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Hemiepiphytic figs kill their host trees: acquiring phosphorus is a driving factor

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Summary

- Hemiepiphytic figs killing their host trees is an ecological process unique to the tropics. Yet the benefits and adaptive strategies of their special life history remain poorly understood.
- We compared leaf phosphorus (P) content data of figs and palms worldwide, and functional traits and substrate P content of hemiepiphytic figs (*Ficus tinctoria*), their host palm and non-hemiepiphytic conspecifics at different growth stages in a common garden.
- We found that leaf P content of hemiepiphytic figs and their host palms significantly decreased when they were competing for soil resources, but that of hemiepiphytic figs recovered after host death. P availability in the canopy humus and soil decreased significantly with the growth of hemiepiphytic figs. Functional trait trade-offs of hemiepiphytic figs enabled them to adapt to the P shortage while competing with their hosts. From the common garden to a global scale, the P competition caused by high P demand of figs may be a general phenomenon.
- Our results suggest that P competition is an important factor causing host death, except for mechanically damaging and shading hosts. Killing hosts benefits hemiepiphytic figs by reducing interspecific P competition and better acquiring P resources in the P-deficient tropics, thereby linking the life history strategy of hemiepiphytic figs to the widespread P shortage in tropical soils.

Introduction

Hemiepiphytes are plants that start as true epiphytes but later establish root contact with the soil, and a subset of these eventually kill and displace their host trees (Putz & Holbrook, 1989; Zotz *et al.*, 2021). Host killing by hemiepiphytes is an endemic phenomenon (Fig. 1a–c) in the tropics, closely related to plant phenotype evolution and life history strategy (Harrison *et al.*, 2003; Lundgren & Marais, 2020). Many *Ficus* species – keystone plants in tropical forests – have evolved the hemiepiphytic ecotype (e.g. *F. religiosa*, *F. benghalensis*, *F. tinctoria*, etc.) that plays a key role in maintaining biodiversity, promoting community regeneration, and cycling nutrient resources (Thomson *et al.*, 1991; O'Brien *et al.*, 1998; Shanahan *et al.*, 2001; Zhang *et al.*, 2020). By focusing on the special life history of hemiepiphytic figs, we could better understand how plants respond to environmental changes and interspecific competition, and their life history strategies.

The host-killing process by hemiepiphytic figs simultaneously involves the mechanical restriction of nutrients and water flow, and competition for limiting resources, such as soil nutrients and water (Compton & Musgrave, 1993; Okamoto, 2015). Some researchers have emphasised that mechanical damage from the aerial root system of hemiepiphytic figs (Supporting Information Fig. S1), these figs are better known as 'stranglers', could be a reason for why their host trees die prematurely (Berg & Corner, 2005; Zotz *et al.*, 2021). But knowledge gaps persist regarding the competition between hemiepiphytic figs and their hosts, fitness advantages gained by the former when the latter die, and adaptive strategies of hemiepiphytes through different growth phases (Lawton & Williams-Linera, 1996; Schmidt & Tracey, 2006; Machado *et al.*, 2018). Previous studies have inferred that acquiring light and escaping mortality risks (e.g. damage from flooding, fire, or terrestrial herbivores) are probably the advantages driving hemiepiphytic figs' canopy access (Putz & Holbrook, 1989; Okamoto, 2015). But once in the canopy, hemiepiphytic figs face drought stress and adjust to the relatively dry environment by modifying their hydraulic traits (Holbrook & Putz, 1996; Hao *et al.*, 2011; Liu *et al.*, 2014). For their germination and seedling growth, hemiepiphytic figs must rely on

Fig. 1 Hemiepiphytic and nonhemiepiphytic *Ficus tinctoria* at different growth stages. (a) Epiphytic seedling stage of hemiepiphytic *F. tinctoria* (aerial roots did not enter the soil and the host palm is alive). (b) Transitional juvenile stage of hemiepiphytic *F. tinctoria* (part of the aerial roots entered the soil and the host palm is alive). (c) Free-standing adult stage of hemiepiphytic *F. tinctoria* (almost all of the aerial roots entered the soil and the host palm had been killed). (d) Canopy humus and other epiphytes in the axillae of oil palm (*Elaeis guineensis*). (e) Seedling stage of nonhemiepiphytic *F. tinctoria*. (f) Juvenile stage of nonhemiepiphytic *F. tinctoria*. (g) Adult stage of nonhemiepiphytic *F. tinctoria*. (h) Leaves of hemiepiphytic and nonhemiepiphytic *F. tinctoria*. All plants shown grew in the Xishuangbanna Tropical Botanical Garden.
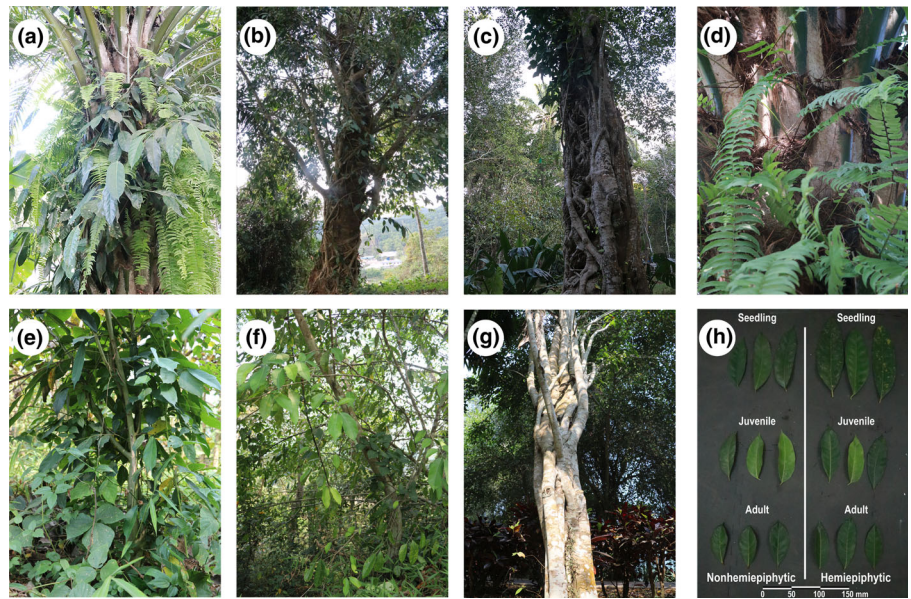
the nutrient and water conditions of microsites provided by host trees (Laman, 1995; Athreya, 1999) and economically use nitrogen (N) at their epiphytic stage (Schmidt & Tracey, 2006). As epiphytic seedlings grow downward from the canopy, corresponding shifts in habitat conditions (e.g. nutrients, water) and ontogeny will alter their functional traits (Putz & Holbrook, 1989; Holbrook & Putz, 1996; Hao *et al.*, 2011).

Plant functional traits – leaf nutrients' content, leaf morphological and photosynthetic traits, etc. – are especially liable to feedback between ecosystem processes, such as resource competition and environmental adaptation (Sterner & Elser, 2002; Westoby & Wright, 2006; Funk *et al.*, 2017; Cope *et al.*, 2021). In resource-limited environments, both nonsubstitutable and limiting elements in organisms often induce competition and are typically considered as forms of selective pressure capable of driving changes in functional traits and possibly inducing evolutionary adaptation under environmental stress (Colom & Baucom, 2020; Lundgren & Marais, 2020). Generally, phosphorus (P) is a limiting nutrient in tropical ecosystems (Wardle *et al.*, 2004; Wright, 2019; Hou *et al.*, 2020), such as in lowland forests of southern China and South America (Zhu *et al.*, 2013; Asner *et al.*, 2015). Plants mainly use water-soluble P, and its availability is relatively low in the tropical soils. Competing for scarce P resources could lead to changed functional traits (Baribault *et al.*, 2012; Carl *et al.*, 2018), with low P availability historically exerting significant selective pressure shaping plant traits' evolution in the tropics (Lovelock *et al.*, 2007). Moreover, P regulates the acquisition and allocation of other nutrients in plants (F. S. Chen *et al.*, 2015) and P is also closely related to community succession and plant growth and adaptations (Garrish *et al.*, 2010; Hidaka & Kitayama, 2011; Turner *et al.*, 2018). Adaptations and trait trade-offs of plants in resource-limited conditions can be reflected in their functional traits, which are plastic and can respond to changing habitats (Funk *et al.*, 2017; Cope *et al.*, 2021). Because hemiepiphytic figs undergo a stark habitat shift, from canopy to

land, functional trait dynamics may be informative for linking their limiting nutrients, functional trait trade-offs, and adaptive strategies.

Because host killing by hemiepiphytes is a long and dynamic process, a space-for-time substitution experiment is a reasonable and effective way to study this long-term ecological interaction (Putz & Holbrook, 1989; Holbrook & Putz, 1996; Schmidt & Tracey, 2006; Frauendorf *et al.*, 2019). Although the host killing by hemiepiphytes arises from mechanical restriction and resource competition, we actually know little of how this process is related to their acquisition of limiting nutrient resources (Lawton & Williams-Linera, 1996; Guevara & Lopez, 2007; Zotz *et al.*, 2021). Furthermore, the host-killing process depends on both ontogeny and habitat shifts, so an appropriate control is also needed to assess the specific causes of associated trait-based changes.

