NATURE IN SINGAPORE **18**: e2025044
Date of Publication: 13 May 2025
DOI: 10.26107/NIS-2025-0044

Nutrient rich anthropogenic soil substrates promote albizia invasion

Weng Ngai **Lam**[1*], G. Kenny **Png**[1], Sherry M. X. **Hung**[2], Jo Lyn **Loo**[1], Madeleine S. **Koeniger**[1] & Jerome W. K. **Kok**[3]

[1]The Asian School of the Environment, Nanyang Technological University, 50 Nanyang Avenue, Singapore 639798, Republic of Singapore. Email: wengngai.lam@ntu.edu.sg ([*]corresponding author)
[2]549 Jurong West Street 42, Singapore 640549, Republic of Singapore
[3]National University of Singapore College, National University of Singapore, 18 College Ave East, Singapore 138593, Republic of Singapore

Abstract. Albizia (*Falcataria falcata*) is an invasive legume species in many tropical countries. In Southeast Asia, albizia often forms monodominant canopies in urban forests, with other non-native tree species in the subcanopy. Such exotic species-dominated forests (EFs) are commonly found in urban areas, representing an alternative stable state that has arisen from an alternative successional trajectory to native species-dominated secondary forests in the region, such as adinandra belukar (AB). It has been proposed that anthropogenic soil substrates (e.g., imported soil, construction rubble) promote albizia invasion, but the complex land use histories of most urban sites prevent the evaluation of this hypothesis. We identified an EF patch that occurs adjacent to an AB patch in Singapore. Historical satellite imagery showed that the EF patch regenerated on a road embankment that was constructed and abandoned in 2009. Soil from the EF patch had greater resin [P], inorganic [N], and pH than the AB patch. Further, leaf traits of EF- and AB-associated tree species from the TRY global trait database showed that the EF-associated species exhibit traits associated with nutrient acquisitive strategies, while those of the AB-associated species were associated with nutrient conservative strategies. These results strongly suggest that the introduction of anthropogenic substrates during soil backfilling following urban land abandonment increases soil pH and nutrient availabilities, which in turn promotes albizia and other fast-growing invasive species to establish an alternative stable state forest-type, differing from natural secondary forests in Singapore. The introduction of nutrient-rich anthropogenic soil substrates likely promotes albizia invasion in Southeast Asia as well as many other nutrient-impoverished tropical ecosystems globally.

Key words. alternative stable state, exotic species-dominated forest, leaf economics spectrum, leaf traits, resource acquisition strategy, soil pH

INTRODUCTION

Albizia (*Falcataria falcata* (L.) Greuter & R.Rankin) is a fast growing, nitrogen-fixing leguminous tree that is considered invasive in many tropical countries (Sherley, 2000). In Southeast Asia, albizia often forms monodominant canopies in urban landscapes, with other non-native tree species in the subcanopy; such forests are locally known as exotic species-dominated forests (EF; Yee et al., 2016). Albizia is known to dramatically increase soil nutrient levels, facilitating the invasion of other non-native plant species and suppressing native species (Hughes & Denslow, 2005; Hughes et al., 2012). Albizia forests have only recently (post-1960s) become a substantial part of the landscape in Singapore (Yee et al., 2016), and may grow in prevalence with increasing land-use change and abandonment. The long-term successional trajectory of such EFs remains unclear, although observations point toward a limited transition toward native species-dominated forest types (Nghiem et al., 2015).

In Singapore, cleared or abandoned areas often become rapidly colonised by fast-growing albizia, resulting in the development of closed-canopy EFs within a matter of years (Yee et al., 2016). But this has not always been so. Before the 1960s, open areas with nutrient-depleted soils from past agriculture tended to be dominated by grasslands or ferns for decades, transitioning slowly into a forest type known as "adinandra belukar" (AB; because it is often dominated by the tree species *Adinandra dumosa* [Pentaphylacaceae]) (Sim et al., 1992). Adinandra belukar represents a unique, species-poor assemblage of tree species that are tolerant of low nutrient conditions, capable of efficient long-distance dispersal, and facilitated by exhaustive agricultural exploitation. It has been proposed that the higher nutrient content of anthropogenic soil substrates used to backfill abandoned sites facilitates albizia invasion (Lam et al., 2020), since natural forests in Singapore and the region tend to be nutrient impoverished (Grubb et al., 1994). However, compelling evidence for this hypothesis has not been presented, largely because the complex land-use histories of most urban sites prevent the evaluation of the causal factors driving these successional trajectories.

To investigate how the introduction of anthropogenic soil substrates may facilitate the dominance of non-native species, we examined the relationships between soil nutrient availability and leaf traits, related to resource use strategies of dominant native and non-native tree species in unmanaged urban forest patches in Singapore with contrasting successional trajectories. We identified an EF patch that occurs adjacent to an AB patch with well-documented land use histories in Singapore. We hypothesised that the EF patch would have significantly higher soil nutrient concentrations than the adjacent AB patch, and tree species associated with this forest type would have leaf traits associated with resource-acquisitive strategies.

MATERIAL & METHODS

Study sites. The study was conducted in equatorial Singapore, at an urban site (Holland Plains at 1°19′46″N 103°46′56″E) which was likely prepared for development in 2009, but subsequently abandoned (Fig. 1A). Comparisons between historical and present-day satellite images obtained from Google Earth Pro (Google, Mountain View, CA) suggest that vegetation was cleared in a narrow stretch of land adjacent to the road, backfilled with rubble (Fig. 1B) to form a road embankment, and that this area was subsequently colonised by albizia trees and grew into EF (hereafter referred to as younger EF because it is no more than 15 years old [YEF]), while adjacent areas remained as AB-precursor scrubland (hereafter also referred to as AB; Fig. 1C–E). Prior to development, vegetation in the area could be classified as AB, while another EF patch was present to the west and south of the site (hereafter referred to as older EF because it was already closed canopy forest in 2000 and thus significantly greater than 24 years old [OEF]; Fig. 1E) according to the earliest available satellite images (2000).

