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Ten years after: what we learned from the Mandai storm forest

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Abstract. Forest disturbances caused by extreme weather events such as severe windstorms are expected to become more prevalent under global climate change. It is imperative that we understand how plant species respond to disturbance-induced habitat changes to be able to predict if forest communities recover from catastrophic events. However, the impacts of wind disturbance on forest succession remains poorly investigated in tropical Asia. We review key findings from three scientific papers arising from studies of the Mandai Forest in Singapore, which was struck by a phenomenal windstorm in 2011, to highlight how they have addressed such knowledge gaps. These studies attempted to link community patterns (i.e., diversity and composition) to species-level demography (i.e., recruitment and size growth) under the influences of multiple assembly processes (i.e., environmental filtering and biotic interaction). We then report new findings investigating potential plant invasions in the Mandai Forest following wind disturbance. Finally, we outline key methodological challenges that led to missed opportunities during the study and propose future directions to address some of the remaining questions related to disturbance ecology in tropical Asia.

Key words. disturbance, secondary succession, community assembly, functional traits, biological invasion

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INTRODUCTION

> *The Kelantan storm… was such a memorable event that it became the fixed date of the era Angin Besar (the Great Wind)… Although Angin Besar is an historical, if somewhat uncertain, date, the actual facts of the storm have long since become an old wives' tale, and I suppose that, in a hundred years or so, the event may appear as fabulous as the famous attack of the sword-fish on Singapore.*
>
> Browne (1949)

In a 1949 issue of The Malayan Forester, F. G. Browne described a catastrophic event which took place around 1883 and devastated multiple patches of dipterocarp forest in the state of Kelantan in Malaysia (then part of Malaya). While qualifying that he was "not an expert in plant ecology", Browne reported these "storm forests" to "draw attention to them and to suggest that they may be worthy of careful, scientific study". This prompted a revisit to the site four years later by J. Wyatt–Smith, who found the low species richness of these wind-disturbed successional forests to be unusual (Wyatt-Smith, 1954). Do forests recover structurally and compositionally from severe wind disturbances? If they do, how long does this take? If they do not, why might this be so? Despite decades of interest in the role of wind disturbances in maintaining the diversity of tropical forests, data to answer these questions remain scarce for the lowland dipterocarp forests of this region.

Globally, the impacts of wind disturbance on forest succession are investigated more frequently in the higher-latitude parts of the Atlantic Neotropics and the Asia-Pacific, while forests in tropical Asia remain poorly studied (Lin et al., 2020). Since the equatorial region (between 10° N and S) is relatively hurricane-free, it is not surprising that there might be a paucity of wind-disturbance studies in this region (Corlett, 2014). However, as extreme weather events are expected to become more frequent and intense with global climate change, there is nevertheless an urgent need to understand and be able to predict the responses of forest communities to such disturbances, which can be comparable in magnitude to commercial logging, especially when past fragmentation exacerbates edge effects and the vulnerability of the forest to further catastrophic events (Laurance & Curran, 2008; Turton, 2013).

An opportunity to address these knowledge gaps appeared in Singapore on 11 February 2011. A powerful rainstorm with wind speeds up to a maximum of 61.2 km h^{-1} (Chua, 2011) hit a patch of secondary forest north of the Upper Seletar Reservoir, in the northern part of the Central Catchment Nature Reserve (1° 24.8′ N, 103° 47.5′ E; Fig. 1; see also map in Appendix S1 of Yee et al., 2019b). Although such wind speeds are relatively low compared to hurricanes or cyclones (which can reach at least double this wind speed, e.g., 119 km h^{-1} recorded in Xi, 2015), extensive tree falls and canopy gaps were created across 40 ha of forested area by this event (Chua, 2011; Appendix S1 of Yee et al., 2019b). Within three months of the event, we began a five-year forest inventory in 40 semi-permanent plots to investigate how the forest in this area—which we call Mandai Forest because it is bisected by Mandai Road running east to west—would recover from the wind disturbance.

This article has three aims. First, we recapitulate the key findings from three scientific papers arising from this study of Mandai Forest (Yee et al., 2019b; Lai et al., 2020, 2021a) to summarise how they have advanced the state of knowledge on forest responses to wind disturbance in this region. Second, we report new findings from investigating potential plant invasions following the disturbance event. Third, we outline a few unresolved questions and missed research opportunities related to wind disturbances to forests and suggest future research directions for Singapore and the surrounding region.

BRIEF OVERVIEW OF FIELD SAMPLING

Field work in Mandai Forest took place from 2011 to 2015. The methodology of field sampling is detailed in Yee (2016) and Yee et al. (2019b). In brief, forty 10 × 10 m^2 plots were established (Appendix S1 in Yee et al. 2019b) using stratified random sampling to ensure a sufficient representation of plots in combinations of the affected versus unaffected areas as well as old versus young secondary forest areas. This was done by overlaying the vegetation map of Yee et al. (2011) with a preliminary mapping of the windstorm-affected areas by the staff of the Conservation Division of the National Parks Board, Singapore. Of the 40 plots, 26 were located in the initially affected areas (but two more plots were later affected by new tree falls in 2013 and 2014 and re-classified thereafter as affected plots). Plots were established at least 40 m apart to prevent inadvertent overlap. More plots were established in the affected areas as this was the intended focus of the short-term monitoring. The plots were surveyed annually between April and August. Within each plot, all stems ≥ 1 cm diameter-at-breast-height (DBH) were identified, measured and tagged. All other vascular plant species were also identified in each plot (although this dataset has yet to be used in a publication until now; see below). Taxonomic nomenclature followed Chong et al. (2009) with updates. Environmental factors were also measured in each plot, including canopy openness, coarse woody debris, leaf litter depth, soil total nitrogen, extractable potassium and extractable phosphorous (see Yee et al., 2019b for more information). During the 2015 census, we collected plant functional traits including specific leaf area (SLA), leaf dry-matter content (LDMC), lamina thickness, wood density, maximum height and seed dry mass from the field, and these were supplemented by data from published databases and the floristic literature (see Lai, 2019; Lai et al., 2020 for more information). At the end of the survey of each plot during the 2015 census, we also removed all the tags from the trees, because funding support had ended and there was no certainty that there would be future surveys that would maintain the tags and prevent them from damaging the trees as they grew. However, the approximate positions of trees ≥ 5-cm DBH within a plot were mapped onto a grid in hopes that it might be useful for future work.

