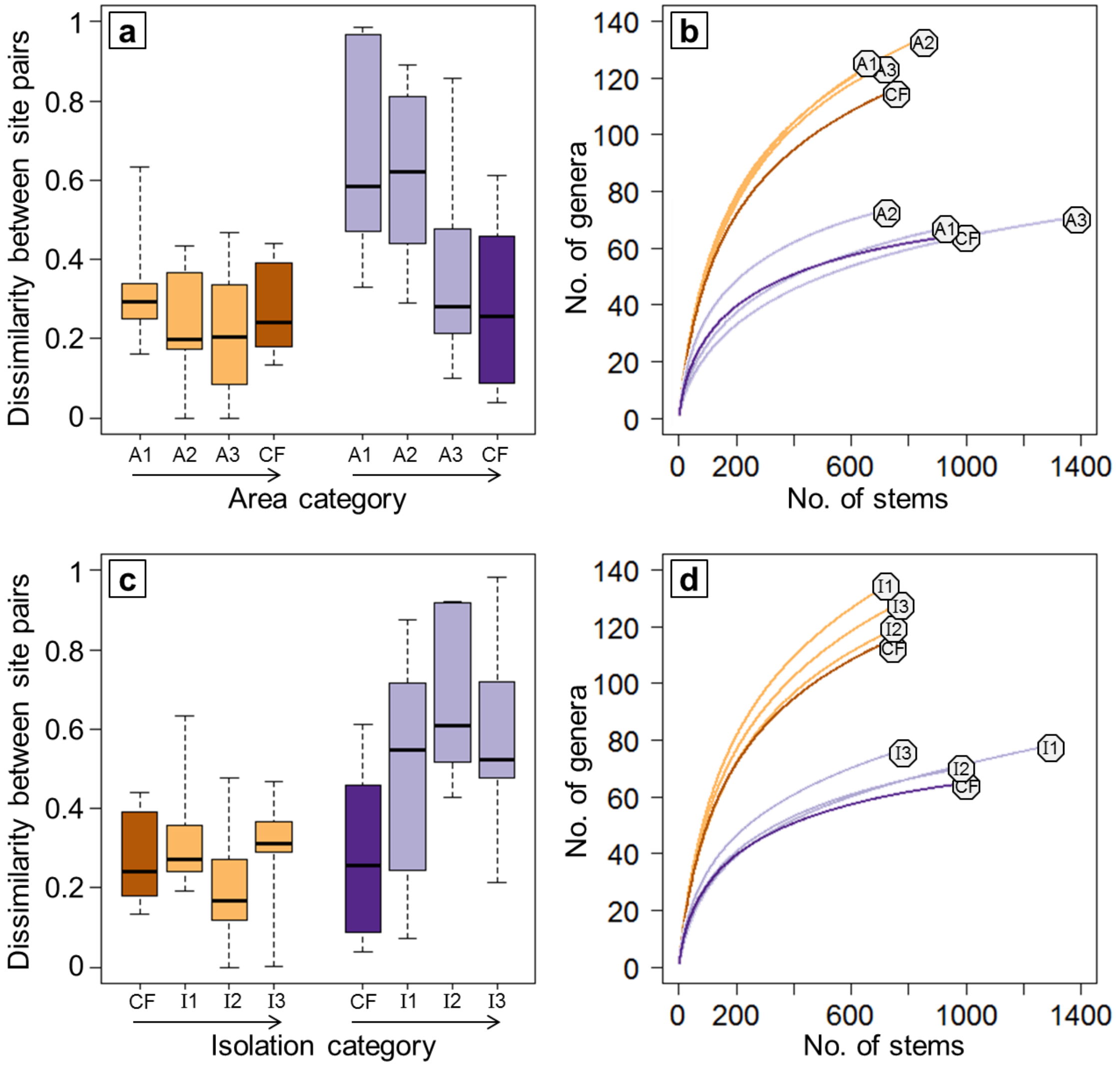

Figure 3.3. Chao-Sørensen dissimilarity between pairs of sites grouped by (a) area or (c) isolation, and observed genus richness, constructed using sample-based rarefaction curves for sites grouped by (b) area and (d) isolation. Site 10 was included in both intermediate groups so that each group contained five sites. A1 represents the smallest fragments, and I3 the most isolated fragments (see Table S3.2 for range of values of area and isolation represented by sites in each group). Boxplots show variation in dissimilarity values: boxplot horizontal lines represent medians, boxes indicate the 25th and 75th percentiles and the whiskers represent the range of values.

Table 3.1. GLM metrics for tree distinctiveness, seedling distinctiveness, and tree-seedling divergence.

Response variable	Predictor variables	df	AICc	Δ_i	Residual deviance	Adjusted R^2
Tree distinctiveness	Area + Isolation	16	-42.89	0.00	0.08	0.12
	Isolation	17	-42.09	0.80	0.09	0.04
	Area	17	-40.25	2.64	0.10	0.00
Seedling distinctiveness	Area	17	-31.50	0.00	0.15	0.37
	Area + Isolation	16	-29.50	2.00	0.15	0.36
	Isolation	17	-24.80	6.70	0.22	0.11
Tree-seedling divergence	Area	17	-38.35	0.00	0.19	0.21
	Area + Isolation	16	-36.44	1.91	0.19	0.16
	Isolation	17	-31.75	6.60	0.24	0.02

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

Table 3.2. Beta regression model metrics relating proportions of genera occurring at each of the 19 sites which were present (i) as both trees and seedlings, (ii) tree genera without seedlings, and (iii) seedling genera without trees.

Response variable	Predictor variables	df	AICc	Δ_i	Pseudo R^2
Trees and seedlings	Area	16	-55.40	0.00	0.45
	Area + Isolation	15	-54.01	1.39	0.47
	Isolation	16	-45.86	9.54	0.10
Trees only	Area	16	-50.55	0.00	0.44
	Area + Isolation	15	-49.49	1.06	0.47
	Isolation	16	-41.04	9.50	0.08
Seedlings only	Area	16	-34.60	0.00	0.12
	Isolation	16	-33.49	1.11	0.07
	Area + Isolation	15	-32.68	1.92	0.13

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

Role of recruitment failure

The proportion of plant genera occurring at each of our 19 sites that were present as both seedlings and trees increased with site area, and the proportion of genera present only as trees declined with area (Table 3.2, Figure 3.4a; n = 19 sites), indicating diminished recruitment in small fragments. By contrast, the proportion of genera present only as seedlings but not trees (‘immigrants’ at a plot scale) was not related to site area. Isolation was a poor predictor in comparison to area in all univariate models, but models including both variables were within 2 AIC units of the best model (containing only area, Table 3.2). We conclude that reproductive failure of certain genera in smaller forest fragments may be responsible for variation in seedling distinctiveness among sites. Results were similar when we repeated the analyses on predominantly animal- and wind- dispersed genera separately (Figure S3.1): fewer genera in smaller fragments were represented by both trees and seedlings, indicating a similar degree of recruitment failure in both groups and leading us to conclude that defaunation was not an important driver of the variation in seedling distinctiveness we observed.

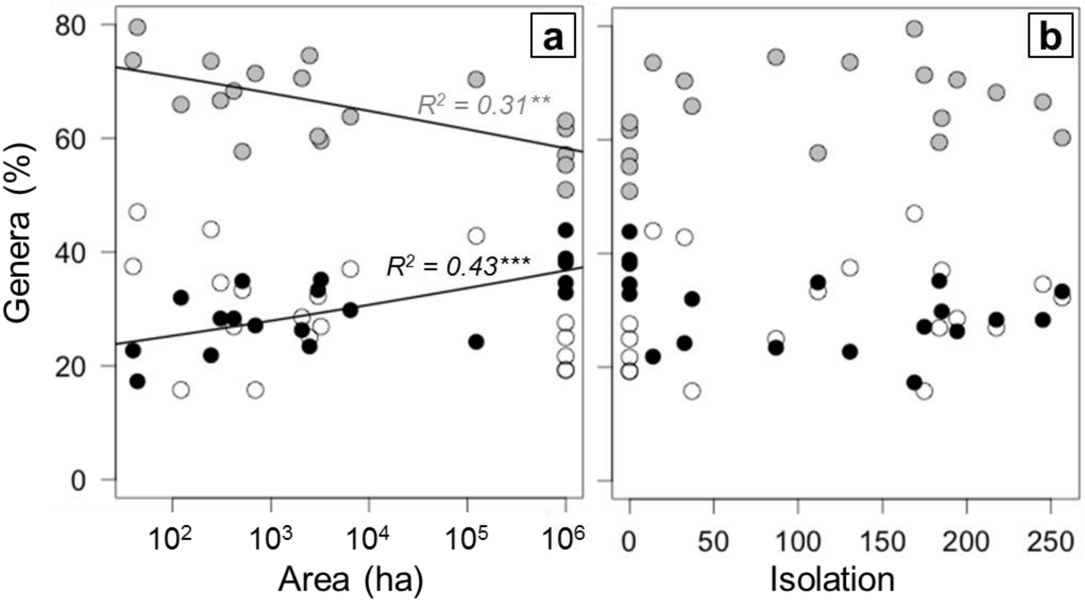

Figure 3.4. The proportion of genera occurring at each of the 19 sites shown as the percentage of genera present as trees and seedlings (black dots = recruitment success), percentage of tree genera without seedlings (grey dots = no evidence of recruitment in the study plots), and percentage of seedling genera without trees (white dots = presumed immigration into the study plots) in each site, in relation to site area (a) and isolation (b). Fitted line shows significant relationship in beta regression models, and r-squared value is pseudo R^2.

3.5 Discussion

Our results demonstrate that there is a strong effect of forest fragmentation on tree recruitment, with the greatest impacts observed in the smallest remaining fragments, and with a possible additional role for fragment isolation. We found that seedling communities in small forest fragments are diverging from those in continuous forest sites, from seedling communities in other forest fragments, and from tree communities in the same forest fragment. Further evidence that plant communities in small fragments are showing the greatest compositional turnover is indicated by a lower proportion of genera represented as both trees and seedlings. It is likely that small fragments will continue to have biodiversity value (through their heterogeneity across landscapes), but each fragment will become decreasingly like the small part of a continuous forest that it once was.

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

Fragmentation is increasing the distinctiveness of seedling communities among sites

Seedling communities in small fragments are not diverging in parallel, and differences in community composition among small fragments are even greater than those among medium or large fragments (Figure 3.3a, Table 3.1). Thus, fragmentation appears to be generating increasingly distinctive plant communities in fragments, which collectively retain considerable diversity (even if each individual fragment has reduced richness); whereas we find no evidence that small and isolated fragments are becoming impoverished in a similar manner – and hence homogenised. Far from homogenising to a common set of (potentially) disturbance-adapted genera, a different set of genera is recruiting seedlings in each fragment.

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

These trajectories of change are likely to be driven by a combination of factors that alter the complex web of ecological processes that occur in forest interior environments, and which are disrupted in forest fragments. Physical differences in fragment size, age, amount of edge and the structure of the surrounding matrix, together influence the penetration of edge effects and the level of disturbance experienced within the fragment (Laurance et al. 2007). Reduced soil moisture in fragments can reduce chances of seedling establishment and survival, and different species have different levels of drought tolerance (O'Brien et al. 2014). Thus, a combination of demographic (e.g., increased stochasticity in small populations) and environmental effects are likely to affect the success and failure of individual species. In addition, dispersal of both pollen and seeds will normally be more limited between more isolated patches of forest, and is likely to alter the reproductive success of tree populations over multiple generations. Many species, including dipterocarps, are predominantly outcrossing and retain deleterious recessive alleles in their populations; they face a heightened risk of inbreeding depression, and hence a reduced capacity to regenerate, if selfing is increased in small and isolated forest fragments (Naito et al. 2008). These factors will combine to create unique conditions in each forest fragment, impeding recruitment of those genera that are ill-adapted to the new conditions, while facilitating the success of others.

Fragmentation is increasing the divergence of communities within sites

We conclude that seedling communities are diverging from the tree communities in the same sites, and that seedling-tree divergence is greatest in the smallest forest fragments. This is consistent with the patterns of distinctiveness that we have just described (seedling but not tree community distinctiveness is elevated in the smallest forest fragments), but it is important to consider seedling divergence separately to distinctiveness because it confirms that the seedling community divergence we observed has arisen through changes (both failures and successes) in recruitment in different locations. The compositional change (from trees to seedlings, leading to the distinctiveness of seedling communities across landscapes) is driven partly by the recruitment failure of existing tree genera within plots (fewer genera are recruiting in small and isolated fragments) and partly by immigration, presumably mainly from adult trees located elsewhere in sites. If one just considers recruitment success (which may influence the trajectory of the future community), more genera of seedlings that we observed in the plots inside small fragments come from parent trees that must be growing outside the plots, whereas the reverse is true for plots in continuous forest (Figure 3.4a). If this increased proportion of immigrant recruitment eventually translates into adult tree composition, it implies a much higher future turnover of the generic composition of trees per plot (i.e., at a scale of 2 ha) in small fragments than in continuous forest.

The difference between the origin of seedlings in small fragments compared to continuous forest arises because the recruitment success of standing trees was lowered in small fragments, but the immigration of new genera (not present as adult trees in the plots), remained similar across all sizes of fragment and in continuous forest (mean number of “parentless” seedling genera in five smallest forest fragments = 7.4 ± 1.4 se, compared to 6.4 ± 0.7 in continuous forest sites; Figure 3.4a). This implies that current seed dispersal rates within fragments are not necessarily lower than in continuous forest. This result is somewhat surprising because defaunation is a frequently reported consequence of fragmentation (Canale et al. 2012), disrupting seed dispersal and limiting movement of seeds away from parent trees (Harrison et al. 2013); thus we might expect there to be a reduced input of seedling genera into plots in smaller fragments from surrounding trees, and for the input of predominantly animal-dispersed genera to be even further reduced. However, we did not find clear differences in the seedling recruitment successes and failures of animal and abiotically dispersed genera that would correspond to the defaunation of fragments (Figure S3.1). Hence we conclude that it is the reduced rate of recruitment of seedlings to parent trees within the plots in small fragments that is driving the observed patterns of increased divergence, not differences in immigration into the plots. Overall, our results support the hypothesis that recruitment differences are driving divergence between small fragments and continuous forest, and are responsible for the diversification of seedling communities across landscapes containing forest fragments.

The landscape perspective

Given the divergence of seedling communities across forest fragments, our results could be a consequence of heterogeneity in altered physical, biological and human forces acting in different combinations and strengths in different locations. We conclude that surviving forest fragments still (for the time being) contain a mixture of forest trees broadly representative of pre-fragmentation communities, that tree recruitment is continuing within forest fragments as well as within continuous forest, and that recruitment has already generated divergence among the seedling communities in different locations, so there is potential for each forest fragment to embark on a different future successional trajectory. As such, although each individual small fragment may support an impoverished subset of species (Stride et al. 2018), a diverging ensemble of forest fragments has the potential to support a considerable diversity of species. Each fragment can potentially support some species and genera that are not found in fragments elsewhere in the landscape, such that the fragments collectively support an equivalent number of genera (for a given number of stems) as would be found in continuous forest (Figure 3.3b, d). Hence, heterogeneous networks of small habitat fragments may have the capacity to make a major contribution to the persistence of biodiversity in otherwise intensively-managed agricultural tropical landscapes.

3.6 Author contributions and acknowledgements

GS, JKH, and CDT conceived and designed the study; GS and AJ collected field data; GS led data analysis and wrote the first draft of the manuscript, with substantial contributions from JKH and CDT to all further revisions. SB, JH and MJMS also contributed to revisions. All authors gave final approval for publication. The authors declare they have no competing interests.

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

CHAPTER 4

Forest fragmentation alters recruitment of tropical trees: a study of dipterocarps on Borneo

4.1 Abstract

Tree regeneration is critical for maintaining the structure, functioning and diversity of forest fragments, but seedling recruitment and survival may be disrupted in forest remnants. This chapter provide important evidence of fragmentation impacts on seedling recruitment of a keystone group of species, the dipterocarps. We examined the impact of rainforest fragmentation on shade-tolerant canopy trees by comparing seedling occurrence (presence/absence) and abundance-when-present of 25 dipterocarp tree species in four forest fragment sites (120 – 2,000 ha) and four sites in an extensive tract of continuous forest (> 1 million ha) in Sabah, Malaysian Borneo (n = 50 trees per site; 7 – 15 species per site). We found that seedling occurrence was reduced in fragments by almost half: only 40.5% of individual trees in forest fragments had conspecific seedlings established nearby, compared to 77% of trees in continuous forest sites. However, when considering only those trees where seedlings occurred (n = 235 trees with seedlings), we found no significant difference overall in the abundance of seedlings between fragments and continuous forest sites. Nonetheless, there was considerable variation in the performance of dipterocarps in forest fragments, with a few species producing a much greater abundance of seedlings in fragments than in continuous forest, but most others producing fewer seedlings. We anticipated that wood density and flower size, acting as proxies for growth rate and pollination syndrome, might predict recruitment success in fragments. However, while species with higher wood density were more likely to have seedlings, this was consistent in both fragments and continuous forest sites, and flower size was not associated with either the occurrence or abundance of seedlings. The variability in recruitment success in fragments between and within species indicates that site-specific factors may have an important impact on the recruitment success of individual trees, and hence future research would benefit from examining larger numbers of individuals per tree species, and increasing the replication of sites. We conclude that if the majority of dipterocarp trees fail to recruit seedlings in fragments, population sizes will continue to decline until some species eventually become extinct from forest fragments; whereas a subset of species are continuing to recruit successfully.

4.2 Introduction

Fragmentation of previously continuous forest landscapes is a world-wide phenomenon and a major threat to biodiversity, ecosystem functioning (Haddad et al. 2015), carbon storage (Qie et al. 2017), and climate regulation (Bala et al. 2007). Loss of species from forest fragments is an increasingly reported trend (Stride et al. 2018, Benedick et al. 2006, Turner 1996), and the loss of functional groups of species such as pollinators and/or seed dispersers from fragments can have important repercussions for the plant communities at these sites (Pérez-Méndez et al. 2016). Recent studies have shown that forest fragments may represent increasingly distinctive tree assemblages as differences in patterns of seedling recruitment are translated into mature tree communities (e.g. Stride et al. in prep), but differences in the success or failure of individual trees to recruit seedlings in fragments compared with more continuous forest have not been quantified. These recruitment patterns are important to study as tropical forests become increasingly fragmented, and patterns of seedling recruitment will dictate the future composition and persistence of forest fragments.

Tropical rainforests represent some of the most biodiverse ecosystems on the planet, and many tree species occurring within these ecosystems have highly restricted distributions and/or exist at low population densities (He et al. 1997), which may be further restricted and reduced by habitat fragmentation. In order for tree populations to persist in forest fragments in the long term, they must continue to flower, fruit, and recruit seedlings. These processes may be impeded by a number of interacting factors arising as a result of fragmentation and isolation of forest remnants. However, the initial effects of habitat fragmentation may be masked by the longevity of individual trees, which can persist for many years in fragments while failing to recruit seedlings, creating an extinction debt in forest fragments that may take many decades to be fully realised (Tilman et al. 1994).

Fragment creation directly reduces the effective population size of trees due to the isolating effect of an (often) inhospitable surrounding matrix of agricultural or urban land (Aguilar et al. 2008). Defaunation of fragments often follows, frequently due to poaching as a result of increased access to fragments (Canale et al. 2012), but also by altering foraging behaviour and limiting movement of animals between patches (Kolb 2008), thereby altering seed dispersal processes. Pollinators can also be affected (Vamosi et al. 2006), and pollen limitation can lead to inbreeding depression in tree progeny in fragments, increasing rates of seed abortion and decreasing seedling survival (Naito et al. 2005, Cunningham 2000). Seedling survival may also be reduced if seeds are not dispersed away from parent trees, leading to increased density-dependent mortality (Wright 2002). In addition, forest fragments often have higher ambient temperature and decreased soil moisture, leading to increased drought stress, greater tree mortality (Phillips et al. 2010), increased rates of flower abscission and fruit abortion (Taylor and Whitelaw 2001), and a decline in the germination rate of seeds and survival of seedlings (Zambrano et al. 2014, Englebrecht et al. 2005). In contrast, reduced population sizes of pre-dispersal seed predators, post-dispersal herbivores, and pathogens in fragments, may result in increased seed survival, seedling germination and seedling establishment (Granados et al. 2017), and the more open canopy of disturbed forest fragments can increase seedling growth rates (Yeong et al. 2016). As a result of these different processes, which are affected in different ways in different fragments, and which will generate different responses in different tree species, it is difficult to predict what the effects of forest fragmentation will be on individual trees.

We know that local seedling genus richness is reduced in forest fragments, and that there is greater beta diversity between seedling communities in small fragments compared with communities in more continuous forest sites (Stride et al. 2018; Stride et al. in prep). However, variation in seedling recruitment success within and among species in continuous forest and fragmented forest has not yet been quantified. It is also unknown whether certain life history characteristics of species may promote recruitment success in forest fragments. For instance, insect-pollinated species with larger flowers tend to be pollinated by larger bodied insects that may be more capable of travelling between isolated patches of forest, thereby linking disjunct populations. By contrast, smaller-flowered species generally only receive pollen from within the fragment, limiting the volume of pollen available as well as its genetic diversity (Kettle et al. 2011). Wood density is often used a proxy for growth strategy (Slik 2005), and low wood-density, fast-growing species may be better equipped to respond to the disturbed environment within forest fragments, leading to a shift in community composition.

We study sites in lowland tropical rainforest on Borneo, where members of the shade-tolerant Dipterocarpaceae family dominate the forest canopy. Here, dipterocarps account for up to 80 percent of the basal area of canopy trees (Ashton et al. 1988) and reach high levels of endemism, and so are important components of the forest ecosystem (Maury-Lechon and Curtet 1998). They share a number of characteristics that make them a good group to study in relation to seedling recruitment patterns following fragmentation, and in this study we focus on a group of 25 dipterocarp species. Dipterocarps are wind dispersed, and have limited secondary seed dispersal. They also have recalcitrant seeds and no soil seed bank, so for successful seedling recruitment to take place, seeds must germinate soon after reaching the forest floor (Umarani et al. 2015). Dipterocarp seedlings are shade-tolerant and although they can survive for many years in the shady understory, nearly all of them will have been recruited subsequent to the isolation of the forest fragments surveyed in this study (Connell and Green 2000). Dipterocarps reproduce synchronously in mast flowering events followed by mass fruiting where individual trees may produce 100,000s of seeds (Ashton et al. 1988). Masting is triggered by the droughts associated with the El Niño Southern Oscillation (ENSO), which occur irregularly on a 3 – 7 year basis, such as in 2015/16 (Cpc.ncep.noaa.gov. 2018, Walsh and Newbery 1999). Successful recruitment rarely occurs outside of these synchronised events (Curran et al. 1999), and so the majority of mature dipterocarps originate during ENSO events. However, fragmentation may alter forest processes and hence disrupt the cues triggering mast flowering, leading to seedling recruitment failure, but evidence is lacking.

To assess how fragmentation may affect seedling recruitment in dipterocarps, we surveyed the recruitment of mature dipterocarp trees in rainforest remnants and in continuous forest in lowland Sabah, Malaysian Borneo. Rainforest remnants represent fragments of relatively undisturbed primary forest that were probably isolated in the 1990s when there was a rapid expansion of oil palm (Yeong et al. 2016), and we test here whether there are differences in patterns of seedling recruitment of individual trees and species between forest fragments and continuous forest sites. We test the hypotheses that (1) seedling recruitment is reduced in forest fragments relative to continuous forest, and that (2) wood density and flower size, acting as proxies for growth rate and pollination syndrome, act as predictors of recruitment success. In this way we assess whether dipterocarp regeneration is disrupted in forest fragments, in order to understand the long-term impact of habitat fragmentation tropical forest ecosystems.

4.3 Material and methods

Study sites

Tree and seedling data were collected in four forest fragments (FF) and four “control” sites in continuous forest (CF), in lowland dipterocarp rainforest (<500 m a.s.l.) in Sabah, Malaysian Borneo, during January – April 2017 (Figure 4.1). FFs were 120 – 2,000 ha in area, located within a fragmented mosaic of forest and agriculture and were surrounded by mature oil palm plantations. The FFs were protected as “Virgin Jungle Reserves” (VJRs) in the 1950s for scientific research and represent primary forest where logging is prohibited, although most FFs have experienced low levels of disturbance from human encroachment, poaching and felling (pers. obs., Brühl et al. 2003). CF sites were located within a tract of forest of > 1 million ha. Two of the CF sites were located within fully-protected undisturbed primary forest (Danum Valley Conservation Area), and the other two sites were within selectively twice-logged forest

(Malua Forest Reserve), logged in the mid-1980s and 2005/6 (Reynolds et al. 2011). Much of the remaining forest in Sabah has been logged, and therefore sampling a range of CF sites represented dipterocarp communities of closed canopy forest typical of the region, to compare with FFs. All sites were >2 km apart.