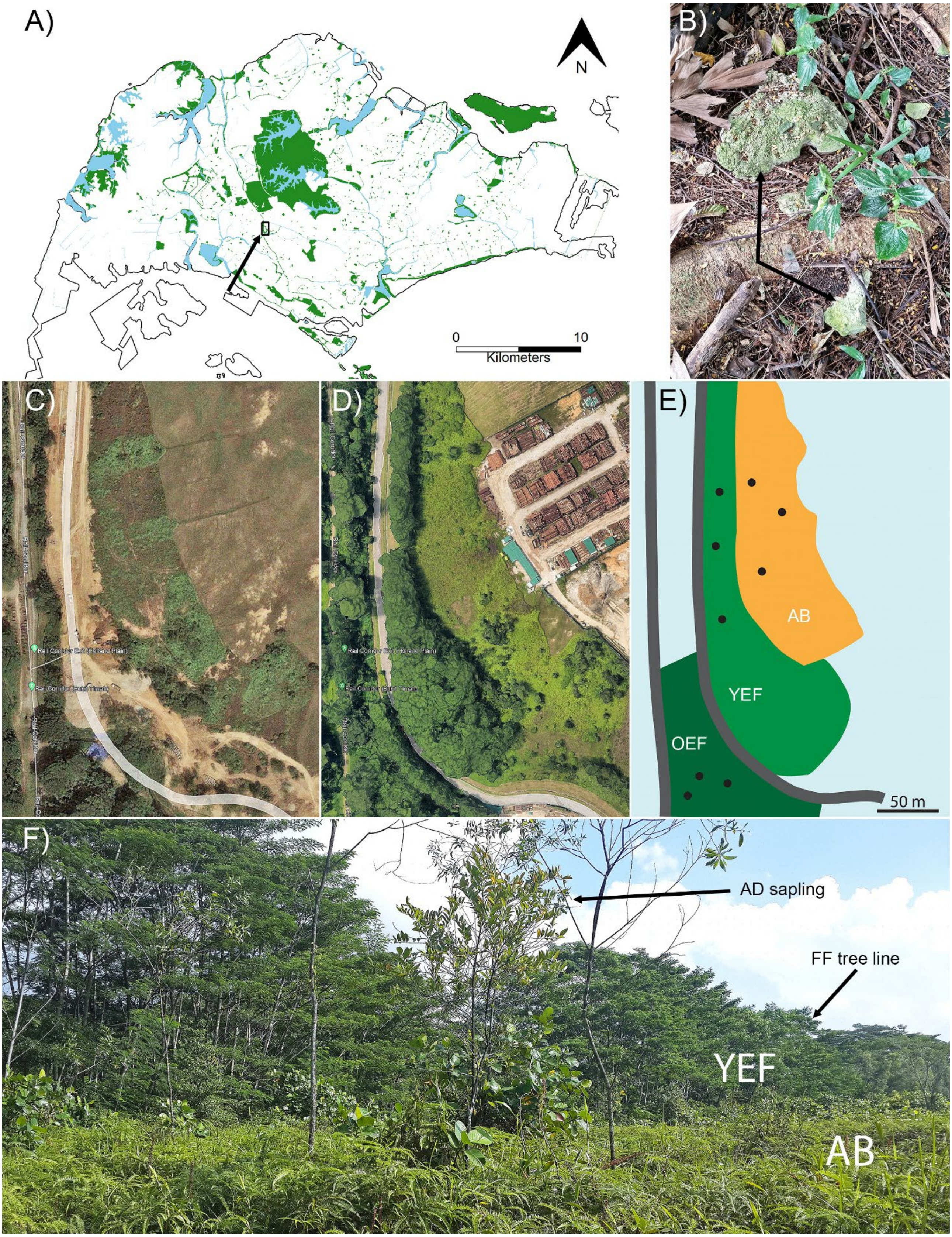

Fig. 1. A, site location within Singapore indicated by black box and arrow; B, concrete and other anthropogenic rubble often observed on the forest floors of exotic species-dominated forests (EFs); C, satellite images of the site in 2009 and D, 2022 show that parts of the cleared areas subsequently developed into an EF patch with tree cover; E, schematic vegetation map of the contrasting vegetation types in 2022 (AB = Adinandra belukar; YEF = younger exotic species-dominated forest; OEF = older exotic species-dominated forest), and the locations of soil cores obtained from them (black circles); F, contrasting vegetation boundary between AB and YEF, with albizia (*Falcataria falcata*; FF) forming a distinct tree line which stands out from the AB-precursor scrubland (note the *Adinandra dumosa* [AD] sapling in the foreground). (Map data A: data.gov.sg; satellite maps C, D: Google, Maxar Technologies; photographs B and F by: Lam Weng Ngai).

Soil chemical analyses. Three soil cores 10 cm (depth) × 5 cm (diameter) were taken each from the AB, YEF and OEF patches (Fig. 1C). Prior to soil chemical analyses, large debris were removed by hand from each soil sample and then homogenised within a bag. We measured soil pH using a 1:2 soil-to-solution ratio and a glass electrode pH meter. Soil total phosphorus [P] was determined by igniting each soil sample at 550°C for 1 h, followed by acid extractions using a 1M H_2SO_4 solution, and then measuring the acid extracts using a molybdate colourimetry method at 880 nm on a Tecan Spark® multimode microplate reader (Tecan, Männedorf, Switzerland) (Turner & Romero, 2009). Readily exchangeable phosphate (resin [P]) was measured by an anion exchange membrane extraction method (Myers et al., 1999), followed by molybdate colourimetry method at 880 nm on a Tecan Spark® multimode microplate reader (Tecan, Männedorf, Switzerland) (Turner & Romero, 2009). Soil total nitrogen [N] and organic carbon [C] were measured on an Elementar vario EL cube CHN elemental analyser (Elementar, Langenselbold, Germany). Soil inorganic [N] (nitrate + ammonia) was extracted using a 1M KCl solution (Øien & Selmer-Olsen, 1980; Gianello & Bremner, 1986), and then measured at 520 nm (nitrate) and 660 nm (ammonia) on a SEAL AA500 flow colourimetry autoanalyzer (Seal Analytical, Norderstedt Germany). Values obtained from this study were compared to those obtained from eight native species-dominated early to late successional secondary forest plots across the Central Catchment Nature Reserve using identical methods, in an unpublished study by Png et al.

Resource acquisition strategies. All tree species in the three forest patches were identified (Table S1), and 12 of the most strongly EF-/AB-associated species (six from each forest type association) were identified for analysis of leaf traits (Table 1). Importantly, these 12 species are well-characterised in the literature as EF- and AB-associated species in many EF and AB sites across Singapore (Sim et al., 1992; Tan et al., 2010; Yee et al., 2016). Data of the following leaf economics spectrum (LES) traits were then acquired from the TRY global plant trait database (Kattge et al., 2020) for these 12 species: specific leaf area (SLA); leaf thickness; leaf N; leaf P. Trait data were obtained from a total of 22 studies (Table S2).

RESULTS

Soil nutrients. Inorganic [N] was significantly higher in OEF than AB ($t = 3.55$; $df = 4$; $p = 0.02$), and in YEF than AB ($t = 2.95$; $df = 4$; $p = 0.04$; Fig. 2A). The inorganic [N] of YEF (22.16 ± 4.08 mg kg^{-1} [mean ± SE]) was close to that of native species-dominated secondary forests recorded in other studies (25.35 ± 1.42 mg kg^{-1}; Fig. 2A; Png et al., unpub. data). Total [N] was marginally lower in AB than in YEF ($t = 2.52$; $df = 4$; $p = 0.06$), and significantly lower in AB than in OEF ($t = 3.63$; $df = 4$; $p = 0.02$; Fig. 2D).

Resin [P] was significantly higher in OEF than AB ($t = 9.04$; $df = 4$; $p < 0.01$), and in YEF than AB ($t = 8.63$; $df = 4$; $p < 0.01$). The resin [P] of AB (0.00272 ± 0.00178 mg kg^{-1} [mean ± SE]) was lower than that of native species-dominated secondary forests estimated by other studies (0.216 ± 0.056 mg kg^{-1}; Png et al., unpub. data) and several magnitudes lower than that of YEF (2.92 ± 1.62 mg kg^{-1}; Fig. 2B). Likewise, total [P] was significantly lower in AB than in YEF ($t = 7.32$; $df = 4$; $p < 0.01$) and OEF ($t = 9.90$; $df = 4$; $p < 0.01$; Fig. 2E).

Soil pH was significantly higher in OEF than AB ($t = 3.22$; $df = 4$; $p = 0.03$), and in YEF than AB ($t = 3.24$; $df = 4$; $p = 0.03$). The pH of native species-dominated secondary forests estimated by other studies (3.57 ± 0.08 [Png et al., unpub. data], as compared to 4.75 ± 0.48 in the AB patch) was significantly lower than that found in all three patches in this study (Fig. 2C).

Soil organic [C] did not differ significantly between the vegetation types (Fig. 3F).

