Fate, Luck or Destiny?
Regeneration of Tropical Rainforest in Singapore

by

Siew Chin Chua

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Committee in charge:

Professor Matthew D. Potts, Chair
Professor David D. Ackerly
Professor Todd E. Dawson

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ABSTRACT

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To date, our understanding of the long-term recovery of secondary forests in the tropics is based on surprisingly little empirical data. In my dissertation, I examined some of the stochastic (dispersal events) as well as deterministic factors (environmental filtering) that are important to community dynamics and thus the on-going regeneration of older tropical secondary forests in Singapore. These secondary forests underwent intensive agricultural activities from the late 1800 to early 1900, and have today, recovered differently after at least 56 years of regeneration. Chapter 1 provided a synopsis of how my research is situated within the larger theoretical framework of tropical forest succession, along with rationale for the focus on older secondary forests in Southeast Asia. In Chapter 2, I compared the floristic composition and structure of a two hectare secondary forest to an adjacent two hectare primary forest in Bukit Timah Nature Reserve, and also examined the extent to which dispersal limitations was limiting forest recovery. In Chapter 3, using nine secondary and three primary forest plots in the Central Catchment Nature Reserve, I determined the effect that changing environmental variables and distance to the nearest mature forest had on seedlings' abundance, diversity as well as the distribution of four broad functional groups. In Chapter 4, using the same twelve research plots, I investigated the linkages between the regenerating environment and functional traits of seedlings and adult trees, as well as analyzed their relative influence on forest recovery. Results from Chapter 2 and 3 demonstrate that forest recovery in Singapore, in terms of species composition, species richness and stand structure, is very slow compared to other old secondary forests elsewhere in the tropics. I found that local Ultisol soils have inherently low nutrients, even when compared to other Dipterocarp forests, and decades of intensive agricultural activities has further resulted in soils whose high aluminum saturation, soil C:N ratio and low available phosphorus inhibit forest regeneration. Overall, forest succession in Singapore is characterized by plant species whose nutrient conserving traits allowed them to specialize on degraded soil, along with the changing light environment, as the forest regrow. The longevity of these plants on degraded land, their ability to slow nutrient returns as well as the strong dispersal limitation in these fragmented forest reserves are important factors that explain the overall slow recovery.

To My Parents

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CHAPTER 1. General Introduction

Forest degradation and deforestation occur disproportionally in the tropics (FAO 2010), and as secondary forests form an increasingly large part of the tropical landscape, their role in sustaining biodiversity (Chazdon et al., 2009; Dent and Joseph Wright, 2009) and ecosystem services is growing (Dent and Joseph Wright, 2009; Guariguata and Ostertag, 2001). The value of secondary forests as refugia for biodiversity as well as for maintaining ecosystem services hinges on aspects of their recovery, including forest structure, floristic composition and the complex ecological linkages among organisms and their environment (Gardner et al., 2009). Understanding the complex processes that affect forest recovery is thus essential, if we are to manage secondary forests to maximize their conservation potential and also to prevent irreversible ecological changes (Groffman et al., 2006).

Previous research has found that secondary forests regain structure and species richness relatively rapidly after disturbance (Letcher and Chazdon, 2009; Norden et al., 2009). However, the recovery of species composition to old growth forests is less certain. Some forests take hundreds of years to converge in composition to old growth forests (Chazdon, 2008a; Corlett, 1995; Finegan, 1996) while other fail to fully recover and form novel ecosystems (Chazdon, 2008b; Lugo and Helmer, 2004). In addition, trajectories of species replacement through succession are particularly difficult to predict. The on-going shifts in species composition over time may thus lead to changes in plants' ecological functions, e.g. differential ability at carbon sequestration and nitrogen fixation, and have implications for the functional diversity and stability of these ecosystems (Tilman et al., 1997; Walker, 1992).

Despite the existence of general frameworks to guide our understanding of secondary forest succession, defined here as the complete clearance of forest for human activities (Chazdon, 2008a; Guariguata and Ostertag, 2001; Peterson and Carson, 2008), challenges remain in using these frameworks to study tropical succession. Current successional frameworks were developed primarily through research done in temperate regions (Peterson and Carson, 2008). As summarized by Chazdon (2008) the conceptual frameworks are based on either the: 1) relative importance of deterministic vs. stochastic processes, with the dominance of the former leading to stable and converging community composition under similar climatic conditions; 2) timing of species colonization (model of initial floristic composition or relay floristics (Egler, 1954)); and 3) relative importance of species' life history traits (Noble and Slatyer, 1980) and species interactions such as tolerance, inhibition and facilitation (Connell and Slatyer, 1977). However, tropical systems are inherently more diverse than temperate systems, in terms of species, structures and ecological processes. In addition, they are further complicated by anthropogenic activities of different types, scales and intensities (Chazdon, 2003; Guariguata and Ostertag, 2001). Thus often times, the processes described in these frameworks are important for certain successional pathways (e.g. as stated in Pickett et al. 1987, the facilitation model implies a linear pathway while the inhibitory model may result in a variety of pathways depending on disturbance frequency); or the processes could only be applicable to a sere community but may lose importance over time (Chazdon, 2003; Pickett et al., 1987), due to complex interacting factors in these diverse systems.

In recent decades, some researchers argued that a focus on *mechanisms* of succession (Huston and Smith, 1987; Pickett et al., 1987), as opposed to imposing conceptual frameworks over an array of systems undergoing different successional pathways (Pickett et al., 1987), would provide insights into the specifics *processes* that drive species replacement as forests regenerate. Such an approach differs from the ones above, as it fundamentally encompasses all possible processes, including those implicit in the other frameworks, but is potentially more precise by explicitly stating the mechanisms to be examined. In essence, this approach acknowledges the complexity and variability of different secondary forests, and seeks to establish an understanding of basic processes, before attempting to generate a broad theory of tropical succession (Pickett et al., 1987).

In this dissertation, I utilize the concepts mentioned above to examine some of the processes important to community dynamics in older tropical secondary forests. There has been less research on older secondary forests in the tropics as compared to that of the earlier stages of succession (Chazdon, 2003) with most being part of chronosequence studies. These space-substituting-time studies quantify vegetation changes in different-aged forests, and have been found to be unsuitable for ascertaining processes influencing succession, due to the variability among sites (Chazdon et al., 2007; Johnson and Miyanishi, 2008). In contrast, a process-based approach is essential, for forest succession is an evolving process between plants and their environment, with biogeochemical processes intricately linking the two; such feedback processes between the existing trees and the environment probably magnify with forest's age and trees' biomass (Garnier et al., 2004; Grime, 1998), and in turn affect subsequent community dynamics. Moreover, forest growth also affects seeding opportunities, as over time more in-situ trees may be able to self-propagate within the site, while improving overall landscape continuity and attracting animal dispersers. Determining the relative importance of dispersal limitation and feedback processes in older secondary forests would help to further our understanding of the long term successional trajectories of tropical forests.

Aside from contributing to the research on older secondary forests, an important aspect of my thesis is also to investigate the effects of low-fertility soils on forest regeneration. Most tropical soils are infertile, due to intense weathering and leeching of nutrients by torrential tropical rain, though rainforest species have evolved and adapted to these conditions. However, past research has shown that soil nutrients recovery in the soil type Ultisols and Oxisols, which form more than 30 % of the world's tropical soils (Richter and Babbar, 1991), along with forest regrowth, are particularly slow (Lu et al., 2002; Moran et al., 2000). We know little about the effects of low-fertility soils on plant functional strategies over forest succession. Current proposed theories of forest succession are similar to the theories of successional processes of natural forest gap dynamics. In gaps, conditions of high light and at times high soil nutrients from decomposing dead plant matter facilitate establishment of short-lived, fast growing pioneer species that acquire resources rapidly; and these species are eventually replaced by late successional species that are slower growing and resource conserving (Bazzaz and Pickett, 1980; Garnier et al., 2004; Huston and Smith, 1987; Odum, 1969). However, long-lived pioneers, which are early colonizers with greater longevity, have been increasingly recognized as a

prominent plant functional group during secondary succession (Chazdon, 2008a; Finegan, 1996; Milton et al., 1994; Peña-Claros, 2001). Since slower plant growth and greater longevity are part of a suite of plant resource conserving traits (Poorter, 2007; Westoby et al., 2002; Wright et al., 2004), some long-lived pioneers might be specialized to grow on degraded soils and inhibit the recruitment of climax species. However in general, little empirical data exists on how differences in soil and other environmental factors facilitate the establishment of short-lived vs. long-lived pioneers, or influence the replacement by other functional groups over time.

Another focus of my thesis is to determine the extent that selected plant functional traits might help in deepening our mechanistic understanding of the forest recovery process, via interactions between the adult trees, the regenerating environment, and the seedlings. Functional traits are biological characteristics that directly or indirectly inform about a species' response to and its functional strategy in the environment (Gitay et al., 1999; Lavorel et al., 1997). Thus examining selected seedling response traits might indirectly elucidate environmental factors that are important to seedling recruitment. When scaled up by plants' biomass, the same (effect) traits of adult tree could also be used to measure the influence of whole plant community on the environment (Lavorel and Garnier, 2002; Quétier et al., 2007). Unsurprisingly, plant functional traits therefore offer great potential at elucidating the unifying processes that drive or inhibit forest regeneration particularly in species rich tropical systems. However, this approach is still at the infancy stage for studying the succession of tropical rainforests (e.g. Lebrija-Trejos et al., 2008; Lohbeck et al., 2013).

Finally, my thesis research was conducted in Singapore's secondary forests, which have been recovering from agricultural activities for 56 – 100 years. Singapore is located in the biodiversity hotspot of Southeast Asia. This region has one of the highest rates of deforestation and land use change, but there has been comparatively little research on the long term recovery of forests, and the limited work conducted showed poor recovery of floristic composition and even species richness in the older secondary forests (Brearley et al., 2004; Turner et al., 1997). Singapore's forests are unique in their early clearance with the arrival of the British in 1819. Gambier plantations were the initial driver of deforestation followed by decades of other exhaustive agricultural activities. These activities severely degraded the Ultisol soil (Burslem et al., 1994; Sim et al., 1992). After 1935, agricultural area sharply declined as the nation urbanized and the remaining forests were left to regenerate. Subsequent protection came from the demarcation of these forests into nature reserves in 1951. Thus, unlike many parts of Southeast Asia, where secondary forests are still relatively young or face continuous disturbance, Singapore secondary forests provide an opportunity to investigate the long term recovery of tropical forests.

To summarize my dissertation, in the second chapter, I compared the floristic composition and structure of a two hectare secondary forest recovering more than 56 years after abandonment from agricultural use to an adjacent two hectare primary forest in Bukit Timah Nature Reserve (BTNR). I also tested the extent to which dispersal limitations is limiting forest recovery. In the third and fourth chapters, the research plots were situated in the larger (2000-ha) contiguous Central Catchment Nature Reserve (CCNR), which contains a mosaic of differently regenerating

secondary forests. I selected forests that were open areas in the 1950s, based on old aerial photographs, but have recovered differently today. The nine secondary forest plots formed a gradient of poorly regenerating fernlands to short-statured and taller secondary forests. In the third chapter, together with three other primary forest plots, also of varying disturbance levels, I determined the effect that changing environmental variables and distance to the nearest mature forest have on seedlings' abundance, diversity as well as the distribution of four broad functional groups. The functional groups included primary forest species, secondary forest species, long-lived pioneers and short-lived pioneers. In the fourth chapter, using the same twelve research plots, I investigated the linkages between the regenerating environment and functional traits of seedlings and adult trees, and analyzed their relative influence on forest recovery. In Chapter 5, I summarized the key findings in the dissertation, along with their implications for management and future research.

CHAPTER 2. Slow recovery of a secondary tropical forest in Southeast Asia

Introduction

Secondary forests now constitute a substantial portion of forest area in the tropics due to widespread and ongoing anthropogenic disturbances and conversions (Asner et al., 2009; Chazdon, 2003). These perturbations take many forms including swidden agriculture, semi-permanent agriculture, grazing and logging. Secondary forests often continue to provide many of the ecosystem functions of primary forests and serve as refugia for biodiversity (Brown and Lugo, 1990; Guariguata and Ostertag, 2001), but the recovery trajectories of secondary forests are varied due to many interacting factors (Chazdon, 2003; Guariguata and Ostertag, 2001).

While some forests have been found to regain their structure relatively quickly and even converge floristically with old growth forests (Letcher and Chazdon, 2009; Norden et al., 2009), others have been found to recover more slowly (Brearley et al., 2004; Corlett, 1991a; Saldarriaga et al., 1988; Turner et al., 1997) or even form novel ecosystems (Lugo and Helme, 2004). In general, forest structure and species richness recover faster than floristic composition (Aide et al., 1996; Brearley et al., 2004; Ferreira and Prance, 1999; Saldarriaga et al., 1988; Turner et al., 1997). In addition, the rate of recovery improves with abundance of generalists in the regional flora, good seed dispersal, presence of remnant trees and proximity to primary forests (Chazdon, 2003; Norden et al., 2009). Conversely, disturbances that severely damage the soil and aboveground vegetation hinders recovery (Chazdon, 2003). Finally, the longevity of some pioneer species as well as their ability to continuously recruit after the formation of a canopy, has also been suggested to slow the recovery of primary forest species (Corlett, 1995; Finegan, 1996; Peña-Claros, 2003). Despite these findings, there remains a need for more research in two key areas. The first is in older secondary forests, which are important to study because these forests often have higher biodiversity and carbon stocks than young secondary forests (Chazdon et al. 2009; Fearnside and Guimarães 1996). Second, there is a need for more research in Southeast Asian disturbed forests. The region is a biodiversity hotspot and is highly threatened by deforestation (Sodhi et al., 2010, 2004). However, research on forest recovery here is comparatively lacking as compared to that in the Neotropics, and past research has largely focused on the early stages (1 - 15 years) of forest recovery (Jepsen, 2006; Nykvist, 1996; Ohtsuka, 2001, 1999; Slik et al., 2002; Yassir et al., 2010, but see Brearley et al., 2004; Turner et al., 1997).

To address these knowledge gaps, we compared and contrasted the physical structure and tree species composition of a secondary forest plot (56 years following agricultural abandonment) with an adjacent primary forest plot. The study site was located in Singapore which contains about 2000-ha of lowland tropical rainforest, most of which is recovering from deforestation that occurred since its founding in 1819 (Corlett, 1992; Corlett, 1991b). Decades later, these secondary forests are ideal for research on understanding recovery processes, particularly that of older secondary forest areas. This is unlike much of Southeast Asia, where deforestation is ongoing. By examining forest recovery in Singapore, we may be able to gain insights into the present status and future recovery trajectory of secondary forests throughout the region.

Our main research questions were:

1. How similar are the secondary forest and the adjacent primary forest, in terms of physical structure, tree species diversity and composition?
2. Do these similarities differ across tree size classes? Comparing the primary and secondary forests, we expect that trees of smaller size classes (e.g. saplings) will be more similar in their structure, diversity and composition.

Methods

Site description

The Bukit Timah Nature Reserve (BTNR; 1°21'N, 103°46'E) is Singapore's largest remaining contiguous primary forest (Corlett, 1988). It has a total area of 163-ha, and consists of 70-ha of primary coastal hill dipterocarp forest surrounded by secondary forests. Mean annual rainfall is 2353 mm. The driest month has an average precipitation of 158.5 mm, and the wettest month 297.9 mm. The mean temperature is 27.0°C. (National Environment Agency, Singapore).

Plot layout

In the eastern part of BTNR, we set up two 2-ha plots – one primary and one secondary. Methods for the establishment of both plots followed the standard methods used by the Center for Tropical Forest Science plot network, as described by Condit (1998). All trees ≥ 1 cm diameter-at-breast-height (DBH) were tagged, measured, mapped and identified to species. Vouchers were collected and verified at the Singapore Herbarium. The primary forest plot, which has an elevation range of 75 to 120 m above sea level, was established in 1993 and has been surveyed five times since then. A full description of the primary forest plot is given by LaFrankie et al. (2005) and Lum et al. (2004). In 2004, we established the secondary forest plot southeast of the primary forest plot (Figure 1). The secondary forest plot lies on the upper slope of a shallow valley, from 50 to 85 m a.s.l. From late 1880s into the mid-1900s, a small Chinese community occupied the area and probably cultivated common subsistence crops such as cassava (Lau & Noor, pers. comm.). A series of aerial photographs taken during the 1950s shows that the study area, which appears to be non-forested and to consist largely of herbaceous vegetation, was not further impacted by humans before being incorporated into the reserve in 1962. Thus, the secondary forest plot is at least 56 years old. Signs of terracing can still be seen in the plot and public walking trails (about 5% of the plot area) currently cut through both plots.

Data analysis

We compared the 2003 primary forest plot census data with the 2004 secondary forest plot data. In analyzing the stand structure and species diversity of the secondary forest plot we excluded ten 20 × 20 m quadrats (located in one corner of the plot) that were found to contain residual primary forest elements. This was ascertained by the presence of large individuals (> 70 cm DBH) of trees species characteristic of primary forest. Thus, there were fifty and forty 20 × 20 m quadrats from the primary and secondary forest plots respectively. However, for the comparison of floristic composition using Nonmetric multidimensional scaling (NMDS)

ordination analyses, we used all 4-ha of surveyed area to create eight 50 × 50 m quadrats within each of the two plots. This was necessary as 20 × 20 m quadrats contained too few trees for our Nonmetric multidimensional scaling (NMDS) ordination analyses. In the Mantel tests, we excised two of the quadrats in the secondary forest plot that were covered more than 50% by the remnant primary forests.

Since each forest age class (i.e. primary and secondary) is represented by a single contiguous area, quadrats nested within each plot are not true replicates. Analyses that lack true treatment replicates are susceptible to spurious relations between two variables that are in fact driven by a spatial gradient, or a third variable that maps to the spatial gradient (Fortin and Gurevitch, 2001; Legendre and Legendre, 1998; Ramage et al., 2013). Despite this reality, the vast majority of studies that address similar questions are pseudoreplicated and devoid of any efforts to account for underlying variation (Ramage et al., 2013). In contrast, we used partial Mantel tests to distinguish the effects of forest age class (primary vs. secondary) from pre-existing spatial and elevation gradients; as such, this paper also serves to demonstrate how meaningful inferences about treatment effects can be drawn from a dataset that lacks true treatment replication.

Stand structure, species diversity and floristic composition

To aid in comparison of our results to other studies, we calculated the stand structure and floristic diversity of the two plots with two different, and commonly employed, DBH cut-offs (≥ 1 and ≥ 10 cm). We compared the most abundant tree species (in terms of basal area) and the most abundant saplings (1-3 cm DBH; in terms of stem counts), across the two plots. In addition, we examined the size class distributions of the most abundant canopy species. Using 20 × 20 m quadrats, we calculated primary and secondary forest species richness (S), Shannon Diversity Index (D), and a stem density-weighted measure of species richness (S_W). S_W was calculated by dividing the species richness of a size class by the average stem density of that size class. We calculated the Jaccard's coefficient of similarity at plot level to compare variation in floristic composition between the primary and secondary forest plots, and excluded the ten 20 × 20 m quadrats with primary forest remnants. Among the 50 × 50 m quadrats, we also created three ordination plots using NMDS (Bray-Curtis dissimilarity index): 1) all trees; 2) only saplings of 1-3 cm DBH size; and 3) only larger trees of ≥10 cm DBH.

Effects of spatial distance, elevation and forest age class

We performed Mantel tests on three predictor variables (spatial distance, elevation and forest age class) to assess the importance of each predictor on dependent matrices of species richness, Shannon diversity and floristic composition in the two plots. We conducted these tests for 1) all trees; 2) only saplings of 1-3 cm DBH size; 3) mid-sized trees of 3-10 cm DBH size, and 4) only larger trees of ≥10 cm DBH. We created individual Euclidean distance matrices for all predictor and response variables with the exception of floristic composition, in which the Bray-Curtis dissimilarity index was used. For the age-class matrices we followed Fortin and Gurevitch (2001) and coded a distance of "1" for quadrat pairs with different forest age classes, and a distance of "0" for quadrat pairs with the same forest age class. We also conducted partial Mantel tests to

test the pure partial effect of each predictor variable on the dependent variable (Manly, 1986). If differences in the dependent variables between forest age classes simply reflect a relatively smooth spatial gradient or are highly affected by elevation, measures of diversity and composition should not be significantly associated with age class after accounting for spatial or elevation distances. This method for addressing the lack of true treatment replication, is relatively simple but rarely used in similar studies (Ramage et al., 2013). Statistical analyses were done using R statistical software v2.13.2 (R Development Core Team, 2011).

Results

There were a total of 12,885 trees from 337 species, 171 genera and 56 families in the primary forest plot. After excising 10 quadrats from the secondary forest plot that contained residual primary forest elements (Figure 1), there were 3,299 individuals from 133 species, 86 genera and 42 families in the remaining 40 quadrats. Patches of the fern *Dicranopteris* spp*.* and pitcher plants *Nepenthes gracilis,* were also present in the secondary forest plot.

Stand structure and species diversity

Overall, mean stem density in the secondary forest plot (1923 ± 134 ha^{-1}) was only 30% of the primary plot, but the secondary forest plot had 130% of the trees larger than 10 cm DBH (535 ± 29 ha^{-1}) as compared to the primary forest plot (Table 1, Table 2); this was due to the high density of mid-sized trees (>10-30 cm DBH) in the secondary forest plot (the primary forest plot had more trees >30 cm DBH). Consistent with the results for stem density, basal area in the secondary forest plot (20.59 ± 1.54 m^2ha^{-1}) was only 58% of the primary forest plot when all trees were used (Table 1, Table 2). Across all size classes, the secondary forest plot was less diverse than the primary forest plot; this was true in terms of species richness (26% of primary forest), species richness weighted by average stem density (41% of primary forest) and Shannon diversity (59% of primary forest) (Table 1, Table 2). However, when small trees (< 10 cm DBH) were excluded, species richness, weighted species richness and Shannon diversity of the secondary plot reached 61%, 61% and 68% of the primary plot respectively (Table 1, Table 2). In the secondary forest plot, stem density and all measures of diversity were higher in the quadrats closer to the primary plot, dropping rapidly with increasing distance (Figure 2).

Floristic composition

The Jaccard's coefficients between the two plots showed that they shared few species (7.9% for all trees and 7.7% for larger trees only, Table 2). This was due to the high dominance of a few secondary forest species, both in terms of basal area and stem density. For example, the secondary forest plot was dominated by five common secondary forest species, *Dillenia suffruticosa* (Dilleniaceae)*, Adinandra dumosa* (Theaceae)*, Campnosperma auriculata* (Anacardiaceae), *Ixonanthes reticulata* (Ixonanthaceae) and *Rhodamnia cinerea* (Myrtaceae) which together made up more than 73% of the basal area in the plot. This is in contrast to the primary forest plot where the top five species, *Shorea curtisii* (Dipterocarpaceae)*, Dipterocarpus caudatus* (Dipterocarpaceae)*, Streblus elongatus* (Moraceae), *Ixonanthes reticulata* and *Koompassia malaccensis* (Fabaceae)*,* made up about 42% of the basal area in the plot (Appendix A, Table 1). The most abundant canopy species in the primary forest plot

showed a typical reverse-J size class distribution whereas the most abundant canopy species in the secondary forest plot showed poor recruitment of small trees (Figure 3). In fact, aside from *Dillenia suffruticosa*, a secondary forest shrub species which made up the top 20% of the sapling population in the secondary forest plot, the next most abundant sapling species included a mix of species found in mature secondary to primary forests. These include *Streblus elongatus, Calophyllum* spp*., Elaeocarpus polystachyus, Baccaurea sumatrana* and *Shorea curtisii* which altogether made up over 40% of the saplings in the secondary forest plot (see Appendix A for details on most abundant species in the two plots); this was especially notable as the high number of sapling-sized *D. suffruticosa* was probably inflated due to coppices that could not be easily differentiated from parent trees. However, aside from *Dillenia suffruticosa,* most of the saplings were located near the primary forest (Figure 2).

Nonmetric multidimensional scaling (NMDS) showed that the composition of adult trees (> 10 cm DBH) in quadrats in the secondary forest plot was distinct from the primary forest plot (Figure 4a) and that the saplings composition was also distinct from the mature trees composition within both plots (Figure 4b). Shepard diagrams for both ordinations exhibited high R^2 for the goodness-of-fit (Appendix B, Figure 1). Within-plot compositional variation was higher in the secondary forest plot than in the primary forest plot, and this was due to the saplings (Figure 4b). Sapling quadrats in secondary forest were highly dispersed while those in primary forest plot were tightly clustered. However, an NMDS biplot of saplings showed that this was likely due to the low quadrat-level stem density but relatively high plot-level diversity in the secondary forest plot, which caused the dissimilarity values of the quadrats to be highly influenced by the presence and absence of few species (Appendix B, Figure 2). In contrast, the higher stem density in the primary quadrats (Table 1) allowed quadrats to share more species despite high plot-level diversity. Finally, quadrats in the secondary forest plot, especially sapling quadrats, were floristically more similar to the primary forest with increasing proximity to the latter (Figure 4 and Appendix B, Figure 2).

Effects of forest age classes, spatial distance and elevation

Our tests of whether differences in diversity and floristic composition between forest age classes were due to their differing histories, as opposed to underlying spatial turnover or elevation effects, revealed that all three predictors were strongly correlated with diversity and floristic composition (Table 3).

The partial Mantel tests showed that among the predictors, forest age class was most strongly correlated with species richness in the primary and secondary forest plots after accounting for the other factors (Table 3). This correlation decreased with increasing tree sizes ($r = 0.677$, 0.619, 0.564 and 0.086, after accounting for spatial distance, for all trees, saplings, mid-sized trees and larger trees respectively; $P < 0.001$, with the exception of the larger trees), and was consistent with the much larger difference in species richness between saplings than between larger trees in the two plots. Conversely, the partial Mantel test showed that both spatial distance and elevation, after accounting for other factors, explained little of the variation found in species richness, although some of the low partial Mantel correlations were highly significant (Table 3). Similarly, we found that forest age class explained the greatest amount of variation in

Shannon diversity as compared to spatial distance and elevation, when elevation and spatial distance were accounted for respectively. The exception was in the saplings, where spatial distance was slightly more strongly correlated with Shannon diversity($r = 0.264$, $P = 0.001$) than forest size class (Table 3). Elevation consistently had low and mostly non-significant effects on species richness and Shannon diversity after accounting for spatial distance. We also conducted supplementary linear regression analyses to further examine relationships between diversity, elevation, and spatial distance (Appendix C). These analyses demonstrated that diversity in the secondary forest plot increased with elevation (and proximity to the primary forest plot), but that no spatial or elevation effects were present in the primary forest plot.

Similar to our results for species richness and Shannon diversity, partial Mantel tests showed that forest age class explained most of the variation in floristic composition ($r = 0.78$, 0.574, 0.676 and 0.510 for all trees, saplings, mid-sized trees and larger trees respectively, after accounting for spatial distance. $P < 0.001$ for all; Table 3). However, the effects of spatial distance were also very high after accounting for forest age class and decreased with increasing tree size ($r = 0.546$, 0.433, 0.350 and 0.305 for all trees, saplings, mid-sized trees and larger trees respectively, with $P < 0.01$ for all; Table 3) Spatial distance and elevation both appeared to be similarly correlated with floristic composition after controlling for forest age class, but again the effect of elevation on floristic composition was mostly weak and non-significant after accounting for spatial distance (Table 3).

Discussion

We found that even after 56 years since the end of intensive agriculture, the secondary forest plot in Bukit Timah Nature Reserve still differed substantially in structure and floristic composition from the adjacent primary forest plot, which is merely on the opposite side of a walking trail. While the high density of large trees in the secondary forest plot (Table 1) has created a shaded understory that has facilitated the replacement of pioneer species with shade-tolerant ones (Appendix A, Table 2), the overall recruitment of primary forest species is slow, and the clear present-day divergence in sapling composition between the primary and secondary forest plots (Figure 4b) suggests that floristic recovery might be a very long process. Below, we compare our findings with previous studies and discuss possible mechanisms that may be slowing forest recovery.

Brearley et al. (2004) summarized the majority of studies that have compared old secondary forests (≥40 years) to primary forests in lowland tropical rainforests. Our findings concerning recovery of floristic composition and structure for trees ≥ 10 cm DBH were consistent with previous studies using the same tree size cutoff; floristic composition tended to remain quite dissimilar to primary forest while forest structure converged rather quickly to that of primary (Table 2). However, with a minimum DBH of 1 cm (i.e. including trees between 1 and 10 cm DBH), our results indicate poor recovery of the secondary forest as compared to other studies (the lowest percentage recovery of stem density, basal area, species richness and Shannon diversity; see Table 2 in this paper and Table 6 in Brearley et al., 2004 for detailed comparisons).

We hypothesize that a few key traits of the dominant species in the secondary forest plot help to explain the poor forest recovery we observed. The first of these traits is the longevity of pioneer species. Individuals of these species can effectively lock up nutrients in their living biomass for a longer time than fast growing pioneer species, reducing nutrient acquisition opportunities for later successional species. Previous studies have shown that the continued persistence of "long-lived pioneers" (Finegan, 1996) can slow down the replacement of light-demanding species by shade-tolerant primary forest species (Finegan, 1996; Corlett, 1995). In our secondary plot many of the most abundant species, including *Adinandra dumosa, Dillenia suffruticosa, Rhodamnia cinerea* and *Fagraea fragrans,* are long-lived and slow growing (Sim et al., 1992; Corlett, 1991a; Corlett, 1995). We posit that these long-living species occupy the space and take up the resources (e.g. nutrients and water) needed for successful recruitment and growth of more shade-tolerant species. In addition, all of the above species coppice readily (pers. obs), allowing them to spread rapidly and compete strongly for resources. *D. suffruticosa* in particular forms dense thickets by producing new plants from adventitious roots when mature (Corlett, 1991a).

The other important traits are high leaf mass per area (which corresponds to higher leaf tissue density and thicker leaves), and low foliar nitrogen and phosphorous of the dominant early successional species. For example, the top species by basal area, *Campnosperma auriculata, A. dumosa, Ixonanthes reticulata*, and *R. cinerea*, have thick leaves (pers. obs; Turner and Tan, 1991; Poorter et al., 2009), and the foliar nitrogen and phosphorous content of *A. dumosa, D. suffruticosa* and *R. cinerea* are very low (Grubb et al. 1994). Both of these leaf traits have been shown to slow decomposition rates (Cornwell et al., 2008), and slow decomposition leads to a buildup of leaf litter that may inhibit seedling establishment and growth (Metcalfe et al., 1998; Metcalfe and Grubb, 1997; Facelli and Pickett, 1991). Recently, Goldsmith et al. (2011) found that higher leaf litter depth in the secondary forest was a likely explanation for the lower seedling density in the secondary forest plot than the primary forest plot at BTNR. Beyond these two traits, both *C. auriculata* and *D. suffruticosa* also have large leaves, which add to the leaf litter depth and continuity. Finally, although *C. auriculata* is commonly found in primary forest gaps, we observed that it had formed an unusually expansive stand, with thick leaf litter, in the area of the secondary forest plot nearest to the primary forest.

Taken together, the traits of the dominant species in the secondary forest plot suggest that the soil in the secondary forest plot may be more infertile than the soil in the primary forest plot. Westoby et al. (2002) showed that low foliar nitrogen and phosphorous content and high leaf mass per area are typical nutrient conserving characteristics of plants that thrive on poor soil; high leaf mass per area in turn is correlated with slow turnover of plant parts and slow growth. In our particular study system, *A. dumosa, D. suffructicos, R. cinerea,* and *F. fragrans* have been commonly found on soil impoverished after decades of exhaustive agricultural use (Corlett, 1991a; Sim et al., 1992). In addition, a final piece of evidence that supports the conjecture that our secondary forest soils were likely impoverished is the striking lack of fast-growing *Macaranga* trees, which are usually one of the first trees to establish in Southeast Asian secondary forests (Brearley et al., 2004; Cheke et al., 1979; Shono et al., 2006). *Macaranga* are also more diverse and abundant in nutrient-rich secondary forest (Wyatt-Smith, 1963), but

almost absent on forest with impoverished soil (Sim et al, 1992). We found only seven *Macaranga* individuals from three species in the secondary forest plot, as compared to 16 *Macaranga* individuals in the primary forest plot.

However, contrary to our expectation, in a recent analysis, the soil from the two plots we investigated showed no significant differences in the levels of many nutrients (Turner, unpubl. data). This might indicate that the soil nutrients in the secondary forest have recovered after 56 years, likely facilitated by the inputs of nutrients from the larger tract of primary forest directly upslope of the secondary forest. Nevertheless, since high nutrient turnover is key to high productivity on poor tropical soils (Ricklefs, 2008), the longer residence time of nutrients in the long-living trees and in the apparent slow decaying leaf litter could slow nutrient turnover rates and affect tree recruitment and growth. Thus, the current dominant species, which probably reflect previous poor soil conditions that have recovered only recently, may have long-lasting negative effects on forest recovery.

Finally, the life history traits of these dominant species also likely explain, at least in part, the compositional disparity between the saplings and mature trees in the secondary forest plot (Figure 4). As light-demanding species, long-lived pioneers recruit poorly under themselves, effectively necessitating a compositionally divergent understory. Although there is a similar disparity between the saplings and mature trees in the primary forest plot (Figure 4), this likely manifests in large because understory tree species with small maximum sizes are excluded from the larger tree size classes.

Beyond the specific traits of the mature dominant species, dispersal limitation may also be partly responsible for the limited compositional recovery of the secondary forest plot. This hypothesis is supported by the rapid drop in stem density and species richness for saplings (and mid-sized trees to a lesser extent) with increasing distance from the primary forest (Figure 2). Large seeded species without animal dispersal agents necessarily re-colonize slowly (Corlett, 1998, Dirzo et al., 2007; Kitamura et al., 2002; Wunderle Jr., 1997), and smaller seeded species that are dispersed by mammal or birds (e.g. *Streblus elongatus, Calophyllum* spp., *Baccaurea sumatrana*) may not establish deep into the secondary forest if their animal dispersers avoid secondary forest (Wunderle Jr., 1997).

Aside from dispersal limitation, a number of other factors could also be contributing to the observed spatial effects on sapling distributions with increasing distance from the primary forest plot. For example, thickets of the fern *D. linearis*, which is known to deter seed establishment (Cohen et al., 1995; Russell et al., 1998), was distributed in areas of the secondary forest plot farthest away from the primary forest. In addition, increasing soil moisture and decreasing radiation from top to bottom of the slope could potentially create abiotic gradients in the two plots. However, we found no relationship between diversity and elevation in the primary forest plot in our supplementary linear regression analyses (Appendix C), despite a greater elevation range in the primary plot than in the secondary plot, suggesting that patterns in the secondary forest plot are probably not directly linked to elevation. Finally, it should also be noted that a fire occurred in the early 1960s at the eastern end of the

secondary forest plot away from the primary forest (Mhd Noor, Lua, pers comm.). This could have resulted in nutrient losses (Mackensen et al., 1996) and created soil fertility differences along the slope gradient. Unfortunately, detailed data on fire intensity and extent are not available. Disentangling all of the above factors is impossible at this point, but we hope that future research will build upon our findings and clarify the key mechanisms.

Summary

Our findings appear to differ from those found elsewhere in the tropics, particularly with regard to the dominance and persistence of long-lived pioneers from the early stages of succession. In the Neotropics for example, it is generally recognized that after initial colonization by short-lived herbs and shrubs, succession transitions from short-lived to long-lived pioneers, which eventually give way to shade-tolerant primary forest species (Finegan, 1996; Peña-Claros, 2003). Species diversity and stem density increase with time, as reflected by the higher species diversity in the understory and subcanopy layer as compared to the canopy layer (Finegan, 1996; Peña-Claros, 2003). In comparison, in the highly degraded forests of Singapore, there exist a suite of long-lived pioneers with life history traits that allow them to slow recolonization by shade-tolerant species, potentially for many decades. Additional factors that may be contributing to the slow recovery of the secondary forest plot include strong dispersal limitation of primary forest species found only in isolated fragments, species-specific barriers to seedling establishment, and inhibition by existing vegetation. In conclusion, our findings add to the paucity of literature on the recovery of older secondary forest, which is highly variable in the tropics and warrants more investigation. Our work also highlights the importance of understanding site- and species-specific barriers to recovery; such knowledge will be essential for management interventions designed to speed forest recovery.

Acknowledgements

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Tables

Table 1. Stand structure and floristic diversity of the primary forest and secondary forest plots. All values are mean ± SE, calculated from 50 and 40 20 × 20 m quadrats in the primary forest and secondary forest plot respectively. Mean species richness, weighted species richness and Shannon diversity per quadrat (0.04 ha), are shown below.

	Primary forest		Secondary forest	
DBH (cm)	**≥ 1**	**≥ 10**	**≥ 1**	**≥ 10**
Stem density (ha^{-1})	6442 ± 181	413.5 ± 17	1923 ± 134	535 ± 29
Basal area (m^2 ha^{-1})	35.10 ± 2.32	30.80 ± 2.34	20.59 ± 1.54	18.28 ± 1.48
Species richness	75.98 ± 1.24	12.28 ± 7.62	19.98 ± 1.88	7.62 ± 0.34
Weighted species richness	0.27 ± 0.00	0.66 ± 0.03	0.11 ± 0.01	0.40 ± 0.02
Shannon diversity	3.70 ± 0.03	2.36 ± 0.04	2.19 ± 0.10	1.61 ± 0.05

n = 50 for primary forest plot, n = 40 for secondary forest plot.

Table 2. Comparison of structural and floristic variables in primary and secondary forest. All values are percentages (secondary forest relative to primary forest). Data from the current study are provided in the first row of each minimum tree size class. Values from other studies, some of which were extracted from Table 6 in Brearley et al. (2004), are provided for context and addressed in the Discussion.

Minimum tree size	Site	Past landuse	Age (years)	Stem density	BA	Species richness	H'	J	Reference
	Bukit Timah Nature Reserve, Singapore	Ag	56	30	58	26	59	7.9	This study
	Luquillo, Puerto Rico	P	51.5	89	79	78	83	-	Aide et al. 1996
1 cm	Luquillo, Puerto Rico	P	60	101	92	115	96	-	Aide et al. 1996
	Rio Negro, Colombia/Venezuela	Sb	60	73	70	88	99	-	Saldarriaga et al. 1988
	Rio Negro, Colombia/Venezuela	Sb	80	102	69	95	100	-	Saldarriaga et al. 1988
	Bukit Timah Nature Reserve, Singapore	Ag	56	130	59	61	68	7.7	This study
	Jau Nat'l Park, Amazonia	SB	40	94	95	60	-	14	Ferreira & Prance, 1999
	Barito Ulu, Central Kalimantan, Indonesia	Ag	55	90	82	65	82	24	Brearley et al. 1994
10 cm	Moruca, Guyana	L/Sb	60	96	70	100	109^{+}	-	van Andel 2001
	Rio Negro, Colombia/ Venezuela	Sb	60	77	-	94	-	-	Saldarriaga et al. 1988
	Rio Negro, Colombia/ Venezuela	Sb	80	118	-	118	-	-	Saldarriaga et al. 1988
	Central Catchment Nature Reserve, Singapore (S1)*	Ag	100	127	66	47	65	-	Turner et al. 1997
	Central Catchment Nature Reserve, Singapore (S1)*	Ag	100	117	68	62	75	-	Turner et al. 1997

P= pasture, Ag = agriculture, Sb = Slash and burn, L= logging,
J = Jaccard's coefficient of similarity, H' = Shannon Diversity Index,
*DBH cut off is 9.55 cm instead of 10 cm

Table 3. Simple and partial Mantel correlations between species richness (S), Shannon diversity (D), floristic dissimilarity (F), treatment (secondary and primary forest plots), spatial distance and elevation. Ninety 20 × 20 m quadrats were used for species richness and Shannon diversity while fourteen 50 × 50 m quadrats were used for floristic composition.

		S	S|treatment	S|spatialdist.	S|elevation	D	D|treatment	D|spatialdist.	D|elevation
All trees	Treatment	0.863***		0.677***	0.758***	0.676***		0.352***	0.490***
	Spatial dist.	0.729***	0.090**		0.465***	0.634***	0.196***		0.387***
	Elevation	0.637***	0.102**	0.068**		0.546***	0.142***	0.031	
Saplings	Treatment	0.822***		0.619***	0.697***	0.575***		0.193***	0.340***
	Spatial dist.	0.692***	0.066*		0.409***	0.594***	0.264***		0.328***
	Elevation	0.615***	0.107***	0.090**		0.526***	0.215***	0.065	
Mid-sized trees	Treatment	0.776***		0.564***	0.659***	0.727***		0.450***	0.577***
	Spatial dist.	0.645***	0.037		0.413***	0.647***	0.139***		0.418***
	Elevation	0.544***	0.011	0.008		0.544***	0.077*	0.001	
Larger trees	Treatment	0.305***		0.086**	0.249***	0.512***		0.293***	0.436***
	Spatial dist.	0.316***	0.123**		0.300***	0.442***	0.049		0.353***
	Elevation	0.185***	-0.039	-0.154		0.308***	-0.077	-0.126	

		F	F|treatment	F|spatialdist.	F|elevation
All trees	Treatment	0.941***		0.780***	0.855***
	Spatial dist.	0.891***	0.546***		0.636***
	Elevation	0.815***	0.461**	0.160	
Saplings	Treatment	0.879***		0.574***	0.719***
	Spatial dist.	0.851***	0.433**		0.606***
	Elevation	0.751***	0.274*	0.027	
Mid-sized trees	Treatment	0.905 ***		0.676***	0.768***
	Spatial dist.	0.842***	0.350**		0.516***
	Elevation	0.786***	0.361**	0.190*	
Larger trees	Treatment	0.835***		0.510***	0.598***
	Spatial dist.	0.793***	0.305**		0.368**

Notes: Column "S", "D" and "F" show simple Mantel correlations of species richness, Shannon diversity and floristic dissimilarity with predictors treatment, spatial distance and elevation. Subsequent three columns show partial Mantel correlations of the same dependent matrices with the same predictors while controlling for treatment, spatial distance and elevation respectively. For example, the top right most value of 0.49 is the correlation of treatment with Shannon diversity after controlling for elevation.

* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$

Figures

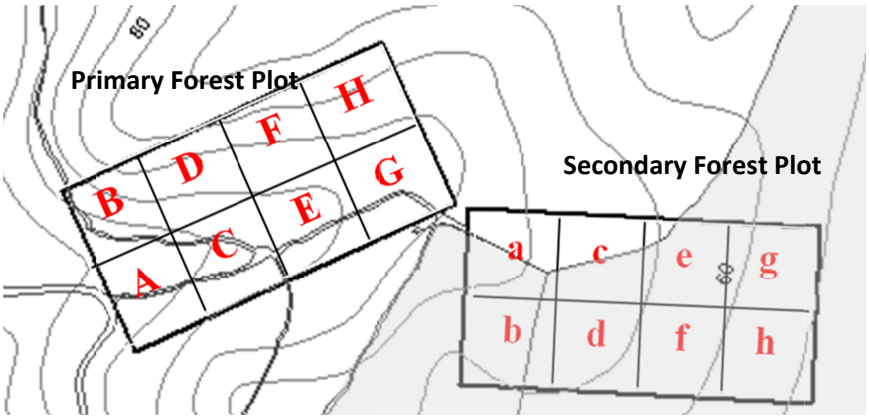


Figure 1. Map showing plot layout and the location of the 50 × 50 m quadrats. Shaded area indicates secondary forest. Unshaded areas indicate old growth forest.

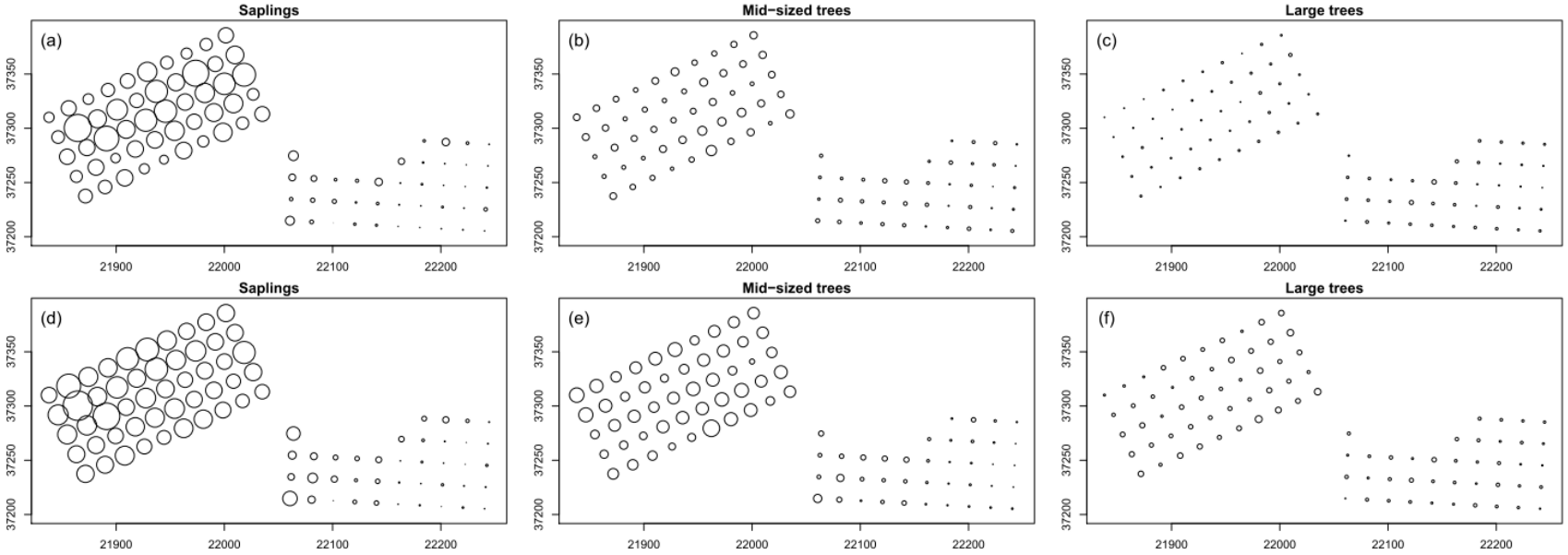


Figure 2. Stem density (panels a, b, c) and species richness (panels d, e, f) in fifty 20 x 20 m primary forest quadrats (left) and forty 20 x 20 m secondary forest quadrats (right). The x- and y-axes are the metric-based cartesian coordinates of the plot. Circle size is proportional to stem density and species richness within each quadrat.

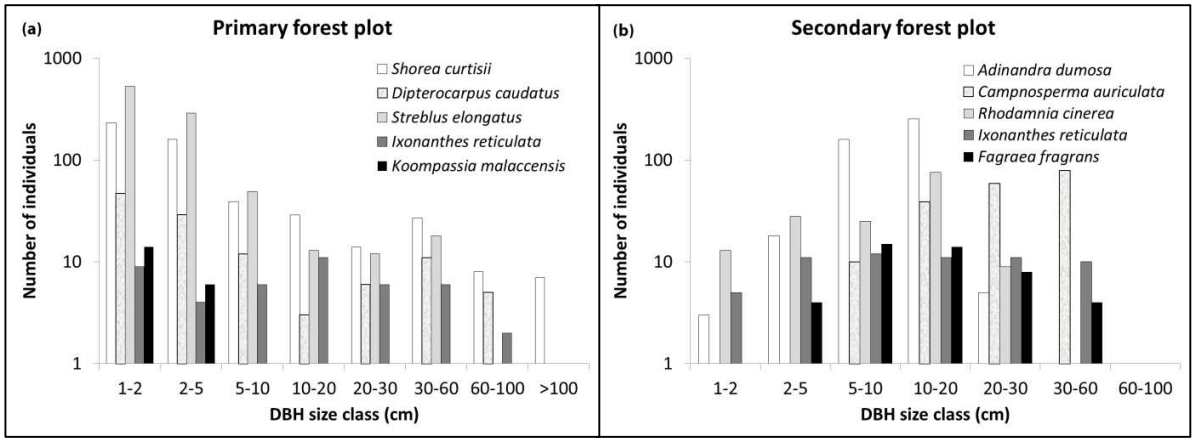


Figure 3. DBH size class distribution of the most abundant canopy tree species (by basal area) in (a) the primary plot and (b) secondary forest plot.

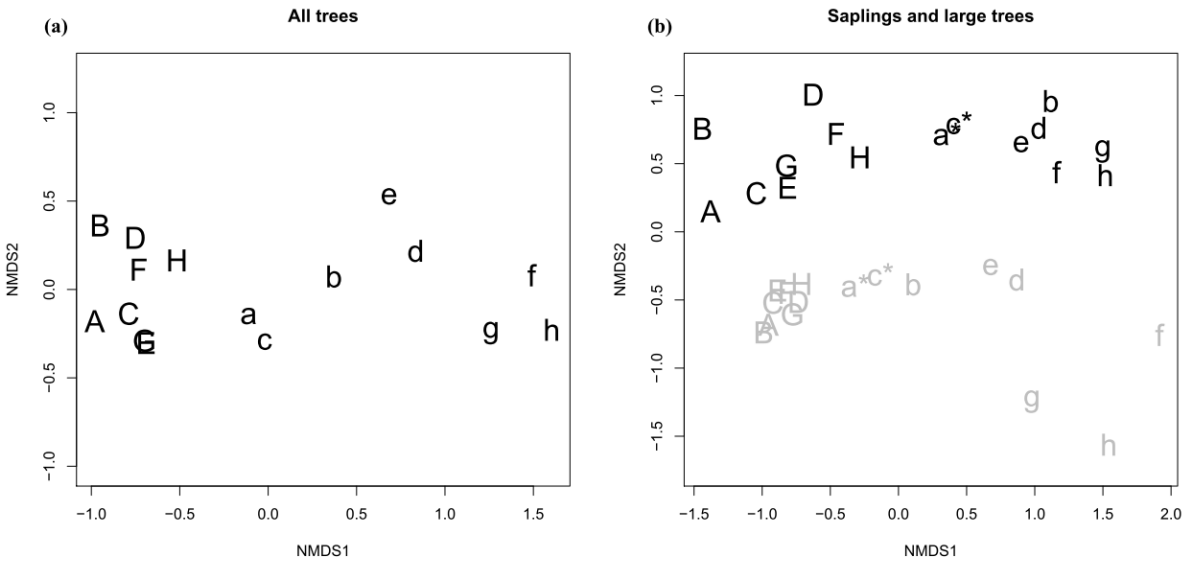


Figure 4. NMDS ordination plots of floristic composition. (a) all trees (b) saplings (i.e. trees ≤ 3 cm dbh) and large trees (i.e. trees ≥ 10 cm). Upper case letters are quadrats in the primary forest plot and lower case letters are quadrats in the secondary forest plot. In Figure 3b, grey letters are saplings ≤ 3 cm dbh and black letters are larger trees ≥ 10 cm dbh.) Spatial locations of the quadrats are shown in Figure 1. Quadrat "a*" and "c*" are quadrats within the secondary forest plot that contain residual old growth elements. See text for details.

CHAPTER 3. Comparative role of the regeneration environment, species functional groups and dispersal on the forests' long term recovery

Introduction

Half of the world's forests consists of areas regenerating from degradation and previous land conversion (FAO, 2010). This is especially true in the tropics, where the majority of deforestation and land use changes are currently occurring (FAO, 2010). Previous research has shown that tropical forests, both primary and secondary, play an important role in conserving biodiversity (Chazdon et al., 2009; Dent and Joseph Wright, 2009) and sustaining ecosystem functions (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). However, the quality and quantity of ecosystem services provided by secondary forests, as well as their ability to conserve biodiversity, have been shown to depend on a forest's recovery state (e.g. age, structure, species composition) (Gardner et al., 2007). For instance, short-statured young secondary forests generally sequester less aboveground carbon than older taller ones; less taxonomically diverse secondary forests usually have lower functional diversity, and hence less resilience to disturbance, than more diverse forests (Tilman et al., 1997; Walker, 1992). Complicating this situation is the fact that secondary forests do not all recover structure and biodiversity at the same rate (Chazdon, 2003). It is thus challenging to predict the trajectory of on-going recovery in secondary forests.

This is especially true for older secondary forests. While secondary forests tend to accumulate species and biomass rapidly in the first few decades after disturbance (Chazdon, 2003; Chazdon et al., 2009; Guariguata and Ostertag, 2001) there is much less known about the long-term successional dynamics of tropical forests. The limited existing knowledge indicates that even though older secondary forests can attain basal area similar to that of old growth forests, factors such as dispersal limitation, soil conditions, and presence of herbaceous species or long-lived pioneers species, can lead to highly variable tree recruitment and recovery of species composition (Chazdon, 2003; Chua et al., 2013; Cohen et al., 1995; Finegan, 1996; Guariguata and Ostertag, 2001; Peña-Claros, 2003). More work is needed to understand the relative importance of these factors and how they interact with one another.

First, as species and biomass accumulate the forest environment changes. Changes in light quality and quantity, air temperature and soil nutrients throughout succession continuously alter which species have the traits most suited to the changing conditions (Anten and Selaya, 2011a; Bazzaz and Pickett, 1980; Noble and Slatyer, 1980). In addition, over time the canopy closes to create a more continuous landscape that encourages animal mediated dispersal (Wunderle Jr., 1997). Despite the potential importance of these processes, almost no research (but see Lebrija-Trejos et al., 2010) has focused on characterizing the environment in recovering tropical forests and determining the relative influence of the regeneration environment and dispersal on current and future forest recovery.

Second, although it is well established that early and late successional species differ in their resource utilization (Bazzaz and Pickett, 1980), especially that of light (Nicotra et al., 1999), few studies have examined how the distribution of resources such as light, water and soil nutrients,

affects recruitment of different plant functional groups: short-lived pioneers (SLP), long-lived pioneers (LLP) and primary forest species (PFS). Seedlings of fast-growing SLP thrive on high light and relatively higher soil nutrients; PFS are shade-tolerant and associated with lower soil fertility (Bazzaz and Pickett, 1980). Slow-growing, LLP are the exception to these general trends in that they have the ability to germinate under high light conditions and persist as canopy trees in mature forests (Finegan, 1996). Not all species within these functional groups have the same resource acquisition strategies, and previous work suggests that some LLP grow well on degraded soil (Burslem et al., 1994; Chua et al., 2013). In short, we still do not fully understand how the differences in the abiotic environment facilitate the establishment of LLP vs. that of SLP, or influence the replacement by other functional groups as recovery progresses.

Beyond our poor understanding of the factors driving the long-term recovery of tropical forests, there is a paucity of information on the recovery of old world tropical forests, particularly those in Southeast Asia, which is a biodiversity hotspot region and highly threatened by deforestation (Sodhi et al., 2010, 2004). We have found only one study that examined forest regeneration of older secondary forests in this region (Brearley et al., 2004). Southeast Asia has climate, topography, taxonomic groups and land use types that are different from more the well-studied Neotropics. Southeast Asia's narrow peninsulas and islands are affected by the monsoon and local maritime environments (Bruijnzeel, 2004). This contrasts with the larger and more continuous landmass of the Neotropics. In addition, Dipterocarp forests in Southeast Asia are not only taxonomically but also structurally and ecologically different from Neotropical forests (Banin et al., 2014; LaFrankie et al., 2006). Finally, the land use histories of the regenerating forests also differ. In the Paleotropics common previous land uses include rubber, palm oil, gambier and spices, in contrast to maize, cacao and pastures in the Neotropics. Thus, the findings from forest regeneration studies from the Neotropics might not be easily generalized to Southeast Asian forests.

To help fill these knowledge gaps, we investigated forest recovery in the Central Catchment Nature Reserve (CCNR) of Singapore. Prior to British colonization in 1819, small trading settlements dotted the coast of Singapore and the interior forests were largely undisturbed (Corlett, 1992). From 1850 to 1900, rapid deforestation occurred as the migrant population swelled and people sought livelihoods in the cultivation of cash crops, so much so that by late 1800s only about 10% of the original forest remained (Cantley 1884). The 20th century saw gradual legal protection of the remnant secondary forests and fragments of old growth forests, with the eventual establishment of CCNR in 1951, under the Nature Reserve Act. Hence, the majority of secondary forests in CCNR are between 60 - 100 years old. A comparison of the aerial photographs taken in the 1950s with more recent photographs shows that the secondary forests in CCNR have recovered at different rates. Areas that had no canopy in 1950s can today either be open land dominated by ferns or short to tall secondary forests. The CCNR forests thus span a continuum of fern-dominated areas to secondary forest with different degrees of recovery to primary forests.

There has been limited previous research in CCNR on forest recovery. Previous work has focused on both large trees (>10 cm DBH) (Turner et al. 1996, Wong et al., 1994) and saplings (Corlett 1991). However, in the sampling study, ages of the sites were inferred from the

vegetation, thus injecting some elements of circularity into the assessment of recovery. In addition, there was some work comparing plant communities and nutrient status of primary forests and that of degraded secondary forests that are recovering from long-term agricultural activities (Burslem et al. 1994, Grubb et al., 1994, Sim et al. 1992). These studies found low nitrogen and phosphorus levels in the degraded forests, as well as strongly phosphorus limited soils in both the degraded and primary forests.

In our study, we assessed forest recovery in the continuum of CCNR forest types to explore the different factors influencing recovery and succession. To provide a common basis for our study, we selected nine secondary forest sites that were all at a similar structural recovery stage in 1950. In addition, we selected three primary forest sites to serve as points of comparison. At all these sites, we conducted an inventory of all trees including saplings and seedlings using a nested sampling design. Sampling adult trees, saplings and seedlings enabled us to assess current as well as future regeneration potential; the latter as indicated by the recruited saplings and seedlings (Dent et al., 2013; Norden et al., 2009; Peña-Claros, 2003). In addition, we quantified the above and below ground abiotic seedling environment and distance to seed sources at each site. We focused on environmental conditions in the seedling stage because these have been found to affect even the traits of adult trees. Thus the regeneration environment have long-lasting effects on plant ecological strategies and the overall community assembly process (Grubb, 1977; Poorter, 2007).

Our research was guided by the following questions:

1. How does the structure, species diversity, composition and functional groups vary among secondary forests and in compoarison to the primary forest?
2. How do the parameters outlined in Q1 differ across tree size classes (large trees, mid-sized, saplings and seedlings)?
3. To what extent can variation in seedling' recruitment be explained by the immediate environment at the establishment sites as well as distance to potential seed sources?

Methods

Site description

Our study was located in the Central Catchment Nature Reserve (1° 22' 32.0514", 103° 48' 13.0674"), the largest contiguous forest reserve in Singapore. The original flora is an extension of the lowland forests of the Malay Peninsula (Corlett, 1992). Today, the reserve consists of 2000-ha of vegetated land, including pockets of Dipterocarp primary forests, secondary forests that are about 60 – 100 year old, as well as four water reservoirs that were constructed and expanded multiple times from 1868 to 1977. Although much of the old growth forests were probably first cleared for gambier (*Uncaria gambier*) plantations in the early 1800 (Wee and Corlett 1986), it is difficult to trace subsequent land use. Gambier is a tropical vine whose leaves are boiled to extract dye for tanning hides, a process which requires an enormous amount of firewood (Corlett, 1992). Forest loss was also exacerbated as gambier could only be sustained on virgin forest soil for a couple of decades, after which productivity declined and

more forests had to be cleared. Old plantations were then replaced by other cash crops, such as cassava, locally known as tapioca, and nutmeg, or subsistence vegetation farms, which likely further decreased soil fertility and degraded the land. With urbanization, farming activities ceased and the remaining forests were left to regenerate naturally, culminating in the establishment of nature reserves in 1951. However, during our field research we observed on-going illegal farming activities occurring at the periphery of the reserve.

Singapore has mean annual rainfall of 2353 mm. The driest month has an average precipitation of 158.5 mm, and the wettest month 297.9 mm. The mean temperature is 27.0°C. (National Environment Agency, Singapore). The terrain of the entire reserve is gently undulating and elevations of the study sites range from 25 – 55 m. The CCNR overlays the Bukit Timah/Central Singapore granite batholith that formed in the early to middle Triassic (Thomas 1991) and occupies a third of the island. Deep weathering on these igneous rocks by the equatorial climate has produced well-developed soils that are classified as Ultisol, an important soil order in the tropics (Richter and Babbar, 1991; Sanchez and Buol, 1975), and Typic Paleudults of the Rengam series (Ives, 1977). The high tropical rainfall facilitates leeching of bases and has resulted in soils that are acidic, have low cation-exchange capacities and are particularly low in phosphorus (Thomas, 1991).

Plot selection and sampling design

We selected plots based on forest structural maps that were created from stereoscopic aerial photographs taken from 1950-1952 by the British Royal Air Force. The resulting 1950s map (National Parks Board, unpublished) has eight forest structural classes, but following Turner et. al. (1996) we collapsed these eight classes into the four classes to facilitate comparison with more recent maps, which are based on lower resolution aerial photographs. The four structural classes are: O: open vegetation (no canopy), S: small pole trees, M: tall mature secondary forests, P: primary forests with canopy of multi strata layers. We initially selected 23 sites that were class O in 1950 and are representative of classes O, S and M in CCNR today. We carried out a two stage sampling. In stage one, we performed a quick structural survey of all trees ≥ 5 cm DBH to verify the current ground status of the plots. We analyzed the structural survey data using Nonmetric Dimensional Scaling Ordination (NMDS) and Hierarchical Clustering (Appendix D, Figure 1). In stage two, we randomly selected nine of the 23 plots, as well as three primary forest plots, for detailed study.

At each of the 12 selected site, we tagged, identified and measured the diameter of trees in a nested sampling design (Figure 1). We surveyed all trees ≥ 1 cm DBH in an inner octahedral plot (50 m across); all trees ≥ 10 cm DBH were surveyed in an additional 11m buffer strip, which included trees that could have influenced abiotic conditions and tree regeneration within the inner plot, as well as serving as seed sources. Thus the entire plot size was 72 m across. We set up 5 × 5 m quadrats within the inner octahedral plot, where all seedlings ≥ 10 cm in height and <1 cm DBH were surveyed (but not tagged) (Figure 1). At each site, the seedling survey stopped when one of the following criteria was met: 200 seedlings sampled (with a minimum of four quadrats) or 20 quadrats sampled. To randomize the location of the quadrats while ensuring that they were well distributed, we divided the tree plot into four sections and apportioned five

potential quadrats within each section. The locations of the potential quadrats were referenced from the center tree of the plot, using randomly generated distances and bearings that fell within each section. We kept rotating through the four sections; setting up one seedling quadrat in each section until the above criteria were met. We carried out environmental measurements in a subset of seedling quadrats. The seedling quadrats were selected based on high species dissimilarity among one another, and the dissimilarity was determined using NMDS ordination of seedling species composition. There were four quadrats in all the plots except for two class O plots that had only three quadrats. In each selected seedling quadrat we measured abiotic and biotic variables, as elaborated below

Quantifying the seedling regeneration environment

We defined the regeneration environment as the immediate environment that was likely influencing the growth and performance of seedlings. We further categorized the regeneration environment into aboveground (AG) and belowground (BG) components, where AG consisted of biotic variables (leaf litter depth and fern cover) and abiotic variables (light, air temperature and vapor pressure deficit) and BG consisted of soil factors.

Leaf litter depth and fern cover

We took four measurements of the leaf litter depth in each of the four 2.5 × 2.5 m smaller quadrats within selected seedling quadrats with a stiff measuring tape. The mean leaf litter depth was then calculated for each seedling quadrat. Percentage coverage of the fern *Dicranopteris* spp. was also visually assessed in each of the smaller quadrats. This was done using a modified Braun–Blanquet cover class scale where >75% cover = 6, 50–75% = 5, 25–50% = 4, 5–25% = 3, 1–5% = 2, and coverage that consisted of easily enumerated individuals = 1.

Air temperature and vapor pressure deficit

From March 2012 to March 2013, we measured relative humidity and air temperatures of the selected seedling quadrats in each site using iButton^{R} sensors (model DS1923). The iButton readings are accurate to 0.0625 ^{o}C and 0.04% relative humidity (Maxim Integrated Products 2009). They were housed in perforated plastic cups and placed 1m from the ground, on a PVC pipe that was staked into the ground. The measurements were logged every 30 minutes for the first five months, and then every 60 minutes for the next seven months. The entire set up was caged to deter damage by wild animals such as the long-tailed macaque (*Macaca fascicularis*) and the wild boar (*Sus scrofa*). For all analyses, we converted relative humidity to vapor pressure deficit (VPD) using temperatures that were logged simultaneously, using the following formula.

$$VPD = \left(\frac{100 - RH}{100}\right) \times (610.7 \times 10^{\frac{7.5 \times T}{237.3 + T}})$$

Thirty-nine iButtons with at least ten months of data, and a minimum of 20 recording days per month, were used in our analyses. Means of daily maximum temperature (Tmax) and means of

daily standard deviation of VPD (sdV) were calculated and used in subsequent analyses. We chose to use daily standard deviations instead of maximum VPD as it better captures the fluctuating conditions that the plants are exposed to. Note minimum daily VPD was almost always zero due to the high humidity.

Light variables

We quantified the canopy structure and gap light transmission by dividing the 5 × 5 m seedling quadrats into four 2.5 × 2.5 m smaller subquadrats and taking hemispherical photographs from a height of 90 cm at the center of each subquadrats, as well as the center of the entire quadrat. We used a 4.5 mm F2.8 Ex DC Circular Fisheye HSM Sigma DC Lens mounted on a Canon digital SLR Camera. Photographs were under-exposed by three stops, to increase contrast between the sky and foliage. The photographs were analyzed using the Gap light analyzer software (GLA version 2.0), and by specifying the monthly spectral fraction in the configuration for GLA, we obtained the percentage of canopy cover (CnpyO), the amount of direct (Dir) and diffuse (Dif) photosynthetic active radiation transmitted by the canopy (Frazer, Canham, & Lertzman, 2000; Frazer, Trofymow, & Lertzman, 1997). The means of these light variables were calculated for each seedling quadrat (see Appendix E for the configuration used in GLA).

Soil factors

In the subquadrats of the selected seedling quadrats, we removed the leaf litter and used a 2-cm diameter soil probe to collect the top 5 cm organic soil. The soils were composited and then air dried. Undecomposed organic materials such as leaves, roots were removed from the soil. The soils were sent to Soils Laboratory of the Smithsonian Tropical Research Institute and analyzed for resin-extractable phosphorus (P), exchangeable cations (Al, Ca, Fe, K, Mg, Mn and Na) with $BaCl_2$, pH in water, $CaCl_2$ and $BaCl_2$, total carbon (TC) and total nitrogen (TN). We used the major cation groups for subsequent data analyses. These include pH in $CaCl_2$, (highly correlated to pH in water and $BaCl_2$), TC, TN, carbon to nitrogen ratio (C:N ratio), P, total exchangeable bases (TEB = Ca + K + Mg + Na), effective cation exchange capacity (ECEC = Al, Ca, Fe, K, Mg, Mn and Na) and aluminum saturation (AlSat = Al/ECEC).

Statistical analysis

To answer Q1 and Q2 we used a variety of standard methods from community ecology to quantify differences in the structure, diversity, and composition between the sites. To answer Q3, we conducted two sets of analyses, the first using all data in primary and secondary forests, and second set only using data from the secondary forests. The first set explored the factors that influence seedling recruitment in the forests, and the second set explored the relative importance of these factors on regeneration. For both sets of analyses we used multiple factor analysis to explore the overall correlation among the seedling community, adult community, regeneration environment and distance to potential seed sources. We used redundancy analysis to test the significance of each environmental variable on variation in seedling composition. Finally, we modeled the relative importance of the different environmental variables on seedling recruitment.

Q1 & Q2. Comparing recovery metrics of secondary forests to primary forests

Stem density, forest structure, diversity and functional groups

We examined structural differences among the twelve plots using hierarchical clustering with Ward's minimum variance method using a Bray-Curtis dissimilarity index. This was done using diameter size classes that were based on the largest stem as well as basal area size classes (which included all stems of a tree). The DBH cut-offs were 1 – 2 cm, 2 – 5 cm, 5 – 10 cm, 10 – 20 cm, 20 – 30 cm, 30 – 60 cm, 60 – 100 cm and > 100 cm. This analysis was carried out for all trees, adult trees only (≥ 10 cm DBH) and smaller trees (1-10 cm DBH). In each of the primary and secondary plots, we also calculated stem density, basal area, species richness, weighted species richness, Shannon Diversity Index and the proportion of species in each of the functional groups described below.

We categorized the species into four broad functional groups: primary forest species (PFS), secondary forest species (SFS), short-lived pioneer species (SLP), and long-lived pioneer species (LLP). Species were categorized as PFS or SPS based on Tree Flora of Malaya Volume 1- 4 (Whitmore 1972a, 1972b, Ng 1978; Ng 1989), Wayside trees of Malaya Volume 1 and 2 (Corner 1988) and online web resources (Slik 2009). Pioneers, species that are able to establish in open areas, were classified based on the same resources as above, as well as previous experimental work that monitored seedling recruitment after removal of fern (unpubl. data). We differentiated SLP and LLP based on species' specific woody density, as stem density is positively correlated with plant longevity (Putz et al., 1983; Wright et al., 2010). Using data from the Global Wood Density Database (Chave et al., 2009, Zanne et al. 2009), we defined pioneers with wood density < 0.4 (g/cm^3) as SLP and those with wood density > 0.5 (g/cm^3) as LLP, which is comparable to the mean wood density of PFS (0.60 ± 0.12 g/cm^3) in our plots with available data. Species with wood density from 0.4 – 0.5 g/cm^3 were omitted from the classification. A list of all species with their wood density and group assignment is found in Appendix F, Table 1.

We carried out one-way ANOVAs to test for significant differences of the stand structure, diversity measures and relative abundance of each functional groups, between primary and secondary forest plots and across different DBH size classes. In all the analyses, we present mean values with standard errors.

Floristic composition

We analyzed differences in floristic composition using Bray-Curtis and Jaccard dissimilarity indices. The Jaccard index is the presence/absence equivalent of the Bray-Curtis index. We compared the floristic similarity (1-dissimilarity index) within and between primary and secondary plots. This was done for big trees, mid-sized trees and saplings. To visualize the floristic differences among plots, we carried out hierarchical clustering with Ward's minimum variance method on the dissimilarity matrices. We further carried out indicator value analysis (IndVal) on the distinctly identified clusters. We did this in a single analysis that combined adult trees (≥ 10 cm DBH), saplings (1-3 cm DBH) and seedlings (<1 cm DBH) only.

Q3. Effects of regeneration environment and distance to seed sources on forest regeneration

Linkages among composition of big trees and seedling, regeneration environment and distance to potential seed sources

We used multiple factor analysis (MFA) (Borcard et al. 2011,Carlson et al., 2010, Escofier and Pagès 1994), to examine the correlation in the structure between five sets of data: seedling community, adult tree community, aboveground variables, belowground variables, and distance to nearest potential seed source (Dist). We used shortest distance to forests with canopy structure corresponding to either mature secondary and primary forests (Turner et al., 1996) as a proxy for Dist. When all the variables are numeric (as in this case), MFA is identical to a PCA performed on all five sets of variables simultaneously, with each of the five data subsets weighted (Borcard et. al. 2011). The correlation is assessed using the RV coefficient, which is akin to the multivariate generalization of the squared Pearson correlation coefficient (Robert and Escoufier, 1976). The RV coefficient ranged from 0 – 1 and is tested by permutations (Daniel Borcard, n.d.; Josse et al., 2008). We applied the Shapiro-Wilk Normality test to the raw data and carried out data transformation to this and other analyses where necessary to improve normality and homoscedasticity.

Determining the effects of regeneration environment on seedlings' composition

We conducted redundancy analysis (RDA) to test the significance of the relationship between the environmental variables and the composition of species that were in the top 70% by abundance in all the surveyed seedlings, while controlling for the partial effect of the density of large trees (≥10 cm DBH). RDA combines multiple regression and principle component analysis. Following Legendre and Gallaher (2001), we carried out Hellinger transformation on the species matrix, which prevents zero counts from contributing towards plots' similarity. It also reduces the weight given to rare species, which is a problem with the often used canonical correspondence analysis. To obtain a parsimonious model, we carried out forward selection of the explanatory variables using the *ordistep* function of the R package "vegan" (Oksanen et al, 2013). We extracted the adjusted R^2 value and conducted a permutation test of the RDA results. The analysis was carried out for all plots as well as for secondary forest plots separately.

Modeling effects of regeneration environment and distance to potential seed sources on seedling recruitment

We built two sets of generalized linear models (GLM) models to evaluate the relative importance of 1) environmental variables on seedling recruitment in all forests (M_{all}), and 2) environmental variables and distance to potential seed sources (Dist) on seedling recruitment in secondary forests only (M_{sec}). Our responses variables were seedling density, species richness and the number of PFS, SFS, SLP and LLP. Since we had count data, we used a Poisson or quasi-Poisson error distribution with log link function. We used automated model selection (function *dredge* in *MuMIn* package of R (Barton 2013)) to rank the models based on greatest maximum likelihood, using Akaike's Information Criterion (AIC) that was adjusted for small sample sizes (AICc) and overdispersion ($QAIC_C$) (Burnham and Anderson 2002). The variances of the $QAIC_C$

were adjusted for overdispersion using estimated values of ĉ from the overdispersion parameter (Bolker 2014).

Components from the PCA analyses of the correlation matrix of the abiotic and biotic measures were used as predictor variables in our models ("predictor components" thereafter). Since the variables were in different measurement scales, we conducted a PCA on the correlation matrix. Thus component loadings are the correlation (Pearson's r) between the components and the original variables. This method reduced the number of variables that entered the model selection, and retained as much as possible, information about the structure of the regeneration environment in the seedling quadrats. This approach also reduces collinearity and the sensitivity of the coefficient estimates to the combination of predictors used (Quinn and Keough 2001). We retained only the components which explained more than the average variance each component would have by chance, as indicated by eigenvalues of the components being larger than one (Norman & Streiner 1994).

Due to the high failure rate of the temperature and relative humidity sensors (data from only 31 seedling quadrats were deemed as comparable after eliminating days with incomplete data), we conducted PCA separately for the aboveground and belowground variables. This allowed us to maximize available data that would relate better to the overall landscape structure of the variables. We also carried out different PCAs for M_{all} & M_{sec} to obtain predictor components that correspond to the structure in all forests and also to secondary forests only. We did a Pearson correlation between the predictor components of AG and BG to determine the degree of collinearity. We also verified our results by analyzing a larger dataset that excluded the iButton data (which showed strong correlation with the light variables).

Our general models were as follows:

M_{all} for pri + sec plots: $Y \sim P_1.A_1 + P_1.A_2 + P_2.B_1 + P_2.B_2 + P_2.B_3$
M_{sec} for sec plots: $Y \sim P_3.A_1 + P_3.A_2 + P_4.B_1 + P_4.B_2 + P_4.B_3 + Dist$

M_{all*} for pri + sec plots: $Y \sim P_1*.A_1 + P_1*.A_2 + P_2.B_1 + P_2.B_2 + P_2.B_3$
M_{sec*} for sec plots: $Y \sim P_3*.A_1 + P_3*.A_2 + P_4.B_1 + P_4.B_2 + P_4.B_3 + Dist$

where prefix "P" denotes different PCAs. P_1* and P_3* are PCA of the aboveground variables that excluded maxT and sdV; A_1, A_2 are component 1 and 2 respectively of the PCA for the aboveground variables; B_1, B_2, B_3 are component 1, 2 and 3 respectively of the PCA for the aboveground variables. Results for M_{all*} and M_{sec*} are in Appendix G.

To make inferences that take model selection uncertainty into consideration, we carried out model averaging over all models within a subset of models that were selected based on the accumulated Akaike weight (≤0.95) (Burnham and Andersen 2002). Inferences were based on model-averaged parameters. Relative importance values (RI) of the parameters from each model were also calculated and compared following Burnham and Andersen (2002).

All satistical analyses were done using R statistical software v3.0.2. (R Development Core Team, 2013).

Results

Q1 & Q2. Comparing recovery metrics of secondary forests to primary forests

Stem density, forest structure, diversity and functional groups

At the plot level, average stem density (5364 ± 637 trees ha^{-1}) of the primary forest plots was about twice that of the secondary forest sites (2441 ± 382 trees ha^{-1}) (P=0.005), although the stem density of large trees (≥ 10 cm DBH) and total basal area of many of the secondary forest plots were not significantly different from that of the primary forest (Table 1), meaning that the differences in stem density was mainly driven by the smaller trees. Seedling density between the primary and secondary forest plots was also not significantly different. However, two of the fern dominated plots (R1 and R3) and one of the short-statured secondary forest (R5), had no or few seedlings.

Our cluster analysis showed that some of the tall secondary forests were structurally similar to the primary forests, especially when smaller trees (<10 cm DBH) were excluded (Appendix H, Figure 1a, 1b). In terms of smaller trees, most of the secondary plots were structurally similar to the primary forests, except for the fern plots R3 and R1 (Appendix H, Figure 1c). Plot R4 had a low density of small trees but high density of mid-sized trees and was an outlier structurally from other secondary forest plots. Similar results were obtained using basal area.

There were a total of 387 unique tree species identified in the 12 secondary and primary plots. The secondary forests plots on average had only about a third (40 ± 3) of the mean species richness of primary forest plots (135 ± 9) (Table 1). Large tree species richness, weighted species richness, Shannon Diversity index, and proportion of PFS were all significantly lower in the secondary forest plots than in the primary forests (P <0.0001 for all, Figure 2). Sapling and seedling diversity in the secondary forest plots also showed similar trends, except that species richness after accounting for stem density was not significantly different from the primary forest plot (Figure 2). In addition, the fern dominated plots (R1 and R3), which were located close to mature forests, had higher weighted species richness than the primary forest plots. Finally, while there were more LLP than SLP among the large trees in the secondary forests, in general with the exception of two plots (R5 and R4), the secondary forests were recruiting more secondary forest species and less pioneer species (both LLP and SLP) in the sapling and seedling classes (Figure 3).

Floristic composition

The composition of the secondary forests was taxonomically distinct from that of the primary forest. The dominant families by basal area (BA) across all three primary forest plots were Dipterocarpaceae (17.78 ± 6.21% of BA), Lauraceae (10.30 ± 3.66% of BA), Olacaceae (7.01 ± 3.61% of BA) and Myristicaceae (6.66 ±1.96% of BA). Other abundant families by stem counts included Euphorbiaceae (23.55 ± 0.69% of density), Meliaceae (8.41 ± 3.67% of density) and

Ebenaceae (7.09 ± 1.26% of density). In contrast, in the secondary forests, two families, Myrtaceae (28.42 ± 3.49% of BA) and Theaceae (15.76 ± 3.34% of BA) made up a third to almost half of the total basal area. Moreover, a single species *Rhodamnia cinerea* represented about half of the trees in the Myrtaceae family, while the trees in the family Theaceae consisted largely of *Adinandra dumosa* individuals. Other abundant families by stem count in the secondary forests were Clusiaceae (15.3 ± 5.50%), Dilleniaceae (8.14 ± 5%, single species *Dillenia suffruticosa*) and Rosaceae (6.20 ± 3.41%, single species *Prunus polystachya*) (see Appendix I for species information for each plot).

Floristic similarities were relatively high within primary forests across all size classes (Figure 4). Floristic similarity was more variable in the secondary forests, and when Bray-Curtis similarity indices were used, large trees among secondary forests plots had higher similarity than smaller trees, especially as compared to saplings. Primary and secondary forest shared the least number of species.

The hierarchical clustering analysis of the large trees, saplings and seedlings in all 12 plots produced the same three clusters of plots, whether Jaccard (presence/absence) or Bray-Curtis (full abundance) dissimilarity was used (Figure 5). Based on Jaccard dissimilarity index, Cluster 3 which consisted of secondary forests' saplings and seedlings had higher similarity with Cluster 2, which consisted of primary forest plots. However, in contrast, based on Bray-Curtis dissimilarity, Cluster 3 was more similar with Cluster 2, which consisted of large trees from secondary forests.

Results from Indval analysis showed that Cluster 1 was characterized by long-lived pioneer species *Adinandra dumosa, Rhodamnia cinerea, Fagraea fragrans,* short-lived pioneer *Macaranga conifer* and secondary forest species *Timonius wallichianus* (Indicator value 0.94, 0.70, 0.47, 0.65 and 0.63 respectively, all $P \leq 0.01$). Cluster 2 had a total of 65 indicator species, including *Aporosa prainiana, Dysoxylum cauliflorum, Hopea griffithii, Knema malayana.* Cluster 3 was characterized by common secondary forest species *Champereia manillana*, *Cinnamomum iners, Anisophyllea disticha, Alstonia angustifolia, Clerodendrum laevifolium* and *Calophyllum ferrugineum* (Indicator value 0.76, 0.58, 0.55, 0.54, 0.53 and 0.50 respectively, all $P \leq 0.05$).

Q3. Effects of regeneration environment and distance to seed sources on forest regeneration

Linkages among composition of big trees and seedling, regeneration environment and distance to potential seed sources

The MFA showed that the seedling communities in the primary and secondary forests were most significantly associated with the big tree communities within each plot (RV coefficient = 0.645, $P < 0.001$) and had decreasing associations with the aboveground, belowground variables and distance to potential seed sources (RV coefficients = 0.404, 0.403 and 0.310, $P < 0.001$ for all). The big tree communities themselves were linked to AG, BG and Dist (RV coefficients = 0.346, 0.609 and 0.397, $P \leq 0.001$ for all) (Table 2). Similar results were obtained for analysis among the secondary forests (Appendix J, Table 1)

Determining the effects of regeneration environment on seedlings' composition

Results from RDA (Table 3) showed that sdV, ECEC, fern cover, and P were most significant in determining the composition of top abundant seedling species in the primary and secondary forest plots. The importance of ECEC reflects the importance of exchangeable Al ions, which constituted on average 87% of ECEC, and are highly correlated with ECEC (r^2 = 0.97). Within secondary forests, the soil variables, P, pH, AlSat and C:N ratio were most significant. Although the adjusted R^2 value was low for both parsimonious models (0.165 and 0.155 for all plots and secondary plots respectively), the permutation tests showed that overall the results were highly significant (P < 0.001).

Modeling effects of regeneration environment and distance to potential seed sources on seedling recruitment

The predictor components used in all the models accounted for > 80% of the variance in AG and BG variables in all the PCAs (Appendix G, Table 1). In general, the aboveground abiotic variables and biotic variables were correlated with different predictor components (A_1s and A_2s respectively). In all models the first belowground predictor components were primarily correlated with low macronutrients (note that phosphorus was correlated only with $P_4.B_1$). The main difference between the models for all data (M_{all}) and that for only secondary plots (M_{sec}) was in the correlation of low soil C:N ratio with low AlSat in $M_{all,}$ but low C:N ratio with high AlSat in M_{sec} (Appendix G, Table 1). Refer to Appendix K for an overall characterization of the regeneration environment in all plots and Appendix G, Table 3 for results of the automated model selection.

M_{all}: Seedling recruitment in primary and secondary forests.

The best fit models show that the species functional groups are distributed along different resource gradients. PFS are associated with $P_1.A_1$ (low light, Tmax and sdV), $P_2.B_2$ (low soil C:N ratio and Al saturation) and $P_1.A_2$ (low macronutrients ofTC, TN, TEB and ECEC) (Table 4 and Appendix G, Table 2). The pioneers in general are associated with higher soil C:N ratio and Al saturation ($P_2.B_2$), although this distinction was strong for the LLP (RI =0.42, model-averaged coefficient = -4.07 ± 1.03***) and not the SLP (RI = 0.28). SLP also had strong association with $P_1.A_1$ (high light, temperature and fluctuating VPD) (RI = 0.83, model-averaged coefficient = 4.2 ± 1.06***, Table 4), although this association was not important when the models were fitted with the larger dataset without the Tmax and sdV (RI = 0.2, Appendix G). More SFS are predicted to be present at sites with low pH, TEB and high P, as supported by the higher RI value (0.54) when the larger dataset was used (Appendix G, Table 2).

Overall, seedling density and species richness are predicted to be higher at sites with less fern cover, less leaf litter, higher diffuse PAR as well as lower soil C:N ratio and Al saturation (Table 4). Species richness is also predicted to be higher at sites with low light, Tmax and sdV.

M_{sec}: Seedling recruitment in secondary forests only

Similar to the above results, $P_3.A_1$ (high fern cover, leaf litter depth and low diffuse PAR) was overall, the most important factor and had negative effects on seedling density, species richness, PFS, SFS and LLP. Increasing distance from potential seed sources was also an

important factor that correlated with decreasing seedling density, species richness, and SFS (Table 4), which was also supported by the analysis with the larger dataset (Appendix G, Table 2). Among the secondary forests, $P_4.B_3$ (high P, high AlSat and low C:N ratio) was predicted to decrease abundance of long-lived pioneers. Results from the larger dataset also showed that SLP was conversely positively correlated with $P_4.B_3$ (RI = 0.48 and 0.71 for LLP and SLP respectively, Appendix G, Table 2). Although none of the belowground predictor components were significant in the models for PFS, we found that PFS in the secondary forests were positively correlated with low C:N ratio and Al saturation (RI = 0.77, model-averaged coeff. = 7.75 ± 3.96.), using the predictor components from $M_{all.}$

Similar to M_{all}, the results from M_{sec} showed that seedling density and species richness were predicted to be higher at sites with less fern cover, leaf litter and higher diffuse PAR (Table 4). Finally, increasing distance to potential seed sources was also predicted to decrease species richness.