Here we present an integrated study that combines an analysis of fig and palm species' leaf P content worldwide and functional trait measurements of hemiepiphytic figs, their host palms, and nonhemiepiphytic conspecifics, with characteristics of corresponding substrates across the host-killing process in the common garden. We asked: (1) How do hemiepiphytic figs benefit from killing their hosts? (2) How do hemiepiphytic figs adapt to the changing habitats? We hypothesised that hemiepiphytic figs benefit from lessening P competition by killing their hosts in the P-deficient tropics, and that hemiepiphytic figs can adapt to changing habitats via functional trait trade-offs during the host-killing process. To test both hypotheses, we first measured, collected, and compared the leaf P content of 81 records of 45 fig species (37 and 44 records of hemiepiphytic and nonhemiepiphytic figs, respectively), 112 records of 99 palm species, and another 2278 records of tropical plants from the common garden (Xishuangbanna Tropical Botanical Garden; XTBG) to a global scale (Tian *et al.*, 2018). Secondly, we selected a common hemiepiphytic fig, *Ficus tinctoria*, with both hemiepiphytic and

nonhemiepiphytic phenotypes (Fig. 1) that is widely distributed in the tropical Asia and Oceania (Wu *et al.*, 2003; Berg & Corner, 2005). We studied the dynamics of leaf functional traits and nutrients in substrates of hemiepiphytic *F. tinctoria*, their host palms (the oil palm, *Elaeis guineensis*), and nonhemiepiphytic conspecifics at different growth stages in a natural common garden inside XTBG, to try and better understand the relationships between P competition and the host-killing process.

Materials and Methods

Study site

This study was conducted in the XTBG, Chinese Academy of Sciences (21°56′N, 101°15′E, 560 m above sea level (asl)), located in Menglun, Yunnan Province, SW China (Fig. S2a). XTBG's total area is 1125 ha, including a 250-ha patch of well preserved primary tropical rainforest. Mean annual temperature is 22.8°C and mean annual precipitation is 1500 mm, 85% of which comes in the rainy season (May–October); the dry season (November–April) and includes a foggy subseason (November–February) and a brief but hot subseason (March–April). During the foggy subseason, a high frequency of radiation fog occurs from midnight until morning (Liu *et al.*, 2014). Here, acidic laterite, with a low P availability (soil available P is 4–5 mg kg^{-1}, soil total P is 0.3–0.7 mg g^{-1}, pH is 4–6; 0–20 cm soil samples), is the common soil type.

Data collection and measurement of leaf P content, from a global scale to the common garden

To understand differential P content across figs, palms, and other plant species from a global scale to the common garden, we collected leaf P$_{mass}$ content records of figs (62 records) and palms (32 records) from 56 publications (please refer to Notes S1–S3 for details) and the TRY database: https://www.try-db.org (Kattge *et al.*, 2020), removing any duplicated records. Overall, 81 and 112 records of figs and palms were acquired spanning 41 and 15 sites worldwide, respectively. The data included 45 fig and 99 palm species. We also analysed the leaf P$_{mass}$ content of 16 common fig species (19 records from 145 individuals) and 80 palm species (80 records from 480 individuals) in the XTBG. Data for leaf P$_{mass}$ content of 15 dominant woody plant species (non-fig and non-palm species; 15 records from 120 individuals) in the local tropical forest were provided by the National Forest Ecosystem Research Station at Xishuangbanna, Chinese Academy of Sciences. To identify the life form and distribution of figs, we used field investigations, the books *Flora of China* (Wu *et al.*, 2003) and *Moraceae* (*Ficus*), in *Flora Malesiana Series I* (Berg & Corner, 2005), and the Fig Tree Classification website (http://www.figweb.org). We took the geometric means of these figs and palms and compared them with those of plant species from the common garden to a global scale (2278 records of tropical plant species, from Tian *et al.* (2018)). Data on soil total P content distribution came from the NASA Earthdata Network: http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1223 (Yang *et al.*, 2013). The

global distribution of soil total P content and the locations of fig and palm records were visualised in ArcGIS v.10.0.

Plant materials

In the XTBG, the studied fig individuals are haphazardly distributed and since 2007 we have measured various functional traits of common ones and palms (Hao *et al.*, 2011; Liu *et al.*, 2014; Ma *et al.*, 2015). Based on our previous work, we chose *F. tinctoria*, a fig species with both hemiepiphytic and nonhemiepiphytic ecotypes (Wu *et al.*, 2003; Berg & Corner, 2005), as the experimental material. Like everywhere else (Putz & Holbrook, 1989; Holbrook & Putz, 1996; Guevara & Lopez, 2007), palms are common hosts of hemiepiphytic figs in the XTBG (Liu *et al.*, 2014; H. H. Chen *et al.*, 2015) and some *F. tinctoria* cause host death. The nonhemiepiphytic *F. tinctoria* (Fig. 1e–g) spends its entire lifetime on the ground. To minimise the influence of different hosts on hemiepiphytic *F. tinctoria*, except for an unidentifiable dead host, all specimens used here were collected from the same host species, oil palm (*E. guineensis*). The planting time of extant host palms was relatively consistent (2003–2006). Since then, they had matured, and oil palms without hemiepiphytic figs were rarely dead. The hemiepiphytic *F. tinctoria* trees were not artificially planted, and the sampled oil palm and *F. tinctoria* were not artificially fertilised.

Plant and substrate sampling

Based on the space-for-time substitution approach, different growth stages of hemiepiphytic and nonhemiepiphytic *F. tinctoria* and host palms were selected from the XTBG. Furthermore, using common garden plants can minimise plastic adjustments to local site conditions and ensure that potential variation in plant functional traits is attributable to ecotype and ontogeny rather than other environmental differences (Hao *et al.*, 2011; Peterson *et al.*, 2016). Nonhemiepiphytic *F. tinctoria* individuals were numbered and their diameters at breast height (DBH) and crown diameters both measured. Distinct growth stages of nonhemiepiphytic *F. tinctoria* were defined by DBH, and classified as nonhemiepiphytic seedling (NHES), nonhemiepiphytic juvenile (NHEJ), and nonhemiepiphytic adult (NHEA) stages. Their hemiepiphytic counterparts were similarly numbered and measured for crown diameter, and noted for whether their roots had entered the soil. Following Liu *et al.* (2014), we defined the growth stages of hemiepiphytic figs as hemiepiphytic seedling (HES), hemiepiphytic juvenile (HEJ), and hemiepiphytic adult (HEA). Because their trunks were inconspicuous and their coalescing roots intertwined their hosts' trunk (Fig. 1a–c), it was difficult to distinguish growth stages of hemiepiphytic figs by DBH alone. Instead, many studies have reported allometric relationships confirming that crown diameter scales significantly with DBH (O'Brien *et al.*, 1995; Hemery *et al.*, 2005). Therefore, crown diameter and DBH of nonhemiepiphytic *F. tinctoria* individuals were used to fit an exponential model (Fig. S3) that approximated the growth stages of hemiepiphytic and nonhemiepiphytic *F. tinctoria* based on their crown diameters. These

were defined as follows: HES ($n = 5$): epiphytic; the host was alive; roots did not penetrate the soil; crown diameter < 2 m (Fig. 1a); HEJ ($n = 10$): transitional; host was alive; part of the root system had entered the soil; 4 m < crown diameter < 8 m (Fig. 1b); HEA ($n = 5$): free-standing (Harrison *et al.*, 2003; Liu *et al.*, 2014); host had been killed; nearly all of the roots were in the soil; crown diameter > 10 m (Fig. 1c). The 'free-standing' stage refers specifically to the last growth stage of the life history of hemiepiphytic *F. tinctoria* in this study. NHES ($n = 5$): without host; DBH < 1.2 cm; crown diameter < 2 m (Fig. 1e); NHEJ ($n = 5$): without host; 2.8 cm < DBH < 14 cm; 4 m < crown diameter < 8 m (Fig. 1f); NHEA ($n = 5$): without host; DBH > 30 cm; crown diameter > 10 m (Fig. 1g).

The *F. tinctoria* and host samples were obtained during the rainy season (October 2018, 2019). Individuals of hemiepiphytic and nonhemiepiphytic *F. tinctoria* were selected and their branches, leaves, and substrates sampled at different growth stages (Fig. S2b,c). The corresponding hosts (oil palms) with hemiepiphytic *F. tinctoria* (epiphytic stage, $n = 5$; transitional stage, $n = 10$) and oil palms without hemiepiphytes ($n = 10$) were sampled. The oil palms' mature and middle-positioned crown leaves were cut by arborists (using professional branch shears) and then their leaf central lobules were sampled.

In parallel, substrates were also sampled: soil and canopy humus of nonhemiepiphytic figs and epiphytic seedlings, respectively, while the other hemiepiphytic figs shared both. Topsoil samples (0–5 cm; root-zone soil) were collected from the ground near the fig trees, whereas canopy humus samples were collected (Fig. S2b) following Liu *et al.* (2014). Substrate samples from each tree were placed in a valve bag and taken to the laboratory where their fresh weight (FW) was measured, then air dried for 20 d, and their dry weight (DW) measured.