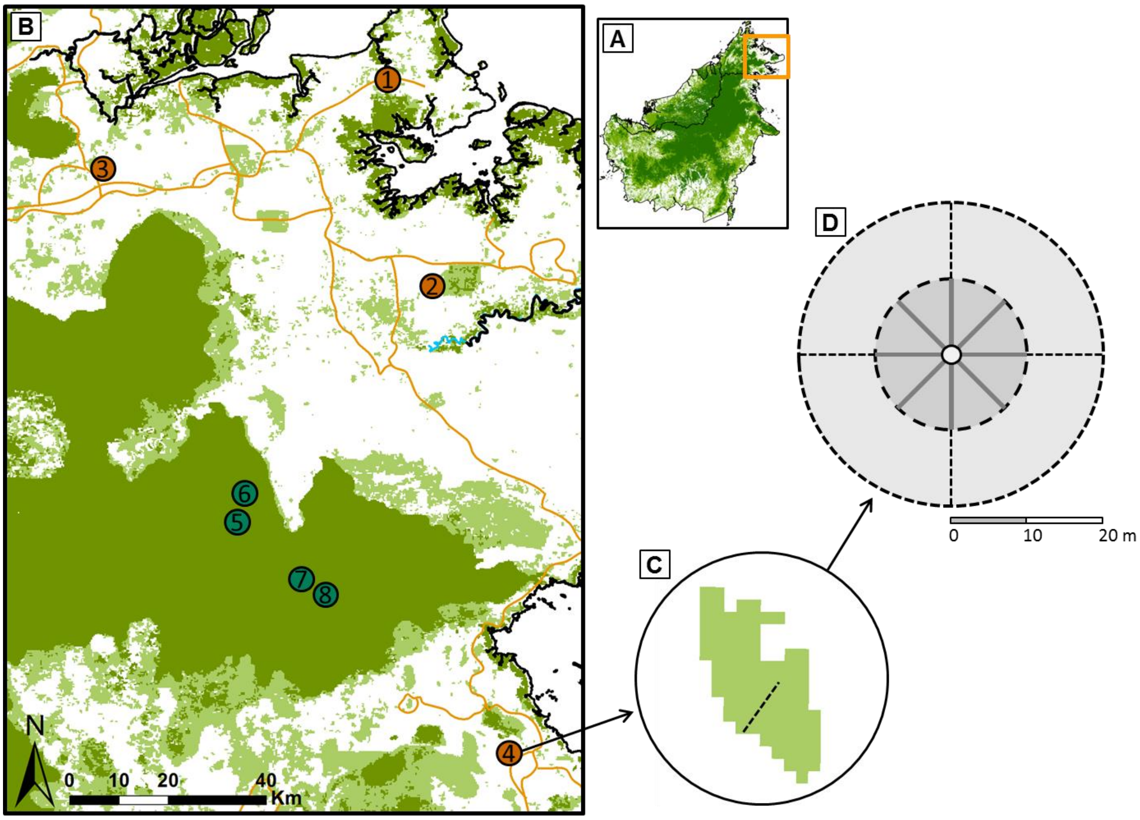


Figure 4.1. (A) Study area location on Borneo. (B) Sites 1 – 4 are numbered in order of increasing size (120 – 2,000 ha), sites 5 – 8 are continuous forest sites; dark green areas indicate forest; light green areas indicate regenerating or degraded forest; white areas indicate agricultural land predominantly covered by oil palm. Forest cover data were obtained from Miettinen et al. 2012. (C) Mother trees were located within eyesight of 1.5km linear transect (dotted line) into centre of forest fragment or continuous forest sites. (D) Diagram of sampling design around each mother tree (central open circle; n = 400 trees sampled in total). Conspecific seedlings were counted along eight 10 m x 20 cm transects (dark grey lines). Dbh and proximity (up to a distance of 20 m from the central mother tree) of the nearest two trees >30 cm dbh in each quarter, and all conspecific trees >30 cm dbh, were recorded.

Locating dipterocarp trees and assessing seedling recruitment

A linear transect (up to 1.5 km long) was set up in each of the eight sites, starting 100 m from the forest edge to avoid the main edge effects (Laurance 2000; Ewers and Didham 2006), and in FFs was angled towards the fragment centre. A list of dipterocarp species present at study sites was established prior to sampling based on prior knowledge of the species composition of the sites (Stride et al. 2018). Given that relatively few species were widespread across all sites, and their low density when present in sites, we selected 25 dipterocarp species (Table 4.1) that occurred in a minimum of two sites (Stride et al. 2018), although subsequently three species were only located in one site each. The majority of seedling (individuals <1.5 m in height and <1 .5 cm dbh) recruitment is likely to have occurred during recent mast fruiting events (e.g. a particularly strong global ENSO event took place in 2015/16; Cpc.ncep.noaa.gov. 2018) and, even though shade-tolerant tree seedlings can survive for a number of years (Connell and Green 2000), it is very unlikely that any seedlings originated before forest fragmentation took place in the 1980s.

Individual trees were targeted in order to efficiently sample seedling density within fragments. It is estimated that ~90% of seeds fall within 10 m of parent trees and germinate where they fall (Smith et al. 2015), and despite the fact that there may be some overlap of individual tree output, sampling seedling abundance within 10 m of parent trees provided robust and quantified evidence of the recruitment effort of the individual trees surveyed.

All qualifying ‘parent’ dipterocarp trees >30 cm diameter at breast height (dbh) within 20 m of the transect were sampled, up to a maximum of 10 individuals per species per site, and 50 individuals overall per site (i.e. 400 stems studied in total). Trees from the 25 study species were only sampled if species identity was assigned with a high degree of confidence. Conspecific tree seedlings were enumerated along eight lines emanating from the mother tree (Figure 4.1D) within a 10 m radius of the trunk of the mother tree. We selected 10 m as a reasonable proxy for the recruitment success because nearly all dipterocarps seeds fall under the crown of the tree, and they have limited secondary dispersal due to lack of a nutritious pericarp. Some of the seedlings that recruited within 10 m of mother trees may have originated from nearby conspecific trees (which we control for through analysis of neighbouring conspecifics, see below), just as some seedlings produced by the mother tree are likely to have dispersed beyond 10 m, up to a maximum dispersal distance of ~80 m (Tamari and Jacalne 1984). However, this data provides an estimate of the seedling density rather than total seedling recruitment of individual trees.

Table 4.1. Dipterocarp species included in study, grouped by location. Sampling location indicates the forest types where species were located: both = species sampled in continuous forest (CF) and forest fragments (FF), CF only and FF only = species only sampled in CF or FF respectively. Number or mother trees sampled, and number of sites where the mother trees were located is also indicated, along with the wood density (data from Chave et al. 2009) and flower length (data from Slik 2009 and Ashton 2004).

ID #	Species	Sampling location	# mother trees	# sites	Wood density	Flower length
1	*Dipterocarpus caudiferus* Merr.	Both	23	5	0.71	50
2	*Dryobalanops lanceolata* Burck	Both	23	6	0.62	12
3	*Hopea nervosa* King	Both	8	4	0.61	3.5
4	*Parashorea malaanonan* Merr.	Both	32	7	0.42	14
5	*Parashorea tomentella* (Symington) Meijer	Both	37	8	0.51	15
6	*Shorea acuminatissima* Symington	Both	18	4	0.39	5
7	*Shorea fallax* Meijer	Both	39	8	0.5	8
8	*Shorea gibbosa* Brandis	Both	17	5	0.46	5
9	*Shorea johorensis* Foxw.	Both	29	5	0.39	8
10	*Shorea leprosula* Miq.	Both	19	6	0.44	6
11	*Shorea macroptera* Dyer	Both	13	3	0.43	5
12	*Shorea parvifolia* Dyer	Both	33	5	0.41	7
13	*Shorea pauciflora* King	Both	21	5	0.53	7.5
14	*Vatica dulitensis* Symington	Both	10	3	0.82	6
15	*Shorea beccariana* Burck	CF only	11	3	0.47	9
16	*Shorea faguetiana* F.Heim	CF only	4	2	0.48	3
17	*Dipterocarpus geniculatus* Vesque	FF only	6	1	0.59	35
18	*Dipterocarpus gracilis* Blume	FF only	10	2	0.60	25
19	*Dryobalanops beccarii* Dyer	FF only	13	2	0.50	10
20	*Hopea ferruginea* Parijs	FF only	5	1	0.58	3
21	*Hopea nutans* Ridl.	FF only	3	1	0.88	4
22	*Shorea guiso* Blume	FF only	4	2	0.71	10
23	*Shorea seminis* Slooten	FF only	10	3	0.72	8
24	*Shorea smithiana* Symington	FF only	6	2	0.36	10
25	*Vatica umbonata* Burck	FF only	6	2	0.79	10

In order to account for variation in the structure of the forest surrounding each mother tree, which influences the light environment and therefore seedling growth and survival, we measured the dbh and distance from the mother tree to the nearest two trees (of any species) >30 cm dbh in each of four quadrants within a 20 m radius of the mother tree, and classified them as dipterocarp or non-dipterocarp, as well as four measures of canopy cover (taken on each compass point) using a spherical densiometer. We used these measurements to calculate tree density, basal area, the fraction of trees that were dipterocarps, and canopy openness. We also measured the dbh and proximity of all conspecific trees >30 cm dbh within 20m radius of each study tree, and included these variables in our analyses to control for the fact that seedlings encountered may have come from more than one mother tree.

Data analyses

We tested the hypotheses that seedling recruitment per tree is reduced in forest fragments compared to continuous forest, and that wood density and flower size are predictors of the sensitivity of species to fragmentation effects (i.e. testing for interaction effects between species identity and forest type on seedling recruitment). We analysed two measures of seedling recruitment, seedling occurrence (binary presence/absence), and seedling abundance when present.

We used a binomial Generalised Linear Mixed Model (GLMM, with a logit link) to model seedling presence or absence per tree in fragments and continuous forest (n = 200 trees in each forest type). We then used a negative-binomial GLMM to analyse seedling abundance when present per tree (zero-truncated data; n = 154 trees in continuous forest, 81 trees in forest fragments). Carrying out these two GLMMs, on seedling occurrence and seedling abundance allowed us to quantify separately the ability of trees to recruit any seedlings, as well as the abundance of seedlings when recruitment occurred.

GLMMs were conducted at the level of individual trees, with species identity and site identity included as random effects (to account for the potential non-independence of data with regards to these two factors), and forest type (CF or FF) included as a categorical predictor variable. The same set of five continuous predictor variables (dbh, conspecific tree density, forest structure, wood density, flower size – see details below) was also included in both seedling presence-absence and abundance models, as follows. To control for the fact that larger trees are more likely to fruit (Numata et al. 2012), we included the dbh of the mother tree in each model, as well as the number of conspecific mature trees (>30 m) within a 20 m radius of the focal tree that may have contributed to the seedling pool. We also controlled for variation in canopy cover and tree density, by including forest structure around each mother tree into models because these factors influence the light environment fostering seedling growth. We quantified forest structure using the first component (PC1) of a Principal Components Analysis combining four variables: the density and basal area of mature trees, proportion of mature dipterocarps, and average canopy openness within 20 m of each focal tree (see SOM for details). High values of PC1 corresponded to high density and basal area of mature trees, and low values of canopy openness, i.e. a low light environment for seedlings. Finally, we included the wood density and flower size of each individual, according to species identity, as well as the interaction of these traits with forest type. For wood density, we used dry weight (g/cm3) data from The Global Wood Density database (Chave et al. 2009, Zanne et al. 2009), and flower size data (flower length) was obtained from the Tree Flora of Sabah and Sarawak (Ashton 2004) and Plants of Southeast Asia (Slik 2009). All five continuous predictor variables (dbh, conspecific tree density, forest structure (PC1), wood density, and flower size) were scaled to have a mean of 0 and variance of 1 prior to analysis, to aid comparison of their relative importance on seedling recruitment. Models including all combinations of predictor variables were run, and the top models (those where delta AICc <2 of the best model) were identified using an AIC approach (Burnham and Anderson 2002). Model averaging of the top models, weighted by AICc, was then used to determine the relative importance and effect size of each variable: effect sizes whose 95% confidence intervals (CIs) did not cross zero were assumed to be significant predictors in each set of models.

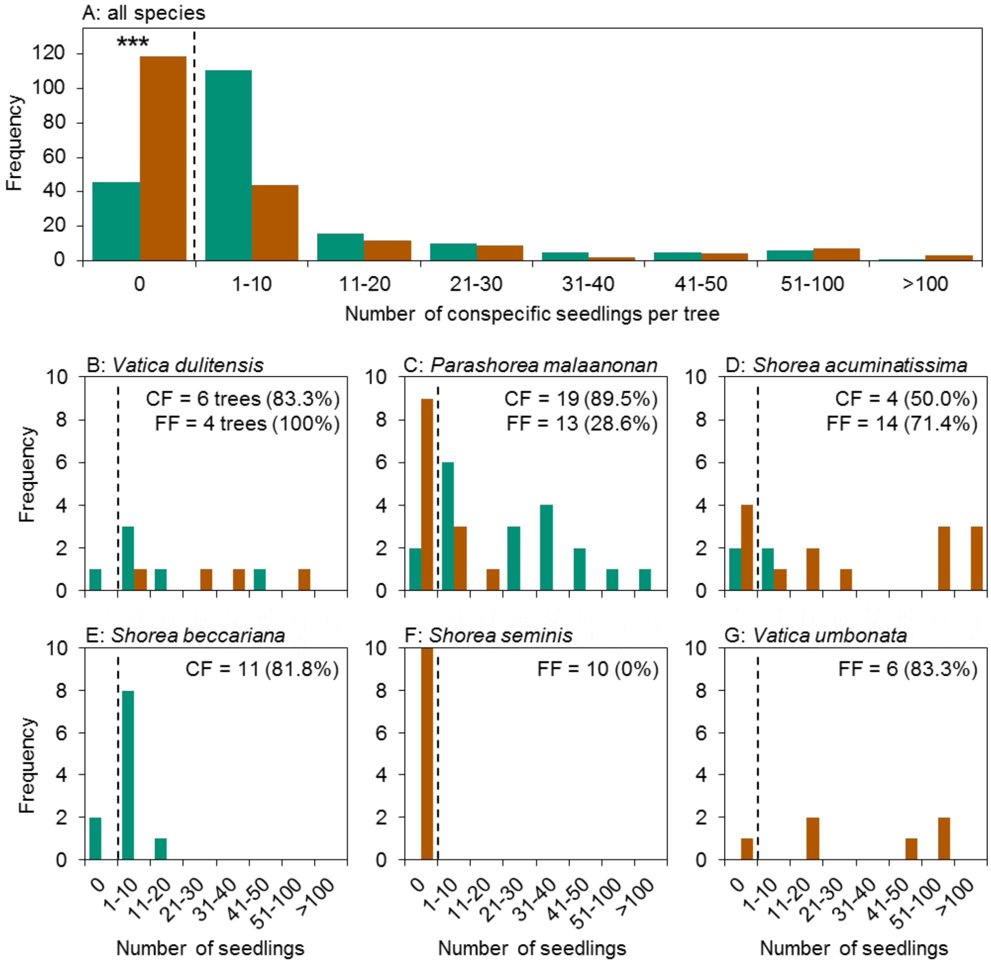


Figure 4.2. Number of conspecific seedlings recruited per tree in continuous forest (green bars) and forest fragments (brown bars). A: Overall frequency distribution of seedling abundance per tree, B – G: example species illustrating variation in seedling recruitment between species and forest types (CF = continuous forest, FF = forest fragments). The number of trees sampled in each forest type is indicted in the top right of each plot, and the percentage of those trees that were recorded with seedlings is in brackets.

Owing to the uneven distribution of species in the landscape, only 14 of our 25 study species were found in both forest fragments and continuous forest sites. In order to separate out the effects of species occurrence at sites from seedling recruitment per species, we then repeated the above GLMMs on the subset of species common to both forest types (14 species, 322 trees; Table 4.1). Compared with the analyses of the full data set, analysing the subset of 14 species allowed us to examine fragmentation effects whilst controlling for the effect of species' identity. However, as the data subset may be biased to include only those species that are most resilient to fragmentation, we present findings from analyses including both the full data set and this sub-set of 14 species. All analyses were performed in R v. 3.2.2 (R Development Core Team 2015).

4.4 Results

A total of 400 trees and 4,418 conspecific seedlings belonging to 25 dipterocarp species in six genera were recorded across our eight study sites. The proportion of trees with conspecific seedlings present ranged from 10 – 66 % in FFs compared to 54 – 92% in CF sites. *Shorea* is the most species-rich genus in the Dipterocarpaceae family, and this was reflected both in the number of *Shorea* species recorded across the sites (11 in CF and 12 in FF; 44% and 48% of species respectively), and the number of *Shorea* trees sampled (133 in CF and 91 in FF; 66.5% and 45.5% respectively). As anticipated, larger trees were more likely to have seedlings present (but did not have greater seedling abundance), and trees with more individuals of the same species nearby were also more likely to have seedlings present, and greater seedling abundance (Table 4.2, Figure 4.4).

Seedling occurrence was significantly lower in forest fragments (40.5% of trees were recorded with conspecific seedlings) than in continuous forest (77% of trees, Figure 4.3a,c), but abundance was unaffected by forest type, probably due to the high level of variation in recruitment in forest fragments (mean abundance-when-present in CF = 12.8 seedlings ± 1.6 SE, mean in FF = 30.2 ± 8.2, Figure 4.3b,d). These results were the same regardless of whether the full dataset of 25 species, or the sub-sample of 14 species common to both forest types, was analysed (Table 4.2, Figure 4.4).

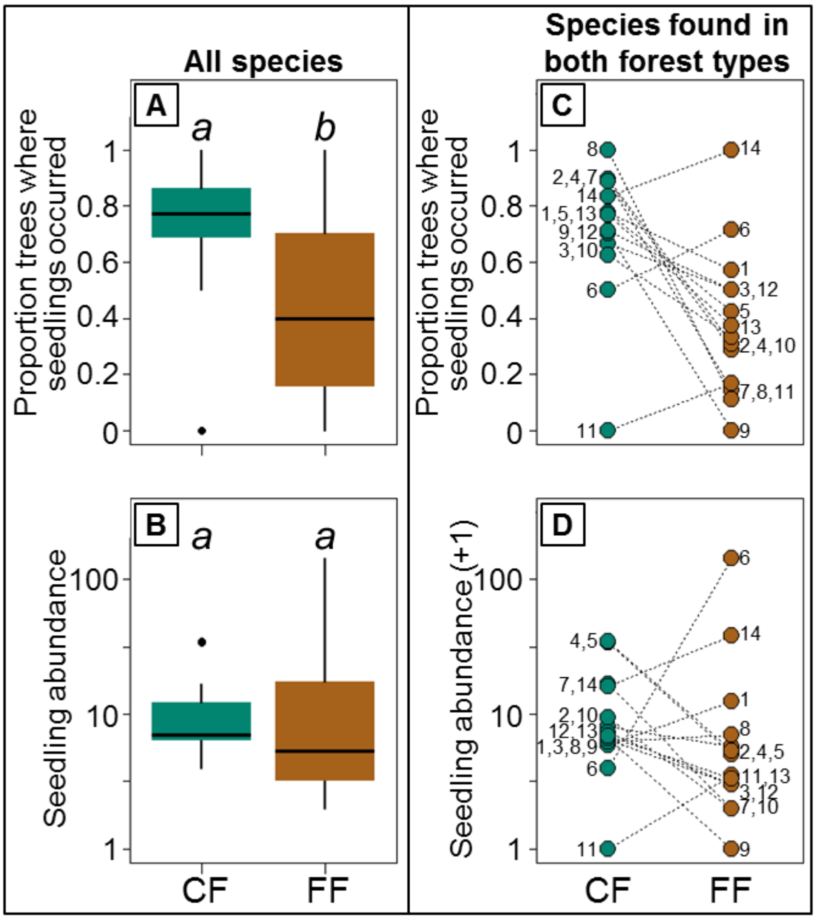


Figure 4.3. Species' sensitivity to fragmentation. (A) Proportion of trees in continuous forest (green bar; 200 trees, 16 species) and forest fragments (brown bar; 200 trees, 23 species) where conspecific seedlings occurred (calculated per species). (B) Mean seedling abundance (when present) of species in continuous forest (154 trees, 16 species) and forest fragments (81 trees, 23 species). Boxplots show variation in values: boxplot horizontal lines represent medians, boxes indicate the 25th and 75th percentiles and the whiskers represent the range of values within 1.5 x interquartile range of the data. Letters indicate significant differences between CF and FF in GLMMs. (C) Difference in proportion of trees with recruitment (seedling occurrence) in CF (green points) and FF (brown points), and (D) mean seedling abundance (here including zeros to allow all 14 species to be plotted) between CF and FF for a subset of 14 species present in both forest types. Numbers indicate species identity (Table 4.1).

There was considerable variation in seedling recruitment among species, and in whether or not species were affected by fragmentation effects (see Figure S4.1 for frequency distributions of seedling abundances of all species). For example, some species performed equally in both forest types (e.g. *Vatica dulitensis*, Figure 4.2B), some performed better in CF than in FF (e.g. *Parashorea malaanonan*, Figure 4.2C), and others performed better in FF than CF (e.g. *Shorea* *acuminatissima*, Figure 4.2D). Two species were only found in CF sites (e.g. *Shorea beccariana*, Figure 4.2E), nine were only found in FF (e.g. *Vatica umbonata*, Figure 4.2G, Table 4.1), and four species of these species failed to recruit any seedlings at all in FF sites (e.g. *Shorea seminis*, Figure 4.2F). Wood density was an important predictor of seedling recruitment overall, and was also included in most top models of seedling abundance (although non-significant), but did not predict sensitivity of species to fragmentation. We found no evidence that flower size was a predictor of either seedling presence or abundance. Thus high wood density species were more likely to show evidence of seedling recruitment, but there were no interactions with forest type.

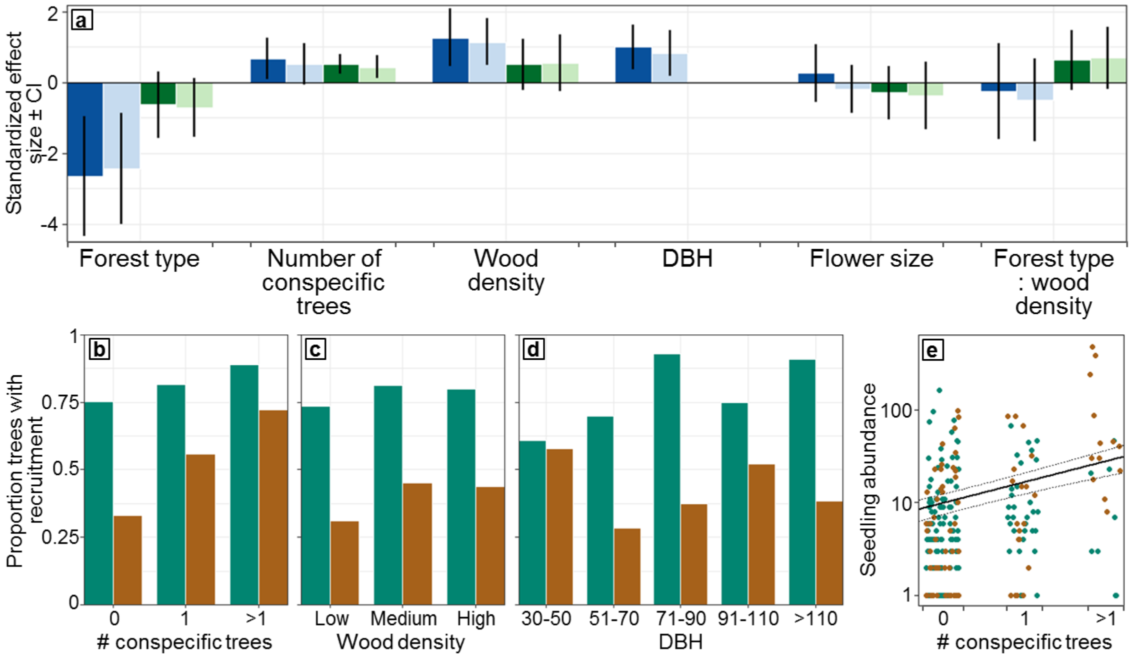


Figure 4.4. (a) Results of averaged seedling occurrence (blue bars) and seedling abundance-where-present (green bars) models based on the full dataset (dark bars) and the data subset containing only 14 species found in both forest types (light bars). Effect sizes whose 95% confidence intervals did not cross zero were assumed to be significant. b – e: significant variables in occurrence and abundance models, based on the full dataset. Proportion of trees with seedlings, grouped by (b) number of conspecific trees nearby, (c) wood density, and (d) DBH of mother tree. (e) Seedling abundance (when present) of trees grouped by number of conspecific trees nearby (each data points represents a tree and symbols are jittered on the x axis to prevent overlap), with fitted line showing predicted relationship (± standard error) in GLMM using full dataset.