Discussion

We found that our secondary forests sites in Singapore have followed different recovery trajectories post-disturbance. Aside from stem density and basal area of large trees, almost all of the recovery metrics (density of smaller trees, species richness, Shannon diversity, proportion of primary forests species and species similarity with old growth) are highly variable and generally lower than comparable measures in primary forest (Table 1, Figure 2 and 5). For example, the secondary forest plots had on average 45% and 29% of the stem density and species richness respectively of the primary forests plots (trees ≥ 1cm DBH). Our findings stand in contrast to studies elsewhere in the tropics, that have generally found greater than 70% recovery of stem density and species richness (See Table 6 in Brearley et al., 2004; Table 2 in Chua et al., 2013). However, these studies have also found variable recovery in species composition in older secondary forests (Dent et al., 2013; Finegan, 1996; Saldarriaga et al., 1988). Overall, our findings along with previous studies (Chua et al., 2013; R T Corlett, 1991; Turner et al., 1997) suggest that Singapore forests regenerate more slowly than most tropical rainforests elsewhere (Aide et al., 1996; Brearley et al., 2004; Ferreira and Prance, 1999; Saldarriaga et al., 1988; van Andel, 2001).

We posit that the slow regeneration in Singapore forests is due in large part to inherent poor soil fertility made worse by disturbance, as well as on-going feedbacks between the regeneration environment and the colonizing vegetation. Other studies have shown that forest regrowth is slow on low fertility soils (Lu et al., 2002; Moran et al., 2000) and old growth forests in Singapore have very low soil fertility, even in comparison to other Dipterocarp forests in the region. In particular, available phosphorus in our primary forest plots ranged from 3.3 – 6.1 mg/kg, while 4.2 – 31.3 mg/kg have been found in other forests in the region (Abdu et al., 2007; Yamashita et al., 2003; Zaidey et al., 2010). In addition, intensive agricultural activities probably further impoverish the soils (Corlett, 1991a; Sim et al., 1992) and encouraged the initial colonization by specialists of low soil nutrients, such as the fern species *Dicranopteris linearis*. Subsequent on-going forest recovery hinges on the interaction of the evolving regeneration

environment with the colonizing vegetation of different functional groups that successfully disperse into the sites. Below we elaborate in detail on how the regeneration environment along with chance dispersal hastens or slows forest recovery.

Our work indicates that past land use had a strong legacy effect on soil conditions. This is evident in the higher soil C:N ratio (19.70 – 32.08% vs. 17.65 – 19.61%) and exchangeable Al (3.53 – 8.79 cmolc/kg vs. 2.69 – 5.91 cmolc/kg) in the secondary forest plots, as compared to the primary forest plots. The differences are not more pronounced because C:N ratio and Al levels also increased from seedling quadrats in the pristine primary forest site to the more disturbed primary forest site. C:N values in our all plots were lower than those found in a previous local study by Sim et al. (1992), but concurred with that by Turner (2012). More importantly, the C:N values are overall higher than that of other Dipterocarp forests, including two secondary forests (See Table 5 in Sim et al. 1992, Abdu et al., 2007; Hamzah et al., 2009; Zaidey et al., 2010), and higher than other humid rainforests (Kauffman et al. 1998). Less data on Al is available from other studies, but in general, lower levels are found in primary Dipterocarp forests (mean of 5.08 cmolc/kg) as compared to secondary forests (mean of 7.96 cmolc/kg) (Abdu et al., 2007; Brearley et al., 2004; Hamzah et al., 2009; Jamaluddin, 2013; Zaidey et al., 2010).

Further, our results from RDA and the GLM models suggest that primary forest species seedlings are more likely to establish at sites with low Al levels (as indicated by ECEC) and low C:N ratio, based on analyses using all data as well as only data from secondary forest plots (Table 3 and 4), and a trend (albeit weaker) for pioneers to establish in soils with opposite conditions. Soil C:N ratio can serve as an indicator of the rate of release of nitrogen to plants, as C:N ratio higher than 20 often indicate a decrease in microbial breakdown of organic matter (Paul and Clark 1989). In other words, mineralization of nitrogen decreases. Since sampling was conducted on the top five cm soil, the higher soil C:N ratio in secondary forests is likely due to the production of nutrient poor dead organic matter, such as leaf litter, a strategy sometimes employed by nutrient use efficient plants in poor soils. In addition, high exchangeable Al reduces plant uptake of calcium and affects other cellular functions (Sanchez, 1976; Robson 1989; Rengel, 2004). In general, Al also decreases available P for plants (Sanchez, 1976; Robson 1989), although such a trend was not observed in our study, probably due to previous depletion of P and its slow recovery. Thus some of the pioneer species might be more adapted to the higher C:N ratio and Al toxicity than PFS, as elaborated below. Finally, these belowground factors are more important than aboveground factors for the establishment of PFS in secondary forests, as shown by our RDA and GLM models based on data using only secondary forests plots (Table 3, 4 and Appendix G, Table 2).

Among the secondary forests, slower recovery in terms of stem density and species richness was observed in plots that had a high proportion of long-lived pioneers. This concurs with other findings that LLP tend to slow forest regeneration and species replacement (Finegan, 1996; Peña-Claros, 2001). Results from our modeling (M_{sec} and M_{sec*}) and RDA indicated that within secondary forests, long-lived pioneers established under different regeneration environments than SLP. LLP are more likely to establish in soils with high C:N ratio, low P and low AlSat and

under aboveground conditions of lower light quantity, air temperature and fluctuations of VPD. The opposite is true for SLP (Table 3, 4 and Appendix G, Table 2). Unlike the other factors, the importance of AlSat is harder to interpret. AlSat is a relative measure of Al levels and exchangeable base cations (AlSat = Al/(Al + TEB)), while TEB in turn is the sum of exchangeable magnesium, calcium, potassium and sodium, most of which are important macronutrients for plants. TEB in the secondary forest plots was much more variable compared to that in primary forests and could be a result of different land use history, variable organic inputs from different regenerating vegetation communities, or increased leaching with rain due to the decreased canopy cover. Nevertheless, assuming no dispersal bias, LLP would be more successful than SLP at sites with soils yet to recover after agricultural depletion of nitrogen and phosphorus. At the same time, our results showed some tendency of LLP to be found at lower light levels than SLP (Table 4 and Appendix G, Table 2). This might imply that some LLP could establish or be successful in a wider range of light conditions than SLP, and could thus persist longer as light levels decrease under the recovering forest. In addition, other studies have shown that some of the LLP species in our study, such as *Adinandra dumosa* and *Rhodamnia cinerea* have very low foliar N and P especially when compared to SLP such as *Macaranga* spp. (Burslem et al., 1994). Thus these LLP produce low quality leaf litter that slows nutrient returns. Overall, these combinations of factors could slow regeneration by creating a positive feedback loop that prolongs the dominance of LLP.

Our results indicate that the presence of persistent herbaceous vegetation can inhibit forest recovery. We found that the fern *D. linearis* presents an effective physical barrier to seedling recruitment. It is commonly found in the tropics and has been previously found to deter forest regeneration (Cohen et al., 1995; Russell et al., 1998). This widespread fern species is a specialist of degraded soils due to its high nutrient use efficiency, especially of phosphorus (Russell and Vitousek, 1997), and its ability to accumulate Al (Kato-Noguchi et al., 2012). Its clonal growth allows it to persist, while its tough fronds have high lignin and low nutrient contents (Amatangelo and Vitousek, 2008), which create slow decomposing leaf litter that could also hinder nutrient recycling. Thus *D. linearis* could potentially vastly slow down nutrient cycling and keep the system in a poor nutrient state. In addition, *D. linearis* has been found to produce allelopathic compounds (Kato-Noguchi et al., 2012). However, we found that the soils in the fern dominated plots were not distinctly different from other plots and these plots were still accumulating secondary forest species after taking stem density into account (Figure 3). In addition, we have also found from our other work (unpubl. results) that within one and a half years of removing ferns and their rootmat, fewer LLP and more SLP, such as *Macaranga* spp., *Ficus* spp. and *Trema* spp., are able to establish. Thus over time, *D. linearis* might be able to increase soil fertility to support the establishment of SLP instead of LLP, which would hasten succession due to the shorter life-span of SLP, promoting more rapid species turnover.

Other than the regeneration environment, forest recovery also appears to be slowed by dispersal limitation. Distance to potential seed sources was the most important factor in modeling abundance of SFS in secondary plots, in our model using all seedling quadrats with soil data. “Dist” was not an important factor for modeling PFS, probably because it was measured as distance to both mature secondary forests as well as primary forests, and there

were fewer primary forests patches in Singapore. Animal mediated dispersal has been shown to be important in maintaining diversity in primary tropical rainforests in general(Corlett, 1998; Wells et al., 2009), as well as for accelerating forest regeneration (Wunderle Jr., 1997). Dispersal is likely limited for SFS because of the importance of animal mediated dispersal. For example, we found that more than 80% of the saplings in the secondary forest plots are animal dispersed. However, we found that dispersal by birds and/or bats, was lower in the fern dominated plots (results not shown) implying that winged animals might be less likely to enter forest gaps, either because of safety or because these places offer less food resources.

While our examination of the regenerating and primary forests of Singapore yielded considerable new insights, we were not able to determine the relative importance of interactions among and between aboveground and belowground factors, which are likely to be important, as plants' strategies change under different resource limitations. Our investigation indicates that controlled experiments would be needed to test differences in specific germination and growth requirements among the species. In addition, we were also only able to investigate one time point and one location. Future work would need to expand the geographical range of study and verify if similar processes are found elsewhere in the tropics.

Summary

Our findings indicate that that the recovery rates of Singapore secondary forests are varied and in general, slower than those found in other studies. The strong correlation between adult tree community structure and that of the seedlings suggests that forest succession in Singapore is strongly influenced by existing vegetation. In-situ seeding by adult trees probably substantially contributed to this relationship, but feedback processes are also important, as suggested by the significant correlations among the adult trees community, seedling community and the regeneration environment. Bringing together all the evidences from above, the following scenarios may have led to the varied recovery trajectories of our nine secondary plots: the abandoned land with extreme low soil fertility and high Al toxicity was first colonized by pioneers that are nutrient use efficient and tolerant of Al, such as the fern *Dicranopteris linearis*. The subsequent successful establishment of long-lived or short-lived pioneers depended on both chance dispersal and recovery state of the regeneration environment. Areas with lower soil fertility, in terms of high C:N, low P and low AlSat, wider range of light quantity, temperature and humidity favored establishment of LLP, while SLP are more likely to establish in soil with low C:N, high P and high AlSat and high light. In general, clonal growth of the fern and LLP longevity as well as the ability of LLP to recruit under shade prolonged the dominance of these pioneers and slowed forest recovery. The thick fern cover and the build up of slow decomposing leaf litter are also mechanical barrier to seed establishment, as both *D. linearis* and LLP tend to produce low quality leaf litter that slows nutrient cycling, although after at least 60 years, soil beneath *D. linearis* appeared suitable for supporting SLP. Conversely, the SLP have shorter lifespan and produce dead organic matter of higher quality, hence improving nutrients recovery while ameliorating the aboveground conditions. These factors facilitate subsequent succession by SFS and PFS, which however may be limited by seed sources. In summary, inherent poor soil fertility made worse by disturbance slows forest regeneration in Singapore.

Both chance dispersal from limited seed sources and environmental filtering determine the successful establishment of species, which further shape the evolving regeneration environment and influence forest recovery.

Acknowledgements
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Tables

Table 1. Stand structure and floristic diversity of the 12 plots. Plot-level values are shown here. Plot area was 0.367 ha for trees with DBH ≥ 10 cm, 0.177 ha for trees with DBH ≥ 1 cm and DBH 1-3 cm, and 0.01 ha for seedlings with DBH <1 cm. Values for seedlings are the mean of four 5 × 5 m^2 seedling quadrats, subsampled 100 times from all sampled quadrats of each big tree plot. Primary forest plots are shaded dark grey and plots with high fern cover are in light grey.

	DBH (cm) ≥ 1					DBH (cm) ≥ 10					DBH (cm) 1 - 3					DBH (cm) <1 cm			
Site	**BA* (m^2 ha^{-1})**	**S (ha^{-1})**	**Nsp**	**Nsp_wt**	**D**	**BA* (m^2 ha^{-1})**	**S (ha^{-1})**	**Nsp**	**Nsp_wt**	**D**	**BA* (m^2 ha^{-1})**	**S (ha^{-1})**	**Nsp**	**Nsp_wt**	**D**	**S (0.01 ha^{-2})**	**Nsp**	**Nsp_wt**	**D**
O1	20.8	3852	120	0.18	3.93	19.31	396	66	0.51	3.92	6.78	2288	83	0.21	3.66	160.40 ± 2.11	47.63 ± 0.49	0.30 ± 0	3.28 ± 0.02
O2	22.02	5781	134	0.13	3.35	16.7	390	63	0.47	3.74	11.39	3893	93	0.14	2.87	680.00 ± 0	55.00 ± 0	0.08 ± 0	2.21 ± 0
O3	26.5	6460	152	0.14	3.78	26.31	447	82	0.53	4	11.76	4147	102	0.14	3.53	117.59 ± 2.00	35.25 ± 0.44	0.30 ± 0	3.11 ± 0.02
R1	12.52	781	37	0.28	3.17	12.07	273	30	0.3	2.84	0.78	220	17	0.46	2.46	44.70 ± 1.92	15.98 ± 0.51	0.39 ± 0.01	2.30 ± 0.03
R2	19.54	2189	41	0.11	2.81	15.58	355	21	0.16	2.03	3.77	1232	34	0.16	2.58	177.36 ± 4.63	21.99 ± 0.19	0.13 ± 0	2.12 ± 0.02
R3	9.28	413	38	0.31	2.53	12.33	194	15	0.21	1.87	0.41	158	10	0.37	1.87	0	0	0	0
R4	19.84	3722	29	0.04	1.74	6.27	303	17	0.16	1.99	2.78	684	18	0.15	2.15	47.58 ± 1.63	14.48 ± 0.32	0.33 ± 0.01	2.15 ± 0.03
R5	9.94	3417	31	0.05	1.96	4.09	186	19	0.3	2.71	11.13	2237	20	0.05	1.55	157.98 ± 4.57	11.9 ± 0.25	0.08 ± 0	1.60 ± 0.01
R6	14.64	2393	45	0.11	3	12.43	559	28	0.14	2.51	3.34	1169	32	0.15	2.8	374.78 ± 4.50	24.46 ± 0.19	0.07 ± 0	1.29 ± 0.02
R7	20.57	2104	40	0.11	2.94	18.27	398	24	0.17	2.42	2.49	774	29	0.22	2.67	86.21 ± 2.82	20.12 ± 0.35	0.25 ± 0.01	2.47 ± 0.02
R8	26.77	3309	41	0.07	2.58	19.16	401	27	0.19	2.62	5.76	1983	32	0.09	2.29	598.00 ± 0	21.00 ± 0	0.04 ± 0	1.26 ± 0
R9	22.42	3637	53	0.08	2.39	16.88	431	36	0.23	2.74	6.03	2130	28	0.07	1.85	1081.00 ± 0	32.00 ± 0	0.03 ± 0	1.75 ± 0

* includes multiple stems. S: stem density, BA: Basal area, Nsp: species richness, Nsp_wt: species richness weighted by stem density, D: Shannon Diversity.

Table 2. Correlations between seedling community of the primary and secondary plots, nearest distance to potential seed sources (Dist), aboveground variables (AG), belowground variables (BG) and in-situ large trees community, using multiple factor analysis (MFA). Upper diagonals contained permutational- based p values. Lower diagonals contained RV coefficients.

Matrix	Seedling	BG	AG	Dist	Big trees
Seedling		**0.000**	**0.000**	**0.000**	**0.000**
BG	**0.404**		**0.023**	**0.026**	**0.001**
AG	**0.403**	**0.274**		0.096	**0.000**
Dist	**0.310**	**0.186**	0.129		0.000
Big trees	**0.645**	**0.346**	**0.609**	**0.396**	

Table 3. Redundancy analysis (RDA) on environmental variables and seedling species composition. Adjusted R^2 value is the percentage of variance explained. Significance test of the RDA results (global test) and that of each canonical axes were determined by permuting the results 999 times.

				Cumulative percentages of canonical variance accounted for by axes 1 - 3		
Data Type	**Parsimonious Model**	**Global test**	**Adjusted R^2 value**	**I**	**II**	**III**
pri + sec seedlings	Spe ~ sdV + ECEC + Fern + P + Condition(density)	***	0.165	40.7***	68***	84.2.
sec seedlings	Spe ~ P + pH + AlSat +CN	***	0.155	34.4***	63.1**	83.2*

. P = 0.0551
*P < 0.05
**P < 0.01
***P ≤ 0.001

Table 4. Relative importance (RI) and model-averaged coefficient estimates (MA-Coeff.) of the models. MA-Coeff. were averaged over all models within a subset of models that had accumulated Akaike weight ≤ 0.95. MA-Coeff. of predictor variables that had RI greater than 0.25 and had significant model-averaged coefficients are in bold. P_1 and P_2 are principal components from the two PCAs conducted on AG and BG variables respectively in both primary and secondary forests; P_3 and P_4 are principal components from the PCA conducted on the AG and BG variables respectively in the secondary forests. Refer to Appendix G, Table 1 for PCA results and Appendix G, Table 2 for modeling results with larger dataset (excluded Tmax and sdV).

Data	Interpretation	Predictor	Density		Species Richness		Pri.Spp.		Sec.Spp.		Short-lived Pioneers		Long-lived Pioneers	
Type		Component	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.
Pri + Sec	**High light, maxT, sdV**	**$P_1.A_1$**	0.24	-0.99 ± 0.71	**0.93**	**-2.09 ± 0.51*** **	**1**	**-8.14 ± 0.92*** **	0.19	-0.26 ± 0.34	**0.83**	**4.2 ± 1.06*** **	0.2	0.87 ± 1.32
Seed-	**Low Dif; high fern cover, leaf litter**	**$P_1.A_2$**	**1**	**-5.11 ± 0.47*** **	**0.98**	**-2.01 ± 0.46*** **	**0.3**	**-1.46 ± 0.53** **	**1**	**-6.79 ± 0.59*** **	0.22	-1.53 ± 1.37	**0.49**	**-3.48 ± 1.08** **
lings	**Low TC,TN,TEB, ECEC**	**$P_2.B_1$**	**0.26**	**1.11 ± 0.18*** **	0.18	-0.17 ± 0.5	**0.37**	**1.57 ± 0.53** **	0.2	-0.89 ± 0.25***	0.21	1.53 ± 1.37	0.26	-2.18 ± 1.10.
n = 31	**Low CN, AlSat.**	**$P_2.B_2$**	**0.97**	**4.26 ± 0.36*** **	**0.45**	**1.42 ± 0.63***	**1**	**4.01 ± 0.53*** **	0.23	1.67 ± 0.32***	0.28	-3.13 ± 2.04	**0.42**	**-4.07 ± 1.03*** **
	Low pH, TEB; high P	**$P_2.B_3$**	0.23	1.49 ± 0.33***	0.2	0.71 ± 0.74	0.15	1.08 ± 0.98	0.21	1.61 ± 0.38***	0.18	0.34 ± 2.28	0.17	0.02 ± 1.32
Sec	**High light, maxT, sdV**	**$P_3.A_1$**	0.15	-0.54 ± 0.23*	0.14	-0.21 ± 0.38	0.23	-1.47 ± 1.57	0.14	-0.56 ± 0.29.	**0.26**	**1.71 ± 0.79***	**0.35**	**-2.29 ± 0.81** **
Seed-	**Low Dif; high fern cover, leaf litter**	**$P_3.A_2$**	**0.94**	**-4.36 ± 0.51*** **	**1**	**-2.66 ± 0.59*** **	**0.97**	**-7.65 ± 3.03***	**0.84**	**-4.59 ± 0.61*** **	0.17	-1.17 ± 1.11	**0.46**	**-2.80 ± 0.91** **
lings	**Distance to potential seed sources**	**Dist**	0.27	-0.04 ± 0.01***	**0.79**	**-0.02 ± 0.01***	0.29	-0.06 ± 0.05	**0.29**	**-0.05 ± 0.01*** **	0.19	0.03 ± 0.02	0.13	-0.01 ± 0.01
n = 20	**Low P, TC, TN, TEB, ECEC**	**$P_4.B_1$**	0.14	0.08 ± 0.49	0.42	-0.83 ± 0.51	0.16	0.45 ± 2.09	0.14	0.11 ± 0.67	0.21	2.01 ± 1.2	0.15	0.53 ± 0.97
	Low pH; high CN,	**$P_4.B_2$**	0.14	0.74 ± 0.29*	0.19	0.5 ± 0.58	0.33	-3.01 ± 2.22	0.14	0.76 ± 0.35*	0.15	0.8 ± 1.42	0.17	1.48 ± 0.98
	Low CN; high AlSat., P	**$P_4.B_3$**	0.15	-1 ± 0.27***	0.14	-0.24 ± 0.58	0.48	2.92 ± 1.74	0.14	-0.7 ± 0.62	0.16	-1.11 ± 1.6	**0.29**	**-2.96 ± 1.29***

Figures

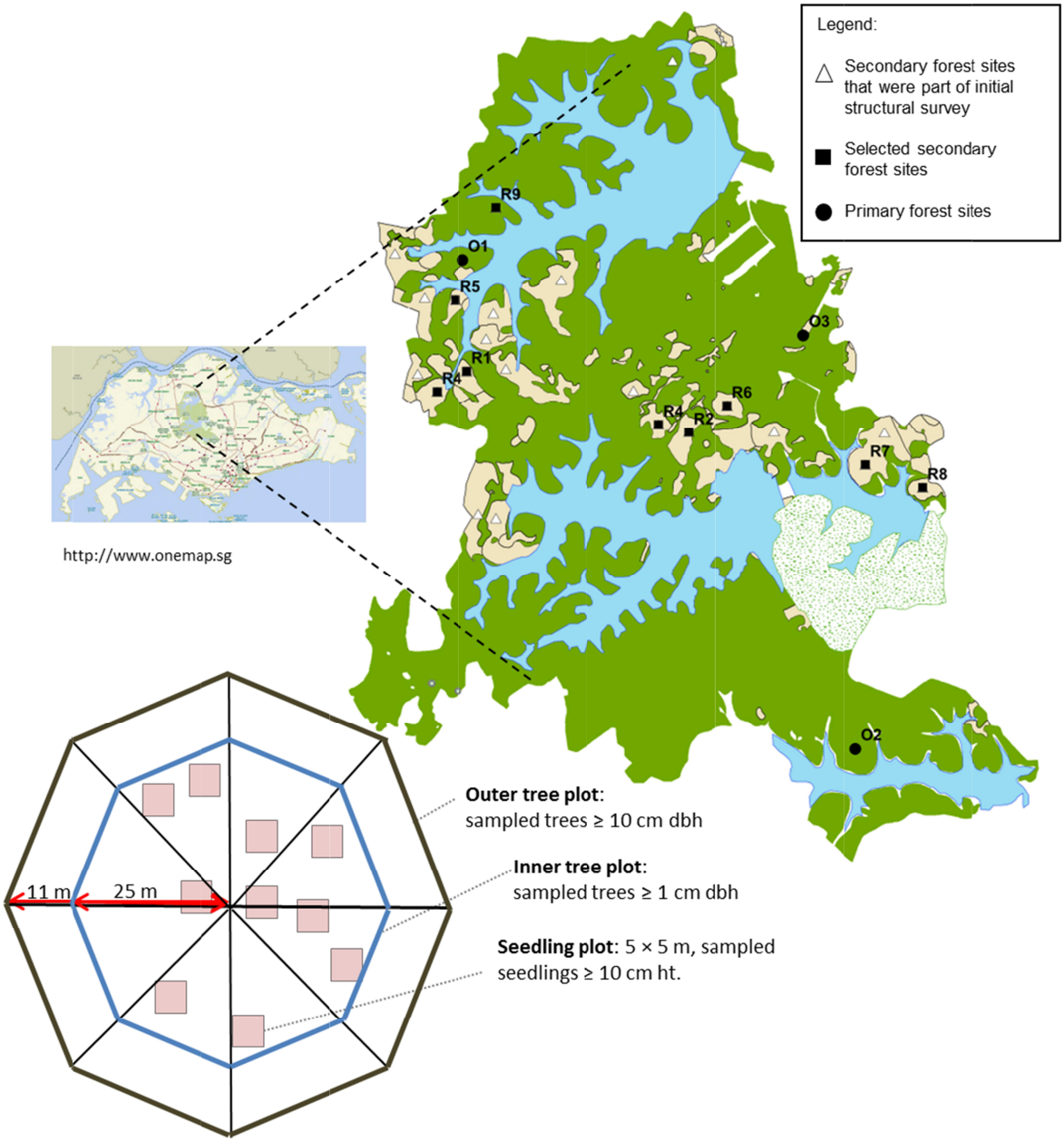


Figure 1. Locations of all secondary forest plots where structural surveys were conducted. Ten of the secondary forest plots and three additional primary forest plots were selected for detailed studies.

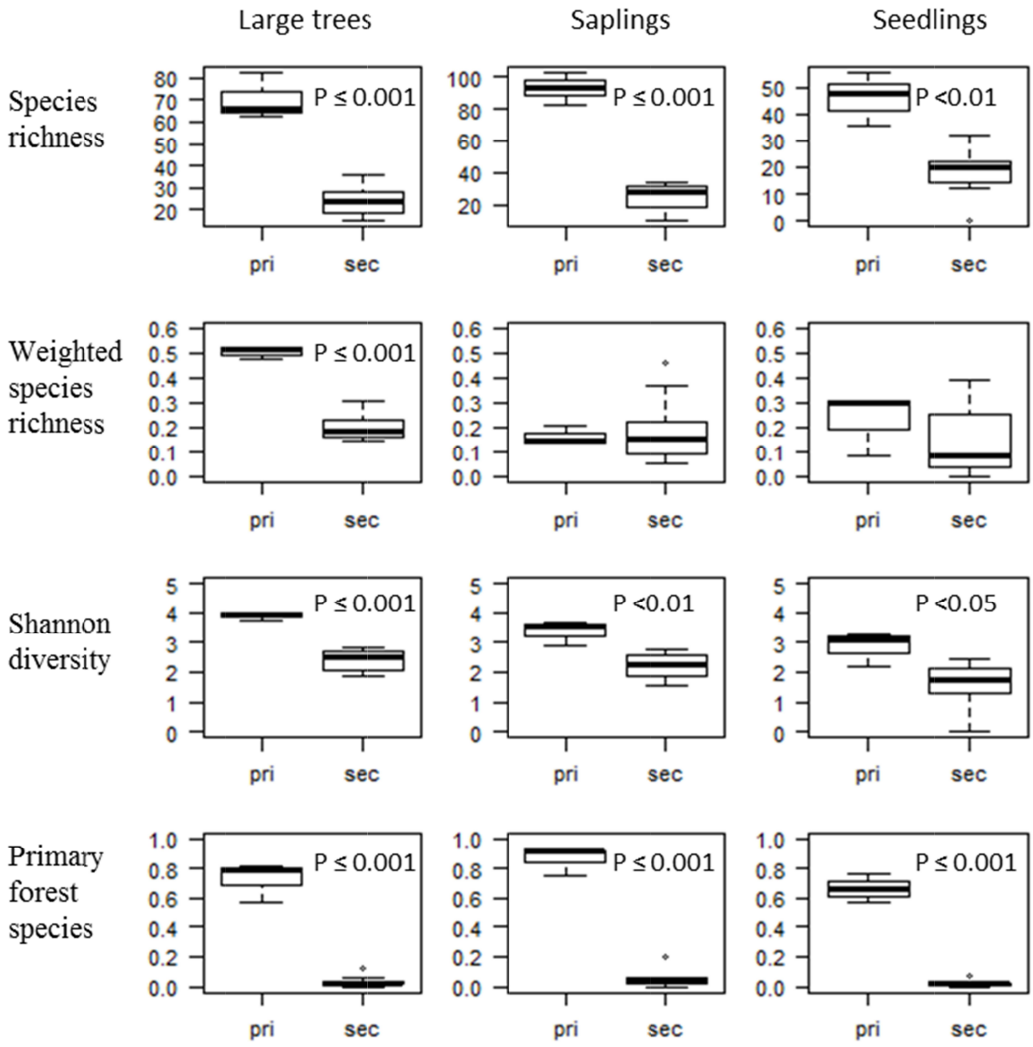


Figure 2. Boxplots of tree density, species richness, weighted species richness (by stem density) and Shannon diversity indices in primary and secondary plots. Values for seedlings are the mean of four 5 × 5 m^2 seedling quadrats, subsampled 100 times from all sampled quadrats at each plot.

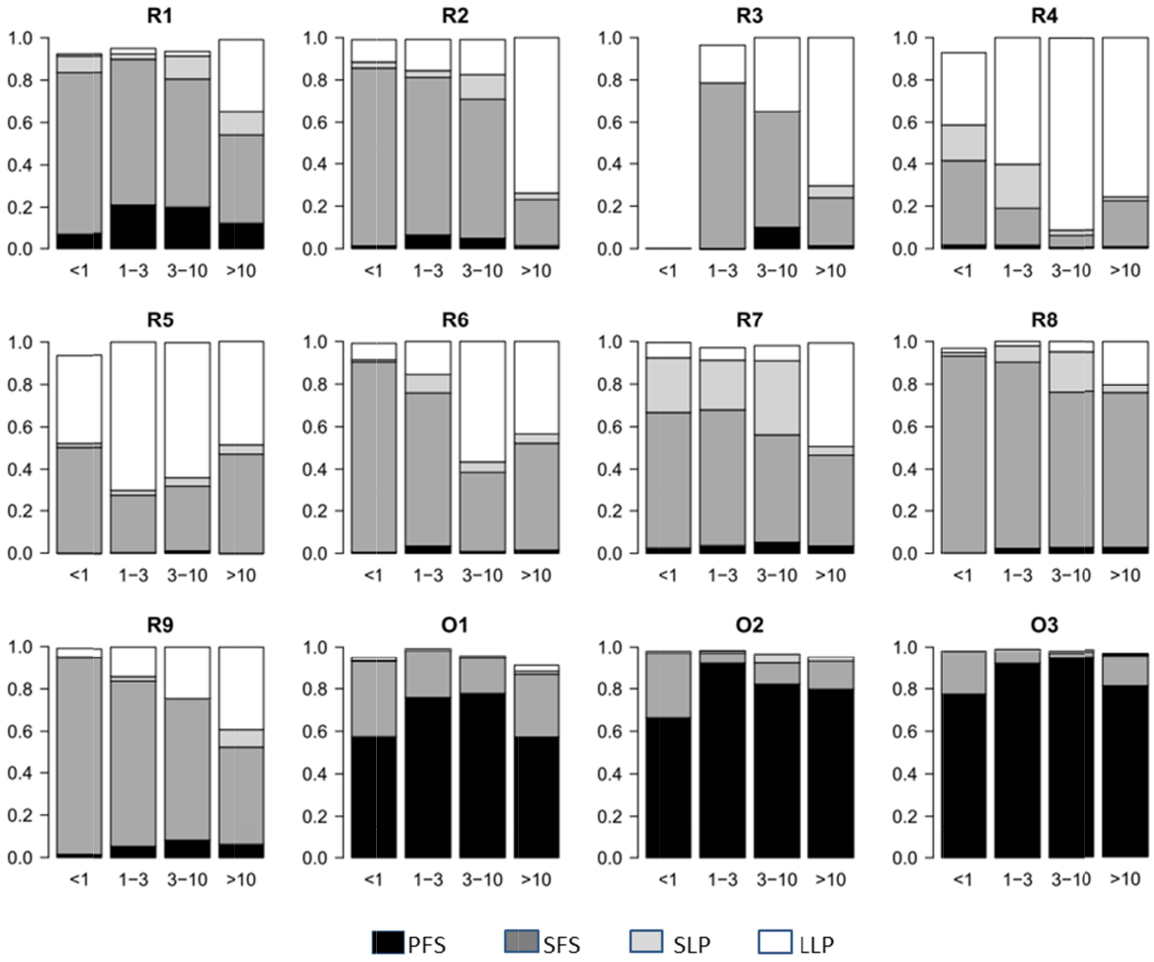


Figure 3. Proportion of primary forest species, secondary forest species, short-lived pioneers and long-lived pioneers by DBH size classes in each survey plot. Pioneers that were not categorized into short-lived or long-lived pioneers due to their intermediary wood density were excluded. The first three sites are fern dominated plots and the last three sites are primary forest plots.

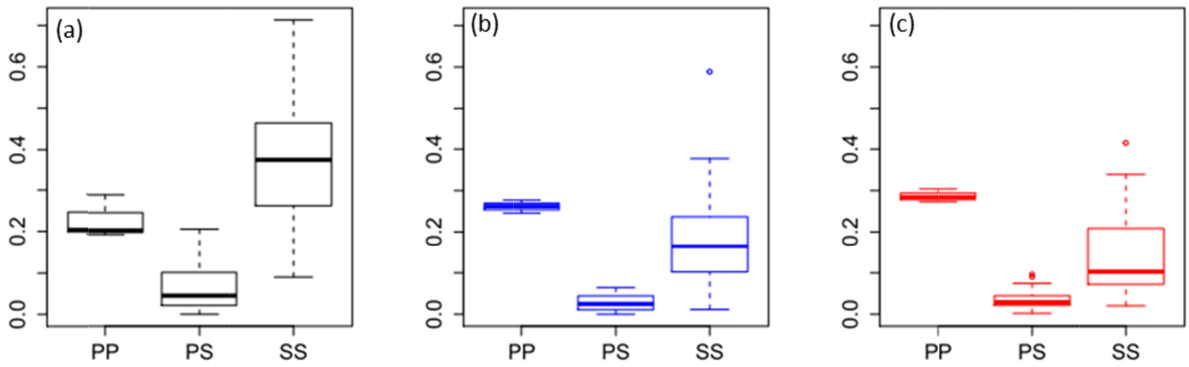


Figure 4. Boxplots showing Bray similarity indices among primary plots (PP), between primary and secondary plots (PS), and among secondary plots (SS) in a) big trees, b) mid-sized trees and c) saplings. Similar results were obtained using Jaccard indices (results not shown).

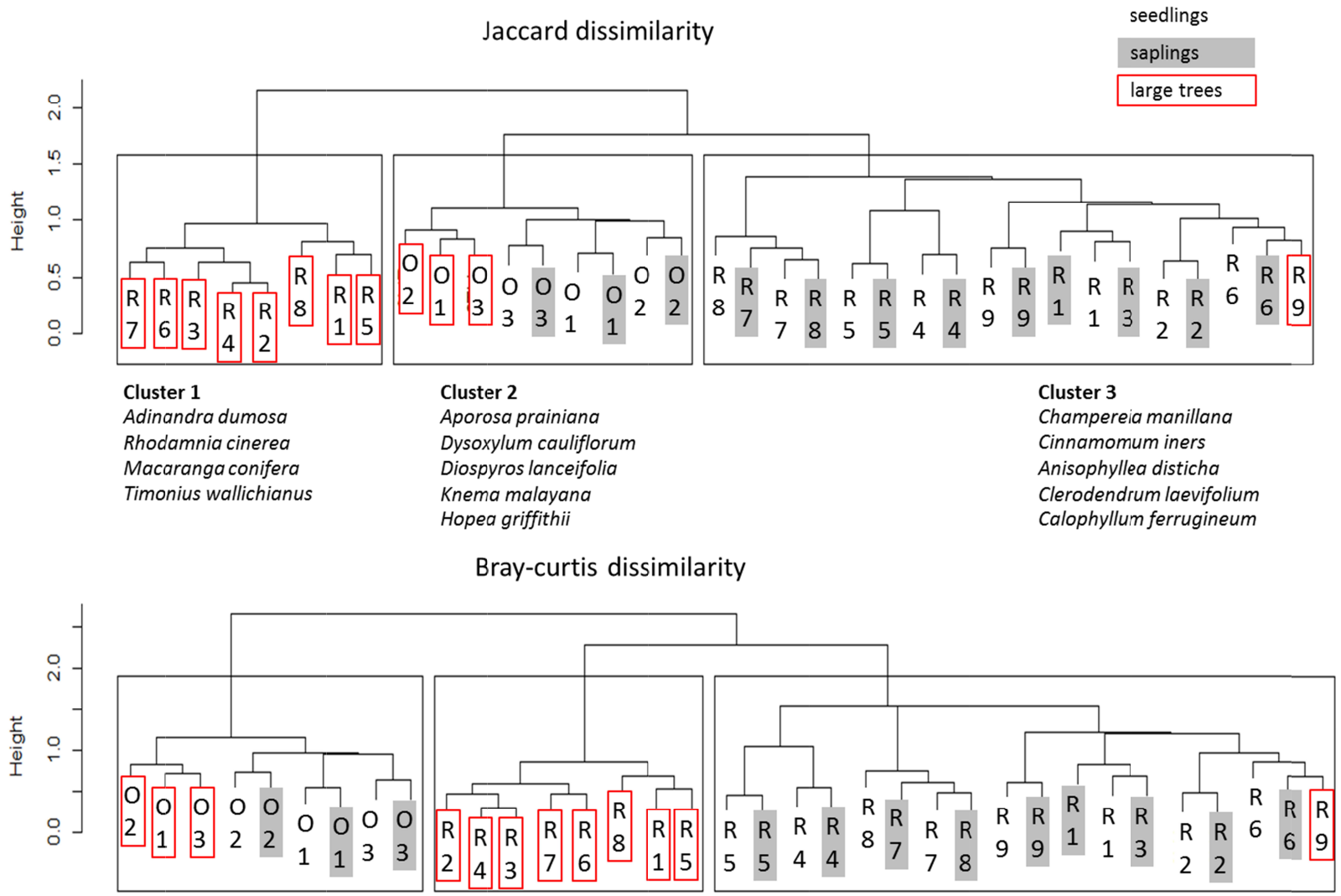


Figure 5. Dendrograms of hierarchical clustering with Ward's minimum variance method on a) Jaccard dissimilarity index and b) Bray-curtis dissimilarity index. Indicator species of the clusters are listed beneath their respective clusters. Plot locations are indicated in Figure 1.

CHAPTER 4. The role of plant functional traits in understanding forest recovery in the secondary forests of the humid tropics

Introduction

After decades of work on forest regeneration, our understanding of and ability to predict secondary forest succession, especially in older secondary forests, is still weak (Guariguata and Ostertag, 2001). The study of forest regeneration during secondary succession, defined here as the complete clearance of forest for human activities (Chazdon, 2008; Guariguata and Ostertag, 2001; Peterson and Carson, 2008), is vital in the tropics today, where secondary forests form the bulk of the tropical landscape due to widespread anthropogenic disturbances (Asner et al., 2009). The potential of these secondary forests to be refugia for biodiversity and to sustain ecosystem functions and services is dependent on their similarity to undisturbed forests. However, tropical forest succession proceeds at varying rates (Corlett, 1995; Finegan, 1996; Letcher and Chazdon, 2009), possibly stagnating over time and taking hundreds of years to converge in terms of species composition to original forests (Finegan, 1996; Guariguata and Ostertag, 2001). Succession may also proceed on different trajectories, resulting in novel ecosystems (Lugo and Helme, 2004).

Current successional theory suggests that as forest regenerates the environment progresses from a high resource state with high light, high nutrient input to a low resource state with low light and low nutrients. Corresponding to the changes in resource levels, fast-growing species that rapidly acquire resources are replaced over time by slow-growing, resource conserving species (Bazzaz and Pickett, 1980; Garnier et al., 2004; Huston and Smith 1987; Odum 1969). Decreasing light especially has been postulated as the main driver (Lohbeck et al., 2013; Wright et al., 2010). However, other studies have documented declining or constant soil nutrients (Feldpausch et al., 2004; Hughes et al., 1999; Johnson et al., 2001) as a forest recovers providing additional support of the change from high to low resource over succession. However, past research have also shown that forests originating on soil with low fertility tend to recover more slowly from disturbances (Corlett, 1991a; Lu et al., 2002), and because of their inherent low fertility, are often colonized by species that are more nutrient conserving (Chua et al., 2013). Overall, we know very little about how resources, in particular soil nutrients, recover after being severely depleted by human disturbances as well as how resources interact with one another to affect the recruitment of plants with different characteristics.

At the same time, succession is an evolving process where the changing structure and diversity of the recovering forest continuously interacts with deterministic (environmental filtering) and stochastic (dispersal events, catastrophic events, etc.) factors to influence subsequent forest dynamics (Huston and Smith 1987). The changing tree community alters the forest environment which favors species whose suite of characteristics is best suited to those conditions. Noble and Slatyer (1980) in particular highlighted the importance of sets of life history traits to predict successional changes. Previous research has also shown that over time as vegetation biomass increases, the influence of existing trees on the regeneration environment, and hence on the colonizing species that could thrive in that environment, become increasingly important (Grime,

1998). Examination of these cause and effect relationships would allow us to gain a more mechanistic understanding of on-going succession in secondary forests.

Plant functional traits offer a way to mechanistically examine interactions between plants and the regeneration environment. Functional traits are defined as biological characteristics that are important for a species' response to the environment (Gitay et al., 1999; Lavorel et al., 1997) and are informative of plant ecological strategies (Westoby and Wright, 2006). For example, fast growing species generally have a suite of traits, such as high specific leaf area (leaf area per mass), leaf nitrogen concentration and low leaf dry matter content (dry mass per fresh mass). These traits facilitate high rates of photosynthesis at low leaf construction cost, but the leaves are often short-lived. In contrast, slow-growing, resource conserving species have leaves with greater longevity and slower photosynthetic returns. This continuum of low cost, fast returns to high cost, slow returns of the leaves has been coined the "leaf economics spectrum"(Reich et al., 1992; Wright et al., 2004). Similarly wood density is related to a trade-off between growth and survival – pioneer species tend to have low stem density with higher hydraulic conductivity, trading low cost wood construction for biomechanic safety, while climax species invest in higher wood density for protection against physical damage and herbivory (Chao et al., 2008; Chave et al., 2009; King et al., 2006).