Measurements of leaf functional traits and substrate nutrients

On rainless days, from 08:00 am to 11:00 am, we measured the photosynthesis of *F. tinctoria* from sun-exposed branch samples. Following Tang & Wang (2011), we used the bevel twig method to measure the *in vitro* maximum net photosynthesis (LI6800; Li-Cor, Lincoln, NE, USA). Photosynthetic irradiance was maintained at 1200 µmol m^{-2} s^{-1} at the leaf surface, leaf cuvette temperature was maintained at 27°C, chamber CO_2 was ambient, and the relative humidity was 70%. We measured the maximum net photosynthesis of five leaves in one sample and averaged it. Intact and mature leaves were randomly collected from the branches of each tree crown, with leaves per individual tree mixed uniformly as a sample, this then measured for FW, leaf thickness, and leaf area (LI3000C; Li-Cor), and this was similarly measured for host palm lobules. After measuring these functional traits, all the plant samples were dried for 2 h at 80°C, then for 48 h at 65°C, to measure their DW. Then, each sample's specific leaf area (SLA) was calculated. For the air-dried substrates, we removed fine roots from the substrates and ground the substrates through a 2-mm sieve. Soil available phosphorus was extracted by NH_4F-HCl and measured by a continuous-flow analyser

(AutoAnalyzer 3; SEAL, Norderstedt, Germany). The remaining substrate samples were oven dried (80°C) for 48 h.

The oven-dried *F. tinctoria* leaves, host palm leaves, and their substrates were adequately triturated to pass through a 0.25-mm mesh sieve for chemical analysis. These prepared samples of plants and substrates were sent to the Public Technology Service Center of the XTBG, where mass-based leaf and substrate nutrients (C (carbon), N, P, K (potassium), Ca (calcium) and Mg (magnesium)) were determined. The mass-based C and N content of leaves (leaf C_{mass} and N_{mass} content) and substrates were measured using a C/N analyser (Vario MAX C/N; Elementar Analysensysteme GmbH, Hanau, Germany). To quantify the mass-based P, K, Ca, and Mg content of leaves (leaf P_{mass}, K_{mass}, Ca_{mass}, and Mg_{mass} content) and substrates, their samples were respectively digested by HNO_3–$HClO_4$ and HNO_3–$HClO_4$–HF mixtures, and then dissolved in HCl. Elemental content was then determined by inductively coupled plasma atomic-emission spectrometry (ICP-AES: iCAP6300; Thermo Fisher Scientific, Bremen, Germany).

Data analysis

Calculation of partial functional traits Leaf C_{mass}, N_{mass}, and P_{mass} content was each divided by SLA to derive the area-based equivalents (i.e., leaf C_{area}, N_{area}, and P_{area} content). The total nutrient content per leaf was calculated as area-based leaf nutrient content × leaf area. Photosynthetic N use efficiency and photosynthetic P use efficiency were calculated as described by Hidaka & Kitayama (2010). We followed the methodology of Chen *et al.* (2019) to quantify trait plasticity of *F. tinctoria* among different growth stages, it expressed as ((LT_{HE} − LT_{NHE})/LT_{NHE}) × 100%, where LT_{HE} is the leaf trait value of hemiepiphytic *F. tinctoria* and LT_{NHE} is the mean value of the corresponding leaf trait(s) for the nonhemiepiphytic counterpart at the same growth stage.

Statistical analysis

All statistical analyses were performed in R software (v.4.0.5). The differences in leaf functional traits and substrate P between *F. tinctoria* and their host palms across growth stages (seedling, juvenile and adult stages), and the differences in leaf P_{mass} content among plant functional groups (figs, palms, and other local dominate woody plants) in the common garden were examined by one-way ANOVA (followed by Tukey's post-hoc test for the pairwise comparisons of means). If the residuals of a fitted one-way ANOVA were not approximately normally distributed, then the nonparametric Kruskal–Wallis test was used instead. Differences in leaf and substrate traits between the hemiepiphytic and nonhemiepiphytic *F. tinctoria*, and the differences in leaf P_{mass} content between the figs and palms worldwide were determined by two-sample *t*-test; if the data did not meet homogeneity of variance or meet a normal distribution, we used the Wilcoxon test. The results were visualised with the GGPLOT2 (Ginestet, 2011) and GGPUBR (Kassambara, 2019) packages.

A linear mixed model (LMM) was used to test the effects of ecotype, ontogeny, and their interactions on the traits of *F.*

tinctoria. Considering that the common garden's microenvironments might modify plant functional traits, we used comprehensive characteristics – substrate C : (N : P) and the substrate water content of each tree – as covariates (Sterner & Elser, 2002; Zheng *et al.*, 2020) and sample site as a random factor, to reduce the impact of varying microenvironments. If the model residuals lacked normality, the dependent variable was log-transformed to meet the normal distribution assumption. The LMM was implemented using the NLME package (Pinheiro *et al.*, 2021).

Pearson correlations between leaf P and other leaf nutrient content were obtained. Principal component analysis (PCA) was used to distinguish the principal components among the six main plant functional traits – firstly removing some trait indicators with strong collinearity and weakly contributing to the axes – using the FACTOMINER package (Le *et al.*, 2008), with the results visualised with the FACTOEXTRA package (Kassambara & Mundt, 2020).

Results

Global pattern of leaf P content in figs and palms

From a global to the common garden scale, figs and palms had a higher leaf P_{mass} content than other plant functional groups
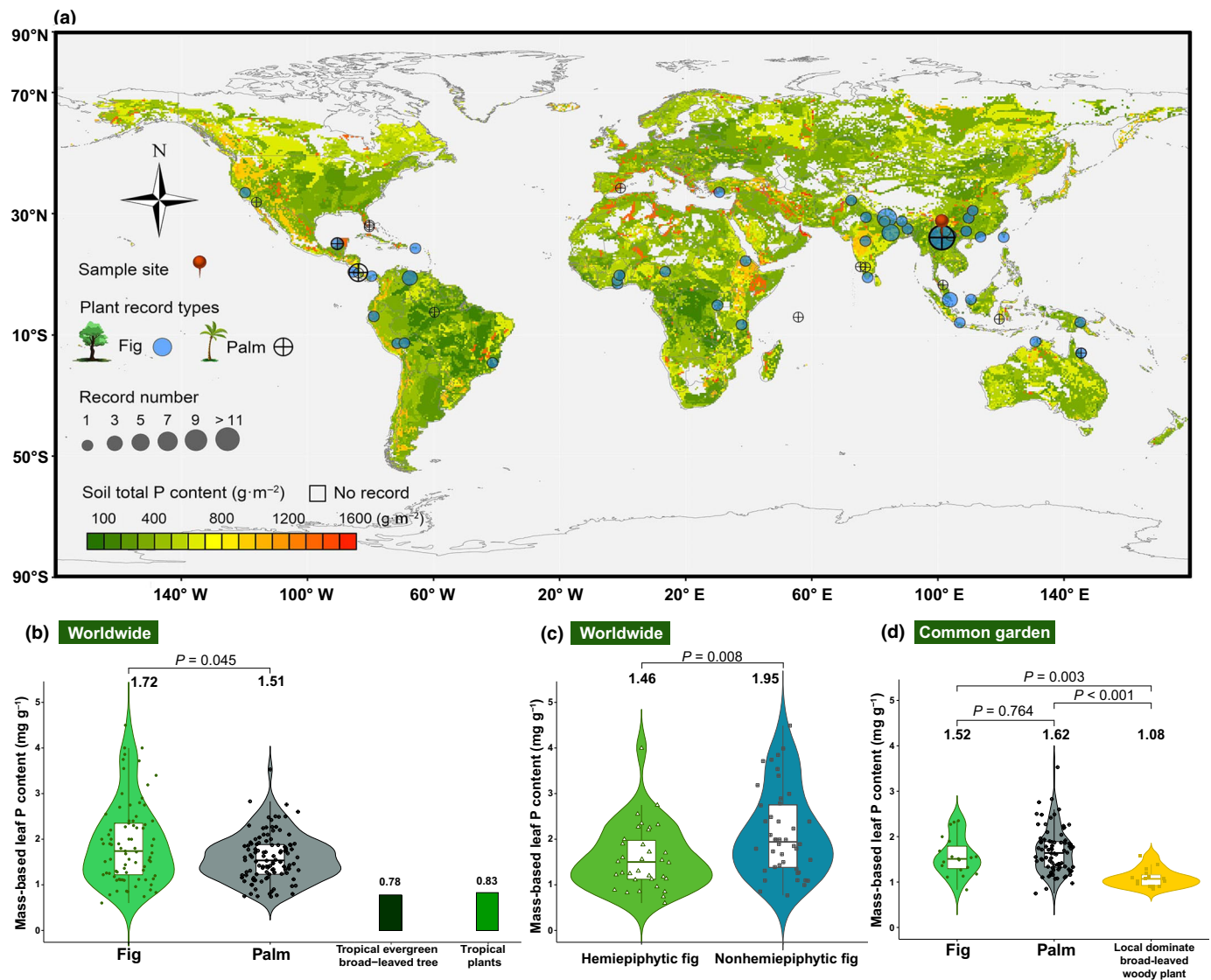
Fig. 2 Higher leaf P content in figs and palms than other plant functional groups in the P-deficient tropics. (a) Locations of the 193 leaf P_{mass} content (mg g^{-1}) observations. There are 81 fig records and 112 palm records. (b) Comparison of leaf P_{mass} content among figs (range: 0.60–4.50, upper quartile: 2.35, median: 1.74, lower quartile: 1.22), palms (range: 0.74–3.53, upper quartile: 1.88, median: 1.54, lower quartile: 1.23), and different tropical plant functional groups using data from Tian *et al.* (2018). (c) Distribution and comparison of leaf P_{mass} content in hemiepiphytic (range: 0.60–4.00, upper quartile: 1.98, median: 1.50, lower quartile: 1.12) and nonhemiepiphytic (range: 0.78–4.50, upper quartile: 2.76, median: 1.95, lower quartile: 1.39) fig species. (d) Distribution and comparison of leaf P_{mass} content in figs (range: 0.83–2.35, upper quartile: 1.79, median: 1.51, lower quartile: 1.30) and palms (range: 0.75–3.53, upper quartile: 1.89, median: 1.64, lower quartile: 1.33) in the common garden, and local dominant tropical woody plants (non-fig and non-palm species, range: 0.50–1.58, upper quartile: 1.16, median: 1.07, lower quartile: 0.93). The unit of the values in parentheses above is mg g^{-1}. Data shown as boxplots, with their data points given as scatter; the number is the geometric average. *P*-values by the Kruskal–Wallis test and Wilcoxon test.

