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RESEARCH ARTICLE

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Strangler fig–host tree associations: Insights into the ecology and management of tropical urban green spaces

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Societal Impact Statement

The strangler fig is known for its hemiepiphytic growth form and conspicuous strangling behavior in the tropics worldwide. It also plays an important role in providing ecological functions in tropical urban ecosystems. This study reveals strangler figs tend to colonize large trees with suitable microsites in a large tropical botanical garden and cause some negative effects on their hosts. We advocate balanced management strategies considering ecological functions, potential risks, and overall values of stranglers and their hosts. These results provide a scientific basis for us to develop better practices for plant management in urban green spaces (especially botanical gardens with high plant biodiversity) in tropical urban ecosystems.

Summary

- Strangler figs colonize trees in tropical cities, which contribute to a unique urban ecology and enrich local ecological functions. Understanding ecological associations between strangler figs and their host trees can improve green space management in tropical urban ecosystems.
- We investigated 9282 trees growing in the Xishuangbanna Tropical Botanical Garden and then analyzed the diversity, characteristics, and network of strangler figs and their host trees.
- We found 13 strangler fig species (319 individuals) widely colonized 67 host species, with palm hosts bearing 52% of all strangler individuals. Strangler figs had a high colonization rate in large trees with appropriate microsites (e.g., persistent palm petioles and the fork of mature trees with rough trunks). Leaf nitrogen and phosphorus content of hosts decreased significantly after strangler figs' aerial roots had entered the ground. The strangler–host network was characterized by relatively high specialization and low nestedness, and simulated management of strangler figs on large hosts and palm hosts could simplify the strangler–host network.

Yu-Xuan Mo and Huang Zou contributed equally to this work.

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- Strangler fig colonization can be managed. Planting trees with large diameters at breast height and rough bark can increase the colonization of stranglers, while cutting off aerial roots can inhibit their establishment. The epiphytic stage is the best time to manage strangler figs. We recommend taking into consideration the trade-offs among ecological functioning, human safety, and the multifaceted value of strangler figs and their host trees and thereby implementing comprehensive management strategies tailored to different contexts for improving green space management in the tropics.

KEYWORDS
ecological network, host tree, strangler fig, tropical botanical garden, urban green space

1 | INTRODUCTION

Understanding the process of plant colonization and establishment is critical for the management of plant communities (Burmeier et al., 2011; Rodrigues et al., 2019). *Ficus* trees are keystone species in the tropics because they play an important role in maintaining biodiversity, for example, by providing food and diverse habitats for many species (e.g., birds, mammals, and insects) in both natural and urban ecosystems (Caughlin et al., 2012; Chong et al., 2021; Shanahan et al., 2001). The foraging and transfer of animals provide opportunities for the spread of figs and thereby also influence the colonization and establishment processes of figs (Caughlin et al., 2012; Doyle, 2000). Due to their well-developed aerial root system, a subset of fig species—the strangler figs (e.g., *Ficus microcarpa*, *F. virens*, *F. tinctoria*)—can colonize trees (Berg & Corner, 2005; Zotz et al., 2021). Strangler figs typically germinate on host trees and send their aerial roots into the soil. Some strangler figs can eventually kill and displace their host trees and become free-standing trees (Figure 1a–c). Strangler figs are notable among hemiepiphytes for their wide distribution and "host strangling" life cycle (Zotz et al., 2021). Their widespread distribution and impact on host trees underscore their ecological importance in various tropical ecosystems. Strangler fig species can also grow on hard surfaces (can even split rock or concrete structures); hence, they occur frequently in urbanized landscapes in the tropics (Chong et al., 2021; Jim, 2018). The conspicuous growth form of these figs is a feature of tropical ecosystems, and it enriches structural complexity in the vertical profile and the ecological functions of forests and cities in the tropics (Chong et al., 2021; Harrison et al., 2003). Apart from host trees in primary forests and walls in cities, many strangler figs can also frequently colonize the trees growing in various secondary plant communities, such as secondary forests (Berg & Corner, 2005) and secondary savannas (Putz & Holbrook, 1989). However, green spaces in tropical urban areas (e.g., botanical gardens that harbor large numbers of plants), as secondary communities with potential and suitable habitats for strangler figs, are mostly ignored (Patel, 1996).

Urban green spaces can provide diverse ecological services and support urban biodiversity (Zou & Wang, 2021). Biodiversity in urban green spaces plays an important role in maintaining ecological balance, mitigating microclimates, and providing opportunities for citizens to connect with nature and observe ecological processes (Lepczyk et al., 2017). Moreover, the diversity of plant species in urban green spaces increases the ecosystem benefits (Ilie & Cosmulescu, 2023). Fig species in urban green spaces also serve ecological functions, such as biodiversity maintenance (Chong et al., 2021) and microclimate regulation (Fahmy et al., 2010). Strangler figs can naturally spread, colonize, and establish themselves in urban green spaces (Figure 1a–d); when the strangler figs colonize and establish themselves in urban green spaces, they inevitably form ecological associations with different organisms, such as their host trees, pollinators, and seed dispersers. Although the pollination ecology (Harrison et al., 2017; Santos et al., 2022) and seed dispersers (Chong et al., 2021; Sheherazade et al., 2017) of strangler fig species have been studied, little is known about the ecological networks, resource competitions (Mo et al., 2022), and the corresponding management of strangler figs and their hosts in urban green spaces. Focusing on these issues is necessary because the strangler–host network refers to direct or potential interactions between different stranglers and their hosts, and these interactions can be further quantified and analyzed to understand patterns and dynamics of the network's stability, host specialization of stranglers, and the possible effects on host trees (Hu et al., 2022).

However, there is also a gap in our understanding of the corresponding ecology and management of strangler figs vis-à-vis their host trees in tropical urban green spaces. Examining these issues is imperative and will allow for better management of urban green spaces because the colonization and establishment of strangler figs could quickly change the landscape of green spaces in tropical urban areas (Lepczyk et al., 2017). As the "shop windows of biodiversity", botanical gardens belong to urban green spaces that play an essential role in biodiversity maintenance, scientific research, science popularization, and tourism (Chen & Sun, 2018; Ward et al., 2010). Strangler figs often successfully establish in tropical botanical gardens (Harrison et al., 2017; Li et al., 2024). Given that tropical botanical gardens collect and conserve various native and introduced tree species (Chen et al., 2009), these could serve as hosts of strangler figs, and stranglers could directly or indirectly threaten their survival as well.

