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Resilience of a forest fragment exposed to long-term isolation in Singapore

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Background: Fragmentation can fundamentally alter the structure of tropical forests. However, the impacts of fragmentation may vary significantly among regions and lead to different outcomes.

Aims: We examined the structure, composition and dynamics of a forest fragment in Singapore to investigate reasons for the apparent resilience of this forest to long-term isolation.

Methods: We conducted 5 censuses of 12,688 trees ≥ 1 -cm dbh in a 2-ha plot on the edge of the fragment between 1993 and 2012.

Results: Stem density and basal area were not significantly different between 1993 and 2012 and were typical of other south-east Asian forests. However, there were short-term decreases in both variables after droughts in 1997 and 2009, both followed by recovery. Total mortality rate over the 19 years was $3.3\% \text{ year}^{-1}$, considerably higher than other tropical forests in Asia, but it was balanced by high recruitment. The 10 most abundant species were primary forest species, pioneer species comprised $<5\%$ of all stems, and none of the 338 species in the plot was exotic. However, species abundances changed more than expected by chance for 86 species, and the rank order of the commonest species changed significantly. Species abundance changes were not related to known species traits.

Conclusions: Despite the long period of isolation, we found a surprising level of resilience of the Bukit Timah forest. While the forest may be more sensitive to the effects of climatic fluctuations at decadal time scales, there were very few signs of forest degradation in this diverse fragment of tropical forest.

Keywords: Bukit Timah Nature Reserve; forest dynamics; forest fragmentation; growth rates; south-east Asia; species composition; tropical forest; turnover

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] Food and Agriculture Organization 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; Castelletta 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 characterise most forest fragments (Tabarelli et al. 2008). Experimental fragments created in the Amazon

showed that fragments experience higher turnover rates than continuous forests, that is, fragments are “hyper-dynamic” (Laurance et al. 1998, 2002, 2006a, 2016; Mesquita et al. 1999). Large trees in fragments have also been reported to have higher mortality rates (Laurance et al. 2000; Arroyo-Rodríguez 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 7 years. In Peninsular Malaysia, fragments were found to be structurally similar to primary forest and had few pioneer species (Thomas 2004).

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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 SEA 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 (LaFrankie et al. 2005; Corlett 2013). 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 (hereafter Bukit Timah), 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, for example, 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.

We investigated the impacts of forest fragmentation on the stand dynamics of a permanent forest plot in Bukit Timah from five censuses, spanning 19 years. We compared our findings with the structure and dynamics of similar lowland primary forests elsewhere in SEA. Based on findings from other forest fragmentation studies (e.g. Laurance et al. 2006a, 2006b), we hypothesised 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.

Materials and methods

Study site

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, unpublished 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 a seasonal, 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 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.

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

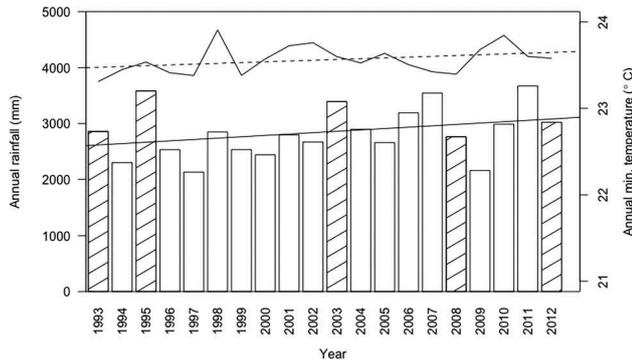


Figure 1. Annual rainfall (bars) and mean minimum annual temperature from a weather station 8.5 km northwest of Bukit Timah, Singapore. Hatched bars represent census years. Solid and dashed straight lines represent the linear fits of annual rainfall and annual minimum temperature, respectively. There were significant increases in both mean annual rainfall (ADF test statistic = -3.51 ; $P \geq 0.059$; 1980–2012) and mean minimum annual temperature (ADF test statistic = -2.72 ; $P \geq 0.297$; 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.

