Drivers of floristic composition in Bukit Timah Nature Reserve: An investigation of leaf functional traits

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Abstract

Forest fragmentation and associated edge effects can lead to considerable ecosystem degradation resulting in high mortality and loss of biodiversity. Bukit Timah Nature Reserve is a forest fragment that has been closely monitored for nearly 20 years. Though fragmentation is typically associated with negative consequences, Bukit Timah showed unexpected resilience to fragmentation effects. Interestingly, alterations in community structure were observed, though significant changes in stem density and basal area did not occur. The aim of this study was to explore the drivers of said compositional change, through examining four species of tropical rainforest trees. Two of these species are currently increasing in abundance (*Shorea curtisii* and *Streblus elongatus*) and two are decreasing in abundance (*Gynotroches axillaris* and *Santiria apiculata*). The study examined leaf mass per area, chlorophyll content, leaf thickness, and stomatal density. The results showed significant differences between species in trait values for all four functional traits, but no overarching trends to explain alteration in species composition were found. The results indicate that the four functional traits assessed are not critical in shaping community composition. Potential other drivers are explored, such as correlation with water transport systems. This is timely and important research in the face of dwindling primary forest in South-East Asia, and represents a global shift in priorities towards protecting ecological biodiversity.

Key Words: Community structure, forest fragmentation, plant performance

Introduction

Tropical primary rainforests are a major global ecological resource. Loss of tropical rainforests due to deforestation is a major threat to climate systems and the biodiversity of the planet (Schwartzman *et al.* 2000). Despite tropical rainforest conservation efforts, over 97 million hectares of tropical and subtropical forest has been lost between 2000 and 2012 (Chow 2015). Selective clearing of forest patches for timber and agricultural plantations can lead to fragmentation of forest stands, resulting in substantial changes to the structure and function of forest fragments. Fragmentation of forest often leads to negative consequences for the stands due to edge effects (Tabarelli *et al.* 2008). Increased light levels and disturbance along the forest perimeter often result in the decline of shade tolerant species, and pioneer species are more likely to thrive (Laurance *et al.* 2000). Decline in species richness, vulnerability to invasion by exotic species, high population turnover, and greater mortality of large trees have also been observed.

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Ngo *et al.* (2016) recently reported on long-term changes in structure and composition of an isolated primary forest fragment in Bukit Timah Nature Reserve in Singapore (hereafter Bukit Timah); surrounded by a secondary forest plot, the reserve has remained undisturbed for 60 years (Swan 1988). The results from five censuses of plants ≥1 cm diameter at breast height (dbh) over a 19-year study period showed that Bukit Timah was surprisingly resilient to the effects of forest fragmentation. The forest did not exhibit significant changes in stem density and basal area over the study period, though alterations in floristic composition were noted.

In total, 58 species increased in abundance, and 28 species were noted to have decreased in abundance. Specifically, species such as *Streblus elongatus* (Miq.) and *Shorea curtisii* (Dyer ex King) showed the greatest increase in abundance, with numbers enlarging by 39 per cent and 20 per cent respectively. In contrast, *Santiria apiculata* (Benn.) and *Gynotroches axillaris* (Blume) decreased in abundance by 14 per cent and 34 per cent respectively. Although changes in floristic composition were observed, the specific drivers behind the alterations were not identified. Thus a question remains regarding what factors are driving the changes in community structure in Bukit Timah.

Understanding the processes that govern community structure has been a major objective in community ecology (McGill *et al.* 2006). One approach to solving this problem has been through the investigation of plant functional traits. Though environmental conditions such as climate and disturbance regime can act as filters to define fundamental niches, plant functional traits determine ecological roles within communities (McGill *et al.* 2006). When significant changes in community composition occur following disturbance events, trait differences between species may be driving the reshaping of community structure (Mouillot *et al.* 2013). This indicates that as changes in abiotic environmental factors occur over time, how well adapted a plant's functional traits are to those specific environmental conditions will substantially affect the distribution and abundance of those species (Cadotte *et al.* 2015). Leaf functional traits are particularly reliable predictors of plant performance in rainforest ecosystems due to the variation in carbon and nutrient investment strategies between species (Poorter and Bongers 2006). Leaf investment according to the leaf economic spectrum (LES) correlates with leaf life span and leaf dry mass per area (LMA), and directly affects the productivity of plant species (Read and Stokes 2006; Wright *et al.* 2004). Though there is a continuum, at the extremes, plants with a rapid-growth strategy tend to produce short-lived leaves with low LMA, while plants with a long-term persistence strategy produce long-lived leaves with higher LMA. Plant species with a persistence strategy typically have a higher survival rate, likely to lead to greater abundance in the long-term (Read and Stokes 2006). In a similar vein, leaf thickness is correlated with leaf toughness, which enables leaves to better withstand physical damage and herbivory (Read and Stokes 2006). Initial investment tends to be high, but superior return on investment is expected with thicker leaves. Tough and thick leaves also offer superior protection from solar radiation and may contribute to greater rates of carbon gain (Read and Stokes 2006). Again, plants with this strategy have higher survival rates and are expected to increase in abundance in the long-term.

