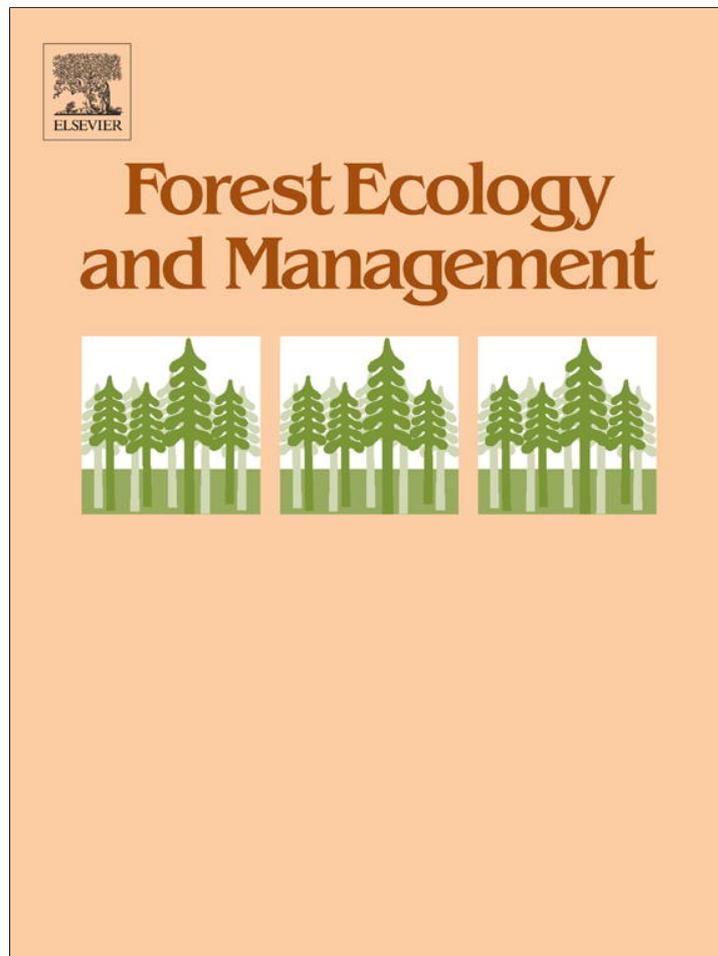


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Slow recovery of a secondary tropical forest in Southeast Asia

Siew Chin Chua^{a,b,*}, Benjamin S. Ramage^b, Kang Min Ngo^a, Matthew D. Potts^b, Shawn K.Y. Lum^a^a Center for Tropical Forest Science, National Institute of Education, Nanyang Technological University, 1 Nanyang Walk, Singapore 637616, Singapore^b Department of Environmental Science, Policy & Management, University of California Berkeley, Berkeley, CA 94720, USA

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ABSTRACT

Understanding the structure and diversity of secondary tropical forests is important as they constitute an increasing proportion of tropical landscapes. However, few studies have investigated the long-term recovery of tropical forests following agricultural abandonment. We compared the physical structure and tree species composition of a 56-year-old 2-ha secondary forest plot with an adjacent 2-ha primary forest in Singapore. All trees ≥ 1 cm in diameter were surveyed. We found that after 56 years of recovery, the secondary forest remains floristically and structurally distinct from the adjacent primary forest. The secondary forest plot had 30% of the stem density, 58% of basal area, 26% of species richness and 59% of the Shannon diversity as compared to the primary forest plot. Nonmetric multidimensional scaling analysis and partial Mantel tests showed that the floristic composition of the two plots was distinct, even after accounting for the underlying spatial gradient in composition. Nevertheless, some shade tolerant species such as *Streblus elongatus* and *Calophyllum* spp. were thriving in the secondary forest. Our findings suggest several possible mechanisms for the slow recovery of the secondary forest, including strong dispersal limitation and the presence of long-lived pioneer species.

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1. 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., 2004, 2010). 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, 1999, 2001; 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

* Corresponding author at: Department of Environmental Science, Policy & Management, University of California Berkeley, Berkeley, CA 94720, USA. Tel.: +1 510 642 5580; fax: +1 510 643 5438.

E-mail address: scchua@berkeley.edu (S.C. Chua).

its founding in 1819 (Corlett, 1991b, 1992). 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.

2. Methods

2.1. 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, 2013, Singapore).

