Dynamics and sustainability of a tropical forest fragment surrounded by an urban sea: Findings from the Bukit Timah Nature Reserve, Singapore

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Chapter 1 – Introduction

1.1 Tropical forests, the threats they face and their importance to humans

Tropical forests are important resources to humans and an essential component of Earth's terrestrial ecosystems. Although they cover only about 10% of Earth's land area, they harbour 50–70% of Earth's biodiversity (Lewis 2006). Among the tangible goods that tropical forests provide to humans include timber, as well as many other non-timber products such as rattan and fruits. Forests also provide numerous intangible ecosystem services, such as rainwater interception and purification, climate regulation and carbon sequestration (Costanza et al. 1997; Ehrlich and Mooney 1983).

Tropical forests are changing rapidly from global and local anthropogenic influences that alter their capacity to provide ecosystem services. Global influences include climate change, global warming and nutrient deposition caused by human burning of fossil fuels (Townsend et al. 1996; Wuebbles and Jain 2001), while local influences include forest fragmentation, hunting of animals, and the introduction of invasive species (Wright 2005). There is still considerable variability and sometimes conflicting results from some studies concerning the responses of tropical forests to climate variations, both between and within regions. For example, trees in the Amazon forest were observed to have increased growth rates averaged over three decades (Lewis et al. 2004a), while trees in a Panamanian forest and Malaysian forest had decreasing growth rates (Feeley et al. 2007). Another study used satellite images of the Amazon to show that the forest became greener during the 2005 drought (Saleska et al. 2007), but a subsequent re-analysis showed that this did not happen (Samanta et al. 2010). Nevertheless, some global trends in changes to forests have been detected. Allen et al. (2010) found that some forests were experiencing higher-than-normal tree mortality rates, while Choat et al. (2012) found that many tree species worldwide are prone to drought stress

and death due to hydraulic failure. Climate models also predict that tropical forests will mitigate global warming through evaporative cooling and carbon sequestration (Bonan 2008), but tend to produce net carbon release into the atmosphere during warm and dry El Niño years, and are susceptible to burning during land clearing (Randerson et al. 2005) due to drier conditions (Malcolm 1998). An additional point to note is that events that occur in one region can affect another region far away, highlighting the global nature of these environmental problems. For example, a simulation model predicted significant changes in rainfall in temperate zones that would have been caused by widespread deforestation in the tropics (Avissar and Werth 2005).

As global climate changes, it is now recognised that society needs to adapt to these changes, and forests have an important role to play here. The relationship between adaptation and forests can occur at two levels – first, by forests adapting to climate change, and second, by forests playing a role in the adaptation of society (Locatelli et al. 2010). The first role is a work-in-progress of monitoring the state of forests as the climate changes. The second role is performed by forests via the ecosystem services mentioned above, which reduce social vulnerability (Locatelli et al. 2010). However, pressures from a burgeoning world population has increased the demand for agricultural goods and led to reductions in forest area (DeFries et al. 2010; FAO 2006; Foley et al. 2007). Tropical forest loss was 7 million ha from 2000 to 2010 (FAO 2016), including pristine forests (FAO 2006). This poses a large threat to wildlife (Gibson et al. 2011), but more importantly their loss decreases the amount of ecosystem services that humans receive, such as buffering against extreme weather events.

Besides the physical, climatic and biodiversity values that tropical forests provide, many of these forests, often found in reserves and nature parks, also bring economic benefits in the form of tourist receipts. A study found that foreign visitors to forest reserves in Costa Rica valued them

higher than what they actually paid (Menkhaus and Lober 1996), while conservation of a rainforest reserve in Sumatra was found to generate higher net values than removal of the forest, one of the reasons being tourism (van Beukering et al. 2003). Tropical forests are important destinations for nature-based tourism, ecotourism and wildlife tourism and this hinges on sustainable development of the destination to ensure minimal environmental degradation and maintain economic value (Prideaux 2014).

1.2 Tropical forests in Singapore

Among tropical countries, Singapore has experienced one of the greatest losses of primary rainforest. Before British colonisation in 1819, the main island was almost fully forested, but the development of Singapore as a port meant that forest had to be cleared for building infrastructure. The early residents also cleared much land for crops such as pepper, gambier, and rubber (Corlett 2013). By the 1990, forest cover in Singapore had been reduced to 4.6% (Kong and Yeoh 1996). The areas that were left untouched were either not profitable to harvest due to steep topography, or were located in the protected water catchments. Currently, about 20% of Singapore is covered in forest, and only 0.16% is primary rainforest (Yee et al. 2011).

The first forest reserves in Singapore in the 1890s consisted of mostly mangroves and some inland forests, although these eventually gave way to agriculture and development (Corlett 1995). Large areas of forests were cleared at various points of time for timber and cash crops. These early years under colonial government saw forests as a resource for only economic gains and other utilitarian needs, as evidenced by the 1894 Annual Report of the Forest Department about the remaining forests in Singapore, “their utility as a source of revenue was subordinated to their climatic and hygenic uses” (Corlett 1995). It was not until 1951 when forests were protected under legislation by the Nature Reserves Act, “for the purposes of propagation, protection and

preservation of the indigenous fauna and flora of Singapore and for the preservation of objects and places of arsthetic, historical or scientific interest" (Corlett 1995). However, the years following independence also saw much urbanisation and further loss of forests and swamps (Wong 1989, from Kong and Yeoh 1996).

The impetus to conserve forests for the sake of its biodiversity, aesthetic and health values only began after Singapore had attained economic success and social stability. Singapore ratified the Convention on Biological Diversity (CBD) in 1995 (U.N. 2017), and launched a National Biodiversity and Strategy and Action Plan for Singapore in 2009 (NParks 2009). The Nature Reserves Act had been renamed the Parks and Trees Act, and lists four functions of nature parks and reserves (Law Revision Commission 2006):

1. The propagation, protection and conservation of the trees, plants, animals and other organisms of Singapore, whether indigenous or otherwise;
2. The study, research and preservation of objects and places of aesthetic, historical or scientific interest;
3. The study, research and dissemination of knowledge in botany, horticulture, biotechnology, or natural and local history; and
4. Recreational and educational use by the public.

Singapore has often been touted as an ecological 'worst-case scenario' (Koh and Sodhi 2004; Sodhi et al. 2004). The huge areas of forest loss caused local extinctions of plants and many animal groups, especially large mammals and birds (Sodhi et al. 2004). Despite these losses, the remaining flora and fauna are still surprisingly high in diversity, with >2000 species of vascular plants, 57 mammal species, 98 reptile species, 25 amphibian species, 355 bird species and >282 butterfly species (NParks 2009). Tree diversity in Bukit Timah Nature Reserve, a primary rainforest in

Singapore, has survived and persisted (Ngo et al. 2016). A mammal, reptile and amphibian survey from 1993 to 1997 in the nature reserves of Singapore found that the Bukit Timah reserve, only 164-ha in size, harboured the highest number of species for all the three animal groups (Teo and Rajathurai 1997), even though other reserves were bigger and continuous with one another.

Besides being biodiversity havens, the remaining forests in Singapore provide other benefits and ecosystem services that parallel those of rural forests in other countries, and their proximity to the city provides even more benefits. They play an important role in reducing the urban heat island (UHI) effect (Solecki et al. 2005), thereby reducing electricity costs and carbon emissions spent on cooling (Akbari 2002; Brack 2002). Forests cool the environment with their shade and when they transpire (Pataki et al. 2011), a process of water loss from leaves during photosynthesis. A study done on the physical environment inside and around the Bukit Timah Nature Reserve showed that temperatures within the forest were 3 degrees cooler than the forest buffer and 7 degrees cooler than the forest exterior (Chatterjea 2014). Similar results of warmer built areas and cooler forests were also found in various parts of Singapore (Chow and Roth 2006). Although the extent of forest cooling effect has not been well-studied in Singapore, Upmanis et al. (1998) found that the cooling effect of a Swedish urban park extended more than 1 km. Forests in urban areas help filter and clean surface water in cities (Dudley and Stolton 2003). In Singapore, an assessment of water quality from two urban watersheds, one containing *ca*. 25% forest, the other predominantly residential, found that the watershed with forest produced water with higher quality (Chui 1997). Forests help to store and sequester carbon, and trees are often the only significant carbon sinks in cities (NEA 2016a). A study on carbon stocks in Bukit Timah Nature Reserve found that the primary forests store a comparable amount of carbon per unit area as other primary forests in the region (Ngo et al. 2013), highlighting their important role as carbon sinks in the city.

In the early 1990s, Singapore sought to use its forest reserves as tourist attractions, after they had been exhausted of their tangible income sources such as timber (Kong and Yeoh 1996). Singapore was marketed as "one of only two cities in the world to have a genuine rainforest" (The Straits Times, 16 Aug 1991). The Singapore Tourism Board included the theme "Nature Trail" among a list of 11 in its Tourism 21 strategy (STPB, 1995, from Henderson 2000) that could be used to promote tourism in the 21st century, and had plans to expand the marketing of Singapore's natural heritage (Kong and Yeoh 1996). Given the multiple functions that forests in Singapore perform, maintaining their integrity over time is important, not only for their economic benefits, but also for the perpetuation of biodiversity and aesthetic values.

Although the government recognises the importance of forest reserves, land scarcity remains the largest constraint during land use planning. By 1991, 10% of the total area of Singapore was reclaimed (Glaser 1991), and above ground and belowground spaces were planned and used in such a way that every piece of public land was used effectively (Lui and Tan 2001). Nature reserves are no exception, serving multiple roles of biodiversity conservation, recreation, and nature education.

1.3 Purpose and organisation of thesis

As mentioned in 1.1, tropical forests can help in the mitigation and adaptation of climate change. In 1.2 the spotlight was on Singapore, a high-urbanised tropical country that has lost >99% of its original forests. To what extent and in what condition will the remaining forests survive in the future and continue to provide their numerous ecosystem services to the residents of Singapore? This thesis aims to answer this question by examining the ecology of a forest reserve in Singapore – the Bukit Timah Nature Reserve. The thesis is arranged as follows. Chapter 2 describes the field and study site and the general methods used. Chapter 3 looks at the primary forest in Bukit Timah from a fragmentation perspective, asking whether the primary forest has degenerated over a period

of 19 years. Chapter 4 examines recovery of an old secondary forest over a period of eight years. Chapter 5 is about tracking short-term growth rates in both primary and secondary forests over seven years and correlating them with weather observations. Chapter 6 is a summary and conclusion of all the previous chapters.

Chapter 2 – Research field site and methods

2.1 Bukit Timah Nature Reserve

The reserve is 164-ha in area, and includes the 164 m hill, Bukit Timah, Singapore's highest natural point. The hill was left forested by the British for "climatic" reasons as a cooling retreat (Sharp and Lum 1996), and it currently has Singapore's largest remaining patch of primary forest (48-ha; Ngo et al. 2016). In 2011, Bukit Timah was designated an ASEAN Heritage Park (ASEAN Centre for Biodiversity 2017).

At 1°17'24.97" N 103°51'7.05" E, Singapore has a tropical climate with abundant rainfall and high uniform temperatures all year round. There are two monsoon seasons in a year, each lasting several months, separated by two inter-monsoonal periods, also lasting several months (NEA 2016b), but these are not considered distinct seasons like in other parts of the tropics. El-Niño and La Niña, weather events that occur once every few years, influence Singapore's weather by altering rainfall patterns and creating the inter-year variation in rainfall (NEA 2017a).

Soils in the tropics are generally very deep and acidic (Bardgett 2005). Soils in primary forest of Bukit Timah were found to be very acidic, with pH 3.5 – 3.8 at 0 – 5 cm depth, similar to other hill dipterocarp forests (Chandler 1985; Grubb et al. 1994). Soil nutrient levels were low, but were even lower in the Bukit Timah secondary forest, especially nitrogen and phosphorus (Grubb et al. 1994). Nutrient levels are typically low because of leaching from the high rainfall, and any available nutrients would be rapidly taken up by vegetation or soil microbes.

Bukit Timah was one of the first forests to be protected by law in the country since the 1930s (Corlett 1988). However, illegal disturbances to the plants and animals of Bukit Timah

continued to be rampant, and two granite quarries at the western edge of Bukit Timah also encroached the forest until the mid 20th century (Corlett 1988; Corlett 1995). From 81-ha in the 1990s (Corlett 1995), the reserve expanded in later years to incorporate some of the connecting secondary forests and scrubland from the surrounding areas to the current area of 164-ha.

Bukit Timah still contains remarkable biodiversity despite the massive forest loss and continued human impacts. Although many mammal and bird species have gone locally extinct (Lim 1997; Sodhi et al. 2004), other taxa, such as flowering plants (Ngo et al. 2016; Turner et al. 1994) and pteridophytes (Wee 1995), are still surprisingly diverse. Small birds, such as the Greater Racket-Tailed Drongo (*Dicrurus paradiseus*), Crimson Sunbird (*Aethopyga siparaja*), Common Emerald Dove (*Chalcophaps indica*) (Lim 1997; pers. obs.), and small mammals such as the Plantain Squirrel (*Callosciurus notatus singapurensis*) and Long-tailed Macaque (*Macaca fascicularis fascicularis*) (Sha et al. 2009; Teo and Rajathurai 1997) are abundant in Bukit Timah.

2.2 Plot set-up and tree surveys

Data were collected from two 2-ha (200 m × 100 m) long-term monitoring plots in Bukit Timah – one in primary and one in secondary forest. The two plots lie within 20 m of each other with no physical barriers between them (Fig. 2.1). A public walking trail runs through the long side of the primary forest plot and also cuts through a corner of the secondary forest plot. Part of the trail near the start of the secondary forest plot once marked the boundary of the Bukit Timah Forest Reserve, the forerunner of today's Nature Reserve. PVC pipes were planted into the ground at 5 m intervals to mark out the plot subquadrats.

The diameters of trees within the plots were measured at 1.3 m height (diameter at-breast-height; dbh), but only trees that were ≥1 cm dbh were recorded, identified to species whenever

possible, tagged with unique numbers, and mapped within the plot. The primary forest plot was set up in 1993, and trees in the plot were measured in 1993, 1995, 2003, 2008 and 2012. The secondary forest plot was set up in 2004, and the trees were measured in 2004, 2008 and 2012. A total of 12687 trees were surveyed in the primary forest plot in 1993, while 3051 trees were surveyed in the secondary forest plot in 2004.

2.3 Figures

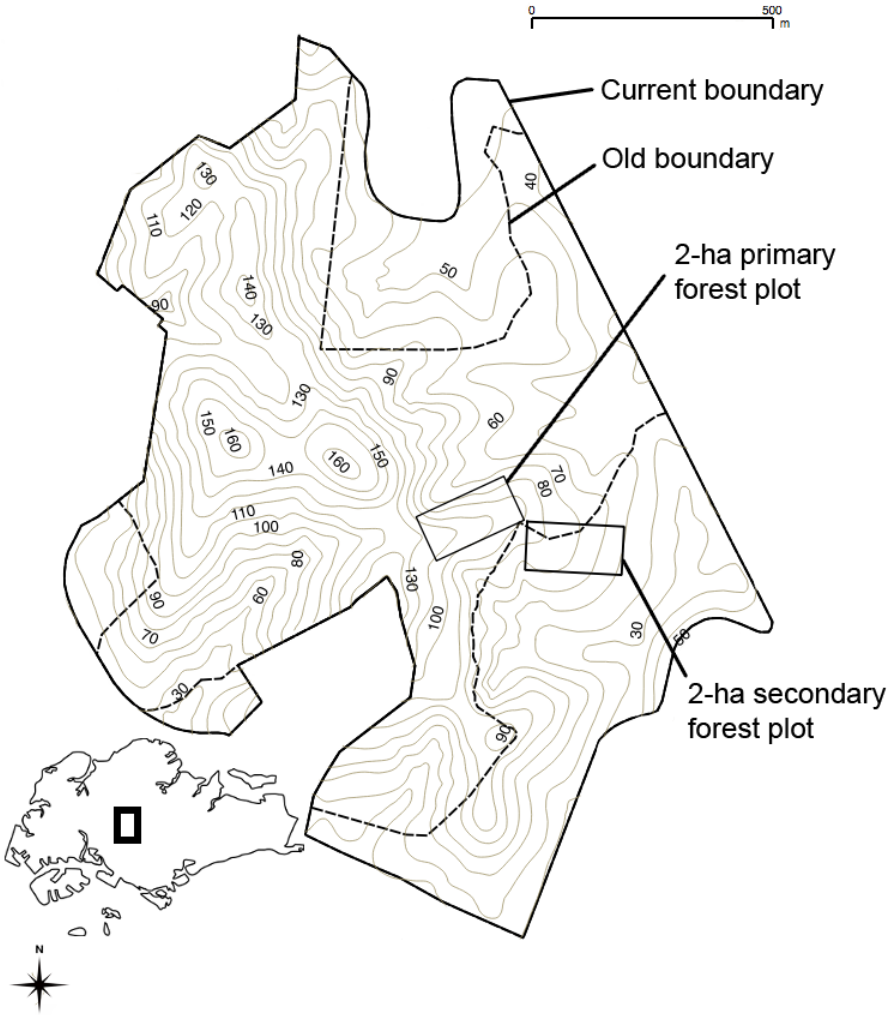

Figure 2.1. Map of Bukit Timah Nature Reserve (164-ha) and its position within Singapore (inset). The positions of the two 2-ha plots are also shown.