Fig. 1. Top: Broken treetops and open canopies in the forests of Mandai following the wind disturbance event in 2011. Middle: Discontinuous canopies along much of the forest edge (here seen in 2011 during boat trips to survey forest plots located near the reservoir's edge). Bottom: Overgrown understory observed in 2013 in a forest plot, with *Miconia crenata* (= *Clidemia hirta*) visible in the foreground (red arrows). (Photographs by: A.T.K. Yee (top, bottom), K.Y. Chong (middle)).

A REVIEW OF KEY FINDINGS

(1) Taxonomic but not functional compositions of recovering affected areas diverged from those of unaffected areas. Yee et al. (2019b) described the recovery of abiotic conditions, forest stand structure and tree diversity and composition in the Mandai Forest over five years following the 2011 windstorm. Soil nutrients, canopy cover, leaf litter depth, coarse woody debris and stand basal area in affected areas recovered rapidly to be comparable to that of unaffected areas within 2–4 years. However, the recovering stand basal area was almost completely constituted by newly recruited small stems, and therefore should not be taken to mean that biomass had recovered as the newly regenerated canopy was still very short in height (<10 m at the end of five years).

Following the rapid increase in stem number and recruitment, the affected areas saw a two-fold increase in species richness and an over three-fold increase in functional-trait diversity. Importantly, although the newly recruited species in affected areas were taxonomically distinct from those in unaffected areas, both types of forest communities were functionally very similar (Fig. 2). Such a divergence in taxonomic but not functional composition indicates that the gap-colonising species in the affected areas were functionally similar to the species in the unaffected areas, perhaps only with slightly higher specific leaf area and/or lower wood density corresponding to cheaper leaf and wood tissue construction by fast-growing species (but see our discussion of potential confounding effects under *Methodological Challenges, Missed Opportunities & Future Directions*).

(2) Wood density, seed mass and maximum height determined post-storm recruitment. Lai et al. (2020) followed up on the functional composition of gap-colonising species by examining specific trait–environment relationships that governed the sapling recruitment of 53 tree or shrub species in the 26 initially-affected plots and two additional plots later affected by new tree falls. The goal was not only to quantify the recruitment of each species along wind-induced environmental gradients, but also to generalise these species–environment relationships using functional traits, which, in theory, should be biological attributes that reflect life-history trade-offs across species in different environmental settings. Species that share similar functional traits are expected to have similar performances in a particular environment, regardless of differences in their biogeographic or evolutionary histories.

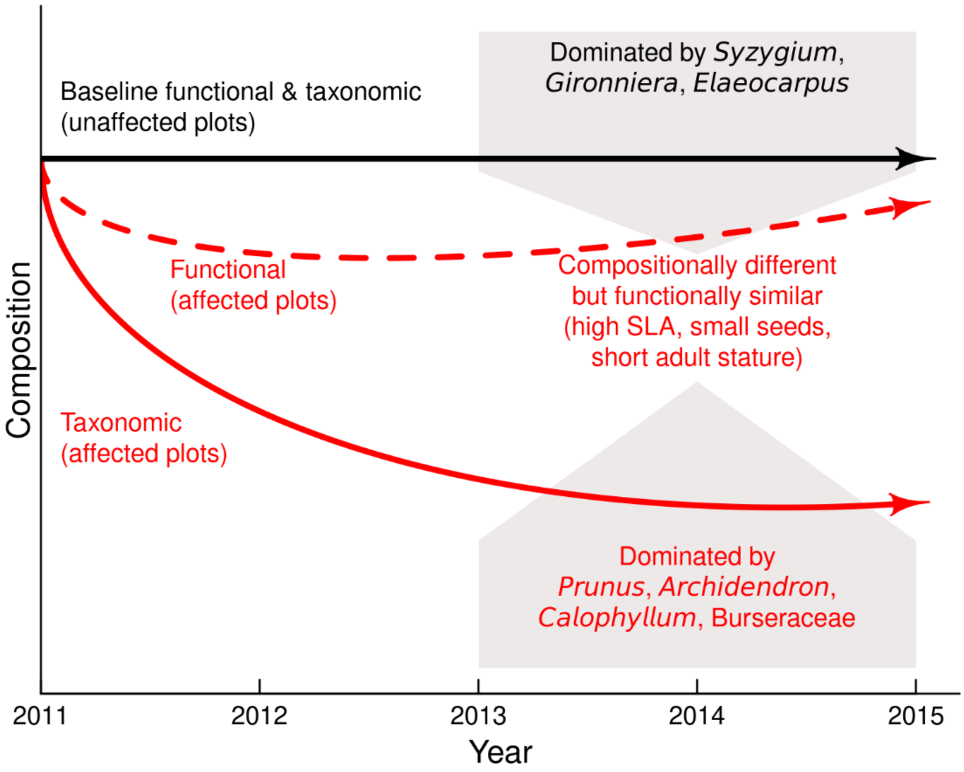

Fig. 2. Simplified schematic of results from Yee et al. (2019b) comparing the five-year successional trajectories of affected areas (red lines) and unaffected areas (black line) in terms of taxonomic (solid lines) and functional (dashed line) compositions.