Table 4.2. Top ranked GLMMs of factors affecting seedling recruitment based on the full dataset and the data subset containing only species found in both forest types (common species subset). Candidate models are ranked according to the Akaike's information criterion (AICc), and variables in bold font were significant in the averaged model (Figure 4.4). Corresponding degrees of freedom (df), log-likelihood estimation (logLik), difference between AICc and lowest AICc value (Δ_i) in model set, Akaike weight (w_i: the probability that each model is the best approximating model), and marginal (R^2m) and conditional (R^2c) r-squared values are presented for binomial GLMMs. Only models with $\Delta i < 2$ were included in the averaged top models.

Response	Candidate models	df	logLik	AICc	Δ_i	w_i	R^2m	R^2c
Seedling occurrence (full dataset)	1. **Forest type** + **DBH** + **conspecific tree density** + **wood density**	7	-204.26	422.8	0	0.55	0.27	0.45
	2. **Forest type** + **DBH** + **conspecific tree density** + **wood density** + flower size	8	-204.06	424.5	1.69	0.24	0.27	0.45
	3. **Forest type** + **DBH** + **conspecific tree density** + **wood density** + forest:wood density	8	-204.19	424.7	1.95	0.21	0.28	0.46
Seedling abundance (full dataset)	1. **Conspecific tree density** + wood density	6	-831.04	1674.4	0	0.22		
	2. **Conspecific tree density**	5	-832.11	1674.5	0.04	0.22		
	3. **Conspecific tree density** + wood density + forest type + forest:wood density	8	-829.23	1675.1	0.66	0.16		
	4. **Conspecific tree density** + wood density + forest type	7	-830.33	1675.2	0.72	0.16		
	5. **Conspecific tree density** + forest type	6	-831.48	1675.3	0.88	0.14		
	6. **Conspecific tree density** + wood density + forest type	7	-830.75	1676	1.55	0.10		
Seedling occurrence (subset dataset)	1. **Forest type** + **DBH** + conspecific tree density + **wood density**	7	-166.07	346.5	0	0.39	0.28	0.45
	2. **Forest type** + **DBH** + **wood density**	6	-167.52	347.3	0.81	0.26	0.26	0.45
	3. **Forest type** + **DBH** + conspecific tree density + **wood density** + forest:wood density	8	-165.72	347.9	1.4	0.19	0.28	0.46
	4. **Forest type** + **DBH** + conspecific tree density + **wood density** + flower size	8	-165.92	348.3	1.79	0.16	0.27	0.45
Seedling abundance (subset dataset)	**1. Conspecific tree density**	5	-677.64	1365.6	0	0.21		
	2. **Conspecific tree density** + wood density	6	-676.78	1366	0.41	0.17		
	3. **Conspecific tree density** + forest type	6	-676.91	1366.3	0.67	0.15		
	4. **Conspecific tree density** + wood density + forest type + forest:wood density	8	-674.81	1366.4	0.8	0.14		
	5. **Conspecific tree density** + wood density + forest type	7	-676.04	1366.7	1.08	0.13		
	6. **Conspecific tree density** + wood density + flower size	7	-676.18	1367	1.36	0.11		
	7. **Conspecific tree density** + flower size	6	-677.57	1367.6	1.98	0.08		

Although up to 6 additional models fell within 2 AICc units of the best model, the analysis provided consistent overall results (Table 4.2). For seedling presence-absence, forest type, DBH, conspecific tree density and wood density were included in all three top models in the full dataset, and in three of the four best subset models (conspecific density was not included in the fourth). For seedling abundance-where-present, conspecific density was the one variable that was consistently included in the top models, for both the whole dataset and for the subset of species that occurred in both forest types (Table 4.2).

4.5 Discussion

Our results demonstrate that forest fragmentation is having a significant impact on the ability of individual dipterocarp trees to recruit seedlings, leading to an almost 50% reduction in trees with seedlings in fragments compared to continuous forest. However, when considering only those trees that were recorded with seedlings, there was no significant difference in seedling abundance between trees in continuous forest and those in forest fragments. This was partly due to the considerable variation in recruitment effort of individual trees in fragments, but indicates that some trees do not face barriers to seedling recruitment in fragments.

Seedling occurrence

A majority of individual trees in forest fragments failed to recruit any seedlings at all. This varied from 90% failure in the fragment with least recruitment (site 2; Figure 4.1), to 44% failure in the fragment with most (site 4), demonstrating that whilst the severity of the impacts of fragment creation is site dependent, all fragments are experiencing a substantial reduction in recruitment relative to trees in the two primary forest sites (sites 7 and 8), in which 91% of trees had seedlings. There may be several competing explanations for the recruitment failure seen in fragments, relating to different parts of the recruitment process from flowering through to germination of seedlings.

Many trees in the aseasonal lowland rainforest of Borneo flower in synchrony, and recent work investigating the proximate cues required to activate flowering genes in two *Shorea* species in tropical rainforests in Southeast Asia found that flowering is initiated by the interaction of cooler daytime temperatures and prolonged drought during the three months prior to flowering (Yeoh et al. 2017). Remote sensing of forests on Peninsula Malaysia also showed that drought was the best predictor of general flowering intensity in every large-scale episode of mass flowering over a ten-year period (Azmy et al. 2016). Furthermore, dipterocarp species have differing sensitivities to these cues, with certain species requiring more severe drought, and others requiring lower temperatures in order for flowering to be initiated (Chen et al. 2018). Thus, abiotic changes in fragments may disrupt flowering cues, due to elevated ambient temperature and drought, and certain species may thrive while others fail in the altered fragment environment. Three of the four fragments sampled in this study had considerably lower levels of soil moisture, a more open canopy, and higher levels of photosynthetically active radiation (PAR) than continuous forest sites (Figure S4.2a –c), coinciding with a lower proportion of trees that were recorded with conspecific seedlings. The fragment with the highest soil moisture and PAR levels, comparable to those found in continuous forest sites (Figure S4.2a –c), had the highest proportion of trees with seedlings, possibly confirming that flowering cues are disrupted by changes in abiotic conditions. However, it could also simply be due to differences in the population density of fruiting dipterocarps: if population densities are higher in continuous forest sites, there is an increased chance of finding one or two conspecific seedlings under sampled trees due to chance dispersal from nearby conspecific trees. The findings are confounded by changes to the community composition of trees and population densities at different sites, and the relatively small number of fragments sampled, but nonetheless suggest that the reduction in seedling recruitment success in fragments could be due to species-specific effects of drought and temperature on the initiation of flowering.

Seedling abundance

In contrast to our finding of reduced seedling occurrence in forest fragments, we found that, when seedlings were present, there was no significant difference in seedling abundance per tree between fragments and continuous forest. However, there were fewer trees recruiting seedlings in fragments (only 81 out of 200 trees), meaning that the analysis may lack some statistical power. There was considerable variation in the performance of species in fragments versus continuous forest sites, demonstrating that some species are able to thrive in forest fragments (three species produced a much greater abundance of seedlings in fragments), some perform similarly in fragments and continuous forest (six species), and some perform worse, despite evidence of the occurrence of seedling recruitment (five species had a much lower abundance of seedlings in fragments; Figure 4d, Table S4.1). For example, *Shorea acuminatissima* performed particularly well in fragments (Figure 4.2d), with (on average) over 140 seedlings recorded per tree, compared to only three per tree in continuous forest. This may be due to its distribution, which was heavily biased towards three forest fragments where it was abundant as a mature tree.

Confounding effects

Greater conspecific mature tree abundance has several implications. To begin with, seedlings within the sample area around one parent tree may have originated from other nearby conspecific mature trees. It is also likely that a species found at high population densities is particularly well-adapted to the location in which it is abundant, meaning that seed germination and seedling survival is more likely due to favourable conditions. Finally, pollen limitation is unlikely to be a factor leading to lack of pollination, meaning that outcrossing is more likely. Maycock et al. (2005) found a negative relationship between the number of flowering conspecifics and the proportion of abscised flowers, and a positive relationship with the proportion of flowering trees producing viable seeds, supporting the conclusion that conspecific tree density was an important factor determining seedling recruitment success. This conclusion is also supported by our models, in which conspecific tree density tree was an important variable in nearly all top models, being positively associated with both seedling presence and seedling abundance when present. Thus, a greater density of conspecific trees is likely to be a result of a favourable local environment while also providing abundant outcross pollen, leading to greater seedling recruitment success.

We also found that mother tree diameter (dbh) was a significant predictor of seedling presence but did not predict abundance when present. Previous studies have shown that larger trees are likely to have more resources available for investment in reproduction (Numata et al. 2012), which suggests that larger trees are more likely to participate in mast fruiting, even if the number of seedlings successfully recruited as a result is not related to tree size.

Species traits (wood density and flower size)

Tree traits can serve as useful proxies for other life history characteristics and can be used to assess species' performance in response to variation in environmental conditions, giving insights into the effects of fragmentation on groups of species that share the same trait (Wright et al. 2010). Wood density is frequently used as a proxy for growth-rate, and species with lower wood density may be able to respond more rapidly to the more open canopy and higher light conditions found in forest fragments (Kunstler et al. 2016). In contrast, however, we found a significant positive effect of wood density on seedling presence regardless of forest type: species with higher wood density were more likely to have recruited seedlings in forest fragments as well as continuous forest. One possible explanation of this may be the enhanced ability of seedlings of high wood density species to survive in the shady understory (Kitajima &

Poorter 2008). Philipson et al. (2014) found that tree species with high wood density had a slower growth rate and greater resistance to mortality, thus seedlings of these species have greater shade tolerance and can persist for longer than light-demanding low wood density species. As a result, seedlings of high wood density species may be the product of a greater number of ENSO-triggered mast fruiting events than those of low wood density species, which have either grown out of the seedling size class or died after fewer years in the shady understory. Another explanation may be the reduced sensitivity to drought of slow-growing species with a conservative strategy of resource use (Ouédraogo et al. 2013), which means that they have a greater capacity to respond to flowering cues, are less likely to abort fruit due to drought stress, and have more resilient seedlings. Thus, they may continue to have the capacity to produce seedlings in both continuous forest and forest fragments, and for those seedlings to survive. This has important implications as forest fragments tend to store less carbon than the equivalent area of intact forest due to elevated rates of mortality of large trees near forest edges (Dantas de Paula et al. 2011), and forest within 0.5 km of an edge is more likely to be a carbon source than a carbon sink (Qie et al. 2017). However, the fact that higher wood density species continue to recruit in these forest fragments means that the fragments should continue to represent important carbon stocks.

Contrary to our expectations we did not find an effect of flower size on seedling recruitment success in fragments, despite the fact that smaller-flowered individuals with correspondingly smaller pollinators are likely to be more susceptible to pollen limitation and selfing due to short dispersal distances and a lack of inter-fragment movement by pollinators (Kettle et al. 2011, Fukue et al. 2007). Selfing can result in higher levels of flower abscission, reduced fruit set, and increased seed abortion (Fukue et al. 2007, Maycock et al. 2005), and thus fewer seedlings. The fact that we did not find an effect of flower size in our models could be a reflection of the difficulty of trait-based analysis on tree communities, which are highly context dependent and site-specific factors may mask any potential effect of flower size (Yang et al. 2018), or due to the relative recency of fragmentation (probably < 30 years ago). Pollinator populations within fragments may (continue to) decline over time, so flower-size may gain relevance as a predictor of seedling recruitment success in future. This study represents a snap-shot in time, and it is possible that other trees, or more trees, may fruit in future ENSO events. Climate change is projected to result in higher temperatures and more variable rainfall in Southeast Asia (IPCC 2013), and an increased intensification of the droughts induced by ENSO events (Fasullo et al. 2018), creating different conditions in fragments (and in continuous forest) temporally as well as spatially. However, the results presented here show no clear effects, more than 20 years after fragmentation took place.

4.6 Conclusions

There was a large range of variation among the fragments in the recruitment ability of individual trees, which is likely to become more pronounced over time as the fragments age, pollinator populations decline, and climate change alters flowering cues. What is evident from this study is that some individuals are recruiting in forest fragments. Even though relatively fewer trees are producing seedlings, forest fragments are likely to persist as closed canopy forest. Although they may comprise an impoverished subset of species, they will continue to provide habitat for forest generalist species even if those relying on specific tree traits are lost, and certain other species may thrive in the new forest conditions. The variation in dipterocarp seedling recruitment among fragments and species is consistent with findings of a previous study in the same landscape, which found that seedling communities in small forest fragments were diverging on different and unpredictable trajectories of change (Stride et al. in prep). The variability in recruitment success between and within species indicates that site-specific factors may have an important impact on the recruitment success of individual trees, and hence future research would benefit from examining larger numbers of individuals per tree species, and increasing the replication of sites. We conclude that if the majority of dipterocarp trees fail to recruit seedlings in fragments, population sizes will continue to decline until some species eventually become extinct from forest fragments; but that a subset of species are continuing to recruit successfully. These results provide substantial evidence of fragmentation impacts on seedling recruitment of a keystone group of species.

4.7 Declarations

This research was funded by a NERC studentship awarded to GS via the ACCE DTP (award ref. NE/L002450/1). GS, JKH, and CDT conceived and designed the study; GS and AJ collected field data; GS led data analysis and wrote the first draft of the manuscript, with substantial contributions from JKH and CDT to all further revisions. SB, JH and MJMS also contributed to revisions. All authors gave final approval for publication. The authors declare they have no competing interests.

CHAPTER 5

General discussion

5.1 Summary of thesis findings

The main aims of this thesis were to (1) investigate the impact of forest fragmentation on current tree diversity and community composition, and how this might change in future, and (2) understand why some trees may be failing to recruit seedlings in small forest fragments.

I examined the genus-level alpha diversity of size classes of trees broadly representing individuals that germinated pre- and post-fragmentation, within plots in 19 sites in continuous forest and forest fragments. I found that fragmentation was leading to a reduction in genus richness of post-fragmentation seedlings, and that this relationship scaled with decreasing fragment size. I then examined genus-level beta diversity of trees and seedlings in the same set of 19 sites, and determined that seedling communities in fragments were diverging in composition from continuous forest sites, from other fragment sites, and from trees communities in the same sites. I also found that seedling communities in small fragments were diverging from one another, showing that these sites are following different trajectories of change. Finally I investigated the impact of fragmentation on the recruitment of individual dipterocarp trees, and found that substantially fewer dipterocarps in fragments showed evidence of recent seedling recruitment compared with those in continuous forest, but that some seedling recruitment was still evident in fragments.

Figure 5.1. *Vatica dulitensis* (Dipterocarpaceae) seedlings following an ENSO-related masting event in logged forest (photo credit: G. Stride).

In this final Chapter, I summarise the key findings of each data Chapter in relation to the specific objectives outlined in the General Introduction (section 1.5), and discuss the implications of my results for trees in small fragments, and the value of small fragments for the conservation of biodiversity. I discuss the variation in the response of tree communities to fragmentation, highlighting some of the key processes in seedling establishment that may be disrupted by fragmentation. I then put my conclusions into a wider context by comparing lowland tropical rainforest in Southeast Asia to other tropical rainforests, to assess how my findings might relate to other tropical regions. Finally, I make some conservation recommendations based on my conclusions, consider some of the important questions that remain for future research, and put forward my final conclusions.

Chapter 2 – **Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants**

Main objectives:

1. Determine the local alpha diversity of trees (representing individuals which germinated prior to fragment formation), saplings, and seedlings (both representing individuals which germinated after fragment formation) in 0.08 ha plots in continuous forest and in forest fragments.
2. Examine effect of forest type (primary, selectively logged, or fragmented) on plot-level alpha diversity of each tree size class.
3. Identify whether fragment area, shape, degree of isolation, and/or level of disturbance, are predictors of alpha diversity of post-fragmentation individuals (seedlings and saplings), in contrast to pre-fragmentation individuals (trees).
4. Examine differences between the three size classes.

In this Chapter, I investigated the impacts of forest fragmentation on the local alpha diversity (measured as number of genera per plot) of stems likely to have been recruited before and after fragment formation. I found a reduction in the genus richness of seedlings, but not saplings or trees, in fragments relative to continuous forest (logged or primary forest). The greatest reduction in seedling genus richness was observed in the smallest, most isolated forest fragments. Sapling genus richness was not reduced in plots in forest fragments (in contrast to seedling genus richness), despite the fact that saplings are likely to comprise mostly of individuals recruited after fragment formation. This result suggested that density dependent mortality (where rare individuals have a higher survival rate) and/or year-to-year variation in which species are recruiting could offset, at a plot-scale, the reductions in genus richness seen in the seedling size class. As a result I concluded that the reduction in seedling genus richness in fragments is probably indicative of reduced recruitment success in forest fragments, but that longer-term studies are required to determine whether this will eventually translate into reduced richness of mature trees, or whether the processes that currently retain high sapling richness will continue in fragments.

Chapter 3 – **Divergent tree seedling communities indicate different trajectories of change among rainforest remnants**

Main objectives:

(1) Using the same data set as in Chapter 2, determine the degree of beta diversity between and within tree and seedling communities (representing individuals recruited pre- and post-fragmentation respectively) in 19 sites in forest fragments and continuous forest.
(2) Determine whether patterns of divergence of seedling (post-fragmentation individuals) from tree communities (pre-fragmentation individuals) within sites, and distinctiveness of tree and seedlings communities between sites, are associated with the size and isolation of sites.
(3) Explore whether changes in seedling community composition are driven by recruitment failure, by identifying differences in presence of genera in sites as trees and/or seedlings.
(4) Investigate whether animal-dispersed genera are disproportionately negatively affected by fragmentation effects.

In Chapter 2, I found a significant reduction in the alpha diversity of seedlings, but no change in the alpha diversity of trees, in forest fragments compared with continuous forest sites, and that seedling alpha diversity declined with fragment area. I wanted to examine whether the changes observed in seedling alpha diversity corresponded to homogenisation or diversification of seedling communities among fragments. I calculated three metrics of beta-diversity based on the Chao-Sørensen dissimilarity of tree and seedling communities. First I calculated the distinctiveness of tree communities and seedlings communities (separately) between sites, and then the divergence of seedlings from tree communities in the same site. I found that seedling communities in small, isolated forest fragments were most distinct from all other seedling communities, and from tree communities in the same fragment. Additionally, seedling communities in small, isolated fragments were more distinct from one another than were those in larger fragments, or those in continuous forest. Fragment sites also contained a higher proportion of genera that were only represented by trees and not seedlings. My results indicate that seedling communities in fragments are diverging from those in continuous forest, and that communities in fragments are following different trajectories of change, and some trees are failing to recruit seedlings. Assuming that seedling communities provide insight into future tree communities, these results imply that, despite a degree of impoverishment of genus richness, fragments make important contributions to landscape scale diversity because they continue to support the recruitment of different genera. Hence, networks of fragments may act as reserves of tree diversity within the landscape.

Chapter 4 – **Forest fragmentation alters recruitment of tropical trees: a study of dipterocarps on Borneo**

Main objectives:

(1) Quantify patterns of seedling recruitment of 25 species of dipterocarp in four forest fragments and four sites in continuous forest (a subset of the 19 sites sampled for Chapters 2 and 3).
(2) Assess whether fragmentation is resulting in recruitment failure and/or reduced abundance of seedlings by mature trees, relative to trees in continuous forest.
(3) Investigate whether wood density and flower size of species act as predictors of recruitment success, and whether these species’ traits interact with forest type to predict recruitment success.

I focused on a group of species in the Dipterocarpaceae in order to investigate the drivers of seedling recruitment failure in forest fragments. Dipterocarps share a number of life history characteristics that make them a useful group to study the effects of fragmentation on trees. Examining fragments isolated around 20 years ago, I found a significant reduction in the number of trees recruiting seedlings in forest fragments, compared to continuous forest. However, when trees showed evidence of recruitment (i.e. seedlings present) there was no significant difference in seedling abundance between continuous forest and forest fragments, although there was much more variation in seedling abundances in forest fragments, probably due to site-specific factors. I also found that higher wood density species were more likely to show evidence of seedling recruitment in both forest types, possibly due to enhanced shade tolerance and greater resistance to mortality. I conclude that forest fragments may experience enhanced levels of drought, which may be disrupting the cues for the initiation of mass flowering, reducing seed production and reducing seedling survival. This may eventually result in the extinction of some dipterocarp species from forest fragments, although a subset of species are continuing to recruit successfully. These results provide substantial evidence of fragmentation impacts on seedling recruitment of a keystone group of species.

The results of these three data chapters reveal that some trees in forest fragments are failing to recruit seedlings, leading to taxonomic impoverishment of seedling communities in individual fragments. However, different genera continue to recruit seedlings in different fragments, indicating that tree communities in fragments are diverging along different trajectories. Consistent with this, some dipterocarps are failing to recruit seedlings in fragments, but others are continuing to recruit successfully. Thus, although fragments have reduced function relative to continuous forest, they continue to support different communities of plants, and hence contribute to landscape-scale diversity.

5.2 What is the importance of small fragments for conservation?

The species-area relationship (SAR) originally described for islands has been found in many taxa occupying habitat fragment ‘islands’, as demonstrated by studies on birds (e.g. Hill et al. 2011), ants (e.g. Brühl et al. 2003), dung beetles (Nichols et al. 2007), bats (e.g. Struebig et al. 2008), and vascular plants (Munguía-Rosas & Montiel 2014). These relationships call into question the value of small fragments for the conservation of biodiversity. I found that the number of tree seedling genera in plots in lowland rainforest fragments on Borneo increased with fragment area (Chapter 2), a pattern which was absent among mature trees or saplings, and which may indicate greater taxonomic impoverishment of seedlings in smaller fragments as a whole. Studies on tropical tree diversity are frequently conducted at the genus-level due to the difficulties of tropical tree identification (e.g. Ewers et al. 2017, Laurance et al. 2004). Although using this higher taxonomic level reduces the resolution of the data, it enables analyses of population trends that wouldn’t be possible at the species level due to the high proportion of rare species occurring at low densities in tropical rainforest. In addition, congeneric species are often ecologically similar (Laurance et al. 2004), and I found a strong correlation between the number of species and number of genera identified per plot (Figure S2.1). Thus, studies conducted on tropical trees at genus- and species- level are likely to reveal trends robust to the resolution of the analysis. My study was based on the assumption that the majority of seedlings (<1cm dbh and <1.5 m in height) and saplings (1 – 5 cm dbh) would have germinated after fragmentation occurred (about 20 years ago), and would therefore provide an insight into the effects of fragmentation not yet visible in the mature tree cohort due to their longevity. The unexpected sapling results that led me to conclude that density dependent mortality and/or year-to-year variation in which genera are recruiting may offset losses, at the plot scale, in seedling richness. These ideas are discussed in detail in Chapter 2 (section 2.5), however my results for seedlings led me to conclude that small fragments are experiencing an overall decline in the genus richness of post-fragmentation seedling recruits.

The reduction I found in seedling alpha diversity in fragments may have important implications for future tree diversity, as well as for the diversity of other forest organisms, which often increase in parallel with plant diversity. The physical structure of the forest is largely determined by the tree community, so a more diverse tree community provides a greater diversity of niches for other species to occupy (Jones et al. 1994). Novotny et al. (2006) attribute the latitudinal gradient in insect species diversity from temperate to tropical regions to the equivalent gradient in plant diversity. They found that the host specificity and number of insect species per host plant were similar in temperate and tropical forests, but that the greater host plant diversity in the tropics provided the opportunities for greater insect diversity (Novotny et al. 2006). As a result, a reduction in the taxonomic richness of trees in fragments is likely to have similar consequences for insects dependent on these plants, as well as other taxa occupying specialised niches, if these niches disappear. Thus, small fragments with an impoverished tree community generally support lower levels of taxonomic richness than larger fragments or continuous forest.

However, in contrast to patterns of alpha diversity, studies considering patterns of beta diversity between fragments within a landscape reveal greater variation in responses to fragmentation. These may differ depending on geographic location, elapsed time since fragmentation, fragment disturbance history, study taxon, and the range of fragment sizes included in the study. I found that although the number of genera of tree seedlings recruited after fragment formation declined with fragment area (Chapter 2), different genera were recruiting in different fragments (Chapter 3). Thus, tree seedling alpha diversity declined with area, but beta diversity increased. Given that the diversity of seedlings offers insight into the diversity and trajectory of change of tree communities in future, this finding has important implications when considering the conservation of overall landscape-scale diversity of forest species within a human-modified landscape. If subsets of tree genera are able to persist long-term in small fragments by continuing to recruit seedlings, they may constitute valuable reservoirs of tree diversity, and hence retain considerable value for diversity conservation. This value is increased if different genera are recruiting in different fragments, as I found, such that the network of fragments embedded in a human-altered landscape maintain a high level of diversity at this broader scale.

