Research Article

Invasive trees in Singapore: are they a threat to native forests?

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Abstract

Asian tropical forests are under extreme stress from clearance, fragmentation, and logging. Because Singapore suffered these same impacts in the 19th century, it can act as an early warning system for the region. We identified invasive exotic tree species from a comprehensive survey, assessed their survival and growth in the open and under a forest canopy, and compared their traits with native pioneers and widely planted exotic species that have failed to naturalize. Nine species were invasive: *Acacia auriculiformis* (ear-leaf acacia), *Cecropia pachystachya* (trumpet tree), *Falcataria moluccana* (Moluccan albizia), *Leucaena leucocephala* (leucaena), *Manihot carthaginensis* subp. *glaziovii* (Ceara rubber tree), *Muntingia calabura* (Jamaican cherry tree), *Piper aduncum* (spiked pepper), *Pipturus argenteus* (white mulberry), and *Spathodea campanulata* (African tulip tree). Under the forest canopy, all grew little and suffered high (75-100%) mortality, with *Spathodea* surviving best. At the open site, mortality was low (0-25%) and height growth rapid (1.6-8.6 cm wk^{-1}), with *Leucaena* growing fastest. The only significant trait difference between native pioneer trees and invasive exotics was the dispersal syndrome; none of the common native pioneers are wind dispersed, while two invasive species are. Among exotics, there were highly significant differences between invasive and non-invasive species in wood density and seed size, with invasive species having only 54% of the mean wood density and 19% of the dry seed mass of non-invasive species. Invasive exotics were also significantly farther from their native ranges than non-invasive species. None of these invasive tree species is a direct threat to the integrity of native closed-canopy forest, but they dominate on newly abandoned land and may pre-empt the recovery of native forest on such sites.

Key words: biological invasions; land-use history; tropical forests; naturalized species

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Introduction

Trees received relatively little attention in the invasive plants literature until recently [1]. They are slower growing and have longer life-cycles than most shrubs and herbs, making potential tree invaders harder to detect and study, and there tends to be a long lag time between introduction and invasion [2, 3]. When exotic tree species do spread beyond their point of introduction, however, they have the potential to be more damaging than smaller plants [1]. They create shade, which is a barrier to the re-establishment of many native species [4, 5]; they can dominate nutrient cycling, potentially changing the site in a more permanent way [6, 7, 8]; and they can make the invaded habitat less suitable for arthropods [9] and native vertebrates [10]. Other reported impacts of some tree invasions include allelopathic suppression of competitors [11, 12], changes in the local fire regime [13], and reduced streamflow [14].

Invasive species are under-studied in tropical Asia compared to other parts of the world [15], with plant invasions of and impacts on natural ecosystems, in particular, receiving little recent attention in the literature [16]. A recent review estimated the total economic and environmental cost of invasive aliens in Southeast Asia as US$33.5 billion a year, but nearly 90% of this was for the agricultural sector [17]. The lack of attention may, in part, reflect a lack of concern, since intact tropical forests on the Asian mainland and continental-shelf islands appear to be relatively resistant to both plant and animal invasions [16, 18]. However, Asian tropical forests are currently under extreme stress from clearance, fragmentation, logging, and rapid urbanization [16], all factors that are expected to make them more vulnerable to invasion.

We investigated invasive trees in Singapore, a densely populated equatorial island nation in Southeast Asia, separated by a narrow strait from the Asian mainland. In Europe, national wealth and human population density are the strongest predictors of biological invasions [19]; in tropical Asia, Singapore ranks highest in both parameters. Singapore has suffered the same impacts as the rest of the region, but up to a century earlier, so it can act as an early warning system for the region as a whole [20]. Forest conversion to monoculture crop plantations and timber extraction, which are now the major threats to tropical forests worldwide, had already transformed Singapore's landscape by the 1880s. Today, only 0.3% of the original primary forest remains, surrounded by a larger area of secondary forests of various ages [21].