(Fig. 2). Globally, the geometric average leaf P_{mass} content of both figs (1.72 mg g^{-1}) and palms (1.51 mg g^{-1}) also surpassed that of other tropical plants (0.83 mg g^{-1}), especially of evergreen woody species (0.78 mg g^{-1}; Fig. 2b). Few values of leaf P_{mass} content in fig and palm records overlapped with those of other tropical plants; for the leaf P_{mass} content of figs and palms, respectively, only 3.7% and 7.1% of the records were lower than 0.83 mg g^{-1}. On a global scale, geometric means of leaf P_{mass} content for hemiepiphytic and nonhemiepiphytic figs were 1.46 mg g^{-1} and 1.95 mg g^{-1}, respectively. The leaf P_{mass} content of hemiepiphytic figs was significantly lower than that of nonhemiepiphytic figs ($P = 0.008$; Fig. 2c). Moreover, the species-level difference matched that detected at the ecotype-level for *F. tinctoria*, and hemiepiphytic *F. tinctoria* also had significantly lower leaf P_{mass} content than its nonhemiepiphytic counterparts (Table S1).

Under common garden conditions, the geometric average leaf P_{mass} content of both figs (1.52 mg g^{-1}) and palms (1.62 mg g^{-1}) was significantly higher ($P < 0.01$) than that (1.08 mg g^{-1}) of

non-fig and non-palm local dominant tree species in local tropical forests. Specifically, the ranges of leaf P_{mass} content of fig, palm and other dominant local dominant woody plants were 0.83–2.35 mg g^{-1}, 0.75–3.53 mg g^{-1} and 0.85–1.58 mg g^{-1} (Notes S3), respectively. Leaf P levels of figs, palms, and other plants under the common garden were similar to the global pattern (Fig. 2d).

Leaf nutrient dynamics of hemiepiphytic and nonhemiepiphytic figs across growth stages

Leaf nutrients' content and their ratios of hemiepiphytic *F. tinctoria* differed significantly from their nonhemiepiphytic conspecifics, especially for those nutrient dynamics linked to P content, and their ratios displayed significant differences during the host-killing process (Fig. 3; Table S1). The leaf P_{mass} content of hemiepiphytic *F. tinctoria* was highest in the epiphytic seedling stage, but declined (by 20.11%) at the transitional juvenile stage ($t = 3.10$, $P = 0.017$), being 33.35% lower than that of their nonhemiepiphytic
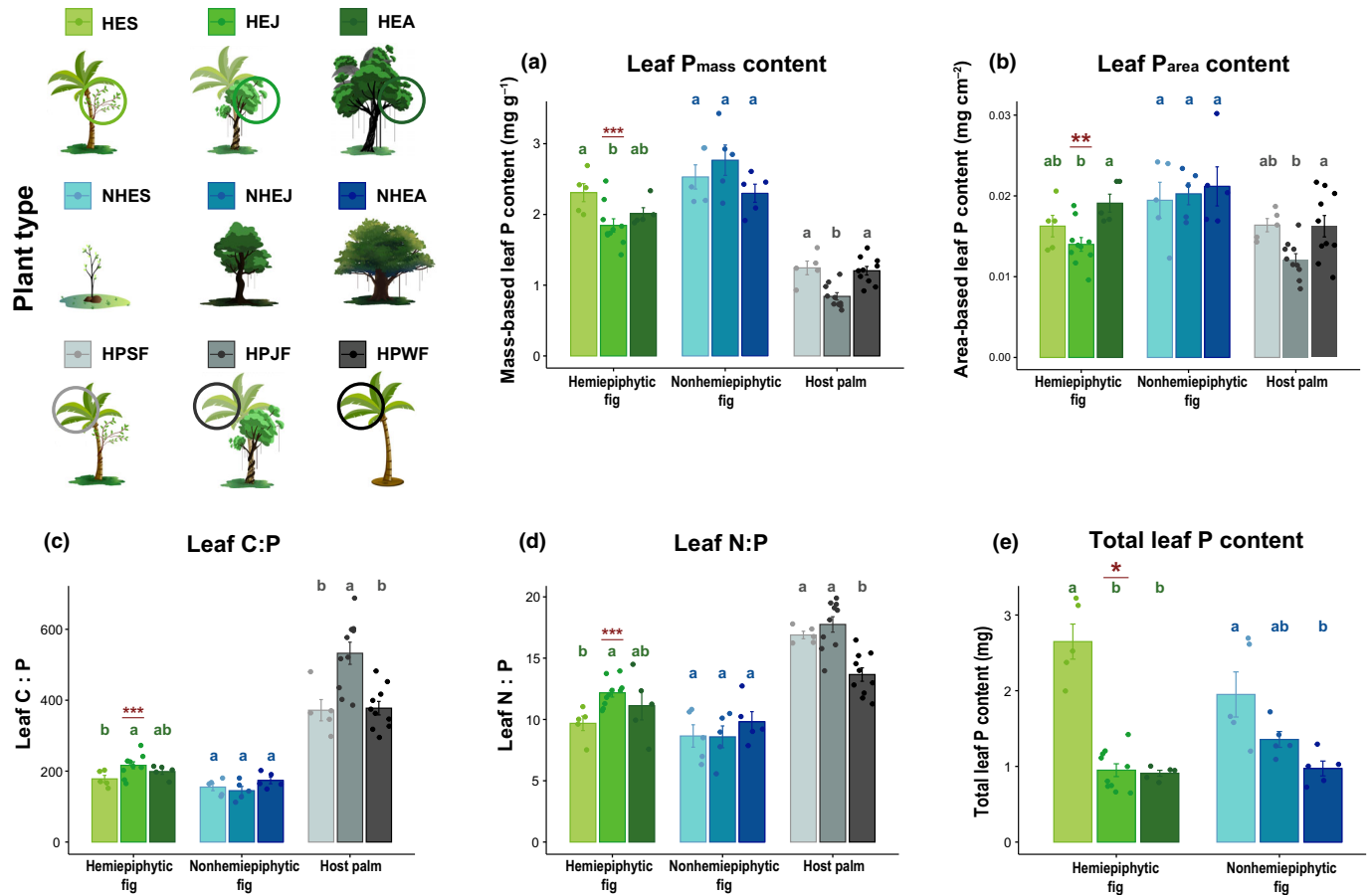
Fig. 3 Leaf P nutrient dynamics of hemiepiphytic and nonhemiepiphytic *Ficus tinctoria* and their host palms at different growth stages. (a) Mass-based leaf P content, (b) Area-based leaf P content, (c) Leaf C : P ratio, (d) Leaf N : P ratio, and (e) Total leaf P content of hemiepiphytic and nonhemiepiphytic *F. tinctoria* and their host palms at different growth stages. HES, hemiepiphytic seedling (epiphytic stage, $n = 5$); HEJ, hemiepiphytic juvenile (transitional stage, $n = 10$); HEA, hemiepiphytic adult (free-standing stage, $n = 5$); NHES, nonhemiepiphytic seedling ($n = 5$); NHEJ, nonhemiepiphytic juvenile ($n = 5$); NHEA, nonhemiepiphytic adult ($n = 5$); HPSF, host palm with seedling fig ($n = 5$); HPJF, host palm with juvenile fig ($n = 10$); HPWF, host palm without fig ($n = 10$). Data shown are the mean (±SE). Different letters with the same colour denote significant differences among the different stages of the same fig ecotype or host palms, at the 0.05 level. *P*-values by ANOVA (or Kruskal–Wallis test). * indicates a significant difference between hemiepiphytic and nonhemiepiphytic *F. tinctoria* within the same growth stage. *P*-values by *t*-test (or Wilcoxon test). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The dynamics of leaf C, N, K, Ca and Mg content of *F. tinctoria* are shown in Supporting Information Fig. S4.