Leaf chlorophyll content is also a critical functional trait that impacts ecosystem functioning. As chlorophyll drives the conversion of light energy into chemical energy, leaf chlorophyll content is likely to impact photosynthetic capacity within plants (Li *et al.* 2018). Leaf chlorophyll content is also positively correlated to gross primary productivity, indicating that higher chlorophyll concentrations lead to greater conversion of light energy into biomass (Li *et al.* 2018). With greater productivity, we can expect plant species with high chlorophyll content to increase in abundance.

Plant evapotranspiration also has a strong impact on water and carbon cycles of forest ecosystems. Specifically, leaf stomata regulate the exchange of carbon and water vapour between plant and atmosphere (Wang *et al.* 2015). Stomatal traits, such as stomatal density, therefore directly affect the water use efficiency and rates of gas exchange in plants (Liu *et al.* 2017). Stomatal density in conjunction with stomatal length is closely correlated to net primary productivity in forest ecosystems (Wang *et al.* 2015). Smaller and denser stomata are linked to higher rates of gas exchange, leading to greater levels of productivity. With greater stomatal density linked to productivity, we can expect plant species with dense stomata to increase in abundance.

The aim of this study was to investigate the potential drivers of changes in community composition in Bukit Timah Nature Reserve. In the context of changing climatic conditions and their likely impact on plant communities, identification of the drivers of community composition has major implications for conservation efforts. Therefore, we explored four leaf functional traits to see whether differences in leaf functional traits were contributing to the increase or decrease in abundance of four key species. We hypothesised that the species increasing in abundance (i.e. *S. elongatus* and *S. curtisii*) would be the species that prioritise a longer-lived strategy, as this would allow them to persist for longer and therefore have a greater chance of procreation and colonisation of the forest fragment. Species that have a rapid-growth and thus short-lived strategy would be hypothesised to decrease in abundance (i.e. *S. apiculata* and *G. axillaris*). Therefore, in line with this theory, species increasing in abundance would have higher levels of LMA, greater leaf thickness, higher chlorophyll content and greater stomatal density. However, it is expected that, as some of these traits exist in a continuum, if a plant does not balance these traits effectively and invests too liberally in the LES, it could negatively affect abundance.

Methods

Study site and species

The study was conducted in the Bukit Timah Nature Reserve located in central Singapore (1.3541°N, 103.7769°E). The reserve covers an area of 164 hectares, with 71 hectares of primary forest consisting predominantly of coastal dipterocarp species (Weerakoon *et al.* 2015). The region has an aseasonal, tropical climate with a mean annual temperature of 26°C (Corlett 1988). Mean annual rainfall is approximately 2,600 mm, with rainfall occurring evenly throughout the year (Corlett 1988).

The four species that were sampled were *Streblus elongatus* (family Moraceae), *Shorea curtisii* (family Dipterocarpaceae), *Santiria apiculata* (family Burseraceae) and *Gynotroches axillaris* (family Rhizophoraceae). These species were selected because prior census data of Bukit Timah indicated that *S. elongatus* and *S. curtisii* were increasing in abundance and *S. apiculata* and *G. axillaris* were decreasing in abundance (Ngo *et al.* 2016).