To do so, Lai et al. (2020) adopted the fourth-corner joint species distribution modelling framework (Niku et al., 2021) and analysed tree recruitment as a function of environment variables, functional traits, and trait × environment interactions. Specifically, the site-by-species count matrix is regressed against the site-by-environment and species-by-traits matrices to obtain the fourth trait-by-environment matrix (hence 'fourth corner'). Unsurprisingly, we found that most of the species had higher recruitment with increasing light availability in canopy gaps. But more importantly, species with lower wood density had greater recruitment in canopy gaps than species with higher wood density (Fig. 3a). This indicates that interspecific responses to light availability in terms of recruitment can potentially be predicted by wood density, where low values indicate cheaper wood construction costs per unit gain in tree height. Along a similar vein, heavy-seeded species are predicted to recruit more than light-seeded species under thick leaf litter depths (Fig. 3b), which was highest in the first of the five censuses following the windstorm (Yee et al., 2019b). Heavy or large seeds contain more reserves that could enable seedlings to push through the germination barriers caused by leaf litter. Species with taller maximum height (i.e., adult stature) also recruited more in older secondary forest plots, whereas short-statured species recruited more in younger secondary forest plots (Fig. 3c). Given that the classification of young and old secondary forests in Singapore (Corlett, 1997; Yee et al., 2011) loosely corresponds to the 'low' and 'tall' physiognomy-based classification of earlier authors (Hill, 1977; Corlett, 1991), the maximum height–forest type relationship probably reflects a historical contingency due to a greater seed source from tall-statured parent trees in old secondary forests, and likewise a greater seed source from short-statured parent trees in young secondary forests. Taken together, wood density, seed mass and maximum height demonstrated the roles of functional traits in species' responses to environmental filtering and dispersal limitation.

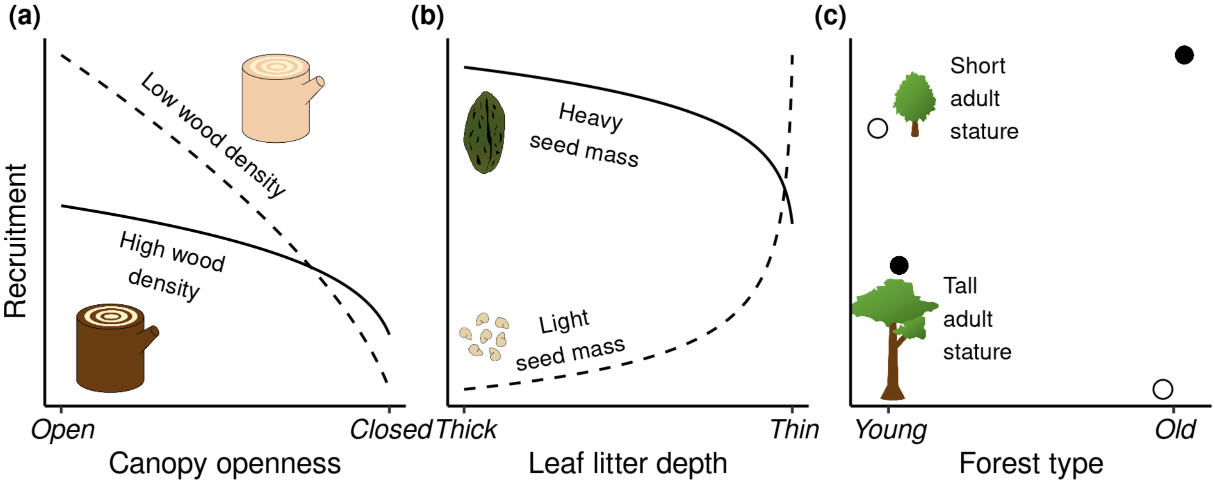

Fig. 3. Simplified schematic of results from Lai et al. (2020) showing the trait-dependent outcomes in recruitment along wind-generated canopy openness and leaf litter depth gradients (each simplified to two extreme categories here), as well as between young and old forest types.

As with many ecological studies, however, there remained some amount of variation in recruitment that was unexplained by environment or traits (see supplemental figures S5 and S6 in Lai et al., 2020). The recruitment of some species—such as *Santiria laevigata*, *Syzygium* spp., *Garcinia scortechinii*, *Dillenia suffruticosa* and *Calophyllum wallichianum* var. *incrassatum*—was explained more strongly than other species by one or more latent variables (Fig. 4), which were estimated in the model to capture the effects of unmeasured abiotic or biotic factors. These species- and site-specific latent variables can also be treated as species loadings and site factors in an ordination (Fig. 4) to visualise residual compositional turnover across sites, and how strongly each species was associated with these compositional changes (Hui et al., 2015). The aforementioned species had high local recruitment in certain plots but not others, and hence were key species that led to compositional turnover across the affected plots. Rather than dismissing model residuals as statistical noise, the latent variables attempt to find non-random structures in the residuals that may contain hidden information about species and sites. For instance, the second latent axis in the ordination of Fig. 4 reveals a compositional gradient that resembles the *Trema–Macaranga* belukar (Wyatt-Smith & Panton, 1995), suggesting that these forest plots might be historically less disturbed by agriculture (Yee et al., 2019a). Uncovering more concrete meaning behind these latent variables, however, would certainly require the integration of domain knowledge across multiple disciplines.