My finding, that small fragments can make significant contributions to landscape-scale tree diversity, corroborates those of other studies conducted in rainforest fragments in Central and South America (e.g. Sfair et al. 2016, Hernández-Ruedas et al. 2014, Arroyo-Rodríguez et al. 2013, Arroyo-Rodríguez et al. 2009, dos Santos et al. 2007). Seedling communities in small fragments are probably following contrasting pathways due to differences in fragment attributes and disturbance history. However, my findings contrast with other studies that have reported taxonomic impoverishment accompanied by homogenization of tree communities in small fragments within a landscape (e.g. Lôbo et al. 2011, Pütz et al. 2011). Homogenization can occur if rare or specialist species decline and common, generalist or pioneer-type species spread and proliferate, thus increasing the similarity in composition between communities (Olden 2006). These studies, that question the conservation value of individual small fragments, are predominantly conducted in the Atlantic forest of northeast Brazil, a globally important biodiversity hotspot which is highly fragmented. Only around 16 % of the original forest remains, distributed amongst fragments of which 80% are smaller than 50 ha, and most forest fragments are composed of disturbed, second-growth forest (Ribeiro et al. 2009). The size of Atlantic forest fragments is in contrast to the forest fragments sampled in this study, of which only the two smallest were smaller than 50 ha (see Figure 2.1, Table 2.1). This difference in the size of ‘small’ fragments in different studies may suggest that there is a size and/or disturbance threshold below which fragments have a poor ability to sustain populations of rare or specialist species, but may also be due to regional differences in the flora and fauna, and the intensity of land use in the intervening matrix.

Carbon sequestration was not a focus of my study, but it is evident that many forest fragments continue to support a high number of large trees, and thus have some value for carbon storage, as well as for conserving landscape diversity. I found that there was no significant difference in the density of large trees (>30 cm dbh) between plots in forest fragments and continuous forest, indicating the potential of fragments for carbon storage (Appendix 1B, Figure S2.3). Undisturbed dipterocarp forest on Borneo has some of the highest carbon stocks per hectare globally due to stem densities of large trees 2 – 4 times higher than forest in the neotropics, and 60% greater average above-ground biomass (Paoli et al. 2008; Slik et al. 2010). However, deforestation, degradation and forest fragmentation are significant sources of greenhouse gas emissions (Qie et al. 2017), and extensive logging and forest clearance over the last half-century has turned tropical lowlands from an important carbon sink to a significant carbon source: Malaysia and Indonesia have some of the highest annual country-level estimates of carbon emissions from deforestation (calculated for 2000 – 2005; Harris et al. 2012). Not only do oil palm monocultures store about 80% less above-ground-carbon than primary forest (Ziegler et al. 2012), but cultivation exposes the soil, resulting in the oxidation of up to 30% of the organic matter held in the top metre of soil and releasing carbon dioxide (Houghton 2005). Forest fragments tend to store less carbon than the equivalent area of intact forest due to elevated rates of mortality of large trees near forest edges (Dantas de Paula et al. 2011), and forest within 0.5 km of an edge is more likely to be a carbon source than a carbon sink (Qie et al. 2017). In order to avoid the worst edge effects I located all plots at least 100m from fragment edges, as it was not a focus of my study to investigate edge effects. This may explain why I did not find significant reductions overall in large tree density in forest fragments (Appendix 1B, Figure S2.3). Changes in community composition towards disturbance-loving, fast-growing pioneer tree species with lower wood densities can also reduce above ground biomass (Bunker et al. 2005), but if heavily disturbed fragments recover their vegetation structure to be more similar to undisturbed forest they may re-gain above ground carbon (Powers & Marín-Spiotta 2017). Contrary to this expectation, I found no difference in the effects of fragment size on the alpha diversity of seedlings, saplings, and trees, when I tested low and high wood density genera separately (Appendix 1B, Table S2.8). Although larger blocks of forest generally experience fewer edge effects and less disturbance than the equivalent area separated into smaller blocks of forest, and thus have a greater capacity for storing carbon, existing small fragments may still have some value in this respect. Fragments are likely to retain substantially higher levels of above ground carbon than oil palm or other crop species, especially relatively undisturbed fragments like those in my study, and thus continue to represent important reservoirs of carbon that should be retained within the landscape.

Turner and Corlett (1996) conclude that even fragments smaller than 100 ha are better than non-forest habitat for the conservation of forest specialist species. Lucey et al. (2016) suggest that a fragment with a core area of 200 ha can support up to 70% of the species richness of the same area of continuous forest. Considering that there are about 54 million patches of fragmented forest in the tropics, that the mean fragment area is only 29 ha, and that they cover an area of more than 1.5 billion ha (Brinck et al. 2017), small fragments represent a substantial area of forest. Despite supporting impoverished assemblages of forest organisms and lower ecosystem functioning relative to primary forest, fragments smaller than 200 ha may sustain assemblages of trees which are no longer found anywhere else, as well as supporting forest specialist species that cannot survive in an agricultural landscape. Fragments can act as stepping-stones, connecting larger areas of forest, and can provide food and shelter to migratory animals (Turner & Corlett 1996). Although fragment connectivity was unimportant relative to area for tree seedling alpha diversity (Chapter 1), the distribution of fragments within the landscape is likely to have important consequences for the permeability of the intervening matrix for other forest species. Fragments can also act as reservoirs of species and genetic diversity, and may be seed sources for natural and assisted recolonization. Tree longevity provides longer time scales over which to act to save tree species, and in 50 or 100 years' time, areas of forest may re-expand if trends for agricultural abandonment in Europe play out in other parts of the world (Navarro & Pereira 2015). Consequently, although continuous forest is clearly superior for the conservation of biodiversity, where fragmentation has already resulted in the formation of small forest fragments they can make a valuable contribution to landscape-scale conservation of biodiversity.

5.3 Why is recruitment so unpredictable?

Fecundity can fluctuate dramatically from year to year due to variations in climate and resource availability, but the advantage of studying seedlings, especially dipterocarp seedlings, is that they represent recruitment effort over a number of years and thus give an overview of the effects of fragmentation on individuals and species in fragments. The results of Chapters 2 and 3 led me to conclude that the decrease in seedling alpha diversity in plots in fragments, and increase in seedling beta diversity between fragments, could be explained by recruitment failure of some trees in some fragments, and this conclusion was supported by the findings of Chapter 4. I did not statistically explore differences between logged and unlogged continuous forest sites due to the low number of sites sampled (two per forest type), but recruitment was notably reduced in logged forest compared to undisturbed primary forest. I found that dipterocarp seedling recruitment was significantly reduced in fragments compared to continuous forest, with only 40% of 200 mature dipterocarp trees in fragments demonstrating any evidence of recruitment, compared to 63% in continuous logged forest sites, and 91% in continuous primary forest sites. However, the fragment sites varied considerably in this respect, with only 10% of trees showing evidence of recruitment in one fragment (site 2, Figure 4.1) but 66% in another (site 4), similar to recruitment in the logged forest sites. Similarly, amongst those trees which showed evidence of having recruited seedlings, mean seedling abundance was relatively high in primary forest (17.8 seedlings per tree within the subplot area), much lower in logged forest (5.6 seedlings per tree), and varied widely amongst fragments. For example, trees in two fragments had mean seedling abundances similar to logged forest sites (~7 seedlings per tree), whereas trees in the smallest fragment (120 ha, site 1) on average recruited 71.2 seedlings, with three trees recruiting over 200 seedlings each. This variation in seedling recruitment between fragments is probably due to the fact that fragmentation can disrupt the sequence of processes that culminate in a tree successfully recruiting a seedling in a number of individual-fragment-specific ways, via changes in fragment characteristics and pollinator, seed disperser, and herbivore populations.

On Borneo, there are no strong seasonal cues for reproduction, and many tree species rely on cues from droughts and low daytime temperatures associated with ENSO events for the initiation of general flowering events and subsequent masting (Sakai et al. 2006). I found that fragments generally had lower levels of soil moisture and a more open canopy (probably corresponding to higher ambient temperature) than continuous forest (Figure S4.2), which may affect the transmission of ENSO cues to trees in forest fragments and disrupt or promote the initiation of mass flowering, depending on the tree. If flowering is initiated there are a number of biotic interactions that may also be altered by fragmentation that are critical for seedling recruitment success. Declines in pollinator abundances are a frequently reported consequence of habitat fragmentation, often resulting in a reduction in seed set (Potts et al. 2010). If the population size of conspecific trees within a fragment is significantly reduced, they may experience increased self-pollination, or pollination by pollen from a sibling tree, resulting in increased rates of flower abscission and production of infertile fruit (Maycock et al. 2005, Ghazoul et al. 1998). Changing populations of insects, birds, and mammals can alter patterns of pre- and post-dispersal seed predation, as well as seed dispersal. Many tree species rely on birds or mammals to move seeds away from parent trees to combat the increased mortality associated with density-dependant Janzen-Connell effects (Caughlin et al. 2015). Dipterocarp recruitment in fragments is, however, unlikely to be substantially impacted by loss of seed dispersers, as they are abiotically dispersed and seeds undergo limited secondary dispersal. Populations of both seed dispersers and predators may grow or (more often) decline as a result of fragmentation (Canale et al. 2012). Finally, germinated seeds may face competition from invasive native or non-native species, and seedling survival may be enhanced by depressed populations of herbivores in fragments (Granados et al. 2017). Consequently, loss of pollinators, seed dispersers, and herbivores can reduce or elevate seedling abundances in way that is likely to vary among fragments.

The failure of many dipterocarp trees in fragments to recruit seedlings contrasts with the fact that some dipterocarps produced seedlings in greater numbers than in continuous forest (Chapter 4). This variation among dipterocarp species may be due to the differing sensitivity of dipterocarp species to phenological cues from ENSO events (Chen et al. 2018) in combination with the factors outlined above. Hobbs and Yates (2003) reviewed and synthesised the results from 29 studies presenting data on the effects of fragmentation on the fecundity of 60 plant species, measured on 85 occasions. Only 3.5% of occasions showed a positive effect of fragmentation on fecundity, while nearly 58% showed significant declines, and the remaining 40% showed no effect. Impacts of fragmentation are thus somewhat variable between and within studies (Hobbs & Yates 2003), and seem to be relatively unpredictable. Tree reproduction can be inhibited at multiple stages of the seedling recruitment process, and the processes and interactions involved may be impacted in a diversity of ways depending of the characteristics of the forest fragment in question. The variation I found in dipterocarp recruitment in fragments demonstrates this point. Thus, more studies are needed in order to determine which stages of the recruitment process are most sensitive to fragmentation, how this varies amongst species with different life history characteristics, and what fragment characteristics have the most deleterious effects.

5.4 Do fragmentation impacts depend on biogeographic region?

My study was conducted in lowland tropical rainforest on Borneo, which is within one of five major regions of lowland tropical rainforest: Asia, Africa, neotropics, Madagascar, and Australasia. Rainforests in these regions share certain ecological characteristics but are distinct in a number of ways as a result of millions of years of almost complete isolation from one another, during which unique biotas have evolved to fill similar niches (Corlett & Primack 2006). Irrespective of their differences, tropical forests throughout these regions face broadly similar threats, one of the most important being from agricultural expansion and intensification, leading to habitat fragmentation and isolation of forest specialist species within habitat patches. As a result of the differences in species composition and species interactions between these regions, as well as differences in climate, the effects of fragmentation on the ecological processes affecting seedling recruitment detailed in the previous section are likely to vary. Despite this, the results of my study reveal some effects of fragmentation that are consistent with those known from other regions, indicating that they have wider applicability than just to fragmented forest on Borneo.

In my study of a Southeast Asian rainforest I found that plot-level seedling alpha diversity increased with fragment area (Chapter 2). Existence of a tree seedling alpha diversity gradient has been demonstrated in a fragmented rainforest in the neotropics (Benítez-Malvido & Martínez-Ramos 2003), but studies of tree seedling diversity in fragmented forest in Asia, Africa, Australasia, and Madagascar are lacking. My study makes a valuable contribution to the scientific literature in this respect. If applicable on a broader scale, my results suggest that most tropical forest fragments experiencing a loss of taxonomic richness in post-fragmentation recruits are likely to have extinction debts pending.

In Chapter 2 I also concluded that density-dependent processes acting on seedlings within plots could be responsible for the recovery of alpha diversity in the sapling size class (at the plot level) to continuous forest levels. This was based on the conclusion that the sapling size class represented many more years of recruitment effort than the seedling size class, and that different genera were recruiting in different years to a greater extent than they do in continuous forest. Janzen-Connell effects on seed and seedling survival have been demonstrated to exist in tropical America, Asia and Africa, although the majority of studies were conducted in the neotropics, and relatively few in Africa (Comita et al. 2014), consistent with a general bias towards the neotropics for tropical ecological studies. It has been suggested that density-dependent effects on seed and seedling mortality would be weaker in Southeast Asia as widespread, unpredictable mast fruiting was thought to have evolved as a predator-satiation mechanism (Curran et al. 1999). However, in a global meta-analysis, Comita et al. (2014) found no evidence that Janzen-Connell effects were weaker in Asia relative to other tropical regions. My conclusions that the maintenance of high sapling alpha diversity is partly due to density dependent effects would support the existence of Janzen-Connell effects in mast fruiting forests. The effect of forest fragmentation on Janzen-Connell effects has not explicitly been tested, but they are likely to be affected by fragmentation because density dependent effects are known to be disrupted by defaunation and disturbance in continuous tropical forest (Terborgh 2013).

Lowland tropical rainforest on Borneo is distinguished from other regions of lowland tropical rainforest in the abundance of trees in the Dipterocarpaceae family. The preponderance of a single family is unusual amongst rainforest regions, and dipterocarp dominance accounts for the greater proportion of abiotically-dispersed species, higher forest canopies, and higher above ground biomass of Borneo forests (Slik et al. 2010). In Chapter 4 I concluded that seedling recruitment failure of dipterocarps in fragments may in part be due to the disruption of the cues for the initiation of mass flowering, and also due to reduced seedling survival due to more severe droughts in fragments. The specific life history characteristics of dipterocarps (discussed in more detail in Chapter 4) mean that if they were replaced by other species, the ecological processes and functioning of the ecosystem might be different (Pennington et al. 2004). Although the family is distributed pantropically, it is only in Southeast Asia that it dominates the canopy and biomass of the forest, and here (in aseasonal zones) mass flowering following ENSO events results in the majority of successful seedling recruitment of many species – not just dipterocarps (Sakai et al. 2006). In contrast, outside of this region, more distinctive dry seasons within an annual cycle tend to serve as a cue for tree flowering phenology, albeit with wide variation between species and populations (Sakai 2001). Although all tropical regions are affected by ENSO events it is only in the aseasonal rainforest in Southeast Asia that ENSO events provide the primary cue for tree flowering on such a large scale. These interacting characteristics of Southeast Asian rainforest (dipterocarp dominance, mass flowering, and the importance of ENSO) may make them more vulnerable to the deleterious impacts of forest fragmentation and climate change than other regions, especially considering that ENSO events are projected to change in intensity and frequency in the future (Fasullo et al. 2018).

As well as considering the attributes of the fragments themselves, it is important to take into account the characteristics of the surrounding human-modified matrix of land, which influence the severity of edge effects and degree of isolation of forest specialist species within fragments. The intensity of the system largely depends on crop type and crop management, but replacement of forest with any agricultural crop typically results in a reduction in species richness due to the structural simplification of the habitat (Fitzherbert et al. 2008). I studied forest fragments that were embedded within oil palm plantations. Oil palm is the most common high-intensity crop in Asia and Africa and supports the fewest species of all common plantation crops (Phillips et al. 2017). In Amazonia, agricultural land use predominantly comprises of soya bean cultivation and pasture land for cattle ranching. Globally, land use as plantation, cropland, or pasture has been found to have a similar negative impact on species richness, and the magnitude of the impact is dictated by the intensity of the system. Consistent with this, an investigation between continents into the effects of land-use on tropical forest diversity showed that the most important difference between regions was the intensity of land-use pressures (Phillips et al. 2017). Conversion of forest to any intensive monoculture significantly reduces local species richness and abundance (Newbold et al. 2015), and poses a substantial barrier to the dispersal of forest specialist species. Hence, the isolation caused by oil palm plantations in my study is likely to have similar effects to that induced by other intensive monocultures, meaning that my findings are potentially generalizable to other regions where agricultural expansion has led to the isolation of fragments of forest.

Although lowland rainforests in different regions of the tropics have some fundamental ecological differences, they are facing similar threats. The response of forest diversity to these threats, namely agricultural expansion and habitat loss and fragmentation, appears to be broadly similar across these regions. It is therefore reasonable to assume that the results of my study are pertinent to other tropical regions where studies into the effects of forest fragmentation on the maintenance of tree diversity are lacking. It is likely that forest fragments in other regions are also experiencing reduced seedling recruitment success of some canopy trees, and that due to fragment-specific factors, fragments are diverging along different trajectories of community compositional change as different species continue to recruit in different fragments. My results demonstrate that, despite this, forest fragments are likely to persist as forest into the future and may continue to represent important reservoirs of biodiversity. This conclusion is based on the assumption that these fragments will continue to benefit from a high level of protection (as Virgin Jungle Reserves), preventing further degradation by logging or poaching, and emphasises the need for stricter enforcement of this protection.

5.5 Conservation of fragmented tropical landscapes and future research needs

Chapters 2 – 4 highlight the importance and short-comings of fragments for the conservation of biodiversity. The results of Chapter 3 show that fragments are important for the maintenance of landscape-scale diversity, but the results of Chapters 2 and 4 demonstrate reduced conservation value relative to continuous forest (especially primary forest) due to the loss of alpha diversity associated with seedling recruitment failure of some species in fragments. Thus, conservation of continuous tracts of forest should be the highest priority, but fragments are important for conserving distinct assemblages of species in human-modified landscapes.

The fragments in my study have reduced tree regeneration relative to primary forest but continue to support seedling recruitment by, across a network of fragments, a diversity of genera. As such they are likely to continue as closed-canopy forest and act as reservoirs of biodiversity within a human-modified landscape that supports substantially fewer species than either fragmented or continuous forest. I collected data in forest fragments that were originally designated protection as Virgin Jungle Reserves in order to preserve the region’s species and genetic diversity. Although there are likely to be extinction debts present, and reductions in fragment diversity vary in relation to fragment area, the fragments continue to support tree regeneration. Lucey et al. (2016) collated data on the species richness of five taxa (ants, birds, butterflies, dung beetles, and dipterocarps) in forest fragments varying in size in Sabah, Malaysia, and found that dipterocarp regeneration was the most severely affected by fragmentation. This result indicates that assessing tree regeneration may be a good way of assessing the continuing longer-term viability of fragments for other taxa. As some tree regeneration evidently continues to take place, this suggests that Sabah’s Virgin Jungle Reserves are succeeding to some extent in their original purpose. In addition, the longevity of individual trees offers a window of conservation opportunity for improvements to fragment area and/or connectivity that would improve the population sizes of trees and provide additional habitat for other forest species, including pollinators and seedling dispersers (Wearn et al. 2012).

Considering that demand for oil palm continues to increase (Fitzherbert et al. 2008), it is important to highlight the conservation value of forest fragments in order to prevent their conversion to further plantations. However, there may be a minimum size below which fragments have limited value for biodiversity conservation, and it can be helpful to provide a recommendation for use by policy makers. Lucey et al. (2017) suggested that fragments should have core area of at least 200 ha in order to maintain dipterocarp regeneration, which would maintain 60 – 70% of the species richness of the same area of continuous forest. However, I found a high abundance of dipterocarp seedlings in a fragment of only 120 ha, suggesting that fragments smaller than 200 ha are capable of supporting tree regeneration, at least in some situations (Chapter 4). As well as this, in Chapter 3 I conclude that despite taxonomic impoverishment, small fragments still contribute to overall landscape diversity, and this may be more important than simply the number of species they support. Jennings et al. (2001) conclude that tree populations require at least one reproductive individual per hectare to avoid inbreeding in the long term, based on the idea that the minimum viable size of a tree population is 50 individuals, which generally contain the majority of the allelic diversity of a species. Tropical trees often occur at low densities, frequently fewer than one reproductive individual per hectare (Primack & Hall 1992). Thus, fragments smaller than 50 ha may have a limited capacity for the maintenance of genetic diversity among tree seedling recruits, although smaller fragments can still contribute to landscape connectivity. I found that connectivity was unimportant relative to fragment size in maintaining taxonomic richness of seedlings, but a landscape-scale approach to conservation is important. Many studies have reported a progressive erosion of biodiversity in fragments smaller than 100 ha (e.g. Gibson et al. 2013, Lôbo et al. 2011), but that this can be ameliorated by increasing connectivity between fragments (Viveiros de Castro & Fernandez 2004). It is important to remember that different taxa have different requirements, and a small fragment may be a valuable component of a landscape-scale conservation strategy for one group of species, while providing little value for another. For populations to persist, small fragments that are clustered provide greater conservation benefits than if they are scattered (Rybicki & Hanski 2013), but movement across the landscape may be facilitated if fragments have more of a corridor-like or stepping stone arrangement (Hodgson et al. 2012). In this way small fragments that are too small to support viable tree populations or populations of large mammals such as orang-utans, can contribute to the connectivity of the landscape and facilitate movement between fragments, maintaining processes such as seed dispersal and pollination. It is clear from my results that small fragments vary in their ability to support tree regeneration, which means that their value is likely to be context specific.

I concluded that failure of many dipterocarps to recruit seedlings could be due to a disruption of cues for the initiation of mass flowering, probably due to elevated drought and ambient temperature in fragments, or due to pollen limitation leading to higher rates of flower abscission, fruit abortion, and seedling mortality. However, the nature of the data I collected for this study means that it provides a snapshot in time of processes that play out over time scales of years to decades. I was able to draw a number of robust conclusions, but I was unable to answer some key questions regarding the critical points at which seedling recruitment is impeded by forest fragmentation, and what specific characteristics of individual fragments lead to recruitment failure.

From my findings I infer how fragmentation may be disrupting tree seedling recruitment. Further studies are required to investigate the actual mechanisms leading to recruitment failure. In order to do this it is necessary to monitor trees through the course of a general flowering and fruiting event, from the initiation of flowering up to seedling establishment. I suggest sampling five widespread dipterocarp species for which sufficient replication per species can be obtained in both continuous forest and forest fragments. Tree-level data is required from a range of fragments and continuous forest sites, and site-level data on soil moisture, air temperature and humidity should be taken through the course of the study. In order to determine the stages at which trees are impeded from recruitment success, flower traps should be employed to monitor the abundance of flowers produced, seed traps to monitor the abundance of seeds, and then seedling surveys at several time intervals following seedling establishment, to monitor abundance and subsequent mortality of seedlings. These data would enable us to determine whether it is flowering failure, flowering success but fruiting failure, fruiting success but seedling establishment failure, or subsequent elevated seedling mortality, that is leading to the reduction in seedling recruitment I observed among dipterocarps in fragments. It would also enable us to determine whether higher levels of drought or higher temperatures in fragments are responsible for the success of certain species over others. In addition, pollinator sampling in the canopy would answer questions on whether pollinators (or certain types of pollinator) have declined following fragmentation. In combination with flower morphology data, this would enhance understanding of the role that pollinator syndrome, pollinator abundance, and pollen limitation has in determining the community composition of dipterocarp seedlings in fragments.

Not only would this type of study inform conservation decisions (such as deciding a minimum viable size for forest fragments), it would aid understanding of the life history characteristics required for persistence in fragments. This type of investigation is needed if we are to understand how tree populations within human-modified landscapes may best be managed for resilience in the face of climate change.

5.6 Conclusions

Some trees in forest fragments are failing to recruit seedlings, leading to reduction in tree seedling richness at the plot level, which is greatest in the smallest fragments. However, fragments are following divergent trajectories of change as different genera continue to recruit seedlings in different fragments, so smaller fragments have higher levels of seedling beta diversity which may continue as seedling cohorts mature. Although fewer dipterocarps are recruiting seedlings in fragments, seedling recruitment continues to occur, albeit on an unpredictable basis, meaning that forest cover should be maintained within forest fragments. Larger fragments have a greater capacity for the conservation of tree diversity and maintenance of ecosystem processes, but smaller fragments represent important reservoirs of taxonomic and genetic diversity which may be important for future forest restoration efforts. Hence, forest fragments continue to make a valuable contribution to landscape-scale diversity.

List of Appendices

Appendix 1 – Supporting information for Chapter 2

Appendix 1A. Chapter 2 abstract translated into Bahasa Melayu.