counterparts ($t = 4.61$, $P < 0.001$; Fig. 3a). However, after host palms died, the leaf P_{mass} content of hemiepiphytic *F. tinctoria* recovered, being similar between hemiepiphytic and nonhemiepiphytic adults. After an initial decrease, leaf P_{area} content of transitional *F. tinctoria* increased by 36.49% after host death ($t = 3.43$, $P = 0.008$), with the leaf P_{area} content significantly lower for transitional juvenile *F. tinctoria* than their nonhemiepiphytic counterparts ($t = 4.08$, $P = 0.001$). By contrast, leaf P_{area} content of nonhemiepiphytic *F. tinctoria* was similar among growth stages (Fig. 3b). Unlike the steady leaf C : N dynamics (Fig. S4), both leaf C : P and N : P ratios of hemiepiphytic *F. tinctoria* fluctuated, first increasing and then decreasing from the epiphytic to free-standing stages. At the transitional stage, the leaf C : P ($t = 4.37$, $P < 0.001$) and leaf N : P ($t = 4.59$, $P < 0.001$) ratios of hemiepiphytic *F. tinctoria* significantly exceeded those of nonhemiepiphytic conspecifics (Fig. 3c, d). The leaf C : N : P ratios at the epiphytic, transitional and free-standing stages of hemiepiphytic *F. tinctoria* were 178 : 10 : 1, 216 : 12 : 1, and 199 : 11 : 1, respectively, being greatest at the transitional stage. The total P content per leaf of the two fig ecotypes declined through ontogeny (Fig. 3e). At the juvenile stage, total P content per leaf of hemiepiphytic *F. tinctoria* was lower ($t = 2.88$, $P = 0.013$) than that of nonhemiepiphytic counterparts.

Leaf P_{mass} content of host palms without figs and with epiphytic *F. tinctoria* was similar, but their values were 43.04% ($t = 4.36$, $P < 0.001$) and 47.82% ($t = 3.95$, $P = 0.002$) higher than those of the host palms with transitional *F. tinctoria*, respectively (Fig. 3a). The leaf P_{area} content of palms was significantly higher without hemiepiphytic figs ($t = 2.93$, $P = 0.020$) than with transitional *F. tinctoria* (Fig. 3b), and leaf P_{area} content had significant positive correlations with the content of other leaf nutrients in both host palms and *F. tinctoria* (Fig. S5). The leaf C : P of host palms with transitional *F. tinctoria* increased significantly, exceeding that of host palms without figs ($t = 4.37$, $P < 0.001$) and with epiphytic figs ($t = 3.70$, $P = 0.004$). The leaf N : P ratio of host palms was also higher with transitional *F. tinctoria* than without figs ($t = 5.33$, $P < 0.001$; Fig. 3c,d). Leaf C : N : P ratios of palm without figs and with epiphytic *F. tinctoria* were 378 : 14 : 1 and 372 : 17 : 1, respectively; however, the ratio of palms with transitional *F. tinctoria* increased to 532 : 18 : 1. Moreover, when the aerial roots of hemiepiphytic *F. tinctoria* grew into the ground, the leaf C_{mass}, N_{mass}, and K_{mass} content of host palms also significantly decreased (Fig. S4).

Leaf morphological and photosynthetic traits at different growth stages

Functional traits related to leaf morphology and photosynthesis of hemiepiphytic *F. tinctoria* significantly changed when growing from epiphytes into free-standing trees, some being strikingly different from nonhemiepiphytic conspecifics (Fig. 4). The leaf thickness of hemiepiphytic and nonhemiepiphytic *F. tinctoria* and the SLA of hemiepiphytic *F. tinctoria* significantly increased ($P < 0.05$); conversely, the leaf area of both fig ecotypes significantly decreased ($P < 0.01$) from seedlings to adults (Fig. 4a–c). Yet leaf area and SLA of host palms were similar across growth stages (Fig. 4b,c). During their growth, the maximum net
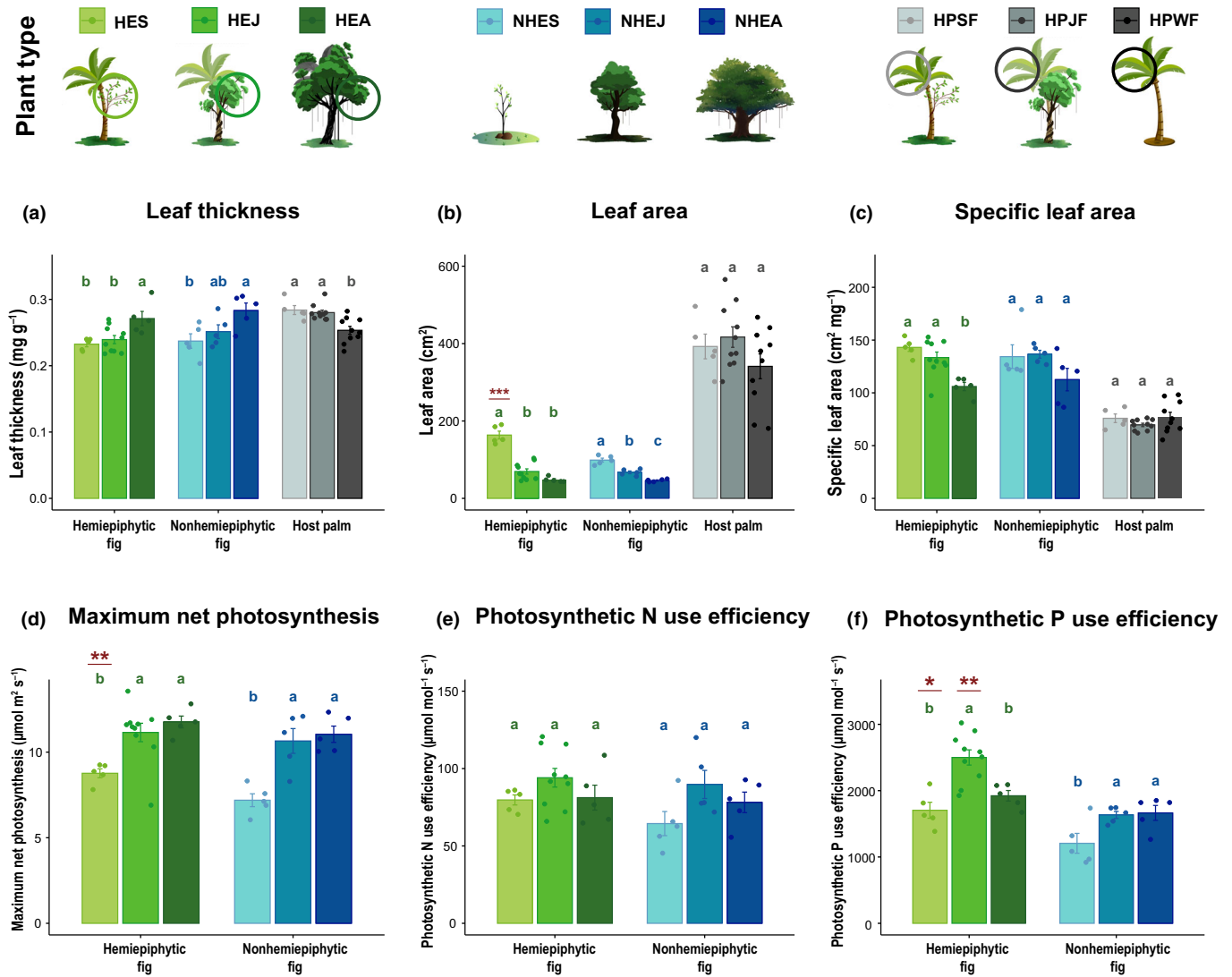
photosynthesis of hemiepiphytic *F. tinctoria* and nonhemiepiphytic conspecifics was significantly enhanced (Fig. 4d). Photosynthetic P use efficiency of hemiepiphytic *F. tinctoria* increased ($t = 4.74$, $P < 0.001$) from the epiphytic to transitional stage, in which it peaked, and then declined ($t = 3.44$, $P = 0.008$) from the transitional to free-standing stage. Photosynthetic P use efficiency of nonhemiepiphytic *F. tinctoria* increased from seedlings to adults ($F = 5.20$, $P = 0.023$). In both seedling ($t = 2.59$, $P = 0.032$) and juvenile ($t = 6.85$, $P < 0.001$) stages, significantly higher photosynthetic P use efficiencies were observed in hemiepiphytic *F. tinctoria* than their nonhemiepiphytic conspecifics (Fig. 4f).