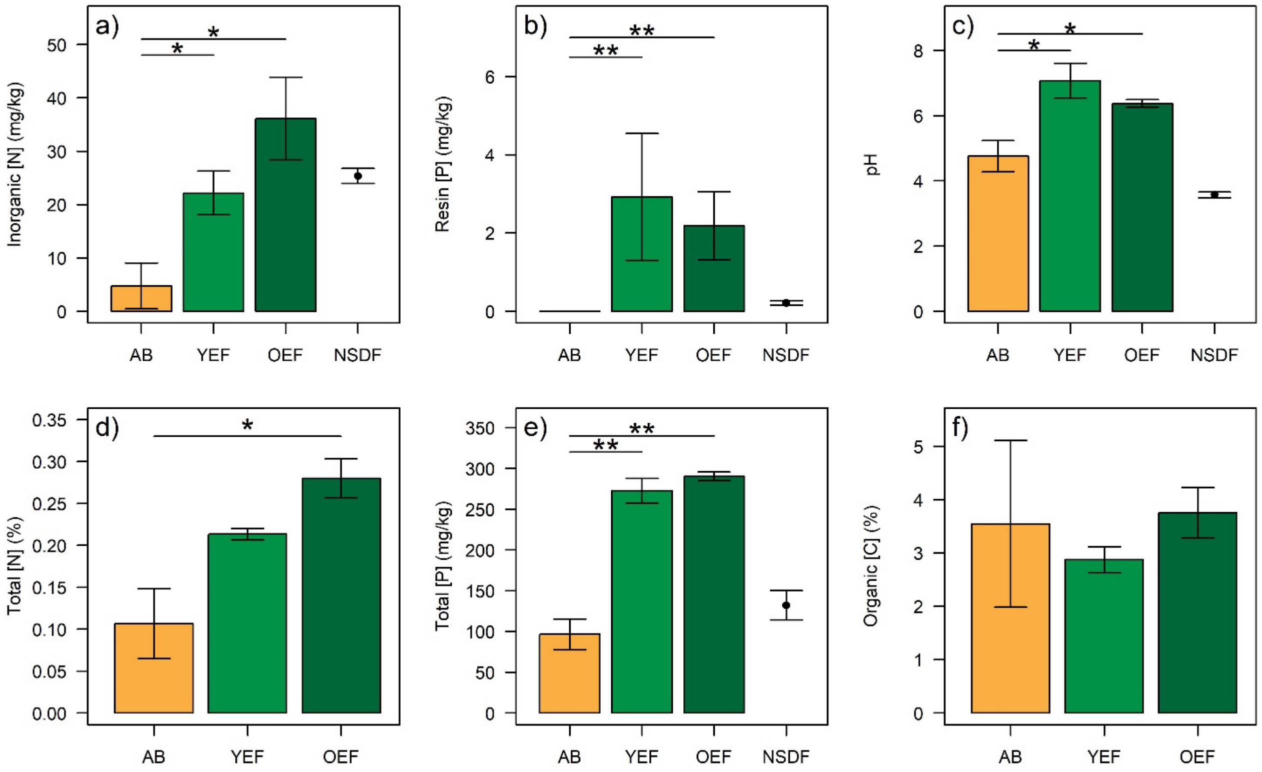

Fig. 2. Bar plots comparing soil: A, inorganic [N]; B, resin [P]; C, pH; D, total [N]; E, total [P]; and F, organic [C] between adinandra belukar (AB), younger exotic species-dominated forest (YEF), and older exotic species-dominated forest (OEF). Mean (filled circles) and standard errors (error bars) of these soil properties in native species-dominated secondary forests (NSDF) are displayed for comparison where available. Bars denote means, and vertical error bars denote standard errors. Horizontal bars with asterisks indicate significantly different means between two groups; *p*-values: 0.01 < * ≤ 0.05; ** ≤ 0.01. *n* = 3.

Resource acquisition strategies. Of the four traits investigated, SLA was the best collected, with trait data available for all 12 tree species, while leaf [P] was only obtained for eight of the 12 species (Table 1). Tree species associated with EF were found to have marginally higher SLA ($t = 2.00$; df = 10; $p = 0.07$; Fig. 3A), marginally thinner leaves ($t = 2.19$; df = 9; $p = 0.06$; Fig. 3B), higher leaf [N] ($t = 2.51$; df = 8; $p = 0.04$; Fig. 3C) and higher leaf [P] ($t = 4.76$; df = 6; $p < 0.01$; Fig. 3D) than species associated with AB. The links between SLA (positive), leaf nutrients (positive) and leaf thickness (negative) and resource acquisitiveness are well established in the literature (Wright et al., 2004). These results thus show that EF-associated tree species are significantly more acquisitive in resource acquisition strategies than AB-associated tree species, which are more conservative.

Table 1. Summary of mean ± standard error trait values obtained from the TRY database of 12 tree species associated with adinandra belukar (AB) and exotic species-dominated secondary forest (EF) vegetation types. Values for which standard error are not reported were obtained from only a single source. *Rhodamnia cinerea* (Myrtaceae) was included for leaf trait analysis to make up a larger sample size of AB-associated species (it is a species with complete leaf trait data), even though it was not observed in this study (Table S1), as it is strongly associated with AB habitats across many other similar patches in Singapore.

Species	**Vegetation type association**	**Specific leaf area ($mm^2\ mg^{-1}$)**	**Leaf thickness (mm)**	**Leaf [N] ($mg\ g^{-1}$)**	**Leaf [P] ($mg\ g^{-1}$)**
Adinandra dumosa **(Pentaphylacaceae)**	AB	7.74 ± 0.66	0.26 ± 0.05	–	–
Dillenia suffruticosa **(Dilleniaceae)**	AB	11.59 ± 0.11	0.28	17.01 ± 0.72	–
Cyrtophyllum fragrans **(Gentianaceae)**	AB	13.01 ± 2.08	0.23	19.25	–
Melastoma malabathricum **(Melastomataceae)**	AB	20.02 ± 1.22	0.25 ± 0.01	18.11 ± 1.05	0.816 ± 0.164
Ploiarium elegans **(Bonnetiaceae)**	AB	8.51	0.42	9.8	0.14
Rhodamnia cinerea **(Myrtaceae)**	AB	6.65 ± 0.62	0.205 ± 0.055	7.6	0.17

Species	Vegetation type association	Specific leaf area (mm^2 mg^{-1})	Leaf thickness (mm)	Leaf [N] (mg g^{-1})	Leaf [P] (mg g^{-1})
Aphanamixis polystachya **(Meliaceae)**	EF	28.82 ± 4.19	0.029	15.75 ± 2.25	2.244 ± 0.155
Claoxylon indicum **(Euphorbiaceae)**	EF	19.26	–	–	–
Ficus fistulosa **(Moraceae)**	EF	13.47 ± 2.77	0.185 ± 0.005	23.8 ± 0.3	1.523 ± 0.027
Mallotus paniculatus **(Euphorbiaceae)**	EF	15.08 ± 0.44	0.158 ± 0.031	32.16 ± 0.89	1.567 ± 0.045
Falcataria falcata **(Fabaceae)**	EF	15.97 ± 4.37	0.169	28.2 ± 2.42	1.29 ± 0.388
Spathodea campanulata **(Bignoniaceae)**	EF	12.79 ± 2.83	0.282	19.31 ± 1.93	1.597 ± 0.151