Serpihan hutan hujan dataran rendah terbentuk berikutan penebangan hutan namun kesan jangka panjang penyerpihan hutan tersebut masih kurang difahami, sebahagiannya adalah berpunca daripada jangka masa generasi pokok yang panjang. Kami mengkaji pokok hutan hujan dalam tiga kelas: anak benih (<1 cm dbh), anak pokok (1-5 cm dbh) dan pokok (> 5 cm dbh) dan ia memberi petunjuk tentang komuniti pokok sebelum dan selepas penyerpihan hutan, dan kesan penyerpihan terhadap pertumbuhan hutan tersebut telah dilaksanakan di Sabah, Malaysia. Kami mendapati bahawa kekayaan anak benih (diukur sebagai bilangan genera per plot) di plot hutan terserpih adalah lebih kurang 30 peratus lebih rendah daripada kekayaan anak benih di plot hutan yang tidak terganggu, dan lebih kurang 20 peratus lebih rendah daripada kekayaan anak benih di plot hutan terhampar yang telah dibalak menggunakan sistem pembalakan terpilih. Keadaan ini membuktikan bahawa terdapat pengurangan pertumbuhan anak benih berlaku di kawasan hutan terserpih. Kekayaan anak benih adalah paling rendah di hutan terserpih yang bersaiz kecil, terasing, dan telah terganggu, yang memberi amaran mempunyai potensi untuk pupus berikutan kesan penyerpihan hutan tidak berlaku bagi pokok. Berbanding anak benih, kekayaan anak pokok tidak menunjukkan penurunan di hutan terserpih yang memberi gambaran bahawa mortaliti ketumpatan bersandar (di mana individu yang jarang mempunyai kadar kehidupan yang lebih tinggi) dan / atau variasi dari tahun ke tahun di mana spesies yang tumbuh, berpotensi mengimbangi pengurangan kekayaan anak benih. Kajian jangka panjang adalah diperlukan untuk menentukan sama ada pertumbuhan anak benih yang gagal atau kerosakan yang tidak berterusan di hutan terserpih yang bersaiz kecil akan menyebabkan pengurangan kekayaan pokok matang, atau sama ada proses yang masih mengekalkan kekayaan anak pokok yang tinggi ini akan berterusan di hutan terserpih.

Appendix 1B. Additional statistical analyses and summary data for Chapter 2.

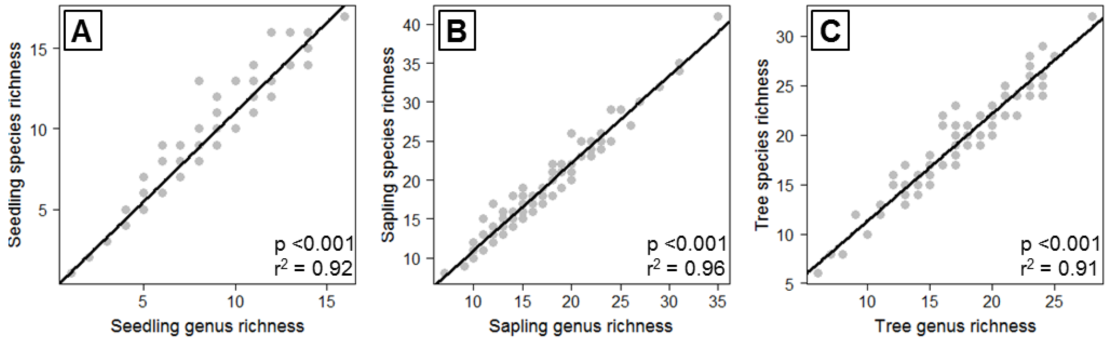
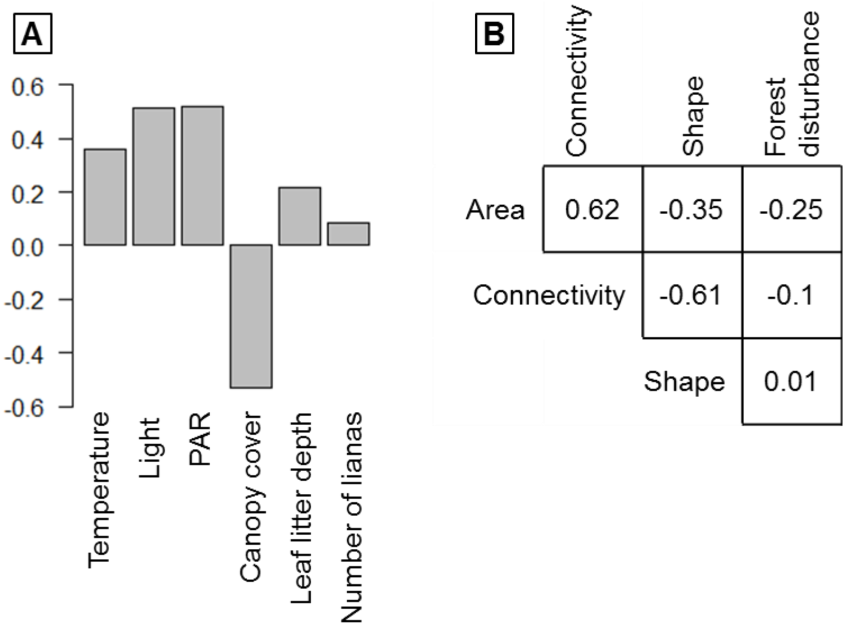


Figure S2.1. Correlation between number of species and number of genera of (A) seedlings, (B) saplings, and (C) trees identified in each plot (n = 93 plots). Black line is fitted using generalized linear regression, and R^2 value is adjusted R^2.



	Connectivity	Shape	Forest disturbance
Area	0.62	-0.35	-0.25
Connectivity		-0.61	-0.1
Shape			0.01

Figure S2.2. A) Variable scores in the first axis of a Principal Components Analysis characterising forest disturbance, accounting for 32.5% of the variation (among plots) in the data. Scores increased with higher light and PAR, higher temperature, and lower canopy cover, which we interpreted as being indicative of a higher level of disturbance. **B)** Matrix of Pearson correlation coefficients calculated between key variables.

Influence of stem density on genus richness

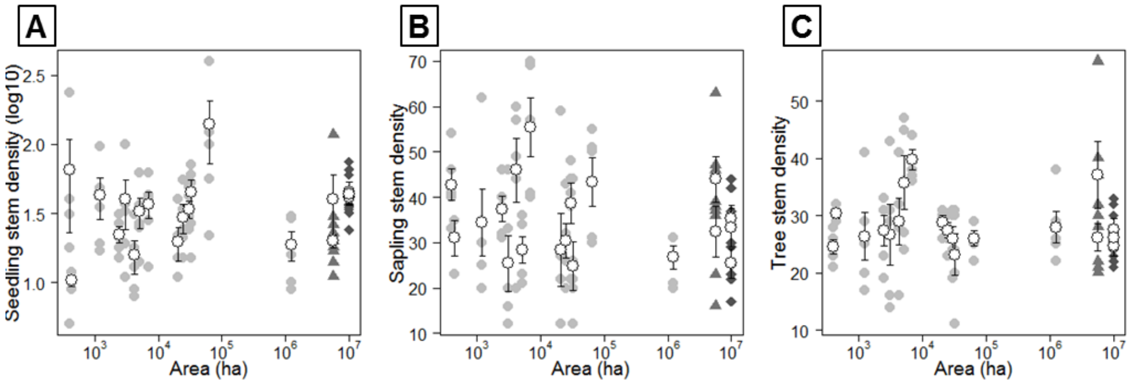


Figure S2.3. Variation in stem density of (A) seedling, (B) sapling, and (C) tree size classes with site area. Light grey circles (fragments), darker grey triangles (logged forest) and dark grey diamonds (primary forest) show number of stems per plot, and black symbols are site means with standard error. There was no significant relationships between stem density and either area, connectivity, or shape (univariate GLMMs).

Table S2.1. Model-averaged coefficients of variables used to predict species richness of seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling species richness	Intercept	2.15	0.04	2.07	2.23	
	Area	**0.38**	**0.09**	**0.20**	**0.57**	**1.00**
	Connectivity	-0.06	0.11	-0.28	0.15	0.29
Sapling species richness	Intercept	2.93	0.04	2.85	3.02	
	Disturbance	-0.11	0.09	-0.28	0.06	0.30
	Shape	-0.05	0.09	-0.23	0.12	0.16
	Connectivity	-0.04	0.09	-0.21	0.14	0.15
Tree species richness	Intercept	2.94	0.03	2.88	2.99	
	Disturbance	**-0.13**	**0.06**	**-0.25**	**-0.02**	**1.00**
	Shape	-0.10	0.06	-0.22	0.02	0.70
	Disturbance:Shape	-0.19	0.19	-0.55	0.18	0.16
	Connectivity	-0.06	0.07	-0.20	0.07	0.14
	Area	-0.05	0.06	-0.17	0.08	0.12

Text S2.1 Rarefaction analysis

Our sampling strategy and main findings pertain to analysis of plot-level local richness. We carried out several analyses to explore whether variation in stem density might affect our findings about fragmentation effects. Given that we only found significant effects of site characteristics for seedlings, we only carried out rarefaction analyses for seedling data. However, there were too few stems per plot for a meaningful rarefaction analysis (< 10 stems per plot in many plots), and so we carried out rarefaction analysis at site-level. We combined plot-level data within each site and removed Site #2 (Sapi A; which only had three plots), rarefied each sample to 50 stems, and regressed these values against each predictor variable. We show trend lines for area, connectivity, and disturbance, as these variables were important in top models of seedling genus richness. Although no univariate regressions were significant, the same trends that were seen in the analysis in the main text were evident (Figure S5). These findings support our results in the main text (Figures 2 and 3) that seedling genus richness was lower in smaller and more disturbed forest fragments.

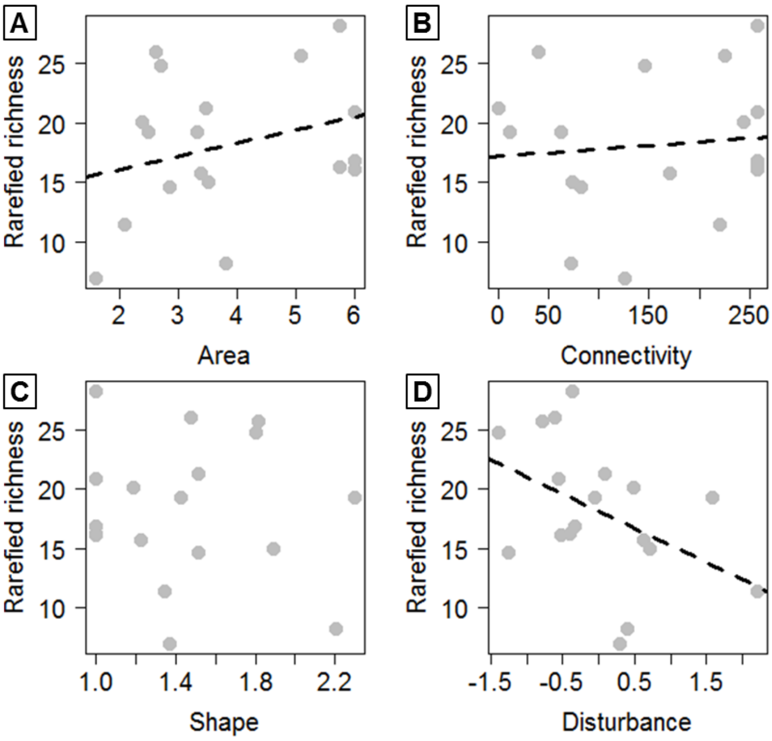


Figure S2.4. Rarefied seedling genus richness plotted against site characteristic predictor variables: (A) area ($\log_{10}$ ha), (B) connectivity, (C) shape, and (D) disturbance. Fitted lines are shown where the relationship was important in top models of seedling genus richness in the main text.

Text S2.2. Equation used to calculate the shape index of each site.

$$= \mathbf{p_{ij} / 2\sqrt{a_{ij}\,\pi}}$$

a_{ij} = area (m^2) of patch$_{ij}$

p_{ij} = perimeter (m) of patch$_{ij}$

Shape = 1 when the patch is circular, and approaches a maximum of 5 when perimeter is very convoluted (Forman & Godron, 1986).

Text S2.3. Equation used to calculate the connectivity of each site.

$$= \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^{2}}$$

a_{ijs} = Area (m^2) of patch$_{ijs}$ within specified neighbourhood (m)* of patch$_{ij}$

h_{ijs} = Edge-to-edge distance between patch$_{ijs}$ and focal patch$_{ij}$

Connectivity = 0 when there are no neighbouring patches of forest within specified neighbourhood*, and increases as forest patches become closer, larger and less fragmented.

*1 – 10 km

Table S2.2. Mean number of species, genera, and families in each size class, and total number of stems, with standard errors (SE), per site (average of 3 – 5 plots per site). Sites are arranged in order of increasing area (Table 2.1).

Site #	**Size Class**	**Species** (±se)	**Genera** (±se)	**Families** (±se)	**Abundance** (±se)
1	Seedlings	4.2 (0.97)	4.2 (0.97)	3.8 (0.86)	66 (42.91)
2	Seedlings	8.33 (0.67)	7.33 (0.33)	6.67 (0.33)	10.33 (0.88)
3	Seedlings	7 (0.84)	6.2 (1.07)	5.2 (0.80)	43 (14.40)
4	Seedlings	6.8 (1.20)	6.8 (1.20)	6 (1.14)	22.4 (2.93)
5	Seedlings	9.4 (0.51)	9 (0.63)	7.2 (0.20)	40 (15.72)
6	Seedlings	7.4 (0.75)	7.2 (0.58)	6.4 (0.40)	15.8 (4.19)
7	Seedlings	11.4 (1.03)	10.8 (1.07)	10 (1.14)	32.8 (8.10)
8	Seedlings	6.4 (0.93)	5.6 (0.51)	4.8 (0.20)	37.2 (8.14)
9	Seedlings	6.8 (0.73)	6.6 (0.68)	5.2 (0.73)	19.8 (5.44)
10	Seedlings	7.4 (0.87)	6.8 (0.73)	6 (0.63)	29.8 (7.01)
11	Seedlings	9 (0.71)	8.4 (0.75)	7.6 (0.40)	34 (4.93)
12	Seedlings	7.6 (0.87)	7 (0.63)	6.4 (0.68)	45.2 (10.46)
13	Seedlings	9.4 (1.25)	8.6 (1.29)	6.2 (1.24)	139.8 (67.09)

14	Seedlings	8 (2.28)	7.8 (2.08)	6.4 (1.03)	18.8 (4.53)
15	Seedlings	9.2 (1.93)	8.2 (1.66)	6.4 (1.21)	40 (19.75)
16	Seedlings	11.2 (1.98)	10 (1.70)	7.8 (1.16)	20 (2.12)
17	Seedlings	12.8 (1.02)	11.8 (0.86)	9.6 (0.75)	41.8 (5.12)
18	Seedlings	12.8 (1.11)	9.6 (1.21)	8.2 (1.20)	44.8 (8.39)
19	Seedlings	11.6 (1.83)	9.6 (1.50)	7.6 1.21)	43.6 (5.84)
1	Saplings	16.4 (2.38)	15 (1.84)	12.4 (1.47)	42.8 (3.48)
2	Saplings	22.67 (2.85)	20.33 (1.76)	16 (2.08)	31 (4.00)
3	Saplings	15.2 (2.18)	14.4 (2.04)	11.2 (1.20)	34.4 (7.34)
4	Saplings	19.2 (0.97)	17.2 (0.97)	13.4 (0.60)	37.4 (2.75)
5	Saplings	16.8 (3.38)	16.2 (3.17)	12.4 (2.16)	25.4 (6.24)
6	Saplings	28 (4.37)	25 (3.58)	18.6 (1.86)	46 (7.09)
7	Saplings	15.8 (2.06)	14.2 (2.06)	11.6 (1.44)	28.4 (2.94)
8	Saplings	21.2 (2.65)	19.2 (2.48)	14.6 (1.78)	55.4 (6.50)
9	Saplings	15.2 (1.50)	14.4 (1.33)	11.2 (1.50)	28.4 (8.03)
10	Saplings	17 (2.17)	15.4 (2.16)	11.8 (2.03)	30.4 (3.80)
11	Saplings	17.8 (1.77)	16 (1.52)	12.8 (0.73)	38.6 (4.47)
12	Saplings	16.8 (4.60)	15.2 (4.27)	11.6 (2.80)	24.8 (5.31)
13	Saplings	23.2 (1.88)	20.6 (1.21)	16 (1.10)	43.4 (5.33)
14	Saplings	17.8 (0.86)	15.4 (1.17)	12.2 (1.39)	26.8 (2.58)
15	Saplings	18.4 (3.26)	17.2 (2.92)	12.8 (1.88)	32.4 (5.64)
16	Saplings	26.4 (2.25)	23.8 (1.88)	18 (1.34)	44 (5.07)
17	Saplings	19.6 (1.81)	17.4 (1.47)	13.2 (1.24)	35.4 (2.82)
18	Saplings	13.6 (1.03)	12.6 (0.81)	9.4 (0.51)	25.4 (3.30)
19	Saplings	20.2 (2.15)	17.8 (1.74)	12.2 (1.39)	33.4 (4.27)
1	Trees	14.6 (2.48)	13.2 (2.08)	10.6 (1.69)	24.6 (1.21)
2	Trees	26 (1.15)	22.67 (0.33)	16 (0.58)	30.33 (0.88)
3	Trees	15.6 (2.06)	14 (1.95)	11.8 (1.59)	26.4 (4.19)
4	Trees	18.8 (2.22)	16.4 (1.94)	13 (0.71)	27.4 (2.71)
5	Trees	17.8 (3.94)	16 (3.03)	11.8 (2.37)	26.6 (5.32)
6	Trees	22.2 (2.42)	20 (2.07)	15.6 (1.21)	29 (4.02)
7	Trees	20.2 (1.24)	18.2 (0.97)	14 (0.45)	35.8 (4.62)
8	Trees	18.6 (2.62)	16.4 (2.14)	13.4 (1.81)	39.8 (1.74)
9	Trees	19 (1.55)	17 (1.87)	12.6 (1.72)	28.8 (1.16)
10	Trees	20.8 (1.24)	20 (1.00)	14 (0.84)	27.4 (1.33)
11	Trees	18.4 (1.17)	16.6 (0.93)	13.8 (0.66)	26 (2.17)
12	Trees	14.4 (2.91)	13.6 (2.79)	10.2 (2.06)	23.2 (3.65)
13	Trees	16.6 (1.21)	15.4 (0.75)	11.4 (0.87)	26 (1.34)
14	Trees	20 (1.30)	18.6 (1.33)	14.2 (0.97)	28 (2.74)
15	Trees	17.2 (2.08)	16 (2.14)	11.6 (1.69)	26.2 (2.42)
16	Trees	24 (2.17)	21.2 (1.85)	15.2 (0.97)	37.2 (5.84)
17	Trees	19.8 (0.92)	17.4 (1.21)	12.6 (0.93)	27.6 (1.86)
18	Trees	18.2 (1.77)	15.6 (1.60)	12.4 (0.93)	24.8 (1.88)
19	Trees	19.4 (1.08)	16.6 (1.33)	13.8 (1.07)	26.2 (1.59)

Influence of soil nutrients on size class richness

We measured the following soil characteristics: soil pH (pH-meter in slurry of water and soil), soil nitrogen, carbon and C:N ratio (using dry combustion C/N analyser), and soil phosphorus (using acid-digestion method described in Grimshaw, 1989). Soil characteristics were measured from four soil cores per plot, that were bulked for each plot prior to analysis at the Forest Research Centre, Sepilok. The soil data were included initially in our analyses, but were not found to be important in predicting diversity differences among plots and sites, and hence they were excluded from the subsequent analyses.

Table S2.3. Mean site values with standard errors (se) for soil nutrient data collected in each site. Sites are arranged in order of increasing area.

Site #	**pH** (±se)	**Total P** (±se)	**Total N** (±se)	**Total C** (±se)	**C:N ratio** (±se)
1	4.31 (0.11)	88.61 (6.53)	0.08 (0.02)	1.39 (0.00)	20.28 (4.19)
2	3.72 (0.09)	126.33 (10.68)	0.10 (0.02)	2.03 (0.26)	23.11 (4.33)
3	4.63 (0.20)	188.34 (19.83)	0.13 (0.03)	1.43 (0.22)	11.81 (1.31)
4	4.64 (0.15)	208.18 (13.47)	0.10 (0.02)	1.40 (0.17)	14.93 (0.88)
5	6.26 (0.45)	281.50 (25.48)	0.32 (0.07)	3.95 (0.98)	12.58 (1.11)
6	4.13 (0.04)	49.03 (8.95)	0.05 (0.01)	1.16 (0.09)	27.95 (6.16)
7	4.84 (0.32)	54.12 (11.04)	0.14 (0.02)	1.93 (0.25)	14.28 (1.37)
8	4.00 (0.16)	75.68 (19.54)	0.13 (0.01)	2.88 (0.62)	22.11 (4.49)
9	5.27 (0.23)	71.63 (4.65)	0.05 (0.00)	1.26 (0.07)	23.56 (1.01)
10	3.94 (0.05)	66.82 (10.28)	0.05 (0.01)	1.34 (0.15)	29.96 (3.13)
11	4.37 (0.08)	280.51 (11.70)	0.21 (0.02)	1.76 (0.14)	8.42 (0.79)
12	5.26 (0.41)	208.31 (35.81)	0.13 (0.01)	1.62 (0.14)	12.11 (0.44)
13	4.00 (0.05)	84.18 (22.16)	0.07 (0.02)	1.30 (0.12)	23.70 (6.24)
14	4.80 (0.14)	348.93 (41.68)	0.15 (0.01)	1.56 (0.16)	10.11 (0.29)
15	3.81 (0.08)	137.99 (7.11)	0.10 (0.02)	1.60 (0.19)	17.85 (2.33)
16	3.88 (0.18)	174.97 (9.39)	0.16 (0.02)	2.08 (0.21)	14.00 (1.56)
17	4.33 (0.13)	316.90 (73.58)	0.13 (0.03)	1.78 (0.13)	15.69 (2.28)
18	3.80 (0.09)	254.11 (23.84)	0.14 (0.03)	1.86 (0.18)	15.25 (2.41)
19	4.63 (0.28)	192.06 (32.32)	0.08 (0.02)	1.33 (0.20)	18.26 (3.27)

Table S2.4. Reciprocal Simpson diversity. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	Predictor	β	SE	Lower CI	Upper CI	RI
Seedling Simpson diversity	Intercept	0.29	0.04	0.22	0.36	
	Area	0.04	0.09	-0.13	0.21	0.46
	Connectivity	-0.03	0.06	-0.15	0.08	0.47
	Area:Connectivity	**-0.37**	**0.16**	**-0.69**	**-0.05**	**0.33**
	Disturbance	0.08	0.05	-0.02	0.17	0.55
	Shape	0.03	0.07	-0.10	0.17	0.27
	Connectivity:Disturbance	0.16	0.10	-0.02	0.35	0.19
Saplings Simpson diversity	Intercept	0.10	0.01	0.09	0.11	
	Connectivity	0.01	0.01	-0.02	0.03	0.21
	Disturbance	0.01	0.01	-0.02	0.03	0.24
Trees Simpson diversity	Intercept	0.09	0.00	0.08	0.09	
	Shape	0.01	0.01	-0.01	0.03	0.38
	Disturbance	**0.00**	**0.00**	**0.00**	**0.01**	**0.17**

Influence of changing buffer size for calculation of connectivity metric

Altering the buffer width from 1 to 10 km, had little or no effect on the outcome of the model. Variables were standardised before being included in the GLMM and this meant there was little variation in values of connectivity, regardless of buffer size.

Table S2.5. Influence of change buffer size for calculation of connectivity metric.

Buffer size (km)	Response variable	Predictor	β	SE	Lower CI	Upper CI
1	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05

2	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
3	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
4	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
5	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
6	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49

		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
7	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
8	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
9	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
10	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.14
		Disturbance	-0.04	0.09	-0.23	0.14

Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
	Disturbance	-0.08	0.08	-0.25	0.08
	Shape	-0.05	0.08	-0.22	0.11
	Connectivity	-0.05	0.08	-0.21	0.12
Tree genera richness	Intercept	2.83	0.03	2.77	2.89
	Disturbance	-0.12	0.06	-0.23	0.00
	Shape	-0.06	0.06	-0.17	0.05

Table S2.6. Influence of changing size class upper/lower bounds on sapling and tree size classes. Model-averaged coefficients of variables used to predict genus richness of seedling (< 1cm dbh), sapling (1 – 2.5 cm dbh), and tree (>10 cm dbh) size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness	Intercept	2.06	0.04	1.98	2.15	
	Area	0.31	0.09	0.12	0.49	**1.00**
	Connectivity	-0.08	0.11	-0.29	0.13	0.24
	Disturbance	-0.04	0.09	-0.23	0.14	0.20
Sapling genera richness	Intercept	2.44	0.05	2.33	2.54	
	Disturbance	-0.10	0.11	-0.31	0.11	0.27
	Connectivity	-0.06	0.11	-0.27	0.15	0.21
Tree genera richness	Intercept	2.23	0.03	2.17	2.30	
	Disturbance	-0.19	0.07	-0.34	-0.05	**1.00**
	Area	-0.03	0.07	-0.18	0.11	0.27

Text S2.4. Wood density as a proxy for growth-rate of genera

In order to test the robustness of our results to the removal of slow-growing genera, we used wood density as a proxy for growth rate (Slik, 2005). We obtained wood density on dry weight (g/cm^3) data from The Global Wood Density database (Chave & al., 2009). We then removed high wood-density (>0.75 g/cm^3), slow-growing genera and repeated our analyses, but found no qualitative difference in our results (i.e. lower richness of seedlings in fragments, but no effects of fragmentation on saplings or trees). These analyses support our assumption that size is a reasonable proxy for pre- and post-fragmentation individuals.