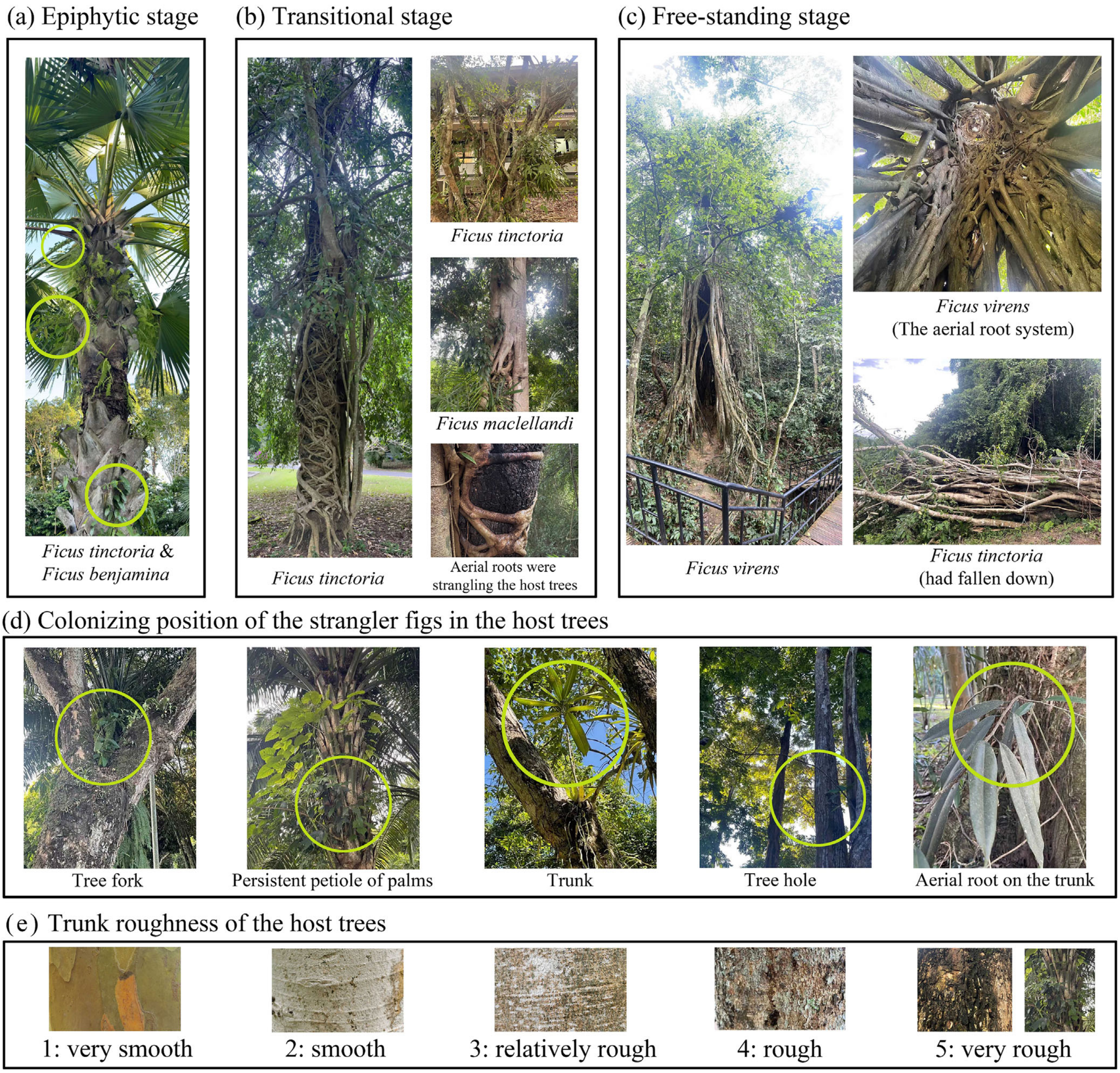


FIGURE 1 The colonization and establishment of strangler figs and characteristics of the host trees. (a) Strangler figs at the epiphytic stage. (b) Strangler figs at the transitional stage. (c) Strangler figs at the free-standing stage. (d) Different colonizing positions of the strangler figs in the host trees. (e) Trunk roughness of the host trees (five levels). All the strangler figs shown grew in the Xishuangbanna Tropical Botanical Garden.

Nevertheless, the management measures (e.g., pruning) for strangler figs and their host trees in tropical green spaces have received little attention. The strangler–host network we focused on in this study is the commensal network formed when the strangler fig has colonized the host tree (from epiphytic to free-standing stages forming obvious strangulation landscape) because this has significant effects on urban green space management. The dynamics of strangler–host network under different simulating scenarios can be used to predict possible changes in network structure and can guide urban greening and management (Hu et al., 2022). The tree risk caused by strangler figs occasionally happens (Figure 1c), which also needs to be considered in the management of urban green space (Judice et al., 2021; Koeser et al., 2015).

In this study, we investigated the diversity and characteristics of strangler figs and their host trees in a large tropical botanical garden as a proxy for understanding the associations of strangler figs in urban green spaces. We analyzed the network relations between the stranglers and their hosts and measured the leaf traits of representative host trees. Specifically, we address the following questions: (I) Can host preference be predicted by tree characteristics; Does mixed host assemblage drive strangler fig–host network abundance? (II) What is the effect of strangler fig burden on host trees, and (III) What are appropriate management interventions for strangler fig incursions in urban green spaces? The findings generated from this study will elucidate patterns of strangler–host networks, contribute to a deeper understanding of the colonization and establishment of strangler figs, and provide insights for improved management of botanical gardens or other urban green spaces with similar conditions in the tropics.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is the Xishuangbanna region, located on the northern edge of the tropics, with a floristic composition like that of the Malay Peninsula (Zhu et al., 2006). This study was conducted from 2021 to 2022 in the Xishuangbanna Tropical Botanical Garden (XTBG), of the Chinese Academy of Sciences (21°56′N, 101°15′E), located in Menglun, Yunnan Province, Southwest China (Figure S1). XTBG received 780,902 visitors annually (2015–2019), and the landscape formed by strangler figs has always been one of popular attractions in the XTBG. The mean annual temperature is 21.7°C, and the mean annual precipitation is 1480 mm (Liu et al., 2014). This area has distinct rainy (May to October, with 85% of annual rainfall) and dry (November to April) seasons. With an average elevation of ca. 560 m a.s.l., the XTBG has a generally flat topography (Figure S1). The XTBG's vegetation coverage is more than 90% and is composed mainly of secondary woodland, secondary forest, primary forest, garden nursery, and artificial grassland. The common soil type here is Ferralsols, whose depth is ca. 2 m in the XTBG, with a soil pH of 3–6 (Mo et al., 2022).

The XTBG has amassed a collection of over 13,000 plant species. There are 81 *Ficus* spp., including 19 strangler figs spp. (15 native, 4 introduced) and 62 non-strangler fig spp. (34 native, 28 introduced). Most of the introduced fig species (except *Ficus religiosa* and *F. binnendijkii*) were cultivated in the *Ficus* collection (established in 1996, under close-to-natural management), whereas native fig species distributed naturally in the forests and woodlands of the XTBG. Among the introduced strangler figs, *F. religiosa* and *F. binnendijkii* have since naturalized and now reproduce naturally, but *F. elastica* and *F. benghalensis* have yet to. Almost all the strangler figs are growing naturally (i.e., their development began in the tree), except for six strangler individuals (now at the free-standing stage) were artificially planted in the *Ficus* collection.

2.2 | Vegetation survey

We established 10 transects in the XTBG, each 1000 m long and GPS-referenced (Figure S1) avoiding areas with few trees like artificial lakes, lawns, and scrublands (because strangler figs need host trees in their early stage). Within 10 m wide on each side of these transects, we carefully searched for strangler figs and recorded all trees with a diameter at breast height (DBH) > 3 cm, totaling 9282 trees (256 hosts, 9026 nonhosts, no strangler included). The survey ensured a sufficient sampling effort for studying the species accumulation of strangler figs (Figure S2).

We surveyed all visible trees within a 10-m width along each transect for strangler figs, recording each fig's species, growth stage, colonizing position, and measuring the height of colonization using a laser distance meter. We identified three growth stages of strangler figs and their common colonizing positions. For figs whose host trees had died and disappeared already, we marked the position as "uncertain." Substrate samples in hosts and nonhosts were collected from these positions during the rainy season and processed to measure their fresh weight, dry weight, and water content (see Note S1 for details). Additionally, we recorded data on the host trees and conducted a random sampling of nonhost trees (957 trees) for investigating their species identity, DBH, height, and trunk roughness (detailed information was provided in Table 1 and Note S1).

2.3 | Host tree sampling strategy and trait measurements

Because sampling and analyzing the leaf samples of host trees and nonhost conspecifics could reflect their actual living conditions, this could guide host tree management. Based on our field survey, we selected *Elaeis guineensis* (Arecaceae, a monocot) and *Senna siamea* (Fabaceae, a eudicot) as representative materials to analyze the influence of strangler figs on their hosts. All strangler figs were identified as *Ficus tinctoria*. To determine the effects of strangler figs on their host trees during the host-killing process, we chose the hosts to span its different phases: hosts with no strangler fig (HNSF; $n = 5$), with an epiphytic strangler fig (HESF; $n = 5$), and with a transitional strangler fig (HTSF; $n = 5$). The sun-exposed, mature, and intact leaves of the two host tree species (similar-sized host and nonhost trees were sampled; Figure S3), 15 central lobules for each *E. guineensis*; 15 leaves for each *S. siamea* at these different phases were sampled (see Note S2 for host tree sampling details).

Firstly, leaf water content and specific leaf area (SLA) of host trees were measured. SLA was calculated by dividing leaf area (leaf area meter, LI-3000C, LI-COR, Lincoln, NE, USA) with its dry weight. For leaf nutrient traits, we ground oven-dried leaves to analyze their carbon (C_{mass}) and nitrogen (N_{mass}) content using a C/N analyzer (Vario MAX C/N, Elementar Analysensysteme GmbH, Hanau, Germany). Phosphorus (P_{mass}) content was measured after leaf sample digestion and analyzed via inductively coupled plasma atomic-emission spectrometry (ICP-AES: iCAP6300, Thermo Fisher Scientific, Bremen, Germany). Then, we also calculated the C:N, C:P, and N:P ratios of the host leaves.

2.4 | Management on strangler figs

After the vegetation survey, 20 strangler fig individuals (at transitional stage, normal growth) in the sampled transects were managed by two different methods; (i) severing of aerial roots (had entered into the soil) of strangler figs that were wrapped around main trunk of host plants, and (ii) severing the main branches of strangler figs. We reinvestigated the growth state of corresponding strangler figs and scored them from 0 to 5 (see Table 1 for details).

TABLE 1 Field survey information of strangler figs and their host trees in the Xishuangbanna Tropical Botanical Garden.