Chapter 3 – Resilience of the Bukit Timah primary forest to fragmentation

3.1 Introduction

Tropical forests are important habitats for biodiversity, and are also large carbon reserves. Tropical forests are rapidly being cleared for various uses such as plantations (FAO 2001; Achard et al. 2002), or degraded. Vast tracts of tropical forest have now been reduced to forest fragments (Skole and Tucker 1993), and fragments are different from the original forest in many ways.

Forest fragments typically experience species loss (Turner 1996; Fahrig 2003). Species richness is generally lower in smaller fragments (Hill and Curran 2003; Castelleta et al. 2005; Cagnolo et al. 2006), and some fragments experience rapid invasion by exotic species (Dislich and Pivello 2002). Forest fragments tend to be influenced by altered environmental conditions near their edges (Murcia 1995; Malcolm 1998). Forest edges experience increased light levels, which promotes the rapid growth of pioneer species (Laurance et al. 2006a) and the decline of shade-tolerant or primary forest species (Cramer et al. 2007; Michalski et al. 2007). Edge effects seem to characterize most forest fragments (Tabarelli et al. 2008). Experimental fragments created in the Amazon showed that fragments experience higher turnover rates than continuous forests, i.e. fragments are 'hyper-dynamic' (Laurance et al. 1998, 2002, 2006b, 2017; Mesquita et al. 1999). Large trees in fragments have also been reported to have higher mortality rates (Laurance et al. 2000; Arroyo-Rodriguez and Mandujano 2006; Oliveira et al. 2008), leading to loss of stand biomass (Laurance et al. 1997; Nascimento and Laurance 2004; Pütz et al. 2011).

Not all fragments suffer the same level of degradation-related changes. Some fragments experience increases in shade-tolerant species (Werneck and Franceschinelli 2004; Higuchi et al. 2008), while for others, species richness declines in small fragments have not been detected

(Cayuela et al. 2006, Sánchez-Gallen et al. 2010). Small forest fragments in Mexico contained high tree species richness (Arroyo-Rodríguez et al. 2008), making small fragments potentially valuable for conservation. Within South-east Asia (SEA), Slik et al. (2011) observed limited edge effects in an old growth tropical forest in Borneo, despite it being adjacent to a burnt forest for seven years. In Peninsular Malaysia, fragments were found to be structurally similar to primary forest, and had few pioneer species (Thomas 2004).

In researching factors that contribute to the resistance of forest fragments to degradation, Thomas (2004) found that a range of traits such as relative density in primary forest, dispersal mode, and low photosynthetic capacity correlated well with persistence in Malaysia. Species that are common in the landscape would have a higher chance of remaining when that landscape becomes fragmented (Thomas 2004). Ballistically-dispersed primary forest species were found in higher proportions in fragments than in primary forest (Thomas 2004). This could result from the fact that loss of animal dispersers from fragments does not affect ballistically-dispersed species, while some animal-dispersed species become disadvantaged (Cordeiro and Howe 2001, 2003). Wind and gyration dispersal is a typical dispersal strategy of old growth canopy trees (e.g., Dipterocarpaceae) in many South-east Asian forests (Corlett 1997; Lee et al. 2002; Davies et al. 2003), unlike other tropical regions where it is usually associated with a pioneer strategy (Slik et al. 2011). In Borneo, the canopy structure of old growth forests is tall and relatively open, possibly making these forests more resilient to edge effects (Slik et al. 2011).

Forests in Singapore have undergone a major transformation since the early 1800s (Corlett 2013; LaFrankie et al. 2005). Less than 0.2% of the original primary forest remains, with secondary forest now covering about 20% of the island (Yee et al. 2011). The largest remaining patch of primary forest, found in Bukit Timah Nature Reserve, is surrounded by secondary forest, where the

original forest used to be exposed to various disturbances, such as timber extraction and agriculture (Corlett 1988, 2011). Large vertebrates, e.g., tigers, have been extirpated from the island (Sodhi et al. 2004). Despite the high number of large vertebrate extinctions in Singapore, some of the surviving small vertebrate fauna are thriving, mainly in the ca. 3000-ha forest mosaic in the centre of the mainland. For example, there are abundant populations of long-tailed macaques, *Macaca fascicularis* Raffles (Lucas and Corlett 1998; Sha et al. 2009; Riley et al. 2015), and plantain squirrels, *Callosciurus notatus* Boddaert (Corlett 1995). A floristic survey of a small forest fragment (4-ha) in Singapore found that 228 plant species had gone extinct, and 174 previously unrecorded species recruited, within a century at the site (Turner et al. 1996). The new records, 94 native and 80 non-native species, constituted about 44% of total species richness during the later inventory (Turner et al. 1996). However, given that the exact sampling locations of the old collections (dating back to the 1890s) could possibly have come from a bigger area before it was reduced to its current size, the floristic changes may not be the result of 'fragmentation effects' alone (Fahrig 2003). In primary forest at Bukit Timah, plant diversity has remained relatively intact (Corlett 1995). Corlett (1988) suggested the possibility of a delayed 'collapse' of the plant community, and a consequent opening up of the forest and decline in mesic habitat-dependent species.

The impacts of forest fragmentation on the stand dynamics of a permanent forest plot in Bukit Timah from five censuses, spanning 19 years, were investigated. The findings from this study were compared with the structure and dynamics of similar lowland primary forests elsewhere in South-east Asia. Based on findings from other forest fragmentation studies (e.g., Laurance et al. 2006a, 2006b), I hypothesized that: (1) pioneer species would become dominant, and continue to dominate due to altered disturbance dynamics; (2) shade-tolerant primary forest species would decline; (3) the number of large-statured trees would decrease, leading to a decline in basal area; (4)

zoochorous species would decline due to the loss of animal dispersers; and, (5) population turnover rates would be high owing to disturbances associated with the fragment edges.

3.2 Methods

3.2.1 Study site

Bukit Timah Nature Reserve (hereafter Bukit Timah) is a 164-ha forest reserve in central Singapore (LaFrankie et al. 2005). Soils of Bukit Timah are nutrient-poor Typic Paleudults of the Rengam series formed on Bukit Timah Granite (Ives, 1977). The forest is coastal hill dipterocarp forest, with a core unlogged area of 48-ha (MS Khoo and S Lum, unpubl. data), dominated by *Shorea curtisii* Dyer ex King, a dipterocarp species usually found at higher elevations in Peninsular Malaysia (Symington et al. 2004). This primary forest is surrounded by two abandoned granite quarries to the west and south, and secondary forest of different successional stages to the east. The secondary forest colonised agricultural land abandoned in the 1950s (Chua et al. 2013). The northern section of the Reserve is dominated by the exotic African Tulip tree (*Spathodea campanulata*), which established following cattle pasture abandonment in the 1970s. A detailed account of the history of Bukit Timah can be found in Corlett (1988, 1995).

The climate is aseasonal, with a wetter period from November to December and a drier period from May to July. Weather data were taken from the nearest weather station with long-term rainfall and temperature records, 8.5 km northwest of Bukit Timah. Mean annual rainfall between 1980 and 2012 was 2688 mm with all months receiving more than 150 mm on average; average daily temperature was 27.0 °C. There have been significant increases in both mean annual rainfall (augmented Dickey-Fuller [ADF] test statistic = -3.51; $P = 0.059$; 1980-2012) and mean minimum annual temperature (ADF test statistic = -2.72; $P = 0.297$; 1985-2012) (Figure 3.1). Within the

census period, two years (1997 and 2009) had annual rainfall more than 1 SD lower than the long-term mean, while four years (1995, 2003, 2007 and 2011) had annual rainfall more than 1 SD greater than the long-term mean.

3.2.2 Field data collection

A 2-ha (200 m × 100 m) plot was established in 1993 by the Centre for Tropical Forest Science (CTFS) within the unlogged primary forest (Figure 3.2) following standard CTFS methods (Manokaran et al. 1990; Condit 1998), where all trees ≥1 cm diameter at breast height (dbh) were measured to the nearest 1 mm, tagged, mapped and identified to species. The plot is located within 10 m of a historical forest boundary. The secondary forest immediately outside of the plot used to be crop plantations, and these were abandoned by 1962 and left to regenerate naturally (Chua et al. 2013). A full description of the plot can be found in LaFrankie et al. (2005). The plot was re-censused in 1995, 2003, 2008 and 2012.

3.2.3 Data analysis

Trees were split into three dbh classes, 1.0 – 1.9 cm, 2.0 – 9.9 cm, and ≥ 10.0 cm for stem abundance and mortality analyses. Kolmogorov-Smirnov tests were used to test for differences in tree size distributions among censuses. Adult stature of species with ≥10 individuals in 2012 (158 species) were classified into three stature classes – understorey (1.0–19.9 cm dbh), canopy (20.0–49.9 cm dbh) and emergent (≥50.0 cm dbh), by taking the mean of the second, third and fourth largest individuals of each species. Where adult trees of known canopy or emergent species were not present in the plot, species were assigned to the correct adult stature using Whitmore and Ng (1972–1989). Dispersal modes of species were classified as biotic or abiotic. Differences in species abundance changes were tested between the three adult stature classes using ANOVA, and between the two dispersal modes using t-test.

Mortality was calculated as $(\ln(n_1) - \ln(S_2))/t$, and recruitment as $(\ln(n_2) - \ln(S_2))/t$, where t is the census interval, n_1 and n_2 are the population sizes at census 1 and census 2 respectively, and S_2 is the number of survivors at census 2. Mortality and recruitment were corrected for differing census intervals using $\lambda_{corr} = \lambda \times t^{0.08}$, where λ is mortality or recruitment rate, and t is census interval in years (Lewis et al. 2004b). This correction reduces the bias that arises during comparisons of mortality and recruitment rates from non-homogenous populations when census intervals differ (Lewis et al. 2004b). In order to take spatial autocorrelation into account, 99.9% confidence intervals (CIs) for mortality and recruitment rates were calculated from 1000 bootstraps of 50 20 m × 20 m squares. This is because spatial autocorrelation generates CIs that are more narrow than they would be if the data were spatially independent (Legendre 1993), therefore non-overlapping CIs at 99.9% level would most likely represent real differences in the mean. Changes in mortality and recruitment between intervals were tested with repeated measures analysis of variance, using 20 m × 20 m squares as sampling units.

To test whether abundances of individual species were increasing or decreasing more than expected given the plot-wide changes, the method developed in Chisholm et al. (2014) was used. This method compares observed changes in the abundance of species against abundance change estimated from a neutral model that includes only demographic variance. By plotting squared species abundance changes versus initial abundance, both species that increased and decreased more than expected given the overall plot-wide changes in abundance were identified.

All tree dynamics analyses were carried out using functions from the CTFS R Package (http://ctfs.si.edu/Public/CTFSRPackage/).

3.3 Results

3.3.1 Stand structure and dynamics

In 1993, stem density was 6344 ha^{-1} and basal area was 36.5 m^2 ha^{-1} in the 2-ha plot at Bukit Timah (Table 3.1). Over the entire 19 years there were no significant differences in stem density or basal area. However, decreases in stem density and basal area were observed in censuses immediately following the two drought years, 1997 and 2009. Changes in total basal area largely followed the same pattern as stem density, where decreases coincided with both drought-affected intervals, and increases followed in wetter periods. Basal area fell to the lowest level in 2012 after the second drought.

Although there were no significant changes in total stem density, there were significant differences in tree size distribution between consecutive census intervals, as well as between the first and last census ($P < 0.01$; Kolmogorov-Smirnov test). The first census in 1993 had the highest number of 1.0–1.9 cm trees and lowest number of trees ≥2.0 cm (Table 3.1). Subsequent recruitment into the ≥2.0 cm size classes caused stem abundances of these size classes to increase.

3.3.2 Floristic composition and dynamics

A total of 338 species were recorded in the plot in 1993 (Table 3.1). The 10 most abundant species were all primary forest species − two emergent, six canopy, and two understorey species (Table 3.2). These species represented nine different families. There were no exotic individuals ≥1.0 cm dbh in the plot.

Pioneer trees made up 3.8-4.6% of all stems among the five censuses (Table 3.1), and none of the pioneer species were common. Fourteen pioneer species were recorded in the plot, with

Archidendron contortum, Pternandra echinata and *Timonius wallichianus* being the most common. Among saplings 1.0-1.9 cm dbh, there were 53 pioneer trees from four species in 1993, and this increased to 59 trees from 11 species in 2012. Pioneer saplings made up only 0.8% and 1.1% of all saplings in 1993 and 2012 respectively.

Of the 158 species with ≥10 individuals, 18 were emergent, 62 were canopy, and 78 were understory species. One hundred and forty-one species were biotically and 17 species were abiotically-dispersed. There were no significant differences in percentage species abundance change (1993 to 2012) between the three adult statures ($F_{(2,155)} = 0.97$, $P = 0.38$; ANOVA) and the two dispersal modes ($t = -0.53$, $P = 0.60$; *t*-test).

Floristic composition changed significantly over the 19 years. The abundance of 86 species changed more than expected under a neutral model of demographic change (Figure 3.3); 58 species increased and 28 species decreased more than expected. Of the 10 most abundant species, four had significant decreases in abundance over the 19 years, three increased significantly, and the abundance of three species did not differ from neutral expectations (Table 3.2). *Streblus elongatus* (Moraceae) and *Shorea curtisii* (Dipterocarpaceae) had 39% and 20% increases in abundance respectively, with *Streblus* becoming the most abundant species in the plot in 2012. In contrast, *Santiria apiculata* (Burseraceae), *Gluta wallichii* (Anacardiaceae) and *Gynotroches axillaris* (Rhizophoraceae) had declines in abundance of 14%, 23%, and 34% respectively.

3.3.3 Demography

Plot-wide mortality over 19 years was 3.3% year^{-1} with significant variation among census intervals ($F_{3,147} = 3.635$, $P = 0.014$; repeated measures ANOVA). Pairwise *t*-tests showed that annual mortality was significantly higher in the last census interval (2008-2012) than the 2003-2008

interval ($P = 0.022$). Although there were no significant changes in mortality ratewhen trees were split into size classes, the mortality rate of large trees tended to mirror the drought intervals (Table 3.3).

Annual recruitment into the ≥1.0 cm dbh size class varied significantly among census intervals ($F_{3,147} = 19.08$, $P < 0.001$; repeated measures ANOVA), and fluctuated even more than mortality (Table 3.3). Recruitment rates were significantly lower in the two census intervals that experienced drought.

3.4 Discussion

Despite a long history of fragmentation and isolation, the patch of primary rain forest at Bukit Timah shows no evidence of 'collapse' or dramatic transformation that might be attributed to fragmentation (Fahrig 2003; Kupfer et al. 2006; Laurance et al. 2011). Stand structure, basal area and the abundance of large trees were similar to those in primary forests in Malaysia (Table 3.4) and did not change significantly through the 19 years of monitoring (Hypothesis 3). The most common species in the plot were all typical shade-tolerant primary forest species, and none of them were pioneer or exotic species (Hypotheses 1 and 2). The proportion of pioneer species in the plot was similar to that found in Pasoh, a Malaysian primary forest (Davies et al. 2003), and there was no significant increase in pioneer species during the study (Condit et al. 1999). The proportion of biotically-dispersed trees did not decline through time (Hypothesis 4), and was similar to other intact forests in the region (Seidler and Plotkin 2006; Harrison et al. 2013). Although population turnover was relatively high compared to Malaysian forests (Table 3.5; Hypothesis 5), the Bukit Timah forest exhibits considerable resistance to the effects of being extremely isolated and surrounded by human activities.