Sample collection

Sample collection was done in one day in the first week of July 2018. The sample collection team walked along the pre-existing hiking paths of Bukit Timah primary forest and collected samples when the target species was identified through visual observation. No transects or quadrats were produced. Three leaves were collected per tree from 5 trees for each of the species, resulting in a total sample size of 60 leaves. Trees were chosen by proximity to Path 1 (see Figure 1), 130–160 m above sea level. Tree age was standardised for by selecting saplings 1.5–3 m in height. Leaf age was standardised by selecting fully expanded leaves near the branch end without epiphylls. Sampled leaves were immediately transferred to plastic bags and kept humidified until they were characterised for the four functional traits in the nearby laboratory at Nanyang Technological University.

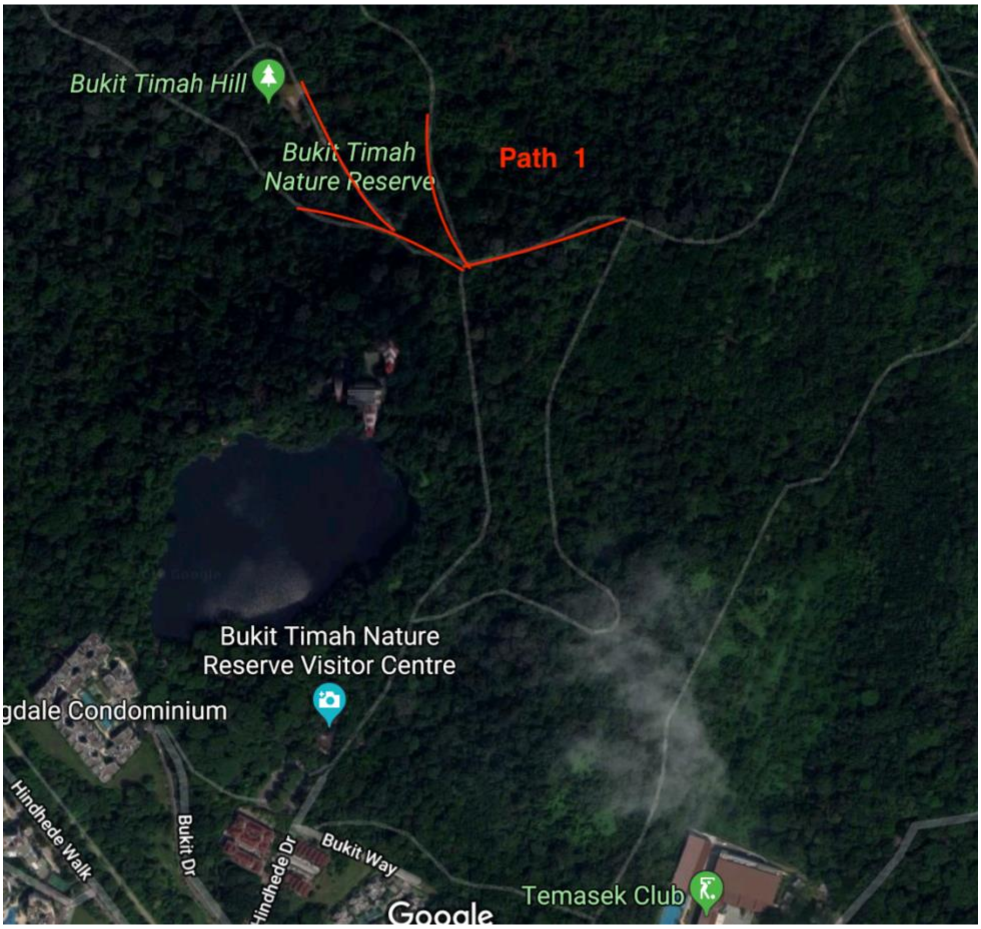

Figure 1: An overhead view of the Bukit Timah Nature Reserve showing the outline of Path 1. Source: Taken from Google Maps.

Chlorophyll content and leaf thickness

SPAD (Soil plant analysis development) measurements were taken using a SPAD chlorophyll meter (Konica Minolta Inc.). Three SPAD measurements were taken per leaf as proxies for chlorophyll content. Leaf thickness was measured using a micrometer caliper. Three measurements were taken per leaf, standardising the location near the midrib. As an exception, as *S. apiculata* produce compound leaves, measurements were standardised by taking measurements from the first left leaflet.