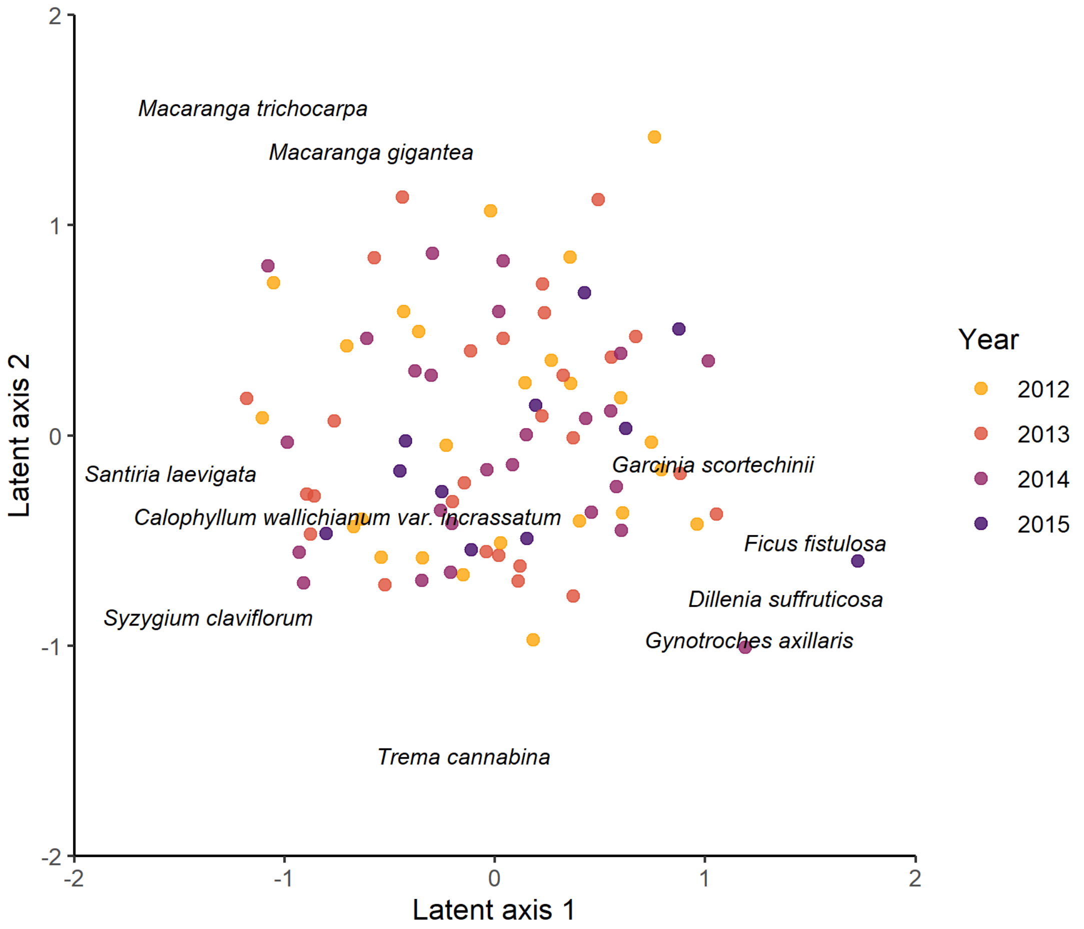

Fig. 4. Model-based ordination showing the positions of forest plots (coloured dots) in the taxonomic compositional space. The species scores of only 10 species with more extreme values are shown for indicative purposes. Note that this ordination is based on recruit composition and is therefore not comparable to that of Yee et al. (2019b), who ordinated both adults and recruits of a larger number of species. Another difference is methodological, in that Yee et al. (2019b) performed distance-based ordination, whereas this study employed latent-variable-model-based ordination. These latent variables represent a combination of unmeasured environmental, biotic and/or dispersal effects; see Hui et al. (2015) for more details.

(3) Biotic interactions were non-additive. Lai et al. (2021a) followed up a question outstanding from Lai et al. (2020): how do biotic interactions (i.e., competition and facilitation) operate during post-windstorm secondary succession? This analysis examined the effects of biotic interactions among ten focal tree species on each of their diameter growth. Unlike most studies on biotic interactions, however, Lai et al. (2021a) also investigated the so-called 'higher-order interactions' (HOIs). Briefly, HOIs are biotic interactions that involve a third, intermediary species outside the interacting species pair. In a typical pairwise (i.e., first-order) interaction, the growth of a focal individual, e.g., of *Archidendron clypearia*, could be inhibited by direct competition from neighbours such as *Gironniera nervosa* (thickest red–blue arrow, Fig. 5a). In a multispecies assemblage, however, it is possible that another species (e.g., *Garcinia parvifolia*) not only directly interacts with the focal individual (thinnest blue arrow, Fig. 5a), but also indirectly interacts by modifying the direct pairwise interaction (intermediate blue arrow, Fig. 5a).