The Singapore government has very actively imported exotic plant materials, starting with mostly economic plants in the nineteenth century, and dominated by ornamental species more recently, particularly after the Garden City campaign was launched in 1967 [22]. A largely unregulated commercial trade also imports numerous alien plants, although relatively few trees. Nowadays, 44% of the total vascular flora in Singapore is exotic [23]. Most of these species grow only in cultivation, but 18% occur spontaneously in the wild, and 12% are considered fully naturalized. We therefore asked the following questions: Which exotic tree species are naturalized in Singapore and which of these are invasive? How well do the invasive species survive and grow in shaded and open sites? How do the invasive exotic trees differ from the native pioneer trees with which they coexist, and from the widely planted exotic species that have failed to naturalize? And, finally, are invasive tree species an actual or potential conservation problem in Singapore and SE Asia?

Methods

Study area

The Republic of Singapore consists of one main island and several smaller ones, with a total land area of 718 km^2. It is situated at the end of the Malay Peninsula, from which it is separated by shallow straits less than 1 km wide at the narrowest point. Singapore is 137 km north of the equator and has a climate of extreme equability, with negligible seasonality in temperature and a mean of >100 mm rainfall in every month. The human population consists of 5.3 million people with a per capita gross national product of US$62,000.

Survey

Possible invasive tree species were identified from the literature on naturalized plant species in Singapore [23] and from the opinions of local botanists. All vegetation types capable of supporting spontaneous tree populations were then surveyed in 2008-10, including open areas, primary and secondary forests, urban habitats, and coastal vegetation. Singapore's small size, dense road network, and large number of active ecologists make it unlikely that any significant invaders were overlooked. Trees were defined as vascular plants exceeding 5 m height at maturity, and their exotic status was determined from an up-to-date checklist [23]. Two species that are native to the region but whose status in Singapore is uncertain, *Morinda citrifolia* (noni) and *Pterocarpus indicus* (Burmese rosewood), were excluded. Conversely, *Pipturus argenteus* (white mulberry), which may be native in the region around Singapore, was included because it is a well-documented recent arrival here. *Ricinus communis* (castor oil plant) is naturalized in Singapore but, unlike in some drier parts of the region, does not reach tree height.

Following Pyšek *et al.* [24], a species was considered naturalized if there was at least one self-replacing population, and naturalized species were considered invasive if they had spread far from where they had been introduced. In the absence of long-term observations, an uneven-aged population structure with some reproductive individuals was taken as evidence for naturalization, and the presence of many individuals at least 1 km from the point(s) of introduction as evidence for invasiveness. In practice, the invasive species were easily distinguished, while there was a continuum between naturalized and casual (i.e., not self-replacing) species, with the role of continuing propagule subsidies from cultivated plants hard to assess. Further studies were therefore restricted to the well-defined invasive group.

Growth experiments

Growth rate appears to be the single best predictor of invasiveness in exotic trees [25]. To assess the invasive potential of the recently arrived (> c. 1960) invasive tree species that may not have had time to reach their potential maximum extent, and to compare them with the well-established species, the survival and growth of eight species (all those identified as invasive except the relatively uncommon *Pipturus argenteus*) were investigated experimentally at two sites selected to represent the expected extremes of the invasibility spectrum in Singapore: a species-rich, 60-70-year old, secondary forest in the Central Catchment Nature Reserve, and an exposed area of mown grassland surrounded by alien-dominated woody vegetation on the campus of the National University of Singapore. Seedlings were raised in a shade house from seeds or, where these were insufficient, wild-collected small seedlings (*Acacia auriculiformis* [ear-leaf acacia] and *Falcataria moluccana* [Moluccan albizia]) or stem cuttings (*Manihot carthaginensis* [Ceara rubber tree]), were hardened, and then planted out when 20-40 cm tall. Five seedlings of each species were sacrificed for measurement of initial biomass. At each site, 15-25 seedlings of each species were planted interdispersed with one another, 75-100 cm apart. In the forest, seedlings were planted in the unmodified understory, avoiding large roots or dead wood. Logistic constraints meant that seedlings had to be planted in two batches eight months apart, but in Singapore's aseasonal climate conditions were very similar for both batches. Seedlings were watered once immediately after planting in the forest and twice within two weeks at the drier open site. Mortality and height were measured monthly and dry biomass (above and below ground) at the end of the experiment: after 54 weeks in the forest and when the plants reached 1.5 m tall at the open site.