Stomatal density

Stomatal density was measured using the adhesive method. A small amount of glue was applied to the abaxial surface of each leaf, then a glass slide was attached and held to the tacky glue. After a period of 1–3 minutes, when the glue had dried slightly to a consistency where the leaf surface tissue could be removed without damaging the leaf, a leaf peel was performed, which created a relief in glue on the slide. The resulting slide with stomatal tissue imprint was then examined under a light microscope at 400× magnification. Photographs of the tissue were taken using a hand-held phone camera (Apple Inc., USA). The number of stomata in the resulting photographs was counted. The specific area of the tissue was not directly measured but ocular area was standardized due to equal magnification. As such, for the purposes of this study, we used this stomatal count as a proxy for stomatal density.

Leaf mass per area (LMA)

To determine LMA, leaf dimensions were obtained by flattening and photographing each of the leaves adjacent to a ruler. The resulting images were analysed through image processing software – ImageJ (National Institute of Health, Maryland, USA) – to determine leaf area. Leaf mass was measured by drying the leaf samples in a microwave. Each leaf was inserted between a makeshift booklet constructed from cardboard and paper towels. The contraption was microwaved at 1,000 W for 30-second bursts until dry. The number of cycles varied from between two to six cycles, depending on the species and leaf size. The resulting leaf mass was then divided by leaf area to obtain leaf mass per area for each leaf.

Statistical analysis

All resulting data was collated in a Microsoft Excel spreadsheet. Statistical analysis was done using R statistical software. Analyses of variance (ANOVA) followed by post-hoc Tukey-Kramer tests were done to test for differences between species in mean chlorophyll content, leaf thickness, leaf mass per area, and stomatal density. These means were represented using histograms made using Microsoft Excel. This analysis also gave *p*-values for each test as a measure of significance of difference, and was represented by differing letters on the histograms. Linear regression analyses were also performed between each of the four leaf functional traits to determine whether there were correlations between traits.

Results

Statistically significant differences in trait values were seen between species for each of the functional traits investigated. However, no overarching patterns were seen in trait values to explain the changes in floristic composition.

Leaf mass per area (LMA) showed significant differences between species (Figure 2a). Mean LMA was highest in *S. curtisii* (79.2 ± 4.6 g m^{-2}), and *S. elongatus* (52.8 ± 2.4 g m^{-2}) was lowest. *S. apiculata* (66.9 ± 6.4 g m^{-2}) and *G. axillaris* (63.2 ± 1.8 g m^{-2}) had intermediate values. Significant differences in LMA were seen between *S. curtisii* and *S. elongates* ($p < 0.001$) and between *S. curtisii* and *G. axillaris* ($p = 0.045$).