In the Mandai Forest data, the model that included complex HOIs received the best support as judged by information criteria, despite having a much greater number of parameters. The direction and magnitude of HOIs on pairwise interactions varied by focal and intermediary species, so in this review we focus on *Archidendron clypearia* as a focal species because it was most sensitive to HOIs (see Figs. 1b and 1c in Lai et al., 2021). Next, we selected *Gironniera nervosa* as the direct neighbour species because its pairwise interaction with *Archidendron clypearia* was most strongly moderated by an intermediary species, *Garcinia parvifolia*. Specifically, the direct biotic effects of *Gironniera nervosa* and *Garcinia parvifolia* on *Archidendron clypearia* were competitive and very weakly facilitative, respectively (Fig. 5a). On the surface, it would appear that, with all else being equal, the combined effect of both neighbour species on *Archidendron clypearia* would be net competitive. Yet, the whole was not the sum of all parts. Non-additivity owing to the facilitative HOI by *Garcinia parvifolia* reversed the competition between *Archidendron clypearia* and *Garcinia nervosa* to net facilitative (thickest arrow switching from red to blue, Fig. 5a). Crucially, ignoring non-additivities in biotic interactions could lead to very different predictions of successional outcomes. Using simulations from models that excluded or included HOIs, it is expected that the omission of HOIs led to a different rank order in final diameters among species, despite few differences in the overall community-level DBH distribution (Fig. 5b). It would be useful to validate these short-term projections with monitoring data in the future.

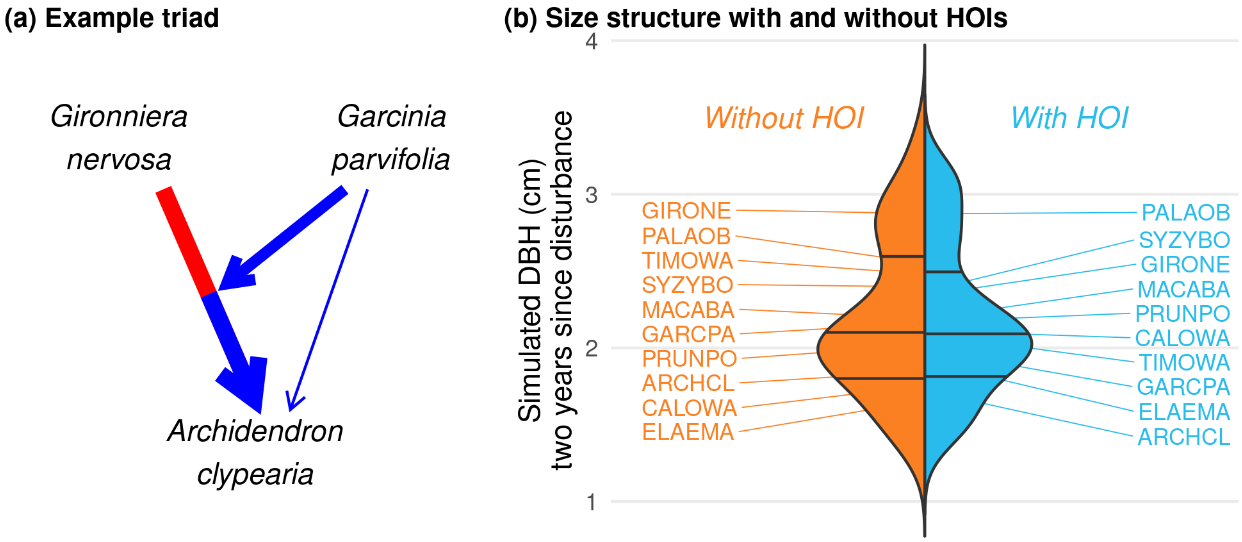

Fig. 5. Simplified schematic of results from Lai et al. (2021a) showing (a) higher-order interaction (HOI) from *Garcinia parvifolia* reversing the direct competitive effect (red) of *Gironniera nervosa* on *Archidendron clypearia* to a facilitative one (blue), and (b) how higher-order biotic interactions (HOIs) may influence the forecasting of successional trajectories in forest tree size structure. Density plots show the two-year projection of diameter-at-breast-height (DBH) of ten tree species with (blue) and without (orange) accounting for HOIs. Horizontal lines delimit DBH quartiles. Note that species ranks by final DBH differ between the two simulated scenarios despite few differences in the overall community-level DBH distribution.

POST-DISTURBANCE PLANT INVASIONS

During our first year of survey, we also noticed that the non-native shrub *Miconia crenata* (previously *Clidemia hirta*; Judd et al., 2018), known to be one of only a few non-native species capable of invading intact forest understories in this region (Teo et al., 2003), seemed to occur more frequently in the areas affected by the windstorm that we passed through on our way to the plots. Invasion of forests by other non-native plant species after tropical storms has been documented before (Bellingham et al., 2005; Laurance & Curran, 2008; Murphy & Metcalfe, 2016). Therefore, we tested the hypothesis that the tree falls would create opportunities for invasion of the forests by non-native species. The vegetation just northwest of and adjacent to our Mandai study area was the epicentre of the naturalization and spread of a Neotropical pioneer tree, *Cecropia pachystachya* (Chong et al., 2017), therefore we also raised the concern that the numerous and extensive tree fall gaps might allow substantial individuals of this species to establish within this part of the nature reserve.