Table 1. Traits used for comparison between native pioneers, invasive aliens, and non-invasive aliens.

Trait	Definition	Explanation	Hypotheses
Mature height (m)	Mean height of mature trees	Important ecological trait.	
Wood density (kg m^{-3})	Oven-dried mass divided by fresh volume	Negative correlation with relative growth rate.	Lower in pioneers and invasives
Dry seed mass (mg)	Oven-dried mass	Large seeds increase stress tolerance but reduce fecundity.	Smaller in pioneers and invasives
Flower sexual system	Hermaphrodite, monoecious, or dioecious	Increased pollination success with sexes on same plant	Dioecy less common in invasives.
Dispersal mode	Flying animal, wind, or mechanical	Flying animals can disperse seeds further and across gaps	Dispersal by animals more common in pioneers and invasives
Residence time (years)	Time since first recorded in Singapore	Propagule pressure increases with time.	Invasive species have longer residence time
Distance from natural range (km)	Straight-line distance from nearest part of natural range	More likely to lose natural enemies with distance	Invasive species from further away

Trait comparisons

Other traits thought to be associated with invasion success in the literature [25] (Table 1) were compared among the invasive species identified in the survey, the 20 commonest native pioneer tree species with which they coexist on wasteland sites outside the Nature Reserves (identified from published and unpublished surveys, and confirmed during our 2008-10 survey), and the 24 commonest exotic tree species that have failed to naturalize despite being widely planted in Singapore for at least 20 years [26] and commonly setting fruit (Ali bin Ibrahim, personal communication). The choice of non-invasive aliens for comparison was intended to exclude species that simply fail to reproduce in Singapore and to ensure that the species chosen had been there long enough to become invasive. Both comparison groups included some species that are invasive outside Singapore, so this is not a test for the traits associated with invasiveness on a global scale.

Traits were assessed from the literature (flower sexual system, dispersal mode, dry seed mass, mature height in Singapore), from on-line databases (wood density; [27, 28]), herbarium records (residence time in Singapore for aliens), and measurements on field-collected material (height, wood density, and seed mass for species not found in the literature or databases). New measurements were from at least five different individuals for each species for seed mass and at least three for wood density. For three species the mean wood density for the genus was used. Distance from the natural range (measured on Google Earth) was used as a proxy for the likelihood of the species encountering natural enemies and suitable mutualists in Singapore. To minimize the risk of falsely rejecting null hypotheses, we made only a small number of planned statistical tests based on hypotheses in the literature. It was not possible to control for phylogenetic effects during statistical analyses because there were only nine invasive species, three of which were legumes.

Results

Survey

Nine tree species were identified as currently invasive in Singapore (Table 2). Six of the invasive species were first recorded >100 years ago and the remaining three arrived in the last 50 years. Five species were deliberately introduced through the Singapore Botanic Gardens for a variety of purposes, while two recent arrivals, *P. argenteus* and *Piper aduncum* [spiked pepper] appear to have spread into Singapore from neighboring countries where they were already naturalized. However, neither was seen in a brief survey in 2010 of the coastal regions of Johor, Malaysia, a few kilometres north of Singapore, suggesting that they were not introduced by natural seed dispersal. We suspect that they arrived as contaminants with the huge volume of ornamental planting material imported from Malaysian nurseries, many of which are farther north where *P. aduncum* has been established for several decades. *Cecropia pachystachya* [trumpet tree] which was also not seen in Johor, is an attractive tree and the current distribution suggests that it may have spread from an undocumented deliberate planting in northern Singapore, since there was no evidence of spread from an earlier planting in the Botanic Garden.