Substrate P content at different growth stages

Concerning changes in the total and available P content of substrates, significant changes were observed across different growth stages of *F. tinctoria*. The soil total P content was greater for hemiepiphytic *F. tinctoria* than their nonhemiepiphytic counterparts at both juvenile and adult stages (Fig. 5a). There were decreasing trends of available P content in substrates from the seedling through adult stages. Once the aerial roots of hemiepiphytic *F. tinctoria* had entered the soil, significant reductions in soil available P content ($\chi^2 = 11.35$; $P = 0.003$) ensued at the transitional stage (by 74.36%) and free-standing stage (by 82.29%; Fig. 5b). When not rooted, hemiepiphytic *F. tinctoria* had significantly higher soil available P content (by 244.23%; $\chi^2 = 4.86$, $P = 0.027$) than nonhemiepiphytic *F. tinctoria*. However, no significant differences in soil available P content were evident between nonhemiepiphytic and hemiepiphytic *F. tinctoria* after their aerial roots entered the soil. The total and available P content in the canopy humus both peaked at the epiphytic stage, then declined significantly with growth. The total P content in the canopy humus of host palms decreased 34.94% ($\chi^2 = 5.81$, $P = 0.054$) as hemiepiphytic *F. tinctoria* grew from epiphytic seedlings into free-standing adults (Fig. 5c). Similarly, available P content in the canopy humus dropped substantially, by 86.22% ($\chi^2 = 6.73$, $P = 0.035$), as hemiepiphytic *F. tinctoria* continued to grow (Fig. 5d).

Variation in and trade-offs among leaf functional traits

The LMMs (Table 1) showed that the fig ecotype significantly affected leaf P_{mass} content, leaf P_{area} content, leaf C : P, leaf N : P, and photosynthetic P use efficiency ($P < 0.001$) of *F. tinctoria*, whereas ontogeny and substrate C : (N : P) did not. This showed that variation in these leaf P-related traits were mainly attributable to the fig ecotype, whose growth and substrate characteristics had negligibly influenced them. Leaf morphology and photosynthesis were significantly ($P < 0.01$) affected by ontogeny (Table S2). Furthermore, the substrate available P content had significant effect on the variation in leaf P_{mass} content of hemiepiphytic *F. tinctoria* ($F = 5.83$, $P = 0.046$) but not nonhemiepiphytic conspecifics (Table S3). Moreover, the plasticity of leaf area in hemiepiphytic *F. tinctoria* was high at the epiphytic stage, while the plasticity of leaf P-related traits in hemiepiphytic *F.*

Fig. 4 Leaf morphological and photosynthetic trait dynamics of hemiepiphytic and nonhemiepiphytic *Ficus tinctoria* and their host palms at different growth stages. (a) Leaf thickness, (b) leaf area, (c) specific leaf area, (d) maximum net photosynthesis, (e) photosynthetic N use efficiency, and (f) photosynthetic P use efficiency of hemiepiphytic and nonhemiepiphytic *F. tinctoria* and their host palms at different growth stages. HES, hemiepiphytic seedling (epiphytic stage, $n = 5$); HEJ, hemiepiphytic juvenile (transitional stage, $n = 10$); HEA, hemiepiphytic adult (free-standing stage, $n = 5$); NHES, nonhemiepiphytic seedling ($n = 5$); NHEJ, nonhemiepiphytic juvenile ($n = 5$); NHEA, nonhemiepiphytic adult ($n = 5$); HPSF, host palm with seedling fig ($n = 5$); HPJF, host palm with juvenile fig ($n = 10$); HPWF, host palm without fig ($n = 10$). Data shown are the mean ($\pm$SE). Different letters with the same colour denote significant differences among the different stages of the same fig ecotype or host palms, at the 0.05 level. *P*-values by ANOVA (or Kruskal–Wallis test). * indicates a significant difference between hemiepiphytic and nonhemiepiphytic *F. tinctoria* within the same growth stage. *P*-values by *t*-test (or Wilcoxon test). *, $P < 0.05$; **, $P < 0.01$.

tinctoria was high at the transitional stage. At the free-standing stage of hemiepiphytic *F. tinctoria*, most of the leaf trait plasticity was low and tended to be stable (Fig. 6a; Table S4).

The PCA of leaf functional traits showed that the first and second axes explained 47.6% and 31.4% of the total variance, respectively (Fig. 6b). The PCA reflected the functional trait trade-offs between total leaf P investment and P allocation and P use efficiency. The first axis loaded the leaf P allocation and investment to the positive side, and photosynthetic P use efficiency to the negative side. Along the second axis, maximum net photosynthesis loaded positively, while SLA did so negatively. Importantly, on the first axis, the position of hemiepiphytic *F. tinctoria* changed from

positive to negative as they grew, whereas the position of non-hemiepiphytic *F. tinctoria* was always positive. On the second axis, the positions of both fig ecotypes shifted from negative to positive as they grew. The PCA revealed that hemiepiphytic and non-hemiepiphytic *F. tinctoria* incurred divergent functional trait trade-offs during their growth, especially in terms of leaf P allocation and investment, and P nutrient use efficiency.

Discussion

Shifts in functional traits can reflect changes to the competitive status and adaptive strategies of plants (Funk *et al.*, 2017; Carl
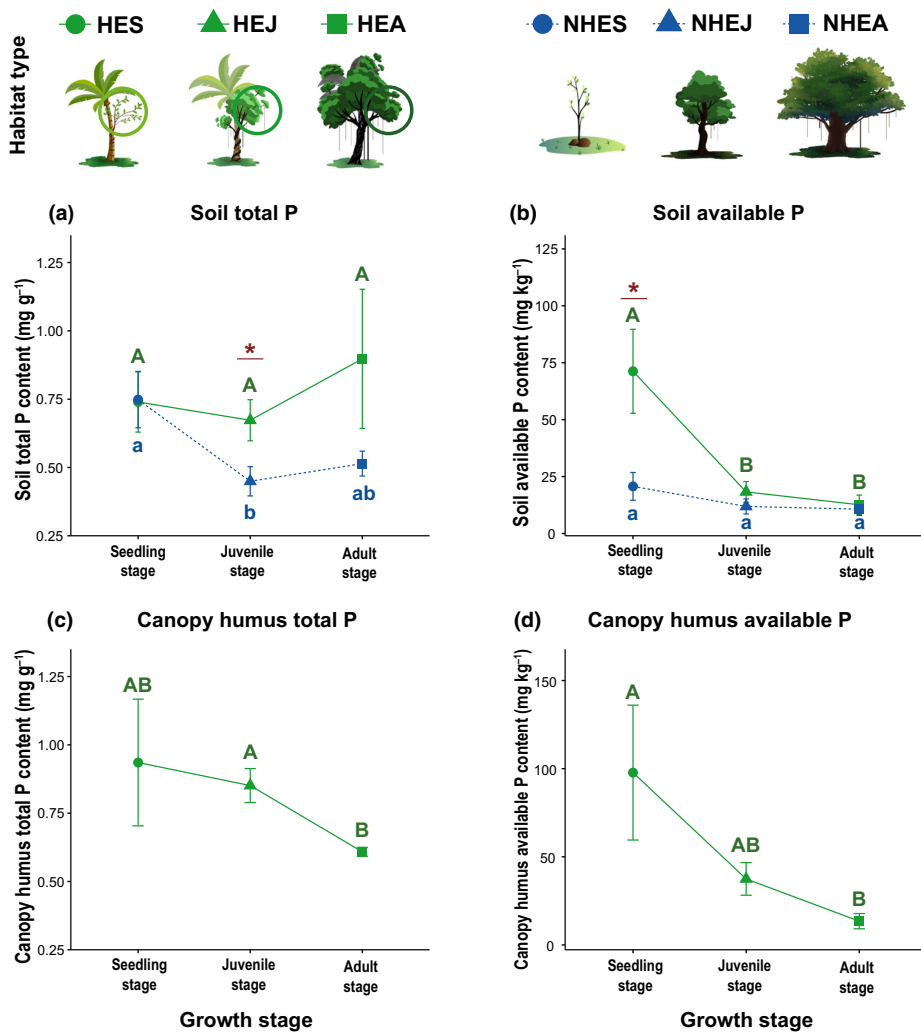
Fig. 5 Dynamics of substrate total and available P content of different habitats at different growth stages. (a) Soil total P content, (b) soil available P content, (c) canopy humus total P content, and (d) canopy humus available P content of hemiepiphytic and nonhemiepiphytic *Ficus tinctoria* at different growth stages. HES, hemiepiphytic seedling (epiphytic stage, $n = 5$); HEJ, hemiepiphytic juvenile (transitional stage, $n = 10$); HEA, hemiepiphytic adult (free-standing stage, $n = 5$); NHES, nonhemiepiphytic seedling ($n = 5$); NHEJ, nonhemiepiphytic juvenile ($n = 5$); NHEA, nonhemiepiphytic adult ($n = 5$). Data shown are the mean ($\pm$1SE). Different capital and lowercase letter denote significant differences among stages of the hemiepiphytic (soil and canopy humus) and nonhemiepiphytic (soil) substrates, respectively, at the 0.05 level. *P*-values by ANOVA (or Kruskal–Wallis test). * indicates a difference between hemiepiphytic and nonhemiepiphytic habitats within the same growth stage of *F. tinctoria*. *P*-values by *t*-test (or Wilcoxon test). *, $P < 0.05$.