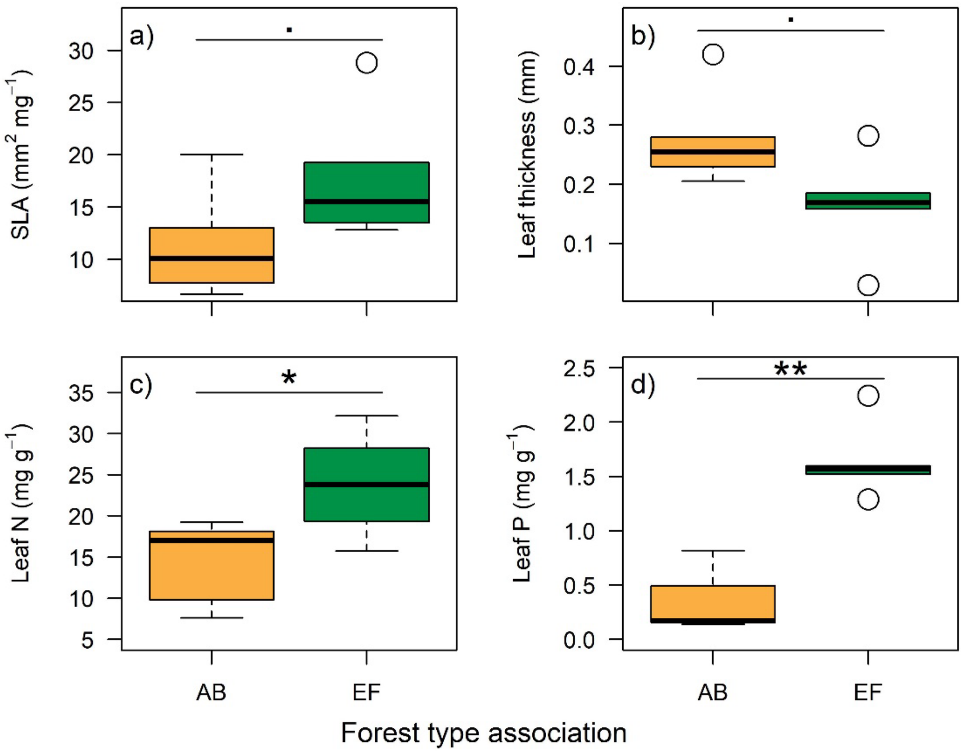

Fig. 3. Box plots comparing leaf traits between adinandra belukar (AB)- and exotic species-dominated forest (EF)-associated tree species. Boxes are interquartile ranges; bold lines in boxes are medians; whiskers are maxima and minima; points are outliers. SLA = specific leaf area; p-values: 0.05 < · ≤ 0.10 ; 0.01 < * ≤ 0.05; ** ≤ 0.01. n = 4–6.

DISCUSSION

In this case study of adjacent exotic species-dominated forest (EF) and adinandra belukar (AB) vegetation patches, historic satellite images showed that the younger EF patch developed on areas that were prepared for development in 2009, while areas that were not affected by that development remained as AB-precursor scrubland. Comparisons of soil nutrients and pH showed that soils from both the younger EF patch and a nearby older EF patch had significantly greater nutrient availability and higher pH than those from the AB patch. Correspondingly, global leaf trait data showed that tree species in the EF patches (which are well-characterised EF-associated species across the region; Yee et al., 2016; Sherley, 2000) were much more resource-acquisitive than tree species in the AB patch (which are well-characterised as AB-associated species across the region; Sim et al., 1992; Turner et al., 1995; Tan et al., 2010; Yee et al., 2016). Together, these results suggest that the introduction of anthropogenic soil substrates (e.g., imported soil and construction rubble) with greater nutrient concentrations and higher pH likely enables albizia and other fast-growing non-native species to establish a unique forest type and alternative stable state to native species-dominated secondary forests containing acidic, nutrient-impoverished soils.

The non-native species occurring within the EF patches generally showed higher leaf N and P concentrations, which suggests greater resource demand, lower resource-use efficiency, and faster growth rates (Reich, 2014). This aligns with the observation that non-native species dominate in the EF patch with higher soil nutrient concentrations, but are largely absent from the nutrient-poor AB patch. In contrast, native species found within the AB vegetation patch were likely adapted to nutrient-poor conditions and showed generally lower leaf N and P concentrations, which suggests greater resource-use efficiency and slower growth (Wright et al., 2004; Reich, 2014). It is important to note that the leaf trait data used in this study was obtained from a global trait database (TRY) and may differ from those collected from our specific study site, although intraspecific trait variation among sites is likely to be relatively small compared to the differences in traits of plant species which have contrasting resource-use strategies. Thus, the differences in leaf nutrient allocation strategies between the native and non-native species of our study site suggests that non-native species associated with EFs may hold a competitive advantage in resource-rich environments, as predicted by our hypothesis, allowing them to competitively exclude native species.

The introduction of anthropogenic soil substrates during soil backfilling likely increased soil nutrient content and availability, particularly P and total N. This likely promoted the growth of various non-native plant species, notably the symbiotic N-fixing albizia species. While albizia is unlikely to be N-limited in nutrient-impoverished, native tropical forest soils due to its ability to symbiotically acquire atmospheric N, increased soil P availability can enhance the investment of albizia in N fixation and the allocation of resources (e.g., N and P) towards its growth and competitiveness (Sprent, 1999). Furthermore, higher soil pH, a potential consequence of backfilling with construction rubble containing mildly alkaline materials (e.g., limestone in cement), can further enhance soil P availability through increased solubilisation of less available soil P fractions (Lambers & Oliveira, 2019), which could further contribute to the competitive advantage of a range of nutrient-acquisitive non-native and EF-associated species. Therefore, the introduction of anthropogenic soil substrates is likely to promote invasion by a diverse assemblage of fast-growing and nutrient-acquisitive plants, including but not limited to the N-fixing albizia, both in Southeast Asia and many other nutrient-impoverished tropical ecosystems globally. As such, our study suggests that urban planners should be more selective in the choice of soils used for backfilling or the construction of road embankments in areas that are likely to be left vacant for prolonged periods of time (Hulme, 2006). The use of soil that more closely matches native conditions can potentially alleviate a key invasion pathway, and consequently support greater native biodiversity across urban landscapes.

Albizia litter can elevate the nutrients of soils on which it is found (Hughes & Uowolo, 2006), but such litter feedback alone is unlikely to explain the large differences in nutrients and pH observed in our study. Comparisons between YEF and OEF patches showed that increases in soil nutrients over ten or more years (the OEF patch is at least ten years older than the YEF patch) were small in comparison to the differences between AB and YEF. Moreover, the distinct tree line separating YEF and AB patches strongly supports our soil nutrient data and the presence/absence of concrete rubble in shallow soil between the vegetation patches, indicating an edaphic driver of vegetation type differences. The shift in soil properties within this and other EF patches was likely due to the deposition of concrete rubble during backfilling activities, presumably to create an embankment and prevent erosion (Fig. 1). Finally, although our study is based on a single site, our findings that the AB and EF vegetation communities represent assemblages of species with contrasting resource acquisition strategies, with soil nutrient availability as a key driver, is consistent with well-established ecological principles regarding resource allocation and community assembly (Schröder et al., 2005; Isbell et al., 2013). Nevertheless, further research, such as expanding the study to include replicate field sites or conducting controlled greenhouse experiments, is warranted to further strengthen our conclusions and test the generality of our findings.

ACKNOWLEDGEMENTS

We thank Ming Yang Lee for assistance with SEAL operation, and Goh Kwan Chien, Carol Zhang, Phoebe Zhou, Muhammad Nasry Abdul Nasir, and Elijah Goh for assistance with fieldwork. This study was partially supported by the National Research Foundation, Singapore, Intra-Create Seed Collaboration Grant (NRF2022-ITS010-0010).