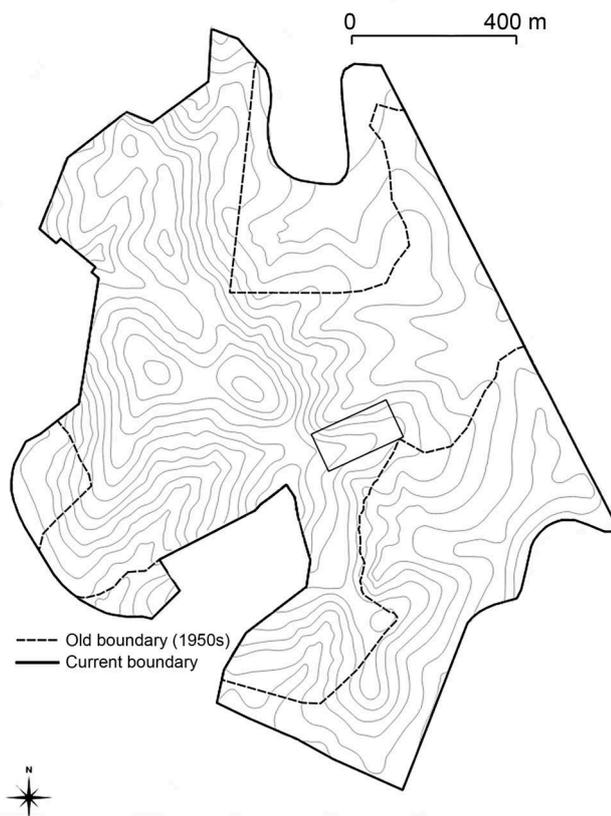


Figure 2. Map of Bukit Timah Nature Reserve (164 ha), Singapore showing the position of the 2-ha plot within the Reserve.

unlogged primary forest (Figure 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.

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) was classified into 3 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. We tested for differences in species abundance changes 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 $\lambda_{\text{corr}} = \lambda \times t^{0.08}$, 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, we calculated 99.9% confidence intervals (CIs) for mortality and recruitment rates from 1000 bootstraps of 50 $20 \text{ m} \times 20 \text{ m}$ 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 $20 \text{ m} \times 20 \text{ m}$ squares as sampling units.

To test whether abundances of individual species were increasing or decreasing more than expected given the plot-wide changes, we used the method developed in Chisholm et al. (2014). 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 vs. initial abundance, we identified both

species that increased and decreased more than expected given the overall plot-wide changes in abundance.

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

Results

Stand structure and dynamics

In 1993, stem density was 6344 ha⁻¹ and basal area was 36.5 m² ha⁻¹ in the 2-ha plot at Bukit Timah (Table 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 1). Subsequent recruitment into the ≥ 2.0 -cm size classes caused stem abundances of these size classes to increase.

Floristic composition and dynamics

A total of 338 species were recorded in the plot in 1993 (Table 1). The 10 most abundant species were all primary

forest species – 2 emergent, 6 canopy and 2 understorey species (Table 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 1), and none of the pioneer species was 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 4 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 understorey 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 (1993–2012) between the three adult stature classes ($F_{(2,155)} = 0.97$, $P = 0.38$; 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); 58 species increased and 28 species decreased more than expected. Of the 10 most abundant species, 4 had significant decreases in abundance over the 19 years, 3 increased significantly, and the abundance of 3 species did not differ from neutral expectations (Table 2). *Streblus elongatus* (Moraceae) and *S. curtisii* (Dipterocarpaceae) had 39% and 20% increases in abundance, respectively, with *Streblus* becoming the most

Table 1. Summary of stand dynamics of the 2-ha primary forest plot in the Bukit Timah forest reserve in central Singapore.

	1993	1995	2003	2008	2012
No. of 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. of 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 (m² 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

Figures in parentheses represent 95% confidence intervals calculated from 1000 bootstrap samples over 20 m × 20 m 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.