et al., 2018; Amaral *et al.*, 2021). Some leaf functional traits mirror plant nutrient conditions; for example, a low leaf P_{mass} content and high leaf N : P ratio could convey P deficiency, albeit this varies interspecifically (Güsewell, 2004; Tian *et al.*, 2018). Fig species typically have a higher P demand than do other tropical plants (Fig. 2b–d), with research showing fig species having a relatively high leaf P_{mass} content (2–4 mg g^{-1}) and relatively low leaf N : P ratios (6–11) under nutrient-sufficient conditions (Xiang & Chen, 2004; Leonel & Damatto, 2008; Garrish *et al.*, 2010; Mendoza-Castillo *et al.*, 2019). Most of our study's corresponding values were within those ranges: respectively, 2.5 mg g^{-1} and 8.9 for nonhemiepiphytic *F. tinctoria*; 2.3 mg g^{-1} and 9.6 for epiphytic *F. tinctoria*; and 2.0 mg g^{-1} and 11.1 for free-standing hemiepiphytic *F. tinctoria*; however, the 1.8 mg g^{-1} and 12.3 for transitional *F. tinctoria* were outside both ranges. The latter's lower leaf P content and higher leaf N : P ratios in transitional *F. tinctoria* suggested that hemiepiphytic figs incur a P shortage when competing for soil resources with their hosts (Putz & Holbrook, 1989; Yu *et al.*, 2019). This interpretation is supported by the decreasing leaf P content and increasing leaf N : P ratio in their host palms, as well as decreasing P content in substrates (Figs 3a–d, 5b–d). Importantly, leaf P

content dynamics (including the leaf C : P and N : P ratios) are mainly affected by the fig's ecotype, providing strong evidence that P-related traits are responsive to the unique life history of hemiepiphytic figs and not dependent on either ontogeny or the microenvironments of the common garden (Table 1). Moreover, the effect of substrate available P content upon the leaf P_{mass} content of hemiepiphytic *F. tinctoria* is significant, but not so for nonhemiepiphytic conspecifics (Table S3). This implies that the P shortage of hemiepiphytic *F. tinctoria* and host palms arises from P competition (Guiz *et al.*, 2018).

The high P demand of figs and palms, the zero distance between hemiepiphytic figs and their hosts, and the widespread P deficiency in tropic soils are key factors generating their intense P competition. First, that figs and palms both have a high P demand is evinced by their higher leaf P_{mass} content vis-à-vis sympatric tropical broad-leaved evergreen trees in the common garden and globally (Fig. 2; Notes S1–S3). Because many fig species, especially pioneer fig trees, grow rapidly in tropical ecosystems (Antunez *et al.*, 2001; Garrish *et al.*, 2010), the 'growth rate hypothesis' predicts this faster growth requires higher P to sustain the increased allocation to P-rich ribosomal RNA to carry out protein synthesis (Sterner & Elser, 2002; Leal *et al.*, 2017).

Table 1 P-related traits of *Ficus tinctoria* and their responses to ecotype (i.e., hemiepiphytic and nonhemiepiphytic ecotypes), ontogeny (i.e., seedling, juvenile and adult growth stages), their interactions (as the fixed effects), substrate C : (N : P) and substrate water content (as the covariates).

Variable	Ecotype (ET)	Ontogeny (OG)	ET × OG	Substrate C : (N : P)	Substrate water content	R^2 of the model
Leaf P_{mass} content	**28.25*****	0.77	**5.65***	0.68	3.19	0.62
Leaf P_{area} content	**16.06*****	3.14	1.53	0.43	1.85	0.51
Leaf C : P ratio	**36.12*****	0.42	**5.24***	1.38	**5.13***	0.67
Leaf N : P ratio	**20.93*****	0.35	3.33	2.14	**7.79***	0.59
Leaf total P content	**8.17***	**40.84*****	**18.36*****	**85.48*****	4.36	0.89
PPUE	**48.23*****	**9.56****	**3.71***	2.29	**6.80***	0.76

Leaf P_{mass} content: mass-based leaf P content; Leaf P_{area} content: area-based leaf P content. PPUE: Photosynthetic P use efficiency. The table shows the *F*-values from a linear mixed model for each variable. The bold text shows the variable has a significant response ($P < 0.05$) to the corresponding factors. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. In these models, the *df* of ecotype is 1, the *df* of ontogeny is 2, the *df* of ecotype × ontogeny is 2, the *df* of substrate C : (N : P) is 1, the *df* of substrate water content is 1. The residual *df* for each model is 27. The other traits of *F. tinctoria* and their responses to ecotype, ontogeny, their interactions, substrate C : (N : P) and substrate water content are shown in Supporting Information Table S2.
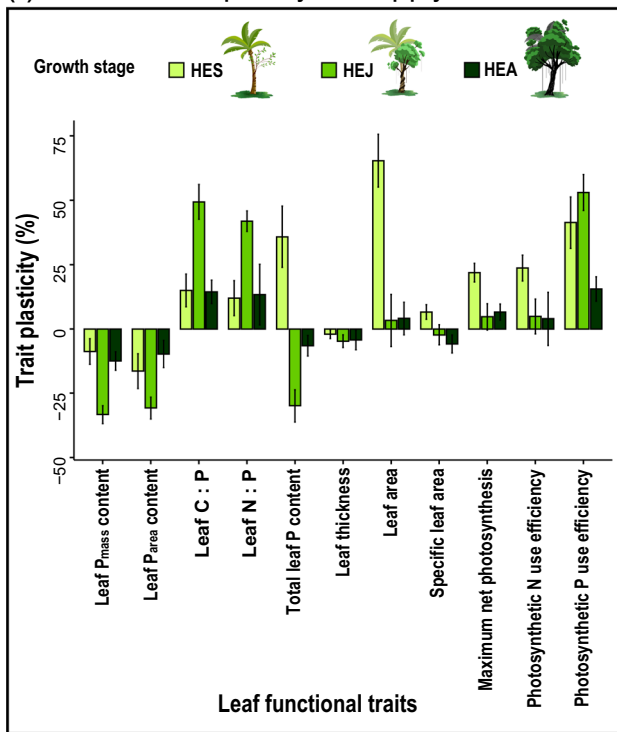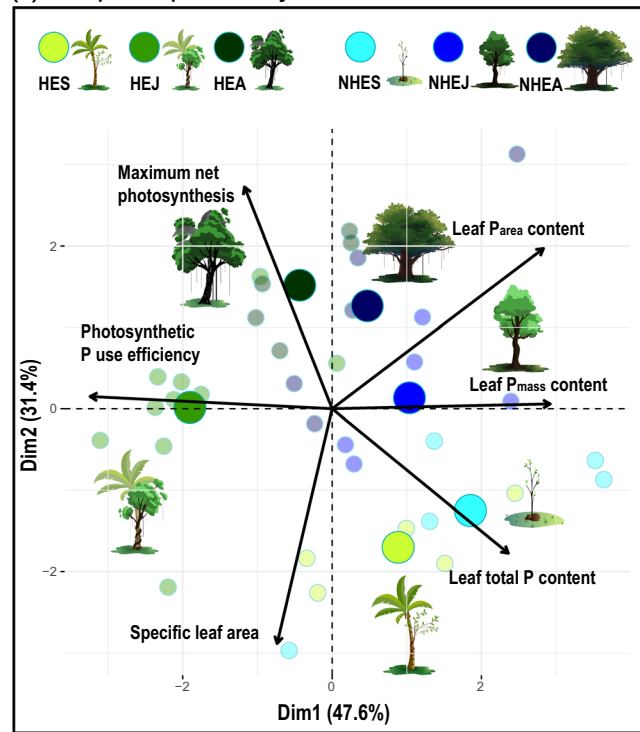
Fig. 6 Plasticity and trade-off of leaf functional traits in *Ficus tinctoria*. (a) Trait plasticity of hemiepiphytic *F. tinctoria* at different growth stages. Data show the mean (±SE). (b) Principal component analysis (PCA) of hemiepiphytic and nonhemiepiphytic individuals of *F. tinctoria*. The large opaque points denote mean values of figs in different growth stages, whereas the small different-coloured translucent points represent fig individuals. HES, hemiepiphytic seedling (epiphytic stage, $n = 5$); HEJ, hemiepiphytic juvenile (transitional stage, $n = 10$); HEA, hemiepiphytic adult (free-standing stage, $n = 5$); NHES, nonhemiepiphytic seedling ($n = 5$); NHEJ, nonhemiepiphytic juvenile ($n = 5$); NHEA, nonhemiepiphytic adult ($n = 5$). The other trait plasticity of hemiepiphytic *F. tinctoria* at different growth stages are shown in Supporting Information Table S4.