LITERATURE CITED

Gianello C & Bremner JM (1986) A simple chemical method of assessing potentially available organic nitrogen in soil. Communications in Soil Science and Plant Analysis, 17: 195–214. https://doi.org/10.1080/00103628609367708

Grubb P, Turner I & Burslem D (1994) Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: Analysis of soil, leaves and litter. Journal of Tropical Ecology, 10: 559–577. doi:10.1017/S0266467400008233

Hughes RF & Denslow JS (2005) Invasion by a N2-fixing tree alters function and structure in wet lowland forests of Hawaii. Ecological Applications 5: 1615–1628.

Hughes RF & Uowolo A (2006) Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: The importance of stand-level controls. Ecosystems, 9: 977–991. https://doi.org/10.1007/s10021-005-0083-9

Hughes RF, Uowolo AL & Togia TP (2012) Recovery of native forest after removal of an invasive tree, *Falcataria moluccana*, in American Samoa. Biological Invasions 14: 1393–1413. https://doi.org/10.1007/s10530-011-0164-y

Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology, 43(5): 835–847. https://doi.org/10.1111/j.1365-2664.2006.01227.x

Isbell F, Tilman D, Polasky S, Binder S & Hawthorne P (2013) Low biodiversity state persists two decades after cessation of nutrient enrichment. Ecology Letters, 16: 454–460.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, Acosta ATR, Adamidis GC, Adamson K, Aiba M, Albert CH, Alcántara JM, Alcázar C, Aleixo I, Ali H, Amiaud B, Ammer C, Amoroso MM, Anand M, Anderson C, Anten NPR, Antos J, Apgaua DMG, Ashman T-L, Asmara DH, Asner GP, Aspinwall MJ, Atkin OK, Aubin I, Baastrup-Spohr L, Bahalkeh K, Bahn M, Baker TR, Baker WJ, Bakker JP, Baldocchi D, Baltzer JL, Banerjee A, Baranger A, Barlow J, Barneche DR, Baruch Z, Bastianelli D, Battles JJ, Bauerle WL, Bauters M, Bazzato E, Beckmann M, Beeckman H, Beierkuhnlein C, Bekker RM, Belfry GC, Belluau M, Beloiu M, Benavides R, Benomar L, Berdugo M, Berenguer E, Bergamin RS, Bergmann J, Bergmann Carlucci M, Berner L, Bernhardt-Römermann M, Bigler C, Bjorkman AD, Blackman CJ, Blanco CC, Blonder B, Blumenthal DM, Bocanegra-González KT, Boeckx P, Bohlman SA, Bohlman GN, Boisvert-Marsh L, Bond WJ, Bond-Lamberty B, Boom A, Boonman CC, Bordin K, Boughton EH, Boukili V, Bowman DMJS, Bravo S, Brendel MR, Broadley MR, Brown KA, Bruelheide H, Brumnich F, Bruun HH, Bruy D, Buchanan SW, Bucher SF, Buchmann N, Bueno CG, Buitink J, Bunker DE, Búrquez A, Butterfield BJ, Byun C, Cabido M, Cahill JF Jr, Camac JS, Camarero JJ, Campany CE, Campetella G, Campos JA, Cano-Arboleda L, Canullo R, Carbognani M, Carvalho F, Casanoves F, Castagneyrol B, Catford JA, Cavender-Bares J, Cerabolini BEL, Cervellini M, Chacón-Madrigal E, Chapin FS, Chapin K, Chelli S, Chen S-C, Chen W, Chevalier L, Chicca M, Choat B, Chung K-F, Ciccarelli D, Coll L, Collins CG, Conti G, Coomes DA, Cornelissen JHC, Cornwell WK, Corona P, Coyea MR, Craine JM, Craven D, Cromsigt JPGM, Csecserits A, Cufar K, Cuntz M, da Silva AC, Dahlin KM, Dainese M, Dalke I, Dalle Fratte M, Dang-Le AT, Danihelka J, Dannoura M, Dawson SK, de Beer AJ, de Frutos A, de Long JR, de Oliveira A, de Oliveira GB, de Vries FT, Dechant B, Delagrange S, Delpierre N, Derroire G, Dias AS, Díaz-Toribio MH, Dietze MC, Dimitrakopoulos PG, Dines T, Dissanayake M, Djordjevic M, Dobrowolski MP, Doktor D, Dolezal J, Dolos K, Döring E, Dos Santos RM, Douma JC, Dreyer E, Drissi R, Du G, Duarte L, Dullinger S, Durka W, Duursma RA, Dymova O, E-Vojtkó A, Eckstein RL, Ejtehadi H, Elser J, Elumeeva TG, Emberson E, Enquist BJ, Eppinga MB, Erfanian MB, Erfmeier A, Esquivel-Muelbert A, Esser G, Estiarte M, Evans MEK, Everwand G, Ewers BE, Ewers RM, Falster DS, Fan Y, Fang J, Farris E, Fazlioglu F, Feng Y, Fernández-Méndez F, Ferrara C, Ferreira J, Fidelis A, Finegan B, Firn J, Flores O, Flynn DFB, Fontana V, Forey E, Forgiarini C, França MB, Frank D, Frenette-Dussault C, Freschet GT, Fry EL, Fyllas NM, Gallagher RV, Ganade G, Ganga F, García-Palacios P, Gargaglione V, Garnier E, Garrido JL, de Gasper AL, Gea-Izquierdo G, Gibson DJ, Gillison AN, Giroldo AB, Glasenhardt MC, Gleason SM, Gliesch M, Goldberg E, Goldstein G, Gomis SM, González-Akre EB, González-M R, González-Robles A, Graae BJ, Granda E, Graves S, Green WA, Gregor T, Gross N, Guerin GR, Guo W, Gutiérrez AG, Haddock L, Haines A, Hakeem KR, Hall JS, Hambuckers A, Han W, Harrison SP, Hattingh WN, Hattori M, He T, He P, Heberling JM, Helm A, Hempel S, Hentschel J, Hérault B, Heres AM, Herz K, Heuertz M, Hickler T, Hietz P, Higuchi P, Hikosaka K, Hirons AD, Hock M, Hogan JA, Holl KD, Honnay O, Hornstein D, Hou E, Hough-Snee N, Hovenden MJ, Hughes RF, Huntley B, Hynd A, Ibanez T, Ichie T, Igić B, Illa E, Isaac ME, Ishihara MI, Ishida A, Ishii H, Ishiwawa M, Ivanov LA, Iversen CM, Izquierdo J, Jackson RB, Jackson BG, Jackson L, Jagodzinski AM, Jandt U, Jansen S, Jenkins T, Jentsch A, Jespersen JR, Jiang G, Johansen JL, Johnson DJ, Jokela EJ, Joly CA, Jordan GJ, Joseph GS, Junaedi DI, Junker RR, Justes E, Kabzems R, Kane JM, Kaplan Z, Kattenborn T, Kavelenova L, Kearsley E, Kempel A, Kenzo T, Kerkhoff AJ, Khalil MI, Khan ML, Kharecha P, Kim H-S, Kim J, Kim M, Kim T-Y, Kimura K, King DA, Kitzberger T, Kjøller R, Klein T, Kleyer M, Klimešová J, Klipel J, Kloeppel B, Klotz S, Knops JMH, Kohyama T, Koike F, Kollmann J, Komac B, Komatsu K, König C, Kraft NJB, Kramer K, Kreft H, Kühn I, Kumarathunge D, Kuppler J, Kurokawa H, Kurosawa Y, Kuyah S, Laclau JP, Lafleur B, Lallai E, Lamb E, Lamprecht A, Larkin DJ, Laughlin D, Le Bagousse-Pinguet Y, le Maire G, le Roux PC, le Roux E, Lee T, Lens F, Lewis SL, Lhotsky B, Li Y, Li X, Lichstein JW, Liebergesell M, Lim JY, Lin YS, Linares JC, Liu C, Liu D, Liu U, Livingstone S, Llusià J, Lohbeck M, López-García Á, Lopez-Gonzalez G, Lososová Z, Louault F, Lukács BA, Lukeš P, Luo Y, Lussu M, Ma S, Maciel Rabelo Pereira C, Mack M, Maire V, Mäkelä A, Mäkinen H, Malhado ACC, Mallik A, Manning P, Manzoni S, Marchetti Z, Marchino L, Marcilio-Silva V, Marcon E, Marignani M, Markesteijn L, Martin A, Martínez-Garza C, Martínez-Vilalta J, Mašková T, Mason K, Mason N, Massad TJ, Masse J, Mayrose I, McCarthy J, McCormack ML, McCulloh K, McFadden IR, McGill BJ, McPartland MY, Medeiros JS, Medlyn B, Meerts P, Mehrabi Z, Meir P, Melo FPL, Mencuccini M, Meredieu C, Messier J, Mészáros I, Metsaranta J, Michaletz ST, Michelaki C, Migalina S, Milla R, Miller JED, Minden V, Ming R, Mokany K, Moles AT, Molnár V A, Molofsky J, Molz M, Montgomery RA, Monty A, Moravcová L, Moreno-Martínez A, Moretti M, Mori AS, Mori S, Morris D, Morrison J, Mucina L, Mueller S, Muir CD, Müller SC, Munoz F, Myers-Smith IH, Myster RW, Nagano M, Naidu S, Narayanan A, Natesan B, Negoita L, Nelson AS, Neuschulz EL, Ni J, Niedrist G, Nieto J, Niinemets Ü, Nolan R, Nottebrock H, Nouvellon Y, Novakovskiy A, Nutrient Network, Nystuen KO, O'Grady A, O'Hara K, O'Reilly-Nugent A, Oakley S, Oberhuber W, Ohtsuka T, Oliveira R, Öllerer K, Olson ME, Onipchenko V, Onoda Y, Onstein RE, Ordonez JC, Osada N, Ostonen I, Ottaviani G, Otto S, Overbeck GE, Ozinga WA, Pahl AT, Paine CET, Pakeman RJ, Papageorgiou AC, Parfionova E, Pärtel M, Patacca M, Paula S, Paule J, Pauli H, Pausas JG, Peco B, Penuelas J, Perea A, Peri PLL, Petisco-Souza AC, Petraglia A, Petritan AM, Phillips OL, Pierce