The three most recently introduced species are also the least abundant, but while *P. argenteus* is sparse but widespread, both *C. pachystachya* and *P. aduncum* are currently expanding their ranges from dense populations in the north of the island. In contrast, the long-established species are present at most suitable sites outside the urban area. Invasive trees are also largely absent from the Nature Reserves in the centre of the island, which are covered in primary and secondary forest dominated by native species [29]. The exceptions were all found in disturbed areas near the margins of the reserves (particularly *Spathodea campanulata* [African tulip tree]) or along major paths. In contrast, invasive trees dominate or co-dominate with a few native species most of the spontaneous woody vegetation outside the nature reserves. In general, it appears that the more recently woody secondary succession has started at a site, the more dominant are invasive trees. All sites abandoned in the last 25 years are at least co-dominated by invasives.

A. auriculiformis, *C. pachystachya*, and *P. aduncum* sometimes form monodominant stands containing few other plant species. *F. moluccana* grows taller (> 30 m) than other pioneer species, both native and exotic, but casts a very light shade and commonly forms a single-species upper canopy over a mixed exotic and native understorey. The other invasive species occur mostly in forest edges, along roadsides, in semi-open early successional vegetation, or in irregular mixtures with native pioneers in closed secondary forest. *F. moluccana* trees adjacent to roads, paths, and gardens are often felled because of the danger from the large branches they shed, and some outlying individuals of *C. polystachya* have been removed, but no attempt has been made to control the other species.

All the invasive species found in Singapore are recorded as naturalized in at least one neighbouring country, except *C. pachystachya*. *Cecropia* species are spreading in Peninsular Malaysia and Java, but, although their precise taxonomic status is unclear, they are morphologically distinct from the invasive form in Singapore (personal observations). *C. pachystachya* is reported as a serious invasive on

Rarotonga Island in the Cook Islands [30]. Another *Cecropia* species, *C. peltata*, was introduced to the Singapore Botanic Gardens in 1902, and there were spontaneous plants in the vicinity by the 1980s [31; RTC personal observations], but this species has shown no sign of spreading further.

Table 2. Invasive tree species in Singapore with first official record, source(s) of seeds/plants introduced, purpose of introduction, dispersal mode in Singapore, native distribution range, and other SE Asian locations where the species is at least naturalized.

Species	Common name	First record	Source	Purpose	Dispersal mode	Native range	Naturalized in SE Asia
Acacia auriculiformis Benth.	ear-leaf acacia	1890	Darwin, Australia	ornamental	bird	N. Australia, New Guinea	widely
Falcataria moluccana (Miq.) Barneby & J.W.Grimes	Moluccan albizia	1909	Bangalore, India	afforestation	wind	E. Indonesia to Solomon Is.	widely
Cecropia pachystachya Trécul[1]	trumpet tree	1967	unknown	ornamental?	bird/bat	South America	not reported elsewhere
Leucaena leucocephala (Lam.) de Wit	leucaena	1888	Florida, USA	ornamental?	mechanical	Central and South America	widely
Manihot carthaginensis (Jacq.) Müll.Arg.	Ceara rubber tree	1879	many sources	rubber	mechanical	South America	locally
Muntingia calabura L.	Jamaican cherry tree	1895	unknown	fruits	bird/bat	Central and South America	widely
Piper aduncum L.	spiked pepper	2003	Malaysia?	spontaneous	bird/bat	Central and South America	widely
Pipturus argenteus (G. Forst.) Wedd.	white mulberry	1979	unknown	spontaneous	bird	Australia to SE Asia.	not reported elsewhere
Spathodea campanulata P.Beauv.	African tulip tree	1909	Bangalore, Penang	ornamental	wind	West Africa	widely