We also carried out our analyses of fragmentation effects separately for high and low wood density groups, and we split our data set according to the median wood density of all genera we encountered in our study (0.55 g/cm3). We found significantly fewer low wood density tree genera present in plots in primary forest than in logged or fragmented forest (ANOVA of tree richness by forest type; high wood density: F(2,90) = 2.57, p = 0.08; low wood density: F(2,90) = 4.55, p = 0.01), however findings from our ANOVA analyses of tree, sapling and seedling richness were qualitatively similar to our original analysis i.e. both low and high wood density seedlings have lower richness in fragments (ANOVA of seedling richness by forest type; high wood density: F(2,90) = 5.60, p = 0.005; low wood density: F(2,90) = 4.60, p = 0.01; ANOVA of sapling richness by forest type high wood density: F(2,90) = 2.87, p = 0.06; low wood density: F(2,90) = 0.23, p = 0.80). Our findings from our GLMMs with respect to examining site characteristics important for richness were also qualitatively similar for the low and high wood density groups. As previously, there was no effect of site area on either high or low wood density sapling richness and so we conclude that differences in plant growth rates are not having major impacts on our designation of post- and pre-fragmentation individuals, or our overall findings.

Table S2.7. Influence of removal of high wood-density (>0.75 g/cm^3), slow-growing genera on size classes. Model-averaged coefficients of variables used to predict genus-level richness of seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness	Intercept	2.00	0.04	1.92	2.08	
	Area	0.28	0.09	0.10	0.46	**1.00**
	Connectivity	-0.06	0.09	-0.24	0.13	0.21
	Disturbance	-0.05	0.11	-0.27	0.16	0.22
Sapling genera richness	Intercept	2.76	0.04	2.68	2.84	
	Disturbance	-0.07	0.08	-0.23	0.09	0.21
	Connectivity	-0.06	0.08	-0.21	0.10	0.19
	Shape	-0.04	0.08	-0.20	0.12	0.17
Tree genera richness	Intercept	2.76	0.03	2.70	2.82	
	Disturbance	-0.13	0.06	-0.24	-0.01	**0.80**
	Shape	-0.05	0.06	-0.17	0.06	0.27

Table S2.8. Model-averaged coefficients of variables used to predict genus-level richness of low and high wood-density seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of each variable are presented. Significant predictors are highlighted in bold.

Response variable	**Predictor**	**β**	**SE**	**Lower CI**	**Upper CI**	**RI**
Seedling genera richness (low wood density)	Intercept	1.16	0.06	1.04	1.27	
	Area	**0.30**	**0.12**	**0.06**	**0.53**	**1.00**
	Shape	-0.07	0.13	-0.33	0.18	0.28
Sapling genera richness (low wood density)	Intercept	1.85	0.05	1.75	1.96	
	Connectivity	-0.21	0.14	-0.48	0.06	0.44
	Shape	-0.20	0.14	-0.46	0.07	0.54
	Area	-0.13	0.11	-0.35	0.09	0.22
	Disturbance	-0.07	0.10	-0.27	0.13	0.09
Tree genera richness (low wood density)	Intercept	1.89	0.04	1.81	1.98	
	Area	-0.14	0.09	-0.32	0.04	0.41
	Connectivity	-0.09	0.09	-0.27	0.08	0.17
	Disturbance	-0.07	0.09	-0.25	0.11	0.13
	Shape	0.06	0.09	-0.11	0.24	0.13
Seedling genera richness (high wood density)	Intercept	1.54	0.06	1.41	1.66	
	Area	**0.31**	**0.14**	**0.04**	**0.59**	**1.00**
	Connectivity	-0.11	0.16	-0.43	0.20	0.20
	Disturbance	-0.07	0.14	-0.34	0.20	0.17
	Shape	0.06	0.13	-0.20	0.32	0.17
Sapling genera richness (high wood density)	Intercept	2.36	0.05	2.27	2.45	
	Disturbance	-0.11	0.09	-0.30	0.07	0.31
	Area	0.09	0.09	-0.10	0.27	0.24
Tree genera richness (high wood density)	Intercept	2.33	0.03	2.26	2.39	
	Disturbance	**-0.18**	**0.07**	**-0.32**	**-0.05**	**1.00**
	Shape	**-0.13**	**0.07**	**-0.27**	**0.00**	**0.72**

Appendix 1C. Distribution of genera by site and size class.

Table S2.9. Abundance of tree genera sampled per site.

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Achariaceae	Hydnocarpus	1	5		2	3		18	1	2	2	1	1	1	1	1	1	4	2	1
	Pangium						1					1								
	Ryparosa															1	1	2	1	
Actinidiaceae	Saurauia					1														
Alangiaceae	Alangium	2		1		1	2			3	1	4	4		1	3	2	2	3	
Anacardiaceae	Buchanania		1		1	1										1	1		1	
	Dracontomelon				1							1			2					1
	Gluta					1							1	3						
	Mangifera								1											
	Melanochyla								3										1	
	Parishia			2																
	Semecarpus	17		24				15						2						
Annonaceae	Alphonsea						1		1											
	Anaxagorea																	2		
	Cyathocalyx										1									
	Dasymaschalon													1						
	Goniothalamus					2												1	1	
	Hubera																	1		
	Maasia	1		1		1	1					1				1	1	2	3	3
	Marsypopetalum	1			1			1												
	Meiogyne				1															
	Monoon	1	1		3			2		4	2	1	2					2	1	3
	Neouvaria	1					1			1	1								1	2
	Phaeanthus					4	1		2		2		1	1					1	3
	Polyalthia							2		8		2		2		2		1		1
	Popowia	1		1		1				4	3								1	
	Sageraea	3						2		1		1				1				1
	Xylopia			1			1							2						
Apocynaceae	Alstonia										1	1								
	Cerbera				2															
	Dyera				2		1		7											
	Kopsia									2										
Burseraceae	Canarium	1	5	1	2	7	1	3	1	1		3		1	4		1		2	1
	Dacryodes			1										2			2			
	Santiria	1	1	1	1		5	4	1			1			1		2	1	1	
Calophyllaceae	Kayea			1										1						
Cannabaceae	Gironniera	3	2				1						1							
	Ziziphus																			2
Capparaceae	Crateva				1						1									
Cardiopteridaceae	Gonocaryum					1														
Celastraceae	Lophopetalum	3		3				2	3	1	1	4	2		1		1	1	1	1
Chrysobalanaceae	Maranthes		2						1											

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Parinari																1			1
Clusiaceae	Calophyllum			1				4						1	1		1	1	1	
	Garcinia			1	4	2	2	2	1	1	1			1		1		1	1	
Combretaceae	Terminalia		2				2		1											
Convolvulaceae	Erycibe												1							
Cornaceae	Mastixia																		1	
Dilleniaceae	Dillenia		1		1		1	1			1	1	1							1
Dipterocarpaceae	Anisoptera																			1
	Dipterocarpus	10	3	13			4		2		4		4	20	2	6	8			
	Dryobalanops		4		3		7	2	19	5	4	1	3		1					
	Hopea				2	5	6	6	30	2						2	16			
	Parashorea		2		3	1	1	1	3	8	8	5	4	4	8	1	1	6	2	4
	Shorea	27	6	6	6	1	13	15	12	10	3	9	1	24	8	8	14	12	14	21
	Vatica	7	2	2	1		1	10	10					1		2	4			
Ebenaceae	Diospyros		3	1	3	8	4	16	7	1	5	7	4		12	1	1	3	2	7
Elaeocarpaceae	Elaeocarpus			3			6		17		4	1	1	3						
	Sloanea									5						1				
Escalloniaceae	Polyosma				1															
Euphorbiaceae	Agrostistachys								1											
	Blumeodendron	1		1		3								2						
	Botryophora					1														
	Croton	1					1						1				1			
	Dimorphocalyx		1						2							7	1	2		
	Endospermum			11							1				1					
	Jatropha														1					
	Koilodepas					2			1		1		6		2	3	7			
	Macaranga			7		2	8	2		2		5				21	32			1
	Mallotus	2	6	2	2	3	2	4	1	1	10	2	11	6	9	4	9	1	20	7
	Melanolepis					3	1													
	Moultonianthus			1										1						
	Neoscortechinia									1										
	Spathiostemon				3	9					7		2		5	1	2	4		1
	Suregada								1											
	Trigonostemon	6	2										1				1			
	Wetria					1														
Fabaceae	Archidendron												1		1					
	Cassia						1													
	Crudia		1						1		3		1				1			
	Cynometra							3			1	1			1					
	Dialium																1			
	Fordia																		1	
	Koompassia							1												
	Ormosia		1		12	5	2					2	1		2	2	2	2		9
	Saraca					8														
	Sindora			1			2								1					

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Sympetalandra							2			2									
Fagaceae	Castanopsis														1					
	Lithocarpus			2	1		1	2	3	3		1		1	1		4	1	3	4
Gentianaceae	Fagraea								1		1						1			
Irvingiaceae	Irvingia		1							1										
Lamiaceae	Callicarpa							1			1						4			
	Clerodendrum						1													
	Gmelina		1								1									
	Teijsmanniodendron		2	1		1		1					1	3			1	1	1	
	Vitex		2					1	1											
Lauraceae	Actinodaphne				1							1	1							
	Beilschmiedia	1	1		5	9			1	1		1	1		4	3	1	4	2	1
	Cinnamomum						1		1											
	Cryptocarya			5		1					1	1						1		
	Dehaasia	1	3		1	1		2		3			1	3	1	7		5	2	1
	Eusideroxylon				5						2	4	8	4						
	Lindera															2				
	Litsea	1	1	3	2	2	6	4	1	3		1	6	1	2	2	1	9	2	4
Lecythidaceae	Barringtonia	3	2	2	1		1	1		2	2			1	2	1	6	2		2
	Planchonia		1				1				1					1				
Magnoliaceae	Magnolia						3	2	1			1			2	1				
Malvaceae	Brownlowia		1									3						1		1
	Diplodiscus									8										
	Durio						1		1							1			1	
	Microcos			2	5	8	2	1	1	2	4	7	1	2	10		1		3	
	Neesia					1	2			1	1	1				1				
	Pentace		2				1			2								3	2	
	Pterocymbium							2												
	Pterospermum				13	2					6	5	13		2			1		1
	Scaphium	1		4					2	3				2		1		1		
	Sterculia														1		1	1		
Melastomataceae	Memecylon										1			3					1	3
	Pternandra			1			5		1	3				2	1	3	2			
Meliaceae	Aglaia		2		1	3	2	1	1	3		2		1		1	1	6	1	6
	Aphanamixis														1			1	2	
	Azadirachta										1		1							
	Chisocheton								1	1				2	4		1	3		
	Dysoxylum				2			1		1	1			1	1	2	1	2	5	2
	Lansium				1					3										
	Reinwardtiodendron					1												1		
	Walsura	2		1			1						3				1			3
Monimiaceae	Kibara														1					
Moraceae	Antiaris																			1
	Artocarpus	1	2	4		1	3								1		1			
	Ficus	1	5		1	4		1		6	2		4				1			

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Parartocarpus									1				2						
	Prainea	1	2	1	1		1		1	1	2	3	1							
Myristicaceae	Gymnacranthera			1																
	Knema	3	2	1		1	3	1	3	3		1	3	1		2	2	2	2	2
	Myristica		1						1		1	1								1
Myrtaceae	Decaspermum		1						1											
	Syzygium	3		4	5		10	7	9	1	4	9	1	4	4	3	7	4	9	5
	Tristaniopsis								1								1			
	Xanthostemon						3		2											
Olacaceae	Ochanostachys	3				1	4						2	2			1			2
	Scorodocarpus															1				
	Strombosia																			4
Oleaceae	Chionanthus			2	1							2		2	1		1		4	
Penaeaceae	Crypteronia															2				
Pentaphylacaceae	Adinandra						1										1			
Phyllanthaceae	Antidesma				1							1							1	
	Aporosa	3			1	3	1	1	5	2	1	1		1	1	1	2	2	4	
	Baccaurea	3		2				1	5		7	1		1	2	1	3	4	3	2
	Bridelia					1		4			1									
	Cleistanthus		1	1	1	1	1	5			3			2				2	3	
	Glochidion				6			4	1	3	1	1			6		3		1	
Polygalaceae	Xanthophyllum	2		1		1		4			1		1	1	1	1	1		5	
Primulaceae	Ardisia							1			1		1				3			
Proteaceae	Helicia												1				2			
Putranjivaceae	Drypetes		3			3				1	1	1	1	2	2		1	2		2
Rhizophoraceae	Carallia																	1		
Rosaceae	Prunus			2										1		11				
Rubiaceae	Aidia	1																		
	Diplospora					1	1													
	Gaertnera						2		6											
	Ixora		1			1							1							3
	Ludekia	2			3						1		2		2		1			
	Nauclea			1	2				2	1										
	Neolamarckia				1					1	1	2			1					
	Pleiocarpidia											1			2	5	2	2		
	Praravinia															1	2			
	Prismatomeris							1		1										
	Rothmannia																	1		
	Urophyllum						1		2						1		1	2		2
Rutaceae	Glycosmis						1													
	Melicope				3	1							2			1	3			
Sabiaceae	Meliosma			1	1															
Salicaceae	Homalium														1	1				
Salvadoraceae	Azima	1	1																	
Sapindaceae	Allophylus															2				

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Dimocarpus				2							1			2		1	3	1	1
	Guioa												1							
	Harpullia											2			2					
	Lepisanthes					2					5	2						1	1	
	Mischocarpus			1				1	1											
	Paranephelium		1		6	2		1		14	4	10	4				1	6	2	2
	Pometia						1													1
	Xerospermum								1											
Sapotaceae	Madhuca			2	1			3		4	3	1		2	2	2	3		1	1
	Palaquium													1						
	Payena				1															
Simaroubaceae	Eurycoma															1				
Stemonuraceae	Stemonurus		1				2	5	11		1									
Tetramelaceae	Octomeles				4						2									
Thymelaeaceae	Aquilaria						1					1					1			
	Gonystylus						1		1											
	Phaleria														1					
Urticaceae	Dendrocnide									1	1			3						
	Oreocnide							1		1										
Violaceae	Rinorea					4		1												
Vitaceae	Leea										1	6			9			12		2

Table S2.10. Abundance of sapling genera sampled per site.

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Achariaceae	Hydnocarpus	1	3		1	4	4	6	1		3	8	4		1	1	1	3	2	
	Pangium						4													
	Ryparosa		1	2			3		2		1		1	3	1		2	6		2
	Trichadenia											1								
Actinidiaceae	Saurauia	2			1			3					1				4	1		
Alangiaceae	Alangium	1	2	1		3	2			2	2	9	1		5	2	2	2	1	
Anacardiaceae	Buchanania		4				1									1	1			
	Dracontomelon									3										
	Gluta				1				1								1			
	Mangifera								2											
	Melanochyla								17											
	Parishia							1						3						
	Semecarpus		1	31				10						8						
Anisophyllaceae	Anisophyllea			1					1					2						
Annonaceae	Anaxagorea		1														1	27		
	Dasymaschalon			1					1											
	Goniothalamus				1	1	1					3	1		1		1			3
	Hubera																	1		
	Maasia	1	1	2					3				2	2						2
	Marsypopetalum	1						2												

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Monoon	3	1		5		1			11	5		3	7					1	1
	Neouvaria						1										1			3
	Phaeanthus		1		3	4	2	3	3			4	1	2	3		1	1	1	
	Polyalthia		4	1	3	6		3	1	4		5		1	1	3	5	3	4	2
	Popowia				3	1			2	2	11	1	1	1	2			2	5	4
	Pseuduvaria																		1	
	Sageraea	5			6			2		7	1	1	1							
	Xylopia			1			2	1				2		1						
Apocynaceae	Alstonia			1								1								
	Cerbera				4															
	Dyera						1				1									
	Kopsia	2			1					4							1	1	3	
Asparagaceae	Dracaena	2																		
Burseraceae	Canarium		1			4	3	1	1		1	1			1	1	2	1		2
	Dacryodes	2					2							2		4				
	Santiria	1	1	1	1		7	2	16			1				1	4			
Calophyllaceae	Kayea		1	1							1		1	1						
Cannabaceae	Gironniera	2				1	1					1				3				
	Ziziphus					1		1		2			1							
Cardiopteridaceae	Gonocaryum																2	1		
Celastraceae	Lophopetalum	4	1		2			1			1	2	1	5	5	2				
Chrysobalanaceae	Maranthes		1						3											
Clusiaceae	Calophyllum					1		1	1					2			1		2	
	Garcinia				1	6	4		6		2		1	1				1		
Combretaceae	Terminalia						2		1			2	1		3					
Convolvulaceae	Erycibe															1				
Dilleniaceae	Dillenia				1		2			1	12	4	1		1			1		
Dipterocarpaceae	Dipterocarpus	1	2	8			6				1	4		11	2	3	13			
	Dryobalanops				1		15		3	1		1	3		1					1
	Hopea					2	5	1	39		6	2	1			19	7			
	Parashorea		1							3	3	4	3					1		2
	Shorea	69	2	9			13	6	7		2		1	18		1	3	2	2	4
	Vatica	6		10				12	19					15		2	6			1
Ebenaceae	Diospyros	1	8	4	7	3	8	21	1	7	6	7	2	18	9	4	2	10	1	14
Elaeocarpaceae	Elaeocarpus						2		20		2									
	Sloanea					1														
Escalloniaceae	Polyosma				2															
Euphorbiaceae	Agrostistachys										6									
	Alchornea					2														
	Blumeodendron					1				2						2				
	Botryophora							2												
	Croton		2				3		2					10	2					9
	Dimorphocalyx		2			3										15	5	10		
	Endospermum										2									
	Homalanthus					2														

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Koilodepas					2						10	1		4	11	8			
	Macaranga			1		1	3					3				1				
	Mallotus	4	5	6	28	3	6	6	9	9	32	9	27	3	11	12	17	14	35	19
	Melanolepis					2														
	Moultonianthus													1						
	Neoscortechinia	1					1			1									1	
	Ptychopyxis			3																
	Spathiostemon					3	1				7		10				2	1		1
	Suregada							3			1									
	Trigonostemon	29	2	1										4						
	Wetria				4															
Fabaceae	Archidendron						2		3		1									
	Cassia						1													
	Crudia										1	1			1	1	1	1		
	Cynometra					1									1					1
	Dialium						2													
	Fordia									1									2	
	Koompassia													1						
	Ormosia				22	11			5			1	2	1		4	12	3		12
	Saraca				2															
	Sindora			1			3													
	Sympetalandra												1		1			1		
Fagaceae	Lithocarpus			1						1				3						
Gentianaceae	Fagraea				1				2	1	1	1	1			1	2	1		
Lamiaceae	Callicarpa	1								1					1			1		2
	Clerodendrum	2					1													
	Teijsmanniodendron		1			1		1					1	2			2			
Lauraceae	Actinodaphne									1										
	Alseodaphne						1													
	Beilschmiedia		2		1	3				3	2			1				7	2	
	Cinnamomum									1									1	
	Cryptocarya			1						5				2						
	Dehaasia		1	6	1			1	2			2		2		2	1	1	1	
	Eusideroxylon			1	3							1	1				1			
	Lindera															3	2			1
	Litsea	5	2	3	6		14	1	8	3		4	3	2	2	3	3	13	7	9
	Notaphoebe							2				1								
Lecythidaceae	Barringtonia	3	1	1			1	5						3						2
	Planchonia		1												1					
Magnoliaceae	Magnolia						1	2	1			1						1		
Malvaceae	Brownlowia		4									2			2		10	2	4	5
	Diplodiscus									6										
	Durio																			2
	Heritiera						1													
	Leptonychia				3															

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Microcos	3	1		1	8	2	1	1	21	1	5	1	4	9	2	2			
	Neesia						5										1			1
	Pentace									5			1					3		1
	Pterospermum				1					3			4							
	Scaphium		1	39			2		4	2			2	1		2	1			
	Sterculia					1	2					1				1				2
Melastomataceae	Memecylon					1	1							2		2	2	1	3	2
	Pternandra		1	2			4		1	3		1				6	16			
Meliaceae	Aglaia		3		2	2	2	1	3	4	1	4	2	1	6		9	8	3	6
	Aphanamixis											1							2	
	Chisocheton				1	1	2		1					3			1	1		
	Dysoxylum		1		1			2	1				1	1		2	1	3	1	4
	Lansium			1		1				2				1						
	Reinwardtiodendron	3			1			1	1	1								4	1	3
	Walsura		2										1	1			1			1
Moraceae	Artocarpus							1									1	1		
	Ficus	1	2		23	4	4	1		1		1	4							
	Prainea				1				3			2	1							
Myristicaceae	Gymnacranthera	1																		
	Horsfieldia						1													
	Knema	4	2	2	3	1	6		1	3	3	2	4	3		1	2		2	10
	Myristica	1	1	2								2		1						
Myrtaceae	Decaspermum							2									1			
	Syzygium	5		9	3	3	11	2	19	1	5	13	1	14	6	3	10	4	5	4
	Tristaniopsis													1				1		
	Xanthostemon						2		3											
Ochnaceae	Campylospermum																1			
Olacaceae	Ochanostachys	8					1						1			1	1	1		
	Strombosia	1																		2
Oleaceae	Chionanthus	3		2	1		7	1	6		1	7	2	9	2	1	2			
Pandaceae	Galearia	2						1		1										
Penaeaceae	Crypteronia															12				
Phyllanthaceae	Antidesma		1		3	1	4			1		1		1	3	1			1	1
	Aporosa	3	1				3		1	1	2	1				2	1	6	7	
	Baccaurea	4		7	1	2		1	8		6	2	1	13	4	2	1	7	4	5
	Cleistanthus	1	6	2		1	2	12	1		4	2	1	3	2		7	1	3	
	Glochidion		1		6	1						4			2		2			
Polygalaceae	Xanthophyllum	6	1	1		1		8		3	3	1			1	3	2	3		1
Primulaceae	Ardisia						3	1	1						2		4		5	
Proteaceae	Helicia																1			
Putranjivaceae	Drypetes			2	3	3					6		2	5	1	3	1		2	
Rubiaceae	Cowiea																		1	
	Diplospora								1						2					1
	Gaertnera						15		25											
	Ixora	8			1	2						1	1		3		1	3		10

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Ludekia				1															
	Nauclea				1					1										
	Pleiocarpidia															2	2			
	Praravinia	1		2										2	2	3		1	5	1
	Prismatomeris		2								2								1	
	Urophyllum	5			2			1	1						1	2	6	1	3	
Rutaceae	Clausena				1															
	Glycosmis		1		1	1							1							1
	Melicope				6	2							1				1			
Sabiaceae	Meliosma			1																
Salicaceae	Flacourtia															1				
Santalaceae	Scleropyrum						1													
Sapindaceae	Dimocarpus				1	1							1		1		1	1		
	Guioa								1											
	Harpullia									1		1			2					
	Lepisanthes				1	6		1				3		2	1					1
	Mischocarpus	1						1	2				1							
	Nephelium						1													
	Paranephelium		1				2			4		15	1	1	2		2	2	2	1
	Pometia						1						1							
	Xerospermum								5											
Sapotaceae	Madhuca			1			1				2			1		1	7			
	Palaquium													1		1				
Simaroubaceae	Eurycoma						1							3		4	1			
Stemonuraceae	Stemonurus	4				1	7	2	3				1							
Symplocaceae	Symplocos															1				
Theaceae	Pyrenaria						2		1											
Thymelaeaceae	Gonystylus		3			1	2													
Urticaceae	Dendrocnide		2											4			1			
	Oreocnide									1										
Violaceae	Rinorea				5	8		2					3	1						
Vitaceae	Leea				1	1				1	2	23	5		20			5		5

Table S2.11. Abundance of seedling genera sampled per site.