When scaled up appropriately by biomass (Garnier et al., 2004; Grime, 1998), plant functional traits and other forest stand level characteristics such as stand basal area, are measures of the whole plant community's effect on the environment (Lavorel and Garnier, 2002; Quétier et al., 2007). For example, the leaf economic traits have been found to predict the litter decomposition and hence nutrient cycling in different tropical land use types (Bakker et al., 2011; Cornwell et al., 2008). Thus traits can be categorized into response traits, which are regenerative traits that influence how species respond to their environment, and effect traits that influence biogeochemical processes (Lavorel and Garnier, 2002; Suding et al., 2008). Overlap in response and effect traits occur when the same trait influences a plant's physiological responses and also affect ecosystem processes such as nutrient cycling. Such overlaps tend to accentuate the feedbacks between plants and the environment (Lavorel and Garnier, 2002; Suding et al., 2008). Finally, when applied to tropical forest succession, functional traits offer great potential to understand the unifying processes that drive or inhibit forest regeneration, even among tropical systems with diverse species. However, it has only been recently that traits have been used to measure plant influences on the changing environment over succession (Cortez et al., 2007; Fu et al., 2009; Garnier et al., 2004; Quétier et al., 2007) and very few of these studies have been conducted in tropical rainforest (Lebrija-Trejos et al., 2008; Lohbeck et al., 2013).

To help fill this knowledge gap, our study focused on using selected plant traits to better elucidate the mechanisms driving forest regeneration in the wet tropical rainforests of Singapore. These forests underwent intense agriculture activities from the mid-1800s to 1900. Today, areas that were open areas as depicted by aerial photographs from the 1950s have recovered differently, in terms of species composition and structure, and range from fernlands to tall mature secondary forests (see Chapter 3). Our study builds on previous work (see

Chapter 3), which showed that areas with low light quantity, low vapor pressure deficits, low soil C:N ratio and high aluminum levels strongly favor establishment of primary forest species and were important predictors of forest recovery. We selected traits that both respond to, as well as affect the environment, including those that are part of the leaf economic spectrum, specifically specific leaf area, leaf dry matter content, leaf nitrogen and phosphorus concentration. We also measured concentrations of other leaf nutrients-potassium, calcium and magnesium-which may be affected by aluminum levels, along with leaf C:N and N:P ratios which are indicative of nutrient limitations (Wright et al., 2004). All these traits were examined in both seedlings and adult trees. In addition in adult trees we measured wood density.

Using study plots in both primary and secondary forests, we first examined relationships between these traits in seedlings and environmental variables that we had previously shown affect seedling regeneration (see Chapter 3). We focused on the seedling stage because environmental filtering at the seedling stage has been shown to have long-lasting effects on plant ecological strategies and the overall community assembly process (Grubb, 1977; Poorter, 2007). Next, we investigated the linkages among seedlings traits, adult tree traits and the environmental variables in the secondary forests plots, and how those linkages related to measures of recovery in terms of seedling and saplings' species richness and stem density.

Our research was guided by the following questions:

1. How do seedling functional traits vary at different stages of forest recovery?
2. Are there key environmental factors that explain the variation in seedling functional traits?
3. Within the secondary forests, how do linkages among environmental variables and functional traits at the seedlings and adult trees level relate to forest recovery in terms of the species richness and stem density of saplings and seedlings?

Methods

Site description

Our study was located in the Central Catchment Nature Reserve (CCNR) (1° 22' 32.0514", 103° 48' 13.0674"), Singapore. The mean temperature is 27.0°C and the mean annual rainfall is 2353 mm, with no month having less than 150 mm of rain on average (National Environment Agency, Singapore). The terrain is gently undulating and elevations of the study sites ranged from 25 – 55 m. The CCNR overlays the Bukit Timah/Central Singapore granite, which has given rise to Typic Paleudults soils of the Rengam series (Ives, 1977). The high tropical rainfall has resulted in infertile, acidic soils that are particularly low in phosphorus (Thomas, 1991). The original forests are an extension of the lowland Dipterocarp forests in the Malay Peninsula. Rapid deforestation took place in the 19th century with the arrival of the British, which resulted in an influx of migrants and the spread of cash crops. Forests were often first cleared for gambier (*Uncaria gambier*) and pepper plantations, although the precise history of our plots remains unclear. As Singapore urbanized into the twentieth century, farming activities ceased and the remaining forests were left to regenerate naturally, culminating in the establishment of nature reserves in

1951. Today, the reserve encompasses 2000-ha, including pockets of primary Dipterocarp forests, 60 – 100 year old secondary forests and four water reservoirs. (For more study area details see Chapter 3)

Plot selection and sampling design

Our plot selection was based on forest structural maps that were created from stereoscopic aerial photographs taken from 1950-1952 and a forest structural classification by Turner et al. (1996). We selected nine plots that were open vegetation (class O, no canopy) in 1950s, and are today representative of three structural classes, namely class O, class S (small pole trees) and class M (tall mature secondary forests). Three primary forest plots were also selected for comparison. At each site, we laid out an octahedral plot, 50 m across, within which seedling quadrats of 5 × 5 m were established and all seedlings ≥ 10 cm in height and <1 cm DBH were surveyed. We surveyed a minimum of four seedling quadrats. Thereafter, the survey stopped with a maximum of 200 seedlings or a maximum of 20 quadrats.

We carried out environmental measurements in a subset of seedling quadrats, four quadrats in all the plots except for two class O plots that had only three quadrats. The quadrats for environmental measurements were selected based on high species dissimilarity, determined using NMDS ordination of seedling species composition. In order to include trees that could have influenced abiotic conditions and seedling regeneration, we identified, measured and tagged all trees ≥ 10 cm diameter at breast height (DBH) within the 50 m plot, as well as in an additional 11m buffer strip (Figure 1). Tree species were cross referenced with specimens from the Singapore Herbarium (SING).

Environmental variables

In each selected seedling quadrat we measured characteristics of the immediate aboveground (AG) and belowground (BG) environment that are likely influencing the growth and performance of seedlings (together the "regeneration environment"). Aboveground, we logged from March 2012 to March 2013 the relative humidity and air temperatures of the selected seedling quadrats using iButton^{R} sensors (model DS1923), which were housed in perforated plastic cups and placed 1m from the ground. The iButtons readings are accurate to 0.0625 ^{o}C and 0.04% relative humidity (Maxim Integrated Products 2009). The measurements were logged every 30 minutes for the first five months, and then every 60 minutes for the next seven months. We used means of daily maximum temperature (maxT) and means of daily standard deviation of vapor pressure deficit (sdV) in the analyses.

We quantified the canopy structure and gap light transmission by dividing the seedling quadrat into four equal subquadrats, and taking hemispherical photographs from a height of 90 cm in the center of each subquadrat, as well as center of the entire seedling quadrat. We used a 4.5 mm F2.8 Ex DC Circular Fisheye HSM Sigma DC Lens mounted on a Cannon digital SLR Camera. The photographs were analyzed using the Gap light analyzer software (GLA version 2.0) which calculated the percentage of canopy cover (CnpyO) as well as the amount of direct (Dir) and diffuse (Dif) photosynthetic active radiation transmitted by the canopy (Frazer, Canham, &

Lertzman, 1999; Frazer, Trofymow, & Lertzman, 1997). The means of these light variables were calculated for each seedling quadrat.

From the four subquadrats of each selected seedling quadrat, we collected the top 5 cm organic soil beneath the leaf litter using a 2-cm diameter soil probe. The soils from each seedling quadrat were composited and then air dried. Undecomposed organic materials were removed from the soil. The soils were sent to Soils Laboratory of the Smithsonian Tropical Research Institute and analyzed for resin-extractable phosphorus (P), exchangeable cations (Al, Ca, Fe, K, Mg, Mn and Na) with $BaCl_2$, pH, total carbon (TC) and total nitrogen (TN). We also took four measurements of the leaf litter depth in each of four subquadrats with a stiff measuring tape. The mean leaf litter depth was then calculated for each seedling quadrat. Refer to Chapter 3 for more information on the quantification of the environmental variables.

Plant traits

Seedling leaf traits were collected from both primary and secondary forests (for Q1 and 2) while adult leaf traits were collected only from secondary forest plots (for Q3). In both seedlings and adult trees, we measured seven leaf traits: specific leaf area (SLA), leaf dry matter content (LDMC), leaf concentration of nitrogen (LNC), phosphorus (LPC), potassium, calcium and magnesium, C:N and N:P ratios. Using the survey data, we pre-determined for each plot, the top 70% of the seedling species by stem number and the top 70% of the tree species by basal area. We then collected the leaves from the selected seedling and tree species. Seedling leaf traits which accounted for on average 90% of the seedling density in each quadrat were collected (3-16 species, which constituted 68 -100% of the number of individual seedlings in the 35 quadrats,). Since many of the seedlings had few leaves, we collected one leaf per seedling and composited leaf specimens from an average of three individuals (ranging from 1 – 7) per species per site. All species except one had at least three individuals sampled. Similarly, the adult leaf traits collected accounted for on average 88% of the plot basal area (16 – 21 species per plot, which constituted 77 – 96% of the total tree basal area in the nine secondary forest plots). We focused only on large trees with DBH ≥ 10 cm DBH or trees with total basal area ≥ 78.5 cm^2 (area with DBH = 10 cm), which took into consideration the high coppicing frequency of many local secondary forest trees species. Leaves from the outer crown of the trees were collected using a long pruner, slingshots, or by catapulting an abrasive fishing line and sawing a thin shoot/branch with the line. At least three leaves from each adult tree and at least three to six individuals per species were collected, except for three species where there were less than two individuals in the entire survey. The cut end of the leaves/shoot was wrapped in damp tissues and the specimens were put in Ziploc bags and transported in a cooler box to the laboratory.

Leaf area and mass measurement were done on entire leaves, including the petioles (Cornelissen et al., 2003). The fresh weight of the leaves was measured within six to 24 hours, during which they were stored in damp paper towels and in a refrigerator. Given the wet local climate with frequent thunderstorms at the time of collection, the leaves should have been near saturated fresh weights at the point of measurement. Leaf areas of individual leaf were measured using a desktop scanner and analyzed with the pixel-counting software ImageJ

(http://rsbweb.nih.gov/ij/). The leaves were oven dried for at least 72 hours at 60 ^{o}C prior to measuring the dry masses. Total carbon and total nitrogen content of the leaves were measured using a Thermo Scientific FLASH 2000 NC Analyzer. We used a Perkin Elmer Inductively Coupled Plasma to analyze for other macronutrients in the leaves, including phosphorus, magnesium, calcium and potassium. In total, leaves were collected from 55 seedling species and 27 tree species.

Using these measurements, we calculated specific leaf area (the one-sided area of the fresh leaf divided by its oven-dry mass, $mm^2\ mg^{-1}$) and leaf dry matter content (the oven-dry mass of a leaf divided by its fresh weight, $mg\ g^{-1}$). We also calculated the C:N and N:P stoichiometry of the leaves. Wood density data were taken from the Global Wood Density Database (Chave et al., 2009, Zanne et al. 2009). In all our analysis, species average values were used. We were not able to get leaf trait data for 15 of the 74 seedling species and for these the average values of species within the genus, or the community aggregated means of that quadrat (see below) were used. These 15 species accounted on average, for 5% or less of the seedling abundance in the quadrats in which they occurred. Similarly, for three of the 27 trees species without wood density data, we used average values of species within the genus.

All abbreviations used for the traits and environmental variables are listed in Appendix L and data of mean trait values of seedling and tree species are found in Appendix M.

Statistical analysis

Unless otherwise stated, throughout this paper, "adult traits" refer to community weighted means (cwm) of traits of the adult trees at each plot, while "seedling traits" refer to cwm of traits of seedlings at each quadrat. Following biomass ratio theory (Garnier et al., 2004; Grime, 1998), cwm for each plot or quadrat was calculated as follow:

$$cwm = \sum_{i=1}^{n} p_i \times trait_i$$

For seedling traits, p_i was calculated based on number of individuals for each species relative to the total number of seedlings in each seedling quadrat, while for adult traits, p_i was the sum of basal area of each tree species relative to the total basal area of trees in each plot. Basal area, rather than abundance was used for adult trees, as it more accurately reflects a species' performance under existing conditions and the effects of dominant species on ecosystem processes**.**

For Q1 and Q2, the analysis was sensitive to extraneous variables due to the small sample sizes and the high level of covariation between variables. Thus we used only the environmental variables that were shown to be important from our previous work (see Chapter 3), namely soil phosphorus, C:N ratio, exchangeable Al and Alsat, along with soil potassium, an important plant nutrient. Although fluctuation in vapor pressure deficit was shown to be an important variable based on previous work, we replaced it with canopy openness, which was highly correlated to sdV (r^2 =0.71, P <0.001). This was because many of the iButtons were lost or malfunctioned. For

Q3, as we were interested in the broad linkages between adult traits, seedling traits and the environmental variables, we included all the environmental variables mentioned above.

We used a combination of the RLQ and the fourth-corner method (Dolédec et al., 1996; Dray and Legendre, 2008; Dray et al., 2014; Legendre et al., n.d.; ter Braak et al., 2012) to answer Q1 and Q2. We carried out the analysis using relative abundance of seedlings species. RLQ simultaneously ordinates site × environmental variable data (table R), site × species data (table L) species × trait variable data (table Q) to identify the main multivariate patterns between the environmental gradients and the plant traits, as influenced by the relative abundance of the seedlings. The fourth corner method may then be applied to the RLQ ordination scores to test for significant correlations between multivariate structures of the traits and environmental variables. The fourth corner method is more precise than simple regression as it uses two models to explicitly test the relationships between the environmental variables with species abundance, as well as that between species abundance and plant traits.

In more detail, an RLQ analysis begins with separate ordinations of the three tables - correspondence analysis (CA) for table L, and principal component analyses (PCA) for table R and Q (since they contain only quantitative variables). The traits in table Q and the environmental variables in table R are then weighted by the sites and species weights obtained from the correspondence analysis of table L. From these a fourth site × trait matrix is calculated by using a linear combinations of the environmental variables and the trait variables so as to maximize their squared cross-covariance (Dray et al., 2014). Next, the fourth corner method may be used to test the correlation between 1) the RLQ sample scores (Axis R1/Axis R2, corresponding to the environmental gradients) and species trait (table Q) and 2) the RLQ species scores (Axis Q1/Axis Q2, corresponding to the trait variables) and the environmental variables (table R). In order to assess the trait trends of secondary and primary forest species, we also broadly categorized the surveyed species based on Tree Flora of Malaya Volume 1- 4 (Whitmore 1972a, 1972b, Ng 1978; Ng 1989), Wayside trees of Malaya Volume 1 and 2 (Corner 1988) and online web resources (Slik 2009) (Appendix L).

Significance of the correlation was then tested by comparing the observed test statistic to its predicted distribution under null hypotheses. In our analysis, we used two null models, Model 2 and Model 4, as proposed by Dray and Legendre (2008). Model 2 permutes the rows of table L (or rows of R) and tests for the non-random distribution of species with fixed traits. Model 4 permutes the columns of L (or rows of Q) and tests for the influence of traits on the species composition under given environmental conditions (Dray and Legendre, 2008; Dray et al., 2014). The global statistical significance of the correlation is significant if the larger of the two P values from both models is lower than α=0.05 (ter Braak et al., 2012). In our case the false discovery rate method (FDR; Benjamini and Hochberg 1995) was used to adjust P values for the multiple testing. We used the ade4 R package (Dray and Dufour 2007) for both the RLQ and fourth corner methods.

To answer Q3, we performed Multiple Factor Analysis (MFA) (Borcard et al. 2011,Carlson et al., 2010, Escofier and Pagès 1994) to first explore the overall correlation among seedling traits,

adult traits and environmental variables within secondary forests only. Total basal area of the plot was used as a proxy for stand structure and was also included as an adult trait. MFA is identical to a PCA performed on all three set of variables simultaneous with each of the three data subset weighted (Borcard et. al. 2011). The RV coefficient which ranges from 0 – 1 is used to assess the correlation of the three sets of variables and is tested by permutations (Borcard et al 2011; Josse et al., 2008). We used the R package FactoMineR (Husson et. al. 2013) for the MFA analysis. Finally, we plotted the relationships of the most significant $Ptrait_{agg}$, $Qtrait_{agg}$ and environmental variables with the seedling and sapling species richness.

All statistical analyses were done using R statistical software v3.0.2. (R Development Core Team, 2013).

Results

Q1 & Q2. Seedling functional traits and key environmental factors over transition from secondary to primary forests

We found that overall seedling traits and the environmental variables in the secondary and primary forests were significantly correlated when analyzed using species abundance (P = 0.0085 for Model 2 and P = 0.021 for Model 4). The first two RLQ axes explain 73.1% and 17.0% respectively of the cross-covariance between the seedling traits and the environmental variables (Figure 1). The first RLQ axis reflects a forest recovery gradient. It corresponds to a transition of seedling quadrats in secondary forests to those in primary forest of decreasing disturbance (Figure 1a), as well as an increase in seedling species richness and density (Figure 2). In general, moving along this axis, leaf foliar nitrogen (Figure 3a), and to a lesser extent phosphorus concentration (adjusted P < 0.1, Figure 3c), increased from secondary to primary forests (Figure 1a and 1e). Similarly, there was a weaker trend of decreasing leaf C:N ratio from secondary to primary forests (adjusted P < 0.1, Figure 3c). Although there was a large amount of trait variation in both secondary and primary forest species (Figure 1c), common secondary species such as *Calophyllum* spp. (e.g. Ca.pc, Ca.tj) and *Rhodamnia cinerea* (Rh.ci) had low leaf nitrogen and phosphorus concentration and high leaf C:N ratio while the opposite was true for primary forest species such as *Nephelium costatum* (Ne.co) and *Strombosia javanica* (St.ja). Correspondingly, light quantity, exchangeable aluminum and aluminum saturation decreased from secondary forests that have poorer recovery of stand structure to primary forests, along with a weaker trend of decreasing soil C:N ratio (Figure 1b, 3b and 3d). The second RLQ axis corresponds to species with high leaf dry matter content and leaf N:P ratio that were found in habitats with low soil potassium and available phosphorus (Figure 1b). However this relationship was not significant.

Q3. Linkages among seedling traits, adult traits and environmental variables and how they relate to forest recovery in secondary forests

The first three axes of the MFA explained more than 65% of the total variance in the combined datasets (Figure 4). Within the secondary forests, seedling traits were more strongly correlated to adult traits (RV = 0.387, P = 0.001) than to environmental variables (RV =0.246, P = 0.03) (Table 2).

The seedling traits formed an axis that corresponds to a gradient of high to low resource acquisition traits (Figure 4a, 4b), going from high specific leaf area, high leaf phosphorus, nitrogen, magnesium and potassium concentration to high C:N and N:P ratio and LDMC. Of the aboveground environmental variables, resource acquisition traits at the quadrat level were negatively correlated with light, fluctuating vapor pressure deficits and leaf litter depth (Figure 4a and 4b). Seedling foliar nutrients were strongly positively correlated with Al saturation (Figure 4a and 4b), which differed from the RLQ results obtained using data from both primary and secondary plots. Adult leaf traits followed similar trends as seedling traits (Figure 4a, 4b). In general, seedlings specific leaf area, adult trees C:N ratio, soil C:N ratio and leaf litter depth were positively correlated to one another (Figure 4a and 4c). Simple bivariate plots showed that of these correlations, the C:N ratio of adult trees was strongly correlated to leaf litter depth, which in turn was strongly correlated to soil C:N ratio (See Appendix N). The adult traits were only weakly correlated to the environmental variables influencing seedling regeneration, despite the overall high correlation between adult traits and the environmental variables (RV = 0.48, $P<0.001$, Table 2). This was because soil nutrient measures, aside from C:N ratio, were either uncorrelated (P, K) or negatively correlated (Ca, Mg) to the foliar nutrients of adult trees, while stand basal area was only weakly correlated to light quantity and vapor pressure deficits (Figure 4a and 4b). Finally, high soil nutrients (soil available P and low soil C:N ratio) was positively correlated with increased stand basal area (Figure 4b and 4c).

At the seedling stage, species richness and density decreased in quadrats with high soil C:N ratio, high leaf litter depth, high quadrat SLA and low stand basal area (Figure 5c and 5f, see Figure 4c for the position of soil C:N ratio and leaf litter depth in the global PCA). These trends remain apparent in the sapling species richness (Figure 6c). The combined effect of high Al saturation and low available phosphorus decreased saplings' species richness (Figure 6b) but not sapling density, as some sites had high sapling density despite low species count (Figure 5e and 6e). A similar weaker trend could be seen in the seedling species richness (Figure 5b). Overall trends of seedling or tree traits with seedling and sapling species richness or stem density were not as apparent as those of environmental variables.

Discussion

We investigated the degree to which plant functional traits and environmental gradients explained the varied recovery status of similarly-aged secondary forests in Singapore. Overall, we found indications that plants are likely more nutrient constrained in the secondary forests as compared to the primary forest. Moving from primary to secondary forest, light availability decreased and soil aluminum levels increased. Below, we discuss in detail the implications of these for forest regeneration on acidic soils. In addition, within the secondary forests, we found that low soil nutrients and high aluminum saturation best explained the poor forest recovery, measured in terms of species richness and stem density of seedlings and saplings. In contrast the measured seedling traits did not correlate to those recovery measures. This differed from the overall trends we found in the primary and secondary forests, and can be attributed to the

ability of the few specialists of degraded soil that could accrue surprisingly high foliar nutrients despite the high aluminum saturation and low nutrients soils.

Several of our findings indicate that the secondary forests are likely more nutrient constrained than the primary forests, which has consequences for forest recovery. This was supported by the increase of quadrat level foliar nitrogen and (to a lesser extent) phosphorus concentrations, from the poorer recovering secondary forests to the primary forests (Figure 1, 2 and 3). At the same time, seedlings with tough leaves that last longer, as indicated by leaf dry matter content, were equally prevalent in both primary and secondary forests that were more P than N limited. This was shown by the strong correlation between seedlings' LDMC and leaf N:P ratio (Figure 1e). (Note as that in the very low nutrient secondary forest plots, seedlings SLA had a surprisingly stronger response to light instead of to soil nutrients, as explained later in the discussion, and thus SLA did not explain very well the overall trait variation in all the seedling quadrats.) All the above indicates that many species in both primary and secondary forests tend to minimize wastage of resources for slower but longer term photosynthetic returns. These results that suggest that secondary forests are more nutrient constrained than primary forests differ from previous work, which suggested that as forests regenerate, light and soil resources decrease, leading to a change from resource acquisition to resource conserving traits (Anten and Selaya, 2011b; Garnier et al., 2004; Lohbeck et al., 2013; Wright et al., 2010). A prevalence of resource conserving traits might be expected in these older secondary forests, which are at least 60 years old. However, our results showed that low foliar N and P at the quadrat level, as well as the corresponding environmental variables, were significantly correlated to poor forest recovery (Figure 2, represented by the first RLQ axis). Resource conserving traits are part of a set of co-occurring life history traits that include slower plant growth and greater longevity (Poorter, 2007; Westoby et al., 2002; Wright et al., 2004), which lead to slower species replacement and hence slower rates of succession (Finegan, 1996). In addition, many of these traits - low foliar N, P and high LDMC and C:N ratio, have been found to slow litter decomposition (Cornwell et al., 2008; Cortez et al., 2007; Kurokawa et al., 2010; Parsons and Congdon, 2008, Paul and Clark 1989) and thus nutrient returns, which would further select for nutrient conserving species. The weak positive correlation between soil C:N ratio and quadrat level C:N ratio found in our study sites suggests that this positive feedback is possible (Figure 3b).

Although the prevalence of resource conserving strategies among many secondary forest species in Singapore concurs with previous research, which emphasized the deleterious effects that past agricultural activities had on soil fertility and forest recovery (Corlett, 1991a; Sim et al., 1992), little is known about the important environmental factors. Interestingly, we found that differences in aluminum levels between primary and secondary forests appear to be an important factor that explains in part the slow recovery. Phytotoxic aluminum is prevalent in acidic tropical soils, as low pH increases the dissolution of aluminum, which primarily affects root functions and uptake of nutrients (Kochian et al., 2005; Rengel, 2004; Sanchez and Buol, 1975). Thus, aluminum toxicity is an important constraint for agriculture on acidic soil. However, native tropical rainforest plants that have evolved on acidic soil have been found to be Al-tolerant, Al-accumulator or even Al-stimulated in terms of growth (Masunaga et al., 1998; Osaki

et al., 1997; Watanabe et al., 2006). Nevertheless, differing levels of aluminum levels appeared to be an important filter for seedlings' response traits as well as forest recovery. It has been shown that intensive agricultural activity can result in soil acidification (Guo et al., 2010), although the relevance of this in soils that are inherently very acidic (pH 3.68-4.16 in our study) is unknown. Moreover, the pH ranges of the primary and secondary forest overlapped. Although both Al and Al saturation were significantly correlated to the low quadrat N and P levels, Al saturation was likely to be the more important factor, as it is the relative quantity of Al^{3+} ions to that of other base cations (Ca^{2+}, Mg^{2+} and K^{+}) at the root plasma membrane, that determines the plant responses (Cronan and Grigal, 1995; Kinraide, 1997). Thus it is possible that torrential tropical rainfall and the loss of tree cover exacerbated the leaching of base cations, which in turn increased aluminum saturation. This might also explain the positive correlation between aluminum and light levels, the latter being an indication of where forest cover is poorer and more leaching of cations by rain would occur. Thus nutrient constraints could account for the unusually low foliar nutrients under high light conditions in these forests.

Turning to the effects that plant functional traits and their linkages with environmental variables have on forest regrowth within secondary forests, we found trends that high soil C:N ratio, increased leaf litter depth and low stand basal area negatively affected seedling establishment, while interactions between high aluminum saturation and low phosphorus decreased saplings' species richness. Seedlings' specific leaf area also increased, probably in response to the lower light conditions beneath the leaf litter. The negative influence of leaf litter agrees with other studies. They found that although some amount of leaf litter could ameliorate microclimate (Baker and Murray, 2010), thick leaf litter was found to negatively affect seedling establishment and growth (Facelli and Pickett, 1991; Metcalfe et al., 1998; Metcalfe and Grubb, 1997). In our study, the correspondingly high soil and C:N ratio (Figure 4a and 4c) of adult trees indicate that slow decomposition has probably led to the thick leaf litter. This was supported by the strong positive simple Pearson correlation between adult C:N ratio to leaf litter depth ($r^2 = 0.67$, $P < 0.001$) and between leaf litter depth and soil C:N ratio ($r^2 = 0.54$, $P < 0.01$) (Appendix N). The soil C:N ratios of our secondary forests (19.70 – 32.08) were much higher than other humid rainforests (Kauffman et al. 1998), including primary and regenerating Dipterocarp forests (See Table 5 in Sim et al. 1992, Abdu et al., 2007; Hamzah et al., 2009; Zaidey et al., 2010). High soil C:N ratio slows microbial breakdown of organic matter and nutrient returns (Paul and Clark 1989); while nutrient efficient plants also tend to produce leaves and leaf litter with high C:N ratio that are slow to decompose. Past research had shown that litter decomposition rates in secondary forests could be similar to primary forests (Barlow et al., 2007) or slower (Mesquita et al., 1998; Parsons and Congdon, 2008), probably as a results of different soil conditions and regenerating species. In our study, slower plant growth and hence lower basal area could also be a result of low soil fertility (Figure 4b and 4c). The poorer regrowth could in turn decrease in-situ seeding opportunities, and has less food resources to attract animal dispersers. At the sapling stage, low soil phosphorus and high aluminum saturation gained importance, as their deleterious effect on species richness was more apparent in sapling than in seedlings (Figure 5b and 6b). It would appear that increase in phosphorus, a known limiting nutrient in tropical soils, allowed for more species to thrive, particularly in soil with high Al saturation. It was also evident from the lesser effects on sapling

density, that the few plant species that could establish on soils with high aluminum and low phosphorus were able to thrive subsequently, resulting in high sapling density (Figure 6e), as elaborated below.

The ability of a few species that could thrive on soil with high aluminum saturation and low phosphorus, and accrete more foliar nutrients than species found at low aluminum saturation (Figure 4b, 5b), may explain in part why seedling traits do not correspond to forest recovery within the secondary forests. In addition, under conditions of high phosphorus, more species were able to have high foliar nutrients even with high aluminum saturation (Figure 4b, 5b). In other words, contrary to the overall trends in primary and secondary forests, where high aluminum levels were correlated with lower seedling foliar N and P concentration and poorer forest growth, in the secondary forests high aluminum saturation was correlated with high foliar nutrients, because of the specialization of some species. Indeed, *Melastoma malabathricum* a common pioneer species of degraded soils in Singapore (Corlett, 1991a; Sim et al., 1992), is not only a hyperaccumulator of aluminum but aluminum stimulates its uptake of phosphorus and hence growth (Osaki et al., 1997), and also reduces iron toxicity to the plant (Watanabe et al., 2001). *M. malabathricum* seedlings are also found in relatively high abundance in two of our sites with high aluminum saturation. Other notably species in our plots that could assimilate relatively high foliar N and P under comparatively low soil nutrients conditions were *Dillenia suffruticosa* and *Champereia manillana* (Appendix O). *D. suffruticosa* in particular, is another common species in the degraded forests. Its rapid clonal growth resulted in high sapling density in plots that have high aluminum saturation and low phosphorus, as the off shoots of *D. suffruticosa* are difficult to distinguish from parent plants, and were enumerated as individuals in the study.

Finally, our research shows the importance of measuring environmental variables along with the plant functional traits, in order to elucidate possible mechanisms driving forest succession, as plant functional traits reflect the strategies of successful seedlings and not necessarily the overall forest recovery. For example, our measured plant traits showed that successful seedlings in the degraded secondary forest with low nutrients and high aluminum saturation were able to maintain high foliar nutrients. Thus, nutrients were not a constraint to the successful seedlings, but soil factors were important to forest recovery. The seedlings traits instead were more responsive to light and possibly drought stress, as indicated by the strong correlation of tougher seedling leaves to light and fluctuations in vapor pressure deficits (Figure 4a and 4b). At the same time, for seedlings growing in degraded soils with thick leaf litter, the carbon cost is high for seedlings to maintain high leaf area to maximize light capture, and yet have thick nutrient conserving leaves. Thus we observed high seedling specific leaf area and low LDMC in thick leaf litter and high soil C:N ratio (Figure 4a and 4c), and only seedlings that could take up nutrients despite the soil conditions, appear to be successful. This also explained the non-significant relationships of seedling SLA with light, leaf litter depth and soil nutrients. Seedling LDMC exhibited similar trends, except for its significant negative correlation with soil C:N ratio, which again indirectly highlighted the importance of light vs. soil nutrients (Appendix N).

Summary

Aluminum saturation appears to play a larger role than previously suspected in tropical succession on acidic, degraded soil. Although tropical plants have evolved on acidic and high aluminum soils, we found that 60 years after regenerating from intensive agricultural activities, poor forest regrowth was correlated with high soil aluminum levels, which appear to affect nutrient uptake in plants, and result in lower leaf nitrogen concentrations in the poorly recovering forest as compared to primary forests. Succession is thus slowed by a positive feedback loop of slower nutrient returns from slow decaying litter and further recruitment of nutrient conserving species. Low nutrients and high aluminum saturation were negatively correlated with seedling and sapling recovery in the secondary forests. Transplanting experiments of primary forest seedlings to the degraded secondary forests would help to elucidate the extent that soil conditions, vs. dispersal really limit the establishment of primary forest species.

We found that many of the plant foliar nutrients of both adult trees and seedlings (P, K, Ca, Mg) were largely invariant of soil nutrients, indicating that the plants are well adapted and able to uptake sufficient nutrients regardless of their environment. The most interesting of which, is the ability of the Al tolerant and Al accumulating species in the degraded secondary forests to accrue higher foliar nutrients than seedlings in soils with low aluminum saturation. Future research tracing the fate of the nutrients, as well as aluminum, as they cycle through the plants and dead organic matter, along with the roles of soil microbes, would probably yield much insight into nutrient recovery and its effects on forest succession. Finally, while plant functional traits reflect strategies of plants in their environment, we advocate that it is crucial to concurrently measure environmental variables for a more complete understanding of the driving factors in succession.

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Tables

Table 1. List of abbreviation used for trait and environmental variables.

Variable	Abbreviation	Name
Plant traits*	BA[+]	Total basal area of plot
	CN	Leaf C:N ratio
	K	Leaf potassium concentration
	LDMC	Leaf dry matter content
	LNC	Leaf nitrogen concentration
	LPC	Leaf phosphorus concentration
	Mg	Leaf magnesium concentration
	NP	N:P ratio
	SLA	Specific leaf area
	Wd	Wood density/specific stem density
Environmental variables	Al	Soil exchangeable aluminum
	Alsat	Soil aluminum saturation
	Ca	Soil exchangeable calcium
	CN	Soil C:N ratio
	Cnopy	Canopy Openness
	K	Soil exchangeaebl potassium
	LL	Leaf litter depth
	Mg	Soil exchangeable magnesium
	P	Soil available phosphorus (resin extracted)
	sdV	Mean standard deviation of daily vapor pressure deficits

*Seedling traits end with suffix ".x" and adult traits end with suffix ".y"

[+] Plot total basal area is not a functional trait but in our MFA analysis, we included it to test the effects of adult trees on environmental variables

Table 2. Correlations between seedling traits, adult traits and environmental variables in the secondary forests using multiple factor analysis (MFA) Upper diagonals contained permutational- based p values. Lower diagonals contained RV coefficients.

	Seedling traits	Adult traits	Env. variables
Seedling traits		***	*
Adult traits	0.387		***
Env. variables	0.236	0.517	

* P <0.05

*** P ≤ 0.001

Figures

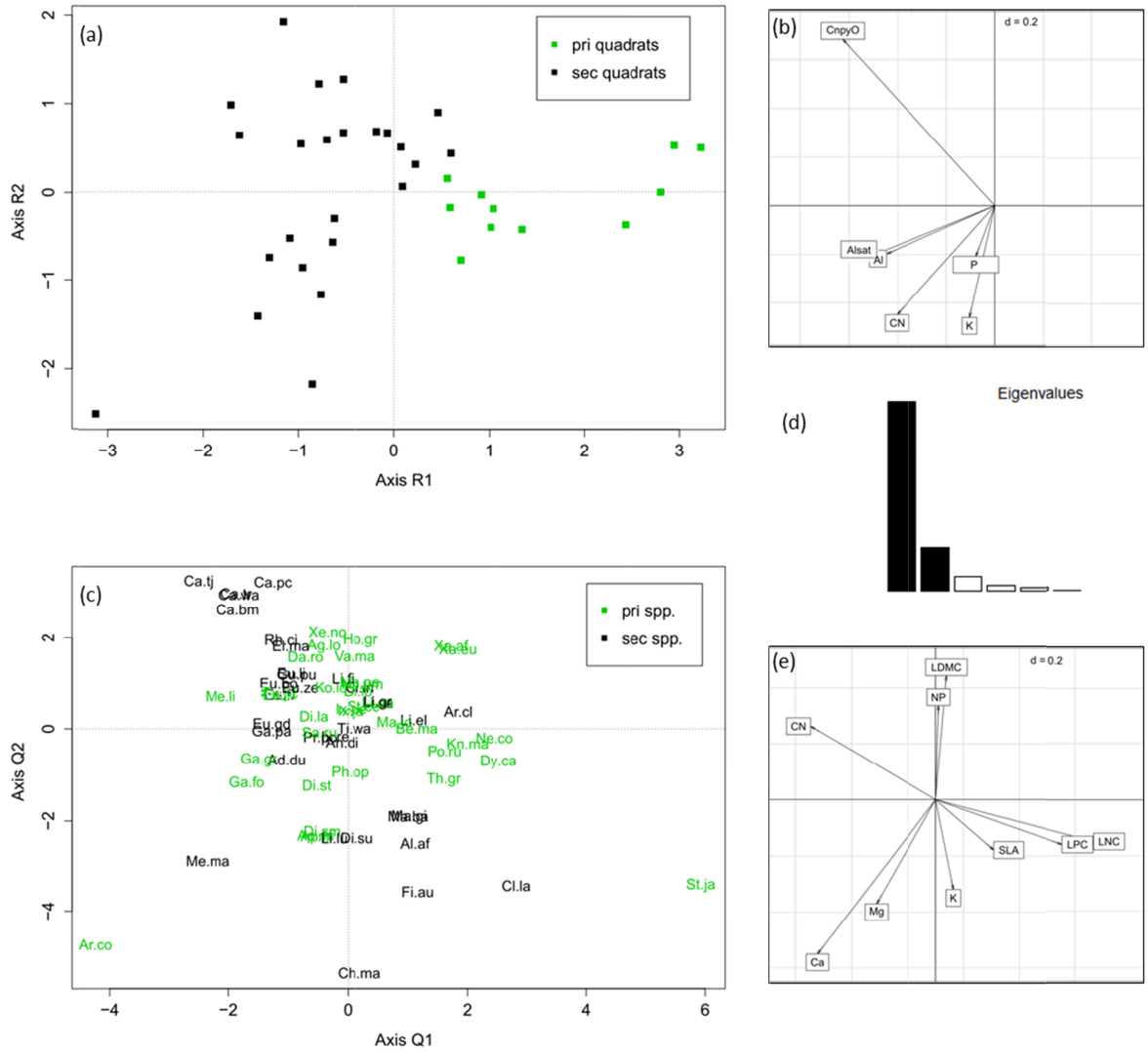


Figure 1. Results of RLQ analysis: (a) distribution of the seedling quadrats by the R (environmental variables) row scores, (b) coefficients for the environmental variables, (c) distribution of species by Q (seedling traits) row scores, (d) the eigenvalues of the first two axes, as indicated in black. See Appendix L for species names corresponding to the species code, and (e) coefficients for traits. Note that values of "d" give the grid size for (b) and (e).

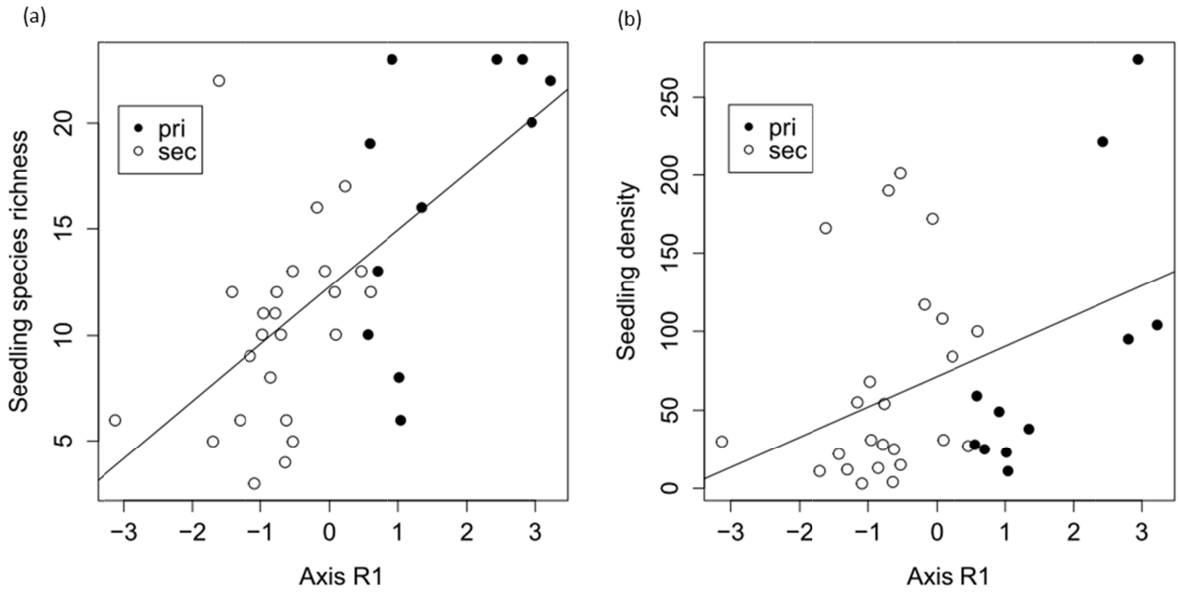


Figure 2. Correlation of the first RLQ axis for environmental variables (Axis R1) with (a) seedling species richness (b) and density of the quadrats in primary and secondary forests.

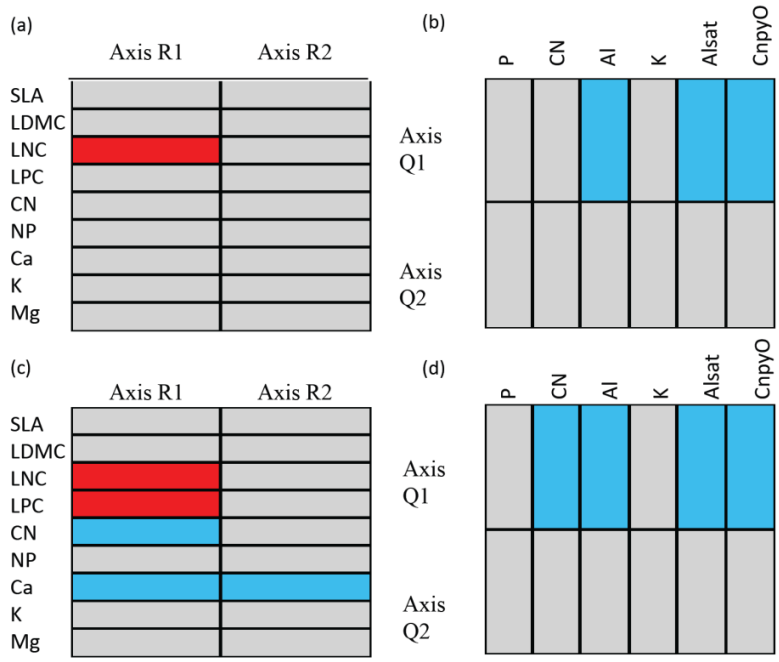


Figure 3. Results of fourth-corner tests between (a) seedling traits and the first two RLQ axes for environmental gradients (Axis R 1/Axis R 2), (b) environmental variables and the first two RLQ axes for seedling traits (Axis Q 1 and Axis Q 2) at adjusted P = 0.05. (c) and (d) show the same tests as (a) and (b) respectively, but at adjusted P = 0.1. Significant positive associations are represented by red cells and significant negative associations by blue cells.