S, Pillar VD, Pisek J, Pomogaybin A, Poorter H, Portsmuth A, Poschlod P, Potvin C, Pounds D, Powell AS, Power SA, Prinzing A, Puglielli G, Pyšek P, Raevel V, Rammig A, Ransijn J, Ray CA, Reich PB, Reichstein M, Reid DEB, Réjou-Méchain M, Resco de Dios V, Ribeiro S, Richardson S, Riibak K, Rillig MC, Riviera F, Robert EMR, Roberts S, Robroek B, Roddy A, Rodrigues AV, Rogers A, Rollinson E, Rolo V, Römermann C, Ronzhina D, Roscher C, Rosell JA, Rosenfield MF, Rossi C, Roy DB, Royer-Tardif S, Rüger N, Ruiz-Peinado R, Rumpf SB, Rusch GM, Ryo M, Sack L, Saldaña A, Salgado-Negret B, Salguero-Gomez R, Santa-Regina I, Santacruz-García AC, Santos J, Sardans J, Schamp B, Scherer-Lorenzen M, Schleuning M, Schmid B, Schmidt M, Schmitt S, Schneider JV, Schowanek SD, Schrader J, Schrodt F, Schuldt B, Schurr F, Selaya Garvizu G, Semchenko M, Seymour C, Sfair JC, Sharpe JM, Sheppard CS, Sheremetiev S, Shiodera S, Shipley B, Shovon TA, Siebenkäs A, Sierra C, Silva V, Silva M, Sitzia T, Sjöman H, Slot M, Smith NG, Sodhi D, Soltis P, Soltis D, Somers B, Sonnier G, Sørensen MV, Sosinski EE Jr, Soudzilovskaia NA, Souza AF, Spasojevic M, Sperandii MG, Stan AB, Stegen J, Steinbauer K, Stephan JG, Sterck F, Stojanovic DB, Strydom T, Suarez ML, Svenning JC, Svitková I, Svitok M, Svoboda M, Swaine E, Swenson N, Tabarelli M, Takagi K, Tappeiner U, Tarifa R, Tauugourdeau S, Tavsanoglu C, te Beest M, Tedersoo L, Thiffault N, Thom D, Thomas E, Thompson K, Thornton PE, Thuiller W, Tichý L, Tissue D, Tjoelker MG, Tng DYP, Tobias J, Török P, Tarin T, Torres-Ruiz JM, Tóthmérész B, Treurnicht M, Trivellone V, Trolliet F, Trotsiuk V, Tsakalos JL, Tsiripidis I, Tysklind N, Umehara T, Usoltsev V, Vadeboncoeur M, Vaezi J, Valladares F, Vamosi J, van Bodegom PM, van Breugel M, Van Cleemput E, van de Weg M, van der Merwe S, van der Plas F, van der Sande MT, van Kleunen M, Van Meerbeek K, Vanderwel M, Vanselow KA, Vårhammar A, Varone L, Vasquez Valderrama MY, Vassilev K, Vellend M, Veneklaas EJ, Verbeeck H, Verheyen K, Vibrans A, Vieira I, Villacís J, Violle C, Vivek P, Wagner K, Waldram M, Waldron A, Walker AP, Waller M, Walther G, Wang H, Wang F, Wang W, Watkins H, Watkins J, Weber U, Weedon JT, Wei L, Weigelt P, Weiher E, Wells AW, Wellstein C, Wenk E, Westoby M, Westwood A, White PJ, Whitten M, Williams M, Winkler DE, Winter K, Womack C, Wright IJ, Wright SJ, Wright J, Pinho BX, Ximenes F, Yamada T, Yamaji K, Yanai R, Yankov N, Yguel B, Zanini KJ, Zanne AE, Zelený D, Zhao YP, Zheng J, Zheng J, Ziemińska K, Zirbel CR, Zizka G, Zo-Bi IC, Zotz G, Wirth C (2020) TRY plant trait database – enhanced coverage and open access. Global Change Biology, 26: 119–188. https://doi.org/10.1111/gcb.14904

Lam WN, Neo L & Tan HTW (2020) Chapter 3: Habitats. In: Lam WN & Tan HTW (eds.) The Pitcher Plants of Singapore. Lee Kong Chian Natural History Museum, National University of Singapore, Singapore, pp. 31–51. http://doi.org/10.26107/LKCNHM-EBOOK-2020-0001 (Accessed 16 April 2025).

Lambers H & Oliveira RS (2019) Plant Physiological Ecology (3rd ed.). Springer Cham, Cham, Switzerland, 736 pp. https://doi.org/10.1007/978-3-030-29639-1

Myers RG, Thien SJ & Pierzynski GM (1999) Using an Ion Sink to Extract Microbial Phosphorus from Soil. Soil Science Society of America Journal, 63: 1229–1237. https://doi.org/10.2136/sssaj1999.6351229x

Nghiem LTP, Tan HTW & Corlett RT (2015) Invasive trees in Singapore: are they a threat to native forests? Tropical Conservation Science, 8: 201–214.