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Achariaceae	Hydnocarpus	1	3		2	1	1	7				2	2		1					
	Pangium						7													
Actinidiaceae	Saurauia	2			1				1				1		1		4	1		5
Alangiaceae	Alangium		1	1			2			1		1	26			6		1	1	1
Anacardiaceae	Buchanania																1			
	Gluta						1													
	Melanochyla								4											
	Semecarpus			6				2						3						
Anisophyllaceae	Anisophyllea													3						

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Annonaceae	Anaxagorea		2															42		
	Goniothalamus												1							1
	Maasia			1													1			
	Monoon					1		1			1									1
	Neouvaria																1			1
	Phaeanthus				1	2						1								
	Polyalthia		1			3				10			1	2	1	2				4
	Popowia		1	1	1	2		4		4	3	2		1	5		1	5	9	5
	Sageraea				1	1				5										
	Xylopia			1						1										
Apocynaceae	Kopsia																	1	10	
Aquifoliaceae	Ilex							3												
Burseraceae	Canarium					2		1	1			1				1	1	1		
	Santiria				1		2	10	1			6								
Cannabaceae	Gironniera														1					
	Ziziphus									1			1							1
Celastraceae	Lophopetalum				2							1	3		1		1	1		
Clusiaceae	Calophyllum							15							5					
	Garcinia					1	2	1									2			
Combretaceae	Terminalia		3																	
Dilleniaceae	Dillenia				1			1		6	1	6	2					2		
Dipterocarpaceae	Dipterocarpus			75								1		12	1		2			
	Dryobalanops						16		26	2			3		1					
	Hopea		1		5		14	2	61	1						13	1			
	Parashorea		1		1					25	27	2	13	40	11			4	27	44
	Shorea	296		38			2	9		4		10	1	578	1	18	4	21	79	44
	Vatica	7		1				5	15					23		95	4			
Ebenaceae	Diospyros					7		19				1		1	2	2	1	2		1
Elaeocarpaceae	Elaeocarpus						2		3		2			3						
Euphorbiaceae	Agrostistachys										3									
	Croton		2			5	4	5	8											12
	Dimorphocalyx				1	10						1			1	2	6			
	Koilodepas					1		1				25				1	1			
	Macaranga			3																
	Mallotus		2	3	49	3	1			20	29	28	36	2	10	11	16	47	26	66
	Melanolepis							4	3											
	Neoscortechinia									4										
	Ptychopyxis													1						
	Spathiostemon					12					2		12		2			3		
	Trigonostemon	6																		
	Wetria				1															
Fabaceae	Crudia																4			
	Dialium							1												
	Fordia															1			10	
	Koompassia							1				1								

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
	Ormosia				3	6							2	1	1	2	2	1		1
Fagaceae	Lithocarpus													8				2	2	
Irvingiaceae	Irvingia			1																
Lamiaceae	Teijsmanniodendron											1		2						
Lauraceae	Beilschmiedia	1	3			1												1		
	Cinnamomum								2											
	Cryptocarya													1						
	Dehaasia	1		1								1		2		1				
	Eusideroxylon											9	1							
	Lindera															9				
	Litsea	1		1	1		3		5	3	6	6	1	1	3	3	9	6	7	3
	Notaphoebe							5												
Lecythidaceae	Barringtonia							1			1									
	Planchonia														3					
Magnoliaceae	Magnolia							1												
Malvaceae	Brownlowia											2			1			2	2	1
	Diplodiscus									1										
	Microcos					9	3		3		22	3			1				3	
	Neesia						1													1
	Pentace		2			53				2								11	23	7
	Pterocymbium							1												
	Pterospermum				22	3					33	43	88		19			23		1
	Scaphium								2					1						
	Sterculia					4														
Melastomataceae	Memecylon															1				1
	Pternandra															1	13			
Meliaceae	Aglaia				2	2	1	7							3	1	5	5	1	1
	Reinwardtiodendron					1	1	1		1			1				1	6		3
	Walsura													1						
Moraceae	Antiaris																			1
	Artocarpus						1	1												
	Ficus		4		2	11		1		4		2	3							
	Prainea	1					2													
Myristicaceae	Knema	2	1				1		1		7		1		1	1		1	3	1
	Myristica	1																		
Myrtaceae	Syzygium			57	1		3	14	38		1	1	2	7		2	8	5	7	5
	Tristaniopsis													1						
	Xanthostemon								5											
Ochnaceae	Schuurmansiella			8																
Olacaceae	Ochanostachys	5						1					1							
Oleaceae	Chionanthus			14	1		1												2	
Phyllanthaceae	Antidesma						5													
	Aporosa											1				1		3	1	
	Baccaurea											1		1		1	1	4	4	
	Cleistanthus				2			10							2	1	1			

		Site numbers																		
Family	**Genus**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Polygalaceae	Xanthophyllum							6				2							1	
Primulaceae	Ardisia					7	1				2									
Putranjivaceae	Drypetes				1						2			1						
Rosaceae	Prunus			1																
Rubiaceae	Gaertnera								1											
	Ixora	3	1										1		6			2		3
	Pleiocarpidia						1										1			
	Praravinia									1							2			
	Psychotria										2									
	Urophyllum		2				1									1	1	2	3	1
Rutaceae	Clausena				1						1									
	Melicope	1																		
Sabiaceae	Meliosma																2			
Santalaceae	Scleropyrum													1						
Sapindaceae	Dimocarpus											1			1			1		1
	Guioa							13					1							
	Mischocarpus			1																
	Paranephelium											2			4			2	1	
Sapotaceae	Madhuca			1						1	1					2	1			
Simaroubaceae	Eurycoma	1												1		21	1			
Stemonuraceae	Stemonurus	1						10	6											
Symplocaceae	Symplocos																		1	
Thymelaeaceae	Aquilaria																1			
Urticaceae	Dendrocnide		1										1	1						
Violaceae	Rinorea				8	44							21							
Vitaceae	Leea				1	8				2	3	6			5			1	1	1

Appendix 2 – Supporting information for Chapter 3

Table S3.1. Values of divergence between cohorts, distinctiveness of community composition in different sites, and percentage of genera present as trees and seedlings (recruitment success), only trees (recruitment failure), or only seedlings (seedling immigration), within the study plots at each site. Area and isolation category of sites indicated in square brackets.

Site #	Area (ha $\log_{10}$)	Isolation	Tree-seedling divergence	Tree distinctive-ness	Seedling distinctive-ness	Recruit-ment success (%)	Recruit-ment failure (%)	Seedling immigration (%)
1	1.60 [A1]	130.70 [C2]	0.34	0.27	0.53	0.23	0.64	0.14
2	1.64 [A1]	168.91 [C2]	0.45	0.29	0.42	0.17	0.67	0.15
3	2.08 [A1]	37.09 [C3]	0.3	0.36	0.37	0.32	0.62	0.06
4	2.39 [A1]	13.91 [C3]	0.36	0.27	0.26	0.22	0.61	0.17
5	2.49 [A1]	245.10 [C1]	0.5	0.21	0.49	0.28	0.57	0.15
6	2.62 [A2]	217.55 [C1]	0.32	0.3	0.36	0.28	0.61	0.1
7	2.71 [A2]	111.76 [C3]	0.24	0.11	0.42	0.35	0.48	0.17
8	2.84 [A2]	174.80 [C2]	0.38	0.26	0.55	0.27	0.68	0.05
9	3.32 [A2]	194.23 [C1]	0.28	0.17	0.31	0.26	0.63	0.11
10	3.39 [A3]	86.85 [C3]	0.35	0.25	0.42	0.23	0.69	0.08
11	3.48 [A3]	256.54 [C1]	0.15	0.11	0.2	0.33	0.51	0.16
12	3.51 [A3]	183.70 [C2]	0.36	0.13	0.31	0.35	0.52	0.13
13	3.81 [A3]	185.11 [C1]	0.18	0.27	0.31	0.3	0.53	0.18
14	5.09 [A3]	32.58 [C3]	0.3	0.25	0.17	0.24	0.58	0.18
15	6.00 [CF]	0.00 [CF]	0.29	0.3	0.37	0.39	0.52	0.09
16	6.00 [CF]	0.00 [CF]	0.19	0.13	0.23	0.33	0.56	0.11
17	6.00 [CF]	0.00 [CF]	0.17	0.31	0.28	0.44	0.46	0.11
18	6.00 [CF]	0.00 [CF]	0.28	0.25	0.3	0.35	0.56	0.1
19	6.00 [CF]	0.00 [CF]	0.14	0.23	0.09	0.38	0.47	0.15

Table S3.2. Mean Chao-Sørensen dissimilarity between pairs of sites within categories based on area or isolation (n = 10 pairwise comparisons per group). Site 10 was included in both A2 and A3, and I2 and I3, so that all groups contained five sites.

Size class	Area or isolation category	Mean	SE	Range of category values
Trees	Smallest (A1)	0.31	0.04	40 – 307 ha
	Medium (A2)	0.24	0.04	419 – 2473 ha
	Largest (A3)	0.21	0.05	2473 – 123,000 ha
	Continuous forest	0.27	0.04	1,000,000 ha
Seedlings	Smallest (A1)	0.66	0.09	40 – 307 ha
	Medium (A2)	0.62	0.06	419 – 2473 ha
	Largest (A3)	0.35	0.07	2473 – 123,000 ha
	Continuous forest	0.30	0.07	1,000,000 ha

Trees	Most isolated (I1)	0.30	0.04	4.96 – 6.71
	Moderately isolated (I2)	0.20	0.05	4.04 – 4.57
	Least isolated (I3)	0.32	0.04	2.76 – 4. 04
	Continuous forest	0.27	0.04	0
Seedlings	Most isolated (I1)	0.58	0.07	4.96 – 6.71
	Moderately isolated (I2)	0.68	0.06	4.04 – 4.57
	Least isolated (I3)	0.49	0.09	2.76 – 4. 04
	Continuous forest	0.30	0.07	0

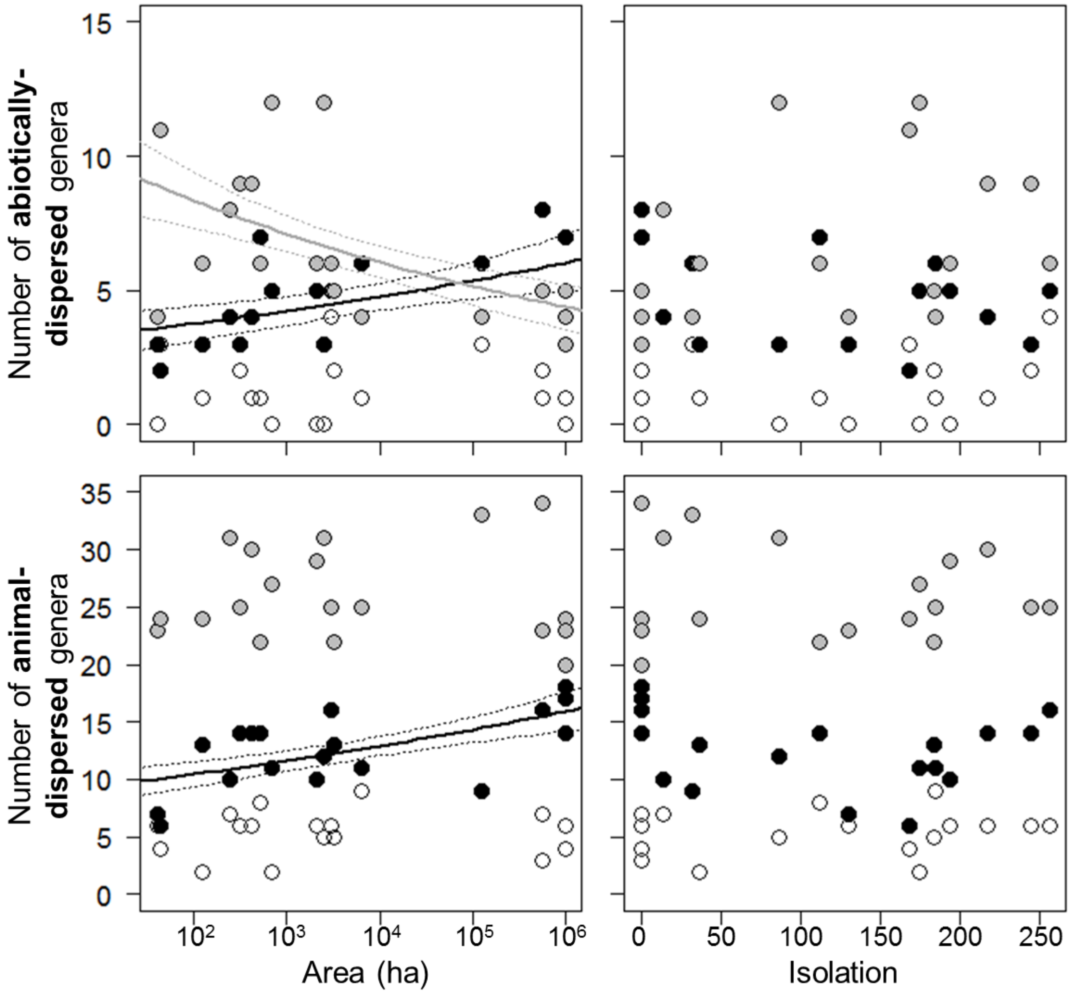


Figure S3.1. The number of (top row) abiotically dispersed and (bottom row) animal dispersed genera occurring at each of the 19 sites that were present as trees and seedlings (= recruitment success), tree genera without seedlings (= no evidence of recruitment in the study plots), and seedling genera without trees (= presumed immigration into the study plots) in each site, in area (left) and isolation (right).). Fitted lines show significant relationships in univariate GLMs of number of genera in each group against site area or isolation.

Appendix 3 – Supporting information for Chapter 4

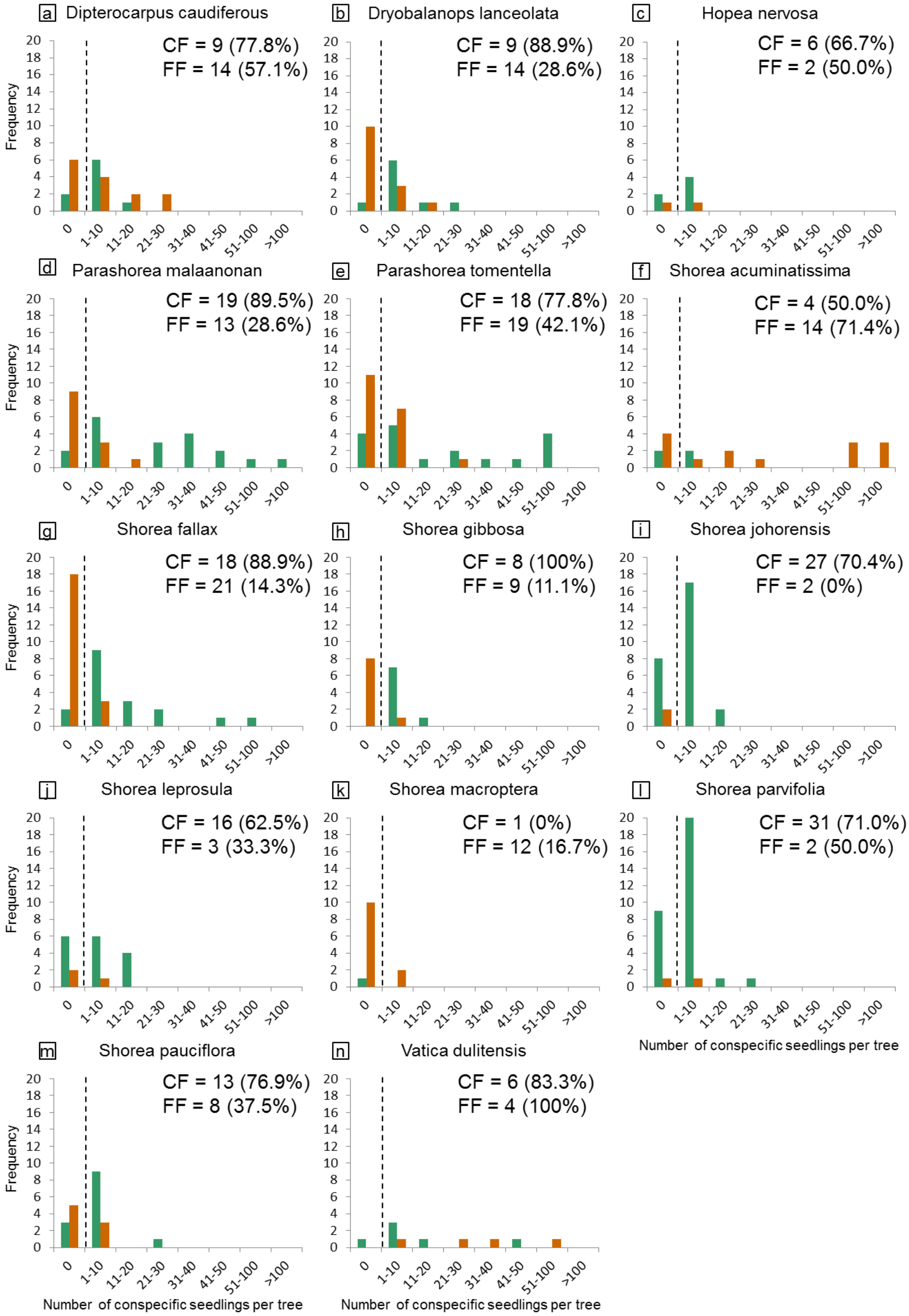


Figure S4.1. See next page for figure legend.

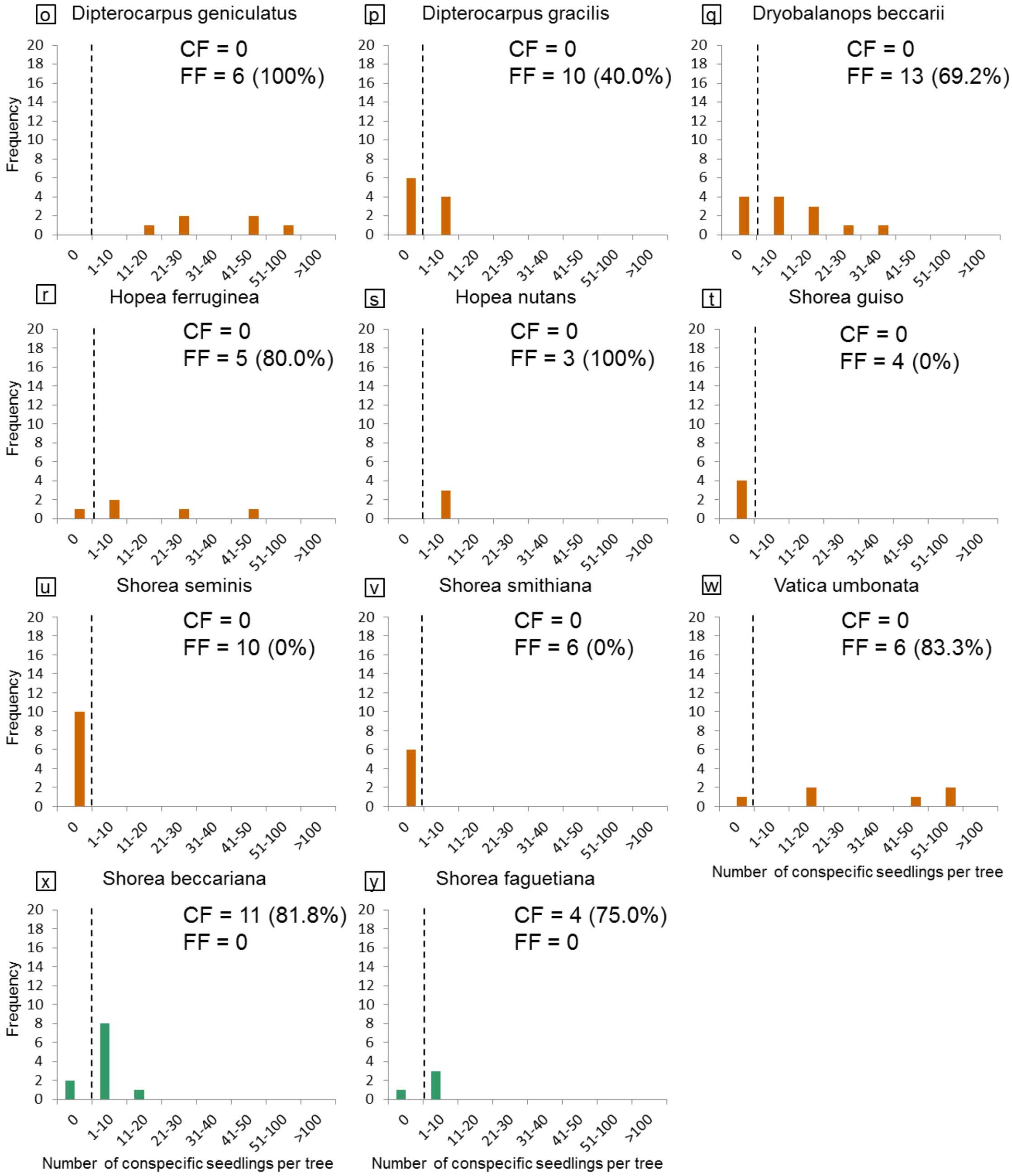


Figure S4.1 continued. Overall frequency distribution of seedling abundance per tree in continuous forest (green bars; CF) and forest fragments (brown bars; FF). a – n: species recorded in both forest types; o – w: species recorded only in forest fragments; x – y: species recorded only in continuous forest. The number of trees sampled in each forest type is indicted in the top right of each plot, and the percentage of those trees that were recorded with seedlings is in brackets.

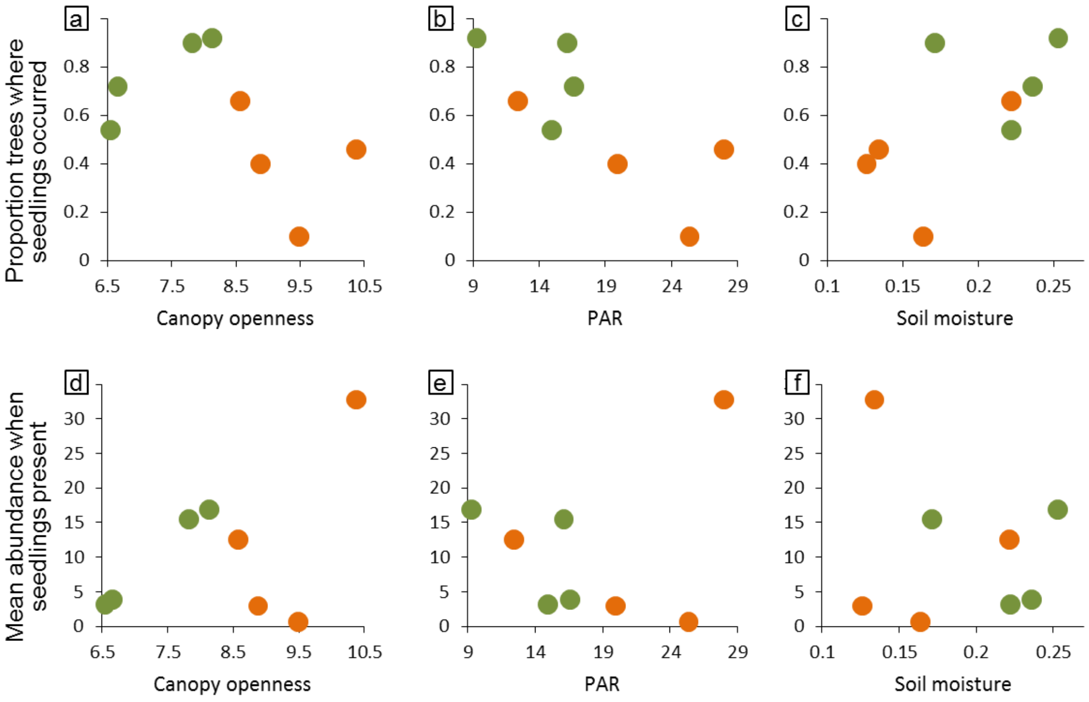


Figure S4.2. Variation in site mean values (green symbols = continuous forest sites, orange symbols = forest fragments) of canopy openness, photosynthetically active radiation (PAR) and soil moisture, plotted against a – c: proportion of trees with conspecific seedlings (n = 50 trees per site), and d – f: mean seedling abundance (per tree) when seedlings were present. PAR and soil moisture data are from Stride et al. (2018).

Table S4.1. Dipterocarp species location and frequency in each site. Site 1 = Labuk Rd, site 2 = Materis, site 3 = Sapi C, site 4 = Kalumpang, site 5 = Malua A, site 6 = Malua B, site 7 = Tembaling (Danum Valley), site 8 = West 15 (Danum Valley). Shaded sites are continuous forest sites.