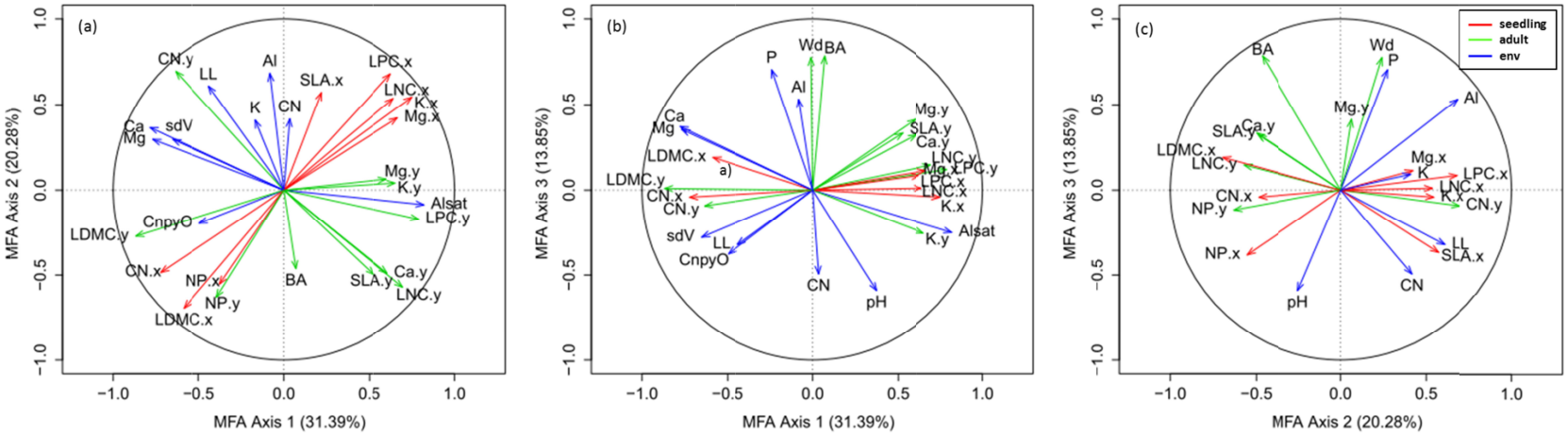


Figure 4. Global PCA plots from Mulitple Factors Analysis showing correlations of traits and environmental variables that are significant at P=0.05. Seedling traits end with suffix ".x" and adult traits end with suffix ".y". Abbreviations used are listed in Table 1.

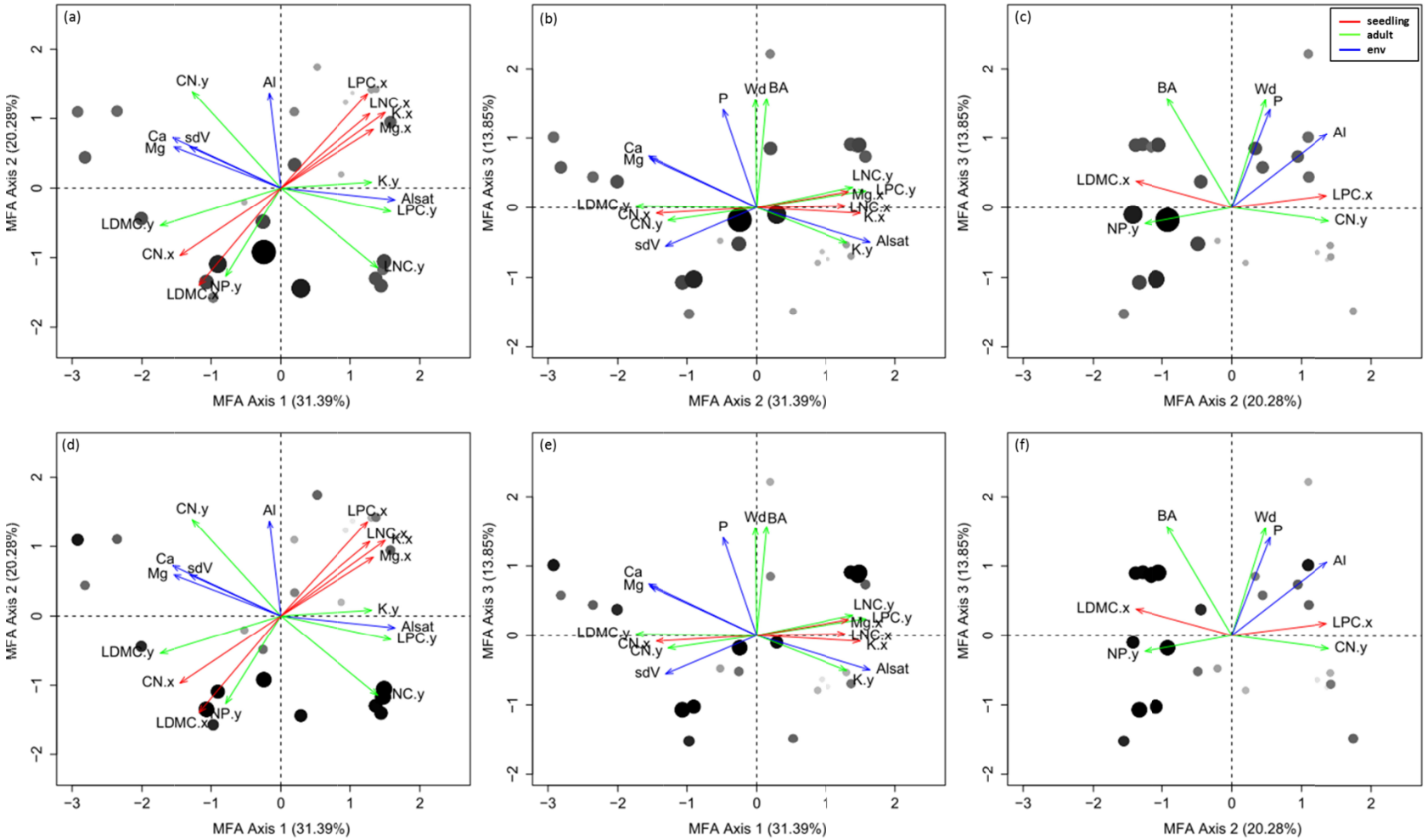


Figure 5. Global PCA biplot showing the distribution of seedling quadrats by the traits and environmental variables, as correlated to the first thre MFA axes. Top three panels (a – c) show point size scaled by seedling species richness and the bottom three panels (d – e) and by seedling density . Only variables that are significant at P=0.001 are shown here. Refer to Figure 4 for the location of other variables. Seedling traits end with suffix ".x" and adult traits end with suffix ".y". Abbreviations used are listed in Table 1.

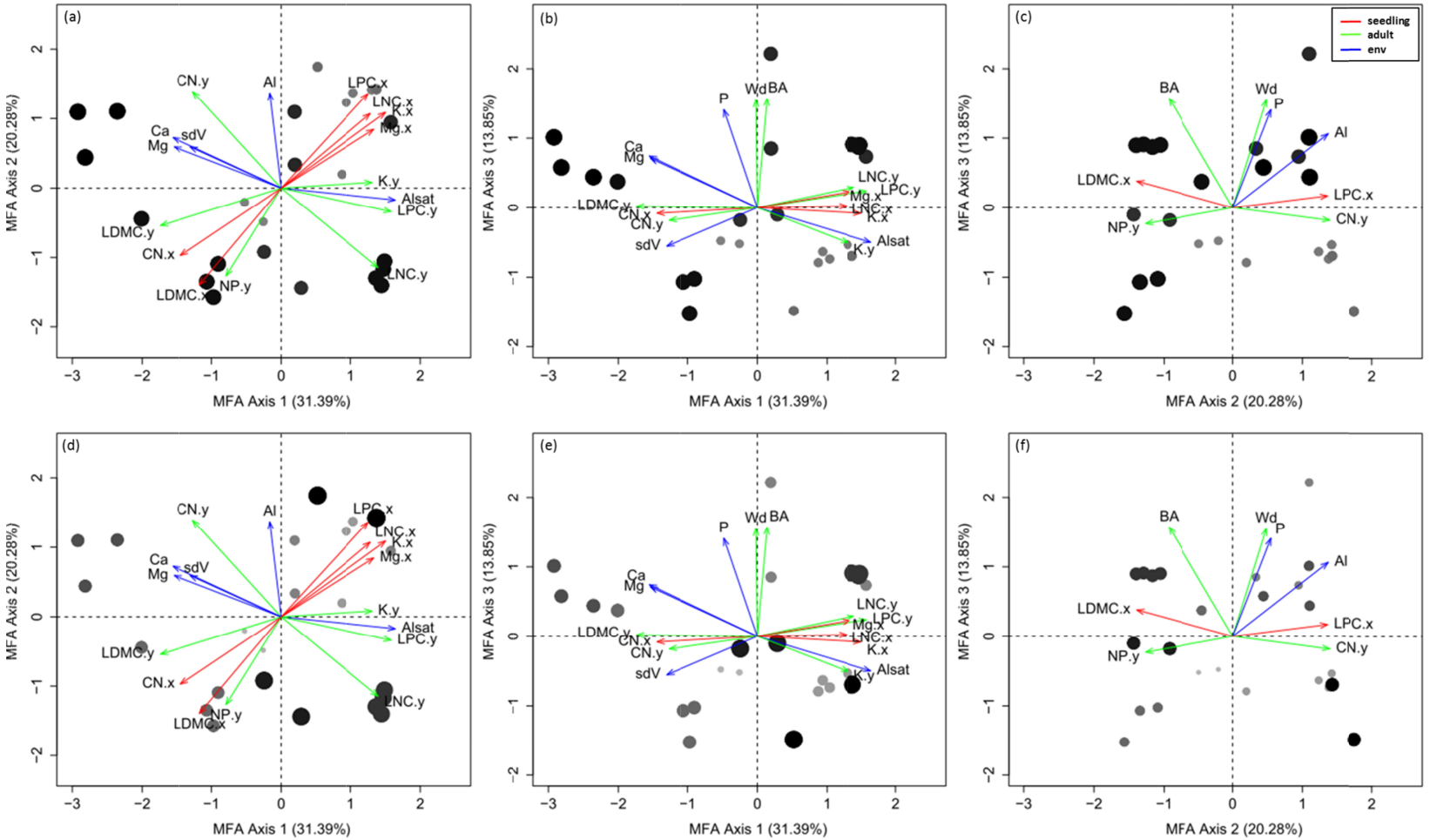


Figure 6. Global PCA biplot showing the distribution of seedling quadrats by the traits and environmental variables, as correlated to the first three MFA axes. Top three panels (a – c) show point size scaled by sapling species richness and the bottom three panels (d – e) by sapling stem density of the respective plots. Only variables that are significant at P=0.001 are shown here. Refer to Figure 4 for the location of other variables. Seedling traits end with suffix ".x" and adult traits end with suffix ".y". Abbreviations used are listed in Table 1.

CHAPTER 5. Conclusions and future research directions

Singapore's forests exemplified the different recovery rates that secondary forests can exhibit even within a small and relatively homogenous landscape. These lowland Dipterocarp forests underwent intensive agricultural activities from the late 1800 to early 1900, and have today, recovered differently after at least 60 years of regeneration. We found that the primary forest plots had much lower soil phosphorus (Yamashita et al., 2003; Zaidey et al., 2010) and the secondary forest plots much higher soil C:N ratio (See Table 5 in Sim et al. 1992, Kauffman et al. 1998) in comparison to other studies of humid tropical rainforests. This finding may be central to explaining the overall slower recovery of stand structure and species richness of these secondary forests, when compared to others that were more than 50 years old (Chapter 2, Table 2). This finding concurs with studies in the Amazon which found that low soil fertility led to poor forest recovery (Lu et al., 2002; Moran et al., 2000). Below, I summarized the key findings from my dissertation, focusing on how poor soil fertility and high aluminum levels affect some of the important processes in forest regeneration and have likely set up a chain of events that have slowed forest recovery.

Summary of key findings

Nutrient constraints, due to levels of aluminum saturation, soil available phosphorus and soil C:N ratio appears to be key to secondary forest succession in Singapore. These factors influence forest recovery in terms of overall species richness and density of seedlings and saplings, seedlings' functional response, and in differentiating the niches of broad functional groups of species.

1) Nutrient constraints affect seedlings' functional response and establishment

Increasing AlSat and soil C:N ratio correlated with decreasing foliar nutrients across the most pristine primary forest plot to the poorly recovering secondary forest plots (Chapter 4, Figure 1 and 3). This is indicative of the resource conserving strategies of seedlings in response to nutrient constraints in the poorly recovering secondary forests. Aluminum saturation disrupts root functions and nutrient uptake by plants (Kochian et al., 2005; Rengel, 2004; Sanchez and Buol, 1975). Although tropical plant species have evolved on acidic and high aluminum soils, forest clearance had probably led to increased leaching of soil base cations and resulted in levels of AlSat that only few species can thrive in. Thus across the primary and secondary forest plots, high levels of AlSat and soil C:N were also highly correlated with decreasing seedling species richness and density (Chapter 4, Figure 2).

Soil phosphorus, a known limiting nutrient in tropical soils, appears to counteract the negative effects of high aluminum soils, and become more important in saplings. The results from Chapter 4 showed that with high phosphorus, sapling species richness in the secondary forests was high despite high AlSat; conversely, the sapling species richness was lowest at sites with high AlSat and low P. However, while P and AlSat affect species richness, their effects on sapling density was much less, as the few plant species that could establish on low P and high AlSat soils were able to thrive subsequently, even accruing high foliar nutrients.

2) Positive feedback between soil and nutrient conserving species slow regeneration

The positive feedback between soil fertility and nutrient conserving species may further slow recovery of soil nutrients, and thus forest regeneration. First, within the secondary forest plots, seedling establishment was negatively affected by correlates of high soil C:N ratio, high tree-level leaf C:N ratio, thick leaf litter depth and low stand basal area (Chapter 4, Figure 5). This is suggestive of a positive feedback loop, where high soil C:N ratio caused nutrient conserving trees to produce poor quality leaf litter that decomposed slowly. The build up of leaf litter depth has been shown to negatively affect seedling establishment (Facelli and Pickett, 1991; Metcalfe et al., 1998; Metcalfe and Grubb, 1997), while at the same time, slow nutrient returns further selects for plants that are nutrient conserving. Further, poorer forest regrowth, as indicated by the correlate of stand basal area, could decrease in-situ seeding opportunities by existing trees and also attract less animal dispersers.

3) Soil factors differentiate niches of broad plant functional groups

Within secondary forests, more primary forest species were found in plots with lower aluminum levels and lower soil C:N ratio, while the opposite was true for pioneer species; soils with higher C:N ratio, lower P and AlSat had more long-lived pioneers and fewer short-lived pioneers (Chapter 3, Table 4). Of these functional groups, long-lived pioneers have been recognized as a sere community whose longevity could determine the eventual succession by climax species (Chazdon, 2008a; Finegan, 1996), but no prior study that I know of has examined the environmental factors important for their establishment. In Singapore forests, long-lived pioneers appeared to be specialists of impoverished soils, and may have supplanted short-lived pioneers even in the early stages of succession.

4) Colonization of degraded soils by *Dicranopteris linearis*

The soil factors are also likely responsible for the initial colonization of the deforested area by the fern, *Dicranopteris linearis*, also a specialist of degraded soil (Russell and Vitousek, 1997) with high aluminum (Kato-Noguchi et al., 2012). Past research has shown that the slow decomposing frond and thick rootmats of *D. linearis*, along with the longevity of the plant, which persists via clonal growth, is an effective barrier to forest regeneration (Cohen et al., 1995; Russell et al., 1998). However, soils in the studied fern plots appeared to have recovered and were not distinctly different from other study plots. Thus, although the fern cover was a strong inhibitor of seedling establishment (Chapter 3, Table 4), regrowth of trees would likely be fast, with the first trees acting as a nucleus (Yarranton and Morrison, 1974), once seed establishment past the mechanical barrier is successful.

Implication for management & future research

The relative importance of dispersal limitations vs. the constraints of the regenerating environment on the establishment of late successional species has consequences for management. The findings from Chapter 2 and 3 suggested that aside from soil factors, the connectivity of the poorly regenerating forests to primary and mature secondary forests was also important to their recruitment of late successional species. Primary forest species recruited poorly into the secondary forests despite the proximity of seed sources at Bukit Timah Nature

Reserve (Chapter 2, Table 3) and distance to potential seed sources was the most important predicting factor for the distribution of secondary forest seedlings at the Central Catchment Nature Reserve (Chapter 3, Table 4). Dispersal limitation and lack of seed sources might be overcome by increasing reforestation efforts, such as collecting growing seeds from primary forests, and transplanting the trees beneath the shade of secondary forests. Planting could also be done strategically to improve landscape connectivity for animal dispersers. However, if the regenerating environment, in particular the soil factors, negatively affect the growth performance of the planted trees, reforestation effort could fail or be less effective. Nursery experiments or in-situ transplants in the secondary forests could help to screen for suitable late successional species that perform well under the regenerating environment. At the same time, seed traps would help to determine the actual dispersal ranges of the primary forest species.

In addition, little research has examined the physiological adaptations of tropical plants to the changing soil conditions over succession. Clearly, adaptation to changing aluminum levels is important. Previous work showed that Al stimulates the growth of the early successional plant species *Melastoma malabathricum*, which was present in our plots. Our preliminary laboratory results also suggest that other plants, *Dillenia suffruticosa* and *Champereia* manillana, are able to hyper-accumulate Al in their leaves. Future research into the various physiological adaptations to Al by these early successional plant species could help to deepen our understanding of the community dynamics of these secondary forests, and might also shed light on the mechanism of aluminum resistance for crop plants. Given the high trait variability among primary forest species (Chapter 4, Figure 1), it is also likely that some primary forest species would perform well in degraded forests.

Other than Al, many of the plant foliar nutrients of both adult trees and seedlings were largely invariant of soil nutrients, while adults and seedlings foliar C:N ratio exhibited opposing trends to soil C:N ratio. The longevity of these leaves and whether some of these foliar nutrients were resorbed prior to leaf senescence would affect nutrient cycling through the system. It would also be interesting to see how much of this was determined by ontogeny, and how much due to changes in species community over time. Future research into the shifts of foliar nutrients, including Al, from seedlings to adult trees, would shed some light on changes in nutrient cycling through the biotic and abiotic nutrient pools and how they are used by microbes as the forests regenerate, as well as the importance of these changes on forest recovery.

Conclusion

To date, our understanding of the long-term recovery of secondary forests in the tropics is based on surprisingly little empirical data. By using the case study of Singapore, I found that local Ultisol soils are inherently low in nutrients and decades of intensive agricultural activities has resulted in soils whose high aluminum saturation, nutrient C:N ratio and low available phosphorus inhibit forest regeneration. Forest succession is characterized by plant species that specialize on the soil conditions in addition to the changing light environment as the forest regrows. The longevity of these plants on degraded land, their ability to slow nutrient returns and the strong dispersal limitation in this fragmented forest reserve explains the overall slow recovery.

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APPENDICES

Appendix A. Top abundant trees and saplings

Table 1. Top 10 tree species by basal area in the primary and secondary forest plots

	Primary forest				Secondary forest			
Rank by BA	**Species**	**BA (m^2)**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2)**	**Indiv (%)**	**Indiv (ha^{-1})**
1	*Shorea curtisii* Dipterocarpaceae	16.1	4.2	258	*Campnosperma auriculata* Anacardiaceae	14.84	6.6	126
2	*Dipterocarpus caudatus* Dipterocarpaceae	4.5	0.9	54	*Adinandra dumosa* Theaceae	5.04	15.1	289
3	*Streblus elongatus* Moraceae	3.9	7	456	*Dillenia suffruticosa* Dilleniaceae	2.32	24	459
4	*Ixonanthes reticulata* Ixonanthaceae	3.3	0.3	20	*Ixonanthes reticulata* Ixonanthaceae	2.09	1.9	37
5	*Koompassia malaccensis* Fabaceae	1.9	0.2	11	*Rhodamnia cinerea* Myrtaceae	1.79	4.8	93
6	*Shorea leprosula* Dipterocarpaceae	1.6	0.1	6	*Fagraea fragrans* Loganiaceae	1.78	1.8	34
7	*Artocarpus scortechinii* Moraceae	1.5	0.4	22	*Alstonia angustiloba* Apocynaceae	1.65	0.4	8
8	*Pellacalyx saccardianus* Rhizophoraceae	1.5	0.4	26	*Timonius wallichianus* Rubiaceae	0.75	3.4	65
9	*Hopea griffithii* Dipterocarpaceae	1.3	0.1	4	*Guioa pubescens* Sapindaceae	0.65	1.5	28
10	*Santiria apiculata* Burseraceae	1	6.4	372	*Streblus elongatus* Moraceae	0.46	2.9	55

Table 2. Top 10 sapling (1-3 cm DBH) species by stem count in the primary and secondary forest plots

Rank by abundance	Primary forest			Secondary forest		
	Species	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Streblus elongatus* Moraceae	609	7.8	*Dillenia suffruticosa* Dilleniaceae	225	20.7
2	*Santiria apiculata* Burseraceae	595	7.6	*Streblus elongatus* Moraceae	70	6.4
3	*Diosypros lanceifolia* Ebenaceae	535	6.8	*Calophyllum ferrugineum* Calophyllaceae	67	6.2
4	*Dacryodes rostrata* Burseraceae	317	4	*Elaeocarpus polystachyus* Elaeocarpaceae	63	5.8
5	*Shorea curtisii* Dipterocarpaceae	301	3.8	*Calophyllum wallichianum* Calophyllaceae	59	5.4
6	*Gluta wallichii* Anacardiaceae	291	3.7	*Baccaurea sumatrana* Phyllanthaceae	55	5.1
7	*Pimelodendron griffithianum* Euphorbiaceae	248	3.2	*Calophyllum pulcherrimum* Calophyllaceae	48	4.4
8	*Gironniera parvifolia* Cannabaceae	236	3	*Shorea curtisii* Dipterocarpaceae	38	3.5
9	*Calophyllum ferrugineum* Calophyllaceae	196	2.5	*Calophyllum teysmannii* Calophyllaceae	31	2.8
10	*Calophyllum pulcherrimum* Calophyllaceae	169	2.2	*Rhodamnia cinerea* Myrtaceae	27	2.5

Appendix B. Supplementary materials for NMDS analysis of BTNR plots

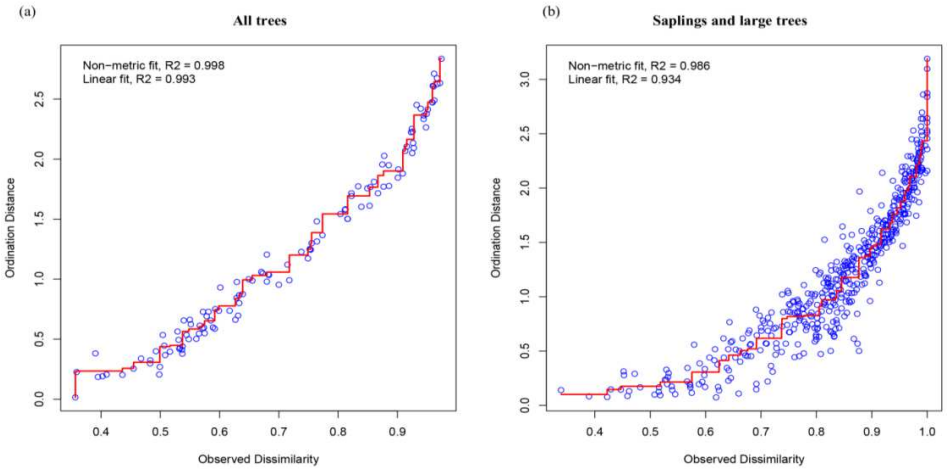


Figure 1. Shepard diagrams for NMDS ordination of (a) all trees in the plots and (b) saplings (1-3 cm DBH) and large trees (≥ 10 cm DBH). Both exhibited high R^2 for the goodness-of-fit.

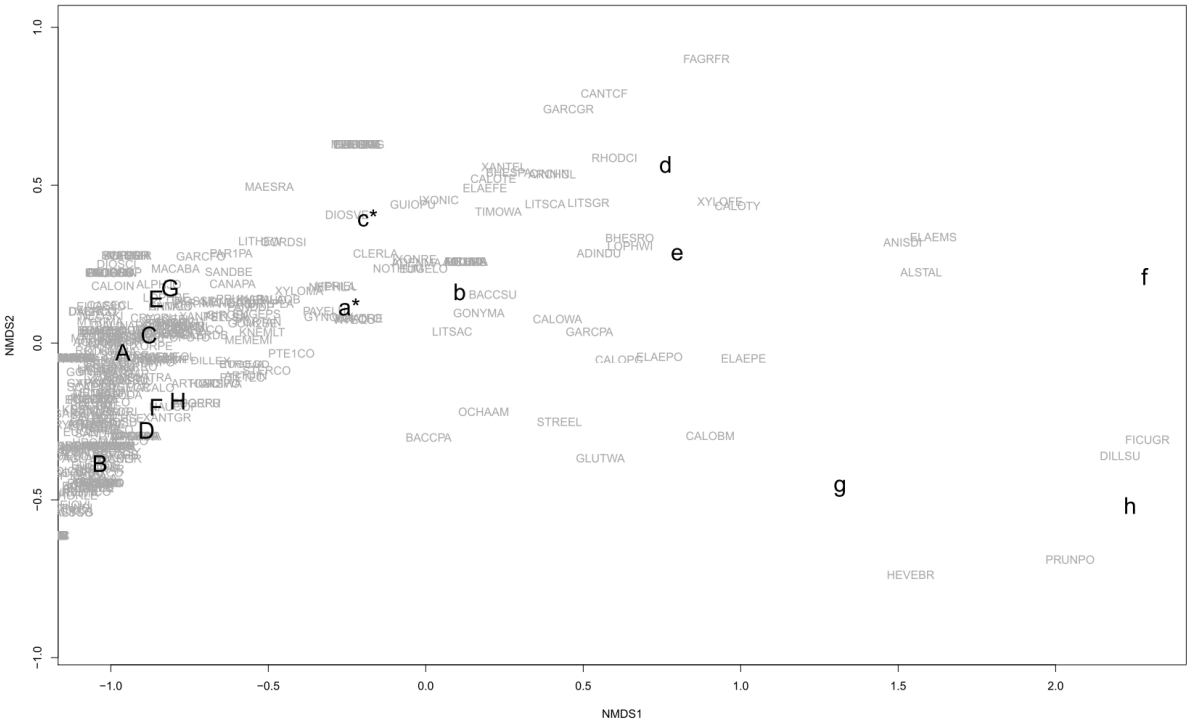


Figure 2. NMDS biplot of 50 × 50 m quadrats and tree species for saplings (i.e. trees ≤ 3 cm dbh) in the primary and secondary forest plots. Upper case letters are quadrats in the primary forest plot and lower case letters are quadrats in the secondary forest plot. Six letter codes indicate tree species. Floristic composition in the secondary quadrats was more similar to that of the primary quadrats with increasing proximity to the primary forests (Chapter 2, Figure 1).

Appendix C. Linear regressions of BTNR plots' recovery measures with elevation

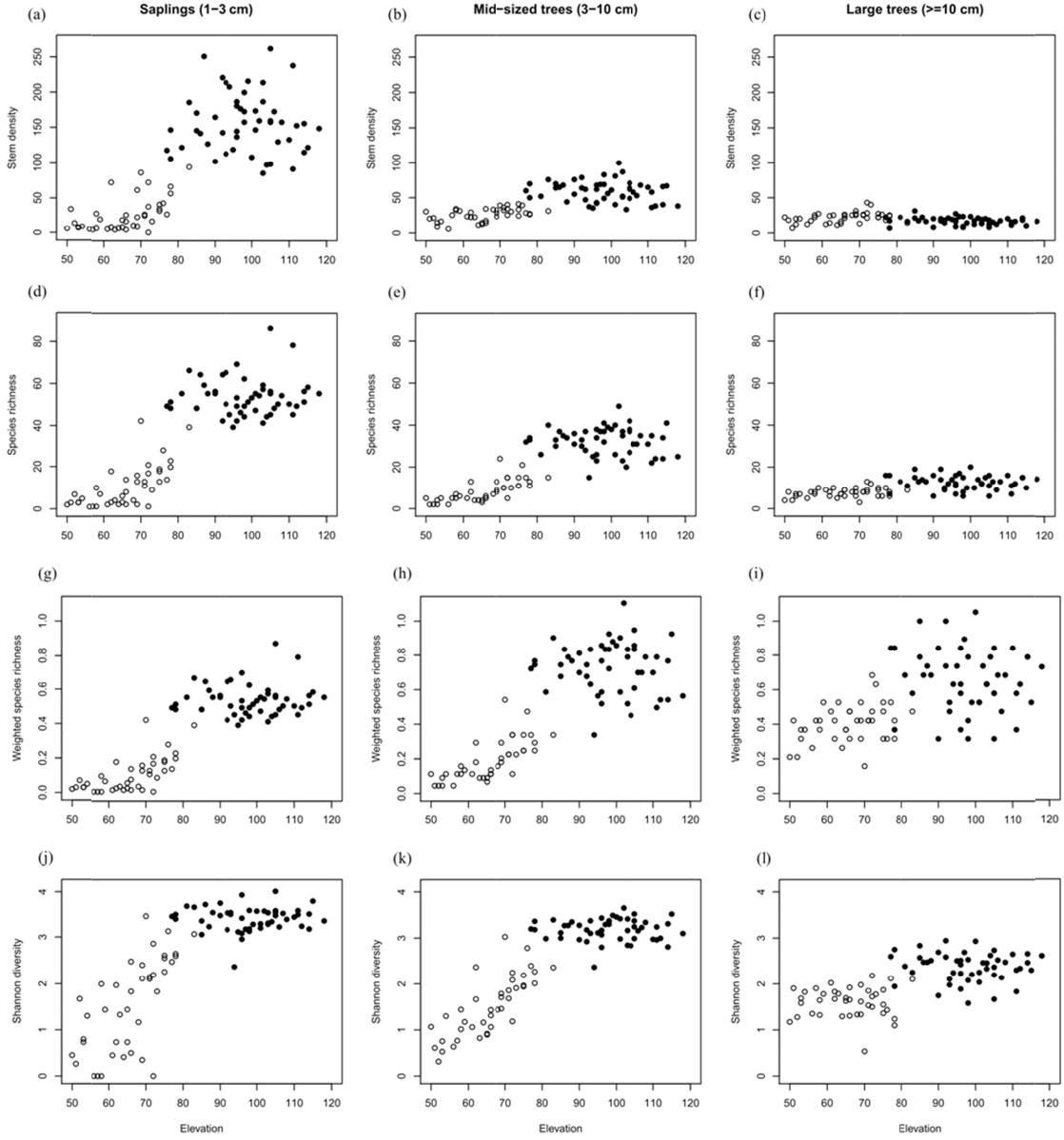


Figure 1. Primary and secondary forest plot stem density (panels a, b, c), species richness (panels d, e, f), species richness weighed by average stem density in that DBH size class (panels g, h, i) and Shannon diversity (panels j, k, l). Filled circles are fifty 20 x 20 m quadrats in primary plot and open circles are forty 20 m x 20 m quadrats in secondary plot. The linear regression showed that there was a significant interaction, in the weighted and non-weighted analyses, between age class and elevation, which served as a proxy for the location of each quadrat relative to the other age class (Figure 1; $p << 0.001$). Secondary forest quadrats that were higher in elevation, and thus closer to the primary forest, had higher species richness. However, the interaction effects were caused mainly by the smaller trees, which indicated that seed dispersal was limited. Linear regression models for large trees (≥ 10 cm) in secondary forest plot showed no significant increase in species richness with proximity to the primary forest plot.

Appendix D. Plot selection and location in CCNR

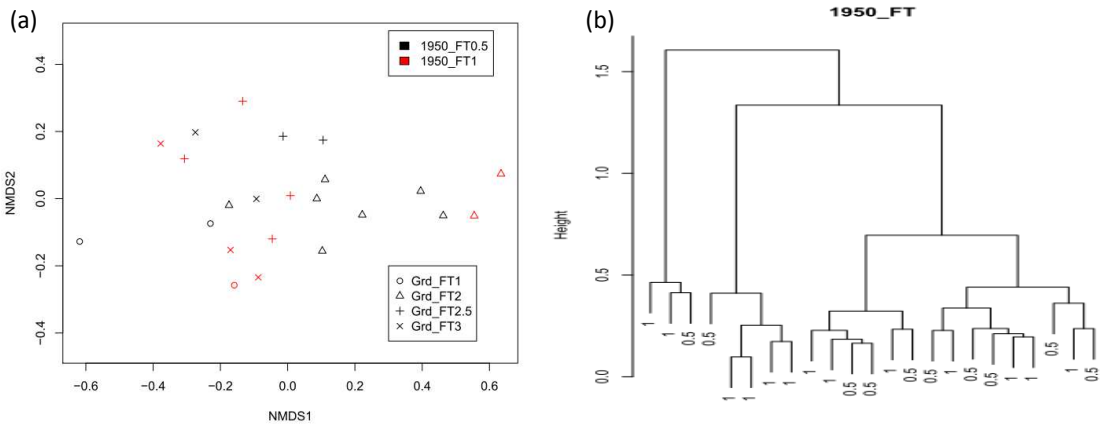


Figure 1. Structural similarity of the plots using (a) Nonmetric Multidimensional Scaling and (b) Hierarchical Clustering (Ward's Minimum Variance). The analysis was based on stem abundance in eight DBH size classes. The graphs verified that the plots in the original 1951 classifications ("0.5" and "1") overlapped in structural similarity today. In (1a) "Grd" referred to the current ground-truth structural classification. Grd_FT1 – Grd_FT3 corresponded to increasing structural complexity. Hierarchical Clustering using two other methods, Single Linkage Agglomerative and Complete Linkage Agglomerative Clustering yielded similar findings (results not shown here).

Table 1. GPS coordinates of study plots

Site	Latitude	Longitude
O1	1° 23' 40.6422"	103° 47' 0.402"
O2	1° 20' 50.8914"	103° 49' 15.7296"
O3	1° 23' 14.3916"	103° 48' 57.6894"
R1	1° 23' 2.0754"	103° 47' 1.8348"
R2	1° 23' 14.3916"	103° 48' 57.6894"
R3	1° 23' 14.3916"	103° 48' 57.6894"
R4	1° 22' 55.0518"	103° 46' 51.495"
R5	1° 23' 26.667"	103° 46' 57.8892"
R6	1° 22' 50.2464"	103° 48' 31.5972"
R7	1° 22' 50.2464"	103° 49' 19.149"
R8	1° 22' 21.7734"	103° 49' 38.859"
R9	1° 23' 58.8798"	103° 47' 11.9574"

Appendix E. Gap light analyzer (GLA) terminology and configurations

Kt, Cloudiness Index (or clearness index)
It is the fraction of extraterrestrial radiation that reaches the earth's surface. Daily Kt is calculated as

$$Kt = \frac{H}{H_0}$$

Where H = amount of global radiation incident on a horizontal ground surface on earth per day. Daily H is obtained from National Environmental Agency, Singapore, 2012 daily meteorological data. Values in mWh cm^{-2} day^{-1} were converted to Wm^{-2} after multiplying by 10/24.
H_0 = amount of extraterrestrial radiation incident on a horizontal surface outside the earth's atmosphere per day. Daily H_0 in Wm^{-2} were generated automatically from the software Gap Light Analyzer, which follows the equation below, integrating solar hours from sunrise to sunset (Duffie 2013).

$$H_0 = \frac{24 \times 3600 G_{sc}}{\pi}\left(1 + 0.033\cos\frac{360n}{365}\right) \times \left(\cos\emptyset cos\delta sin\omega_s + \frac{\pi\omega_s}{180}\, sin\emptyset sin\delta\right)$$

where G_{sc}, solar constant = 1367 Wm^{-2}, n = day of the year, Ø = Latitude of the location, δ = declination, which is the angular position of the sun at solar noon, ω_s = sunset hour angle, calculated from $\cos\omega_s = -\tan\emptyset\, tan\,\delta$.
Mean daily Kt for each month were calculated from daily Kt.

R_p/R_s Spectral Fraction
The fraction of global radiation incident, contributed by all wavelengths (0.25 µm – 25 µm) on a horizontal surface (R_s), that will be received as photosynthetically active radiation (PAR, with wavelengths 400 – 700 nm). Daily R_p/R_s is predicted from daily cloudiness index Kt using an empirical relationship:

$$\frac{R_p}{R_s} = 1 - exp(-0.499Kt^{-0.219})$$

Mean daily R_p/R_s for each month were calculated.

H_b/H Beam Fraction
The fraction of total solar radiation incident on a horizontal ground surface on earth (H) that is direct solar radiation (H_b). Daily R_p/R_s is predicted from daily cloudiness index Kt using an empirical relationship:

$$\frac{H_b}{H} = 1 - exp(-0.3.044Kt^{2.346})$$

Mean daily H_b/H for each month were calculated.

τ_b Clear-Sky Transmission Coefficient
The beam radiation transmitted through clear atmosphere, corrected for tropical climate is calculated from the equation (Hottel 1976):

$$\tau_b = a_0 + a_1 \, exp(\frac{-k}{cos\theta_z})$$

where a_0 =(0.4237 – 0.00821(6 – A)^2) × 0.95; a_1 = (0.5055 + 0.00595(6.5 – A)^2) × 0.98; k = (0.2711 + 0.01858(2.5 – A)^2) ×1.02; A, mean elevation of sites = 0.043 km and θ_z = zenith angle. Mean τ_b for a day is the average of τ_b with changing zenith angles throughout the day (i.e. θ_z = 0^o, 10^o, 20^o, 30^o, 40^o, 50^o, 60^o, 70^o, 80^o and 90^o).

Table 1. Configurations used in the software Gap Light Analyzer for all sites

Image	Initial Cursor Point	North
	Magnetic Correction*	0^o 12' – 0^o 13' East
	Projection distortion	Lambert's Equal Area
Resolution	Solar Time Step	1 minute
	Growing season start-end	January 1 – December 31
	Number of azimuth region	36
	Number of zenith regions	9
Radiation	Data Source	Modeled
	Solar constant	1367 W m^{-2}
	K_t, Mean daily cloudiness index (clearness index) by month	0.383 – 0.508
	R_p/R_s Mean daily spectral fractions by month	0.44 – 0.45
	H_b/H Mean daily beam fraction by month	0.273 – 0.448
	Model	Universal Overcast Sky
	τ_b Mean clear-sky transmission coefficient integrated over a day	0.454

*Configuration for the tab "Site" in GLA is specific for each seedling quadrat and is shown in Table B2.