Plant type	Investigated information	Additional information
Strangler figs	Species identity	**(I)** Native or introduced **(II)** Endangered species (protected by law or policy) or not
	Growth stages	**(I)** Epiphytic stage (living with a live host tree, no aerial roots penetrated the soil) **(II)** Transitional stage (living with a live host tree, some aerial roots penetrated the soil) **(III)** Free-standing stage (host tree is dead; most aerial roots penetrated the soil.)
	Colonization height	**(I)** Actual height measured in the field.
	Colonizing positions	**(I)** Fork of hosts (FH) **(II)** Persistent petiole of palms (PPP) **(III)** Tree trunk of hosts (TTH) **(IV)** Tree hole of hosts (THH) **(V)** Aerial roots (of figs or lianas) on the host tree trunk surface (ARH) **(VI)** Uncertain
	Substrate (mixture of canopy humus and litter) in colonizing positions	**(I)** Fresh weight **(II)** Dry weight **(III)** Water content
	The vitality state after management	**(I)** Score 0: Dead, no green leaves on branches, no reborn branches, and dry bark **(II)** Score 1: Close to death, nearly no green leaves on branches, no reborn branches, and nearly dry bark **(III)** Score 2: Severely restrained growth, alive with few green leaves and few reborn branches **(IV)** Score 3: Restrained growth, alive with some green leaves and some reborn branches **(V)** Score 4: Nearly unaffected growth, alive with many green leaves and reborn branches **(VI)** Score 5: Normal growth, unaffected growth
Host trees and non-host trees	Species identity	**(I)** Native or introduced **(II)** Endangered species (protected by law or policy) or not
	Diameter at breast height (DBH)	**(I)** Actual DBH measured in the field
	Height	**(I)** Actual height measured in the field.
	Trunk roughness	**(I)** Score 1: Very smooth, without fissures, furrows, or other obvious topography **(II)** Score2: Smooth, with shallow fissures **(III)** Score 3: Relatively rough, shallowly furrowed **(IV)** Score 4: Rough, with some fissures or furrows **(V)** Score 5: Very rough and with abundant deep fissures and furrows or other topography

2.5 | Data analysis

2.5.1 | Network analysis

The network approach offers the computation of several metrics to describe topological structure and to quantitatively analyze community stability. We constructed a matrix-based bipartite network where nodes represent host trees and strangler figs and links represent their interactions (colonization events). Each cell in the matrix represents the number of observed interactions between the corresponding host and strangler fig species (Pu et al., 2021). Using the R package "bipartite" (Dormann et al., 2009), we calculated key parameters of the network such as connectance (indicating the overall interaction density), nestedness (NODF: reflecting network organization), H_2' (reflecting stranglers' specialization), and other parameters were shown in Table S1. We further compared the observed network parameters to those from null models (random network), which allowed us to determine if the observed network structure deviates significantly from random expectations. By employing these parameters, we aim to understand the complexity and stability of the strangler–host network, identify key host species that support strangler fig colonization, and assess the potential impacts of different management on the network structure.

Furthermore, removal based on indices of strangler figs or their hosts could be informative to explore the dynamics of their network structure under different management scenarios. To assess how the strangler–host network responds to various management scenarios, simulations of strangler figs–host network dynamics were conducted following the method of Hu et al. (2022). These scenarios included removing strangler figs based on host tree DBH (from small to large, HDBH (S ~ L); from large to small HDBH (L ~ S)), growth stage (from epiphytic to transitional SFG (E ~ T); transitional to epiphytic SFG (T ~ E)), host species numbers (from few to many HSN (F ~ M), from many to few HSN (M ~ F)), and random removal (SFR). The network's connectance, NODF, specialization (H_2'), and modularity were then analyzed to understand the dynamics during these different management processes (see Note S3 for data analysis details).

2.5.2 | Statistical analysis

We analyzed the differences between host and nonhost trees, including DBH, height, trunk roughness, and substrate weight, using *t*-tests or Wilcoxon rank sum tests. Variations in substrate weight among different colonization positions and host traits across strangler fig growth stages were assessed with ANOVA or Kruskal–Wallis tests, followed by Tukey HSD or pairwise Wilcoxon tests. Spearman correlations examined the link between substrate weight and fig colonization frequency. For visualizations, we used R packages "ggplot2" (Ginestet, 2011) and "ggpubr" (Kassambara, 2019).

We utilized Generalized Linear Mixed Models (GLMMs) and Linear Mixed Models (LMMs) to analyze the impact of host characteristics (i.e., DBH, trunk roughness, and host height) and colonization traits (i.e., colonizing position and height of stranglers) on strangler figs' colonization and establishment. The models also tested the influence of strangler growth stage and host species on host tree traits. Sampling transects were incorporated as random factors in these models. The significance of effects was determined using log-likelihood-ratio tests, comparing GLMMs and LMMs with and without specific factors (Lu et al., 2020). There are no nested explanatory variables in the GLMMs and LMMs. These analyses were conducted using the "lme4" package (Bates et al., 2015). The detailed information on statistical analysis is described in the Note S3.

All statistical analyses were performed in R software, version 4.0.5 (R Core Team, 2021).

3 | RESULTS

3.1 | Species composition of strangler figs and their host trees

We found 319 individuals of strangler fig from 13 species (11 native and 2 introduced species; Table 2). *F. tinctoria* was the most common species, accounting for 54% (171 individuals) of all strangler figs, followed by *F. maclellandii* (12%) and *F. benjamina* (10%). By contrast, the abundances of other strangler fig species were relatively low. Moreover, 48% of the strangler figs were at the epiphytic stage, while the other, 44% had rooted into the soil and were growing together with the host tree (transitional stage), and a few individuals (8%) had already killed their host trees (free-standing stage).

The 256 host individuals (2.8% of the investigated trees) belonged to 67 tree species (Table S2) in 27 families (Table 3). Because 13 individuals of host trees were completely or almost disintegrated, they were not identified. Sometimes, more than one strangler fig individuals colonized the same part of the host, and this phenomenon was commonly seen in Arecaceae (i.e., palm species)

TABLE 2 Species and growth stage of strangler figs in the Xishuangbanna Tropical Botanical Garden.

				Growth stages		
***Ficus* species**	**Section**	**Native or introduced**	**Total number**	**Epiphytic**	**Transitional**	**Free-standing**
F. tinctoria	*Palaeomorphe*	Native	171	65 (38%)	94 (55%)	12 (7%)
F. maclellandii	*Urostigma*	Native	38	32 (84%)	5 (13%)	1 (3%)
F. benjamina	*Urostigma*	Native	32	26 (81%)	4 (13%)	2 (6%)
F. subulata	*Palaeomorphe*	Native	26	1 (4%)	25 (96%)	0 (0%)
F. curtipes	*Urostigma*	Native	18	12 (67%)	6 (33%)	0 (0%)
F. virens	*Urostigma*	Native	13	2 (15%)	4 (31%)	7 (54%)
F. altissima	*Urostigma*	Native	5	1 (20%)	0 (0%)	4 (80%)
F. binnendijkii	*Urostigma*	Introduced	5	5 (100%)	0 (0%)	0 (0%)
F. concinna	*Urostigma*	Native	4	4 (100%)	0 (0%)	0 (0%)
F. glaberrima	*Urostigma*	Native	2	2 (100%)	0 (0%)	0 (0%)
F. microcarpa	*Urostigma*	Native	2	2 (100%)	0 (0%)	0 (0%)
F. religiosa	*Urostigma*	Introduced	2	2 (100%)	0 (0%)	0 (0%)
F. geniculata	*Urostigma*	Native	1	0 (0%)	1 (100%)	0 (0%)
Total	2	-	319	154 (48%)	139 (44%)	26 (8%)

F. tinctoria and *F. subulata* are from *Sycidium* subgenus, and the rest are all from *Urostigma* subgenus.
Strangler fig species were ranked by their number of individuals.
All fig species listed were not endangered species.

TABLE 3 Families of the host trees colonized by strangler figs in the Xishuangbanna Tropical Botanical Garden.

Family	Total number	Species number	Endangered plant individuals	DBH ± SE (cm)	Height ± SE (m)	Trunk roughness ± SE
Arecaceae	133	11	2	47.67 ± 1.01	12.39 ± 0.24	4.9 ± 0.0
Fabaceae	42	12	0	59.59 ± 5.24	15.21 ± 0.67	3.7 ± 0.2
Moraceae	17	10	0	47.72 ± 7.31	14.43 ± 1.01	2.8 ± 0.2
Bignoniaceae	6	4	0	38.64 ± 8.58	14.54 ± 1.93	3.7 ± 0.5
Malvaceae	6	3	3	48.77 ± 7.68	16.26 ± 2.07	3.7 ± 0.3
Anacardiaceae	4	1	0	83.00 ± 9.68	13.22 ± 0.49	3.3 ± 0.3
Dipterocarpaceae	3	2	1	65.61 ± 18.24	16.9 ± 3.11	4.0 ± 1.0
Sapindaceae	3	2	1	28.43 ± 6.12	5.62 ± 0.35	4.0 ± 0.6
Lecythidaceae	3	1	0	81.83 ± 28.38	15.64 ± 4.50	3.3 ± 0.7
Fagaceae	2	2	1	26.95 ± 4.85	14.55 ± 1.54	3.0 ± 0.0
Lamiaceae	2	2	0	44.45 ± 9.65	22.38 ± 3.56	3.0 ± 0.0
Lauraceae	2	2	0	48.33 ± 23.93	14.42 ± 2.49	4.0 ± 0.0
Myrtaceae	2	2	0	35.48 ± 19.63	7.34 ± 2.14	3.0 ± 2.0
Euphorbiaceae	2	1	0	140.53 ± 9.39	23.07 ± 0.25	4.5 ± 0.5
Lythraceae	2	1	0	74.27 ± 6.27	15.73 ± 1.18	3.5 ± 0.5
Magnoliaceae	2	1	0	22.40 ± 2.70	11.27 ± 0.83	3.0 ± 0.0
Meliaceae	2	1	0	78.24 ± 3.24	17.37 ± 0.37	5.0 ± 0.0
Myristicaceae	2	1	0	28.10 ± 13.70	16.81 ± 2.45	2.5 ± 0.5
Annonaceae	1	1	0	26.74	15.68	4.0
Apocynaceae	1	1	0	40.10	13.59	4.0
Ebenaceae	1	1	0	3.80	3.02	3.0
Elaeocarpaceae	1	1	0	9.60	6.99	2.0
Guttiferae	1	1	0	101.22	14.07	5.0
Phyllanthaceae	1	1	0	10.80	6.29	2.0
Rhamnaceae	1	1	0	40.75	10.85	5.0
Rosaceae	1	1	0	38.20	5.05	5.0
Uncertain hosts	13	-	-	-	-	-
Total	256	67	8	50.71 ± 1.59	13.40 ± 0.26	4.3 ± 0.1