Table 2. Abundance changes of the 10 most common species in a 2-ha permanent plot in primary forest Bukit Timah, Singapore.

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

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.

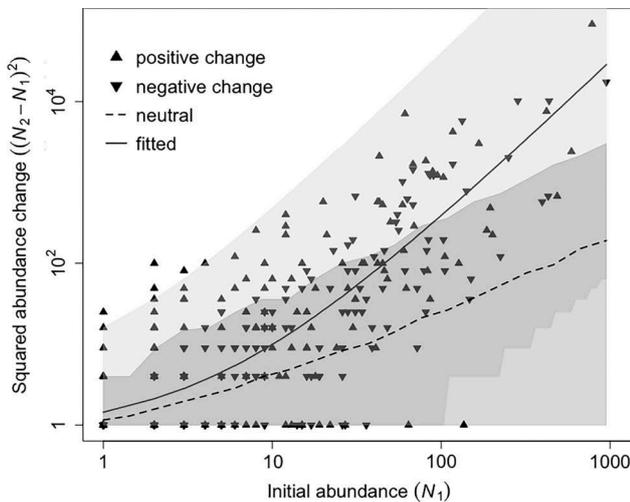


Figure 3. Squared abundance changes in a 2-ha permanent plot in primary forest, Bukit Timah, Singapore over 19 years plotted against initial abundance. Each point represents one species. The dashed line with shaded dark grey 95% confidence interval shows the neutral model prediction. The black curve with shaded light grey 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).

abundant species in the plot in 2012. In contrast, *Santiria apiculata* (Burseraeaceae), *Gluta wallichii* (Anacardiaceae) and *Gynotroches axillaris* (Rhizophoraceae) had declines in abundance of 14%, 23%, and 34%, respectively.

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 rate when trees were split into size classes, the mortality rate of large trees tended to mirror the drought intervals (Table 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). Recruitment rates were significantly lower in the two census intervals that experienced drought.

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 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 was 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 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 were 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 $\geq 88\%$ 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

Table 3. Annual mortality and recruitment rates during census intervals in a 2-ha permanent plot in primary forest, Bukit Timah, Singapore.

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

Values in parentheses indicate 99.9% confidence intervals from 1000 bootstrap samples of 20 × 20 m squares. Figures with the same superscript letters have overlapping confidence intervals. Drought-affected intervals are highlighted.

Table 4. Comparison of basal area recorded at Bukit Timah with that reported from other tropical south-east Asian forest sites.

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

Figures are averages of multiple surveys or plots if available.

Table 5. Comparison of mortality rates from Bukit Timah with that reported from other tropical south-east and south Asian forest sites.

Site	Years	Duration (years)	Annual mortality (%)	Reference
Bukit Timah	1993–1995	2	2.9	This study
Singapore	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)
Sungei Menyala, Malaysia	1971–1984	13	2.1*	Manokaran and Swaine (1994)
	1947–1985	38	2.0*	Manokaran and Swaine (1994)
Bukit Lagong, Malaysia	1949–1985	36	1.4*	Manokaran and 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)

Only papers using the same calculation methods were included. *Trees ≥10-cm dbh.

predominantly pioneer genus, *Macaranga*, had not only 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 dispersed 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). We did not find such trends 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 per cent (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 understorey 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). We did not find these patterns 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 – 4 had decreases and 3 had increases. Six of these seven species were canopy and emergent species, while one was an understorey species. Of the declining species, only *G. axillaris* had very low recruitment (0.6%) over the

19 years. The other declining species, *S. apiculata*, *G. wallichii* and *Calophyllum ferrugineum*, had average to higher-than-average recruitment rates but mortality always exceeded recruitment. The most abundant species in 2012, *S. 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 (fourth 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 SEA (Table 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 CO₂ (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). We found 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.

Conclusions

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 was 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.

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