Table 2. Configurations used for tab "Site" in the Gap Light Analyzer

Site	Seedling Plot	Latitude	Longitude	Date	Magnetic declination (min, sec)	Slope (^{o})	Aspect (m)	Elevation (m)
R4	B14D5.5	1° 22' 55.0518"	103° 46' 51.495"	10-Dec-11	0° 12' East	7.81	95.24	47.7
R4	B45D12.5	1° 22' 55.0518"	103° 46' 51.495"	10-Dec-11	0° 12' East	8.14	90.22	45.7
R4	B130D14	1° 22' 55.0518"	103° 46' 51.495"	10-Dec-11	0° 12' East	8.82	103.51	45
R4	B212D19.5	1° 22' 55.0518"	103° 46' 51.495"	10-Dec-11	0° 12' East	8.01	95.4	49.5
R7	B5D11.5	1° 22' 50.2464"	103° 49' 19.149"	10-Nov-11	0° 13' East	6.1	111.23	41.3
R7	B83D9.7	1° 22' 50.2464"	103° 49' 19.149"	10-Nov-11	0° 13' East	9.07	109.85	38.4
R7	B93D5	1° 22' 50.2464"	103° 49' 19.149"	10-Nov-11	0° 13' East	9.07	109.85	38.4
R7	E188D6.1	1° 22' 50.2464"	103° 49' 19.149"	10-Nov-11	0° 13' East	6.69	117.85	40.4
R7	237D13.5	1° 22' 50.2464"	103° 49' 19.149"	10-Nov-11	0° 13' East	6.69	117.85	40.4
R8	B26D19	1° 22' 21.7734"	103° 49' 38.859"	3-Nov-11	0° 13' East	2.67	116.79	30.4
R8	B50D12.5	1° 22' 21.7734"	103° 49' 38.859"	3-Nov-11	0° 13' East	3.94	161.48	29.5
R8	B263D12.5	1° 22' 21.7734"	103° 49' 38.859"	3-Nov-11	0° 13' East	4.58	163.91	30.1
R8	B212D19.5	1° 22' 21.7734"	103° 49' 38.859"	3-Nov-11	0° 13' East	5.59	168.06	28.7
O1	B344D19.5	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	6.83	358.84	40.3
O1	B204D11	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	6.47	358.64	44.2
O1	B50D12.5	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	7.56	0.88	42.2
O1	E26D29	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	7.12	3.14	40.2
O1	E81D18.5	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	7.53	5.28	40.1
O1	E190D17.3	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	3.13	10	45.5

O1	E244D8	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	6.47	358.64	44.2
O1	B267D18.5	1° 23' 40.6422"	103° 47' 0.402"	23-Nov-11	0° 12' East	6.95	355.91	44
O2	B231D23	1° 20' 50.8914"	103° 49' 15.7296"	2-Feb-12	0° 13' East	4.59	172.73	50.4
O2	B83D11	1° 20' 50.8914"	103° 49' 15.7296"	8-Feb-12	0° 13' East	6.12	123.99	49.9
O2	B170D8	1° 20' 50.8914"	103° 49' 15.7296"	1-Feb-12	0° 13' East	5.47	146.91	50
O2	B330D9.6	1° 20' 50.8914"	103° 49' 15.7296"	2-Feb-12	0° 13' East	4.45	139.48	51
O3	B294D21.5	1° 23' 14.3916"	103° 48' 57.6894"	13-Dec-11	0° 13' East	10.78	197.29	44.1
O3	B50D12.5	1° 23' 14.3916"	103° 48' 57.6894"	11-Dec-11	0° 13' East	14.26	202.87	46.3
O3	B212D19.5	1° 23' 14.3916"	103° 48' 57.6894"	11-Dec-11	0° 13' East	9.19	199.91	42.1
O3	B83D11	1° 23' 14.3916"	103° 48' 57.6894"	13-Dec-11	0° 13' East	14.26	202.87	46.3
O3	E5D11.5	1° 23' 14.3916"	103° 48' 57.6894"	11-Dec-11	0° 13' East	12.86	199.19	45
O3	E204D11	1° 23' 14.3916"	103° 48' 57.6894"	6-Dec-11	0° 13' East	9.19	199.91	42.1
O3	E244D7	1° 23' 14.3916"	103° 48' 57.6894"	11-Dec-11	0° 13' East	9.19	199.91	42.1
O3	E267D18.5	1° 23' 14.3916"	103° 48' 57.6894"	19-Dec-11	0° 13' East	10.78	197.29	44.1
O3	E344D19.3	1° 23' 14.3916"	103° 48' 57.6894"	13-Dec-11	0° 13' East	13.92	204.85	48.7
R2	B190D17.3	1° 23' 14.3916"	103° 48' 57.6894"	16-Jan-12	0° 13' East	7.09	125.96	41.9
R2	B50D12.5	1° 23' 14.3916"	103° 48' 57.6894"	25-Jan-12	0°12'East	7.55	137.45	43.2
R2	E14D5.5	1° 23' 14.3916"	103° 48' 57.6894"	18-Jan-12	0° 13' East	5.98	138.28	44.4
R2	E14D5.5	1° 23' 14.3916"	103° 48' 57.6894"	25-Jan-12	0°12'East	5.98	138.28	44.4
R2	E83D11	1° 23' 14.3916"	103° 48' 57.6894"	16-Jan-12	0° 13' East	7.55	137.45	43.2
R2	E204D11	1° 23' 14.3916"	103° 48' 57.6894"	25-Jan-12	0°12'East	6.98	134.19	43.2
R2	B273D18.5	1° 23' 14.3916"	103° 48' 57.6894"	18-Jan-12	0° 13' East	5.04	140.3	44.3
R2	E231D23	1° 23' 14.3916"	103° 48' 57.6894"	18-Jan-12	0° 13' East	5.45	127.72	43.2
R3	B206D18	1° 23' 14.3916"	103° 48' 57.6894"	2-Mar-12	0° 12' East	10.96	106	49.7
R3	B263D11	1° 23' 14.3916"	103° 48' 57.6894"	2-Mar-12	0° 12' East	9.28	90.24	50.3
R3	B26D18	1° 23' 14.3916"	103° 48' 57.6894"	2-Mar-12	0° 12' East	7.66	75.36	47.8
R1	B263D12.5	1° 23' 2.0754"	103° 47' 1.8348"	28-Feb-12	0° 12' East	5.64	272.21	34.7
R1	B150D19	1° 23' 2.0754"	103° 47' 1.8348"	30-Nov-11	0° 12' East	5.71	281.46	36.3
R1	B212D23	1° 23' 2.0754"	103° 47' 1.8348"	30-Nov-11	0° 12' East	5.34	289	34.9
R1	B294D21.5	1° 23' 2.0754"	103° 47' 1.8348"		0° 12' East	5.99	267.79	33.2
R1	E83D11	1° 23' 2.0754"	103° 47' 1.8348"	30-Nov-11	0° 12' East	7.65	254.9	36.6
R5	B83DD11	1° 23' 26.667"	103° 46' 57.8892"	9-Nov-11	0°12'East	2.48	84.06	43.2
R5	B294D21.5	1° 23' 26.667"	103° 46' 57.8892"	7-Nov-11	0°12'East	0.99	75.18	44.1
R5	B231D23	1° 23' 26.667"	103° 46' 57.8892"	maybe 8 nov 11	0°12'East	2.54	150.33	43.9
R5	B170D8	1° 23' 26.667"	103° 46' 57.8892"	9-Nov-11	0°12'East	3.28	144.98	43.5
R5	E81D18.5	1° 23' 26.667"	103° 46' 57.8892"	2-Nov-11	0° 13' East	3.53	86.17	42.5
R5	E81D18.5	1° 23' 26.667"	103° 46' 57.8892"	8-Nov-11	0°12'East	3.53	86.17	42.5
R5	E190D17.3	1° 23' 26.667"	103° 46' 57.8892"	2-Nov-11	0° 13' East	3.28	144.98	43.5
R5	E344D19.3	1° 23' 26.667"	103° 46' 57.8892"	8-Nov-11	0°12'East	3.3	32.24	43.4
R9	B263D12.8	1° 23' 58.8798"	103° 47' 11.9574"	31-Oct-11	0°12'East	3.41	101.54	33.7
R9	B5D11.5	1° 23' 58.8798"	103° 47' 11.9574"	24-Oct-11	0° 13' East	3.85	56.66	32.7

R9	B81D18.5	1° 23' 58.8798"	103° 47' 11.9574"	31-Oct-11	0°12'East	3.1	96.39	31.3
R9	B190D17.3	1° 23' 58.8798"	103° 47' 11.9574"	24-Oct-11	0° 13' East	4.59	132.26	32.2
R6	B330D9.6	1° 22' 50.2464"	103° 48' 31.5972"	9-Dec-11	0° 13' East	7.4	351.47	49
R6	B344D19.3	1° 22' 50.2464"	103° 48' 31.5972"	9-Dec-11	0° 13' East	7.4	351.47	49
R6	B81D18.5	1° 22' 50.2464"	103° 48' 31.5972"	9-Dec-11	0° 13' East	6.2	0.13	51
R6	B263D12.5	1° 22' 50.2464"	103° 48' 31.5972"	9-Dec-11	0° 13' East	5.28	339.59	50.6
R6	E204D11	1° 22' 50.2464"	103° 48' 31.5972"	9-Dec-11	0° 13' East	5.28	339.59	50.6

Appendix F. Classification of functional groups in Chapter 3

Table 1. Classification of seedling species into four functional groups: short-lived pioneers (SLP), long-lived pioneers (LLP), secondary forest species (SFS) and primary forest species (PFS). SLP and LLP are differentiated base on wood density values. SLP are pioneers with wood density < 0.4 g/cm^3) and LLP are pioneers with wood density > 0.5 g/cm^3. "NA" denotes pioneers with intermediate wood density values and hence not classified into neither SLP nor LLP. Wood density (Wd) data was courtesy of Chave et al. 2009 and Zanne et al. 2009.

Species	Family	Functional group	Wood density* (g/cm^3)
Euodia glabra	Rutaceae	SLP	0.310
Ficus fistulosa	Moraceae	SLP	0.380
Macaranga bancana	Euphorbiaceae	SLP	0.382
Macaranga conifera	Euphorbiaceae	SLP	0.330
Macaranga gigantea	Euphorbiaceae	SLP	0.295
Macaranga griffthiana	Euphorbiaceae	SLP	0.382
Macaranga heynei	Euphorbiaceae	SLP	0.382
Trema cannabina	Cannabaceae	SLP	0.342
Trema tomentosa	Cannabaceae	SLP	0.342
Adinandra dumosa	Theaceae	LLP	0.540
Guioa pubescens	Sapindaceae	LLP	0.548
Ixonanthes reticulata	Ixonanthaceae	LLP	0.626
Rhodamnia cinerea	Myrtaceae	LLP	0.801
Syzygium zeylanicum	Myrtaceae	LLP	0.664
Clerodendrum laevifolium	Lamiaceae	NA	0.574
Dillenia suffruticosa	Dilleniaceae	NA	0.450
Ficus aurata	Moraceae	NA	0.406
Ficus globosa	Moraceae	NA	0.406
Ficus grossularioides	Moraceae	NA	0.420
Melastoma malabathricum	Melastomataceae	NA	0.440
Adenanthera bicolor	Fabaceae	SFS	0.850
Alstonia angustifolia	Apocynaceae	SFS	0.613
Anisophyllea disticha	Anisophylleaceae	SFS	0.670
Archidendron clypearia	Fabaceae	SFS	0.323
Arthrophyllum diversifolium	Araliaceae	SFS	0.365
Calophyllum ferrugineum	Clusiaceae	SFS	0.550
Calophyllum macrocarpum	Clusiaceae	SFS	0.640
Calophyllum pulcherrimum	Clusiaceae	SFS	0.617
Calophyllum tetrapterum	Clusiaceae	SFS	0.550
Calophyllum teysmanii	Clusiaceae	SFS	0.540
Calophyllum wallichianum	Clusiaceae	SFS	0.530
Champereia manillana	Opiliaceae	SFS	0.690
Cinnamomum iners	Lauraceae	SFS	0.499

Cratoxylum formosum	Hypericaceae	SFS	0.715
Dysoxylum cauliforum	Meliaceae	SFS	0.715
Elaeocarpus mastersii	Phyllanthaceae	SFS	0.550
Elaeocarpus petiolatus	Elaeocarpaceae	SFS	0.455
Ficus heteropleura	Moraceae	SFS	0.406
Garcinia parvifolia	Clusiaceae	SFS	0.435
Gironniera nervosa	Ulmaceae	SFS	0.450
Gnetum gnemon	Gnetaceae	SFS	0.610
Gymnacranthera forbesii	Myristicaceae	SFS	0.540
Gynotroches axillaris	Rhizophoraceae	SFS	0.520
Hevea brasiliensis	Euphorbiaceae	SFS	0.467
Lindera lucida	Lauraceae	SFS	0.452
Litsea castanea	Lauraceae	SFS	0.410
Litsea elliptica	Lauraceae	SFS	0.450
Litsea firma	Lauraceae	SFS	0.408
Litsea grandis	Lauraceae	SFS	0.433
Palaquium obovatum	Sapotaceae	SFS	0.550
Prunus polystachya	Rosaceae	SFS	0.500
Syzygium borneense	Myrtaceae	SFS	0.664
Syzygium filiforme var. clarimyrtus	Myrtaceae	SFS	0.710
Syzygium grande	Myrtaceae	SFS	0.923
Syzygium lineatum	Myrtaceae	SFS	0.680
Timonius wallichianus	Rubiaceae	SFS	0.760
Vitex pinnata	Verbenaceae	SFS	0.683
Actinodaphne pruinosa	Lauraceae	PFS	0.510
Aglaia rufinervis	Meliaceae	PFS	0.670
Agrostistachys borneensis	Euphorbiaceae	PFS	0.820
Aidia densiflora	Rubiaceaee	PFS	0.753
Antidesma cuspidatum	Phyllanthaceae	PFS	0.800
Aporosa benthamiana	Phyllanthaceae	PFS	0.623
Aporosa frutescens	Phyllanthaceae	PFS	0.623
Aporosa microstachya	Phyllanthaceae	PFS	0.670
Aporosa miqueliana	Phyllanthaceae	PFS	0.720
Aporosa nervosa	Phyllanthaceae	PFS	0.623
Aporosa prainiana	Phyllanthaceae	PFS	0.630
Ardisia colorata	Myrsinaceae	PFS	0.591
Artocarpus lanceifolius	Moraceae	PFS	0.565
Beilschmiedia madang	Lauraceae	PFS	0.470
Calophyllum rubiginosum	Clusiaceae	PFS	0.550
Canarium pilosum	Burseraceae	PFS	0.465
Casearia capitallata	Salicaceae	PFS	0.625
Castanopsis lucida	Fagaceae	PFS	0.530

Chassalia chartacea	Rubiaceae	PFS	.
Croton oblongus	Euphorbiaceae	PFS	0.510
Dacryodes nervosa	Burseraceae	PFS	0.569
Dacryodes rostrata	Burseraceae	PFS	0.550
Dimocarpus longan ssp. malesianus	Sapindaceae	PFS	0.700
Diospyros lanceifolia	Ebenaceae	PFS	0.660
Diospyros styraciformis	Ebenaceae	PFS	0.683
Diospyros sumatrana	Ebenaceae	PFS	0.605
Diospyros venosa	Ebenaceae	PFS	0.683
Elaeocarpus stipularis	Phyllanthaceae	PFS	0.445
Galearia fulva	Pandaceae	PFS	0.635
Garcinia forbesii	Clusiaceae	PFS	0.742
Garcinia griffthii	Clusiaceae	PFS	0.742
Garcinia scortechinii	Clusiaceae	PFS	0.640
Glycosmis chlorosperma	Rutaceae	PFS	0.439
Goniothalamus macrophyllus	Annonaceae	PFS	0.440
Gonystylus confusus	Thymelaeaceae	PFS	0.560
Gonystylus maingayi	Thymelaeaceae	PFS	0.590
Hopea griffithii	Dipterocarpaceae	PFS	0.665
Irvingia malayana	Irvingiaceae	PFS	.
Ixora javanica var. retineria	Rubiaceae	PFS	0.793
Ixora pendula	Rubiaceae	PFS	0.793
Knema intermedia	Myristicaceae	PFS	0.533
Knema laurina	Myristicaceae	PFS	0.470
Knema malayana	Myristicaceae	PFS	0.630
Koilodepas longifolium	Euphorbiaceae	PFS	.
Lasianthus attenuatus	Rubiaceae	PFS	.
Litsea accendens	Lauraceae	PFS	0.425
Litsea costalis	Lauraceae	PFS	0.340
Macaranga lowii	Euphorbiaceae	PFS	0.675
Maclurodendron porteri	Rutaceae	PFS	0.550
Mallotus penangensis	Euphorbiaceae	PFS	0.590
Meiogyne vingata	Annonaceae	PFS	.
Memecylon lilacinum	Melastomataceae	PFS	0.820
Memecylon paniculatum	Melastomataceae	PFS	0.720
Microdesmis caseariifolia	Pandaceae	PFS	.
Myristica cinnamomea	Myristicaceae	PFS	0.570
Nephelium costatum	Sapindaceae	PFS	0.778
Nothaphoebe umbelliflora	Lauraceae	PFS	0.443
Ochanostachys amentacea	Olacaceae	PFS	0.770
Pentace triptera	Malvaceae	PFS	0.520
Phaeanthus ophthalmicus	Annonaceae	PFS	.

Polyalthia angustissima	Annonaceae	PFS	0.554
Polyalthia rumphii	Annonaceae	PFS	0.580
Popowia fusca	Annonaceae	PFS	0.597
Pouteria malaccensis	Moraceae	PFS	0.660
Prismatomeris glabra	Rubiaceae	PFS	.
Sandoricum koetjape	Meliaceae	PFS	0.473
Santiria rubiginosa	Burseraceae	PFS	0.683
Shorea pauciflora	Dipterocarpaceae	PFS	0.533
Strombosia ceylanica	Olacaceae	PFS	0.730
Strombosia javanica	Olacaceae	PFS	0.527
Syzygium glaucum	Myrtaceae	PFS	0.664
Syzygium incarnatum	Myrtaceae	PFS	0.664
Syzygium pseudoformosum	Myrtaceae	PFS	0.664
Tarenna mollis	Rubiaceae	PFS	0.680
Thottea grandiflora	Aristolochiaceae	PFS	.
Vatica maingoyi	Dipterocarpaceae	PFS	0.707
Xanthophyllum affine	Polygalaceae	PFS	0.613
Xanthophyllum eurhynchum	Polygalaceae	PFS	0.650
Xanthophyllum vitellinum	Polygalaceae	PFS	0.730
Xerospermum noronhianum	Sapindaceae	PFS	0.770
Xylopia malayana	Annonaceae	PFS	0.585

Appendix G. Supplementary modeling results

Table 1. Results from four principal component analyses, conducted on above- and belowground variables (P_1 and P_2) in primary and secondary forests, and above- and belowground variables (P_3 and P_4) in secondary forests only. A_1, A_2 = component 1 and 2 respectively of the PCA for aboveground variables; B_1, B_2, B_3 = component 1, 2 and 3 respectively of the PCA for aboveground variables. Values in bold indicated the variables that correlated most strongly with that component. Note that results from P_1* and P_3* are not shown here, but are similar to that of P_1 and P_3.

	Aboveground				Belowground				
Data Type	**Transfo-rmation**	**Vari-able**	**$P_1.A_1$ (66.8%)**	**$P_1.A_2$ (19.3%)**	**Transfo-rmation**	**Vari-able**	**$P_2.B_1$ (51.3%)**	**$P_2.B_2$ (19.1%)**	**$P_2.B_3$ (13.2%)**
Pri + Sec seedlings n = 31		CnpyO	**0.415**	-0.331		pH	0.280	-0.019	**-0.690**
	log	Dir	**0.419**	-0.326	log	P	-0.339	0.203	**0.512**
	log	Dif	0.393	**-0.422**	1/	TC	**0.442**	0.293	0.104
	(1/)^4	maxT	**-0.427**	-0.284	log	TN	**-0.456**	-0.058	-0.049
	log	sdV	**0.431**	0.154	(1/)^4	CN	0.151	**0.590**	0.103
	log	LL	0.192	**0.459**	log	TEB	**-0.403**	0.291	**-0.401**
	log(x+1)	Fern	0.305	**0.539**		ECEC	**-0.418**	-0.185	-0.188
					^5	AlSat	0.207	**-0.634**	0.203
Sec seedlings n = 29	**Transfo-rmation**	**Vari-able**	**$P_3.A_1$ (59.2%)**	**$P_3.A_2$ (29.4%)**	**Transfo-mation**	**Vari-able**	**$P_4.B_1$ (52.3%)**	**$P_4.B_2$ (16.9%)**	**$P_4.B_3$ (13.2%)**
		CnpyO	**0.568**	-0.033		pH	0.269	**-0.512**	-0.134
	log	Dir	**0.559**	-0.065	log	P	**-0.344**	0.129	**0.383**
	log	Dif	**0.578**	-0.027	1/	TC	**0.425**	-0.236	0.056
	log	LL	-0.059	**0.725**	log	TN	**-0.448**	0.016	0.166
	log(x+1)	Fern	0.166	**0.685**	(1/)^4	CN	0.006	**-0.633**	**0.624**
					log	TEB	**-0.409**	-0.339	-0.354
						ECEC	**-0.420**	-0.112	0.185
					^5	AlSat	0.291	0.372	**0.505**

Table 2. Relative importance (RI) and model-averaged coefficient estimates (MA-Coeff.) of the models. MA-Coeff. are averaged over all models within a subset of models that had Akaike weights summed up to 95%. MA-Coeff. of predictor variables that had RI greater than 0.3 and had significant model-averaged coefficients were in bold. P_1* and P_2 are principal components from the two PCAs conducted on AG (exluded maxT and sdV) and BG variables respectively in both primary and secondary forests; P_3 and P_4 are principal components from the PCA conducted on the AG (exluded maxT and sdV) and BG variables respectively in the secondary forests.

Data	Interpretation	Predictor	Density		Species Richness		Pri.Spp.		Sec.Spp.		Short-lived Pioneers		Long-lived Pioneers	
Type		Component	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.	RI	MA-Coeff.
Pri + Sec	**High light**	**P_1*.A_1**	0.22	0.52 ± 0.35	**0.48**	**-0.94 ± 0.42***	**1**	**-6.02 ± 0.92*****	**0.33**	**1.44 ± 0.47****	0.24	1.16 ± 0.96	**0.31**	**1.87 ± 0.69****
Seed-	**High fern cover, leaf litter**	**P_1*.A_2**	**0.6**	**-2.17 ± 0.35*****	**0.95**	**-1.5 ± 0.37*****	0.17	-0.05 ± 0.51	**0.73**	**-2.96 ± 0.43*****	**0.31**	**-2.02 ± 1.06.**	**0.29**	**-1.74 ± 0.74***
lings	**Low TC,TN,TEB, ECEC**	**P_2.B_1**	**0.38**	**1.4 ± 0.34*****	0.2	0.15 ± 0.4	**0.86**	**3.24 ± 0.49*****	0.2	-0.15 ± 0.58	0.2	0.08 ± 1.13	0.22	-1.07 ± 0.83
n = 41	**Low CN, AlSat.**	**P_2.B_2**	**0.94**	**2.72 ± 0.4*****	**0.99**	**1.94 ± 0.44*****	**1**	**5.09 ± 0.42*****	0.21	0.71 ± 0.7	0.25	-1.63 ± 1.15	**0.38**	**-2.81 ± 0.84****
	Low pH, TEB; high P	**P_2.B_3**	**0.46**	**2.53 ± 0.66*****	0.27	0.69 ± 0.58	0.29	-2.19 ± 0.86*	**0.54**	**3.46 ± 0.69*****	0.2	-0.14 ± 1.38	0.21	-0.94 ± 1.04
Sec	**High light**	**P_3*.A_1**	0.19	0.57 ± 0.25*	0.19	0.25 ± 0.38	0.21	0.87 ± 1.44	0.2	0.67 ± 0.28*	0.2	0.87 ± 1.09	0.21	-1.06 ± 0.88
Seed-	**High fern cover, leaf litter**	**P_3*,A_2**	**0.51**	**-1.84 ± 0.34*****	**0.98**	**-1.73 ± 0.42*****	**0.78**	**-3.54 ± 1.64***	**0.44**	**-1.88 ± 0.37*****	0.21	-0.75 ± 1.34	**0.41**	**-2.34 ± 0.97***
lings	**Distance to potential seed sources**	**Dist**	**0.91**	**-0.06 ± 0.01*****	**0.43**	**-0.02 ± 0.01***	0.27	-0.03 ± 0.03	**0.92**	**-0.08 ± 0.01*****	0.16	0 ± 0.02	0.21	-0.02 ± 0.01
n = 29	**Low P, TC, TN, TEB, ECEC**	**P_4.B_1**	0.26	1.2 ± 0.47*	0.27	-0.68 ± 0.4	0.31	1.72 ± 1.73	0.25	**1.25 ± 0.5***	0.29	2.1 ± 1.16.	0.18	-0.30 ± 0.81
	Low pH; high CN,	**P_4.B_2**	0.17	0.54 ± 0.31.	0.17	-0.1 ± 0.51	0.44	-2.96 ± 1.97	0.18	0.65 ± 0.34.	0.23	-1.38 ± 2.26	0.19	0.70 ± 0.96
	Low CN; high AlSat., P	**P_4.B_3**	0.19	0.5 ± 0.51	0.19	-0.15 ± 0.48	0.43	2.3 ± 1.72	0.19	0.57 ± 0.53	**0.71**	**3.72 ± 1.02*****	**0.48**	**-3.45 ± 1.36***

Table 3. Results of automated selection of GLMs. M_{all} are models using all primary and secondary plots that have full abiotic data. M_{sec} are models using only secondary plots. Models without mean maximum temperatures and mean standard deviation of vapor pressure deficits are on the right panel and denoted by "*". Models that used AIC_C instead of $QAIC_C$ were denoted by "†". The response variables are seedling density (Den), species richness (Sp.rich), primary forest species (PRI), secondary forest species (SFS), short-lived pioneers (SLP) and long-lived pioneers (LLP). Refer to Table 2 in this appendix for the abbreviations of predictor variables.

M_{all} n=31						M_{all}*, n =41					
Models	**K**	**LogLik**	**QAICc**	**Δ**	**Akaike Weight**	**Models**	**K**	**LogLik**	**QAICc**	**Δ**	**Akaike Weight**
Den ~ P1.A2 + P2.B2	3	-677.92	37.77	0	0.41	Den ~ P1*.A2 + P2.B2	3	-1031.44	50.51	0	0.21
Den ~ P1.A2 + P2.B1 + P2.B2	4	-653.98	39.64	1.86	0.16	Den ~ P1*.A2 + P2.B2 + P2.B3	4	-999.91	51.85	1.34	0.11
Den ~ P1.A2 + P2.B2 + P2.B3	4	-663.79	40.05	2.27	0.13	Den ~ P1*.A2 + P2.B1 + P2.B2	4	-1007.3	52.15	1.63	0.09
Den ~ P1.A1 + P1.A2 + P2.B2	4	-664.36	40.07	2.3	0.13	Den ~ P2.B2 + P2.B3	3	-1077.55	52.36	1.85	0.08
Den ~ P1.A2 + P2.B1 + P2.B2 + P2.B3	5	-639.7	42.14	4.37	0.05	Den ~ P2.B1 + P2.B2 + P2.B3	4	-1022.52	52.76	2.24	0.07
Den ~ P1.A1 + P1.A2 + P2.B1 + P2.B2	5	-650.71	42.6	4.83	0.04	Den ~ P2.B1 + P2.B2	3	-1092.71	52.97	2.46	0.06
Den ~ P1.A1 + P1.A2 + P2.B2 + P2.B3	5	-657.14	42.87	5.1	0.03	Den ~ P1*.A1 + P1*.A2 + P2.B2	4	-1029.93	53.06	2.54	0.06
Den ~ P1.A1 + P1.A2	3	-814.44	43.46	5.69	0.02	Den ~ P2.B2	2	-1158.45	53.15	2.64	0.06
						Den ~ P1*.A2 + P2.B1 + P2.B2 + P2.B3	5	-975.44	53.62	3.11	0.04
						Den ~ P1*.A1 + P1*.A2 + P2.B2 + P2.B3	5	-993.75	54.36	3.85	0.03
						Den ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2	5	-998.9	54.57	4.05	0.03
						Den ~ P1*.A1 + P2.B1 + P2.B2 + P2.B3	5	-1001.28	54.66	4.15	0.03
						Den ~ P2.B1 + P2.B3	3	-1137.99	54.79	4.28	0.02
						Den ~ P1*.A1 + P2.B2 + P2.B3	4	-1075.05	54.87	4.35	0.02
						Den ~ P1*.A1 + P2.B1 + P2.B2	4	-1084.28	55.24	4.72	0.02
						Den ~ P2.B3	2	-1213.53	55.36	4.85	0.02

Sp.rich. ~ P1.A1 + P1.A2	3	-101.9	80.84	0	0.33
Sp.rich. ~ P1.A1 + P1.A2 + P2.B2	4	-98.48	81.3	0.47	0.26
Sp.rich. ~ P1.A1 + P1.A2 + P2.B3	4	-101.44	83.38	2.54	0.09
Sp.rich. ~ P1.A1 + P1.A2 + P2.B1	4	-101.68	83.54	2.7	0.09
Sp.rich. ~ P1.A1 + P1.A2 + P2.B2 + P2.B3	5	-98.14	84.17	3.33	0.06
Sp.rich. ~ P1.A1 + P1.A2 + P2.B1 + P2.B2	5	-98.41	84.35	3.52	0.06
Sp.rich. ~ P1.A2 + P2.B2	3	-108.32	85.33	4.49	0.04

PFS ~ P1.A1 + P2.B2	3	-102.9	53.89	0	0.34
PFS ~ P1.A1 + P2.B1 + P2.B2	4	-98.47	54.85	0.96	0.21
PFS ~ P1.A1 + P1.A2 + P2.B2	4	-98.86	55.01	1.12	0.19
PFS ~ P1.A1 + P1.A2 + P2.B1 + P2.B2	5	-94.31	56.15	2.26	0.11
PFS ~ P1.A1 + P2.B2 + P2.B3	4	-102.09	56.4	2.51	0.1
PFS ~ P1.A1 + P2.B1 + P2.B2 + P2.B3	5	-98.1	57.79	3.89	0.05

Sp.rich. ~ P1*.A2 + P2.B2	3	-133.89	118.61	0	0.27
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B2	4	-130.73	118.63	0.02	0.27
Sp.rich. ~ P1*.A2 + P2.B2 + P2.B3	4	-132.88	120.39	1.78	0.11
Sp.rich. ~ P1*.A2 + P2.B1 + P2.B2	4	-133.57	120.95	2.34	0.08
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B2 + P2.B3	5	-130.36	121.08	2.47	0.08
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2	5	-130.72	121.38	2.77	0.07
Sp.rich. ~ P1*.A2 + P2.B1 + P2.B2 + P2.B3	5	-132.55	122.87	4.26	0.03

PFS ~ P3.A2	3	-20.76	49.02	0	0.15
PFS ~ P3.A2 + DIST + P4.B3	4	-19.52	49.71	0.7	0.1
PFS ~ P3.A2	3	-21.19	49.88	0.87	0.1
PFS ~ P3.A1	3	-21.27	50.04	1.02	0.09
PFS ~ P3.A2	2	-22.8	50.3	1.28	0.08
PFS ~ P3.A1 + P3.A2 + P4.B3	4	-20.17	51.01	1.99	0.05
PFS ~ P3.A1 + P3.A2 + P4.B2	4	-20.19	51.05	2.03	0.05
PFS ~ P3.A2 + DIST + P4.B2	4	-20.27	51.2	2.18	0.05
PFS ~ P3.A2	3	-22.2	51.91	2.89	0.03
PFS ~ P3.A2 + P4.B2 + P4.B3	4	-20.62	51.91	2.9	0.03
PFS ~ P3.A2 + P4.B1 + P4.B3	4	-20.68	52.03	3.02	0.03
PFS ~ P3.A2	3	-22.48	52.45	3.44	0.03
PFS ~ P3.A1 + P3.A2 + P4.B1	4	-21.01	52.68	3.67	0.02
PFS ~ P3.A2 + P4.B1 + P4.B2	4	-21.11	52.89	3.88	0.02
PFS ~ P3.A2 + DIST + P4.B2 + P4.B3	5	-19.31	52.9	3.89	0.02
PFS ~ P3.A2 + DIST + P4.B1 + P4.B3	5	-19.34	52.96	3.94	0.02
PFS ~ P3.A1 + P3.A2 + DIST	4	-21.18	53.02	4	0.02
PFS ~ P3.A1 + P3.A2 + DIST + P4.B3	5	-19.46	53.21	4.2	0.02
PFS ~ DIST + P4.B1 + P4.B3	4	-21.29	53.24	4.23	0.02
PFS ~ DIST	3	-23.12	53.73	4.72	0.01

						PFS ~ P3.A1 + P3.A2 + DIST + P4.B2	5	-19.81	53.91	4.9	0.01
SFS ~ P1.A2	2	-652.53	29.63	0	0.36	SFS ~ P3.A2	2	-497.8	21.84	0	0.25
SFS ~ P1.A2 + P2.B2	3	-634.5	31.65	2.02	0.13	SFS ~ P3.A2	3	-441.26	23.37	1.54	0.12
SFS ~ P1.A2 + P2.B3	3	-639.32	31.82	2.19	0.12	SFS ~ P3.A1	3	-481.79	24.54	2.71	0.06
SFS ~ P1.A2 + P2.B1	3	-645.89	32.05	2.42	0.11	SFS ~ DIST	2	-595.92	24.66	2.83	0.06
SFS ~ P1.A1 + P1.A2	3	-650.42	32.21	2.58	0.1	SFS ~ P3.A2	3	-492.27	24.84	3.01	0.06
SFS ~ P1.A2 + P2.B1 + P2.B2	4	-625.36	34.19	4.56	0.04	SFS ~ P3.A2	3	-492.48	24.85	3.01	0.06
SFS ~ P1.A2 + P2.B2 + P2.B3	4	-628.14	34.29	4.66	0.03	SFS~(Null)	1	-703.13	24.96	3.12	0.05
SFS ~ P1.A2 + P2.B1 + P2.B3	4	-633.71	34.49	4.86	0.03	SFS ~ P3.A2	3	-497	24.98	3.14	0.05
SFS ~ P1.A1 + P1.A2 + P2.B2	4	-633.97	34.49	4.86	0.03	SFS ~ P3.A2 + DIST + P4.B2	4	-434.22	26.79	4.95	0.02
SLP ~ P1.A1	2	-42.45	38.31	0	0.27	SLP ~ P3.A1	2	-37.33	26.3	1.73	0.1
SLP ~ P1.A1 + P2.B2	3	-41.33	40.13	1.82	0.11	SLP ~ P4.B1	2	-37.9	26.59	2.02	0.08
SLP ~ P1.A1 + P2.B1	3	-41.47	40.24	1.92	0.1	SLP ~ DIST	2	-38.32	26.8	2.23	0.07
SLP ~ P1.A1 + P1.A2	3	-41.64	40.36	2.05	0.1	SLP ~ P3.A2	2	-38.56	26.92	2.35	0.07
SLP ~ P1.A1 + P2.B3	3	-42.35	40.88	2.57	0.08	SLP ~ P4.B2	2	-39.08	27.18	2.61	0.06
SLP ~ (Null)	1	-50.6	41.88	3.57	0.05	SLP ~ P4.B3	2	-39.29	27.29	2.72	0.06
SLP ~ P2.B2	2	-47.88	42.33	4.02	0.04	SLP ~ P3.A1	3	-35.82	28.71	4.14	0.03
SLP ~ P1.A1 + P1.A2 + P2.B2	4	-40.64	42.48	4.17	0.03	SLP ~ P3.A1	3	-36.5	29.05	4.48	0.02
SLP ~ P1.A1 + P2.B1 + P2.B2	4	-40.79	42.59	4.28	0.03	SLP ~ P3.A1	3	-36.63	29.11	4.54	0.02
SLP ~ P1.A1 + P1.A2 + P2.B1	4	-41.11	42.83	4.52	0.03	SLP ~ P3.A1	3	-36.75	29.18	4.61	0.02
SLP ~ P1.A1 + P2.B2 + P2.B3	4	-41.19	42.89	4.58	0.03	SLP ~ DIST	3	-37.22	29.41	4.84	0.02
SLP ~ P1.A1 + P2.B1 + P2.B3	4	-41.44	43.07	4.76	0.03	SLP ~ P3.A1	3	-37.24	29.42	4.85	0.02
SLP ~ P1.A1 + P1.A2 + P2.B3	4	-41.62	43.21	4.9	0.02	SLP ~ P3.A2	3	-37.26	29.43	4.86	0.02
						SLP ~ P3.A2	3	-37.41	29.51	4.94	0.02
						SLP ~ P4.B1	3	-37.42	29.51	4.94	0.02
LLP ~ (Null)	1	-132.61	37.14	0	0.12	LLP ~ P3.A2	2	-88.18	34.76	0.05	0.12
LLP ~ P1.A2	2	-123.01	37.23	0.09	0.12	LLP ~ P3.A1	2	-90.26	35.41	0.7	0.09
LLP ~ P2.A2	2	-123.1	37.25	0.11	0.12	LLP ~ P3.A2	3	-81.97	36.01	1.3	0.06
LLP ~ P1.A2 + P2.B2	3	-113.67	37.58	0.44	0.1	LLP ~ P3.A1	3	-82.94	36.31	1.6	0.06
LLP ~ P1.A2 + P2.B1	3	-116.99	38.4	1.26	0.07	LLP ~ P3.A1 + P3.A2 + P4.B3	4	-72.31	36.64	1.93	0.05
LLP ~ P1.A1	2	-130.11	38.98	1.84	0.05	LLP ~ P3.A1	3	-84.52	36.8	2.09	0.04
LLP ~ P1.A2 + P2.B1 + P2.B2	4	-108.2	39.09	1.95	0.05	LLP ~ P4.B2	2	-94.87	36.83	2.12	0.04
LLP ~ P2.B1	2	-130.81	39.15	2.02	0.04	LLP ~ P4.B3	2	-95.07	36.9	2.18	0.04
LLP ~ P1.A1 + P1.A2	3	-121.07	39.4	2.26	0.04	LLP ~ P3.A2	3	-85.15	36.99	2.28	0.04

LLP ~ P2.B1 + P2.B2	3	-121.51	39.51	2.37	0.04	LLP ~ DIST	2	-96.38	37.3	2.59	0.03
LLP ~ P2.B3	2	-132.61	39.6	2.46	0.04	LLP ~ P4.B1	2	-97.03	37.5	2.79	0.03
LLP ~ P2.A2 + P2.B4	3	-122.59	39.77	2.64	0.03	LLP ~ P3.A2	3	-87.47	37.71	3	0.03
LLP ~ P1.A2 + P2.B4	3	-122.69	39.8	2.66	0.03	LLP ~ P3.A2	3	-88.02	37.88	3.17	0.03
LLP ~ P1.A1 + P2.B2	3	-122.86	39.84	2.7	0.03	LLP ~ P3.A1	3	-89.13	38.23	3.51	0.02
LLP ~ P1.A1 + P1.A2 + P2.B2	4	-113.62	40.42	3.29	0.02	LLP ~ P3.A1	3	-90.08	38.52	3.81	0.02
LLP ~ P1.A2 + P2.B2 + P2.B4	4	-113.67	40.44	3.3	0.02	LLP ~ P3.A1	3	-90.21	38.56	3.85	0.02
LLP ~ P1.A1 + P1.A2 + P2.B1	4	-116.53	41.14	4	0.02	LLP ~ P3.A2 + P4.B1 + P4.B3	4	-80	39.02	4.31	0.01
LLP ~ P1.A2 + P2.B1 + P2.B4	4	-116.57	41.15	4.02	0.02	LLP ~ P3.A1 + P3.A2 + P4.B2	4	-80.71	39.24	4.53	0.01
LLP ~ P1.A1 + P2.B1	3	-129.5	41.48	4.34	0.01	LLP ~ P3.A2 + P4.B2 + P4.B3	4	-81.17	39.38	4.67	0.01
LLP ~ P1.A1 + P2.B4	3	-129.74	41.54	4.4	0.01	LLP ~ DIST	3	-93.3	39.52	4.8	0.01
LLP ~ P2.B1 + P2.B4	3	-130.81	41.8	4.67	0.01	LLP ~ P3.A2 + DIST + P4.B3	4	-81.78	39.57	4.86	0.01

M_{sec}, n=20

Models	K	LogLik	QAICc	Δ	Akaike Weight
Den ~ P3.A2	2	-446.75	23.36	0	0.33
Den ~ P3.A2	3	-407.21	25.13	1.76	0.14
Den ~ P3.A2	3	-436.34	26.16	2.8	0.08
Den ~ P3.A1	3	-440.87	26.32	2.96	0.08
Den ~ P3.A2	3	-441.27	26.33	2.97	0.07
Den ~ P3.A2	3	-446.71	26.53	3.17	0.07

M_{sec}*, n = 29

Models	K	LogLik	QAICc	Δ	Akaike Weight
Den ~ P1*.A2 + P2.B2	3	-1031.44	50.51	0	0.21
Den ~ P1*.A2 + P2.B2 + P2.B3	4	-999.91	51.85	1.34	0.11
Den ~ P1*.A2 + P2.B1 + P2.B2	4	-1007.3	52.15	1.63	0.09
Den ~ P2.B2 + P2.B3	3	-1077.55	52.36	1.85	0.08
Den ~ P2.B1 + P2.B2 + P2.B3	4	-1022.52	52.76	2.24	0.07
Den ~ P2.B1 + P2.B2	3	-1092.71	52.97	2.46	0.06
Den ~ P1*.A1 + P1*.A2 + P2.B2	4	-1029.93	53.06	2.54	0.06
Den ~ P2.B2	2	-1158.45	53.15	2.64	0.06
Den ~ P1*.A2 + P2.B1 + P2.B2 + P2.B3	5	-975.44	53.62	3.11	0.04
Den ~ P1*.A1 + P1*.A2 + P2.B2 + P2.B3	5	-993.75	54.36	3.85	0.03
Den ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2	5	-998.9	54.57	4.05	0.03
Den ~ P1*.A1 + P2.B1 + P2.B2 + P2.B3	5	-1001.28	54.66	4.15	0.03
Den ~ P2.B1 + P2.B3	3	-1137.99	54.79	4.28	0.02

†Sp.rich. ~ P3.A2	3	-58.62	124.74	0	0.27
†Sp.rich. ~ P3.A2 + DIST + P4.B1	4	-57.42	125.5	0.76	0.18
†Sp.rich. ~ P3.A2 + DIST + P4.B2	4	-58.26	127.19	2.44	0.08
†Sp.rich. ~ P3.A1 + P3.A2 + DIST	4	-58.52	127.7	2.96	0.06
†Sp.rich. ~ P3.A2	3	-60.1	127.71	2.97	0.06
†Sp.rich. ~ P3.A2 + DIST + P4.B3	4	-58.6	127.86	3.12	0.06
†Sp.rich. ~ P3.A2 + DIST + P4.B1 + P4.B2	5	-56.95	128.18	3.44	0.05
†Sp.rich. ~ P3.A2	2	-61.81	128.32	3.57	0.04
†Sp.rich. ~ P3.A2 + DIST + P4.B1 + P4.B3	5	-57.18	128.65	3.91	0.04
†Sp.rich. ~ P3.A1 + P3.A2 + DIST + P4.B1	5	-57.26	128.81	4.06	0.04
†Sp.rich. ~ P3.A2 + P4.B1 + P4.B3	4	-59.53	129.72	4.97	0.02

Den ~ P1*.A1 + P2.B2 + P2.B3	4	-1075.05	54.87	4.35	0.02
Den ~ P1*.A1 + P2.B1 + P2.B2	4	-1084.28	55.24	4.72	0.02
Den ~ P2.B3	2	-1213.53	55.36	4.85	0.02
Sp.rich. ~ P1*.A2 + P2.B2	3	-133.89	118.61	0	0.27
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B2	4	-130.73	118.63	0.02	0.27
Sp.rich. ~ P1*.A2 + P2.B2 + P2.B3	4	-132.88	120.39	1.78	0.11
Sp.rich. ~ P1*.A2 + P2.B1 + P2.B2	4	-133.57	120.95	2.34	0.08
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B2 + P2.B3	5	-130.36	121.08	2.47	0.08
Sp.rich. ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2	5	-130.72	121.38	2.77	0.07
Sp.rich. ~ P1*.A2 + P2.B1 + P2.B2 + P2.B3	5	-132.55	122.87	4.26	0.03

†PFS ~ P3.A2	3	-20.76	49.02	0	0.15
†PFS ~ P3.A2 + DIST + P4.B3	4	-19.52	49.71	0.7	0.1
†PFS ~ P3.A2	3	-21.19	49.88	0.87	0.1
†PFS ~ P3.A1	3	-21.27	50.04	1.02	0.09
†PFS ~ P3.A2	2	-22.8	50.3	1.28	0.08
†PFS ~ P3.A1 + P3.A2 + P4.B3	4	-20.17	51.01	1.99	0.05
†PFS ~ P3.A1 + P3.A2 + P4.B2	4	-20.19	51.05	2.03	0.05

PFS ~ P1*.A1 + P2.B1 + P2.B2	4	-181.39	56.23	0	0.49
PFS ~ P1*.A1 + P2.B1 + P2.B2 + P2.B3	5	-178.07	58.17	1.94	0.19
PFS ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2	5	-181.3	58.97	2.74	0.13
PFS ~ P1*.A1 + P2.B2	3	-205.94	59.66	3.42	0.09
PFS ~ P1*.A1 + P2.B2 + P2.B3	4	-199.22	60.61	4.38	0.06
PFS ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B2 + P2.B3	6	-177.25	60.9	4.67	0.05