The low numbers of pioneer species in the Bukit Timah forest was unusual compared to other forest fragments. Even though pioneer species were found in gaps in Bukit Timah, and were also present in other forested parts of Singapore, they were not increasing in numbers in the plot. Pioneer trees that were <20.0 cm dbh consistently made up ≥88% of all pioneer trees, evidence that the existing pioneers were not remnants of a more degraded forest. The number of pioneer species decreased after the two droughts, suggesting that pioneer species also responded to drought stress like other species. In a Panamanian forest, the abundance of pioneers also declined more often than shade-tolerant species over a 13-year period that included a run of dry years and long dry seasons (Condit et al. 1996a). In a Bornean forest, the predominantly pioneer genus, *Macaranga*, had very high mortality after the 1997 drought, but also high seedling recruitment caused by the increased canopy openness (Slik 2004). Pioneer seedlings from a Bolivian forest had traits that maximised above-ground light capture and efficient root extension for below-ground resource capture (Markesteijn and Poorter 2009), but the high resource demand of pioneers may also predispose them to drought mortality (Reich 2014).

Abundance changes of biotically-dispsersed species did not differ from that of abiotically-dispersed species. In Amazonian fragments, old-growth taxa that declined in abundance tended to be sub-canopy trees that were animal-dispersed and had obligate outbreeding systems (Laurance et al. 2006b). A study made in a Bornean rainforest found that the extirpation of all animals with a body mass >1 kg increased stem density and decreased the species diversity of saplings (Harrison et al. 2013). Such trends were not found in Bukit Timah. The large population of macaques (Sha et al. 2009) and small rodents may have acted as seed dispersers even for large seeds (Lucas and Corlett 1998; Brewer and Rejmánek 1999), while fulfilling their usual role as seed predators. There are no immediate threats to these animals, except for the trapping of macaques in areas surrounding the reserve (Sha et al. 2009). Fourteen percent (206 individuals) of the total macaque population was

removed in 2007 (Sha et al. 2009), but this does not seem to have had much effect on their role as seed dispersers.

The abundance of 86 tree species in the Bukit Timah plot changed more than expected by chance over the 19-year study. There were no obvious patterns in the characteristics of species that increased and decreased in abundance. Both the increasing group and decreasing group had a mix of canopy, emergent and understorey species, as well as primary forest and pioneer species. On the 50-ha plot at BCI in Panama, species varied in their response to an intense El Niño-associated drought event (Condit et al. 1996b). At least 16 species of shrubs and small trees affiliated with moist habitats declined close to extinction within the plot, and drought-tolerant species increased in abundance (Feeley et al. 2011). Results from another forest in Costa Rica monitored for 20 years showed that deciduous, compound-leaved canopy species increased in abundance at the expense of evergreen, simple-leaved understory species (Enquist and Enquist 2011). These changes were attributed to increasingly dry years as well as longer and stronger dry seasons (Condit et al. 1996a; Enquist and Enquist 2011). These patterns were absent at Bukit Timah, despite the occurrence of two droughts over 19 years. In a lowland primary forest in Sabah, Malaysia, Newbery and Lingenfelder (2004) also found mixed responses of the 19 most abundant species to an intense drought, similar to our findings at Bukit Timah. Given the contrasting responses of species despite similarities in life history, examining their functional traits and drought tolerances may help to explain their differential abundance changes.

Seven of the 10 most abundant species on the plot had significant changes in abundance throughout the 19 years – four had decreases and three had increases. Six of these seven species were canopy and emergent species, while one was an understorey species. Of the declining species, only *Gynotroches axillaris* had very low recruitment (0.6%) over the 19 years. The other declining

species, *Santiria apiculata*, *Gluta wallichii*, and *Calophyllum ferrugineum*, had average to higher-than-average recruitment rates but mortality always exceeded recruitment. The most abundant species in 2012, *Streblus elongatus*, had large increases in trees <10.0 cm dbh, predominantly due to low mortality of these trees. Starkly different outcomes were also observed in two emergent species, *S. curtisii* and *G. wallichii*. Both species had similar starting abundances (426 for *S. curtisii* and 435 for *G. wallichii*), and both are abiotically-dispersed, but *S. curtisii* had 177 more individuals than *G. wallichii* after 19 years. Interestingly, *C. ferrugineum*, which was found to have proliferated in the Botanic Gardens Jungle fragment in Singapore (Turner et al. 1996), experienced a 17.5% reduction in Bukit Timah (10th rank in plot). In a lowland forest in Sabah, Malaysia, *Dacryodes rostrata* had greatly elevated mortality after an intense drought (Newbery and Lingenfelder 2004), while abundance change of this species in Bukit Timah (4th rank in plot) was not different from the neutral expectation. Future on-site or common garden eco-physiological experiments could help elucidate whether these differences in abundance change might be related to differential levels of drought tolerance among the common species.

Overall tree turnover in the plot was higher than values observed in forests from other tropical Asian sites in Malaysia and Sri Lanka (Manokaran and Swaine 1994; Condit et al. 2006). Mortality rates were 1-2% above the rates recorded in lowland and hill forests in South-east Asia (Table 3.5). Is this a result of fragmentation, or is it a characteristic of coastal hill forests? In a Bornean old growth forest, creation of a forest edge by fire did not lead to large changes in species composition and light conditions, but mortality of larger trees increased towards the forest edge (Slik et al. 2011). High turnover in fragments is usually a result of edge effects, where trees experience increased wind-throw in Amazonia and microclimatic changes (Laurance et al. 1998). Mean annual tree turnover has been found to correlate positively with species richness in tropical forests (Phillips et al. 1994). However, Bukit Timah (Fisher's alpha = 67.3) has lower tree diversity

than Pasoh (Fisher's alpha = 125.8; Davies et al. 2003), Malaysia, so species richness is unlikely to be the explanation for elevated turnover rates at Bukit Timah. Given the lack of evidence for edge effects, a possible reason for the higher turnover rates is that Bukit Timah, being a hill emerging from the lowlands, is exposed to higher light levels and wind, and therefore higher turnover rates might have been inherent.

Turnover rates fluctuated among censuses in this study in relation to the timing of drought events. Even in undisturbed forests, turnover rates change over time. Long-term inventory data showed that tree turnover has been increasing across Neotropical tropical forests (Phillips 1996; Lewis et al. 2004a), possibly due to an increase in resource availability such as CO_2 (Lewis et al. 2004a). Mortality rates increased significantly after severe droughts in Amazonian, Panamanian and Bornean primary rainforests (Condit et al. 1995; Nakagawa et al. 2000; Slik 2004; Phillips et al. 2009). There was a significant increase in overall mortality rate at Bukit Timah after the 2009 drought, but not after the 1997 drought. However, recruitment rates decreased significantly during both droughts. This, together with the stand structure of Bukit Timah, suggests that the forest is more susceptible to drought stress than to fragmentation effects. Nonetheless, effects of fragmentation could interact with and exacerbate drought effects through cumulative stresses, such as forest desiccation and fire occurrence (Cochrane and Laurance 2008; Briant et al. 2010). For example, tree turnover and liana abundance in Amazonian forest interior increased over a 32-year period, with the magnitude of these changes being higher at fragment edges, and this was attributed to the synergistic effects of fragmentation and large-scale environmental drivers (Laurance et al. 2014).

Our results show that small forest fragments can retain high tree diversity and resilience against fragmentation effects. This is the first published long-term study of a tropical forest

fragment, even though other short-term studies have also recorded fragment resilience (e.g. Cayuela et al. 2006; Arroyo-Rodríguez et al. 2008). Although the preservation of large areas of forest is still the best scenario for biodiversity conservation, fragments should not be overlooked for their biodiversity potential. As large areas of forest in the region are removed (Miettinen et al. 2011), even in protected areas (Curran et al. 2004), the conservation of the hundreds of thousands of forest fragments must be a priority for local governments and NGOs.

3.5 Conclusion

Observed changes in Bukit Timah seem to be driven by the effects of climatic fluctuations at decadal time scales, rather than a directional degradation of the forest associated with fragmentation. Despite the long-term anthropogenic disturbances that Bukit Timah has been exposed to, the tree flora still holds considerable diversity. The 10 most abundant trees in Bukit Timah were primary forest species, and the number of pioneer species and individuals were low. Many species had varying abundance changes despite similarities in adult statures and dispersal modes. Species abundance change of biotically-dispersed species were not lower than those of abiotically-dispersed species, suggesting that the faunal species loss did not adversely affect recruitment of these species. Tree mortality and recruitment rates were higher than other comparable tropical Asian rainforests, but the contribution of fragmentation effects to this observation is uncertain. Turnover rates also fluctuated over time and showed evidence of response to the two drought events. Our results from 19 years of monitoring did not indicate that Bukit Timah had or was undergoing systematic degradation. However, given the high turnover rates and drought-related responses observed in Bukit Timah, changes in climate patterns, such as an increased frequency and intensity of dry periods, could have a stronger impact on this fragment compared to intact forests.

3.6 Tables and figures

Table 3.1. Summary of stand dynamics of the 2-ha primary forest plot. Figures in parentheses represent 95% confidence intervals calculated from 1000 bootstrap samples over 20×20m squares. Figures with the same superscript letters have overlapping confidence intervals. Broken trees were not included in the size classes. Censuses immediately following the 1997 and 2009 drought years are highlighted.

	1993	1995	2003	2008	2012
No. individuals (ha^{-1})					
All trees	6344^{a} (5867-6807)	6712^{a} (6284-7124)	6436^{a} (6086-6753)	6861^{a} (6506-7235)	6455^{a} (6109-6804)
1.0-1.9 cm	3238^{a} (2921-3569)	3070^{ac} (2813-3323)	2543^{b} (2342-2747)	2914^{ab} (2708-3112)	2638^{bc} (2446-2817)
2.0-9.9 cm	2685^{a} (2448-2933)	2942^{a} (2724-3154)	2854^{a} (2682-3012)	2993^{a} (2829-3152)	2987^{a} (2816-3150)
≥10.0 cm	407^{a} (376-437)	421^{a} (394-448)	420^{a} (386-457)	441^{a} (407-476)	413^{a} (383-447)
Pioneer species (all sizes)	231	224	190	215	193
No. species					
All trees	338	345	345	351	354
'Extinct' from plot		2	10	11	6
'New' recruits in the plot		9	10	17	9
Pioneer species	11	12	11	12	12
Basal area ($m^2.ha^{-1}$)					
All trees	36.5 (32.0-41.5)	37.2 (33.0-41.4)	35.1 (30.8-39.8)	36.6 (32.0-41.1)	30.4 (26.4-34.7)
Pioneer species	1.5	1.4	1.1	1.0	0.9

Table 3.2. Abundance changes of the 10 most common species in Bukit Timah. Species with abundance changes significantly greater than neutral model expectations are indicated by **. The letter codes are adult stature classes: (Under-storey) 1.0-19.9 cm; (Canopy) 20.0-59.9 cm; (Emergent) ≥ 60.0 cm dbh. Numbers in parentheses are species abundance ranks.

Species	1993	2012	% change
Santiria apiculata (C) Burseraceae	951 (1)	816 (2)	-14.2**
Streblus elongatus (C) Moraceae	781 (2)	1086 (1)	+39.1**
Diospyros lanceifolia (U) Ebenaceae	592 (3)	641 (3)	+8.3**
Dacryodes rostrata (C) Burseraceae	486 (4)	514 (4)	+5.8
Gluta wallichii (E) Anacardiaceae	435 (5)	334 (8)	-23.2**
Gironniera parvifolia (U) Ulmaceae	431 (6)	410 (6)	-4.9
Shorea curtisii (E) Dipterocarpaceae	426 (7)	511 (5)	+20.0**
Pimelodendron griffithianum (C) Euphorbiaceae	396 (8)	373 (7)	-5.8
Gynotroches axillaris (C) Rhizophoraceae	284 (9)	186 (15)	-34.5**
Calophyllum ferrugineum (C) Calophyllaceae	251 (10)	207 (13)	-17.5**

Table 3.3. Annual mortality and recruitment rates during census intervals. Values in parentheses indicate 99.9% confidence intervals from 1000 bootstrap samples of 20×20m squares. Figures with the same superscript letters have overlapping confidence intervals. Drought-affected intervals are highlighted.

	1993-1995	1995-2003	2003-2008	2008-2012
Mortality (% yr^{-1})	2.9^{a}	2.9^{a}	2.7^{a}	3.4^{a}
	(2.3-3.7)	(2.4-3.3)	(2.3-3.1)	(2.7-4.2)
Recruitment (% yr^{-1})	5.4^{a}	2.6^{b}	5.6^{a}	2.5^{b}
	(3.9-7.4)	(2.0-3.2)	(4.7-6.8)	(2.0-3.0)
Mortality (% yr^{-1}) by dbh size class (cm)				
1.0-1.9	3.5^{a}	3.4^{a}	3.1^{a}	3.5^{a}
	(2.8-4.5)	(2.6-4.0)	(2.6-3.8)	(2.5-4.3)
2.0-9.9	2.2^{a}	2.4^{a}	2.0^{a}	2.5^{a}
	(1.6-3.0)	(2.0-2.9)	(1.6-2.5)	(2.0-3.2)
≥10.0	2.4^{a}	3.0^{a}	2.2^{a}	2.9^{a}
	(1.2-3.9)	(2.0-4.1)	(1.5-3.1)	(1.7-4.7)

Table 3.4. Comparison of basal area with other tropical Asian forest sites. Figures are averages of multiple surveys or plots if available.

	Basal area ($m^2.ha^{-1}$)		
Site	≥1.0 cm dbh	≥10.0 cm dbh	Reference
Bukit Timah, Singapore	36.5		This study
		32.6	
Pasoh, Malaysia	33.2		Davies et al. (2003)
Lambir Hills, Malaysia	43.3		Lee et al. (2002)
Andulau, Brunei		35.2	Davies & Becker (1996)
Ladan, Brunei		40.2	Davies & Becker (1996)
Sungei Menyala, Malaysia		31.8	Manokaran & Swaine (1994)
Bukit Lagong, Malaysia		41.1	Manokaran & Swaine (1994)
Pasoh, Malaysia		29.1	Manokaran & Swaine (1994)
Bornean old-growth forests		37.1	Slik et al. (2010)

Table 3.5. Comparison of mortality rates from other tropical Asian forest sites. Only papers using the same calculation methods were included. *Trees ≥10cm dbh.

Site	Years	Duration (years)	Annual mortality (%)	Reference
Bukit Timah, Singapore	1993-1995	2	2.9	This study
	1995-2003	8	2.9	This study
	2003-2008	5	2.7	This study
	2008-2012	4	3.4	This study
	1993-2012	19	3.3	This study
Pasoh, Malaysia	1987-1990	3	1.1	Condit et al. (2006)
	1990-1995	5	1.5	Condit et al. (2006)
	1995-2000	5	1.9	Condit et al. (2006)
	1971-1984	13	2.1*	Manokaran & Swaine (1994)
Sungei Menyala, Malaysia	1947-1985	38	2.0*	Manokaran & Swaine (1994)
Bukit Lagong, Malaysia	1949-1985	36	1.4*	Manokaran & Swaine (1994)
Lambir, Malaysia	1992-1997	5	1.5	Condit et al. (2006)
Sinharaja, Sri Lanka	1995-2001	6	1.6	Condit et al. (2006)

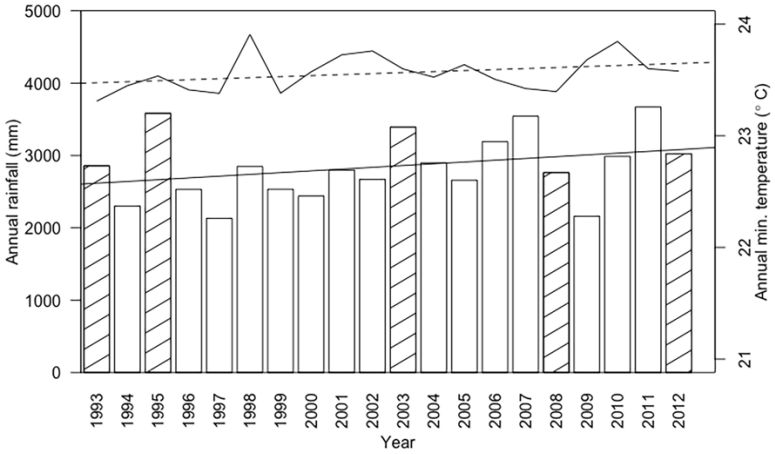

Figure 3.1. Annual rainfall (bars) and mean minimum annual temperature from a weather station 8.5 km northwest of Bukit Timah. Hatched bars represent census years. Solid and dashed straight lines represent the linear fits of annual rainfall and annual minimum temperature respectively. There were significant increases in both mean annual rainfall (augmented Dickey-Fuller [ADF] test statistic = -3.51; p = 0.059; 1980-2012) and mean minimum annual temperature (ADF test statistic = -2.72; p = 0.297; 1985-2012). Two drought (1997, 2009) and four 'wet' (1995, 2003, 2007, 2011) years occurred during the 19-year census period, when annual rainfall fell below and above 1 SD of mean rainfall respectively.