Seven additional tree species were classified somewhere on the casual-naturalized continuum, but not invasive in Singapore. These species vary greatly in their current abundance and distribution. *Alstonia macrophylla* (deviltree) is widely naturalized in semi-shaded sites on Sentosa Island, just south of Singapore, but the species has been in Singapore since 1879 and does not appear to be spreading much beyond the area where it was planted. *Hevea brasiliensis* (Para rubber tree) is the most abundant and widespread of the additional species, but although the shade-tolerant saplings dominate the understorey of some areas of secondary forest, they are rarely found beyond the crowns of mature trees and most or all of these appear to be remnants of the very extensive commercial plantings in the first half of the twentieth century. Similarly, *Andira inermis* is widespread as spontaneous, relatively shade-tolerant saplings, but all or almost all these are within bat-dispersal distance (< 100 m for large seeds [32]) of mature planted trees. *Ptychosperma macarthurii* (Macarthur palm) is better established, but the spontaneous population is still subsidized by seeds dispersed from extensive ornamental plantings and further study is needed to assess its current status [33]. *Elaeis guineensis* (oil palm) has been widely planted in the past and apparently spontaneous individuals are widespread in the south of Singapore. Seeds are dispersed by crows (*Corvus* spp.), which carry ripe fruits to nearby trees for processing (RTC, personal observations), but there is no strong evidence for a self-replacing wild population. Finally, *Ficus religiosa* (bo tree) is abundant as seedlings and saplings on artificial structures, but spontaneous adults are rare and the seed rain is dominated by planted individuals.

Eleven additional species are classified as naturalized trees in the 2009 Singapore checklist [23], but no evidence for a persistent, self-replacing population was found for any of these during this study. One of these, *Flacourtia jangomas* (coffee plum) is also listed in the latest global checklist of invasive alien trees and shrubs [34] on the basis of a record from Singapore, but the only reported self-replacing populations, on the islands of Pulau Ubin and Pulau Tekong, seem to be in decline. An earlier list of naturalized species [35] also included *Anacardium occidentale* (cashew tree), which was a rare casual species in our survey, and *Morinda citrifolia,* which is largely coastal and may be native.

Table 3. Means and standard deviations of growth rates of the invasive tree species tested at the open site in Singapore.

Species	Common name	Height growth ($cm.week^{-1}$)	Relative growth rate ($mg.g^{-1}day^{-1}$)
Acacia auriculiformis	ear-leaf acacia	4.8 (0.9)	27.1 (3.9)
Cecropia pachystachya	trumpet tree	2.3 (1.2)	13.0 (3.4)
Falcataria moluccana	Moluccan albizia	4.1 (1.8)	26.7 (5.7)
Leucaena leucocephala	leucaena	8.6 (2.1)	34.5 (4.4)
Manihot carthaginensis	Ceara rubber tree	2.8 (0.8)	23.2 (3.0)
Muntingia calabura	Jamaican cherry tree	4.2 (2.0)	17.3 (1.3)
Piper aduncum	spiked pepper	1.6 (0.8)	7.6 (3.2)
Spathodea campanulata	African tulip tree	2.0 (1.4)	5.6 (5.3)

Growth experiments

In the forest experimental site, mortality was high (75-100%) and height growth of the survivors low (0-0.4 cm wk^{-1}) in all species. *Manihot* (all dead by week 9), *Muntingia* (all by week 10), and *Falcataria* (all by week 17) performed worst and *Spathodea* best (25% survival at week 54, but with only 8 cm mean height growth). The other species with survivors at week 54 were *Leucaena* (3), *Cecropia* (2), and *Piper* (2). *Acacia* was planted late and had to be harvested at week 17, when one unhealthy seedling survived. In the open site, mortality was low (0-25%) and height growth rapid (1.6-8.6 cm wk^{-1}) (Table 3). Relative biomass growth rates ranged from 7.6 mg g^{-1}day^{-1} in *Piper* to 34.5 mg g^{-1}day^{-1} in *Leucaena* and were highly correlated among species with height growth (Spearman's r_s = 0.87, $P < 0.001$). Flowering occurred in *Manihot* (105 days after planting), *Leucaena* (114 days), *Muntingia* (140 days), and *Piper* (225 days) before the end of the experiment.