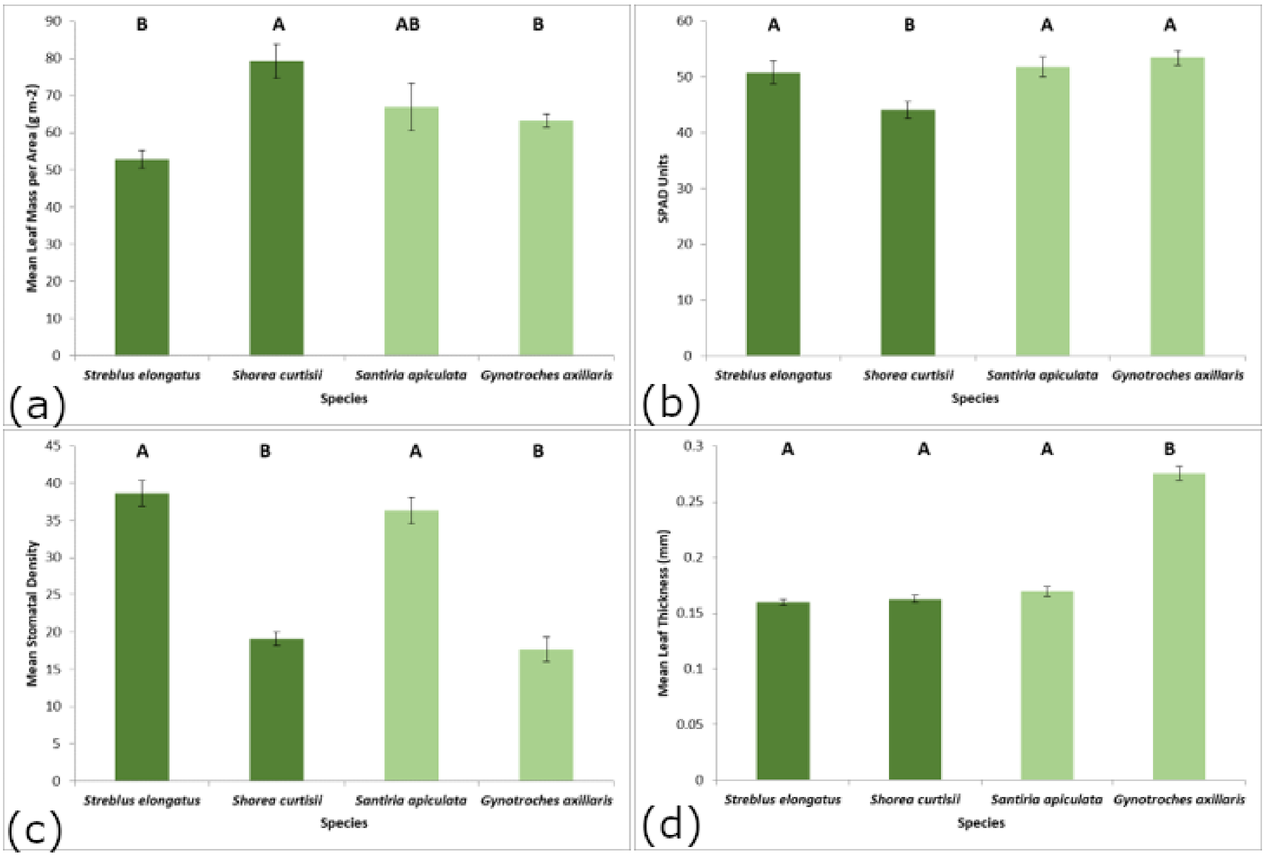

Figure 2: Leaf functional traits of four species present in Bukit Timah Nature Reserve. a) Mean leaf mass per area ($g\ m^{-2}$), b) SPAD units, c) stomatal density, and d) leaf thickness. Error bars represent standard error. Species are arranged left to right by percentage change in abundance, from greatest increase to greatest decrease, where dark green is an increasing and light green a decreasing species. A, AB, B above bars indicate statistically significant differences at $p < 0.05$ according to Tukey-Kramer tests.

S. curtisii had significantly lower chlorophyll content than *S. elongatus* ($p = 0.027$), *S. apiculata* ($p = 0.008$), and *G. axillaris* ($p < 0.001$) (Figure 2b). Chlorophyll content was lower in *S. curtisii* (44.1 ± 1.4 SPAD units), while *S. elongatus* (50.8 ± 2.0 SPAD units), *S. apiculata* (51.8 ± 1.7 SPAD units), and *G. axillaris* (53.4 ± 1.3 SPAD units) had similar values.

Significant differences in stomatal density were seen between *S. elongatus* and *S. curtisii* ($\mathrm{p} < 0.001$), *S. elongatus* and *G. axillaris* ($p < 0.001$), *S. apiculata* and *S. curtisii* ($p < 0.001$), and *S. apiculata* and *G. axillaris* ($p < 0.001$) (Figure 2c). *S. elongatus* (38.6 ± 1.7 stomata per ocular area) and *S. apiculata* (36.3 ± 1.8 stomata per ocular area) had relatively high stomatal density compared to *S. curtisii* (19.1 ± 0.9 stomata per ocular area) and *G. axillaris* (17.7 ± 1.6 stomata per ocular area).

Leaf thickness was significantly higher in *G. axillaris* (0.275 ± 0.005 mm), than in *S. curtisii* (0.163 ± 0.003 mm), *S. elongatus* (0.160 ± 0.003 mm), or *S. apiculata* (0.169 ± 0.004 mm), which had similar values ($p < 0.001$, Figure 2d).

Linear regressions analysis among the four functional traits were fit for each species and resulted in only one significant correlation. Stomatal density and leaf thickness have a negative correlation ($R^2 = 74\%$) that is significant ($p < 0.0005$), and held true for all four selected species (Figure 3).