Øien A & Selmer-Olsen AR (1980) A laboratory method for evaluation of available nitrogen in soil. Acta Agriculturae Scandinavica B, 30: 149–156. https://doi.org/10.1080/00015128009435259

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. Journal of Ecology, 102: 275–301.

Schröder A, Persson L & De Roos AM (2005) Direct experimental evidence for alternative stable states: a review. Oikos, 110: 3–19.

Sherley G (2000) Invasive species in the Pacific: A technical review and draft regional strategy. South Pacific Regional Environment Programme, Apia, Samoa, 190 pp.

Sim JWS, Tan HTW & Turner IM (1992) Adinandra belukar: an anthropogenic heath forest in Singapore. Vegetatio, 102: 125–137. https://doi.org/10.1007/BF00044729

Sprent JI (1999) Nitrogen fixation and growth of non-crop legume species in diverse environments. Perspectives in Plant Ecology, Evolution and Systematics, 2: 149–162.

Tan HTW, Chou LM, Yeo DCJ & Ng PKL (2010) The Natural Heritage of Singapore, Third Edition. Prentice Hall, Singapore, 271 pp.

Turner IM, Ong BL & Tan HTW (1995) Vegetation analysis, leaf structure and nutrient status of a Malaysian heath community. Biotropica, 27: 2–12.

Turner BL & Romero TE (2009) Short-term changes in extractable inorganic nutrients during storage of tropical rain forest soils. Soil Science Society of America Journal, 73: 1972–1979. https://doi.org/10.2136/sssaj2008.0407

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ & Villar R (2004) The worldwide leaf economics spectrum. Nature, 428: 821–827.

Yee ATK, Chong KY, Neo L & Tan HTW (2016) Updating the classification system for the secondary forests of Singapore. Raffles Bulletin of Zoology, 32: 11–21

APPENDIX

Table S1. List of all tree species found during comprehensive surveys in young exotic species-dominated forests (YEF), old EF (OEF) and adinandra belukar (AB; native species-dominated secondary forests) patches in this study. EF (green) and AB (orange) species chosen for leaf trait analyses (Table S3) are highlighted for clarity. These species were chosen because (i) they were only found in one forest type here; (ii) they are consistently found in that same forest type in many other locations across Singapore and as reported by other studies of EF/AB.

Species	**OEF**	**YEF**	**AB**
Alstonia angustiloba (Apocynaceae)	1	1	
Andira inermis (Fabaceae)	1	1	
Aphanamixis polystachya (Meliaceae)	1	1	
Bridelia tomentosa (Phyllanthaceae)	1	1	
Calophyllum soulattri (Calophyllaceae)	1	1	
Cinnamomum iners (Lauraceae)	1	1	
Claoxylon indicum (Euphorbiaceae)	1	1	
Clausena excavata (Rutaceae)		1	
Dimocarpus lichi (Sapindaceae)		1	
Falcataria falcata (Fabaceae)	1	1	
Ficus benjamina (Moraceae)	1	1	
Ficus fistulosa (Moraceae)	1	1	
Ficus microcarpa (Moraceae)	1	1	
Ficus variegata (Moraceae)	1	1	
Leea indica (Vitaceae)	1		
Manihot carthaginensis (Euphorbiaceae)	1		
Mallotus paniculatus (Euphorbiaceae)	1	1	
Morella esculenta (Myricaceae)	1	1	
Neolitsea cassia (Lauraceae)		1	
Nephelium lappaceum (Sapindaceae)		1	
Pipturus argenteus (Urticaceae)	1	1	
Ricinus communis (Euphorbiaceae)	1		
Spathodea campanulata (Bignoniaceae)	1	1	
Sterculia parvifolia (Malvaceae)	1		
Syzygium grande (Myrtaceae)	1	1	
Syzygium myrtifolium (Myrtaceae)		1	
Syzygium polyanthum (Myrtaceae)	1	1	
Terminalia catappa (Combretaceae)	1	1	
Vitex pinnata (Lamiaceae)		1	
Acacia auriculiformis (Fabaceae)		1	1
Arthrophyllum jackianum (Araliaceae)		1	1
Syzygium cerasiforme (Myrtaceae)		1	1
Adinandra dumosa (Pentaphylacaceae)			1
Cyrtophyllum fragrans (Gentianaceae)			1
Dillenia suffruticosa (Dilleniaceae)			1
Melastoma malabathricum (Melastomataceae)			1
Ploiarium elegans (Bonnetiaceae)			1

Table S2. Datasets from TRY from which leaf trait data was obtained.

Dataset	**Reference**	**Species**	**Traits**
Traits of Bornean Trees Database	Kurokawa H & Nakashizuka T (2008) Leaf herbivory and decomposability in a Malaysian tropical rain forest. Ecology, 89: 2645–2656.	*Dillenia suffruticosa*	N, SLA
Reich-Oleksyn Global Leaf N, P Database	Reich PB, Oleksyn J & Wright IJ (2009) Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. Oecologia, 160: 207–212.	*Rhodamnia cinerea, Acacia auriculiformis, Spathodea campanulata, Aphanamixis polystachya, Acacia auriculiformis, Falcataria falcata, Melastoma malabathricum*	N, P, SLA
Global Leaf Element	Watanabe T, Broadley MR, Jansen S, White PJ, Takada J, Satake K, Takamatsu T, Tuah SJ & Osaki M (2007) Evolutionary control	*Mallotus paniculatus*	K