		Overall	**No.**	**Site number**							
Genus	**Species**	**freq.**	**sites**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Dipterocarpus	caudiferus	23	5	9	2	3		6	3		
	geniculatus	6	1	6							
	gracilis	10	2		5		5				
Dryobalanops	beccarii	13	2		5	8					
	lanceolata	23	6		8	1	5	2	4	3	
Hopea	ferruginea	5	1				5				
	nervosa	8	4		1	1		2	4		
	nutans	3	1				3				
Parashorea	melaanonan	32	7	2	3	3	5		4	6	9
	tomentella	37	8	3	8	6	2	2	4	7	5

		Overall	No.	Site number							
Genus	**Species**	**freq.**	**sites**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Shorea	acuminatissima	18	4	5	2		7	4			
	beccariana	11	3					7	3	1	
	fallax	39	8	6	4	6	5	3	4	5	6
	faguetiana	4	2						1	3	
	gibbosa	17	5		1	8		1	2	5	
	guiso	4	2		3		1				
	johorensis	29	5			2		5	4	8	10
	leprosula	19	6		2		1	4	1	4	7
	macroptera	13	3	7		5		1			
	parvifolia	33	5				2	5	7	8	11
	pauciflora	21	5	5		3		7	4		2
	seminis	10	3	4	2	4					
	smithiana	6	2	3	3						
Vatica	dulitensis	10	3				4	1	5		
	umbonata	6	2		1		5				

Table S4.2. List of parent trees, tag number (Tree ID) and location.

Site #	Tree ID	Species	Latitude	Longitude
1	101	Parashorea malaanonan	4.94980	117.80724
1	102	Shorea johorensis	4.94971	117.80738
1	103	Parashorea malaanonan	4.94963	117.80773
1	104	Shorea parvifolia	4.94961	117.80781
1	105	Dryobalanops lanceolata	4.94908	117.80786
1	106	Parashorea malaanonan	4.94925	117.80786
1	107	Parashorea tomentella	4.94907	117.80861
1	108	Parashorea tomentella	4.94895	117.80868
1	109	Parashorea tomentella	4.94892	117.80922
1	110	Parashorea tomentella	4.94869	117.80937
1	111	Shorea johorensis	4.94876	117.80950
1	112	Shorea faguetiana	4.94879	117.80962
1	113	Dryobalanops lanceolata	4.94866	117.80968
1	114	Shorea gibbosa	4.94873	117.80981
1	115	Shorea faguetiana	4.94881	117.80999
1	116	Parashorea malaanonan	4.94889	117.80980
1	117	Shorea fallax	4.94848	117.81001
1	118	Shorea leprosula	4.94837	117.80979
1	119	Shorea gibbosa	4.94847	117.80967
1	120	Shorea parvifolia	4.94819	117.81000
1	121	Shorea fallax	4.94802	117.80980
1	122	Dryobalanops lanceolata	4.94790	117.80974
1	123	Parashorea tomentella	4.94799	117.80969
1	124	Shorea johorensis	4.94806	117.80997
1	125	Shorea johorensis	4.94800	117.81009
1	126	Shorea gibbosa	4.94846	117.80942

Site #	Tree ID	Species	Latitude	Longitude
1	127	Shorea fallax	4.94981	117.80703
1	128	Shorea parvifolia	4.94986	117.80670
1	129	Shorea parvifolia	4.95026	117.80639
1	130	Shorea faguetiana	4.95142	117.80581
1	131	Shorea johorensis	4.95167	117.80583
1	132	Shorea gibbosa	4.95182	117.80584
1	133	Shorea fallax	4.95273	117.80626
1	134	Shorea parvifolia	4.95269	117.80635
1	135	Parashorea malaanonan	4.95295	117.80640
1	136	Shorea leprosula	4.95308	117.80643
1	137	Shorea parvifolia	4.95294	117.80622
1	138	Shorea leprosula	4.95281	117.80584
1	139	Shorea leprosula	4.95303	117.80575
1	140	Shorea fallax	4.95321	117.80552
1	141	Shorea johorensis	4.95321	117.80589
1	142	Shorea gibbosa	4.95352	117.80557
1	143	Shorea beccariana	4.95346	117.80541
1	144	Shorea parvifolia	4.95382	117.80545
1	145	Shorea johorensis	4.95418	117.80530
1	146	Shorea johorensis	4.95443	117.80533
1	147	Parashorea tomentella	4.95462	117.80525
1	148	Parashorea malaanonan	4.95503	117.80523
1	149	Shorea parvifolia	4.95482	117.80523
1	150	Parashorea tomentella	4.95488	117.80489
2	201	Parashorea malaanonan	4.96554	117.78875
2	202	Shorea parvifolia	4.96562	117.78880
2	203	Shorea parvifolia	4.96565	117.78865
2	204	Shorea johorensis	4.96574	117.78847
2	205	Parashorea malaanonan	4.96592	117.78839
2	206	Shorea leprosula	4.96709	117.78873
2	207	Shorea parvifolia	4.96650	117.78882
2	208	Parashorea tomentella	4.96673	117.78866
2	209	Shorea johorensis	4.96617	117.78864
2	210	Shorea leprosula	4.96732	117.78846
2	211	Shorea parvifolia	4.96736	117.78861
2	212	Shorea fallax	4.96744	117.78846
2	213	Shorea fallax	4.96867	117.78904
2	214	Shorea parvifolia	4.96882	117.78902
2	215	Shorea johorensis	4.96897	117.78912
2	216	Shorea fallax	4.96911	117.78916
2	217	Shorea johorensis	4.96913	117.78930
2	218	Shorea parvifolia	4.96926	117.78862
2	219	Shorea leprosula	4.96906	117.78858
2	220	Shorea johorensis	4.96885	117.78875
2	221	Shorea parvifolia	4.96970	117.78869
2	222	Shorea fallax	4.96985	117.78882
2	223	Parashorea malaanonan	4.96964	117.78922

Site #	Tree ID	Species	Latitude	Longitude
2	224	Shorea johorensis	4.96956	117.78935
2	225	Parashorea malaanonan	4.96965	117.78954
2	226	Shorea parvifolia	4.96548	117.78861
2	227	Shorea johorensis	4.96546	117.78894
2	228	Parashorea malaanonan	4.96526	117.78865
2	229	Shorea pauciflora	4.96511	117.78860
2	230	Shorea pauciflora	4.96505	117.78824
2	231	Shorea fallax	4.96503	117.78827
2	232	Shorea johorensis	4.96541	117.78806
2	233	Shorea johorensis	4.96487	117.78861
2	234	Parashorea tomentella	4.96479	117.78864
2	235	Shorea parvifolia	4.96449	117.78857
2	236	Shorea johorensis	4.96350	117.78851
2	237	Parashorea malaanonan	4.96344	117.78864
2	238	Shorea parvifolia	4.96336	117.78893
2	239	Parashorea malaanonan	4.96327	117.78892
2	240	Shorea leprosula	4.96314	117.78876
2	241	Shorea parvifolia	4.96291	117.78884
2	242	Parashorea tomentella	4.96250	117.78847
2	243	Shorea fallax	4.96173	117.78824
2	244	Parashorea malaanonan	4.96306	117.78798
2	245	Shorea leprosula	4.96357	117.78739
2	246	Parashorea tomentella	4.96399	117.78781
2	247	Parashorea malaanonan	4.96393	117.78807
2	248	Shorea leprosula	4.96605	117.78783
2	249	Parashorea tomentella	4.96631	117.78704
2	250	Shorea leprosula	4.96618	117.78772
3	301	Parashorea tomentella	5.51215	118.02138
3	302	Dryobalanops lanceolata	5.51239	118.02017
3	303	Dryobalanops lanceolata	5.51178	118.02005
3	304	Parashorea tomentella	5.51224	118.01990
3	305	Dryobalanops lanceolata	5.51226	118.01963
3	306	Dipterocarpus gracilis	5.51237	118.01959
3	307	Parashorea tomentella	5.51283	118.01756
3	308	Dryobalanops lanceolata	5.51278	118.01810
3	309	Dryobalanops lanceolata	5.51308	118.01789
3	310	Parashorea tomentella	5.51255	118.01782
3	311	Parashorea malaanonan	5.51265	118.01807
3	312	Shorea guiso	5.51313	118.01684
3	313	Parashorea tomentella	5.51323	118.01678
3	314	Shorea seminis	5.51364	118.01684
3	315	Shorea smithiana	5.51360	118.01714
3	316	Dryobalanops beccarii	5.51257	118.01636
3	317	Shorea acuminatissima	5.51201	118.01633
3	318	Shorea acuminatissima	5.51221	118.01531
3	319	Shorea guiso	5.51232	118.01513
3	320	Dryobalanops beccarii	5.51242	118.01486

Site #	Tree ID	Species	Latitude	Longitude
3	321	Vatica umbonata	5.51256	118.01490
3	322	Shorea smithiana	5.51237	118.01486
3	323	Shorea seminis	5.51243	118.01469
3	324	Hopea nervosa	5.51199	118.01464
3	325	Shorea fallax	5.51199	118.01468
3	326	Dryobalanops lanceolata	5.51188	118.01452
3	327	Parashorea malaanonan	5.51172	118.01448
3	328	Dipterocarpus gracilis	5.51147	118.01213
3	329	Shorea guiso	5.51168	118.01219
3	330	Parashorea tomentella	5.51166	118.01203
3	331	Shorea smithiana	5.51186	118.01190
3	332	Dryobalanops beccarii	5.51228	118.01177
3	333	Dryobalanops beccarii	5.51242	118.01041
3	334	Dipterocarpus gracilis	5.51226	118.01045
3	335	Dryobalanops lanceolata	5.51257	118.01016
3	336	Dipterocarpus gracilis	5.51257	118.01012
3	337	Parashorea tomentella	5.51161	118.01031
3	338	Shorea fallax	5.51196	118.01003
3	339	Dryobalanops beccarii	5.51221	118.01004
3	340	Shorea fallax	5.51215	118.00942
3	341	Shorea fallax	5.51249	118.01056
3	342	Dryobalanops lanceolata	5.51163	118.01375
3	343	Dipterocarpus caudiferus	5.51264	118.02137
3	344	Dipterocarpus caudiferus	5.51281	118.02101
3	345	Shorea leprosula	5.51254	118.02089
3	346	Shorea gibbosa	5.51376	118.02067
3	347	Shorea leprosula	5.51427	118.02120
3	348	Parashorea malaanonan	5.51452	118.02097
3	349	Parashorea tomentella	5.51463	118.02140
3	350	Dipterocarpus gracilis	5.51490	118.02141
4	401	Vatica umbonata	4.66306	118.15210
4	402	Shorea acuminatissima	4.66287	118.15194
4	403	Vatica umbonata	4.66266	118.15199
4	404	Shorea acuminatissima	4.66252	118.15198
4	405	Shorea fallax	4.66240	118.15199
4	406	Shorea acuminatissima	4.66245	118.15222
4	407	Shorea fallax	4.66231	118.15181
4	408	Shorea acuminatissima	4.66217	118.15139
4	409	Shorea fallax	4.66104	118.15152
4	410	Shorea acuminatissima	4.66099	118.15157
4	411	Vatica umbonata	4.65950	118.15158
4	412	Vatica umbonata	4.65936	118.15187
4	413	Vatica dulitensis	4.65905	118.15208
4	414	Parashorea malaanonan	4.65894	118.15189
4	415	Vatica dulitensis	4.65884	118.15182
4	416	Parashorea malaanonan	4.65889	118.15169
4	417	Dipterocarpus gracilis	4.65872	118.15178

Site #	Tree ID	Species	Latitude	Longitude
4	418	Shorea fallax	4.65853	118.15211
4	419	Parashorea tomentella	4.65857	118.15200
4	420	Hopea nutans	4.65796	118.15262
4	421	Hopea ferruginea	4.65795	118.15282
4	422	Hopea nutans	4.65776	118.15277
4	423	Dryobalanops lanceolata	4.65780	118.15284
4	424	Hopea ferruginea	4.65770	118.15294
4	425	Parashorea tomentella	4.65748	118.15288
4	426	Dryobalanops lanceolata	4.65748	118.15251
4	427	Parashorea malaanonan	4.65768	118.15242
4	428	Dipterocarpus gracilis	4.65731	118.15275
4	429	Dipterocarpus gracilis	4.65719	118.15298
4	430	Hopea nutans	4.65717	118.15309
4	431	Dryobalanops lanceolata	4.65701	118.15315
4	432	Hopea ferruginea	4.65691	118.15276
4	433	Dipterocarpus gracilis	4.65705	118.15275
4	434	Vatica dulitensis	4.65641	118.15306
4	435	Dryobalanops lanceolata	4.65698	118.15271
4	436	Shorea fallax	4.65633	118.15326
4	437	Dipterocarpus gracilis	4.65643	118.15337
4	438	Hopea ferruginea	4.65577	118.15316
4	439	Vatica umbonata	4.65564	118.15284
4	440	Shorea acuminatissima	4.65564	118.15275
4	441	Hopea ferruginea	4.65547	118.15249
4	442	Vatica dulitensis	4.65885	118.15248
4	443	Shorea guiso	4.65927	118.15286
4	444	Shorea parvifolia	4.65936	118.15276
4	445	Shorea leprosula	4.65957	118.15266
4	446	Shorea acuminatissima	4.65950	118.15264
4	447	Parashorea malaanonan	4.65973	118.15279
4	448	Parashorea malaanonan	4.65954	118.15275
4	449	Dryobalanops lanceolata	4.65985	118.15285
4	450	Shorea parvifolia	4.66027	118.15252
5	501	Dipterocarpus geniculatus	5.89270	117.93149
5	502	Dipterocarpus caudiferus	5.89304	117.93170
5	503	Shorea fallax	5.89311	117.93185
5	504	Dipterocarpus caudiferus	5.89320	117.93200
5	505	Shorea fallax	5.89342	117.93187
5	506	Shorea acuminatissima	5.89359	117.93165
5	507	Dipterocarpus caudiferus	5.89350	117.93166
5	508	Shorea fallax	5.89378	117.93188
5	509	Shorea acuminatissima	5.89391	117.93168
5	510	Shorea macroptera	5.89384	117.93166
5	511	Shorea macroptera	5.89370	117.93122
5	512	Dipterocarpus caudiferus	5.89364	117.93110
5	513	Shorea fallax	5.89340	117.93117
5	514	Dipterocarpus geniculatus	5.89463	117.93198

Site #	Tree ID	Species	Latitude	Longitude
5	515	Dipterocarpus caudiferus	5.89471	117.93190
5	516	Dipterocarpus caudiferus	5.89492	117.93168
5	517	Shorea acuminatissima	5.89502	117.93150
5	518	Dipterocarpus caudiferus	5.89490	117.93134
5	519	Dipterocarpus geniculatus	5.89508	117.93115
5	520	Dipterocarpus caudiferus	5.89506	117.93066
5	521	Shorea fallax	5.89492	117.93199
5	522	Dipterocarpus geniculatus	5.89671	117.93174
5	523	Dipterocarpus caudiferus	5.89680	117.93179
5	524	Shorea fallax	5.89688	117.93188
5	525	Dipterocarpus geniculatus	5.89665	117.93198
5	526	Shorea macroptera	5.89875	117.93165
5	527	Shorea macroptera	5.89881	117.93111
5	528	Shorea macroptera	5.89854	117.93098
5	529	Shorea macroptera	5.89983	117.93241
5	530	Parashorea tomentella	5.89951	117.93260
5	531	Parashorea tomentella	5.89932	117.93252
5	532	Shorea pauciflora	5.89985	117.93246
5	533	Shorea pauciflora	5.90007	117.93276
5	534	Shorea smithiana	5.89975	117.93277
5	535	Shorea smithiana	5.89973	117.93300
5	536	Shorea seminis	5.89681	117.93227
5	537	Shorea pauciflora	5.89661	117.93261
5	538	Dipterocarpus geniculatus	5.89655	117.93330
5	539	Shorea smithiana	5.89647	117.93422
5	540	Shorea seminis	5.89689	117.93498
5	541	Shorea pauciflora	5.89684	117.93493
5	542	Parashorea malaanonan	5.89685	117.93468
5	543	Parashorea malaanonan	5.89718	117.93472
5	544	Parashorea tomentella	5.89705	117.93493
5	545	Shorea macroptera	5.89641	117.93500
5	546	Shorea pauciflora	5.89488	117.93197
5	547	Shorea seminis	5.89483	117.93210
5	548	Shorea seminis	5.89474	117.93325
5	549	Shorea acuminatissima	5.89465	117.93367
5	550	Shorea acuminatissima	5.89460	117.93323
6	601	Shorea fallax	5.72445	117.41195
6	602	Shorea fallax	5.72458	117.41216
6	603	Parashorea tomentella	5.72515	117.41212
6	604	Parashorea tomentella	5.72508	117.41235
6	605	Shorea seminis	5.72503	117.41204
6	606	Hopea nervosa	5.72530	117.41205
6	607	Parashorea tomentella	5.72539	117.41180
6	608	Dryobalanops beccarii	5.72553	117.41199
6	609	Dryobalanops beccarii	5.72579	117.41182
6	610	Parashorea tomentella	5.72557	117.41149
6	611	Shorea macroptera	5.72582	117.41156

Site #	Tree ID	Species	Latitude	Longitude
6	612	Dryobalanops beccarii	5.72615	117.41157
6	613	Dryobalanops beccarii	5.72727	117.41151
6	614	Shorea gibbosa	5.72708	117.41145
6	615	Shorea pauciflora	5.72724	117.41133
6	616	Shorea pauciflora	5.72735	117.41175
6	617	Dryobalanops beccarii	5.72707	117.41189
6	618	Shorea macroptera	5.72694	117.41197
6	619	Shorea gibbosa	5.72688	117.41282
6	620	Dryobalanops beccarii	5.72695	117.41242
6	621	Parashorea tomentella	5.72715	117.41074
6	622	Shorea pauciflora	5.72737	117.41068
6	623	Shorea fallax	5.72751	117.41080
6	624	Shorea fallax	5.72765	117.41061
6	625	Dryobalanops beccarii	5.72762	117.41052
6	626	Shorea johorensis	5.72727	117.41026
6	627	Shorea fallax	5.72774	117.41093
6	628	Shorea gibbosa	5.72781	117.41109
6	629	Shorea gibbosa	5.72918	117.41072
6	630	Shorea gibbosa	5.72925	117.41049
6	631	Shorea macroptera	5.73092	117.40993
6	632	Shorea gibbosa	5.73074	117.40951
6	633	Dipterocarpus caudiferus	5.73150	117.40932
6	634	Shorea fallax	5.73177	117.40924
6	635	Shorea seminis	5.73175	117.40890
6	636	Shorea seminis	5.73117	117.40893
6	637	Dipterocarpus caudiferus	5.72765	117.41176
6	638	Shorea macroptera	5.72780	117.41162
6	639	Dryobalanops beccarii	5.72652	117.41086
6	640	Shorea johorensis	5.72613	117.40984
6	641	Shorea gibbosa	5.72675	117.41034
6	642	Parashorea malaanonan	5.72706	117.41341
6	643	Shorea gibbosa	5.72708	117.41337
6	644	Shorea seminis	5.72423	117.41201
6	645	Shorea macroptera	5.72436	117.41195
6	646	Parashorea malaanonan	5.72447	117.41152
6	647	Dryobalanops lanceolata	5.72538	117.41108
6	648	Parashorea malaanonan	5.72471	117.41176
6	649	Dipterocarpus caudiferus	5.72449	117.41254
6	650	Parashorea tomentella	5.72457	117.41222
7	701	Shorea parvifolia	5.09671	117.66585
7	702	Shorea johorensis	5.09663	117.66565
7	703	Shorea parvifolia	5.09671	117.66638
7	704	Dipterocarpus caudiferus	5.09691	117.66663
7	705	Shorea johorensis	5.09671	117.66662
7	706	Shorea beccariana	5.09643	117.66663
7	707	Shorea pauciflora	5.09627	117.66682
7	708	Shorea pauciflora	5.09620	117.66698

Site #	Tree ID	Species	Latitude	Longitude
7	709	Shorea gibbosa	5.09645	117.66723
7	710	Shorea parvifolia	5.09651	117.66727
7	711	Shorea beccariana	5.09671	117.66709
7	712	Dipterocarpus caudiferus	5.09612	117.66595
7	713	Shorea parvifolia	5.09618	117.66608
7	714	Shorea johorensis	5.09636	117.66584
7	715	Shorea beccariana	5.09630	117.66559
7	716	Shorea fallax	5.09616	117.66533
7	717	Shorea pauciflora	5.09599	117.66654
7	718	Dipterocarpus caudiferus	5.09586	117.66653
7	719	Shorea fallax	5.09512	117.66672
7	720	Shorea pauciflora	5.09514	117.66690
7	721	Parashorea tomentella	5.09492	117.66595
7	722	Shorea johorensis	5.09489	117.66664
7	723	Shorea beccariana	5.09435	117.66651
7	724	Dipterocarpus caudiferus	5.09434	117.66638
7	725	Vatica dulitensis	5.09372	117.66640
7	726	Dipterocarpus caudiferus	5.09278	117.66696
7	727	Shorea pauciflora	5.09261	117.66699
7	728	Dryobalanops lanceolata	5.09250	117.66709
7	729	Dryobalanops lanceolata	5.09245	117.66726
7	730	Shorea pauciflora	5.09228	117.66706
7	731	Shorea parvifolia	5.09203	117.66622
7	732	Shorea johorensis	5.09194	117.66774
7	733	Shorea beccariana	5.09160	117.66694
7	734	Shorea fallax	5.09159	117.66748
7	735	Hopea nervosa	5.09206	117.66643
7	736	Hopea nervosa	5.09203	117.66788
7	737	Shorea macroptera	5.09212	117.66771
7	738	Shorea leprosula	5.09115	117.66752
7	739	Shorea beccariana	5.09189	117.66673
7	740	Dipterocarpus caudiferus	5.09243	117.66675
7	741	Shorea leprosula	5.09025	117.66774
7	742	Shorea pauciflora	5.09012	117.66803
7	743	Shorea leprosula	5.08911	117.66823
7	744	Shorea acuminatissima	5.08866	117.66898
7	745	Shorea acuminatissima	5.08891	117.66850
7	746	Shorea acuminatissima	5.08793	117.66768
7	747	Shorea leprosula	5.08796	117.66757
7	748	Shorea acuminatissima	5.08841	117.66760
7	749	Parashorea tomentella	5.09011	117.66764
7	750	Shorea beccariana	5.09050	117.66731
8	801	Shorea parvifolia	5.11811	117.67321
8	802	Shorea beccariana	5.11809	117.67333
8	803	Shorea parvifolia	5.11803	117.67306
8	804	Shorea beccariana	5.11804	117.67292
8	805	Shorea parvifolia	5.11831	117.67257

Site #	Tree ID	Species	Latitude	Longitude
8	806	Shorea parvifolia	5.11898	117.67238
8	807	Vatica dulitensis	5.11958	117.67147
8	808	Hopea nervosa	5.11965	117.67122
8	809	Parashorea malaanonan	5.11961	117.67118
8	810	Shorea johorensis	5.11946	117.67125
8	811	Shorea fallax	5.11961	117.67103
8	812	Shorea johorensis	5.11946	117.67089
8	813	Shorea pauciflora	5.11939	117.67098
8	814	Parashorea malaanonan	5.11968	117.67061
8	815	Dipterocarpus caudiferus	5.11959	117.67038
8	816	Parashorea tomentella	5.12024	117.67037
8	817	Dryobalanops lanceolata	5.12031	117.67048
8	818	Vatica dulitensis	5.12040	117.67067
8	819	Shorea johorensis	5.12033	117.67073
8	820	Parashorea tomentella	5.11977	117.67085
8	821	Shorea johorensis	5.11981	117.67068
8	822	Parashorea malaanonan	5.12054	117.67022
8	823	Vatica dulitensis	5.12069	117.67042
8	824	Shorea pauciflora	5.12094	117.67041
8	825	Shorea gibbosa	5.12083	117.67037
8	826	Shorea fallax	5.12075	117.67013
8	827	Shorea leprosula	5.12067	117.67010
8	828	Hopea nervosa	5.12108	117.67000
8	829	Shorea gibbosa	5.12116	117.66951
8	830	Shorea fallax	5.12109	117.66929
8	831	Parashorea tomentella	5.12116	117.66924
8	832	Parashorea malaanonan	5.12073	117.66934
8	833	Shorea fallax	5.12095	117.66905
8	834	Shorea parvifolia	5.12107	117.66891
8	835	Hopea nervosa	5.12097	117.66874
8	836	Dryobalanops lanceolata	5.12119	117.66873
8	837	Dryobalanops lanceolata	5.12109	117.66849
8	838	Shorea parvifolia	5.12095	117.66835
8	839	Shorea parvifolia	5.12099	117.66857
8	840	Dipterocarpus caudiferus	5.12075	117.66857
8	841	Shorea pauciflora	5.12059	117.66823
8	842	Shorea beccariana	5.12036	117.66813
8	843	Shorea faguetiana	5.12000	117.66813
8	844	Dipterocarpus caudiferus	5.12017	117.66799
8	845	Vatica dulitensis	5.11934	117.67238
8	846	Shorea pauciflora	5.12005	117.67290
8	847	Parashorea tomentella	5.12086	117.67254
8	848	Dryobalanops lanceolata	5.12155	117.67370
8	849	Hopea nervosa	5.12066	117.67322
8	850	Vatica dulitensis	5.11898	117.67347

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