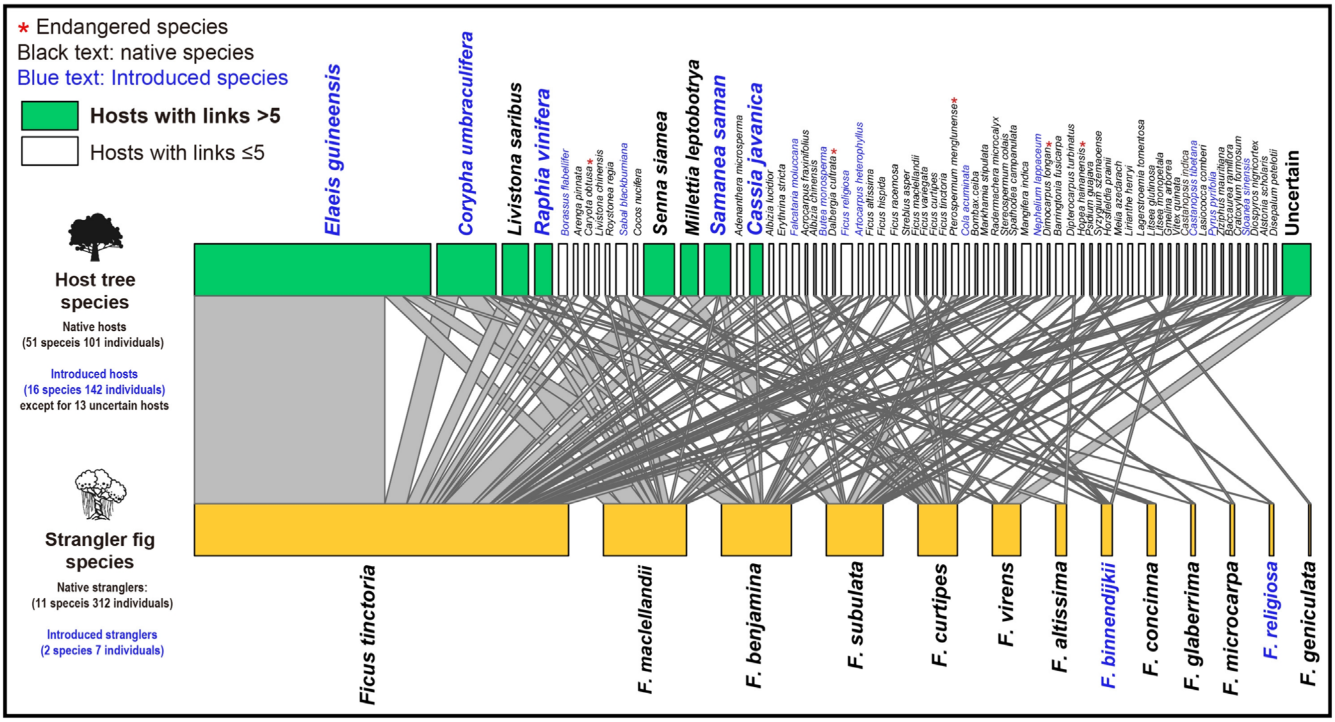
Note: Some host trees were completely (or almost) disintegrated; these 13 individuals could not be identified.

hosts (Figure 1a). Palms (Arecaceae) accounted for more than 50% (133 individuals) of all the host trees, with the *E. guineensis* (92 individuals loaded with 108 strangler figs, 71 individuals without stranglers) being the most common host. Only eight individuals of the host trees were endangered plant species currently protected by law or policy.

3.2 | The strangler–host network

In the strangler–host network (Figure 2), *F. tinctoria* maintained the most links (171 among 35 host species), followed by *F. maclellandii* (38 among 13 host species), *F. benjamina* (32 among 17 host species), *F. subulata* (26 among 14 host species), *F. curtipes* (18 among 12 host species), and *F. virens* (12 among 5 host species, but 7 hosts could not be identified)—the number of links for all other strangler figs was <5. Among the host trees, *E. guineensis* sustained the highest number of links (108 among 4 strangler species; introduced), followed by *Corypha umbraculifera* (27 among 6 strangler species; introduced), *S. siamea* (14 among 2 strangler species; native), *Livistona saribus* (12 among 4 strangler species; native), and *Samanea saman* (12 among 4 strangler species; introduced). The introduced host species (*E. guineensis*, *C. umbraculifera* and *S. saman*) accounted for about half of all links in the strangler–host network (Figure 2; Table S2).

Compared to the random network, the strangler–host network exhibited high specialization and low nestedness (Figure 2). For the key parameters, the connectance (0.13) of the strangler–host network was notably lower than those in the random network (0.16). The NODF of the strangler–host network (23.48) was significantly lower than that of the random network (44.38), indicating lower nestedness in the strangler–host network. The strangler–host network's H_2' (0.47) was significantly higher than the random network's H_2' (0.17), suggesting the specialization in strangler–host associations. The other network parameters are shown in the Figure 2.



The parameters of the strangler-host network

Parameters	Meanings of the Parameters	Strangler-host network	Random network
Connectance	Number of observed interactions divided by the total number of possible interactions	0.13***	0.16
NODF	Nestedness based on overlap and decreasing fill (the values from 0 to 100, and the 0 indicates the low nestedness)	24.38***	44.38
H2'	A quantitative measurement that reflects the specialization, (from 0: no specialization to 1: perfect specialization)	0.47***	0.17
Interaction evenness	A metric to detect potential interaction dominance in the ecological network	0.56***	0.62
Generality	A weighted mean effective number of strangler fig species per host tree species	2.15***	3.42
Vulnerability	A weighted mean effective number of host species per strangler fig species	9.29***	14.79
Linkage density	Marginal totals-weighted diversity of interactions per species	5.72***	9.10

FIGURE 2 Network between strangler figs and their host trees. Each bar is a species: orange ones represent strangler figs, green and white ones represent host trees. Each gray line, termed a link, combines different bars to represent the interactions of host trees and strangler figs. The size of a bar corresponds to the amount of interacting partners, and the width of an interaction is proportional to its observed frequency. The parameter meanings and corresponding parameters of strangler–host network and random network are given below the illustrated network. *** denotes significant difference in corresponding parameters between strangler–host network and random network, $p < 0.0001$.

3.3 | The characteristics difference among hosts and nonhosts and different colonization positions

Based on the comparison of DBH, tree height and trunk roughness between host and nonhost trees, we found significantly higher DBH (mean: 51.0 cm vs. 15.9 cm) and tree height (mean: 13.4 m vs. 9.2 m) as well as rougher trunk (mean: 4.3 vs. 2.8) in host tree than nonhost tree ($p < 0.001$; Figure 3a–c). These results indicated that strangler figs had a higher colonization rate in larger trees with rougher trunks. Moreover, the substrate amount in persistent petiole of palms (PPP), fork of hosts (FH), and tree trunk of hosts (TTH) was significantly higher ($p < 0.05$) than that of corresponding positions of nonhost trees. While substrate amount in the tree hole of hosts (THH) and aerial roots on the host tree surface (ARH) had no significant difference from that of nonhosts ($p > 0.05$, Figure 3d).

We found strangler fig individuals varied in their colonization frequency among different colonizing positions, in the order of PPP > FH > THH > TTH > ARH (Figure 3e). Despite the relatively large variation present in substrate fresh weight (host trees: 2–667 g vs. nonhost trees: 1–175 g), it also differed significantly ($\chi^2 = 20.66$, $p < 0.001$) among the five colonizing positions (Figure 3f), whose ranking was PPP > FH > THH > TTH > ARH. The colonization frequency of strangler figs was positively correlated ($R^2 = 0.85$, $p < 0.0001$) with the fresh weight of the substrate (Figure 3g). Concerning the host characteristics, having a rough trunk (≥3) supported the majority of strangler fig individuals (Figure 3h). The colonizing height of transitional strangler figs was lower (i.e., more frequently occurred at ≤3 m) than that of epiphytic or free-standing ones (Figure 3i). The DBH and height of palm hosts were relatively similar, yet both measures of other dicotyledon hosts were more heterogeneous (Figure 3j,k; Table 3).