†PFS ~ P3.A2 + DIST + P4.B2	4	-20.27	51.2	2.18	0.05
†PFS ~ P3.A2	3	-22.2	51.91	2.89	0.03
†PFS ~ P3.A2 + P4.B2 + P4.B3	4	-20.62	51.91	2.9	0.03
†PFS ~ P3.A2 + P4.B1 + P4.B3	4	-20.68	52.03	3.02	0.03
†PFS ~ P3.A2	3	-22.48	52.45	3.44	0.03
†PFS ~ P3.A1 + P3.A2 + P4.B1	4	-21.01	52.68	3.67	0.02
†PFS ~ P3.A2 + P4.B1 + P4.B2	4	-21.11	52.89	3.88	0.02
†PFS ~ P3.A2 + DIST + P4.B2 + P4.B3	5	-19.31	52.9	3.89	0.02
†PFS ~ P3.A2 + DIST + P4.B1 + P4.B3	5	-19.34	52.96	3.94	0.02
†PFS ~ P3.A1 + P3.A2 + DIST	4	-21.18	53.02	4	0.02
†PFS ~ P3.A1 + P3.A2 + DIST + P4.B3	5	-19.46	53.21	4.2	0.02
†PFS ~ DIST + P4.B1 + P4.B3	4	-21.29	53.24	4.23	0.02
†PFS ~ DIST	3	-23.12	53.73	4.72	0.01
†PFS ~ P3.A1 + P3.A2 + DIST + P4.B2	5	-19.81	53.91	4.9	0.01
SFS ~ P3.A2	2	-497.8	21.84	0	0.25
SFS ~ P3.A2	3	-441.26	23.37	1.54	0.12
SFS ~ P3.A1	3	-481.79	24.54	2.71	0.06
SFS ~ DIST	2	-595.92	24.66	2.83	0.06
SFS ~ P3.A2	3	-492.27	24.84	3.01	0.06
SFS ~ P3.A2	3	-492.48	24.85	3.01	0.06
SFS~(Null)	1	-703.13	24.96	3.12	0.05
SFS ~ P3.A2	3	-497	24.98	3.14	0.05
SFS ~ P3.A2 + DIST + P4.B2	4	-434.22	26.79	4.95	0.02
SFS ~ P1*.A2	2	-1083.56	44.21	0	0.17
SFS ~ P1*.A2 + P2.B3	3	-1027.33	44.72	0.51	0.13
SFS ~ P2.B3	2	-1127.67	45.74	1.53	0.08
SFS ~ P1*.A1 + P1*.A2 + P2.B3	4	-983.26	45.8	1.59	0.08
SFS ~ P1*.A1 + P1*.A2	3	-1071.05	46.24	2.03	0.06
SFS ~ P1*.A2 + P2.B2	3	-1074.57	46.36	2.15	0.06
SFS ~ P1*.A1 + P2.B3	3	-1077.78	46.47	2.26	0.05
SFS ~ P1*.A2 + P2.B1	3	-1079.56	46.53	2.32	0.05
SFS ~ P1*.A2 + P2.B1 + P2.B3	4	-1023.14	47.18	2.97	0.04
SFS ~ P1*.A2 + P2.B2 + P2.B3	4	-1027.27	47.32	3.11	0.04
SFS~(Null)	1	-1244.72	47.46	3.25	0.03
SFS ~ P1*.A1 + P1*.A2 + P2.B2	4	-1036.64	47.65	3.44	0.03
SFS ~ P1*.A1 + P1*.A2 + P2.B2 + P2.B3	5	-965.79	47.95	3.74	0.03
SFS ~ P2.B1 + P2.B3	3	-1124.48	48.09	3.88	0.02
SFS ~ P2.B2 + P2.B3	3	-1125.02	48.11	3.9	0.02

SFS ~ P1*.A1 + P2.B1 + P2.B3	4	-1061.73	48.52	4.31	0.02
SFS ~ P1*.A1 + P1*.A2 + P2.B1 + P2.B3	5	-983.1	48.55	4.34	0.02
SFS ~ P1*.A1 + P1*.A2 + P2.B1	4	-1069.36	48.78	4.57	0.02
SFS ~ P1*.A2 + P2.B1 + P2.B2	4	-1069.92	48.8	4.59	0.02
SFS ~ P1*.A1 + P2.B2 + P2.B3	4	-1074.86	48.97	4.76	0.02

SLP~(Null)	1	-39.45	24.57	0	0.23
SLP ~ P3.A1	2	-37.33	26.3	1.73	0.1
SLP ~ P4.B1	2	-37.9	26.59	2.02	0.08
SLP ~ DIST	2	-38.32	26.8	2.23	0.07
SLP ~ P3.A2	2	-38.56	26.92	2.35	0.07
SLP ~ P4.B2	2	-39.08	27.18	2.61	0.06
SLP ~ P4.B3	2	-39.29	27.29	2.72	0.06
SLP ~ P3.A1	3	-35.82	28.71	4.14	0.03
SLP ~ P3.A1	3	-36.5	29.05	4.48	0.02
SLP ~ P3.A1	3	-36.63	29.11	4.54	0.02
SLP ~ P3.A1	3	-36.75	29.18	4.61	0.02
SLP ~ DIST	3	-37.22	29.41	4.84	0.02
SLP ~ P3.A1	3	-37.24	29.42	4.85	0.02
SLP ~ P3.A2	3	-37.26	29.43	4.86	0.02
SLP ~ P3.A2	3	-37.41	29.51	4.94	0.02
SLP ~ P4.B1	3	-37.42	29.51	4.94	0.02

SLP~(Null)	1	-83.93	43.11	0	0.22
SLP ~ P1*.A2	2	-81.95	44.53	1.42	0.11
SLP ~ P2.B2	2	-82.73	44.88	1.77	0.09
SLP ~ P1*.A1	2	-83.08	45.05	1.94	0.08
SLP ~ P2.B1	2	-83.91	45.43	2.32	0.07
SLP ~ P2.B3	2	-83.92	45.44	2.33	0.07
SLP ~ P1*.A2 + P2.B2	3	-80.78	46.45	3.34	0.04
SLP ~ P1*.A1 + P1*.A2	3	-81.05	46.57	3.46	0.04
SLP ~ P1*.A2 + P2.B3	3	-81.71	46.88	3.77	0.03
SLP ~ P1*.A2 + P2.B1	3	-81.83	46.93	3.82	0.03
SLP ~ P1*.A1 + P2.B2	3	-82.44	47.21	4.1	0.03
SLP ~ P2.B2 + P2.B3	3	-82.64	47.31	4.2	0.03
SLP ~ P2.B1 + P2.B2	3	-82.69	47.33	4.22	0.03
SLP ~ P1*.A1 + P2.B1	3	-82.9	47.43	4.32	0.03
SLP ~ P1*.A1 + P2.B3	3	-83.03	47.49	4.38	0.02
SLP ~ P2.B1 + P2.B3	3	-83.9	47.89	4.78	0.02

LLP~(Null)	1	-97.05	34.71	0	0.12
LLP ~ P3.A2	2	-88.18	34.76	0.05	0.12
LLP ~ P3.A1	2	-90.26	35.41	0.7	0.09
LLP ~ P3.A2	3	-81.97	36.01	1.3	0.06
LLP ~ P3.A1	3	-82.94	36.31	1.6	0.06
LLP ~ P3.A1 + P3.A2 + P4.B3	4	-72.31	36.64	1.93	0.05
LLP ~ P3.A1	3	-84.52	36.8	2.09	0.04
LLP ~ P4.B2	2	-94.87	36.83	2.12	0.04
LLP ~ P4.B3	2	-95.07	36.9	2.18	0.04
LLP ~ P3.A2	3	-85.15	36.99	2.28	0.04
LLP ~ DIST	2	-96.38	37.3	2.59	0.03

LLP~(Null)	1	-156.53	42.38	0	0.15
LLP ~ P2.B2	2	-148.83	42.84	0.46	0.12
LLP ~ P1*.A1	2	-150.73	43.3	0.92	0.1
LLP ~ P1*.A2	2	-153.66	44.01	1.64	0.07
LLP ~ P2.B3	2	-155.13	44.37	1.99	0.06
LLP ~ P2.B1	2	-155.54	44.47	2.09	0.05
LLP ~ P1*.A2 + P2.B2	3	-145.85	44.58	2.2	0.05
LLP ~ P1*.A1 + P2.B2	3	-146.43	44.72	2.34	0.05
LLP ~ P1*.A1 + P1*.A2	3	-147.67	45.02	2.64	0.04
LLP ~ P2.B1 + P2.B2	3	-147.78	45.05	2.67	0.04
LLP ~ P2.B2 + P2.B3	3	-148.79	45.29	2.91	0.04

LLP ~ P4.B1	2	-97.03	37.5	2.79	0.03	LLP ~ P1*.A1 + P2.B1	3	-150.6	45.73	3.35	0.03
LLP ~ P3.A2	3	-87.47	37.71	3	0.03	LLP ~ P1*.A1 + P2.B3	3	-150.65	45.74	3.37	0.03
LLP ~ P3.A2	3	-88.02	37.88	3.17	0.03	LLP ~ P1*.A2 + P2.B1	3	-150.77	45.77	3.4	0.03
LLP ~ P3.A1	3	-89.13	38.23	3.51	0.02	LLP ~ P1*.A2 + P2.B3	3	-150.96	45.82	3.44	0.03
LLP ~ P3.A1	3	-90.08	38.52	3.81	0.02	LLP ~ P1*.A2 + P2.B1 + P2.B2	4	-142.62	46.39	4.02	0.02
LLP ~ P3.A1	3	-90.21	38.56	3.85	0.02	LLP ~ P2.B1 + P2.B3	3	-154.22	46.61	4.23	0.02
LLP ~ P3.A2 + P4.B1 + P4.B3	4	-80	39.02	4.31	0.01	LLP ~ P1*.A1 + P1*.A2 + P2.B2	4	-143.76	46.67	4.29	0.02
LLP ~ P3.A1 + P3.A2 + P4.B2	4	-80.71	39.24	4.53	0.01	LLP ~ P1*.A2 + P2.B2 + P2.B3	4	-145.33	47.05	4.68	0.01
LLP ~ P3.A2 + P4.B2 + P4.B3	4	-81.17	39.38	4.67	0.01	LLP ~ P1*.A1 + P2.B1 + P2.B2	4	-145.92	47.2	4.82	0.01
LLP ~ DIST	3	-93.3	39.52	4.8	0.01	LLP ~ P1*.A1 + P1*.A2 + P2.B1	4	-146.15	47.25	4.88	0.01
LLP ~ P3.A2 + DIST + P4.B3	4	-81.78	39.57	4.86	0.01	LLP ~ P1*.A1 + P2.B2 + P2.B3	4	-146.4	47.31	4.94	0.01

Appendix H. Structural analysis of CCNR plots

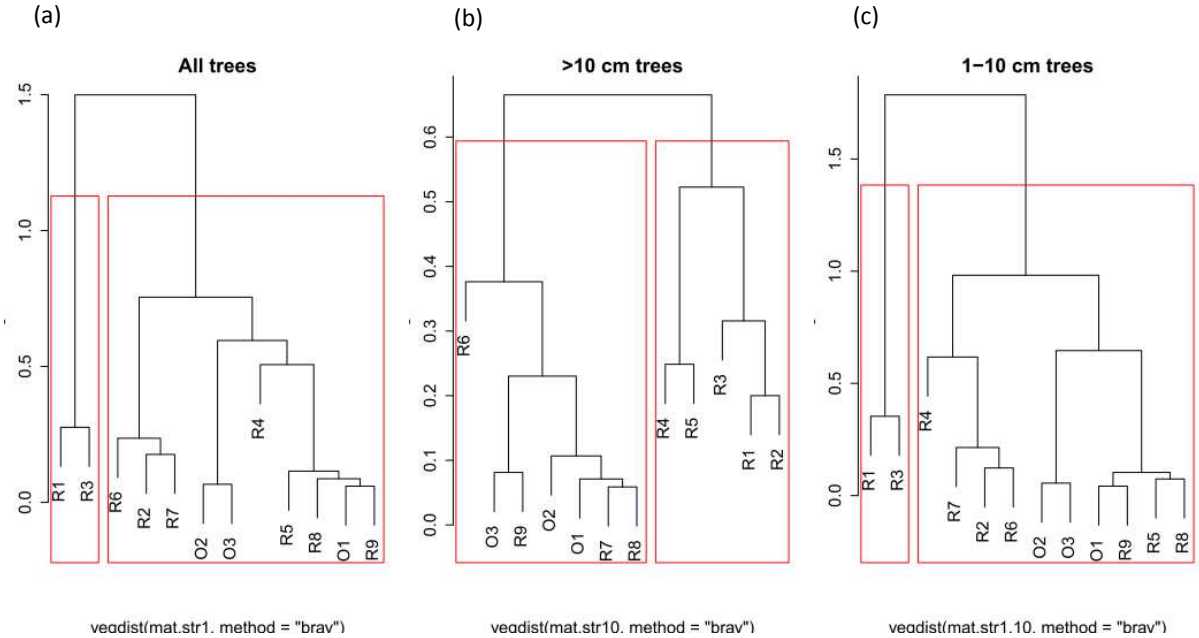


Figure 1. Dendrograms showing hierarchical clustering (Ward's minimum variance) of the forest structure in secondary and primary plots, based on the abundance of trees in pre-determined diameter size classes. Primary forest plots are in grey. Note that the smaller height differences in branch length in panel (b) denoted higher structural similarity among trees >10 cm DBH, as compared to the smaller trees. Similar results were obtained using basal area.

Appendix I. Top abundant species in CCNR plots

Table 1. Top 10 tree species (≥ 10 cm DBH) by basal area in the plots.

	O1				O2				O3			
Rank by BA	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**
1	*Litsea elliptica*	2.2	2.8	11	*Strombosia javanica*	2.1	8.4	33	*Shorea pauciflora*	3.7	0.6	3
2	*Hopea griffithii*	2.0	8.3	33	*Aglaia macrocarpa*	1.2	0.7	3	*Hopea griffithii*	3.6	11.0	49
3	*Myristica maingayi*	1.3	1.4	5	*Nephelium costatum*	0.8	4.9	19	*Koompassia malaccensis*	1.7	0.6	3
4	*Dipterocarpus elongatus*	0.8	1.4	5	*Nothaphoebe umbelliflora*	0.8	2.1	8	*Pternandra tuberculata*	1.6	0.6	3
5	*Adenanthera bicolor*	0.7	1.4	5	*Dysoxylum cauliflorum*	0.5	7.7	30	*Ochanostachys amentacea*	1.2	3.0	14
6	*Rhodamnia cinerea*	0.7	2.8	11	*Knema malayana*	0.5	4.9	19	*Kokoona reflexa*	1.0	1.8	8
7	*Timonius wallichianus*	0.6	4.1	16	*Pometia pinnata*	0.5	0.7	3	*Prunus polystachya*	1.0	1.8	8
8	*Syzygium ridleyi*	0.6	0.7	3	*Litsea costalis*	0.5	1.4	5	*Kibatalio maingayi*	1.0	1.2	5
9	*Macaranga gigantea*	0.6	1.4	5	*Popowia fusca*	0.5	7.7	30	*Palaquium impressinervum*	0.7	0.6	3
10	*Beilschmiedia madang*	0.5	2.8	11	*Horsfieldia sparsa*	0.4	1.4	5	*Diospyros sumatrana*	0.7	8.5	38
Sum			26.9				39.9				29.9	

Table 1. Cont.

	R1				R2				R3			
Rank by BA	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**
1	*Rhodamnia cinerea*	3.0	13.0	35	*Rhodamnia cinerea*	7.9	34.6	123	*Adinandra dumosa*	4.1	46.5	90
2	*Adinandra dumosa*	1.3	19.0	52	*Adinandra dumosa*	3.0	28.5	101	*Rhodamnia cinerea*	3.3	9.9	19
3	*Gynotroches axillaris*	1.1	5.0	14	*Guioa pubescens*	0.6	10.0	35	*Cratoxylum arborescens*	1.1	1.4	3
4	*Macaranga conifera*	1.1	10.0	27	*Ixonanthes reticulata*	0.6	0.8	3	*Guioa pubescens*	1.0	14.1	27
5	*Garcinia parvifolia*	0.7	5.0	14	*Litsea elliptica*	0.5	3.8	14	*Macaranga conifera*	0.8	5.6	11
6	*Timonius wallichianus*	0.7	8.0	22	*Syzygium lineatum*	0.5	2.3	8	*Timonius wallichianus*	0.6	5.6	11
7	*Cratoxylum maingayi*	0.7	5.0	14	*Gynotroches axillaris*	0.5	1.5	5	*Prunus polystachya*	0.3	1.4	3
8	*Elaeocarpus mastersii*	0.6	6.0	16	*Macaranga conifera*	0.4	2.3	8	*Calophyllum pulcherrimum*	0.3	1.4	3
9	*Myrica esculanta*	0.5	1.0	3	*Litsea firma*	0.3	3.8	14	*Garcinia parvifolia*	0.2	1.4	3
10	*Syzygium lineatum*	0.4	4.0	11	*Elaeocarpus mastersii*	0.2	1.5	5	*Syzygium lineatum*	0.2	4.2	8
Sum			76.0				89.2				91.5	

Table 1. Cont.

	R4				R5				R6			
Rank by BA	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**
1	*Rhodamnia cinerea*	2.0	32.4	98	*Syzygium zeylanicum*	0.7	13.2	25	*Elaeocarpus mastersii*	2.7	22.9	128
2	*Adinandra dumosa*	1.2	33.3	101	*Litsea elliptica*	0.5	5.9	11	*Ixonanthes reticulata*	1.5	3.4	19
3	*Syzygium grande*	0.6	2.7	8	*Syzygium borneense*	0.3	4.4	8	*Adinandra dumosa*	1.4	20.0	112
4	*Acacia auriculiformis*	0.6	3.6	11	*Rhodamnia cinerea*	0.3	8.8	16	*Rhodamnia cinerea*	1.4	11.2	63
5	*Litsea elliptica*	0.4	3.6	11	*Dillenia suffruticosa*	0.3	7.4	14	*Guioa pubescens*	1.0	5.9	33
6	*Alstonia angustifolia*	0.3	4.5	14	*Adinandra dumosa*	0.3	14.7	27	*Cratoxylum arborescens*	0.7	5.4	30
7	*Elaeocarpus mastersii*	0.3	3.6	11	*Syzygium lineatum*	0.2	4.4	8	*Syzygium lineatum*	0.6	3.9	22
8	*Syzygium lineatum*	0.1	2.7	8	*Elaeocarpus mastersii*	0.2	5.9	11	*Timonius wallichianus*	0.6	7.8	44
9	*Acacia mangium*	0.1	0.9	3	*Macaranga conifera*	0.1	2.9	5	*Macaranga conifera*	0.5	3.4	19
10	*Dillenia suffruticosa*	0.1	2.7	8	*Timonius wallichianus*	0.1	5.9	11	*Litsea elliptica*	0.4	3.4	19
Sum			90.1				73.5				87.3	

Table 1. Cont.

	R7				R8				R9			
Rank by BA	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**	**Species**	**BA (m^2 ha^{-1})**	**Indiv (%)**	**Indiv (ha^{-1})**
1	*Fagraea fragrans*	4.5	4.1	115	*Timonius wallichianus*	3.6	28.6	115	*Rhodamnia cinerea*	4.7	33.5	145
2	*Adinandra dumosa*	3.9	30.8	16	*Syzygium grande*	2.7	4.1	16	*Ixonanthes reticulata*	2.7	5.7	25
3	*Rhodamnia cinerea*	2.7	13.7	38	*Prunus polystachya*	2.0	9.5	38	*Garcinia parvifolia*	1.7	8.9	38
4	*Timonius wallichianus*	1.2	8.9	27	*Adinandra dumosa*	1.7	6.8	27	*Syzygium claviflorum*	0.6	1.3	5
5	*Prunus polystachya*	1.0	8.9	35	*Guioa pubescens*	1.6	8.8	35	*Calophyllum teysmanii*	0.6	0.6	3
6	*Syzygium grande*	1.0	2.7	38	*Hevea brasiliensis*	1.6	9.5	38	*Euodia glabra*	0.6	1.9	8
7	*Gynotroches axillaris*	0.6	1.4	3	*Pertusadina eurhyncha*	1.4	0.7	3	*Timonius wallichianus*	0.5	5.7	25
8	*Litsea elliptica*	0.6	4.8	8	*Litsea firma*	1.0	2.0	8	*Macaranga gigantea*	0.5	2.5	11
9	*Campnosperma auriculata*	0.6	0.7	8	*Garcinia parvifolia*	0.5	2.0	8	*Campnosperma auriculata*	0.4	2.5	11
10	*Lindera lucida*	0.4	4.1	19	*Rhodamnia cinerea*	0.4	4.8	19	*Elaeocarpus mastersii*	0.4	3.2	14
Sum			80.1				76.9				65.8	

Table 2. Top 10 sapling (1-3 cm DBH) species by stem count in the plots.

	O1			O2			O3		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Dysoxylum cauliflorum*	50	12.3	*Koilodepas longifolium*	275	39.9	*Koilodepas longifolium*	105	14.3
2	*Ixora javanica var. retineria*	37	9.1	*Mallotus penangensis*	53	7.7	*Diospyros sumatrana*	103	14
3	*Xerospermum noronhianum*	28	6.9	*Aglaia rufinervis*	42	6.1	*Agrostistachys borneensis*	68	9.3
4	*Koilodepas longifolium*	25	6.2	*Knema malayana*	33	4.8	*Hopea griffithii*	66	9
5	*Hopea griffithii*	16	4	*Dacroydes rostrata*	23	3.3	*Pentace triptera*	26	3.5
6	*Macaranga lowii*	15	3.7	*Dysoxylum cauliflorum*	21	3	*Macaranga lowii*	25	3.4
7	*Diospyros lanceifolia*	15	3.7	*Xerospermum noronhianum*	16	2.3	*Popowia fusca*	14	1.9
8	*Dacroydes rostrata*	14	3.5	*Nephelium costatum*	13	1.9	*Vatica pauciflora*	14	1.9
9	*Agrostistachys borneensis*	14	3.5	*Agrostistachys borneensis*	10	1.5	*Ixora pendula*	13	1.8
10	*Memecylon lilacinum*	13	3.2	*Knema laurina*	8	1.2	*Ardisia colorata*	13	1.8
Sum			56.1			71.7			60.9

Table 2. Cont.

	R1			R2			R3		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Champereia manillana*	9	23.1	*Calophyllum ferrugineum*	66	30.3	*Calophyllum pulcherrimum*	11	39.3
2	*Garcinia parvifolia*	6	15.4	*Guioa pubescens*	30	13.8	*Guioa pubescens*	5	17.9
3	*Santiria griffithii*	4	10.3	*Garcinia parvifolia*	21	9.6	*Anisophyllea disticha*	2	7.1
4	*Syzygium filiforme var. clarimyrtus*	3	7.7	*Cinnamomum iners*	13	6	*Calophyllum ferrugineum*	2	7.1
5	*Garcinia eugeniaefolia*	3	7.7	*Syzygium lineatum*	11	5	*Champereia manillana*	2	7.1
6	*Rhodamnia cinerea*	1	2.6	*Prunus polystachya*	10	4.6	*Calophyllum teysmanii*	1	3.6
7	*Anisophyllea disticha*	1	2.6	*Elaeocarpus mastersii*	9	4.1	*Alstonia angustifolia*	1	3.6
8	*Calophyllum wallichianum*	1	2.6	*Lindera lucida*	9	4.1	*Calophyllum teysmanii*	1	3.6
9	*Clerodendrum laevifolium*	1	2.6	*Actinodaphne malaccensis*	6	2.8	*Syzygium lineatum*	1	3.6
10	*Elaeocarpus mastersii/ Garcinia griffithii/ Xanthophyllum eurhynchum/ Syzygium lineatum/ Santiria rubiginosa/ Syzygium subdecussatum*	1	2.6	*Litsea firma/Macaranga bancana*	5	2.3	*Garcinia parvifolia*	1	3.6
Sum			77.1			82.6			96.5

Table 2. Cont.

	R4			R5			R6		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Dillenia suffruticosa*	38	31.4	*Dillenia suffruticosa*	204	51.5	*Alstonia angustifolia*	41	19.8
2	*Adinandra dumosa*	27	22.3	*Champereia manillana*	77	19.4	*Syzygium borneense*	22	10.6
3	*Clerodendrum laevifolium*	13	10.7	*Syzygium zeylanicum*	65	16.4	*Rhodamnia cinerea*	22	10.6
4	*Euodia glabra*	11	9.1	*Calophyllum pulcherrimum*	8	2	*Calophyllum ferrugineum*	20	9.7
5	*Rhodamnia cinerea*	7	5.8	*Clerodendrum laevifolium*	5	1.3	*Clerodendrum laevifolium*	16	7.7
6	*Syzygium borneense*	4	3.3	*Syzygium borneense*	4	1	*Elaeocarpus mastersii*	16	7.7
7	*Alstonia angustifolia*	3	2.5	*Euodia glabra*	4	1	*Syzygium lineatum*	11	5.3
8	*Artocarpus dadah*	3	2.5	*Rhodamnia cinerea*	4	1	*Garcinia parvifolia*	8	3.9
9	*Syzygium lineatum*	3	2.5	*Alstonia angustifolia*	3	0.8	*Dillenia suffruticosa*	5	2.4
10	*Cinnamomum iners/ Cratoxylum maingayi*	2	1.7	*Calophyllum teysmanii/ Guioa pubescens*	3	0.8	*Anisophyllea disticha*	4	1.9
Sum			91.8			95.2			79.6

Table 2. Cont.

	R7			R8			R9		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Prunus polystachya*	34	24.8	*Prunus polystachya*	164	46.7	*Calophyllum pulcherrimum*	188	49.9
2	*Clerodendrum laevifolium*	24	17.5	*Cinnamomum iners*	23	6.6	*Garcinia parvifolia*	60	15.9
3	*Champereia manillana*	11	8	*Timonius wallichianus*	22	6.3	*Ixonanthes reticulata*	42	11.1
4	*Calophyllum ferrugineum*	9	6.6	*Syzygium lineatum*	18	5.1	*Calophyllum wallichianum*	16	4.2
5	*Syzygium borneense*	5	3.6	*Macaranga bancana*	18	5.1	*Calophyllum tetrapterum*	15	4
6	*Anisophyllea disticha*	4	2.9	*Hevea brasiliensis*	11	3.1	*Rhodamnia cinerea*	10	2.7
7	*Ixonanthes reticulata*	4	2.9	*Litsea elliptica*	10	2.8	*Clerodendrum laevifolium*	7	1.9
8	*Macaranga bancana*	4	2.9	*Clerodendrum laevifolium*	8	2.3	*Maclurodendron porteri*	4	1.1
9	*Macaranga conifera*	4	2.9	*Elaeocarpus mastersii*	8	2.3	*Aporosa miqueliana*	3	0.8
10	*Timonius wallichianus*	4	2.9	*Syzygium grande*	8	2.3	*Calophyllum teysmanii/ Dysoxylum cauliflorum*	3	0.8
Sum			75			82.6			79.6

Table 3. Top 10 seedlings species in the plots. N is average stem number per 5 × 5 m seedling quadrat. Plot R3 had zero seedlings.

	O1			O2			O3		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Xerospermum noronhianum*	5.8	13.8	*Dysoxylum cauliflorum*	51	29.4	*Agrostistachys borneensis*	3.5	11.6
2	*Dysoxylum cauliflorum*	4	9.6	*Mallotus penangensis*	43	24.8	*Diospyros sumatrana*	3.3	10.9
3	*Garcinia parvifolia*	2.6	6.3	*Strombosia javanica*	33.3	19.2	*Thottea grandiflora*	2.9	9.6
4	*Dimocarpus longan ssp. malesianus*	2.3	5.4	*Knema malayana*	7.5	4.3	*Memecylon lilacinum*	1.4	4.6
5	*Agrostistachys borneensis*	2.1	5.1	*Strombosia ceylanica*	4.3	2.4	*Koilodepas longifolium*	1.3	4.3
6	*Strombosia ceylanica*	1.8	4.2	*Nothaphoebe umbelliflora*	3.3	1.9	*Ixora pendula*	1.2	4
7	*Litsea elliptica*	1.3	3	*Koilodepas longifolium*	3	1.7	*Phaeanthus ophthalmicus*	1	3.3
8	*Calophyllum pulcherrimum*	1.3	3	*Dacroydes rostrata*	2.3	1.3	*Prunus polystachya*	1	3.3
9	*Ixora javanica var. retineria*	1.3	3	*Agrostistachys borneensis*	1.8	1	*Mallotus penangensis*	0.9	3
10	*Macaranga lowii*	1.1	2.7	*Aglaia rufinervis*	1.8	1	*Litsea firma*	0.8	2.6
			56.10			87.00			57.20

Table 3. Cont.

	R1			R2			R4		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Calophyllum pulcherrimum*	3.5	26.4	*Syzygium lineatum*	17	40.5	*Dillenia suffruticosa*	2.7	22.2
2	*Litsea elliptica*	1.3	9.4	*Garcinia parvifolia*	4.9	26.5	*Clerodendrum laevifolium*	2	16
3	*Garcinia parvifolia*	1.1	8.5	*Guioa pubescens*	4.3	11.5	*Litsea elliptica*	1.5	11.9
4	*Anisophyllea disticha*	0.6	4.7	*Calophyllum ferrugineum*	3.9	5.3	*Melastoma malabathricum*	0.8	6.2
5	*Champereia manillana*	0.5	3.8	*Calophyllum pulcherrimum*	3	4.7	*Alstonia angustifolia*	0.7	5.3
6	*Timonius wallichianus*	0.4	2.8	*Litsea elliptica*	2.7	2.2	*Rhodamnia cinerea*	0.6	4.9
7	*Litsea firma*	0.3	1.9	*Cinnamomum iners*	2	1.6	*Cinnamomum iners*	0.5	4.1
8	*Pouteria malaccensis*	0.3	1.9	*Elaeocarpus mastersii*	0.9	1.6	*Adinandra dumosa*	0.5	3.7
9	*Calophyllum tetrapterum*	0.3	1.9	*Champereia manillana*	0.7	0.9	*Syzygium borneense*	0.4	2.9
10	*Trema cannabina*	0.3	1.9	*Macaranga bancana*	0.7	0.6	*Guioa pubescens/Timonius wallichianus/Palaquium obovatum*	0.3	2.5
			63.20			95.40			79.70

Table 3. Cont.

	R5			R6			R7		
Rank by abund.	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Champereia manillana*	16.3	40.5	*Elaeocarpus mastersii*	71	73.7	*Prunus polystachya*	5.6	25.6
2	*Syzygium zeylanicum*	10.6	26.5	*Guioa pubescens*	4.4	4.6	*Clerodendrum laevifolium*	2.6	11.7
3	*Dillenia suffruticosa*	4.6	11.5	*Garcinia parvifolia*	3	3.1	*Syzygium grande*	2.1	9.4
4	*Melastoma malabathricum*	2.1	5.3	*Ixonanthes reticulata*	2.4	2.5	*Macaranga bancana*	1.2	5.5
5	*Calophyllum pulcherrimum*	1.9	4.7	*Calophyllum pulcherrimum*	2	2.1	*Ficus aurata*	1.1	5.2
6	*Elaeocarpus mastersii*	0.9	2.2	*Syzygium lineatum*	2	2.1	*Anisophyllea disticha*	1.1	4.9
7	*Ficus aurata*	0.6	1.6	*Alstonia angustifolia*	1	1	*Champereia manillana*	0.9	4.2
8	*Anisophyllea disticha*	0.6	1.6	*Timonius wallichianus*	1	1	*Guioa pubescens*	0.9	3.9
9	*Syzygium grande*	0.4	0.9	*Litsea elliptica*	0.8	0.8	*Cinnamomum iners*	0.6	2.6
10	*Guioa pubescens/Arthrophyllum diversifolium/Calophyllum tetrapterum/Syzygium lineatum/Elaeocarpus petiolatus*	0.3	0.6	*Melastoma malabathricum/Litsea firma*	0.8	0.8	*Lindera lucida*	0.6	2.6
			95.40			91.70			75.60

Table 3. Cont.

	R8			R9		
Rank by abund	**Species**	**N**	**Indiv (%)**	**Species**	**N**	**Indiv (%)**
1	*Prunus polystachya*	105.3	70.3	*Calophyllum teysmanii*	126.5	46.7
2	*Syzygium grande*	16.5	11	*Calophyllum pulcherrimum*	69.3	25.6
3	*Litsea firma*	6.3	4.2	*Garcinia parvifolia*	15.8	5.8
4	*Ficus globosa*	4.8	3.2	*Syzygium borneense*	12.5	4.6
5	*Guioa pubescens*	2.8	1.8	*Litsea firma*	10	3.7
6	*Cinnamomum iners*	2.5	1.7	*Alstonia angustifolia*	9.5	3.5
7	*Elaeocarpus mastersii*	1.8	1.2	*Ixonanthes reticulata*	5	1.8
8	*Calophyllum ferrugineum*	1.8	1.2	*Dillenia suffruticosa*	4.3	1.6
9	*Ficus aurata*	1.5	1	*Xanthophyllum affine*	2.5	0.9
10	*Lindera lucida*	1.3	0.8	*Melastoma malabathricum*	2	0.7
			96.40			94.90

Appendix J. Results from MFA of secondary plots only

Table 1. Correlations between seedling community of secondary forest plots, nearest distance to potential seed sources, (Dist) belowground variables (BG), aboveground variables (AG) and the in-situ large trees community, using multiple factor analysis (MFA). Upper diagonals contained permutation-based p values. Lower diagonals contained RV coefficients.

Matrix	Seedling	BG	AG	Dist	Big trees
Seedling		**0.004**	**0.011**	**0.014**	**0.000**
BG	**0.344**		0.144	0.332	**0.040**
AG	**0.297**	0.149		0.232	**0.016**
Dist	**0.243**	0.075	0.084		**0.000**
Big trees	**0.758**	**0.247**	**0.259**	**0.463**	

Note: This analyses used a larger dataset with only soil variables that were shown to be important in the RDA analysis (AlSat, CN, P and pH, see below), and excluded data of max daily air temperature (maxT) and fluctuation in VPD (sdV) which had high failure rates.

Appendix K. Characterizing the regenerating environment

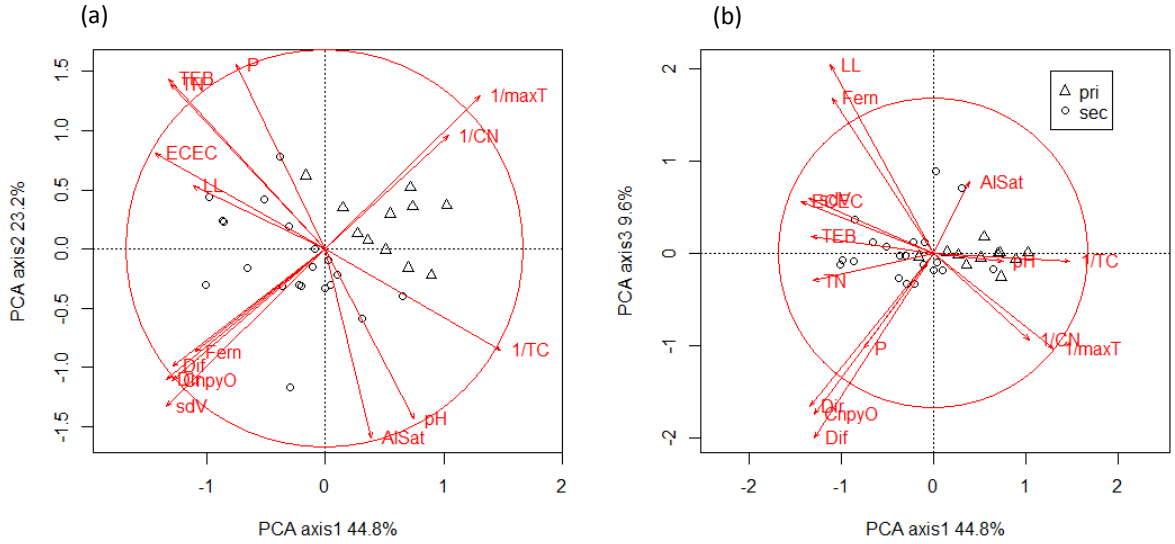


Figure 1. PCA biplots of the environmental variables in the seedling quadrats of primary and secondary forests plots. (Abbreviations: TC = total carbon, TN = total nitrogen, TEB = total exchanges bases, AlSat = aluminum saturation, ECEC = effective cation exchange capacity, CN = soil C:N ratio, Dif = diffused PAR, Dir = direct PAR, maxT = mean maximum daily temperature, sdV = mean daily standard deviation of VPD and LL = leaf litter depth).

In the PCA on the 31 (out of 48) seedling quadrats that had complete data of the regenerating environment,t the first three principal components explained 77.5% of the variance (Figure 5). In general, the gradient of the following variables corresponded to the distribution of the least disturbed primary forest quadrats (in terms of proximity to roads) to forested secondary ones, and to the fern-dominated quadrats: decreasing light, maxT, sdV, soil C:N ratio, fern cover and leaf litter. Aboveground, canopy openness, amount of diffused and direct PAR, sdV and maxT were positively correlated. Thick leaf litter and fern cover were also positively correlated. In general, the fern *D. linearis* thrived under high light conditions. However, light quantity also decreased beneath the fern's canopy, as indicated by the third principal component. Belowground, most of the primary seedling quadrats also had low total exchangeable bases (TEB), total nitrogen (TN), ECEC and phosphorus (P), while the secondary forest plots exhibited high variation in these soil variables. The soil pH in both primary and secondary forests overlapped and was very low, and ranged from pH 3.74 – 4.09 in primary forests to pH 3.42 – 4.48 in secondary forests. Although the results from these 31 plots showed relatively high Al saturation (AlSat) in some of the primary plots, when all available soil data from 48 plots were analyzed, the primary plots in general had lower AlSat.

Appendix L. Species abbreviation and categorization in Chapter 4

Table 1. Abbreviation of species used in Figure 1 and the categorization of primary/secondary forest species in Chapter 4.

Species Code	Species	Family	Category
Ad.du	*Adinandra dumosa* Jack	Theaceae	sec
Ag.ex	*Aglaia exstipulata* (Griff.) W. Theob.	Meliaceae	pri
Ag.lo	*Agrostistachys borneensis* (Wight) Benth	Euphorbiaceae	pri
Al.af	*Alstonia angustifolia* Wall. ex A. DC.	Apocynaceae	sec
An.di	*Anisophyllea disticha* (Jack) Baill.	Anisophylleaceae	sec
An.cu	*Antidesma cuspidatum* Müll. Arg	Phyllanthaceae	pri
Ap.fr	*Aporosa frutescens* Blume	Phyllanthaceae	pri
Ap.mi	*Aporosa microstachya* (Tul.) Müll. Arg.	Phyllanthaceae	pri
Ar.cl	*Archidendron clypearia* (Jack) I. C. Nielsen	Fabaceae	sec
Ar.co	*Ardisia colorata* Roxb	Myrsinaceae	pri
Be.ma	*Beilschmiedia madang* Blume	Lauraceae	pri
Ca.bm	*Calophyllum ferrugineum* Ridl.	Clusiaceae	sec
Ca.pc	*Calophyllum pulcherrimum* Wal. Ex Choisy	Clusiaceae	sec
Ca.tj	*Calophyllum teysmanii* Miq.	Clusiaceae	sec
Ca.tr	*Calophyllum tetrapterum* Miq.	Clusiaceae	sec
Ca.wa	*Calophyllum wallichianum* Planch. & Tr.	Clusiaceae	sec
Ch.ma	*Champereia manillana* (Blume) Merr.	Opiliaceae	sec
Ci.in	*Cinnamomum iners* Reinw.	Lauraceae	sec
Cl.la	*Clerodendrum laevifolium* Blume	Lamiaceae	sec
Di.su	*Dillenia suffruticosa* (Griff. ex Hook. f. & Thomson) Martelli	Dilleniaceae	sec
Di.lo	*Dimocarpus longan ssp. Malesianus* Lour.	Sapindaceae	pri
Di.la	*Diospyros lanceifolia* Roxb	Ebenaceae	pri
Di.st	*Diospyros styraciformis* King & Gamble	Ebenaceae	pri
Di.sm	*Diospyros sumatrana* Miq	Ebenaceae	pri
Dy.ca	*Dysoxylum cauliforum* Hiern	Meliaceae	pri
El.ma	*Elaeocarpus mastersii* King	Phyllanthaceae	sec
Eu.bo	*Syzygium borneense* (Miq.) Miq.	Myrtaceae	sec
Eu.fi	*Syzygium filiforme var. clarimyrtus* e (Wall. ex Duthie) Chantaran. & J. Parn.	Myrtaceae	sec
Eu.gd	*Syzygium grande* (Wight) Walp	Myrtaceae	sec
Eu.gc	*Syzygium glaucum* (King) P. Chantaranothai & J. Parn.	Myrtaceae	pri
Eu.in	*Syzygium incarnatum* Merr. & L.M. Perry	Myrtaceae	pri
Eu.li	*Syzygium lineatum* (DC.) Merr. & L.M. Perry	Myrtaceae	sec
Eu.pf	*Syzygium pseudoformosum* (King) Merr. & L.M. Perry	Myrtaceae	pri

Eu.sp	*Syzygium sp.*	Myrtaceae	sec
Eu.ze	*Syzygium zeylanicum* (L.) DC.	Myrtaceae	sec
Fi.au	*Ficus aurata* Miq.	Moraceae	sec
Ga.fo	*Garcinia forbesii* King	Clusiaceae	pri
Ga.gr	*Garcinia griffthii* T. Anderson	Clusiaceae	pri
Ga.pa	*Garcinia parvifolia* Miq.	Clusiaceae	sec
Gi.ne	*Gironniera nervosa* Miq.	Ulmaceae	sec
Gu.pu	*Guioa pubescens* (Z. & M.) Radlk	Sapindaceae	sec
Ho.gr	*Hopea griffithii* Kurz	Dipterocarpaceae	pri
Ix.re	*Ixonanthes reticulate* Jack	Ixonanthaceae	sec
Ix.ja	*Ixora javanica var. retineria* (Blume) DC.	Rubiaceae	pri
Ix.pe	*Ixora pendula* Jack	Rubiaceae	pri
Kn.ma	*Knema malayanai* Warb.	Myristicaceae	pri
Ko.lo	*Koilodepas longifolium* Hook. f.	Euphorbiaceae	pri
Li.lu	*Lindera lucida* (Blume) Boerl.	Lauraceae	sec
Li.ac	*Litsea accedens* (Blume) Boerl.	Lauraceae	pri
Li.ca	*Litsea castanea* Hook. f.	Lauraceae	sec
Li.co	*Litsea costalis* (Blume) Kosterm	Lauraceae	pri
Li.el	*Litsea elliptica* Blume	Lauraceae	sec
Li.fi	*Litsea firma* Hook. f.	Lauraceae	sec
Li.gr	*Litsea grandis* Hook. f.	Lauraceae	sec
Ma.ba	*Macaranga bancana* (Miq.) Mull. Arg.	Euphorbiaceae	sec
Ma.gi	*Macaranga gigantea* (Rchb. f. & Zoll.) Mull. Arg.	Euphorbiaceae	sec
Ma.lo	*Macaranga lowii* King ex Hook. f.	Euphorbiaceae	pri
Ma.pe	*Mallotus penangensis* Müll. Arg.	Euphorbiaceae	pri
Me.ma	*Melastoma malabathricum* L.	Melastomataceae	sec
Me.li	*Memecylon lilacinum* Z. & M.	Melastomataceae	pri
Ne.co	*Nephelium costatum* Hiern	Sapindaceae	pri
No.um	*Nothaphoebe umbelliflora* (Blume) Blume	Lauraceae	pri
Ph.op	*Phaeanthus ophthalmicus* (Roxb. ex G. Don) J. Sinclair	Annonaceae	pri
Po.ru	*Polyalthia rumphii* Merr.	Annonaceae	pri
Pr.po	*Prunus polystachya* (Hook. f.) Kalkm	Rosaceae	sec
Rh.ci	*Rhodamnia cinerea* Jack	Myrtaceae	sec
Sa.ru	*Santiria rubiginosa* Blume	Burseraceae	pri
St.ce	*Strombosia ceylanica* Gardn.	Olacaceae	pri
St.ja	*Strombosia javanica* Blume	Olacaceae	pri
Th.gr	*Thottea grandiflora* Rottb.	Aristolochiaceae	pri
Ti.wa	*Timonius wallichianus* (Korth.)	Rubiaceae	sec
Ur.hi	*Urophyllum hirsutum* (Wight) Hook. f.	Rubiaceae	pri
Va.ma	*Vatica maingoyi* Dyer	Dipterocarpaceae	pri
Xa.af	*Xanthophyllum affine* Korth.	Polygalaceae	pri
Xa.eu	*Xanthophyllum eurhynchum* Miq.	Polygalaceae	pri
Xe.no	*Xerospermum noronhianum* (Blume) Blume	Sapindaceae	pri

Appendix M. Trait data

Table 1. Mean trait values of seedling species.