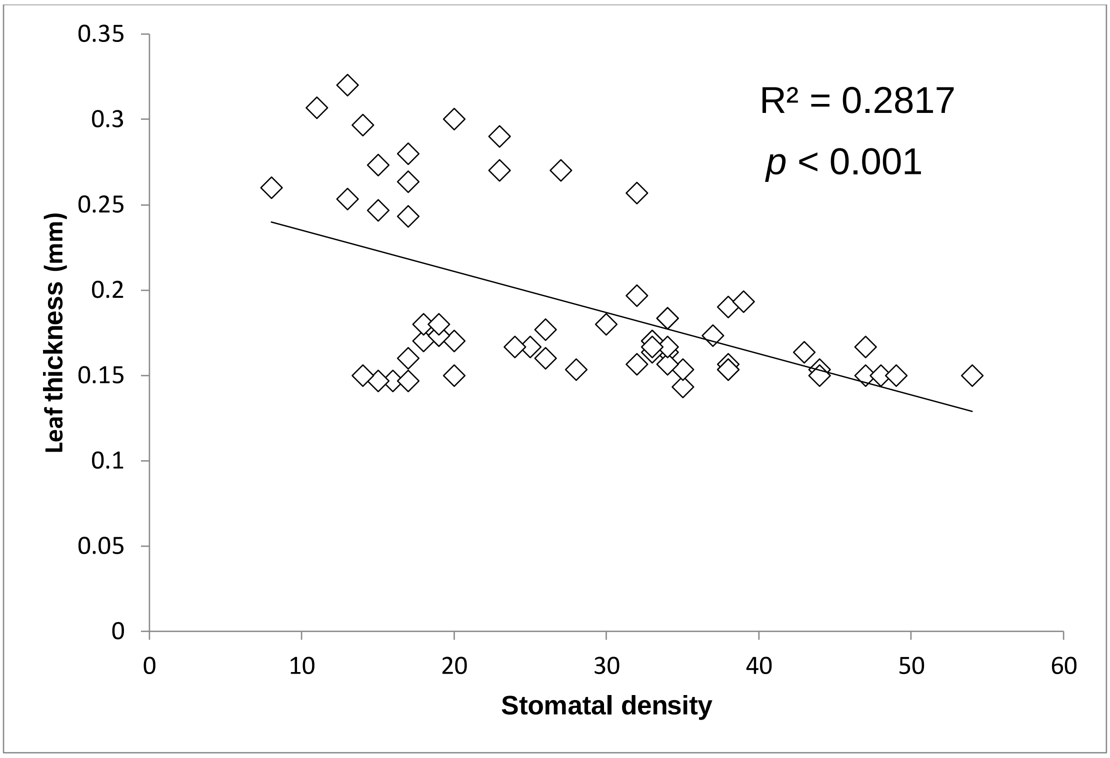

Figure 3: Stomatal density – leaf thickness reveals a negative correlation between the two components ($R^2 = 0.28173$, $p < 0.001$).

Discussion

The results show significant variability in leaf functional trait values between species, but did not support our hypotheses regarding drivers of compositional change in Bukit Timah. In terms of leaf mass per area, the two species increasing in abundance had the highest and lowest LMA, while the two decreasing species had intermediate values (Figure 2a). In chlorophyll content, the increasing *Shorea curtisii* had lower chlorophyll content compared to the other three species (Figure 2b). *Streblus elongatus* and *Santiria apiculata* both had significantly higher stomatal density compared to *S. curtisii* and *G. axillaris* (Figure 2c). Mean leaf thickness was low for all species except for *G. axillaris*. A negative correlation between stomatal density and leaf thickness was also observed for all 4 species, but it is unclear whether this correlation is of consequence for community composition (Figure 3). No trait exists in a vacuum. Correlations may exist between these traits and potentially others that we did not sample in this study. We believe that our assessment that slower-growth strategies that enable a plant to live a longer life has some merit, as there is precedence in literature that this economic strategy allows plants to procreate for longer (in arid environments (Carvajal 2018). We expected a positive correlation between abundance and LMA, leaf thickness, chlorophyll content and stomatal density, as this could indicate a more conservative investment in the LES and therefore a longer-lived strategy. However, we did not find any overarching pattern in the leaf functional trait variability that explained the increase or decrease in abundance of the species investigated. It may be that there are additional pressures on plant abundance that we were not aware of. Additionally, the Bukit Timah primary rainforest exists as an island in an ocean of secondary forest. This secondary forest likely influences the existing primary rainforest in unknown ways. This would be an area of interest for future studies, as the interactions between primary and secondary forests is poorly understood.