Trait comparisons

The only trait difference between native and invasive pioneers that was significantly different at the 0.05 level was the dispersal syndrome (Chi-square test; p = 0.049) (Table 4): none of the native pioneers are wind dispersed, while two invasive species (*Falcataria* and *Spathodea*) are. Invasive species also tended to be shorter (Mann-Whitney U test; p = 0.067) and to have less dense wood (p = 0.082) than coexisting natives. In contrast, there were highly significant differences between invasive and non-invasive exotics in wood density (Mann-Whitney U test; p < 0.0001) and seed size (p = 0.007), with invasive species having only 54% of the mean wood density and 19% of the dry seed mass of non-invasive species. However, there is considerable overlap between the two groups and these two characters are not sufficient to identify potential invasives. Flower sexual system also differed between the two groups (Chi-square test; p = 0.039), but in the opposite direction to that which was expected: all but one of the non-invasive species have hermaphrodite flowers while two invasive species are dioecious and one monoecious. Invasive exotic species were significantly farther from their native ranges than non-invasive species (Mann-Whitney U test; p = 0.015).

Table 4. Means and standard deviations of quantitative traits and percentages of qualitative traits for native pioneer trees, invasive alien trees, and non-invasive alien trees. The bottom two rows give p-values for pair-wise Mann-Whitney tests for quantitative traits and chi-square tests for qualitative tests; p < 0.05 in bold.

	Height (m)	Wood density (kg m^{-3})	Seed mass (mg)	Distance to natural range (km)	Residence time (yr)	Sexual system	Dispersal mode
Native	18.5 (6.8)	501.2 (197.7)	400.6 (1186.5)			47% herm. 42% dioec. 11% monoec.	90% flying 0% wind 10% other
Invasive	13.9 (11.8)	383.3 (125.0)	82.5 (211.6)	10,800 (7,100)	85.6 (46.4)	67% herm. 22% dioec. 11% monoec.	56% flying 22% wind 22% other
Non-invasive	19.1 (8.6)	709.5 (178.9)	426.9 (409.1)	4,300 (6,000)	97.5 (35.7)	96% herm. 4% monoec.	28% flying 50% wind 22% other
Native *vs.* invasive	0.067	0.082	0.290			0.576	**0.049**
Invasive *vs.* non-invasive	0.092	**< 0.001**	**0.014**	**0.030**	0.450	**0.039**	0.236

Discussion

Singapore's small size may tend to inflate the fraction of species treated as exotic relative to larger, continental areas [36], but even allowing for this, some sites in Singapore have more coexisting invasive tree species than anywhere else we have seen in the humid tropics between northern Australia and southern China (personal observations). However, the total number of invasive tree species represents only 1.1% of the exotic tree species recorded in Singapore [23], suggesting that the risk of a particular exotic tree species becoming invasive is low, in agreement with other studies [37]. Strikingly, none of the five most widely grown exotic tree species in Singapore (*Albizia saman*, *Swietenia macrophylla*, *Khaya senegalensis*, *Tabebuia rosea*, and *Xanthostemon chrysanthus*), each with >10,000 individuals planted [26], is invasive, although casual seedlings of *A. saman*, *K. senegalensis*, and *T. rosea* are fairly common [38]. This shows that propagule pressure alone is not sufficient to drive invasion. Conversely, the widely planted forestry tree, *Acacia mangium*, which is naturalizing throughout the humid tropics of SE Asia on poor soils [39], is only casual in Singapore, where it has rarely been planted. Other naturalization failures are likely to reflect Singapore's extremely equable equatorial climate, which lacks the seasonal cues on which tropical plant reproduction often depends. Possible candidates for this barrier to naturalization include the globally widespread tropical invasive trees, *Castilla elastica*, *Miconia calvescens*, *Psidium cattleianum*, and *Syzygium jambos*, which have all been cultivated in Singapore, but only *C. elastica* and *S. jambos* produce the occasional self-sown sapling.