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 75–120 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 (Fig. 1). The secondary forest plot lies on the upper slope of a shallow valley, from 50 to 85 m a.s.l. Gambier and pepper were grown in parts of the secondary forest plot around 1845 (National Archives of Singapore). Signs of terracing also suggested that pineapples were planted, possibly in the late 1800s. Thereafter 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,

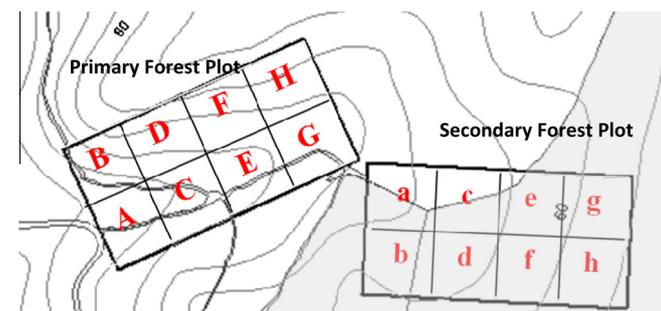


Fig. 1. Map showing plot layout and the location of the 50 × 50 m quadrats. Shaded area indicates secondary forest. Unshaded areas indicate old growth forest.

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. Public walking trails (about 5% of the plot area) currently cut through both plots.

2.2. Data analysis

We compared the 2003 primary forest plot census data with the 2004 secondary forest plot data. In analysing 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 was 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.

2.2.1. 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.

2.2.2. 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 Core Team, 2013).

3. 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 (Fig. 1), there were 3299 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.

3.1. Stand structure and species diversity

Overall, mean stem density in the secondary forest plot ($1923 \pm 134 \text{ ha}^{-1}$) was only 30% of the primary plot, but the secondary forest plot had 130% of the trees larger than 10 cm DBH ($535 \pm 29 \text{ ha}^{-1}$) as compared to the primary forest plot (Tables 1 and 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 ($20.59 \pm 1.54 \text{ m}^2 \text{ ha}^{-1}$) was only 58% of the primary forest plot when all trees were used (Tables 1 and 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) (Tables 1 and 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 (Tables 1 and 2). In the secondary forest plot, stem density and all measures of diversity were higher in the quadrats

Table 1

Stand structure and floristic diversity of the primary forest and secondary forest plots. All values are mean \pm SE, calculated from fifty and forty 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.

| DBH (cm) | Primary forest | | Secondary forest | |
|---|------------------|------------------|------------------|------------------|
| | ≥ 1 | ≥ 10 | ≥ 1 | ≥ 10 |
| Stem density (ha^{-1}) | 6442 \pm 181 | 413.5 \pm 17 | 1923 \pm 134 | 535 \pm 29 |
| Basal area ($\text{m}^2 \text{ ha}^{-1}$) | 35.10 \pm 2.32 | 30.80 \pm 2.34 | 20.59 \pm 1.54 | 18.28 \pm 1.48 |
| Species richness | 75.98 \pm 1.24 | 12.28 \pm 7.62 | 19.98 \pm 1.88 | 7.62 \pm 0.34 |
| Weighted species richness | 0.27 \pm 0.00 | 0.66 \pm 0.03 | 0.11 \pm 0.01 | 0.40 \pm 0.02 |
| Shannon diversity | 3.70 \pm 0.03 | 2.36 \pm 0.04 | 2.19 \pm 0.10 | 1.61 \pm 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 Section 4.

| Minimum tree size | Site | Past landuse | Age (years) | Stem density | BA | Species richness | H' | J | References |
|-------------------|---|--------------|-------------|--------------|----|------------------|------------------|-----|-----------------------------|
| 1 cm | 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) |
| | 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. (1998) |
| 10 cm | 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 and Prance, (1999) |
| | Barito Ulu, Central Kalimantan, Indonesia | Ag | 55 | 90 | 82 | 65 | 82 | 24 | Brearley et al. (2004) |
| | Moruca, Guyana | L/Sb | 60 | 96 | 70 | 100 | 109 ^a | – | 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. (1998) |
| | Central Catchment Nature Reserve, Singapore (S1) ^a | Ag | 100 | 127 | 66 | 47 | 65 | – | Turner et al. (1997) |
| | Central Catchment Nature Reserve, Singapore (S1) ^a | 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.

^a DBH cut off is 9.55 cm instead of 10 cm.