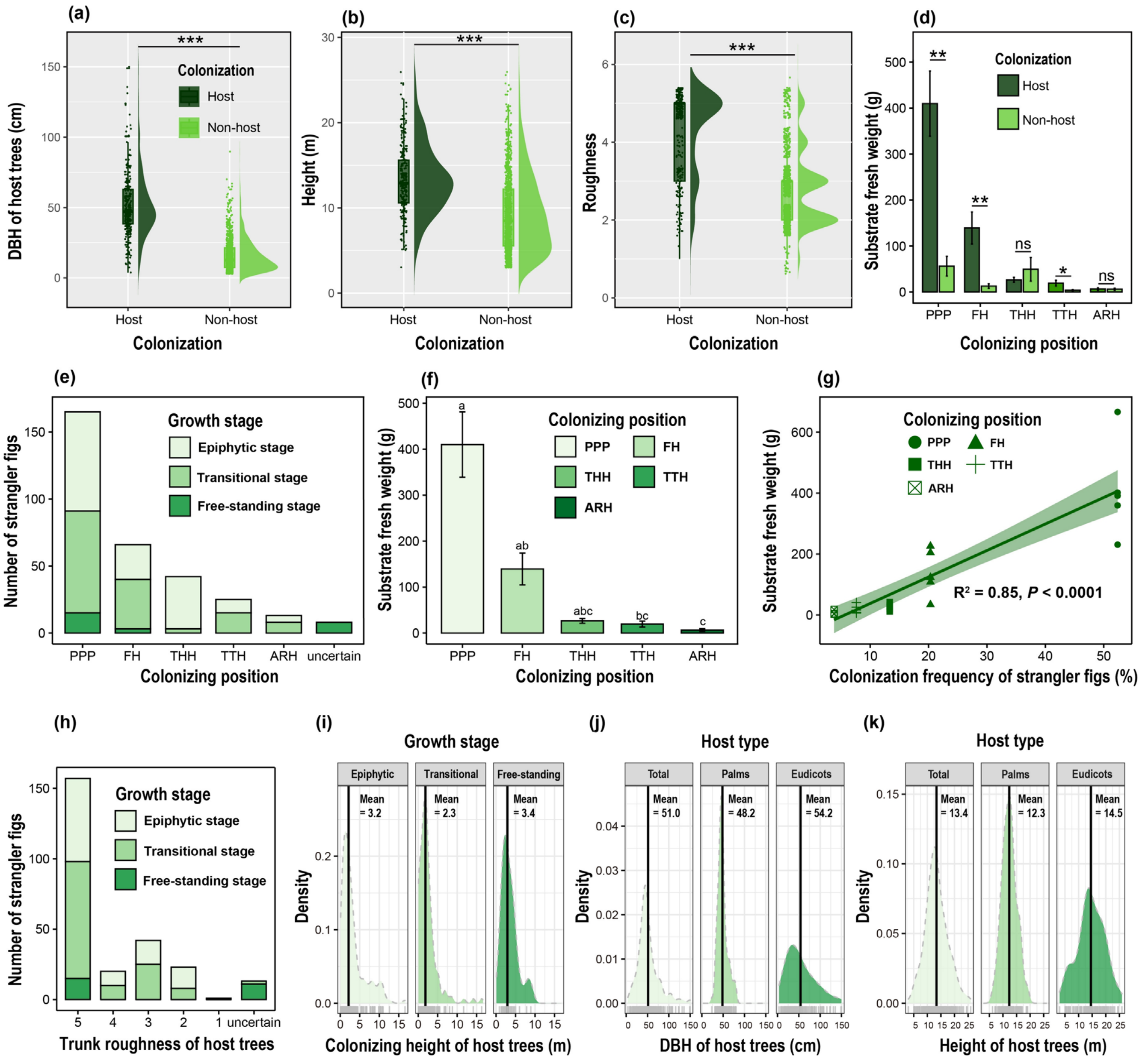


FIGURE 3 Differences among colonizing positions, substrate characteristics, and host tree characteristics of strangler figs. (a–d) Differences of diameter at breast height (DBH), height, trunk roughness, and substrate fresh weight between host and nonhost trees. Different letters denote significant differences (Kruskal–Wallis test) among the substrate characteristics of differing positions, *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns $p > 0.05$. The error bars mean standard error. (e) Difference of strangler fig abundance at different colonizing positions. (f) Difference in substrate fresh weight at different colonizing positions. Different letters denote significant differences among the substrate characteristics of differing positions, $p < 0.05$ (Kruskal–Wallis test). The error bars mean standard error. (g) Substrate fresh weight is positively correlated with the number of strangler figs at corresponding positions. The green area: 95% confidence interval. (h) Difference in strangler fig abundance across host trunk roughness categories. (i) Probability density distribution of stranglers' colonizing height at different growth stages. (j,k) Probability density distributions of host trees' DBH and height. ARH, aerial root (of strangler figs or lianas) on the host trunk surface; FH, fork of hosts; PPP, persistent petiole of palms; THH, tree hole of hosts; and TTH, tree trunk of host trees.

The DBH and trunk roughness of hosts significantly affected appearance of strangler figs, whereas host height was a negligible predictor of the outcome (Table S3). Colonizing position, colonizing height, host DBH, and height significantly affected whether the aerial roots of strangler figs entered the soil or not, yet the host trunk roughness had no significant effect.

3.4 | Factors affecting host leaf traits of stranglers

Our results showed that strangler figs' growth and host species were both important factors ($p < 0.05$) affecting the leaf nutrient status and morphological traits of the host trees (Table S4). Specifically, the leaf nutrients of host trees were reduced by strangler figs'

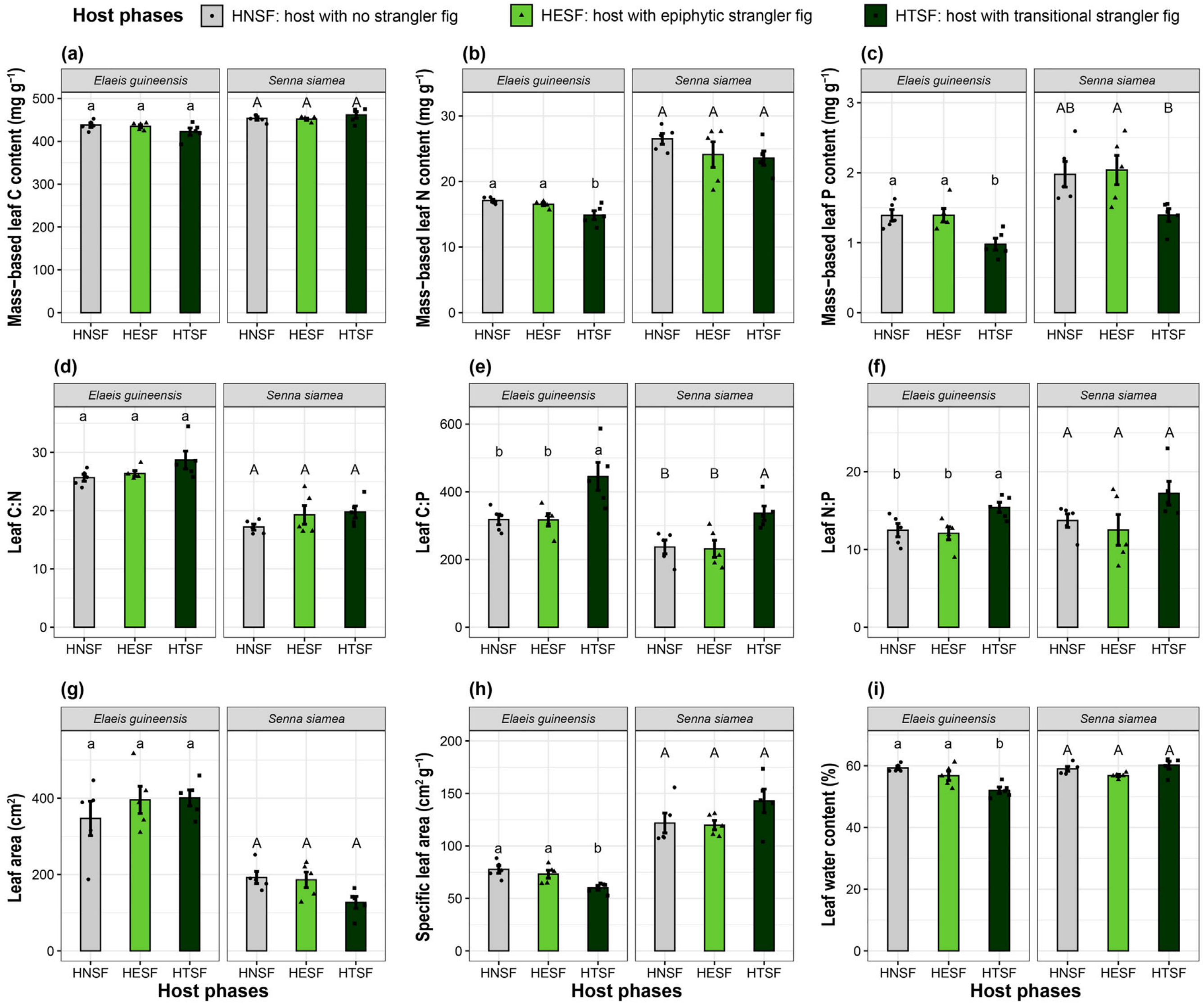


FIGURE 4 Leaf traits of host trees with strangler figs at different growth stages. (a–f) Hosts' leaf nutrient traits. (g–i) Hosts' leaf morphological traits. Different letters (lowercase: *Elaeis guineensis*; capital letter: *Senna siamea*) denote significant differences among the different phases of the hosts, at the $p < 0.05$ level. The error bars mean standard error.