Family	Species	Species Code	SLA (mm/mg)	LDMC	LNC (mg/g)	LPC (mg/g)	CN	NP	Ca (ug/g)	K (ug/g)	Mg (ug/g)
Theaceae	*Adinandra dumosa*	Ad.du	24.25	4.43	13.44	0.65	36.02	20.58	5552.85	14491.31	3250.69
Meliaceae	*Aglaia exstipulata*	Ag.ex	21.86	2.53	28.83	0.66	28.83	44.05	8576.57	15843.79	2219.91
Euphorbiaceae	*Agrostistachys borneensis*	Ag.lo	12.38	2.16	18.18	0.48	20.00	39.53	6203.20	6646.94	1062.63
Apocynaceae	*Alstonia angustifolia*	Al.af	39.28	4.96	31.11	0.63	22.09	49.52	9786.35	23956.35	4417.89
Anisophylleaceae	*Anisophyllea disticha*	An.di	25.67	2.93	19.85	0.66	20.69	33.23	4986.16	4183.58	5428.97
Phyllanthaceae	*Aporosa frutescens*	Ap.fr	24.56	4.37	21.64	0.71	21.64	30.30	11835.02	7121.72	5768.84
Fabaceae	*Archidendron clypearia*	Ar.cl	26.33	3.04	34.43	0.66	34.43	52.57	3710.09	9291.05	3235.80
Myrsinaceae	*Ardisia colorata*	Ar.co	14.43	3.53	15.51	0.42	29.44	37.05	19709.53	12506.13	14897.00
Lauraceae	*Beilschmiedia madang*	Be.ma	20.10	3.42	26.20	0.87	19.64	30.31	3059.02	8888.45	2646.80
Clusiaceae	*Calophyllum ferrugineum*	Ca.bm	11.12	2.32	11.52	0.33	11.52	35.52	3870.43	3230.70	1800.15
Clusiaceae	*Calophyllum pulcherrimum*	Ca.pc	14.46	1.91	12.86	0.33	16.45	39.54	3217.51	3405.89	1181.56
Clusiaceae	*Calophyllum teysmanii*	Ca.tj	10.49	2.34	9.48	0.27	9.48	35.62	3524.45	2949.46	1386.80
Opiliaceae	*Champereia manillana*	Ch.ma	18.48	3.86	32.05	1.48	32.05	22.42	18996.77	32214.26	6516.20
Lauraceae	*Cinnamomum iners*	Ci.in	18.07	2.87	19.53	0.64	20.74	30.83	4086.14	8378.06	1400.40
Lamiaceae	*Clerodendrum laevifolium*	Cl.la	45.97	5.48	40.05	1.18	28.55	34.53	7292.39	25595.84	4589.83

Burseraceae	*Dacryodes rostrata*	Da.ro	17.12	2.40	14.32	0.44	21.73	32.84	4860.48	7521.39	1446.12
Dilleniaceae	*Dillenia suffruticosa*	Di.su	22.67	5.70	20.45	1.11	24.93	19.41	7379.79	20622.82	4032.17
Sapindaceae	*Dimocarpus longan ssp. malesianus*	Di.lo	18.56	2.31	20.14	0.81	26.06	24.86	5370.80	5881.25	1952.11
Ebenaceae	*Diospyros lanceifolia*	Di.la	14.84	2.46	20.78	0.55	21.81	38.36	8744.38	9570.43	3201.58
Ebenaceae	*Diospyros sumatrana*	Di.sm	28.91	4.37	21.16	0.60	21.16	35.52	8807.09	21104.66	6728.04
Meliaceae	*Dysoxylum cauliforum*	Dy.ca	30.45	4.02	37.45	0.94	26.54	39.69	3525.83	12324.89	2869.29
Phyllanthaceae	*Elaeocarpus mastersii*	El.ma	21.10	2.49	15.62	0.34	19.62	51.53	6817.14	3364.74	2228.99
Myrtaceae	*Syzygium*	Eu.sp	15.78	2.33	16.04	0.50	16.04	32.02	8089.83	3332.56	3088.50
Myrtaceae	*Syzygium borneense*	Eu.bo	17.55	2.79	14.38	0.47	21.05	30.95	5314.08	5251.20	2903.45
Myrtaceae	*Syzygium grande*	Eu.gd	13.68	2.96	14.73	0.68	14.73	22.38	6843.47	7076.58	3590.48
Myrtaceae	*Syzygium lineatum*	Eu.li	18.60	2.61	13.86	0.55	13.86	25.22	4952.79	4264.76	1755.15
Myrtaceae	*Syzygium zeylanicum*	Eu.ze	19.78	2.81	12.83	0.69	12.83	18.73	3473.79	9191.58	1608.06
Moraceae	*Ficus aurata*	Fi.au	45.29	4.71	29.74	0.96	29.74	31.00	6955.48	14995.45	8722.00
Clusiaceae	*Garcinia forbesii*	Ga.fo	17.05	4.34	15.45	0.54	29.27	28.86	13114.24	6612.25	2937.79
Clusiaceae	*Garcinia parvifolia*	Ga.pa	19.32	4.27	15.76	0.44	20.37	35.95	9077.46	3571.39	3107.95
Ulmaceae	*Gironniera nervosa*	Gi.ne	28.76	3.26	32.45	0.71	14.08	45.95	3030.89	6379.72	2691.61
Sapindaceae	*Guioa pubescens*	Gu.pu	18.19	2.35	16.95	0.48	16.95	35.22	5700.73	3698.92	3767.07
Dipterocarpaceae	*Hopea griffithii*	Ho.gr	21.07	2.17	20.68	0.45	23.56	45.75	4409.40	5643.47	1623.93

Ixonanthaceae	*Ixonanthes reticulata*	Ix.re	24.91	3.83	20.49	0.49	20.49	42.46	7701.65	7160.56	2905.88
Rubiaceae	*Ixora pendula*	Ix.pe	15.74	2.44	25.15	0.52	25.15	48.30	8804.97	11884.55	2972.33
Euphorbiaceae	*Koilodepas longifolium*	Ko.lo	20.20	2.12	18.27	0.61	20.96	29.98	7763.77	6544.81	1846.74
Lauraceae	*Lindera lucida*	Li.lu	24.89	4.34	25.07	0.90	25.07	27.76	15062.41	6702.78	3406.81
Lauraceae	*Litsea elliptica*	Li.el	27.22	3.61	25.88	0.68	25.18	38.19	4685.84	8884.84	1626.44
Lauraceae	*Litsea firma*	Li.fi	20.68	2.87	18.45	0.56	18.45	33.31	3831.63	5646.94	1923.07
Euphorbiaceae	*Macaranga bancana*	Ma.ba	36.16	3.51	26.93	0.97	26.93	27.62	9497.02	11438.56	3487.94
Euphorbiaceae	*Macaranga lowii*	Ma.lo	33.77	2.76	21.28	0.65	21.28	32.59	3747.55	8110.36	2926.93
Euphorbiaceae	*Mallotus penangensis*	Ma.pe	18.56	2.27	21.36	0.59	20.87	36.07	7614.19	5071.77	1219.54
Melastomataceae	*Melastoma malabathricum*	Me.ma	22.70	4.28	16.26	0.57	20.83	28.93	21796.26	6731.93	3727.93
Melastomataceae	*Memecylon lilacinum*	Me.li	13.26	2.27	13.72	0.36	13.72	37.85	12340.82	3459.52	3199.17
Lauraceae	*Nothaphoebe umbelliflora*	No.um	17.66	2.72	18.22	0.74	18.22	24.54	2321.62	7301.83	1885.35
Annonaceae	*Polyalthia rumphii*	Po.ru	29.50	4.48	29.71	0.76	29.71	39.35	5178.58	13207.60	1753.07
Rosaceae	*Prunus polystachya*	Pr.po	16.19	2.81	19.67	0.65	19.67	30.59	7887.67	11466.53	3244.52
Myrtaceae	*Rhodamnia cinerea*	Rh.ci	15.69	2.49	13.44	0.44	19.15	31.51	3154.74	6218.54	2028.20
Olacaceae	*Strombosia ceylanica*	St.ce	14.28	2.93	23.36	0.60	23.36	39.91	5826.05	10059.80	2338.78
Olacaceae	*Strombosia javanica*	St.ja	42.55	5.36	49.12	3.15	49.12	16.33	2721.53	20538.59	2508.98
Aristolochiaceae	*Thottea grandiflora*	Th.gr	41.49	6.14	27.32	0.66	27.32	41.72	5472.74	13058.44	2545.88
Rubiaceae	*Timonius wallichianus*	Ti.wa	33.67	4.09	19.16	0.47	19.89	40.65	6539.95	6885.53	1890.06

Rubiaceae	*Urophyllum hirsutum*	Ur.hi	25.13	3.65	19.77	0.47	19.77	41.81	12486.52	7025.29	5809.47
Dipterocarpaceae	*Vatica maingoyi*	Va.ma	9.97	2.37	18.70	0.66	18.70	28.33	3091.08	7920.20	1113.28
Polygalaceae	*Xanthophyllum affine*	Xa.af	16.66	2.44	29.49	0.63	29.49	47.52	1258.25	8278.45	1088.17
Sapindaceae	*Xerospermum noronhianum*	Xe.no	14.41	2.11	16.37	0.54	16.37	30.27	3224.02	4585.91	1167.05

Table 2. Mean trait values of tree species. Wood density (Wd) data was courtesy of Chave et al. 2009 and Zanne et al. 2009.

Family	Species	Species Code	SLA (mm/mg)	LDMC	LNC (mg/g)	LPC (mg/g)	CN	NP	Ca (ug/g)	K (ug/g)	Mg (ug/g)	Wd (g/cm^3)
Fabaceae	*Acacia auriculiformis*	Ac.au	9.61	0.36	31.49	0.63	18.02	50.05	3771.30	6387.05	1386.36	0.680
Theaceae	*Adinandra dumosa*	Ad.du	8.06	0.40	11.21	0.38	46.12	30.12	3621.48	6741.97	2373.09	0.540
Clusiaceae	*Calophyllum teysmanii*	Ca.tj	5.36	0.52	8.55	0.25	58.79	33.80	3370.44	3301.83	2582.26	0.540
Lauraceae	*Cinnamomum iners*	Ci.in	10.64	0.41	19.14	0.56	26.11	34.00	5309.09	9541.49	1332.49	0.499
Hypericaceae	*Cratoxylum arborescens*	Cr.ar	9.91	0.42	12.53	0.48	40.00	26.59	4805.43	6661.79	1495.98	0.433
Dilleniaceae	*Dillenia suffruticosa*	Di.su	10.97	0.26	20.23	1.01	23.89	20.31	5040.18	9884.08	3067.11	0.450
Phyllanthaceae	*Elaeocarpus mastersii*	El.ma	9.67	0.50	15.03	0.43	33.24	35.55	4149.91	4347.67	1543.63	0.550
Myrtaceae	*Syzygium borneense*	Eu.bo	7.78	0.47	13.69	0.51	37.23	26.91	4069.76	5216.66	1681.09	0.664*
Myrtaceae	*Syzygium claviflorum*	Eu.cl	7.30	0.47	13.00	0.49	46.30	25.73	3392.34	6975.62	1571.82	0.624
Myrtaceae	*Syzygium grande*	Eu.gd	6.62	0.48	13.50	0.46	38.75	29.09	5564.98	4260.93	1955.20	0.923
Myrtaceae	*Syzygium lineatum*	Eu.li	8.44	0.49	12.48	0.46	38.90	28.26	5937.83	3316.99	1813.66	0.680
Myrtaceae	*Syzygium zeylanicum*	Eu.ze	12.08	0.40	10.66	0.51	46.51	19.35	3867.59	6233.42	1176.63	0.664*
Rutaceae	*Euodia glabra*	Eu.gl	9.46	0.33	25.82	0.95	19.83	27.22	4134.11	6919.33	2091.67	0.310
Loganiaceae	*Fagraea fragrans*	Fa.fr	11.89	0.33	17.76	0.62	28.25	28.55	6489.35	2960.54	3038.41	0.688
Clusiaceae	*Garcinia parvifolia*	Ga.pa	11.83	0.33	18.75	0.58	26.09	32.73	7602.44	4141.63	2554.63	0.435
Sapindaceae	*Guioa pubescens*	Gu.pu	7.33	0.50	15.60	0.54	34.61	29.32	3250.16	4321.78	2120.63	0.548*
Rhizophoraceae	*Gynotroches axillaris*	Gy.ax	9.30	0.34	17.60	0.49	27.66	36.24	3543.99	4442.22	1908.36	0.520
Euphorbiaceae	*Hevea brasiliensis*	He.br	15.57	0.40	37.82	1.64	13.35	23.03	5174.10	7637.57	2997.59	0.467
Ixonanthaceae	*Ixonanthes reticulata*	Ix.re	10.82	0.38	18.81	0.49	26.59	38.99	4846.87	6779.40	2356.38	0.626
Lauraceae	*Litsea elliptica*	Li.el	9.78	0.44	20.71	0.64	26.62	32.34	6770.73	5381.57	1463.54	0.450
Euphorbiaceae	*Macaranga conifera*	Ma.co	12.43	0.40	22.94	0.94	21.29	24.91	7646.59	8097.15	2659.65	0.330
Euphorbiaceae	*Macaranga gigantea*	Ma.gi	7.83	0.45	16.60	0.84	29.53	19.74	14664.30	9226.71	1994.10	0.295
Rubiaceaee	*Pertusadina eurhyncha*	Pe.eu	13.32	0.44	17.15	0.62	28.80	27.70	1501.86	3421.94	1833.72	0.680
Rosaceae	*Prunus polystachya*	Pr.po	7.87	0.49	16.87	0.62	31.47	27.60	5511.59	8024.47	1759.36	0.500
Myrtaceae	*Rhodamnia cinerea*	Rh.ci	9.58	0.50	13.37	0.52	39.37	26.46	3464.97	5150.53	1533.71	0.801
Bignoniaceae	*Spathodea campanulata*	Sp.ca	14.03	0.32	22.79	1.27	19.84	17.89	27325.26	11868.35	2795.77	0.351
Rubiaceae	*Timonius wallichianus*	Ti.wa	20.35	0.31	21.93	0.76	22.23	29.13	8335.58	9584.60	1857.01	0.760

*genus-level wood density values

Appendix N. Bivariate plots of selected cwm trait values and environmental variables

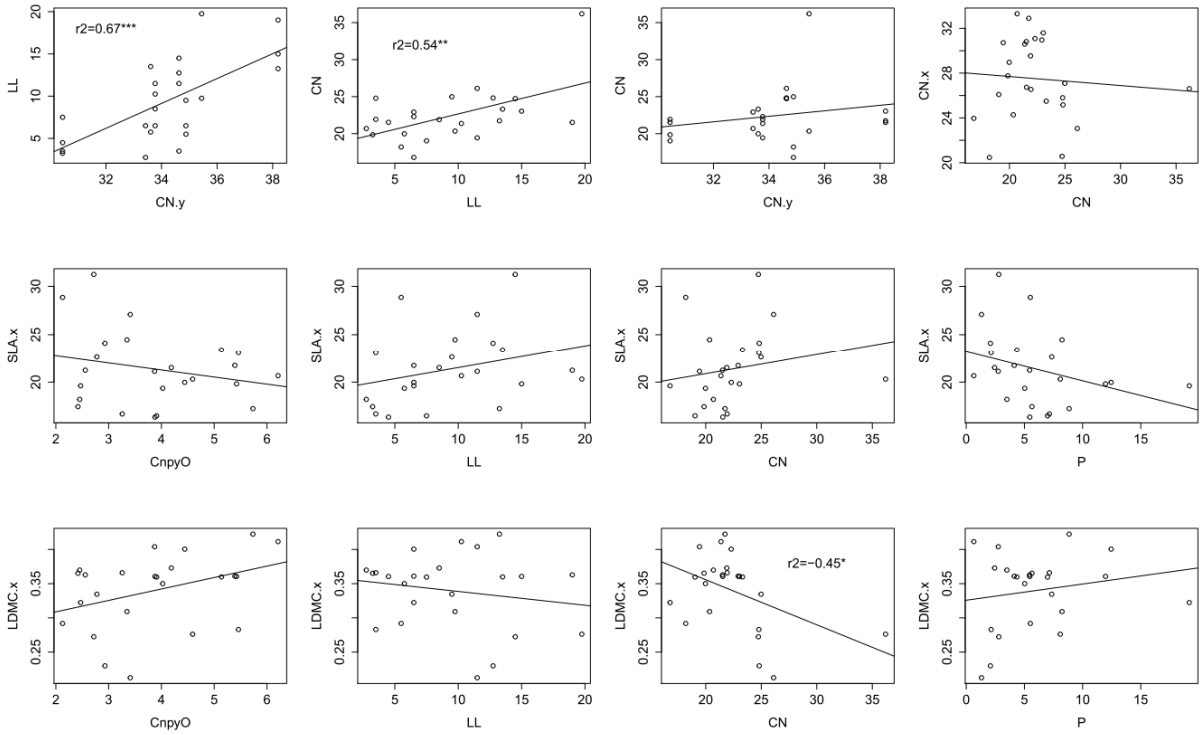


Figure 1. Bivariate plots of community weighted means of selected traits and environmental variables in the secondary forest plots. Only significant Pearson correlations are shown. Seedling traits end with suffix ".x" and adult traits end with suffix ".y". See Table 1 for the list of abbreviation.

Appendix O. Graphs of foliar nutrients and soil nutrients

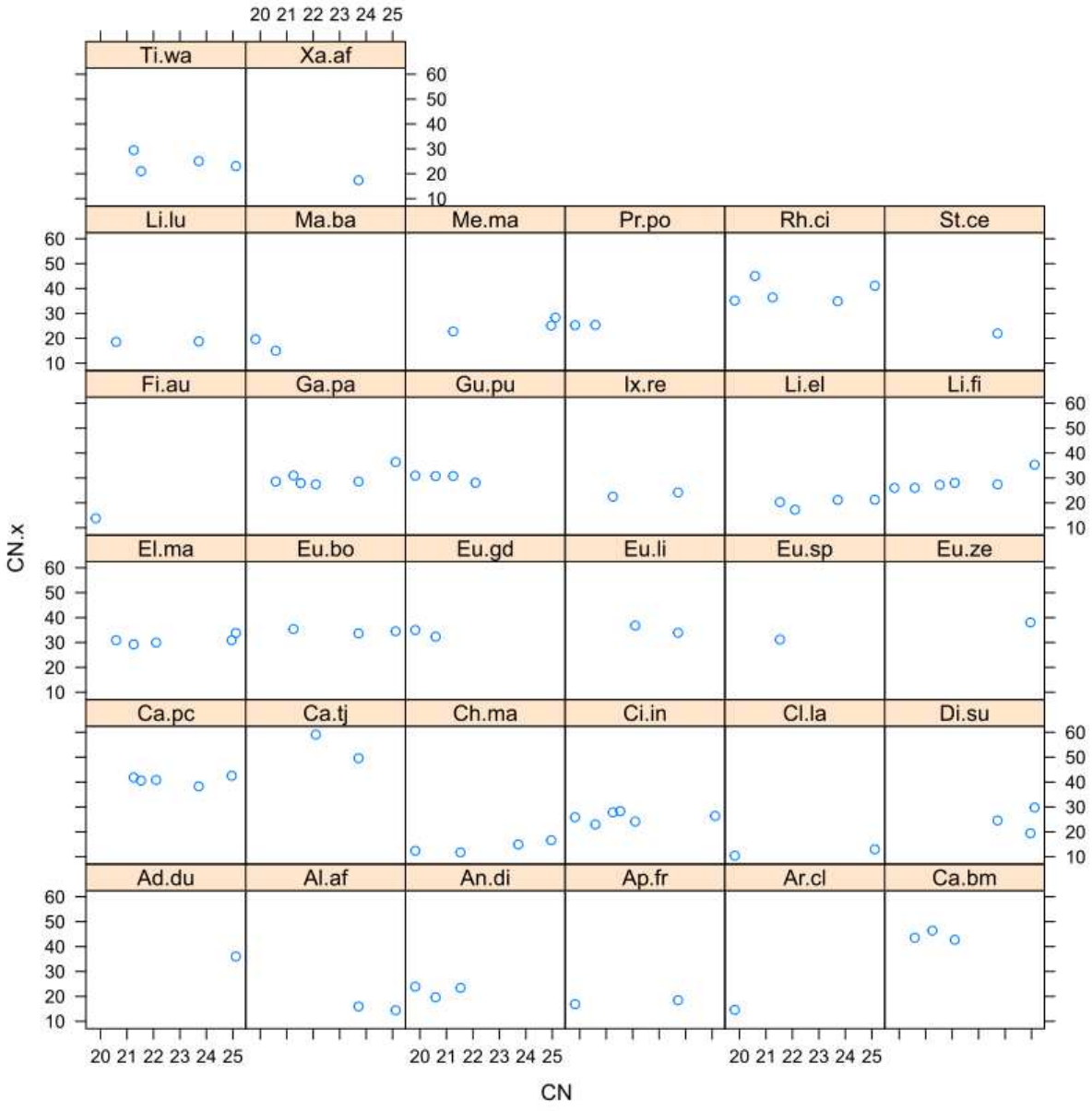


Figure 1. Leaf C:N ratio of seedlings species plotted by plots' soil C:N ratio.

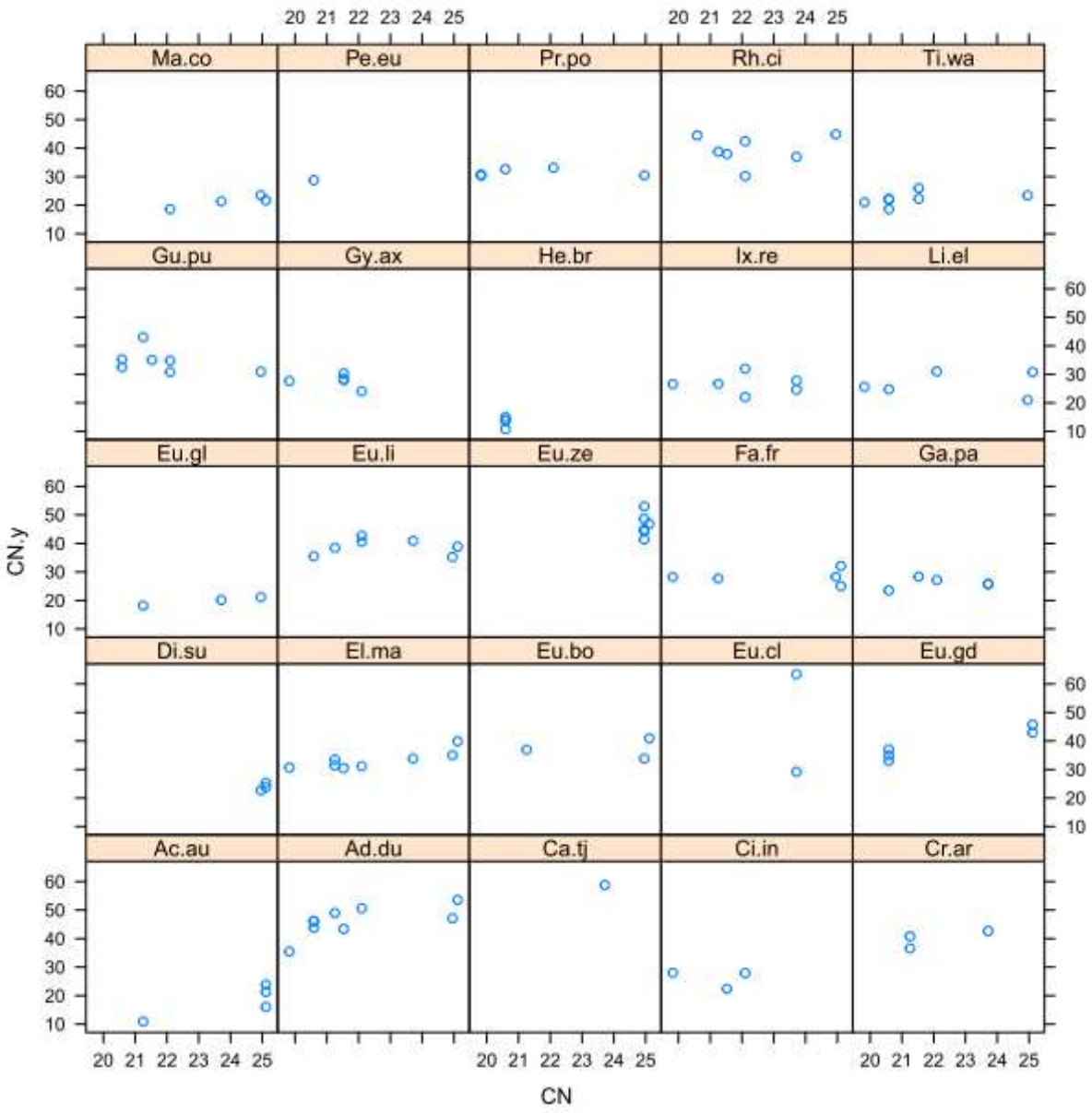


Figure 2. Leaf C:N ratio of saplings species plotted by plots' soil C:N ratio.

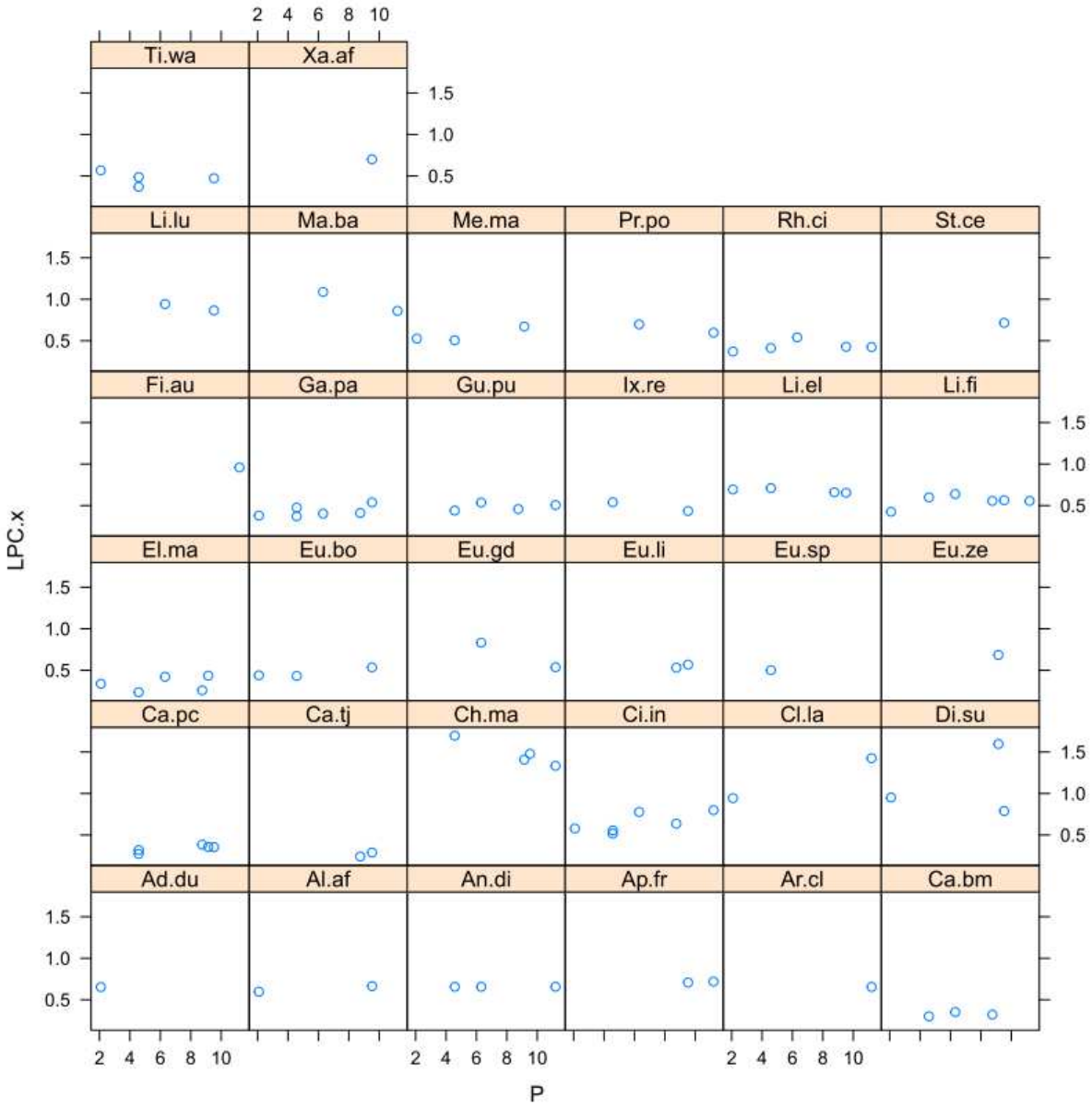


Figure 3. Leaf phosphorus content (mg g^{-1}) of seedlings species plotted by plots' available phosphorus (mg kg^{-1}).

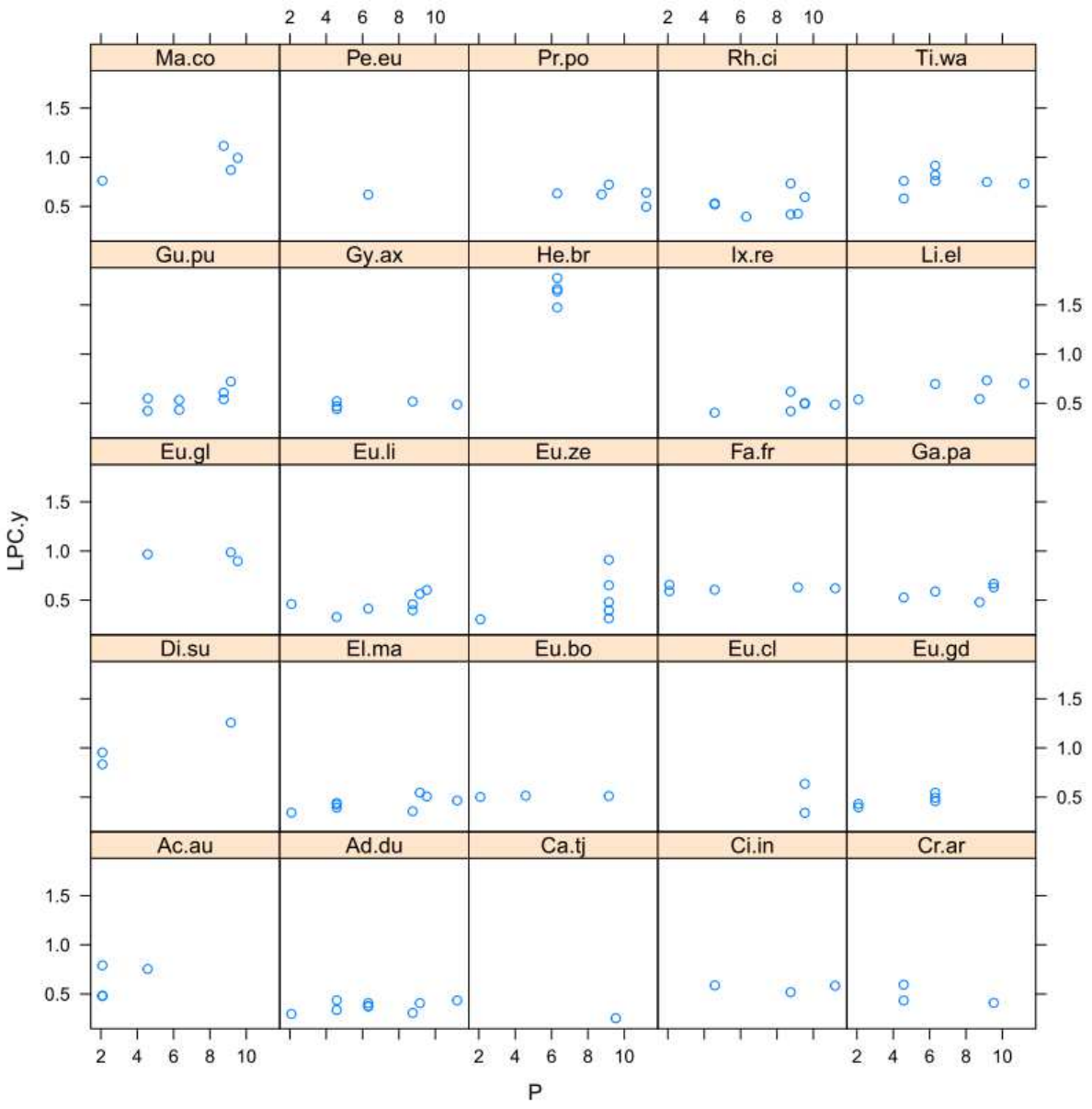


Figure 4. Leaf phosphorus content (mg g^{-1}) of saplings species plotted by plots' available phosphorus (mg kg^{-1}).

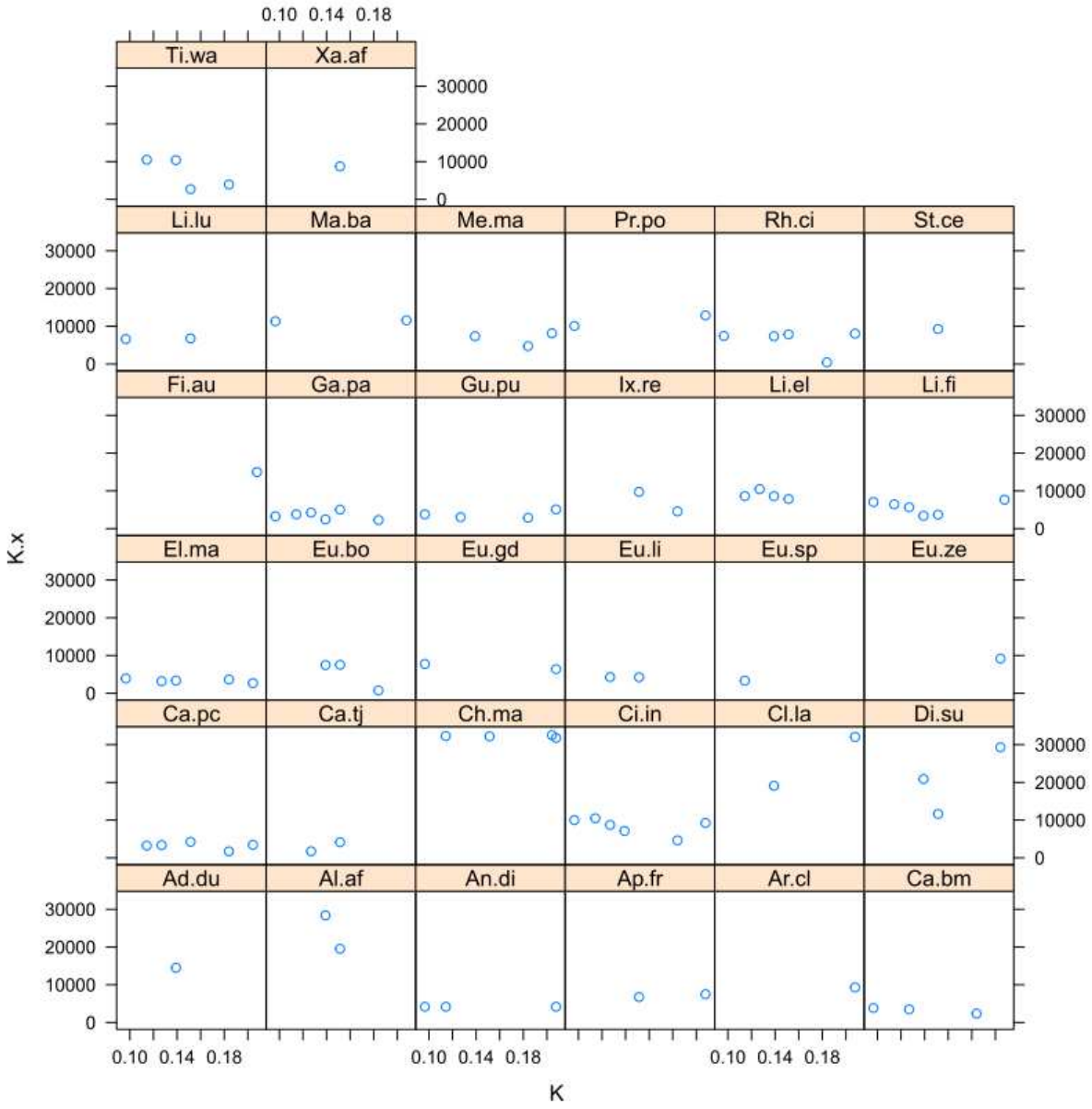


Figure 5. Leaf potassium concentration (ug g^{-1}) of seedlings species plotted by plots' exchangeable potassium (cmolc kg^{-1}).

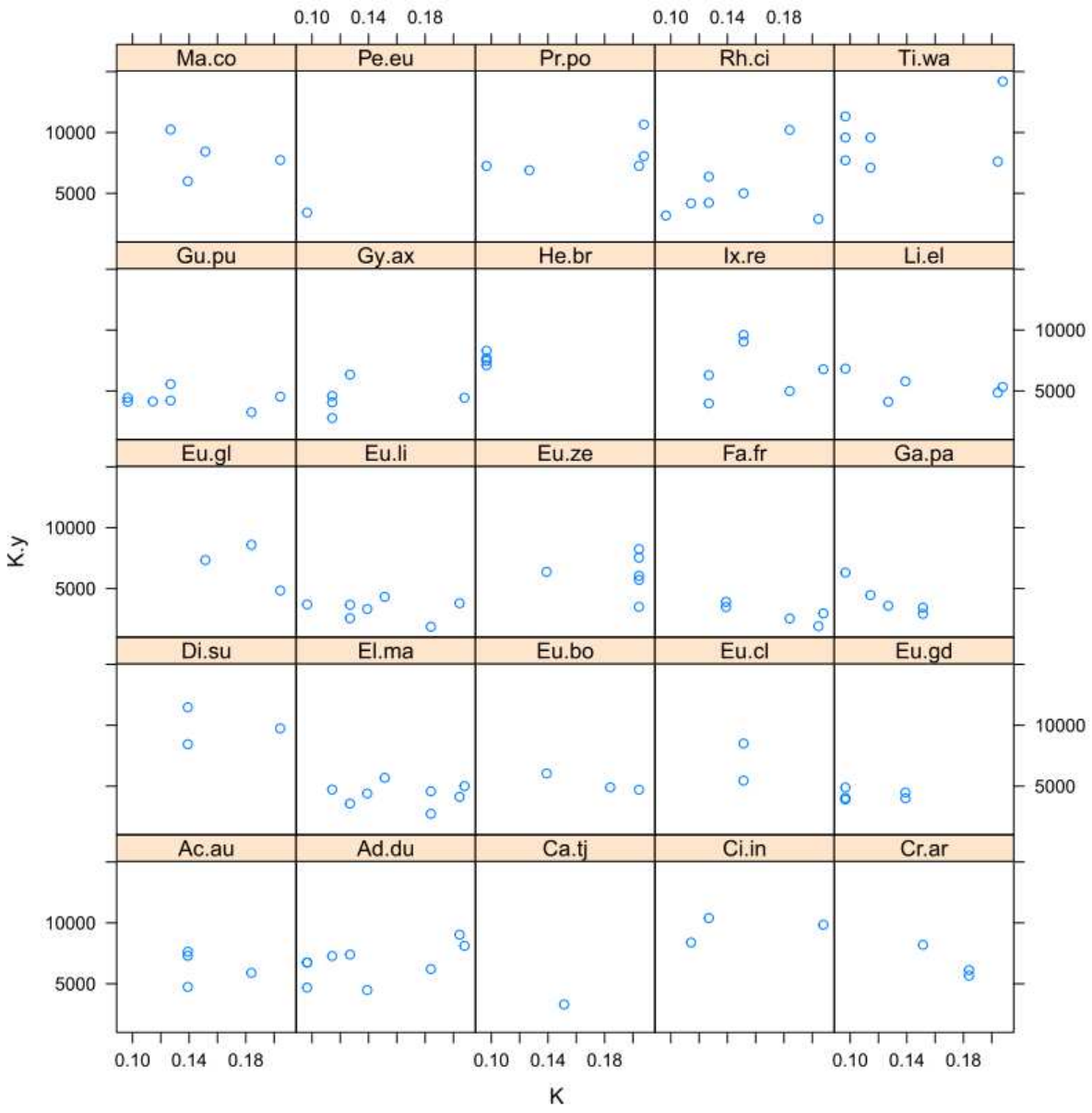


Figure 6. Leaf potassium concentration (ug g^{-1}) of saplings species plotted by plots' exchangeable potassium (cmolc kg^{-1}).