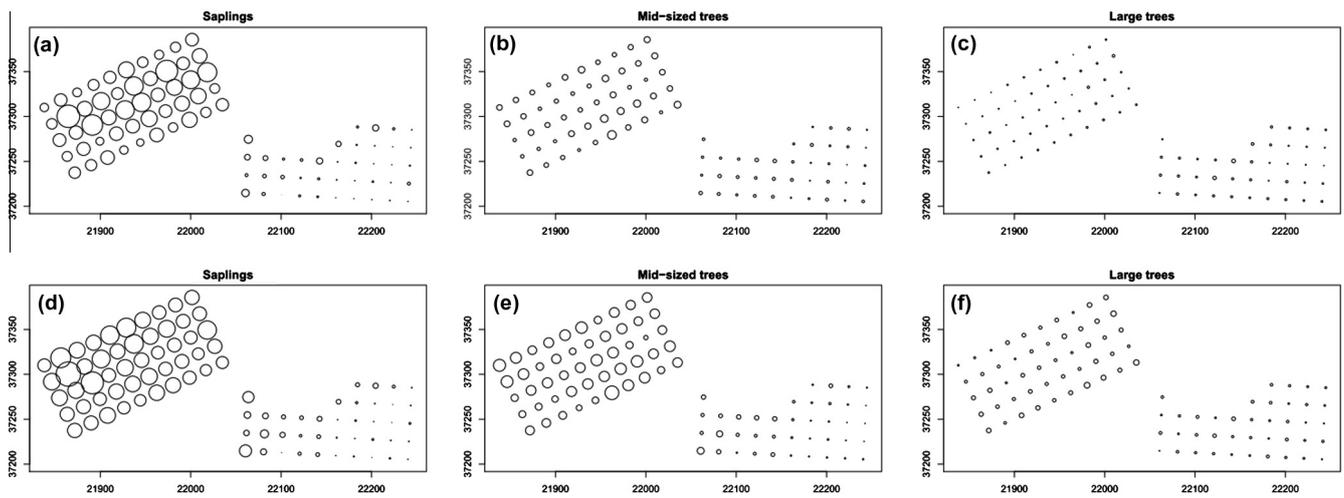


Fig. 2. Stem density (panels a–c) and species richness (panels d–f) in fifty 20 × 20 m primary forest quadrats (left) and forty 20 × 20 m secondary forest quadrats (right). The x- and y-axes are the metric-based cartesian coordinates of the plot. Circle size is proportional to stem density and species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

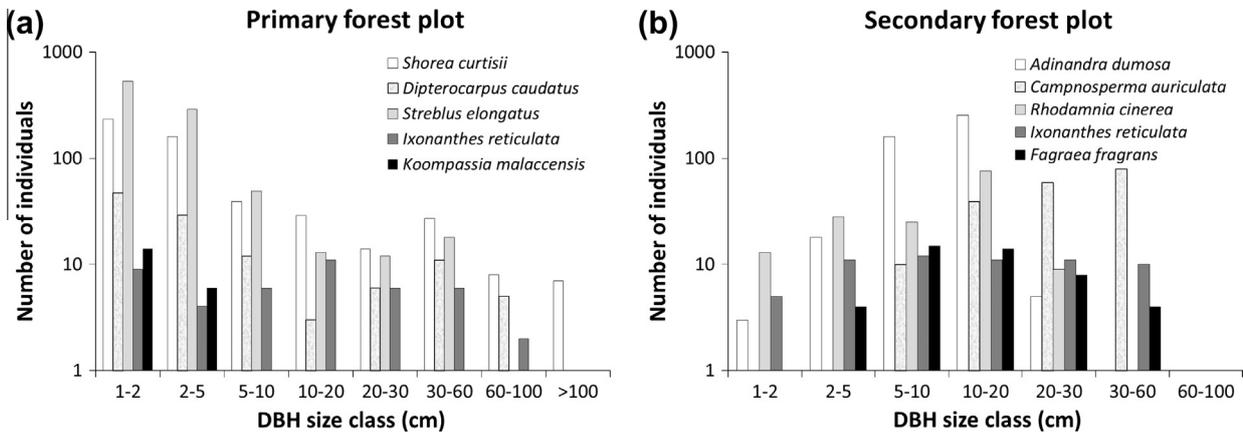


Fig. 3. DBH size class distribution of the most abundant canopy tree species (by basal area) in (a) the primary plot and (b) secondary forest plot.

closer to the primary plot, dropping rapidly with increasing distance (Fig. 2).