growth, and interspecific differences were also detected (Figure 4). For *E. guineensis*, its leaf N_{mass} content was significantly lower in the HTSF phase than either the HNSF or HESF phase ($p < 0.05$), but this difference was not found for *S. siamea* (Figure 4b). Moreover, the leaf P_{mass} content of *E. guineensis* in the HTSF phase was 42.13% and 42.33%, respectively, lower than that in the HNSF and HESF phases ($p < 0.05$). Similarly, the leaf P_{mass} content of the host *S. siamea* in the HTSF phase was 42.45% and 46.76% lower than that in the HNSF ($p = 0.073$) and HESF ($p < 0.05$) phases, respectively (Figure 4c). With the content of leaf nutrients changed, the leaf C:P and N:P ratios of the host also changed (Figure 4d–f), being greatest in the HTSF phase ($p < 0.05$). In the *E. guineensis* host, both its SLA and leaf water content were significantly lower ($p < 0.05$) in the HTSF phase but not so in *S. siamea* host (Figure 4h,i).

3.5 | Influences of different management on stranglers and strangler–host network

Different management had different influences on survival of strangler figs and strangler–host network (Figure 5). After severing aerial roots of strangler figs, most of the strangler individuals (80%) died (Figure 5a). Although severing branches could restrict the growth of strangler figs, their survival rate was found to be slightly decreased (Figure 5b). These results indicated that compared with the severing branches, severing aerial roots was easier to eliminate the strangler figs (Figure 5c).

As the removal intensity increased, the connectance of the strangler–host network gradually increased, with the HSN (F $\sim$ M) and SFG (E $\sim$ T) scenarios changing earlier and higher than other scenarios (Figure 5d). For NODF dynamics, HDBH (L $\sim$ S) and HSN (M $\sim$ F)

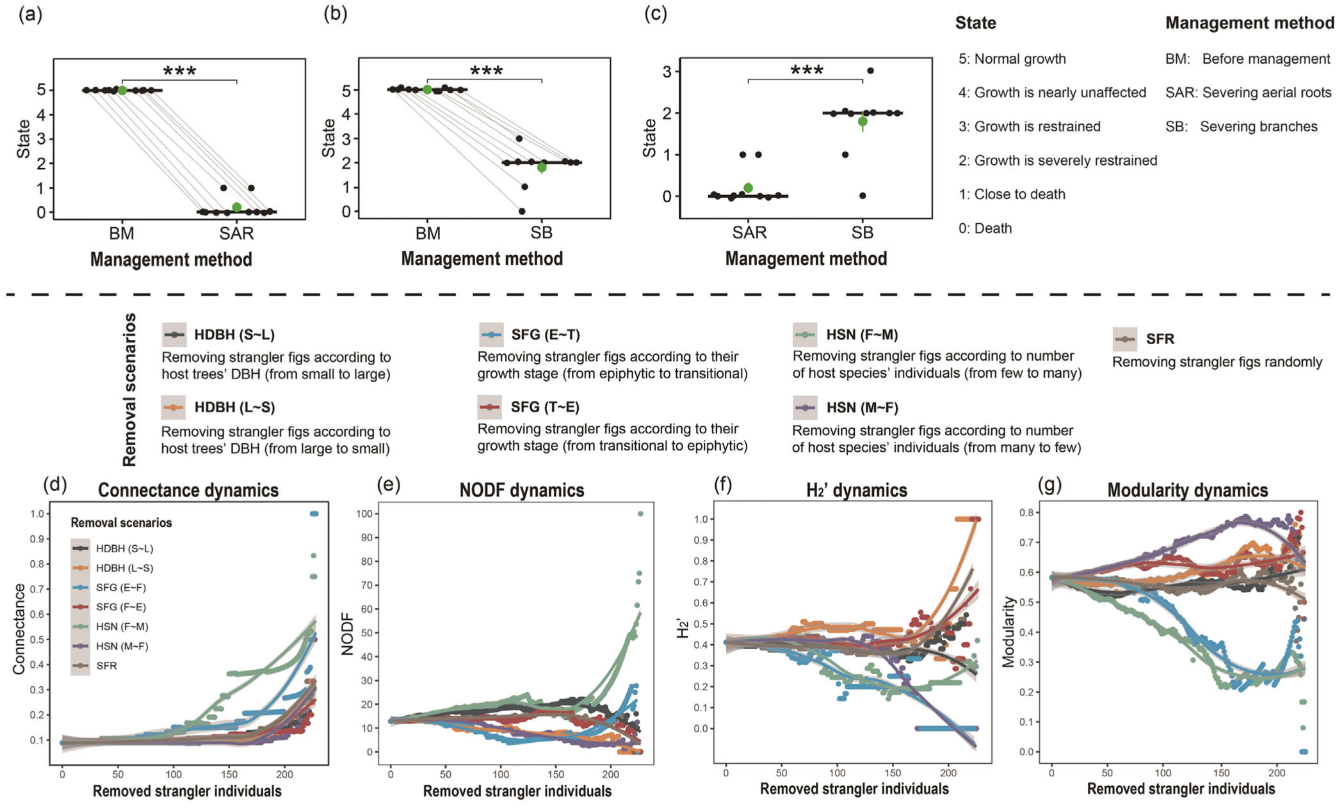


FIGURE 5 Influences of different management on strangler figs and strangler–host network. (a) The stranglers' state after severing their aerial roots. (b) The stranglers' state after severing their branches. (c) The state comparison after severing aerial roots and branches of strangler figs. The dynamics of (d) connectance, (e) NODF (reflecting network nestedness), (f) H_2', and (g) modularity of strangler–host network under different removal scenarios. *** indicates significant differences in different management methods, $p < 0.001$.

scenarios gradually decreased, while HDBH (S ~ L), SFG (T ~ E), and the HSN (F ~ M) and SFG (E ~ T) scenarios ultimately increased with strangler removal (Figure 5e). H_2' dynamics showed upward trends for HDBH (L ~ S), SFG (T ~ E), and SFR scenarios, with sharp increase after removing more than 150 stranglers, while SFG (E ~ T) and HSN (M ~ F) scenarios showed downward trends (Figure 5f). Additionally, as removal intensity increased, the modularity of the HSN (F ~ M) and SFG (E ~ T) scenarios declined, whereas it increased for the HSN (M ~ F), SFG (T ~ E), and HDBH (L ~ S) scenarios (Figure 5g).

4 | DISCUSSION

4.1 | Possible reasons for host preference among strangler figs

The species composition and network pattern of strangler figs and their host trees indicate that, although the host association of strangler figs is relatively broad, they can show preferences for particular host taxa (Table 2; Table 3; Figure 2). Generally, strangler figs frequently colonize big trees' suitable microsites (Harrison et al., 2003; Male & Roberts, 2005) especially those enabling them to intercept and store substrate (Figure 3). Based on our data and previous studies, we propose several hypotheses about the host preference exhibited by strangler figs in the XTBG. One of the possible reasons for the observed host specialization pattern of stranglers is due to the suitability of the specific host trees for colonization and establishment. In primary forests, the high colonization rate of strangler figs is likely attributed to both microsites (e.g., colonizing position) and characteristics of hosts (Doyle, 2000; Harrison et al., 2003; Male & Roberts, 2005). Our results suggest this interplay of ecological factors can be extended to the urban green space (Table S3; Figure 3). Similarly, other studies have reported that *Copernicia* and *Sabal* palms are common hosts for strangler figs in secondary communities of the Neotropics (Caughlin et al., 2012; Guevara & Lopez, 2007). In many palms, their petiole bases can persist along the trunk for a long time and provide a suitable microsite, which could intercept substrate to sustain the growth of strangler figs colonizing it. Firstly, the substrate of PPP harbors higher concentrations of nutrients (Guevara & Lopez, 2007; Mo et al., 2022) and water potential (Swagel et al., 1997) than does the soil. Secondly, the fresh weight of PPP's substrate is relatively high (Figure 3), which could better support the establishment of strangler seedlings. Thirdly, unlike the other colonizing positions such as FH and THH that often provide only a single microsite for stranglers to occupy, there are many PPPs in a palm trunk (Figure 1a,b,d), which could continuously supply nutrients and water as strangler figs grow from the canopy downward to the ground. Despite the positive feedback of substrate accumulation at the original colonizing positions and other crevices or receptacles created by the continued growth of strangler figs, the benefits of this feedback likely are more substantial in palm hosts than others (Figure 1a,b). Hence, PPP could provide sufficiently larger water and nutrient pools than other colonizing positions, which effectively improves the likelihood of strangler figs' successful establishment. This may explain why there is a high colonization frequency of strangler figs at the persistent petiole of palm trees in the sampled botanical garden (XTBG).