In the second year of survey, as we had predicted, the proportion of affected plots with *Miconia crenata* increased, but not in the unaffected plots (Fig. 6). In this year, thick stands of up to a person's height could be encountered along some of the trails. From the second to the fourth year, *Miconia crenata* was present in all affected plots in young secondary forest and 12 out of the 13 of the affected plots in old-growth forest (see bottom photograph in Fig. 1). However, in the fifth year, *Miconia crenata* began to decline along the trails and disappear from some of the plots (Fig. 6), likely because of canopy closure.

Two years later, Wong (2017) sub-sampled in three forest patches north of the Upper Seletar Reservoir, including the Mandai Forest and two others bordering the Bukit Timah Expressway, and also found that *Miconia crenata* occurrence decreased with increasing canopy cover and leaf litter depth. However, Wong (2017) only found *Miconia crenata* in less than 10% of the fifty-five 100-m^2 transects studied (i.e., each transect with the same sampling area as our square plots). Compared to the larger extent of forest surveyed by Wong (2017), the unaffected plots of the Mandai forest had a 3–5-fold greater prevalence of *Miconia crenata* (Fig. 6), suggesting that the occurrence of *Miconia crenata* may have been elevated at the landscape-level in the Mandai area following the storm. This corresponds to the observation of Yee et al. (2019b) that there appeared to have been partial canopy loss even in the plots that were classified as unaffected in the study.

Although *Cecropia pachystachya* was recorded in one affected plot in 2012 and another affected plot from 2013 to 2014, these seedlings never reached a large enough size to qualify for measurement of DBH and had all died out by 2015. A stand of *Cecropia pachystachya* that established within a tree fall area (not within our plots) near the south side of Mandai Road was likewise observed by us to be ephemeral.

While it remains to be seen if the occurrence of *Miconia crenata* in affected young secondary forest plots will return to levels similar to that of unaffected plots beyond our five-year study duration, it appears—at least superficially—that native-dominated forests such as Mandai Forest are able to resist prolonged, extensive invasion by these non-native species despite this catastrophic disturbance event. Nevertheless, invasion could eventually still be promoted if there is an overall change in disturbance regime and not just a once-off event (Chong et al., 2021a).

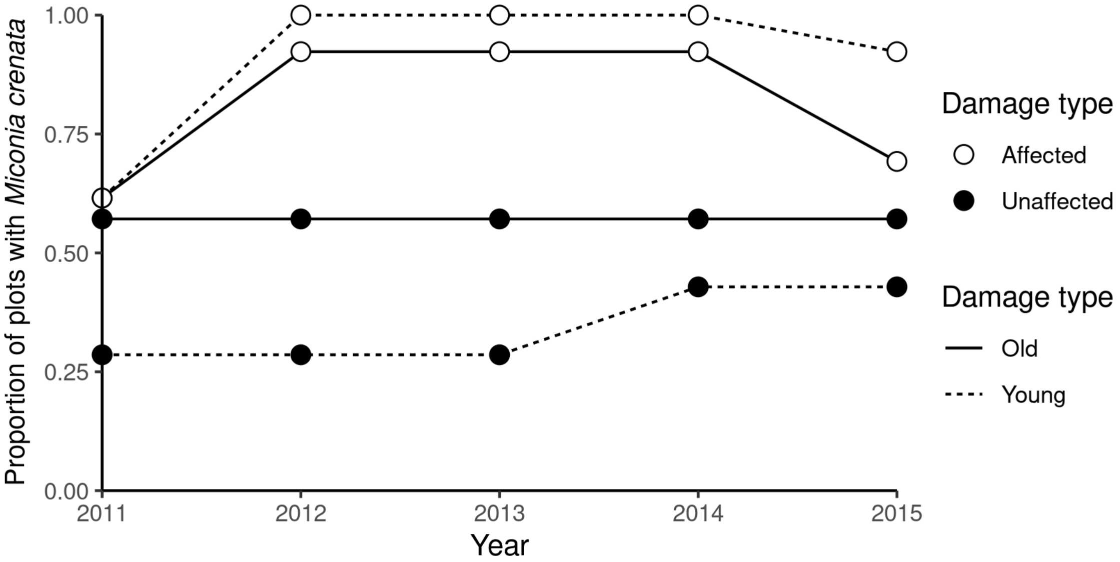

Fig. 6. Proportion of plots with presence of *Miconia crenata* over the five years of the study.

METHODOLOGICAL CHALLENGES, MISSED OPPORTUNITIES & FUTURE DIRECTIONS

After five years of fieldwork followed by five years of data analyses and writing, many unanswered questions remain about the assembly processes occurring in the Mandai storm forest. These questions will require data beyond the temporal extent of our original five-year study period. In the following sections, we position the Mandai storm forest as a potential study system for longer-term work that would address some of the important knowledge gaps in disturbance ecology, echoing Browne's call to draw scientific interest to such 'storm forests'. We outline key methodological challenges that led to missed opportunities and propose future directions to address some of the remaining questions.

The Mandai Forest study employed a quick-and-dirty approach with pros and cons. We responded quickly and took the rare opportunity to study such an event. In the challenging post-storm terrain, plots were limited to 100 m^2 in size and 40 in number (smaller-grained but with a larger extent). This rapid response allowed us to capture the most dynamic phase of secondary succession in terms of stand structure. One of the key trade-offs for such small plots is the undocumented effects on tree demographics from outside of the plot area. We also eventually gave up on estimating the category of damage to each tree (see Metcalfe et al., 2008), and resorted to estimating coarse woody debris by percent ground cover, which may not be as representative as estimates by volume or mass. We also only recorded presences (instead of abundances) of climber species on trees (which has not been used in any analysis yet).