It is also possible that the lack of definitive results is due to the limitations of the study. The four study species were chosen for exhibiting the greatest changes in abundance over long-term monitoring (Ngo *et al.* 2016), but the plant community in Bukit Timah consists of many more species. The four functional traits investigated were also selected according to the equipment available. Differences in LMA, chlorophyll content, leaf thickness and stomatal density in the study species are not critical drivers of community composition in Bukit Timah. Though leaf functional traits can be good predictors of plant performance under certain conditions, it is becoming increasingly clear that short-term measurements of functional traits at the leaf level are not necessarily effective for predicting long-term changes at the community level (Diaz and Cabido 1997). However, the lack of conclusive results is not necessarily a drawback. This study was a preliminary study to assess a limited number of species and functional traits that could be investigated with the equipment and time available. The study by no means encompasses all the functional traits or species that could be studied. With the results indicating that the above functional traits examined do not explain changes in abundance, investigation of other traits on a wider range of species could shed light on the drivers of community composition in Bukit Timah.

Bukit Timah did not exhibit significant changes in stem density and basal area over the 19-year study period, but higher mortality, lower stem density and lower recruitment rates were observed in censuses following droughts in 1997 and 2009 (Ngo *et al.* 2016). Though recovery from the drought events was rapid, water stress appears to have a substantial effect on the plant communities in Bukit Timah. Drought stress severely affects plant productivity, as mechanisms to curb water loss effectively suppress carbon exchange from the atmosphere (Farooq *et al.* 2009). Prolonged stomatal closure can lead to carbon starvation and, in extreme cases, to mortality. Hydraulic failure can also occur due to embolism within the hydraulic architecture of plants (Choat *et al.* 2007). When an air bubble forms due to cavitation within xylem vessels, water transport is severely restricted and potentially leads to desiccation and mortality. With drought stress appearing to substantially affect community structure in Bukit Timah, assessment of functional traits related to water transport may be of particular interest. Several functional traits are related to water transport. For example, wood density is a major trait that controls for the susceptibility to embolism (Mouillot *et al.* 2013). Plants with higher wood density have stronger fibres associated with xylem vessels, thereby being more effective at inhibiting cavitation (Apgaua *et al.* 2015). Vessel lumen area and vessel density are also traits that affect water conductance. Larger vessel lumen area equates to greater water transport capacity, but also increases susceptibility to embolism (Choat *et al.* 2007). Greater vessel density combined with smaller vessel lumen area reduces the potential for cavitation due to the multiple conduits water can pass through, but results in lower conductance for each vessel. With an obvious trade-off between the two traits, different plants have evolved different strategies to manage water deficit (Apgaua *et al.* 2015). Additionally, stomatal density and their subsequent water use is subject to complex interactions in the humid environment of the tropical rainforest understory. This complexity is reflected in literature, with some arguing that greater stomatal density is correlated with better stomatal conductance and therefore a higher photosynthetic rate (Kusumi *et al.* 2012); and some believing that a great stomatal density would induce extensive water loss rates and thus impede the plants functioning (Lawson and Blatt 2014). It is likely that there is a limit for the density of stomata that a plant will have, as their density influences the photosynthetic rate, until a point where water loss is greater than the photosynthetic rate gained. Competitive plants could potentially be able to balance this compromise more effectively.