Furthermore, the forks of big trees are also usually colonized by strangler figs in tropical primary forests (Harrison et al., 2003; Male & Roberts, 2005). Similar to these observations, our study also found that FH has the second highest colonization frequency in the XTBG (Figure 3f). A persistent palm petiole, large trees' forks, or the rough trunk of host trees usually form suitable microsites for the colonization and establishment of strangler figs; however, certain microsites such as THH and ARH (Patel, 1996) occasionally form in trees with a relatively small DBH or smooth trunk. This probably explains why strangler figs not only exhibit preferences for particular hosts (for suitable microsites) but also colonize other various hosts because some host trees can easily form suitable microsites, whereas others form them accidentally. After a certain disturbance event (e.g., fierce wind and tree-fall), there could be a dislodgement of strangler figs from their host trees, especially at the epiphytic stage. Long-term monitoring of strangler figs and multiple comparisons of these results are needed in future research. Moreover, palms and figs, as good landscaping plant materials, are popular and widely used tree species for urban greening and landscape construction in gardens, parks, or roadsides in tropical urban areas (Fehr et al., 2020; Panyadee et al., 2016). Compared with natural forests, the density of strangler figs in XTBG (16 ha^{-1}) far surpasses that (3 ha^{-1}) in a primary dipterocarp forest of Sarawak (Harrison et al., 2003) and is nearly twice that (9 ha^{-1}) in a rain forest of Queensland (Male & Roberts, 2005). Hence, the colonization probability of strangler figs could increase in tropical urban green spaces, especially where both figs and palms (or other big trees) have been planted. Clearly, our comparison to natural systems such as rainforests in Sarawak and Queensland has nontrivial limitations: Most notably, we would not expect a similar frequency of oil palms, and strangler figs typically colonize a variety of hosts. However, datasets on strangler fig density in comparable (artificial) areas are absent to our knowledge. Further work would certainly benefit from examining population dynamics across a range of geographically dispersed urban spaces.

Another possible reason for high specialization of strangler figs may also be related to the dispersal agents of their seeds (Caughlin et al., 2012; Doyle, 2000). The fruits of fig species, strangler figs included, of course, are regarded as the "key resource" for various animal populations (Shanahan et al., 2001; Zhang et al., 2020). They constitute a vital dietary component for many birds and mammals, especially in cities where food resources are relatively scarce; hence, these animals are common seed dispersers for strangler figs in both natural and urban ecosystems (Chong et al., 2021; Nogueira & Peracchi, 2003). Furthermore, mature strangler figs feature greater structural complexity than other trees, which may provide shelter for animals in urban ecosystems (Chong et al., 2021). Palm fruits are food sources for frugivorous birds and bats (Spennemann, 2018), and palms can provide an appropriate habitat for these flying animals (Evelyn & Stiles, 2003; Teuscher et al., 2015). Frequent activities—such as foraging, resting, or nesting—and movement of seed dispersers between the strangler fig trees and host trees may broaden the seed rain shadow, which could be another reason for the high occurrence frequency of strangler figs on palms (or other big trees). In our study site, *F. tinctoria* is the most common strangler fig species (Table 2; Figure 2), whose fruit production peaks in winter (January to mid-February). Thus, *F. tinctoria* provides food for birds (at least 15 species) in this season when the general availability of fruits is relatively low and insufficient (Chen et al., 2015). The phenology and seed dispersers of *F. tinctoria* interact to enhance the seed dispersal of this strangler fig species, which could explain its dominance in XTBG. Therefore, it is not unreasonable to presume that analogous fruit-feeding and seed-dispersal behaviors of animals may also occur in tropical urban ecosystems, to facilitate the colonization and establishment of strangler figs there (Chong et al., 2021; Patel, 1996). However, we recognized that some processes (e.g., seed dispersal and germination), forming the strangler–host network, are important but were not directly observed in our study. These processes warrant further study to understand the mechanism of forming strangler–host ecological associations.

4.2 | Impact of strangler figs on their hosts

It is easy to observe the visible influences of a strangler fig on its host, which entail damage to the external phloem of host trees as well as shading of their crown foliage (Harrison et al., 2003; Zhang et al., 2020). In stark contrast, some effects on hosts from strangler figs are unnoticeable, such as their altered nutrient status. We have shown here that strangler figs at XTBG reduced the leaf N_{mass} and P_{mass} content and increased the C:N and C:P and N:P ratios of their hosts in the HTSF phase (Figure 4; Table S4). This implies that the host trees incurred nutrient deficiency when they grew together with transitional strangler figs (Mo et al., 2022) but varies between host species. Unlike the leaf N deficiency of *E. guineensis* hosts, the leaf N content of *S. siamea* (Fabaceae) hosts did not significantly decrease in the HTSF phase (Figure 4b), maybe because of the nitrogen-fixation capacity in *S. siamea*. Intense competition likely ensues between the hosts and strangler figs during the transitional stage (Lawton & Williams-Linera, 1996), and our results support this conclusion. In addition, the crown of strangler figs broadens after the aerial roots entered the soil (Figure 1a–d), which will partly shade the host's crown (Li et al., 2024; Zotz et al., 2021) and may also reduce its maximum net photosynthesis and carbon assimilation (Hernandez et al., 2020).

Nevertheless, the influence of strangler figs on their hosts' ecophysiology and fitness is complex, varying across growth phases and different host trees (Figure 4; Table S4). For example, host nutrient status is rarely affected by strangler figs at the epiphytic stage, yet host nutrient status does worsen when stranglers reach the transitional stage (Mo et al., 2022). For a long time, the influence of strangler figs on their hosts was viewed as being necessarily negative, with such effects as mechanical damage, competition, and dynamic loading (Lawton & Williams-Linera, 1996; Zotz et al., 2021). Intriguingly, Richard and Halkin (2017) found that transitional strangler figs could support their host trees in the face of severe disturbance (storms). The ways in which strangler figs influence their hosts' vital rates, and functioning may be important, especially for managing botanical gardens or other urban green spaces because some host trees of the strangler figs are commonly planted for urban greening and landscaping. Consequently, by explicitly considering the functions and ecological associations of strangler figs and their hosts, we could learn to effectively conserve and manage them according to specific circumstances across the urban landscape.

4.3 | Recommendations for management of strangler figs and their hosts

There is the evident frequent utilization of strangler figs, palms, and/or other big trees in urban green spaces, along with the occurrence of stranglers' seed dispersal by animals in tropical cities (Caughlin et al., 2012; Fehr et al., 2020). The strangler–host network results indicate that, in the XTBG, most of links exist between strangler figs and the introduced hosts, namely, *E. guineensis* and *Samanea saman* (Figure 2). In urban ecosystems, there are many introduced plants (Fehr et al., 2020; Silva et al., 2020) especially in their botanical gardens (Chen et al., 2009). These introduced plants could broaden the host breadth of strangler figs. Although we found that ca. 97% of the investigated tree individuals were not colonized, the absolute number of the host trees affected by strangler figs was nontrivial. Moreover, the total amount of endangered plants colonized by strangler figs was low (Table 3), suggesting the stranglers' management for endangered plants may not be necessary.

Previous studies have shown that connectance and nestedness play fundamental roles in diminishing the extent of disturbances and stabilizing the dynamics of biological communities (Baumgartner, 2020; Hu et al., 2022). In comparison with the other hemiepiphyte–host network in a subtropical forest (Pu et al., 2021), the strangler–host network is distinguished by lower connectance (0.13 vs. 0.33) and nestedness (NODF: 24.38 vs. 46.10) and higher specialization (H_2': 0.47 vs. 0.08). Similarly, other epiphyte-host networks in New Zealand, southern Chile, and Argentina (Ceballos et al., 2016; Taylor et al., 2016) also show higher nestedness (NODF = 32–77; mean = 56.30) and lower specialization ($H_2' = 0.08$–0.35; mean = 0.16) than our study. These features and their discrepancy imply the strangler–host network is not stable and has weak resilience to disturbance in the botanical garden. Accordingly, appropriate artificial management intervention could be effective at altering the structure of the strangler–host network. If we remove strangler figs according to HDBH ($L \sim S$) or SFG ($T \sim E$) scenario that will increase the specialization and decrease the stability of the strangler–host network (Figure 5f,g). For management, choosing the two removal methods may lead subsequent management of the strangler–host network easier.