Another compromise that we made was in trait collection. We delayed trait collection until the last census to concentrate efforts on stem measurement and plant identification in the first few censuses. Moreover, resolving species identities is crucial for collecting trait specimens from the correct species. This, however, means that some of the leaves collected in the last census were from sub-canopy positions within reach, although effort had been made to maximise the number of leaves collected from sun-exposed adults. Yee et al. (2019b) found that the functional trait composition of affected plots did not significantly deviate from that of unaffected plots. However, there was a weak tendency towards higher community-weighted mean SLA values in the affected plots (Lai, 2019). Furthermore, Lai et al. (2020) also showed that leaf traits did not moderate species recruitment across environments. Given that collections of leaf function trait measurements were all from the last census, we are unable to confidently conclude if the findings of weak successional divergence in SLA and lack of leaf–environment interaction are true or obscured by leaf heteroblasty or other forms of phenotypic plasticity that may have occurred over the first four years. Ironically, other traits that are less readily available for field collection, i.e., wood cores and seeds, are less variable across ontogenetic stages and environments (Moles et al., 2005; Chave et al., 2006; Kraft et al., 2010) and could be more confidently filled in from alternative data sources such as floristic accounts, herbarium collections, and twig-wood allometry (see Appendix/Supporting Information in Yee et al., 2019b; Lai et al., 2020). Despite the relative ease of making fresh collections of leaf traits, these could paradoxically be the most difficult trait data to accurately measure to reflect functional strategies at fine spatiotemporal scales owing to their inherent variability. We therefore suggest that future trait-based studies of succession could consider leaf collection and trait measurements over time to test if ontogenetic changes in leaf traits are substantial and rapid over the course of early succession.

Valuable lessons from the Mandai Forest on the short-term dynamics of post-disturbance succession further highlight the importance of longer-term data in piecing together a more complete ecological picture of post-storm succession. Funding for our Mandai storm forest study came to an end after five years, yet the legacy impacts of a windstorm operate on longer timescales. From our field observations and the data, we suspect that the fifth year was when the regenerating forest was just about to enter a self-thinning phase (Yee et al., 2019b; Chong, 2020). Although trees >5 cm DBH were tagged for future resurvey, mortality during the thinning phase should be more prominent for trees 1–5 cm DBH, therefore, considerable information about tree mortality has already been lost at the time of writing this paper. Yee et al. (2019b) examined overall diversity and composition, which are emergent community-level patterns arising from various underlying species-level demographic processes, such as size growth, recruitment and mortality (Fig. 7). We were only able to further investigate tree recruitment (Lai et al., 2020) but there were not sufficient mortality data across species as the forest was just about to self-thin. Without mortality data, we could not have a complete study of whole-plant life-cycle processes in the regenerating forest to predict population dynamics in response to future disturbances. Ongoing research in the Nee Soon Freshwater Swamp Forest, across the reservoir and south of the Mandai Forest, has picked up lessons from the Mandai study and will integrate the collection of tree growth, mortality, fruit production and recruitment data. In these studies, the combination of different vital rates is showing promising utility in agent-based models to forecast forest structure under different land-use regimes. We encourage more demographic data from longer-term monitoring of secondary forests, such as those in Mandai and the rest of the Central Catchment Nature Reserve, which have not benefitted from long-term follow-up studies as compared to the ForestGeo plots at the Bukit Timah Nature Reserve, for instance (Lum & Ngo, 2021).

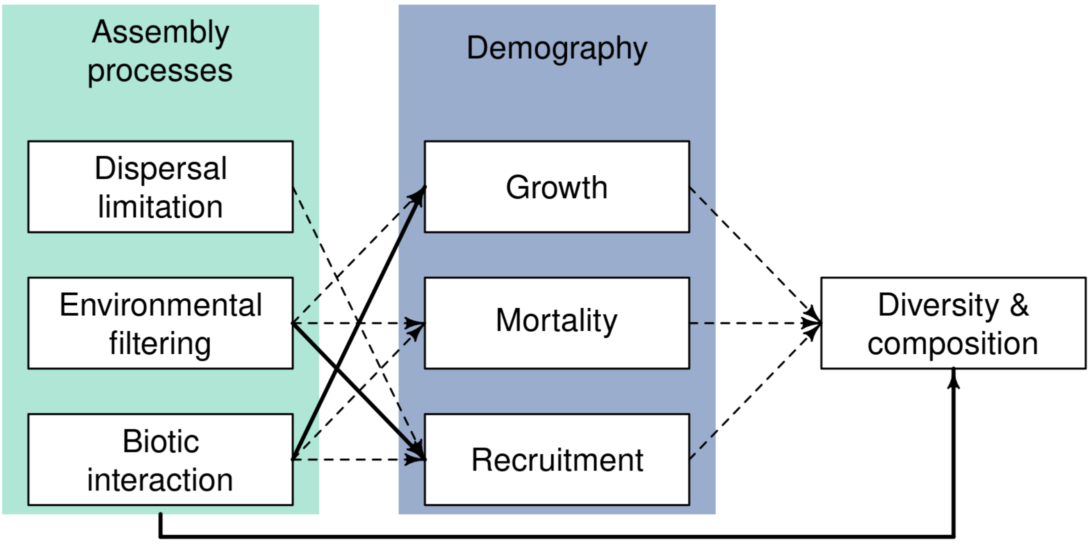

Fig. 7. Efforts and gaps from the Mandai storm forest studies. Solid arrows are relationships addressed by the Mandai studies, whereas dashed arrows indicate knowledge gaps.