Dataset	**Reference**	**Species**	**Traits**
Composition Database	of leaf element composition in plants. New Phytologist, 174: 516–523.		
Global A, N, P, SLA Database	Reich PB, Oleksyn J & Wright IJ (2009) Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. Oecologia, 160: 207–212.	*Rhodamnia cinerea, Acacia auriculiformis, Spathodea campanulata, Aphanamixis polystachya, Acacia auriculiformis, Falcataria falcata*	N, P, SLA
The Tansley Review LMA Database	Poorter H, Niinemets L, Poorter L, Wright IJ & Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist, 182: 565–588.	*Adinandra dumosa, Dillenia suffruticosa, Cyrtophyllum fragrans, Mallotus paniculatus, Ploiarium elegans, Rhodamnia cinerea*	SLA
The Americas N&P database	Kerkhoff AJ, Fagan WF, Elser JJ & Enquist BJ (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. American Naturalist, 168: E103–E122.	*Ploiarium elegans*	N, P
Leaf Biomechanics Database	Onoda Y, Westoby M, Adler PB, Choong AMF, Clissold FJ, Cornelissen JHC, Diaz S, Dominy NJ, Elgart A, Enrico L, Fine PVA, Howard JJ, Jalili A, Kitajima K, Kurokawa H, McArthur C, Lucas PW, Markesteijn L, Perez-Harguindeguy N, Poorter L, Richards L, Santiago LS, Sosinski Jr E, Van Bael S, Warton DI, Wright IJ, Wright SJ & Yamashita N (2011) Global patterns of leaf mechanical properties. Ecology Letters, 14: 301–312.	*Adinandra dumosa, Dillenia suffruticosa, Cyrtophyllum fragrans, Mallotus paniculatus, Ploiarium elegans, Rhodamnia cinerea, Ficus fistulosa, Melastoma malabathricum*	SLA, LT
GLOPNET - Global Plant Trait Network Database	Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets L, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ & Villar R (2004) The worldwide leaf economics spectrum. Nature, 428: 821–827.	*Spathodea campanulata, Adinandra dumosa, Dillenia suffruticosa, Mallotus paniculatus, Cyrtophyllum fragrans, Rhodamnia cinerea, Claoxylon indicum, Ficus fistulosa, Melastoma malabathricum*	SLA, N, P
Leaf Nitrogen and Phosphorus for Chinas Terrestrial Plants	Chen Y, Han W, Tang L, Tang Z & Fang J (2011) Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. Ecography, 34. https://doi.org/10.1111/j.1600-0587.2011.06833.x	*Aphanamixis polystachya, Mallotus paniculatus, Ficus fistulosa*	P
Nutrient Resorption Efficiency Database	Vergutz L, Manzoni S, Porporato A, Novais RF & Jackson RB (2012) A global database of carbon and nutrient concentrations of green and senesced leaves. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. https://doi.org/10.3334/ORNLDAAC/1106	*Aphanamixis polystachya, Spathodea campanulata*	N, P, SLA
CTFS Luquillo Forest Dynamics Plot	Swenson NG, Anglada-Cordero P & Barone JA (2011) Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. Proceedings of the Royal Society B, 278: 877–884.	*Spathodea campanulata*	N, P, SLA
Photosynthesis Traits Worldwide	Maire V, Wright IJ, Prentice IC, Batjes NH, Bhaskar R, van Bodegom PM, Cornwell WK, Ellsworth D, Niinemets L, Ordonez A, Reich PB & Santiago LS (2015) Global soil and climate effects on leaf photosynthetic traits and rates. Global Ecology and Biogeography, 24: 706–717.	*Adinandra dumosa, Dillenia suffruticosa, Mallotus paniculatus, Melastoma malabathricum*	N, P, SLA
Tree species functional traits from Dinghushan Biosphere Reserve, southern China	Li R, Zhu S, Chen HYH, John R, Zhou G, Zhang D, Zhang Q & Ye Q (2015) Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest? Ecology Letters, 18: 1181–1189.	*Mallotus paniculatus*	N, P, SLA
The Global Leaf Traits	unpub.	*Aphanamixis polystachya, Ficus fistulosa, Cyrtophyllum fragrans, Acacia auriculiformis, Spathodea campanulata, Falcataria falcata, Melastoma malabathricum*	N, P, SLA
SLA and height data of exotic plant species in highland forest of Java and Bali	unpub.	*Acacia auriculiformis, Aphanamixis polystachya, Ficus fistulosa, Cyrtophyllum fragrans, Acacia auriculiformis, Spathodea campanulata, Falcataria falcata, Melastoma malabathricum*	N, P, SLA, LT
UppangalaTraits	Schmitt S, Raevel V, Rejou-Mechain M, Ayyappan N, Balachandran N, Barathan N, Rajashekar G & Munoz F (2021) Canopy and understorey tree guilds respond differently to the environment in an Indian rain forest. Journal of Vegetation Science, 32: 1–9. https://doi.org/10.1111/jvs.13075	*Aphanamixis polystachya*	LT, SLA
Leaf Economics Traits of Woody Species in Dinghushan	He P, Wright IJ, Zhu S, Onoda Y, Liu H, Li R, Liu X, Hua L, Oyanoghafo OO & Ye Q (2019) Leaf mechanical strength and photosynthetic capacity vary independently across 57 subtropical	*Ficus fistulosa, Mallotus paniculatus*	N, P, LT, SLA

Dataset	**Reference**	**Species**	**Traits**
Biosphere Reserve, Southern China	forest species with contrasting light requirements. New Phytologist, 223: 607–618.		
Hawaiian Leaf Traits Database	Penuelas J, Sardans J, Llusia J, Owen S, Carnicer J, Giambelluca TW, Rezende EL, Waite M & Niinemets L (2010) Faster returns on leaf economics and different biogeochemical niche in invasive compared with native plant species. Global Change Biology, 16: 2171–2185.	*Falcataria falcata*	N, P, SLA
Onoda 2017 leaf dataset	Onoda Y, Wright IJ, Evans JR, Hikosaka K, Kitajima K, Niinemets L, Poorter H, Tosens T & Westoby M (2017) Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist, 214: 1447–1463.	*Falcataria falcata*	SLA, N
Functional Traits of Trees	Paine CET, Amissah L, Auge H, Baraloto C, Baruffol M, Bourland N, Bruelheide H, Dainou K, de Gouvenain RC, Doucet J-L, Doust SJ, Fine PVA, Fortunel C, Haase J, Holl KD, Jactel H, Li X, Kitajima K, Koricheva J, Martinez-Garza C, Messier C, Paquette A, Philipson CD, Piotto D, Poorter L, Posada JM, Potvin C, Rainio K, Russo SE, Ruiz-Jaen M, Scherer-Lorenzen M, Webb CO, Zahawi RA & Hector A (2015) Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. Journal of Ecology, 103: 978–989. https://doi.org/10.1111/1365-2745.12401	*Falcataria falcata*	SLA
Tropical Traits from West Java Database	Shiodera S, Rahajoe JS & Kohyama T (2008) Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. Journal of Tropical Ecology, 24: 121–133.	*Melastoma malabathricum*	SLA, N
BAAD: a biomass and allometry database for woody plants	Falster DS, Duursma RA, Ishihara MI, Barneche DR, FitzJohn RG, Vahammar A, Aiba M, Ando M, Anten N, Aspinwall MJ, Baltzer JL, Baraloto C, Battaglia M, Battles JJ, Bond-Lamberty B, van Breugel M, Camac J, Claveau Y, Coll L, Dannoura M, Delagrange S, Domec JC, Fatemi F, Feng W, Gargaglione V, Goto Y, Hagihara A, Hall JS, Hamilton S, Harja D, Hiura T, Holdaway R, Hutley LB, Ichie T, Jokela EJ, Kantola A, Kelly JWG, Kenzo T, King D, Kloeppel BD, Kohyama T, Komiyama A, Laclau JP, Lusk CH, Maguire DA, le Maire G, Makela A, Markesteijn L, Marshall J, McCulloh K, Miyata I, Mokany K, Mori S, Myster RW, Nagano M, Naidu SL, Nouvellon Y, OGrady AP, OHara KL, Ohtsuka T, Osada N, Osunkoya OO, Peri PL, Petritan AM, Poorter L, Portsmuth A, Potvin C, Ransijn J, Reid D, Ribeiro SC, Roberts SD, Rodriguez R, Saldana-Acosta A, Santa-Regina I, Sasa K, Selaya NG, Sillett SC, Sterck F, Takagi K, Tange T, Tanouchi H, Tissue D, Umehara T, Utsugi H, Vadeboncoeur MA, Valladares F, Vanninen P, Wang JR, Wenk E, Williams R, Ximenes FA, Yamaba A, Yamada T, Yamakura T, Yanai RD & York RA (2015) BAAD: a biomass and allometry database for woody plants. Ecology, 96: 1445. https://doi.org/10.1890/14-1889.1	*Melastoma malabathricum*	SLA, N
The China Plant Trait Database	Wang H, Harrison SP, Prentice IC, Yang Y, Bai F, Togashi HF, Wang M, Zhou S & Ni J (2017) The China Plant Trait Database. Pangaea. https://doi.org/10.1594/PANGAEA.871819	*Melastoma malabathricum*	SLA, N, P
Heishiding Performance Trait Environment Data	unpub.	*Aphanamixis polystachya, Ficus fistulosa, Cyrtophyllum fragrans, Spathodea campanulata, Falcataria falcata, Melastoma malabathricum*	SLA, N, P
Koeniger M. PhD thesis	unpub.	*Cyrtophyllum fragrans, Falcataria falcata, Spathodea campanulata*	N, LT