Arguably, given the pronounced negative effects of strangler figs on their hosts, we should explore taking key steps to protect the host trees under particular circumstances. Considering that microsite is a significant factor influencing the stranglers' colonization and establishment (Doyle, 2000; Harrison et al., 2003), regular management of the microsite (e.g., removing persistent petioles from palms) could offer a simple yet efficient way to reduce the colonization and establishment of strangler figs in urban areas (Figure 3). Furthermore, using native tree species may also reduce the colonization probability of strangler figs (Figure 2). If the esthetic value of a landscape was seriously disrupted by strangler figs, they also ought to be eliminated. Moreover, if strangler figs colonize protected plants (i.e., species with endangered status in law or policy), we ought to quickly remove those stranglers to avoid severely damaging the hosts. Ideally, we would remove such strangler figs when they are at the epiphytic stage because at this time they negligibly impact their hosts (Figure 4; Mo et al., 2022). For those strangler figs already rooted into the soil, severing their aerial roots could be a more efficient management than severing branches to kill stranglers (Figure 5a–c). Because the severing aerial roots of strangler figs can cut off their water and nutrient acquisition from the soil, the transpiration of the leaves is still present, and the underground part has no supply of photosynthetic products, these make strangler figs more likely to die. While tree-pruning has been practiced since antiquity, our results provided insights into effective measures to manage the strangler figs in urban green spaces in a modern context. Because the negative effects (e.g., mechanical damage, nutrient deficiency, and shading) have already occurred on hosts (transitional phase), compensation measures, such as N or P fertilization and wound therapy on the host trees, warrant consideration to foster their recovery after removing strangler figs.

However, not every strangler fig in a given urban area must be removed because the colonization and establishment of strangler figs is a natural process. Most strangler figs are native species (Table 2), and they typically require several decades to become free-standing trees. On the one hand, strangler figs are crucial for sustaining animal populations through the provisioning of food and habitat (Chong et al., 2021; Nogueira & Peracchi, 2003). Retaining some strangler figs will help to conserve and maintain local animal communities, especially in urban ecosystems where biodiversity is already relatively low. On the other hand, humans could benefit from conserving some strangler fig species *in situ*. For instance, some strangler fig species are heritage trees that have multiple cultural, historical, and amenity values (Thaiutsa et al., 2008; Zhang et al., 2017). Besides, the host-killing process engaged by strangler figs is a vivid biological example and aid for better understanding the complex tropical ecosystems, which is also a unique landscape in the tropics. Strangler figs also can be attractive wonders for use in natural education programs in tropical botanical gardens, and we can even artificially create strangulation spectacles (if need be). Tree risk is an important issue in urban green space management, whose assessment methods usually consider three key aspects: (1) likelihood of impact to target, (2) likelihood of

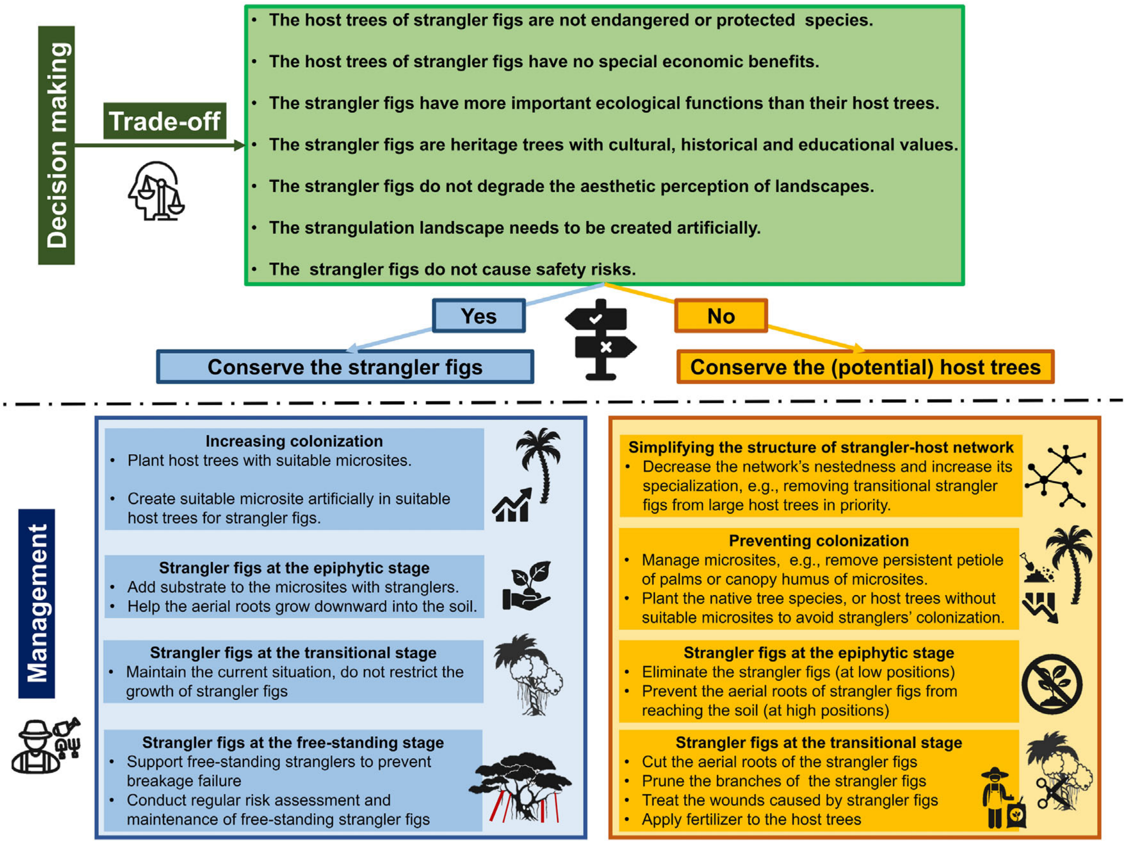


FIGURE 6 Suggestions for managing strangler figs and their host trees in tropical urban ecosystems.

failure, and (3) consequences of failure should a target be struck (Judice et al., 2021; Koeser et al., 2015). Due to the death and decomposition of their host trees, free-standing stranglers are prone to falling (Figure 1c), and some poorly anchored epiphytic strangler seedlings may also fall from their hosts, these would cause tree risks. The free-standing stranglers probably generate a bigger modal impact force, with a higher probability of their falling parts hitting a human or property target, than do epiphytic seedlings, due not only to their huge size but also greater visitors' attendance. Therefore, installing necessary supports and implementing regular risk assessments and management practices to conserve free-standing strangler figs and protect people in cities would be prudent, especially in botanical gardens with many tourists. Further, we suggest following conditions should be met when we decide to conserve strangler figs: (I) Host trees of strangler figs are not endangered species and have no specific economic benefits. (II) Strangler figs can (partly) substitute the functions of their hosts and/or harbor multiple values in culture, history, or education. (III) Strangler figs do not disrupt the esthetic feeling of landscapes. (IV) Strangler figs do not pose security risks. If the above conditions are not met, the host tree individuals should be protected.

Based on our results (Figures 3–5, Tables 2–3), we suggest that comprehensive management measures can be taken to change the colonization and establishment rates of strangler figs in tropical urban green spaces via microsite management, network construction, and regulation of stranglers and their hosts at different stages. For practicality, we present a flowchart of decision-making and management aspects concerning strangler figs and their host trees that is applicable to tropical urban ecosystems (Figure 6). Our recommendations can be applied to a range of urban green spaces including arboreta, parks, and gardens; other green spaces such as urban corridors and roof gardens require further study.

5 | CONCLUSION

Our results revealed that strangler figs prefer large-sized host trees, which can frequently form suitable microsites (especially those capable of intercepting and storing the substrate and seed) for strangler figs' colonization and establishment. Frequent utilization of strangler figs, palms, and/or other big trees, coupled with stranglers' seed dispersal by animals, should also increase the stranglers' colonization and establishment in tropical urban ecosystems. Furthermore, strangler figs likely compete for soil resources with their host trees, and this could lead to their hosts suffering nutrient deficiency once stranglers are rooted in the soil. Based on the patterns of the constructed strangler–host network and the influences of strangler figs on their hosts, implementing appropriate management could be necessary and effective. We should consider the trade-offs among multiple conditions and functions of strangler figs vis-à-vis their host trees.

For example, targeted severing aerial roots can inhibit stranglers' establishment without harming valuable hosts, selecting host trees with large DBH, and rough bark can increase the colonization of stranglers, and management for stranglers should be carried out at their epiphytic stage. These comprehensive strategies, tailored to different contexts, will improve urban greening and management of botanical gardens in the tropics.

AUTHOR CONTRIBUTIONS

Conceptualization: Yu-Xuan Mo, Huang Zou, Liang Song, and Wen-Yao Liu. *Data curation, formal analysis, and visualization*: Yu-Xuan Mo, Huang Zou, Hai-Xia Hu, Liang Song, and Yuan Li. *Funding acquisition, project administration, and supervision*: Liang Song and Wen-Yao Liu. *Investigation*: Yu-Xuan Mo, Huang Zou, and Yun-Xin Zhang. *Methodology*: Yu-Xuan Mo, Huang Zou, Hai-Xia Hu, Su Li, Xiao-Yan Pu, and Tao Hu. *Writing—original draft*: Yu-Xuan Mo and Huang Zou. *Writing—review and editing*: Hai-Xia Hu, Su Li, Hua-Zheng Lu, Sujan Balami, Liang Song, and Wen-Yao Liu.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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