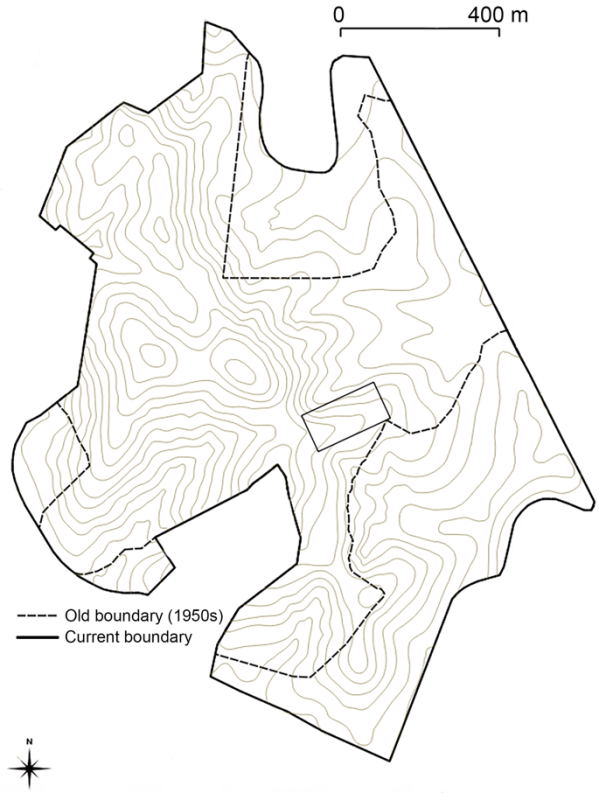

Figure 3.2. Map of Bukit Timah Nature Reserve (164-ha) showing the position of the 2-ha plot within the reserve.

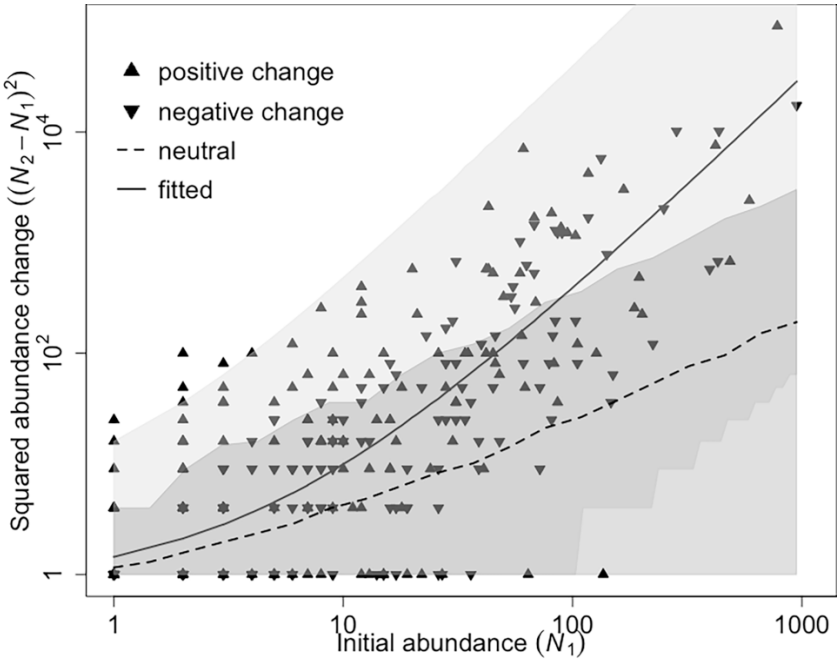

Figure 3.3. Squared abundance changes in Bukit Timah over 19 years plotted against initial abundance. Each point represents one species. The dashed line with shaded dark gray 95% confidence interval shows the neutral model prediction. The black curve with shaded light gray 95% confidence interval shows the fitted model. Species whose abundances did not change ($(N_2-N_1)^2 = 0$) are not shown on the log axes (48 species).

Chapter 4 – Recovery and tree dynamics of the Bukit Timah secondary forest

4.1 Introduction

Half of tropical forests in the world are secondary (ITTO 2002), and this proportion continues to increase as primary forests are being converted to pastures or agricultural land (Gibbs et al. 2010) and subsequently abandoned (Lang & Knight 1983; Nepstad et al. 1996; Rivera & Aide 1998). Although Brown & Lugo (1990) stated that secondary forests more than 60–80 years old were "often indistinguishable from primary forests", there is increasing evidence that these old secondary forests require an even longer time for species composition and forest structure to recover to levels resembling primary forest (Brearley et al. 2004; Chua et al. 2013; Riswan et al. 1985; Turner et al. 1997).

Secondary forest succession has been theorised to follow four phases (Oliver 1981). The first phase usually involves the rapid growth of herbaceous plants and colonising trees, also known as pioneer species. These trees are able to create a closed canopy layer within 5-10 years after land abandonment (Chazdon 2008). The next phase brings about forest structure development, as the pioneer trees grow further in diameter and height, thereby reducing the amount of light reaching the understorey. This in turn reduces the density of light-demanding herbaceous plants and the seedlings of pioneer species (Capers et al. 2005), and favours the establishment of shade-tolerant species. This phase usually occurs 10-20 years after abandonment (Chazdon 2008), and is succeeded by the third phase, also called the "understorey reinitiation stage" (Oliver 1981). This phase, occurring over decades to centuries, involves the establishment and growth of old-growth species in the understorey (Denslow and Guzman 2000, Guariguata et al. 1997) and a gradual

replacement of pioneer canopy trees with old-growth species (Chazdon 2008). The last phase, the "old-growth stage", is one of relatively stable composition (Peet 1992), containing a mix of canopy species that were not present during early succession (Chazdon 2008), and should have the greatest resemblance to old-growth forests in terms of forest structure and species composition.

Compared to studies that examined early tropical forest secondary succession (e.g. Ewel et al. 1983; Guariguata et al. 1997; Kammesheidt 1999; Nepstad et al. 1996; Rivera and Aide 1998), fewer studies have been done on older secondary forests (≥ 50 years; Brearley et al. 2004; Chua et al. 2013; Lang and Knight 1983; Saldarriaga et al. 1988). Secondary forests ≥ 50 years old usually already have a tree canopy, and are very likely to be in the understorey reinitiation stage. Forest structural variables of old secondary forests, such as basal area and stem density, were similar to or approaching those found in old-growth forests (Brearley et al. 2004; DeWalt et al. 2003). However, tree species composition in old secondary forests was often found to differ significantly from old-growth forests (Chazdon 2003; Finegan 1996; Guariguata and Ostertag 2001). Despite these differences, secondary forests often harbor high animal diversity, sometimes even in young secondary forests (Castro-Luna et al. 2007; DeVries et al. 1997; Heinen 1992; Raman et al. 1998; Vasconcelos 1999), highlighting their importance for biodiversity conservation.

Besides changes to aboveground vegetation, secondary forest soils also often undergo changes in nutrient levels. Soil carbon (C) and nitrogen (N) usually escape the ecosystem temporarily after forest removal (Detwiler 1986; Houghton et al. 1991) via combustion and decomposition, while the levels of other nutrients like potassium, calcium and phosphorus vary depending on land use history and time elapsed since abandonment (Allen 1985; Certini 2005; Eden et al. 1991; McNabb et al. 1997). These changes are reversible if the forest is allowed to recover (da S. Martins et al. 1991; Reiners et al. 1994), or if disturbances are not repetitive over short periods of

time (Davidson et al. 2007; Don et al. 2011). The recovery of soil to pre-disturbance levels depends on the forest type, soil type, and land use, but once plants start growing in abandoned land, soil recovery processes also begin through plant-soil interactions (Guariguata and Ostertag 2001).

Being Southeast Asia's country with the highest per capita gross domestic product (World Bank 2016), Singapore has, not surprisingly, lost much of its forests, both primary and secondary growth, to urban development. Beginning in the early 19th century, forest cover has dwindled to its current 22.6% of total land area, much of it being young secondary forest (Yee et al. 2011). Old secondary forests cover only 1.37% of total land area, and surround the small primary forest fragments remaining in Singapore (0.16%; Yee et al. 2011). Both primary and old secondary forests are currently located in protected nature reserves (Law Revision Commission 2006). Even after a century of natural recovery, the tree communities in these old secondary forests differed significantly from primary forests in species richness and composition (Turner et al. 1997). However, Turner et al. (1997) only observed trees greater than 30 cm girth at breast height, or 9.5 cm diameter at breast height (dbh), excluding the sapling size classes which are indicators of future forest composition. A study comparing adjacent primary and secondary forests in Singapore also found that adult tree composition differed significantly, but saplings (≤3 cm dbh) were floristically more similar to primary forest with increasing proximity to primary forest (Chua et al. 2013). Other studies done in Bolivia and Costa Rica also found that sapling communities were more similar between secondary and primary forests than adult trees (Guariguata et al. 1997; Peña-Claros 2003). These observations concur with the understory reinitiation stage of forest recovery, where one of the predictions is that primary forest species will recruit into the younger size classes as the pioneer trees mature (Oliver 1981).

Using three measurements of trees collected from a permanent research plot in an old secondary forest in Bukit Timah Nature Reserve, Singapore, I present temporal and spatial dynamics of the forest over eight years. This secondary forest is more than 60 years old (Chua et al. 2013), and is less than 10 m away from the adjacent primary forest, but basal area, stem density and species richness were still significantly lower than primary forest (Chua et al. 2013). Previous studies on secondary forests have predominantly used chronosequences (Chazdon 2003; Chazdon et al. 2007), which assumes that each chronosequence site experienced similar disturbances and had similar environmental conditions, like soil fertility and vegetation composition, before the disturbances. There are few studies that track temporal dynamics in tropical secondary forests (but see Chazdon et al. 2007; Norden et al. 2015). Although there had been structural and floristic studies about younger secondary forests in the region (Malaysian 17 and 30-year-old forests; Kochummen 1966; Kochummen & Ng 1977), our study provides a systematic and more mechanistic understanding of forest recovery in Southeast Asia. This study is expected to contribute to literature on forest recovery in tropical Asia in light of evidence that long-term forest recovery rates are lowest in tropical Asia compared to other continents (Cole et al. 2014).

Following the predictions of the understory reinitiation stage (Oliver 1981) and evidence from young secondary forests in Central America (Chazdon et al. 2005), I hypothesize that 1) mortality of the dominant species in the secondary forest will increase over time, and this thinning is expected to occur at higher rates in smaller tree sizes than in bigger trees (Chazdon 2008; Chazdon et al. 2005); 2) The number of shade-tolerant/primary forest species and individuals will increase over time in the understory, and that 3) their recruitment will be concentrated near the primary forest at first but will disperse further into the secondary forest over time. Because of the mixed results from previous studies about secondary forest soils, I hypothesize that 4) the primary and secondary forest in Bukit Timah will have the same level of soil nutrients, given the long

recovery time and lack of continued disturbances at the site. I also examined the dynamics and growth rates of species shared by both the primary and secondary forests.

4.2 Methods

4.2.1 Field data collection

The secondary forest plot was established in 2004, less than 20 m southeast from a 2-ha primary forest plot (Chua et al. 2013). The total size of the secondary forest plot is also 2-ha, but because part of the northwest corner of the plot is primary forest, this portion was excluded and only the 1.6-ha (forty 20 × 20 m quadrats) secondary forest portion of the plot was used for all analyses in this chapter.

All trees ≥1 cm diameter-at-breast-height (dbh; 1.3m) were enumerated in 2004, 2008 and 2012. The most abundant species in the plot in 2004 were, in descending order, *Dillenia suffruticosa* (Griff.) Martelli, *Adinandra dumosa* Jack, *Campnosperma auriculatum* (Blume) Hook. f., *Rhodamnia cinerea* Jack (Chua et al. 2013). These four species were considered dominant species in the secondary forest plot, because they made up >50% of all stems and >60% of total basal area (Chua et al. 2013).

For comparisons with primary forest, I used data from an adjacent 2-ha plot, which also had all stems ≥1 cm dbh enumerated (Ngo et al. 2016). I used data from 2003 and 2012 because they overlap with the survey period of the secondary forest plot.

4.2.2 Soil sampling, ion exchange, and chemical analyses

Soils were sampled in alternate 20 × 20 m quadrats in both the primary (26 quadrats) and secondary (20 quadrats) forest plots. One 10 cm core was taken from the center of each sampled quadrat. Soils were air-dried at ambient laboratory temperature for 10 days and then sieved (< 2 mm) prior to analysis. Soil pH was determined in both deionized water and 10 mM $CaCl_2$ in a 1:2 soil to solution ratio using a glass electrode. Total carbon and nitrogen were determined by automated combustion and gas chromatography with thermal conductivity detection using a Thermo Flash 1112 analyzer (CE Elantech, Lakewood, NJ, USA). Exchangeable cations were determined by extraction in 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio), with detection by inductively-coupled plasma optical-emission spectrometry on an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA) (Hendershot *et al*. 2008). Total exchangeable bases (TEB) was calculated as the sum of Ca, K, Mg, and Na; effective cation exchange capacity (ECEC) was calculated as the sum of Al, Ca, Fe, K, Mg, Mn, and Na; base saturation was calculated by (TEB ÷ ECEC) × 100. A measure of extractable phosphorus (often considered to be 'plant-available' phosphorus) was determined by extraction with anion exchange resin strips in the laboratory, with phosphate detection by automated neutralization and molybdate colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO, USA) (Turner and Romero 2009). Nitrogen mineralization was quantified using in-situ resin bags, containing mixed cation/anion exchange resins. Resin bags contained 5 g of mixed-bed anion and cation exchange resins (Dowex Marathon Mr-3) sealed inside 220 µm polyester mesh. Bags were buried in the upper 10 cm of soil in 26 locations within each plot, at the same points where soils were sampled for analysis. After incubation *in situ* for approx. 20 days the resin bags were collected, rinsed with deionized water to remove adhering soil, extracted with 75 mL of 0.5 M HCl. Nitrate (+nitrite), ammonium, and phosphate were determined by automated colorimetry on a Lachat QuikChem 8500 (Hach Ltd., Loveland, CO, USA).

4.2.3 Data analysis

Tree species were classified as primary forest species, generalist species (common in both primary and secondary forests), secondary forest species, or exotic species using flora guides (Corner 1988; Slik 2009; van Steenis 1948; Whitmore & Ng 1972-1989).

Mortality was calculated as $(\ln(n_1) - \ln(S_2))/t$ and recruitment as $(\ln(n_2) - \ln(S_2))/t$, where t is the census interval, n_1 and n_2 are the population sizes at census 1 and census 2, respectively, and S_2 is the number of survivors at census 2 (Condit et al. 1999). Distance to primary forest was calculated as the perpendicular distance from the center of each 20 × 20 m quadrat to the nearest primary forest boundary. The relationship between number of primary forest and generalist trees with the distance to primary forest was analyzed using linear regression.

For species shared between the primary and secondary forest plots (six species with >40 individuals), the primary forest always had the largest individuals. Because growth rates are dependent on size, I removed individuals in the primary forest that were larger than the biggest individual in the secondary forest so that their growth rates were comparable.