3.2. 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), *Camnosperma 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), *I. reticulata* and *Koopassia malaccensis* (Fabaceae), made up about 42% of the basal area in the plot (Supplementary material 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 (Fig. 3). In fact, aside from *D. 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 *S. elongatus*, *Calophyllum* spp., *Elaeocarpus polystachyus*, *Baccaurea sumatrana* and *S. curtisii* which altogether made up over 40% of the saplings in the secondary forest plot (see Supplementary materials 1 and 2 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 *D. suffruticosa*, most of the saplings were located near the primary forest (Fig. 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 (Fig. 4a) and that the saplings composition was also distinct from the mature trees composition within both plots (Fig. 4b). Shepard diagrams for both ordinations exhibited high R² for the goodness-of-fit (see Supplementary material 3). Within-plot compositional variation was higher in the secondary forest plot than in the primary forest plot, and this was due to the saplings (Fig. 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

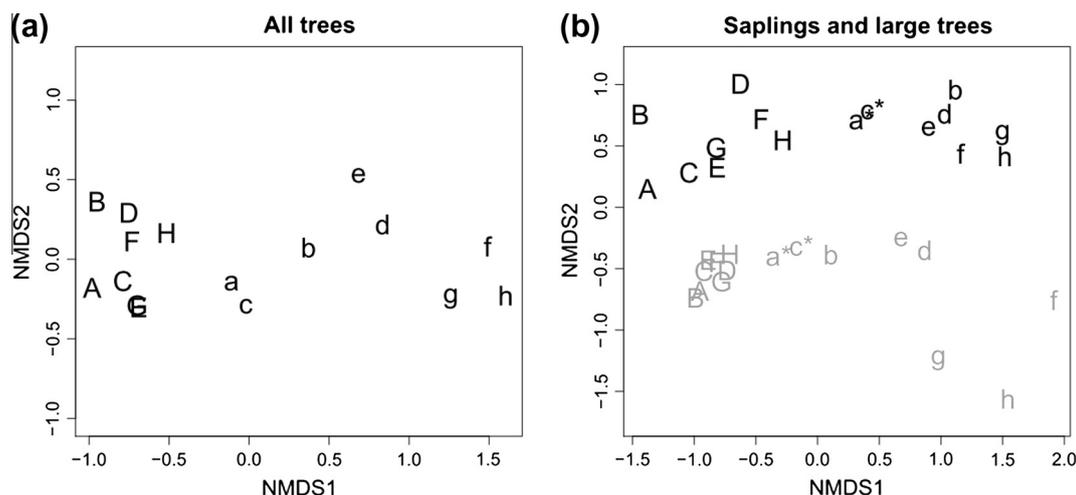


Fig. 4. NMDS ordination plots of floristic composition. (a) all trees and (b) saplings (i.e., trees ≤ 3 cm DBH) and large trees (i.e., trees ≥ 10 cm). Upper case letters are quadrats in the primary forest plot and lower case letters are quadrats in the secondary forest plot. In Fig. 3b, grey letters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

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** | | | | |
| | Elevation | 0.778*** | 0.406*** | 0.288* | – | | | | |

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.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

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 (Supplementary material 4). 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 (Fig. 4 and Supplementary material 4).

3.3. 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 Shannon diversity was slightly more strongly correlated with spatial distance ($r = 0.264, P = 0.001$) 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 (Supplementary material 5). 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, with $P < 0.001$ 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).

4. 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 (Supplementary material 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 (Fig. 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.

Breareley 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 Breareley 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 *A. dumosa*, *D. suffruticosa*, *R. cinerea* and *Fagraea fragrans*, are long-lived and slow growing (Sim et al., 1992; Corlett, 1991a, 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, *C. auriculata*, *A. dumosa*, *I. 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. suffruticos*, *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 (Fig. 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 (Fig. 4), this likely manifests in large part 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 (Fig. 2). Large seeded species without animal dispersal agents necessarily re-colonize slowly (Corlett, 1998; Dirzo et al., 2007; Kitamura et al., 2002; Wunderle, 1997), and smaller seeded species that are dispersed by mammal or birds (e.g., *S. elongatus*, *Calophyllum* spp., *B. sumatrana*) may not establish deep into the secondary forest if their animal dispersers avoid secondary forest (Wunderle, 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 (Supplementary material 5), 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.

5. Conclusion

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 transits 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.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.07.053>.

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