The nine invasive tree species in Singapore differ considerably in their biological characteristics and also in their pathways to invasion success, suggesting that predicting which tree species will become invasive will be difficult. Coutts *et al.* [40] show that the rate of spread of an invasive species is expected, in general, to be driven primarily by dispersal ability, with mean dispersal distances the best single predictor. However, the small size of Singapore in relation to normal seed dispersal distances, and the wide initial planting of some species, may make this factor less important. *M. carthaginensis* depends on ballistic seed dispersal (with possibly secondary dispersal by ants) and *F. moluccana* and *S. campanulata* have relatively large, wind-dispersed seeds, but all three were widely planted in the past, so their distributions within Singapore do not appear to be dispersal-limited today. *L. leucocephala* also has limited natural dispersal by mechanical means, but its persistent seed bank [41] probably ensures dispersal with soil, and it is common around construction sites. All the other invasive species have small seeds in fleshy fruits that are readily swallowed by ubiquitous open-country birds (yellow-vented bulbul, *Pycnonotus goiavier*, mynas, *Acridotheres* spp., and others) and, in some species, by fruit bats (*Cynopterus brachyotis*). This should permit dispersal distances of >1 km per generation [32], which is consistent with the rapid spread of the newest invaders, none of which were widely planted. On the other hand, *Cecropia*, *Muntingia*, *Piper*, and *Pipturus* all have considerably smaller seeds than most native pioneers, which may limit their ability to invade natural gaps in native forests, as suggested for *Cecropia peltata* in Malaysia [31].

Implications for conservation

Both the survey and the planting experiment suggest that none of the currently invasive tree species in Singapore is a threat to the integrity of native closed-canopy forest. *Spathodea* appears to have the most shade-tolerant saplings and is present in the margins of the Nature Reserves, but these incursions appear to be a reflection of past disturbance and there is no sign of active invasion into closed forest. However, two of the species considered naturalized but not (yet) invasive, *Hevea brasiliensis* and *Andira inermis*, potentially are a threat because of their shade-tolerant saplings. *Hevea* is likely to be permanently constrained by poor seed dispersal, but *A. inermis* is dispersed well by fruit bats and is of greater concern. Removal of all adult trees of both species from the nature reserves and their immediately vicinity would be a sensible precaution. The populations of the other species listed above as potentially invasive should be monitored. The trait comparisons suggest that the currently invasive exotic trees are distinguished by smaller seeds and less dense wood—presumably proxies for the pioneer traits of good dispersal and rapid height growth. However, the opposite traits—large seeds and denser wood—are likely to be associated with potential for invading closed-canopy forests [42, 43], and these species may be of greater concern in the long run [44]. Fortunately, any invasion by such species is likely to be slow and should be detectable by surveying the fringes of the reserves at regular intervals for shade-tolerant saplings of additional exotic species.