4.3 Results

4.3.1 Plot-level dynamics

There was a slight increase in the total number of trees from 2004 to 2012 (Table 4.1), but some patterns were observed when split into different size classes. There were consistent increases in the abundance of 1.0–4.9 cm dbh trees, while consistent decreases were observed in the bigger trees, especially in the 5.0–9.9 cm size class (Table 1). Despite the slight decrease in the number of larger trees (≥10 cm dbh), basal area increased by 15.6% within the eight-year period.

There was a rapid increase in the total number of species from 2004 (125 species) to 2012 (148 species; 18.4%; Table 1). Most of this increase was contributed by primary forest species (18 species), followed by generalist species (4 species), and secondary forest species (1 species). There was only one exotic species throughout the survey period – the rubber tree (*Hevea brasiliensis*).

Recruitment rates were constant in the two census intervals 2004–2008 and 2008–2012, but mortality increased for all size classes in the 2008–2012 interval, with a 0.5x increase for all trees (Table 4.2).

4.3.2 Dynamics of species types

Stem abundance increased consistently at every census for primary forest and generalist species, decreased consistently for secondary forest species, and remained constant for exotic species (Fig. 4.1). Basal area of generalist species increased rapidly, from 11.3 to 14.1 m^2/ha by 2012, but this was mainly due to the growth of the large trees of one dominant species, *C. auriculatum*. Basal area of primary forest and exotic species also increased consistently but at a slower pace than generalist species. There were no net changes in the basal area of secondary forest species over the eight years. Although the combined basal area of all primary forest species was <2 m^2/ha (7.3%), they included 83 out of 148 species (56%) in the plot in 2012 (Table 4.1).

4.3.3 Distance from primary forest

There was a significant negative relationship between stem abundance and distance from primary forest for both primary forest and generalist species ($p < 0.01$; Fig. 4.2a & b). This pattern was stronger for primary forest species (slope = -0.35 in 2004), and became more pronounced over time (slope = -0.42 in 2012). Therefore, even though primary forest species became more abundant over

time, most of the recruitment occurred near the primary forest, with limited dispersal beyond 60 m from the primary forest (Fig. 4.2a). There were no patterns between secondary forest species abundances and distance from primary forest in 2004 ($p = 0.121$), but in 2012 there was a significant decrease in stem abundance with decreasing distance from primary forest ($p = 0.011$; Fig. 4.2c).

4.3.4 Dynamics of dominant species

Two of the dominants species, *C. auriculatum* and *R. cinerea*, are generalist species, while the other two, *A. dumosa* and *D. suffruticosa*, are secondary forest species. *A. dumosa*, *C. auriculatum*, and *D. suffruticosa* showed clear declines in abundance at every census interval (Fig. 4.3). *C. auriculatum,* the tallest canopy species in the plot, had fewer than five individuals in the 1.0–4.9 cm dbh size class in 2004, and no longer had recruits in the later censuses. For the other three species, only *R. cinerea* had consistently lower mortality rates than the plot average for all tree sizes. Extremely high mortality rates were observed in both *D. suffruticosa* and *A. dumosa* in the 1.0–4.9 cm size class, and in the 5.0–9.9 cm size class of *C. auriculatum* in both census intervals.

4.3.5 Species shared between primary and secondary forests

Most of the species shared between primary and secondary forests with >30 individuals in both forest types (6 species) were generalist species (Table 4.3). Two species, *Streblus elongatus* and *Shorea curtisii*, were among the most common in the primary forest. These six species had more trees in the primary forest than secondary forest plot except *Ixonanthes reticulata* (generalist) and *Timonius walliachianus* (secondary forest). All six species had higher tree growth rates in the secondary forest except for *S. curtisii* (Table 4.3).

4.3.6 Soil nutrients and ion exchange

Soils were generally very acidic and mineral content very low in both forests. Soil nutrient concentrations were very similar between primary and secondary forest except for Al saturation, base saturation, carbon content, C:N ratio and NO_3^- exchange (Table 4.4). Secondary forest soils had significantly higher C:N ratio and Al saturation than primary forest soils, both signs of soil degradation from previous agricultural activities. NH_4^+ and NO_3^- turnover were generally very high in both primary and secondary forests, although NO_3^- exchange was significantly lower in secondary forest (Table 4.4).

4.4 Discussion

Although the secondary forest in Bukit Timah does not resemble the adjacent primary forest after more than 60 years of natural regeneration, there are strong signs that the forest is experiencing rapid change. Three out of four dominant species in the plot were declining without self-regeneration, and are likely to be phased out or greatly reduced in abundance in the next decade. Other secondary forest species also declined in abundance at every census. Eighteen new primary forest species recruited into the plot within eight years, most of them being single individuals. Stem abundance and basal area of primary forest and generalist species increased every census, while exotic species had a very insignificant presence throughout the survey period. These observations support the hypotheses that dominant trees in the secondary forest would decline, especially among the smaller trees, and that primary forest species would increase in the understorey, both of which substantiate the "understorey reinitiation stage" of Oliver (1981). However, primary forest species and generalist species abundances decreased with increasing distance from the primary forest, while the opposite was observed for secondary forest species in 2012. Common species shared between the primary and secondary forests generally had higher abundances in the primary forest, but tree growth rates were higher in the secondary forest. There were no significant differences between soil

nutrients in primary and secondary forest except for a lower base saturation and NO_3^-, and higher C and C:N ratio in secondary forest.

The declining dominant species were *C. auriculatum*, and *A. dumosa* and *D. suffruticosa*. *R. cinerea*, was the only dominant species that maintained its abundance. Other secondary forest species also had declining abundance, such as *Guioa pubescens*, *Fagraea fragrans*, and *Ficus grossularioides*. A study in a Costa Rican secondary forest also found that the dominant pioneer species declined at light-use sites after 39 years of recovery (Chazdon et al. 2007), but it was not clear if the sapling community had recovered. In a 60-year-old secondary forest in Panama, pioneer species had very high mortality in the larger size classes, but overall species composition changed very little (Lang & Knight 1983).

Previous research considered secondary forest dominated by *A. dumosa* as adinandra belukar heath forest, including the Bukit Timah secondary forest (Sim et al. 1992). They were called anthropogenic heath forests due to their resemblance to natural heath forests, such as poor soils and the ability of heath tree species to tolerate them (Sim et al. 1992). Adinandra belukar often contain a suite of species that include *A. dumosa*, *D. suffruticosa*, *R. cinerea*, *F. fragrans*, *F. grossularioides* and the fern *Dicranopteris linearis* (Sim et al. 1992), all of which are common in the Bukit Timah secondary forest plot. In particular, *D. linearis* forms a thicket up to 3 m over *ca*. 0.16-ha in some areas in the plot (pers. obs.), with living fronds growing atop dead fronds. It was described as a 'climbing' fern in Hawaiian rainforests (Russell et al. 1998), but it neither twines nor possesses hooks for climbing like true climbing plants. The strong allelopathic properties of *D. linearis* (Chong and Ismail 2006; Kato-Noguchi et al. 2012), together with its dark understorey, result in its prolonged dominance in severely disturbed landscapes (Cohen et al. 1995; Russell et al.

1998). In addition, *D. linearis* is able to grow well on Al-saturated soils (Chua et al. 2016), giving it an advantage over Al-intolerant species.

Nevertheless, *D. linearis* can be suppressed naturally over time where a canopy is present, even if it is made out of climbers linked to different tree crowns (Kochummen & Ng 1977). Although *D. linearis* coverage was not assessed, it is interesting to note that one typical pioneer species, *Macaranga bancana*, increased from 1 tree in 2004 to 32 trees in 2012. These *M. bancana* recruits were found growing in a cluster at the edges of *D. linearis*. The reasons for their recent establishment is unknown, but they are light-demanding and grow quickly, raising the possibility that *D. linearis* will be suppressed further and lead to accelerated recruitment of primary forest species.

Closer to the primary forest, an almost pure stand of *C. auriculatum* had established and dominated the canopy, something which has never been recorded from other secondary forests in the region. *C. auriculatum* is a canopy species usually found in regenerating gaps within the primary forest, but never observed to grow in large swathes such as in the Bukit Timah secondary forest plot. Most of the *C. auriculatum* in the plot were large trees (mean dbh 31 cm) without signs of self-regeneration, so with the rapid recruitment of primary forest species under its canopy I predict that the canopy will become more heterogeneous over time barring major disturbances.

There were no significant differences in soil chemistry between the primary and secondary forests, except soil carbon content, C:N ratio, Al saturation (higher in secondary forest), NO_3^- exchange and base saturation (higher in primary forest). Soil characteristics from previous studies in Singapore primary and secondary forests have been largely consistent with our results, but there were large variances in C:N ratios, total P, and total exchangeable bases (Table 4.5). Soil pH was

consistently low at 3.6-4.0 for both primary and secondary forests. Sim et al. (1992) reported higher C:N ratios in both primary and secondary forests, while total P tended to be higher in primary forests in two other studies compared to our results (Grubb et al. 1994; Sim et al. 1992). There was also higher Al saturation and much lower base saturation than Chua et al. (2016) for both primary and secondary forests, likely due to differences in sampling locations and perhaps land use history in the case of secondary forests.

Soil nutrient recovery has only been reported in one other old secondary forest in Central Kalimantan, Indonesia (Brearley et al. 2004), and they also found high similarities in soil nutrient levels between the secondary forest and an adjacent primary forest. In a similar vein to Bukit Timah, this 55-year-old secondary forest also differed in floristic composition to its adjacent primary forest, although forest structure was similar (Brearley et al. 2004). In Bukit Timah, the secondary forest was also significantly different floristically and structurally from the adjacent primary forest after 56 years of natural recovery (Chua et al. 2013), even though current soil nutrient levels were largely similar. Given these observations, soils in secondary forests may recover more rapidly than the vegetation composition and structure in the absence of continued disturbances, but more studies on soils in old secondary forests are needed to confirm this.

The increase in the number of primary forest species reflects their growth from the seedling stage rather than recruitment from seed, because our sampling method captured only saplings and trees ≥1 cm dbh. Most of the existing and recruiting primary forest species were concentrated near the primary forest boundary, largely overlapping the canopy *C. auriculatum* trees. *C. auriculatum* leaves are thick, waxy, and create a thick leaf litter when their leaves are shed. Even though Goldsmith et al. (2011) found that thick leaf litter hindered seedling recruitment in the plot, the study used the primary forest as a benchmark against the secondary forest. However, given that

secondary forest species are often unable to regenerate under their own canopy, unlike primary forest seeds (Whitmore 1989; Yamamoto 2000), this benchmark may have been an unfair one. The large overlap in spatial distribution between *C. auriculatum* and primary forest species shows that thick leaf litter may have delayed but not inhibited the establishment and growth of primary forest species.

Although the decreasing gradient of primary forest species with increasing distance from the primary forest is not surprising, this gradient became stronger over time, giving the impression that primary forest species were not spreading further into the secondary forest. However, in the areas furthest from the primary forest, eight primary forest species new to those areas had recruited by 2012, although most of them had only one tree per species. Therefore even though recruitment of primary forest species occurred throughout the plot, their densities were much higher nearer the primary forest. Slow recovery of species richness has been observed in other old secondary forests as well (Brearley et al. 2004; Lang and Knight 1983; Kochummen & Ng 1977), and dispersal limitation is usually one of the main explanations. In Bukit Timah, given that soil conditions were similar between primary and secondary forests, dispersal limitation is also the most likely reason for the slow recovery of primary forest species. Large mammal and bird dispersers like Sambar Deer and hornbills have not been recorded for decades (Corlett 1988), but some of the smaller mammals still exist in high abundance, such as the plantain squirrel and long-tailed macaque (Sha et al. 2009). Are these small mammals ineffective seed dispersers? Observations of mammals and birds feeding on *C. auriculatum* fruits found that macaques spat out seeds under the tree crowns while squirrels like destroyed the seeds (Corlett and Lucas 1989). The feeding behaviour of these two abundant mammals would likely be similar for the fruits of other species, and may explain poor recruitment of primary forest species in secondary forest.

Interestingly, species shared between both primary and secondary forests almost always had higher growth and increasing abundance in the secondary forest, except for *S. curtisii*. The superior performance of these species in the secondary forest may be due to more favourable conditions such as higher light levels and lower competition than in primary forest. However, *S. curtisii*, the most common dipterocarp species in Bukit Timah, while thriving in the primary forest (Ngo et al. 2016), seemed to be doing less well in the secondary forest. Both recruitment and growth rates of *S. curtisii* in the secondary forest were lower than in primary forest. This species depends on general flowering events, which occur supra-annually, for the recruitment of seedlings. This may have restricted its number of chances for seed recruitment, but does not explain the lower growth rates in the secondary forest. Collection of trait data or experiments on plant physiology will offer more clues to the contrasting performances of species. This also demonstrates that species growth rates are influenced by the environment, and broad generalisations about species groups like 'fast-growing' and 'slow-growing' are very context-dependent.

This chapter has demonstrated that rapid and significant changes occurred within eight years in an old secondary forest whose recovery was thought to have stagnated. Old secondary forests are not unique to Singapore. The Southeast Asian region has experienced high deforestation rates in the past few decades (FAO 2001) and which continue to more recent years (Miettinen et al. 2011). Our results contribute to a greater understanding of secondary forest recovery dynamics in Singapore as well as in the region. As secondary forests become more prevalent, long-term studies on secondary forests will provide more knowledge on the factors that influence the speed and trajectory of recovery. This is important for guiding management decisions that aim to restore biodiversity, carbon sequestration capabilities, and a suite of other ecosystem services.

4.5 Table and figures

Table 4.1. Stand information of the Bukit Timah secondary forest plot.

	2004	2008	2012
No. individuals (/ha)			
All trees	1861.3	1927.5	1906.9
1.0–4.9 cm	836.3	881.3	976.9
5.0–9.9 cm	476.9	432.5	331.9
≥10 cm	547.5	544.4	521.9
Basal area (m^2/ha)	19.2	20.6	22.2
No. of species			
All trees	125	139	148
Primary forest species	65	75	83
Generalist species	45	48	49
Secondary forest species	14	15	15
Exotic species	1	1	1

Table 4.2. Mortality and recruitment rates of trees in the Bukit Timah secondary forest plot.

	2004–2008	2008–2012
Recruitment (%/yr)	3.3	3.5
Mortality (%/yr)		
1.0–4.9 cm	2.7	3.7
5.0–9.9 cm	2.2	4.0
≥10 cm	1.3	1.8
All trees	2.2	3.6

Table 4.3. Species shared between the secondary and primary forest plots and their abundances and growth rates.

		No. individuals				Growth rate (mm/yr)	
	Species class	Primary forest plot		Secondary forest plot		Primary forest plot	Secondary forest plot
Census year		2003	2012	2004	2012	2003–2012	2004–2012
Streblus elongatus (Moraceae)	Generalist	909	1086	72	125	0.66*	1.81
Shorea curtisii (Dipterocarpaceae)	Primary	517	511	37	34	1.42*	0.91
Calophyllum ferrugineum (Clusiaeae)	Generalist	240	207	64	80	0.48*	0.92
Calophyllum pulcherrimum (Clusiaceae)	Generalist	226	213	61	89	0.64*	1.59
Ixonanthes reticulata (Ixonanthaceae)	Generalist	44	27	59	57	1.11	5.36
Timonius wallichianus (Rubiaceae)	Secondary	67	56	92	102	1.15*	1.88

*To correct for biases that may arise from differences in tree size, those individuals in the primary forest plot that were larger than the maximum size in the secondary forest plot were removed, and growth rates calculated from the remaining trees.

Table 4.4. Soil characteristics (0–10 cm) of the 1.6-ha secondary forest plot, and from an adjacent 2-ha primary forest in Bukit Timah. Soils were sampled in the center of 20 m × 20 m quadrats. 26 quadrats and 20 quadrats were sampled in the primary and secondary forests respectively. Errors represent standard errors. Different letters beside the figures indicate significant differences from *t*-tests.

