



## Slow recovery of a secondary tropical forest in Southeast Asia



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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  $\geq 1$  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

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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  $\geq 1$  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,

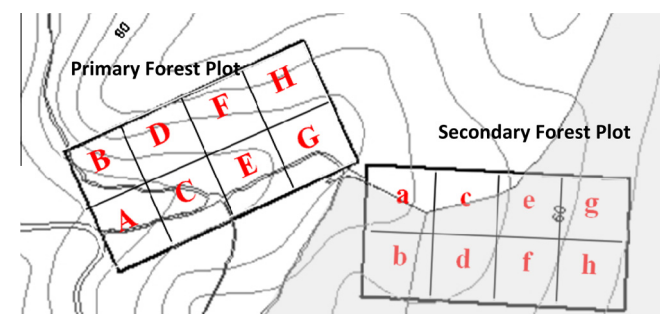


Fig. 1. Map showing plot layout and the location of the 50 × 50 m quadrats. Shaded area indicates secondary forest. Unshaded areas indicate old growth forest.

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 ( $\geq 1$  and  $\geq 10$  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  $\geq 10$  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

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