A key strategy for reducing the risk from alien plant invasions is to prevent their introduction by a formal risk assessment of species before they are imported [45]. The most widely used risk assessment for plants is the Australian Weed Risk Assessment System (A-WRA). A test of the transferability of A-WRA scores from other tropical localities showed that these can be used directly in Singapore, reducing the number of species that would require new assessments [46]. However, Singapore is a tiny, trade-dependent economy, protective of its number one global rankings for both ‘ease of doing business’ and ‘trading across borders’ (World Bank Group; www.doingbusiness.org/rankings). The introduction of new border controls would not be seen as compatible with this. A more practical alternative may be to assess alien species *after* they have become established in Singapore, either in cultivation or in the wild. This has the additional advantage of including the many accidental introductions, which would not be prevented by pre-border screening. A focus on species that can potentially invade the closed-canopy native forests in Singapore’s Nature Reserves would further reduce the burden of enforcement, and eliminating high-risk species from a 1-km width quarantine zone around the Reserves would be a practical way to minimize invasion risk. Moreover, most tree planting in Singapore is by government agencies and a small number of private developers, so a voluntary policy might work.

In contrast to the situation in native, closed-canopy forests, invasive exotics dominate all stages of plant succession on most land that has been abandoned in recent decades. When protected from further disturbance these sites eventually develop an invasive-dominated closed-canopy forest. This contrasts strikingly with the native secondary forest that developed on land abandoned from the late nineteenth century through to around the middle of the twentieth century [29]. This pattern resembles that reported for New York, where exotic trees dominate most ‘regenerated patches’, on sites that had been cleared for urban use and then abandoned, but native trees continue to dominate in areas that were forested when incorporated into the city [47]. Three factors may account for these two very different successional trajectories in Singapore, but the evidence is insufficient at present to assess their relative importance. One possibility is that it reflects differences in soil conditions: earlier sites were simply abandoned after farming to exhaustion, while more recent sites were generally bulldozed clear of a mixture of small settlements, tree crops, and vegetable farms. An alternative or additional explanation is that the earlier sites were all within dispersal distance of native forests, while more recent sites have typically been isolated from native forest and exposed to a rain of invasive tree seeds. A third possibility is that invasive species are superior to native pioneers on sites where propagules of both are available. This could occur if the invasive trees had advantageous traits that are not present in the native flora: two possibilities suggested by this study are nitrogen fixation (three invasives, but no native pioneers) and wind-dispersed seeds (two invasives, but very few native pioneers, none common). Moreover, release from natural enemies could create an alien advantage even in the absence of differences in other traits [16]. This was not directly assessed in this study, but the observation that invasive exotic species are significantly farther from their native ranges than non-invasive exotic species is consistent with enemy release being a factor, and this needs further study.

A key question for the future of Singapore's vegetation is: what happens next to these alien-dominated forests? Will the invasives gradually displace the remaining native species? Will the natives gradually replace the invasives? Or, will Singapore end up with 'novel forests' in which native and invasive species coexist? Parallel situations can be found on oceanic islands, such as Puerto Rico [48], Hawaii [4], and the Ogasawara (Bonin) Islands [49], but Singapore has a hyperdiverse continental rainforest flora, with 860 native tree species, including a diverse pioneer flora. In this situation, the high diversity of species and functional groups would be expected to capture most available resources and thus minimize the potential for plant invasions [16, 18]. Yet this is clearly not the case. If Singapore is vulnerable to invasive trees preempting forest recovery, then so, potentially, is everywhere else in the increasingly human-dominated continental tropics. The same invasive tree species, with several others, dominate increasing areas on the urban fringes of Asian cities and scattered patches in rural areas (personal observations). Scale is important, however, and dispersal limitation greatly reduces the immediate threat to most non-urban areas, except from widely grown exotic plantation trees, including several species of *Acacia*.

Finally, Singapore and most of SE Asia are expected to be 2-4°C warmer by the end of this century, with less predictable changes in rainfall [50], creating a climate that has not existed anywhere on Earth since the Pliocene. The thermal and other tolerances of Singapore's native flora are unknown, but most of the native, naturalized, and cultivated exotic trees come from relatively open vegetation types in drier tropical climates, where temperature maxima are likely to exceed those currently experienced in Singapore. Tolerance of drought and temperature extremes may add to the invasive potential of the exotic tree species that have already escaped from cultivation and may allow other species to do so in future.

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