	Primary forest	Secondary forest
pH_{BaCl2}	3.6 ± 0.03*[a]	3.7 ± 0.05[a]
Al (cmolc/kg)	5.3 ± 0.20[a]	5.5 ± 0.33[a]
Ca (cmolc/kg)	0.11 ± 0.02[a]	0.08 ± 0.01[a]
Fe (cmolc/kg)	0.14 ± 0.01[a]	0.12 ± 0.02[a]
K (cmolc/kg)	0.12 ± 0.01[a]	0.11 ± 0.01[a]
Mg (cmolc/kg)	0.09 ± 0.006[a]	0.09 ± 0.013[a]
Mn (cmolc/kg)	0.01 ± 0.002[a]	0.01 ± 0.002[a]
Na (cmolc/kg)	0.04 ± 0.004[a]	0.04 ± 0.004[a]
TEB (cmolc/kg)	0.36 ± 0.03[a]	0.30 ± 0.04[a]
ECEC (cmolc/kg)	5.84 ± 0.22[a]	5.90 ± 0.37[a]
Al saturation (%)	91.19 ± 0.01[a]	92.94 ± 0.00[b]
Base saturation (%)	6.37 ± 0.57[a]	4.95 ± 0.31[b]
Total C (%)	2.90 ± 0.16[a]	4.27 ± 0.34[b]
Total N (%)	0.17 ± 0.006[a]	0.19 ± 0.014[a]
C:N ratio	17.0 ± 0.5[a]	22.4 ± 0.4[b]
Resin P (mg P/kg)	4.22 ± 0.40[a]	3.63 ± 0.69[a]
Total P (mg P/kg)	71.40 ± 2.29[a]	74.66 ± 3.31[a]
Bulk density (g/cm^3)	1.11 ± 0.05[a]	0.95 ± 0.07[a]
Soil available P and N		
PO_4^- (μg P/bag/day)	2.5 ± 1.2[a]	0.1 ± 0.02[a]
NO_3^- (μg N/bag/day)	81.9 ± 7.8[a]	40.5 ± 5.3[b]
NH_4^+ (μg N/bag/day)	67.4 ± 23.9[a]	87.3 ± 56.6[a]
Total inorganic N (μg N/bag/day)	149.4 ± 23.5[a]	127.8 ± 11.7[a]

*Data from 3 quadrats were missing.

Table 4.5. Soil chemical characteristics from studies done in forests of Singapore.

Primary forest	Depth (cm)	pH (H_2O)	C:N	N (%)	Total P (μg/g)	K (cmolc/kg)	Al sat (%)	TEB (cmolc/kg)	Reference
Bukit Timah 2-ha plot	0–10	3.88	17.0	0.17	71.40	0.12	91.19	0.36	This study
Bukit Timah Fern Valley (western part)	0–20	4.09	36.2	0.16	58.0	NR	NR	NR	Sim et al. (1992)
Bukit Timah (eastern part)*	0–10	3.8	NR	0.12	65	3.50†	NR	NR	Grubb et al. (1994)
Bukit Timah Fern Valley (western part)	NR	4.1	NR	NR	NR	NR	NR	NR	Grubb et al. (1994)
Bukit Timah Jungle Fall (western part)	NR	3.8	NR	NR	NR	NR	NR	NR	Grubb et al. (1994)
Central Catchment (mean)	0–5	3.95**	18.81	NR	NR	NR	83	0.61	Chua et al. (2016)
Secondary forest									
Bukit Timah 1.6-ha plot	0–10	4.00	22.4	0.19	74.66	0.11	92.94	0.30	This study
Adinandra belukar (mean of various sites)	0–20	3.59	38.2	0.08	20.5	NR	NR	NR	Sim et al. (1992)
Adinandra belukar (Kent Ridge)	0–10	4.3	NR	0.08	50	15.99†	NR	NR	Grubb et al. (1994)
Central Catchment (tall mature forest mean)	0–5	3.90**	21.33	NR	NR	NR	84	0.80	Chua et al. (2016)
Central Catchment (small pole trees mean)	0–5	4.01**	26.15	NR	NR	NR	86	0.74	Chua et al. (2016)
Central Catchment (open vegetation mean)	0–5	3.89**	22.16	NR	NR	NR	84	0.89	Chua et al. (2016)

NR – not reported. Al sat – Al saturation (Al / ECEC) × 100. *Mean values from 0–5 and 5–10 cm depths. **pH in $CaCl_2$. †Total K. This corrects the published data, for which incorrect units were given (David Burslem, personal communication)

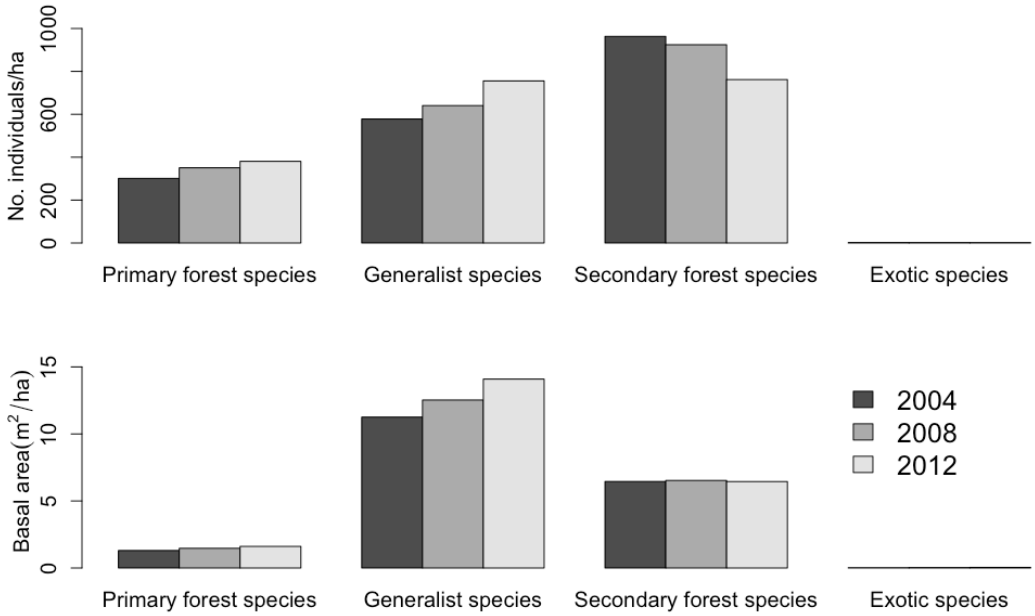

Figure 4.1. Changes in abundance and basal area of species types over time in the Bukit Timah secondary forest plot.

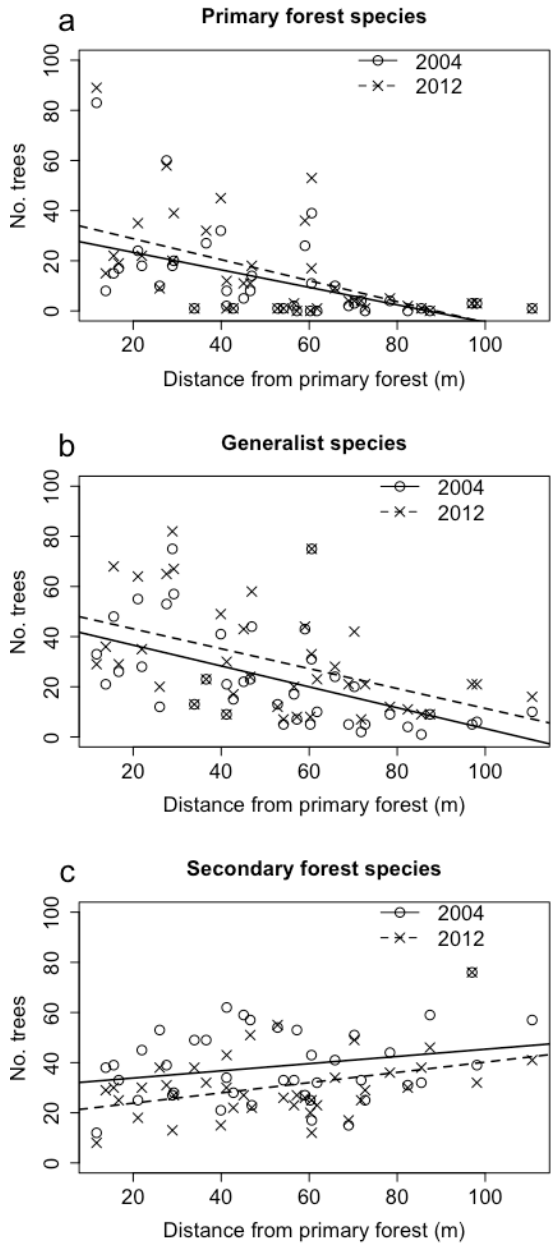

Figure 4.2. Relationship between distance from primary forest and tree abundance of each species types in the Bukit Timah secondary forest plot.

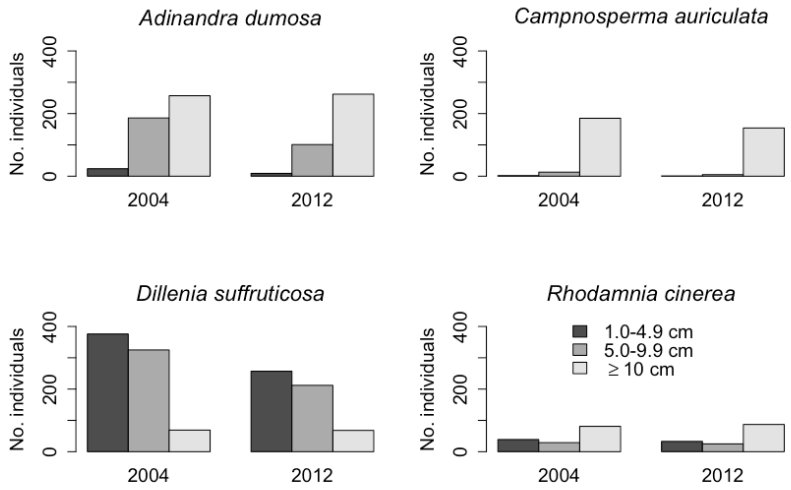

Figure 4.3. Abundance changes from 2004 to 2012 of the four dominant species in the secondary forest plot.

Chapter 5 – Growth rates of trees in primary and secondary forests of Bukit Timah

5.1 Introduction

Trees have a big influence on atmospheric carbon dioxide (CO_2) levels. The most obvious evidence of this is the annual fluctuation in global atmospheric CO_2 (Keeling et al. 1976), when temperate trees in the northern hemisphere enter autumn and winter and photosynthesis rates are greatly reduced. From this, it is natural to deduce that tree growth rates will have impacts on future atmospheric CO_2. Although CO_2 makes up only a small proportion of gases in the atmosphere (currently 0.041%; Dlugokencky and Tans 2017), it is an important greenhouse gas, and its increase in the last century has caused noticeable and irreversible changes in climate and weather patterns worldwide (Solomon et al. 2009).

The rise in atmospheric CO_2 levels in the last century has been theorised to increase tree growth rates globally (Lloyd and Farquhar 1996) due to carbon fertilisation. However, climate change encompasses more than just elevated CO_2, it also alters numerous other environmental variables such as temperature, terrestrial nutrient deposition, and precipitation patterns. These environmental changes affect both short- and long-term tree growth, but their effects might differ depending on latitude, climate and altitude.

Field experiments have tried to examine the effect of different factors on tree growth in isolation, such as by increasing CO_2 (Norby et al. 2010; Oren et al. 2001), temperatures (Jump et al. 2006; Lloyd et al. 2011), various nutrients (Högberg et al. 2006; Nadelhoffer et al. 1999), and even water exclusion (da Costa et al. 2010). Most of these experiments were done in temperate forests,

with relatively fewer studies in tropical forest ecosystems (but see da Costa et al. 2010; Rowland et al. 2015). Experiments may distinguish effects on tree growth among various factors, but in nature, trees are exposed to these changing factors in concert, and it has been shown in numerous experiments that some of these factors interact with one another to produce different responses in tree growth. For example, a 11-year CO_2 enrichment experiment found that tree growth was enhanced for the first 6 years of the experiment, but this enhancement disappeared in later years, likely caused by nitrogen limitation (Norby et al. 2010). Although such long-term experiments provide valuable new insights to tree growth in a changing climate, they are difficult to sustain due to budget and logistical constraints.

Besides experimental research, observational studies on tree growth is another way to track tree responses to environmental changes and stress. In climates with distinct growing and dormant seasons, tree trunks 'store' a record of their annual growth rates through growth rings. The study of tree rings, dendrochronology, has contributed much knowledge about tree responses to climate and weather changes, as well as historical events (e.g. Schweingruber et al. 1979). For example, a study about tree-ring reconstruction from trees in New Zealand found evidence to support the Medieval Warm Period, an event that was hypothesized to occur from A.D. 1000 to 1300, even though this event was highly variable in time and space (Cook et al. 2002). Another 2326-year tree-ring reconstruction in Asia also found support for the Medieval Warm Period, as well as the Little Ice Age (Zhang et al. 2003), hypothesized to occur from A.D. 1500 to 1850 (Mann 2002). More recent events can also be inferred from tree rings. For example, tree rings were used to track mass earth movements, such as landslides, in the French Alps (Braam et al. 1987), and tree rings from juvenile and adult trees of a light-demanding species in western Thailand were used to infer recruitment patterns of the species (Vlam et al. 2014). However, this technique cannot be applied to trees without growth rings, such as tropical trees growing in aseasonal climates. Trees growing in tropical

aseasonal Southeast Asia typically do not have tree rings (Whitmore 1984), so measuring the productivity of these trees usually involves physical measurements of diameter or height.

Studies on tree growth usually take on two vastly different time scales. On one hand, field-based physiological experiments, usually involving gas measurements from the leaves within minutes, provide information about chemical reaction rates occurring in the leaves, like photosynthesis and respiration. On the other hand, plot-based measurements of tree trunks over several years give information about cumulative effects of environmental changes and stress on tree growth. It may be difficult to scale up individual biological processes, such as photosynthetic rate, to predict tree growth and performance, because many other factors affect tree growth. Similarly, it is difficult to determine the exact environmental causal factors on tree growth or mortality from tree measurements at supra-annual intervals, because multiple events occur within such long intervals.

Short-term tree growth rates are a way to study tree responses to environmental changes and stress. There is evidence to suggest that tropical trees respond to water availability (Baker et al. 2003; Bullock 1997; Whigham et al. 1990; Worbes 1999). In an experiment done on planted *Pinus radiata* trees in Australia, Myers (1988) found that the cumulative water stress within one growing season significantly influenced the annual stem growth of the trees. In a temperate forest in the U.S., eddy covariance methods combined with tree measurements revealed that trees respond to both hourly and daily variations in ambient conditions, as well as monthly and seasonal anomalies that reflect weather and climate variations (Barford et al. 2001). As climate changes, such short-term information on tree growth is necessary for projecting forest net primary productivity and tree mortality, which affect long-term ecosystem carbon balance and global warming trends.

In Singapore, even though there are no distinct wet and dry seasons, rainfall is highly variable year to year (NEA 2017b), and includes influences from the El Niño Southern Oscillation (NEA 2017a). Trees typically do not have growth rings in their trunks (Abdul Azim and Okada 2014). Nevertheless, the annual rainfall variability is expected to influence forest tree growth and mortality rates. However, intra-annual forest tree measurements have never been published in Singapore or in Southeast Asia. Most plot-based studies in the region are usually done in supra-annual, usually 5-year intervals (e.g. Condit et al. 1999; Feeley et al. 2007), which is too long to capture finer-scale responses of tree growth to short-term environmental fluctuations. Field-based physiological experiments have also been done in the region, but most of them focus on one-time inter-species comparisons (e.g. Inoue et al. 2015; Kenzo et al. 2004, 2006, 2008).

Using both long and short tree measurement interval data from the primary and secondary forest plots of Bukit Timah, I ask the following questions: 1. Trees that die from environmental stress will have very low growth rates just before they die. 2. Tree growth rates will be positively correlated with rainfall. 3. Secondary forest species will have the highest growth rates and sensitivity towards rainfall, followed by generalist species and primary forest species.

5.2 Methods

The study site is the 2-ha primary and secondary forest plots of Bukit Timah Nature Reserve (section 2.2). Trees that were selected were measured much more frequently than in the previous two chapters. Because absolute growth rates increase with tree size, and because small trees were much more abundant than large trees, trees were grouped into four size classes – 5.0–9.9 cm, 10.0–19.9 cm, 20.0–39.9 cm, and ≥40.0 cm. A stratified sampling approach was used such that each size class had a comparable number of trees (Fig. 5.1; Table 5.1). Tree diameters at-breast-height (cm) were measured using a diameter tape.