Water availability has a strong effect on the development of hydraulic architecture, with species growing in differing environments exhibiting pronounced differences in xylem anatomy (Choat *et al.* 2007). Species growing in drier habitats tend to have greater resistance to embolism and cavitation compared to species growing in wetter areas. Hence species habitat preference may be a good indicator of susceptibility to drought. For example, *Shorea curtisii* tends to dominate ridges and upper slopes of hill dipterocarp forests in the Malay Peninsula (Kondo *et al.* 2016). This implies that *S. curtisii* is probably drought tolerant to some extent, as soil water movement tends to be enhanced in areas of steep topography resulting in drier soils (Mori *et al.* 2013). Similarly, *Streblus elongatus* commonly has a scattered distribution among lowland forests and dry woods (Keng 1990; Prawirohatmodjo *et al.* 1998). In addition, anecdotal observations indicate that this species has some level of drought tolerance, as it is also found in secondary forests and coastal hills, which are subjected to drying winds from offshore (Shawn Lum, personal observations). *Santiria apiculata* is also commonly found in lowland woods with dry soils, and is rarely found on swampy grounds (van Steenis 1958). In contrast, *Gynotroches axillaris* is commonly found in water catchment areas. The species shows habitat preference for marshes, swamps, and areas along creeks in tropical rainforests (van Steenis 1958). These habitat preferences indicate that *G. axillaris* requires higher levels of moisture and has a low level of drought tolerance. With water stress likely to be an important factor in regulating community composition in Bukit Timah, the habitat preferences and hydraulic traits of *S. curtisii, S. elongatus* and *G. axillaris* appear to be strong candidates to explain the patterns of change in abundance in these species. *S. curtisii* and *S. elongatus* may have hydraulic traits that give them a competitive advantage leading to the increase in abundance, and *G. axillaris* may be decreasing in abundance due to disadvantageous water transport physiology and morphology when under water deficit. Future studies into hydraulic architecture and water conductance capacity may yield some enlightening answers. Interestingly, *S. apiculata* appears to have some degree of drought tolerance, but has been decreasing in abundance. It is possible that the main drivers for *S. curtisii, S. elongatus* and *G. axillaris* are related to water transport, but *S. apiculata* is decreasing due to a combination of other factors. Traits are not selected for independently, as selection acts on the plant as a whole (Diaz *et al.* 1998). Though a single trait can act as a powerful driver, it is likely a multitude of traits interact to govern performance in plants.

Though functional traits thought to be indicators of ecological strategy differences among species within and between communities, these traits interact strongly with environmental gradients to influence performance and maintenance (McGill *et al.* 2006). With drought effects likely to be a factor in governing community structure, soil moisture may be an interesting abiotic factor to investigate. Soil moisture levels have substantial effects on the hydrological cycle and biological processes that govern forest ecosystems (Mori *et al.* 2016). Topography, rainfall, evaporative processes and soil characteristics can influence soil moisture levels substantially, leading to spatial and temporal variation. In addition to moisture, soil nutrient concentration can have considerable effects on plant growth. For example, spatial variation in key nutrients such as phosphorous, calcium, potassium and magnesium has been identified as a substantial driver of Dipterocarp forest composition in Borneo (Khairil *et al*. 2014). As functional traits do not act in isolation, assessment of soil conditions within Bukit Timah may contribute to further understanding of factors influencing community composition.

In light of changing climate systems leading to higher temperatures and more intense and frequent drought events (Kharin *et al.* 2007), research into the drivers of community composition is increasingly relevant. With changes in environmental factors, migrations in vegetation communities and alterations in composition are likely to occur (Diaz and Cabido 1997). These changes are likely to alter ecosystem functioning substantially. Understanding how functional traits mediate competitive interactions and respond to abiotic factors can lead to better conservation strategies. Knowledge of these drivers also has real world applications;

for example, influencing decisions around restoration of rainforests through the planting of different species. If the impact of environmental factors on floristic composition was known, this could be used to predict species success within a certain environment. This could reduce loss of plants due to incorrect placement and allow species to exist within their suited niche, which represents a more driven and systematic approach to regeneration and recovery. Additionally, with deforestation rates predicted to increase in intensity, we can expect forest fragmentation to accelerate (Chow 2015). The Ngo *et al.* (2016) study showed that small forest fragments can show resilience to fragmentation effects, and demonstrates the potential merit of conserving even small forest fragments. With continuing fragmentation likely to occur in the future, the conservation value of these fragments is undeniable (Tabarelli *et al.* 2008). Using Bukit Timah as a model ecosystem, findings can then be applied to other tropical rainforest fragments across South-East Asia.

Conclusions

Our results showed significant variability in leaf functional trait values between species. Nevertheless, we did not identify any overarching pattern in the leaf functional trait variability that explained the increase or decrease in abundance of the species investigated. With previous censuses indicating water stress being a notable factor leading to decreased stem density and increased mortality, we strongly suspect functional traits related to water transport are important drivers of community structure. In future studies, we recommend the investigation of water transport traits in a wider range of species. The contributions to conservation strategies and management practices would be immense if further studies of plant functional traits can identify key drivers of community composition.

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