Secondary forests constitute about a quarter of Singapore's land area (Yee et al., 2019a) and about 65% of Southeast Asia (Estoque et al., 2019). The many unanswered questions which remain from our studies imply that there are opportunities for collective research efforts that could better inform decisions regarding the management of such forests. We anticipate future efforts to prioritise getting the most out of established sites, before moving on to supplement or validate previous findings with experiments or new field studies. Some of these missing trait and demographic data could be obtained with relatively less effort by leveraging on the 40 pre-existing Mandai Forest plots. Although it will be difficult to track the fate of individual 1–5-cm DBH trees from which tags were removed in 2015, it may still be possible to estimate population-level mortality by censusing the total number of surviving trees per species and trace the larger trees ≥ 5-cm DBH in 2015 that were mapped, in order to provide information on mortality and diameter growth. The plots could also be expanded to 20 × 20 m^2 to match the plot size and design in the Nee Soon catchment (Chong et al., 2021b) as well as in the nature parks (see Neo et al., 2017; Lai et al., 2021b). It is also imperative to continue resolving the identities of many species in the Mandai storm forest inventory. This will facilitate future trait collections that could prioritise poorly sampled species (fewer than half of the species in Mandai had good coverage of leaf, stem and seed traits that fulfil standard protocol by Pérez-Harguindeguy et al., 2013; see appendices of Yee et al., 2019b for a summary of trait coverage) and could be extended to poorly represented but disturbance-relevant traits, e.g., resprouting (Vesk & Yen, 2019; Lin et al., 2020; Su et al., 2020). The 'traits' of a plant species need not be restricted to morpho-physiological characteristics that describe its Grinellian niche (i.e., abiotic requirements), but could also be attributes that quantify its Eltonian niche, such as biotic associations or multitrophic roles (Dehling & Stouffer, 2018) or other ecosystem functions, such as primary production and nutrient cycling (e.g., Lam et al., 2021).

CLOSING REMARKS

A short communication on the impacts of wind damage at a site in Central Kalimantan by Proctor et al. (2001) was one of very few reports on this subject from this region following Wyatt-Smith's (1954) investigation into the aftermath of Angin Besar. Just as Angin Besar was to Kelantan, Proctor et al. (2001) described their culprit storm as "of an unprecedented ferocity (within the memories of local field assistants up to 45 years of age)". Likewise, the extent of tree falls in Mandai has been unprecedented in Singapore at least in current memory. Did the storm that hit Mandai Forest result in overall negative impacts on the forest, e.g., through the killing of large trees that could either have been relics from the original forest or at least have taken a long time to reach that size since the recovery of the forest from past human disturbance? Or was it a much-needed 'jumpstart' to the forest that removed long-lived pioneers and restarted the process of succession after persistence in an arrested state? These are questions that would take a long-term approach to answer.

Disturbances such as storms, landslides or even fires are part of regular ecosystem processes, but for Singapore's relatively fragmented remaining forest patches, every such event will be a cause for concern, and even more so if they increase in frequency with climate change. Broken and shortened canopies can be seen along the edges of many of the forested peninsulas around the reservoirs in the Central Catchment Nature Reserve (e.g., middle photograph of Fig. 1). Many of them likely suffered from recent blowdowns that were not detected due to the relative lack of visibility. Tree falls have been observed to have occurred in and around several of the plots established in the Nee Soon catchment (see Chong et al., 2021b) since the series of studies began there in 2013.

Has our study of the Mandai storm forest been useful to inform future responses to storm disturbances to the forest reserves? We think that certain actions are *not* needed in the case of wind disturbances: leaf litter and coarse woody debris should not be removed and instead should be left on-site for nutrient recycling to occur naturally, and active reforestation of tree fall gaps did not appear to be necessary unless the aim is to enhance the community composition of secondary forests with old growth species. However, this recommendation of non-action may not apply for other types of disturbances such as landslides or fires which eliminate the seed and sapling banks that are critical for rapid recovery. Another important question that requires future surveys or even experimental manipulations to answer is whether climber infestation takes over in some gaps (Schnitzer et al., 2021), and therefore if, when, and to what extent trimming of climbers may help to accelerate forest recovery.

At the same time, even while we have anecdotes that tree falls have increased in frequency following the onset of stronger storms recently, most of such events occur at scales too small for a meaningful study in isolation. Extreme weather events, while worrying in their potential impacts, are rare opportunities that can be taken advantage of to establish a robust study, as we did in Mandai Forest where we set up a before-after-control-impact design plot network. Another approach may be to set up pairs of plots, one of each pair in the affected area and the other in a nearby similar but unaffected area, every time that a disturbance event occurs. This can follow a standardised design and, over time, as plot pairs are accumulated, they can form a valuable dataset for analysis. This may address biases that may be introduced if we study only extreme events of the largest scale (Lin et al., 2020). It could also be part of a broader systematic approach to properly quantify the timing and extent of such disturbance events so that we no longer rely only on qualitative anecdotes. Beyond Singapore, such a distributed plot design could be a way to overcome difficulties in the study of impacts and forest regeneration following treefalls, through collaboration in this (hurricane-free) region, similar in spirit to distributed experiments such as NutNet (https://nutnet.org/).

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