The dates when the trees measured are listed in Table 5.2. The shortest measurement interval was 5.4 months, and the longest was 7.4 years. Growth rate was calculated as (dbh2 – dbh1) / time for each measurement interval, and is expressed in mm/yr. Errors in the data were checked by removing growth rates that were < -5%/yr and >75 mm/yr (Condit et al. 1993), because these were not plausible and were likely caused by human errors. For calculating growth rates of trees that died within the study period, mean growth rates before their recorded mortality was used.

Rainfall from five closest weather stations to Bukit Timah were averaged, and the Standardised Precipitation Index was used to detect rainfall deviations and abnormalities (McKee et al. 1993). Growth rates for each size class were tested for differences between the primary and secondary forest using *t*-test, with mean growth rates from each measurement interval as replicates. The sum of rainfall within each measurement interval was calculated for each tree, and multiple linear regression was used to test the relationship between growth, rainfall and tree size.

5.3 Results

5.3.1 Rainfall patterns

Rainfall was not seasonal, but over a period of 37 years (1980-2016), rainfall varied from year to year. Mean rainfall in this period was 2595.5 mm/yr, with the wettest year (2006) receiving 3403.3 mm and the driest year (1983) receiving 1543.3 mm of rain. These two years also marked the two extremes in rainfall pattern within this period (Fig. 5.2), with most years receiving ‘normal’ rainfall and ‘very wet’ years becoming more frequent after 2000.

5.3.2 Tree growth rates

The mean growth rates across all measurement intervals and size classes was 3.7 and 2.7 mm/yr for the primary and secondary forest plots respectively, with considerable variation between intervals in both plots (Fig. 5.3). Some growth rates were significantly different from one another, with the primary forest having more significant fluctuations than the secondary forest. As with rainfall patterns, there were no apparent trends or seasonality in growth rates.

When split by tree size, the smaller trees in the primary forest plot had significantly higher growth compared to trees of the same sizes in the secondary forest plot (Table 5.3). This pattern was vice versa for the bigger trees, where trees in secondary forest had significantly higher growth rates. The expectation for hypothesis 3, that secondary forest species will have higher growth rates than primary forest species, was only partially correct.

5.3.3 Tree growth rates before mortality

As predicted by hypothesis 1, most trees had significantly lower growth rates than surviving trees before mortality, except for the 10.0–19.9 cm size class. Growth rates increased with tree size, within expectations for surviving trees, but such a pattern was not observed in dying trees.

5.2.4 Relationship between tree growth and rainfall

For the primary forest trees, there was a significant negative relationship between rainfall and tree growth rates when data from all measurement intervals were included (Fig. 5.4a), but this relationship disappeared after excluding the intervals that were longer than 2 years. There were also no relationships between rainfall and tree growth in the secondary forest (Fig. 5.4b). It is interesting to note that growth rates from the shortest measurement intervals had the most variation compared

to longer intervals. These results are counter to our expectation in hypothesis 2 that growth rates were correlated with rainfall.

5.3.5 Growth rates of common species

The most common dipterocarp species in Bukit Timah – *Shorea curtisii*, had much higher growth rates than the other common species for trees ≥10.0 cm (Table 5.5). The largest size class (≥40.0 cm) had an even higher growth rate than *Campnosperma auriculatum*, the most common canopy species in the secondary forest plot. Surprisingly, the small trees of both common primary forest species, *S. curtisii* and *Streblus elongatus*, had much higher growth rates than those in the secondary forest (Table 5.5).

5.4 Discussion

Data from the weather stations around Bukit Timah showed that rainfall varied significantly between years, even though the climate was aseasonal. Tree growth rates also varied significantly between measurement intervals, but this does not seem to be caused by rainfall directly. The trees that died during the study period had significantly lower growth rates than surviving trees prior to mortality. There were significant differences in growth rates between the primary and secondary forest trees in all size classes – the smaller trees (<20.0 cm) in the primary forest grew significantly faster than in secondary forest, while the larger trees (≥20.0 cm) in the secondary forest grew significantly faster than in primary forest. The dominant species in the secondary forest had very low growth rates in the small trees (5.0-9.0 cm), much lower than *S. curtisii* and *S. elongatus*.

Although trees in the secondary forest were expected to have higher growth rates than those in the primary forest at all sizes, the smaller trees had significantly lower growth rates. This may be due to the canopy cover already present in the secondary forest, which made the understorey

unconducive for the growth of light-demanding species. As shown in Chapter 4, the three out of four dominant species in the secondary forest, all light-demanding species, were not self-regenerating over time. Their high mortality and low growth rates in the small size classes point to possible stress, one of which could be the lack of light. This reasoning is strengthened by the significantly higher growth rates of the larger trees in the secondary forest, for which light is much less limiting.

The depressed growth rates of dying trees provides evidence that stressed trees devote fewer resources to trunk expansion compared to healthy trees (Dobbertin 2005). Although the cause of mortality was generally unknown unless the symptoms appeared on the bark or canopy, trees may channel more resources to isolating injuries and pathogens, or may be coping from a sudden loss of large amounts of biomass, in the case of snapped branches or trunks from neighbouring treefalls or from lightning strikes. Lightning usually kills the canopy tree struck, as well as other large trees within 10 m of the struck tree (pers. obs.). It is often difficult to ascertain the exact cause of mortality, because when signs of mortality become visible, such as termite trails on the trunk, it is usually at the late stages of tree decline, and these signs may be secondary causes of mortality instead of the initial trigger.

Although both temporal growth rates and rainfall fluctuated between years, they were not correlated to each other. The lack of correlation of short-term growth rates to rainfall in all tree sizes and forest types was surprising, because as shown in Chapter 2, the two drought events in 1997 and 2009 seemed to influence tree turnover in the primary forest. Long-term declines in growth rates had been detected in tropical forests in Panama and Malaysia (Feeley et al. 2007), while droughts have been linked to leaf shedding and flushing in a tropical forest in Borneo (Ichie et al. 2004). In the same forest in Borneo, Nakagawa et al. (2012) found that general flowering, but not drought,

negatively affected tree growth rates. These results indicate that resources for trunk growth are redistributed to other parts of the tree during different phases of a tree's ontogeny. Other environmental factors may affect tree growth too, such as temperature and solar radiation (Dong et al. 2012).

Growth rates differed significantly among the most common species in both primary and secondary forests. Surprisingly, *Shorea curtisii*, the most common dipterocarp species in Bukit Timah, had the highest growth rates in all size classes. Many dipterocarp species are tolerant of low light levels in the forest understorey, but are capable of growing rapidly in the presence of high light levels (Sasaki and Mori 1981), such as in a forest gap. Gaps were not quantified during the study period, but more gaps were observed during the 2012 survey of the primary forest plot (pers. obs.), and could have contributed to the high growth rates of *S. curtisii*. On the other hand, growth rates were very low for the small trees of secondary forest species. As mentioned in the above paragraphs, since these are light-demanding species, their slow growth may reflect a lack of light in the understorey.

Overall, the fluctuations in tree growth rates within years should have environmental causes, but rainfall does not seem to be the main cause. Besides examining other weather data, monitoring of tree phenology might also help to determine the resource allocation of trees besides trunk growth. Differential species growth rates may lead to shifts in species composition of the forest, but the extent to which short-term growth rates will contribute to long-term forest composition is unknown.

5.5 Tables and figures

Table 5.1. Average number of trees selected in each dbh size class for frequently-measured trees.

	Dbh size class (cm)			
	5.0–9.9	10.0–19.9	20.0–39.9	≥40.0
Primary forest plot	52	59	45	68
Secondary forest plot	59	122	37	32

Table 5.2. Tree measurement dates for frequently-measured trees.

Primary forest plot	Secondary forest plot
May 1993	-
Dec 1995	-
Apr 2003	Jul 2004
Oct 2007	Oct 2007
Jan 2009	Dec 2008
Jul 2009	May 2009
Feb 2010	Dec 2009
Jul 2010	Jun 2010
Jan 2011	Dec 2010
Jul 2011	Jun 2011
Jan 2012	Dec 2011
Jul 2012	Jun 2012
Jan 2013	Dec 2012
Jul 2013	Jun 2013
Feb 2016	Jan 2016

Table 5.3. Mean growth rates (mm/yr) of trees in the primary and secondary forest plots. Errors indicate 95% confidence intervals. Different letters indicate significant differences at α = 0.05 from *t*-tests.

	Dbh size class (cm)			
	5.0–9.9	10.0–19.9	20.0–39.9	≥40.0
Primary forest plot	1.39 ± 0.62[a]	2.97 ± 0.90[a]	3.27 ± 1.24[a]	4.49 ± 1.12[a]
Secondary forest plot	0.50 ± 0.48[b]	1.42 ± 0.40[b]	4.62 ± 1.41[b]	7.08 ± 2.48[b]

Table 5.4. Mean growth rates (mm/yr) of trees that died by 2016 and those that remained alive at 2016. Errors represent 95% confidence intervals. Different letters within the same size class represent significant differences in mean tested by *t*-test.

Size class (cm)	Died by 2016	Alive at 2016
5.0–9.9	0.00 ± 0.43[a]	1.33 ± 0.38[b]
10.0–19.9	1.11 ± 0.92[a]	2.19 ± 0.35[a]
20.0–39.9	-0.13 ± 1.00[a]	4.20 ± 0.90[b]
≥40.0	1.35 ± 1.00[a]	5.28 ± 0.81[b]

Table 5.5. Growth rates of common species in the Bukit Timah primary and secondary forest plots. Data from both the primary and secondary forests were used in growth calculations for each species.

	Primary forest species		Secondary forest species			
Adult stature	Emergent	Canopy	Canopy	Canopy/sub-canopy	Canopy/sub-canopy	Sub-canopy/understorey
Size class (cm)	*Shorea curtisii* (N=36)	*Streblus elongatus* (N=22)	*Campnosperma auriculatum* (N=47)	*Adinandra dumosa* (N=70)	*Rhodamnia cinerea* (N=57)	*Dillenia suffruticosa* (N=32)
5.0-9.9	1.08	1.42	-	0.30	0.33	0.22
10.0-19.9	7.32	0.56	1.31	1.45	1.02	0.58
20.0-39.9	6.50	1.65	4.96	2.78	3.52	-
≥40.0	6.23	1.84	6.02	0.40	-	-

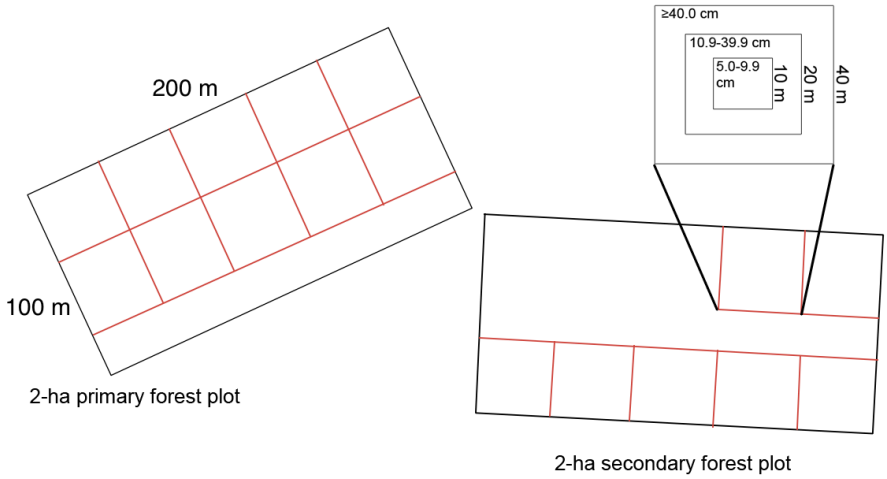

Figure 5.1. Sampling scheme for frequently-measured trees.

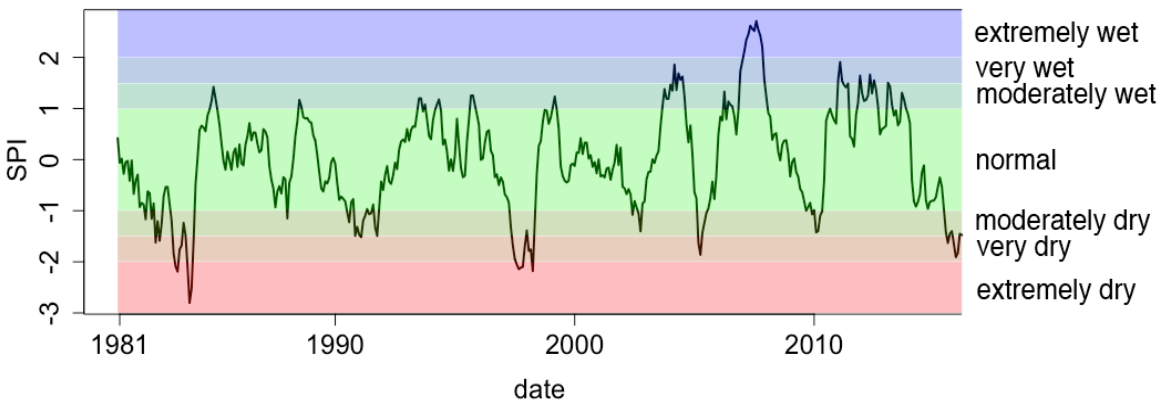

Figure 5.2. The 3-month Standardised Precipitation Index from five weather stations closest to Bukit Timah. The green band in the centre represents the range of 'normal' rainfall, while the blue bands represent excessive rain, and the red bands represent rain shortage.

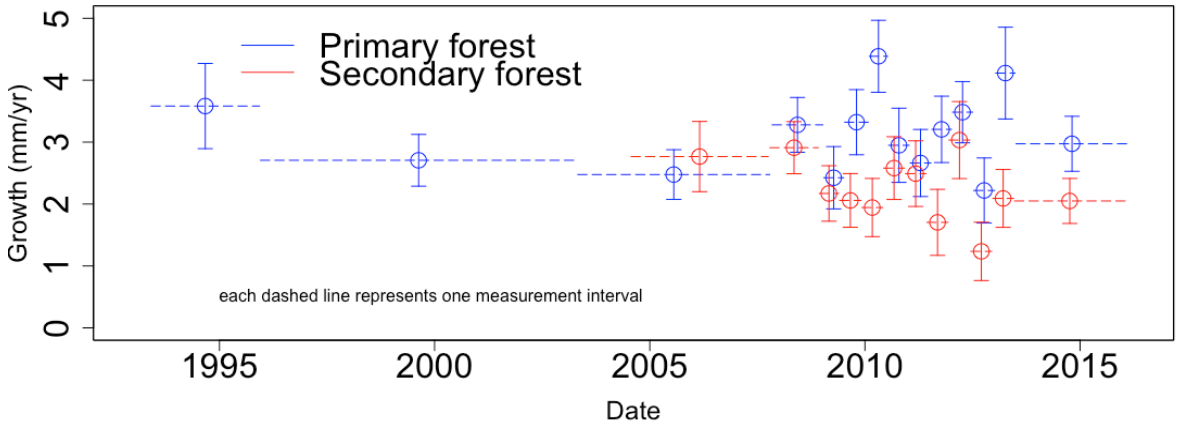

Figure 5.3. Mean growth rates across time for the primary and secondary forest plots. Error bars indicate 95% confidence intervals.

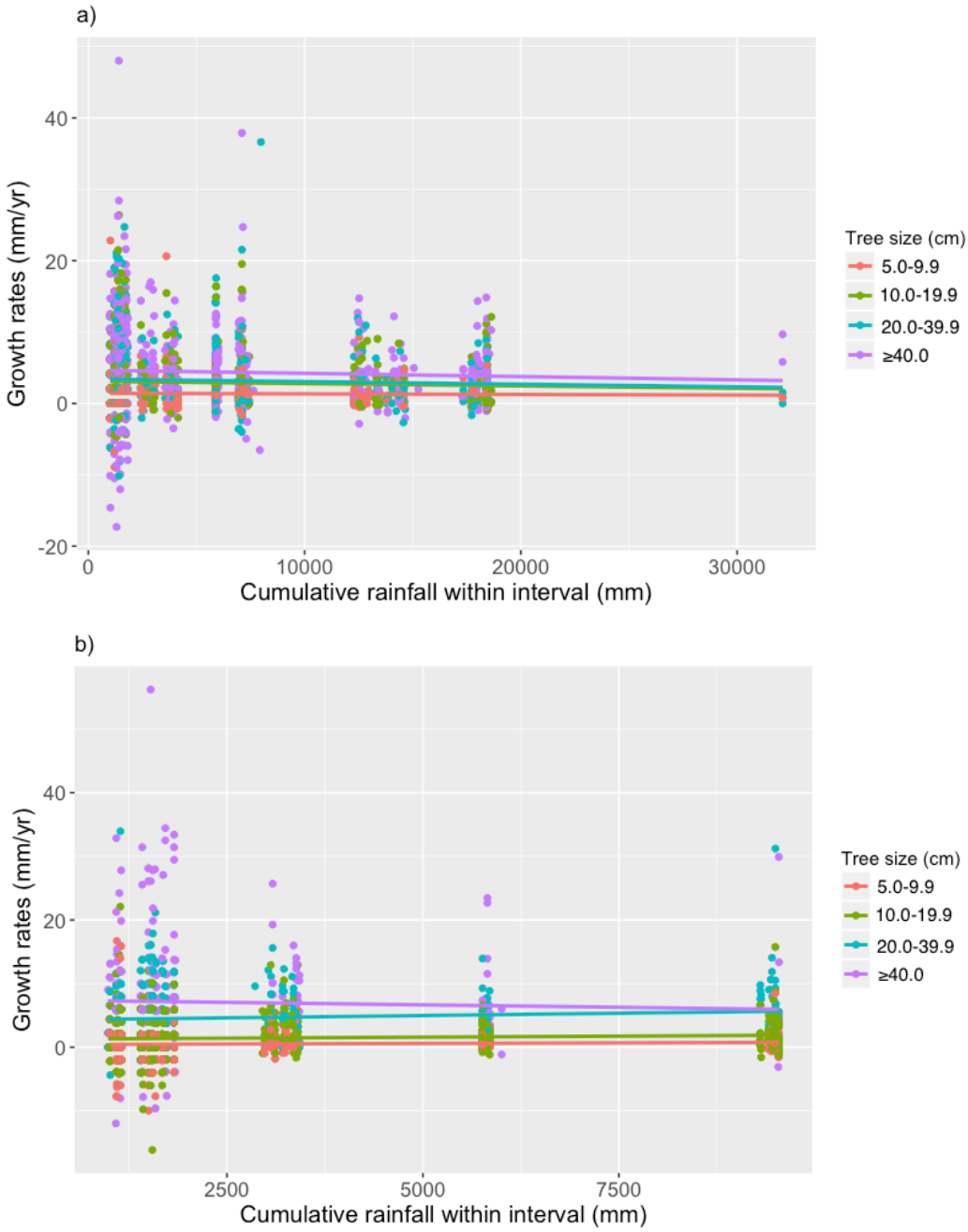

Figure 5.4. Plots of cumulative rainfall within measurement intervals for each tree for the a) primary forest plot and the b) secondary forest plot.

Chapter 6 – General discussion and conclusions

6.1 General summary

Evidence from chapter 3 showed that the primary forest in Bukit Timah was still intact despite its small size, although it was showing signs of responding to the changing climate. Chapter 4 showed that the secondary forest recovered very slowly for the past 60 years, but there were rapid changes occurring in the understory that will likely lead to greater resemblance to primary forest in the near future. Using frequent measurements of selected trees in both primary and secondary forests in Bukit Timah, chapter 5 showed that tree growth rates varied within and between years, and that short-term tree growth was not responding to rainfall. Such long-term monitoring of forest trees coupled with selective short-term measurements are relatively rare in the tropics, but the fact that Bukit Timah is positioned in the centre of a city also makes this a novel case study of the fate and survival of fragmented forest reserves in urban centres.

The resistance of the Bukit Timah primary forest to degradation is a good sign for biodiversity conservation. As shown in many previous surveys of flora and fauna (e.g. Koh and Sodhi 2004; Teo and Rajathurai 1997; Turner 1994), Bukit Timah holds the greatest diversity relative to its size compared to other reserves. The same result is reflected in numerous other studies that compare the species richness of primary and degraded forests in the region (e.g. Gibson et al. 2011) – primary forests generally has higher diversity. However, the Bukit Timah primary forest is not without vulnerabilities – it is subject to influences from a changing climate. For example, tree recruitment rates of saplings decreased by half after a drought. Low recruitment rates may be compounded by the fact that many species in this forest fruit only during general flowering events, a phenomenon that occurs once every 5 years or so in Bukit Timah. A study on four dipterocarp species at the forest reserve to the east of Bukit Timah showed that seeds were subject to high levels

of predation and seed viability was low (Chong et al. 2016). Active intervention like planting may be necessary if and when recruitment rates decrease drastically for prolonged periods, but currently, systematic phenology monitoring at Bukit Timah and other primary forests in Singapore is lacking. Nursery stocks maintained by the National Parks Board (NParks) usually have their origins from Malaysia, Thailand or other countries in the region, but their main purpose is to cultivate fruit trees and shrubs for parks and gardens (NParks 2016b). Previous plantings observed in the primary forest plot had been done in an ad hoc fashion without clear long-term goals. It is hoped that the results obtained here provides additional information to guide future management decisions.

The Bukit Timah secondary forest has come a long way from its open agricultural past to the current forested appearance. Despite its location beside the primary forest without any physical barriers except for a 2 m wide trail, it has not inherited the structure and floristic composition of the primary forest after more than 50 years of natural recovery (Chua et al. 2013). Even though the secondary forest appears very sparse and has a relatively open canopy dominated by only a few species, there are positive changes occurring in the understorey that may not be noticeable at a glance. The recruitment of primary forest and generalist species, their continued growth, the high mortality of secondary forest and dominant species, augur well for the recovery of the secondary forest. It will still take decades before these developments make discernible changes in forest structure, but the results show that forest recovery consists of several steps and phases occurring concurrently, and that big changes in forest structure needs to be preceded by smaller comparatively changes in the understorey.

Research on forest fragments have shifted towards examining the landscape matrix instead of focussing on only the fragments themselves, because the matrix has a large influence on area and isolation effects (Kupfer et al. 2006). In Bukit Timah's case, the urban matrix that surrounds it is

unlikely to change for at least the next several centuries. However, the complete isolation of Bukit Timah ended after 2013 when the Eco-Link@BKE, a bridge connecting Bukit Timah and the Central Nature Reserve, was completed (NParks 2015). Some rare mammals have used the bridge to make crossings to Bukit Timah, such as civet cats and pangolins (NParks 2015) – encouraging signs for the recovery of Bukit Timah fauna. Primary forest species from Bukit Timah may eventually also spread into the Central Nature Reserve, speeding up recovery of the secondary forests there, but this will take much longer than the spread of animals. The fragmented Bukit Timah seems to have survived the worst of direct human disturbances, and the recent addition of the Eco-Link@BKE is an important connection between the oldest forests remaining in Singapore. However, these forests are nevertheless vulnerable to global climate changes, as shown in the chapters above.

6.2 Bukit Timah and nature reserves in Singapore's society

Bukit Timah Nature Reserve continues to be relevant to Singapore as it presses on with developments to its infrastructure, economy, and social fabric. The health benefits that forests in Singapore bring to humans have been recorded since the mid 19th century, from the personal notes of a doctor (Kong and Yeoh 1996). As Singaporeans become more health-conscious, spending time in forest reserves, whether for active exercise or for simple relaxation, is becoming more popular with residents. This is exemplified by a 275% increase in the number of visitors to Bukit Timah from 1990 to 2010 (NParks, Bukit Timah exhibit), even though the population of Singapore increased by 67% in the same period. One of the present global trending health therapies is 'forest bathing', basically a short, leisurely walk through a forest. It involves breathing in phytoncides, volatile organic substances produced by some temperate cypress species (Li et al. 2006; 2009), and such walks have been scientifically proven to be beneficial for health (Park et al. 2010). Although phytoncides have not been tested for in the forests of Singapore, walking through a forest is widely

accepted as a relaxing activity, and is a major nature-based leisure and educational activity in Singapore.

Nature reserves also play an indirect role in the economy of Singapore. While timber harvesting provided income in the early 19th century until the eventual depletion of forests, the remaining forests were deemed too poorly-stocked for further commercial exploitation, and were subsequently used for research, education and recreation (Kong and Yeoh 1996). Nature reserves have been promoted as tourist destinations since the early 1990s for bird-watching and nature walks (Kong and Yeoh 1996). These reserves, together with the pervasive planted greenery, were marketed under the umbrella of a "Garden City" campaign, which later evolved into a "City in a Garden" (NParks 2016a), and this 'green' image was a key magnet for foreign investors and tourists.

Government policies on nature have always taken a utilitarian stance since Singapore's independence. Mr Lee Kuan Yew, the first prime minister of Singapore, sought to transform a third-world slum into a 'garden' city by initiating tree planting campaigns and policies that incorporate greenery into city planning. Paradoxically, this campaign was initiated after large areas of forests were cleared to make way for residential and industrial uses (Yuen 1996). Forests were replaced by buildings, roads and artificial greenery – easily planted and removed as deemed necessary. Nevertheless, the campaigns and greening policies were successful – Singapore became a prosperous city complete with lush greenness that few other tropical cities could boast.

Economic and infrastructure developments often come before environmental protection, sometimes ironically side-stepping the legislations meant to protect nature reserves. Singapore's 1992 National Report to the UN Conference on Environment and Development outlined some principles when dealing with environmental issues (Anon. 1992). The people's economic needs

came first, followed by population control, pollution prevention, environmental impact assessments, environmental education, legislature, enforcement and lastly monitoring and review of the situation (Anon. 1992 pp. 9). It can be understood from this order of priority that if Singapore's economy necessitated the removal of nature reserves, the decision will be justified by its inevitability and lack of other options. However, the report also pointed out that as people became more affluent and attained higher education levels, the demand for a higher quality of life also grew, and having more recreational space was one of the demands (Anon. 1992 pp. 10).

There are two well-publicised examples where the government yielded to the voices of the people in favour of nature (Wee and Hale 2008). In 1991, the Public Utilities Board of Singapore proposed to build a 18-hole golf course in the Lower Peirce Reservoir, but this was met with much opposition from the Nature Society (Singapore) (NSS), a local non-governmental organisation (Hesp 1995; Kong and Yeoh 1996). The NSS performed an Environmental Impact Assessment (EIA) and concluded that many species of plants and animals would be lost, and a nearby freshwater swamp habitat would be damaged if the golf course were built (Wee 1992). The second example is Chek Jawa, a 100-ha piece of wetland on an island, Pulau Ubin, east of the Singapore mainland. The area was designated for reclamation by the government in 2001, but local volunteers discovered its rich biodiversity and petitioned for the preservation of the area (Tan 2001; Wee and Hale 2008). The reclamation plans were eventually shelved, and NParks was tasked with its management.

However, urban development is constantly encroaching on whatever little forest that is left. One of the most heated exchanges in the early 1990s between the government and nature groups was the development of Senoko, a wetland and mangrove at the northern tip of Singapore (Hesp 1995). It was earmarked for industrial and residential development in the 1980s, but the 1990

recession postponed the development. Surveys done by the NSS found 189 species of birds (57% of total number recorded in Singapore), and some of these were endangered species (Wee 2017). Despite intense lobbying and unprecedented public support, the government went ahead with the development (Neo 2007). In a more recent example, the government announced in 2013 plans for building a new subway line (the Cross Island MRT Line, or CRL) that would run underneath a portion of the Central Nature Reserve, east of Bukit Timah (Anon. 2016). Although the CRL runs underground, building the line necessitates works aboveground as well, and several nature groups, including NSS, have voiced concerns about the negative effects on the forest, and even proposed an alternative route for the line that avoids the forest (NSS 2013). Final plans for the line are still unconfirmed, but the alternative route proposed would cost more and may force 216 households to relocate. These alternatives may be a small price to pay when considering that forests need at least a few centuries, a much longer timescale than those considered by land use planners, to recover to their original state. Bukit Timah seems to have been spared these encroachments for the time being, but given that materialistic gains are always given priority in land use planning (Neo 2007), there may well come a day when this reserve containing Singapore's oldest forest is forced to take a place on the balance against development.

To ensure the long-term continuity of Bukit Timah and other nature reserves in their natural state, the general public needs to appreciate them. Studies of nature perception in Singapore found that youth have little interest in and affinity for nature (Kong et al. 1999), and that Singaporeans preferred manicured landscapes, like parks and gardens, over natural landscapes like forests (Khew et al. 2014). Reasons for these attitudes have been attributed to growing up in a highly urban environment where aesthetic landscapes predominate, parents who were over-protective, and the availability of other recreational activities (Khew et al. 2014; Kong et al. 1999). These results point to a lack of exposure to natural landscapes by many Singaporeans, because a minority of the

respondents surveyed in these two studies had some exposure to nature at some point in their lives, such as in kampong settings, living abroad, or taking an ecology or conservation course (Khew et al. 2014; Kong et al. 1999). Numerous other research point to the effect of childhood experiences in influencing adult lifestyle habits and landscape preferences. Children who spent time with nature tended to have positive perceptions of natural environments and outdoor recreational acitivies (Bixler et al. 2002), show a sense of responsibility towards nature (Cheng and Monroe 2012), and pursue jobs and activities related to nature, e.g. conservation, in adulthood (Asah et al. 2012; Tanner 1980). Currently, the science syllabus of Singapore mainsteam education covers some concepts about ecology and biodiversity (MOE 2016), and the concept of environmental conservation is introduced in primary school (MOE 2013), but is non-existent at the pre-university level, where the focus is on technical details of biological processes (MOE 2016). Although NParks introduced school programs to increase biodiversity by creating suitable habitats in schools coupled with biodiversity surveys done by students, the pool of students involved may be limited. To achieve effective biodiversity conservation, education about the irreplaceability of natural habitats need to be inculcated from young through formal education. Quoting Tan (1995), "The fate of nature conservation in Singapore will very much depend upon the political will, which is turn is shaped by the priorities of the people of Singapore" (Nathan 1998).

6.3 Conclusion

The results from all three chapters generally show that the primary forest in Bukit Timah Nature Reserve has retained its integrity despite the small size and exposure to long-term direct anthropogenic disturbances, and will continue to survive into the near future. The primary forest will likely expand into current secondary forest areas if continued undisturbed, but complete recovery of secondary forest will likely take centuries. Following observations of tropical forests from other countries and regions, the Bukit Timah forest is vulnerable to short-term weather

abnormalities, such as drought. Other environmental factors besides rainfall influence tree growth in Bukit Timah as well, but more data from weather stations or satellites are needed to pinpoint them. Spatial expansion of Bukit Timah is unlikely, because the urban matrix around Bukit Timah will remain urban in the near future. The latest boost to ameliorate the fragmented state of Bukit Timah is the Eco-Link@BKE, a bridge that allows plants and animals to travel between Bukit Timah and the Central Nature Reserve. Continued monitoring of the forests, with increased efforts in vegetation phenology monitoring at Bukit Timah, will provide a better understanding of reproductive patterns of trees, which is crucial for the long-term sustainability of tree populations in Bukit Timah.

Bukit Timah is an important biodiversity haven in Singapore. However, being a land-scarce country, this forest reserve is obliged to fulfill other roles. Bukit Timah serves as a popular weekend destination for increasing numbers of residents, a nature-education destination for students, and a nature-based tourist attraction. While public visitation is an important step in biodiversity conservation, trail wear and noise levels need to be managed to reduce human impacts on the forest. Finally, surveys about public perceptions towards nature among residents show although they know the importance of biodiversity conservation, knowledge about the biodiversity itself is low, and landscape preferences are skewed towards manicured parks, which harbor much lower levels of biodiversity compared to nature reserves. A greater emphasis on ecology and evolution topics in the mainstream school syllabus would create better understanding of Singapore's own biodiversity and natural heritage among students, which would in turn encourage pro-conservation thoughts and actions. If the technical and scientific tools for propagating native forest trees are in place, as well as society's awareness of Singapore's rich biodiversity, Bukit Timah and other nature reserves can be 'sustained' for a long time to come.

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