Furthermore, compared with the nonhemiepiphytic figs, hemiepiphytic figs lacked more P (Figs 2, 3). Second, close proximity of plants implied strong competition (Radtke *et al.*, 2003), so the zero distance between hemiepiphytes and their hosts suggests their intense competition. Third, P is commonly a limiting nutrient element in our study area (Han *et al.*, 2005; Mani & Cao, 2019) and other tropical ecosystems (Wright, 2019; Hou *et al.*, 2020), and competing for deficient soil nutrients is a widespread ecological process in plant communities (Baribault *et al.*, 2012; Carl *et al.*, 2018; Turner *et al.*, 2018). These reasons

support the idea that against the background of P deficiency in tropics, P competition between hemiepiphytes and their hosts is a general phenomenon. Early studies (Putz & Holbrook, 1989; Guevara & Lopez, 2007) also indirectly support our conclusion, having found a decreased leaf P_{mass} content and increased rate of root arbuscular mycorrhizal (AM) colonisation in Neotropical hemiepiphytic figs when they rooted into the soil (Table S5). Given the higher plant density and lower soil P availability in tropical forests, P competition between hemiepiphytic figs and their hosts in their natural habitats is likely to be more intense

than in our common garden (Comita *et al.*, 2014; Guiz *et al.*, 2018). Nevertheless, host death enables hemiepiphytic figs to monopolise crucial limiting resources, especially P, as demonstrated by the recovered leaf P content and diminished leaf C : P and N : P ratios (Fig. 3a–d). The host-killing process by hemiepiphytic figs benefits them by mitigating P competition, confirming our hypothesis.

Aerial roots of hemiepiphytic figs can mechanically damage the external phloem of dicot hosts and restrict the flow of nutrients and water, probably a critical reason for host death (Lawton & Williams-Linera, 1996; Zotz *et al.*, 2021). Yet, as common hosts for hemiepiphytic figs (Putz & Holbrook, 1989; Guevara & Lopez, 2007; Liu *et al.*, 2014), palm stems consist of primary tissues with scattered internal vascular bundles that transport water and nutrients (Tomlinson, 2006). Therefore, constriction applied to the stem surface by fig roots probably does not sever (but may reduce) the nutrient and water transportation in palms (Fig. S1). Fairhurst & Härdter (2003) reported an optimum leaf P_{mass} content of $1.4 \, \mathrm{mg \, g^{-1}}$ for oil palm; however, when living with transitional hemiepiphytic *F. tinctoria* the leaf P_{mass} content falls below that to $0.8 \, \mathrm{mg \, g^{-1}}$, so oil palms incur P deficiency stress. In addition, the leaf P_{area} content of the two *F. tinctoria* ecotypes and host palms had positive correlations with other area-based nutrient content (Fig. S5). Accordingly, declining P may reduce other essential nutrients in the plants (Sterner & Elser, 2002; Tian *et al.*, 2018; Penuelas *et al.*, 2019), which could contribute to the death of host palms. When P deficient, plants could change their interaction with soil microorganisms to facilitate P capture (Andrino *et al.*, 2021). Once the aerial roots of hemiepiphytic figs enter the soil, they can greatly enhance AM colonisation (from *c.* 5% to 60%) to expand their nutrient absorption area and acquire more scarce P resources (Guevara & Lopez, 2007). Hemiepiphytes also have no trunk, so they may have extra resources available for developing their root system further to access substrate nutrients or to produce more branches and leaves to shade their host palms. Hemiepiphytic figs competing for light with their hosts in the canopy stratum is another probable factor promoting host death (Lawton & Williams-Linera, 1996; Zotz *et al.*, 2021). These efficient strategies make hemiepiphytic figs apt at acquiring both belowground and aboveground resources (P and light) during the transitional stage until its less competitive host palms are killed via chronic resource shortages. Furthermore, our study relied on a space-for-time substitution and extensive empirical data collection. To validate our conditional findings, long-term observations across the whole life history of hemiepiphytic figs are needed, especially their belowground ecological processes (e.g. soil microbial community changes), to better understand the competition between them and their hosts.

Trade-offs could be a consequence of the cost of plasticity for underlying phenotypic traits (Chevin *et al.*, 2010). Plasticity and trade-offs in functional traits could help plants adjust to resource competition (Yu *et al.*, 2019; Cope *et al.*, 2021). Hemiepiphytic *F. tinctoria* show strong leaf trait plasticity across growth stages, equipping them to better utilise resources via functional trait trade-offs in changing habitats (Fig. 6). These can reflect the adaptation strategies of hemiepiphytic figs through ontogeny. At their epiphytic stage, because host palms' canopy humus provides enough P for seedling growth (Putz & Holbrook, 1989) and light availability is relatively high, the cost of building a trunk can be partly avoided, leaving epiphytic seedlings not lacking P (Figs 3, 5). Therefore, hemiepiphytic figs can invest more nutrients into a higher leaf area to capture more light and intercept more water from rain and fog (Liu *et al.*, 2014). As transitional juveniles, the canopy humus no longer supplies enough nutrients (especially P) and water resources for subsequent growth of large hemiepiphytic fig trees (Fig. 5c,d). Accordingly, hemiepiphytic figs develop super aerial root systems and penetrate soil to obtain nutrient and water resources for growth. With their expanding canopy and rooted state, transitional figs can acquire light and water resources more easily than do epiphytic seedlings (Holbrook & Putz, 1996; Liu *et al.*, 2014), as reflected in the latter's reduced leaf area (Figs 1h, 4b). Under P-deficient conditions, hemiepiphytic figs reduce their leaf P_{mass} and P_{area} content and increase their root AM colonisation (Putz & Holbrook, 1989; Guevara & Lopez, 2007) to acquire P for growth. Transitional hemiepiphytic figs employ enhanced P-related trait plasticity to cope with P-limited conditions (Fig. 6a): despite their lower leaf P_{mass} content, they significantly increased their photosynthetic P use efficiency to maintain regular photosynthesis (Hidaka & Kitayama, 2010, 2011), whereas they lowered leaf P_{area} content and leaf area to reduce total P investments per leaf (Fig. 3e). Transitional figs optimise leaf area and P allocation and may trade off P components (Mo *et al.*, 2019) to lessen their dependence upon substrate P resources and better adapt to P deficiency. Moreover, decomposing fallen fruit or litter from host palms will input more nutrients (P, N and C) into the topsoil (Singh *et al.*, 2010) than in a habitat without host palms (Table S1; Fig. S2c). After host death, the decomposition of dead host residues would supply nutrients for the growth of hemiepiphytic figs. As their hosts die and disappear, the increasing leaf thickness and decreasing SLA of hemiepiphytic figs (Fig. 4a–c) in going from epiphytic seedlings to free-standing adults should enable them to better deal with higher light intensity and transpiration (Holbrook & Putz, 1996; Coble & Cavaleri, 2014). Hemiepiphytic figs adapt to changing habitats via functional trait trade-offs across growth stages, in support of our hypothesis.

The nonhemiepiphytic growth form can acquire a relatively stable and continuous supply of nutrient and water resources (Liu *et al.*, 2014). So why do many *Ficus* species have hemiepiphytic phenotypes? Hemiepiphytic fig seeds are dispersed by animals (e.g. birds and bats) and initially germinate and grow in the canopy (Heer *et al.*, 2010; H. H. Chen *et al.*, 2015), where seedlings maximise P and light intake and escape multiple stresses (Lawton & Williams-Linera, 1996; Okamoto, 2015). Although hemiepiphytic figs will ultimately root in soil and face P deficiency, their increased tolerance and competitiveness through ontogeny are beneficial for adapting to stresses on the ground. Habitat conditions imposing low-resource availability and high risk upon vulnerable seedlings will increase fitness costs and decrease their long-term survivability (Niinemets, 2010). On an evolutionary scale, the hemiepiphytic

phenotype of figs can reduce extinction rates in comparison with primarily nonhemiepiphytic lineages, because it lets figs occupy diverse habitats in highly risky and competitive tropical ecosystems (Machado *et al.*, 2018). Intense competition for scarce P is a prevailing stress for plants in the tropics (Turner *et al.*, 2018; Hou *et al.*, 2020), with figs having evolved the hemiepiphytic phenotype to better cope with environmental stresses. Shifts in nutrient, competition, light and water conditions will feed back into functional traits and their plasticity, resulting in fig resource-mediated adaptive strategies and phenotypic evolution (Putz & Holbrook, 1989; Holbrook & Putz, 1996; Schmidt & Tracey, 2006; Guevara & Lopez, 2007; Hao *et al.*, 2010, 2011; Liu *et al.*, 2014; H. H. Chen *et al.*, 2015). Functional trait trade-offs of hemiepiphytic figs are driven by deficient and changing resource availabilities (e.g. P, light, water). Based on results from ourselves and others, we propose a path diagram for the adaptive strategy of hemiepiphytic figs in changing habitats (Fig. 7), which could serve as a paradigm for understanding plant life history strategy and adaptation to changing habitats.

Conclusion

Our results demonstrate that the high P demand of figs, P deficiency in tropics, and zero distance between hemiepiphytic figs and their host trees lead to intense P competition between them. Hemiepiphytes adapt to changing environments via functional trait trade-offs to better utilise limited resources. We suggest that by killing their hosts, the hemiepiphytic figs benefit from reduced P competition for which acquiring P could be a driving factor. These findings provide a new perspective on the evolution of host killing in hemiepiphytes and link this behaviour to the widespread P shortages in tropical soils.

Acknowledgements
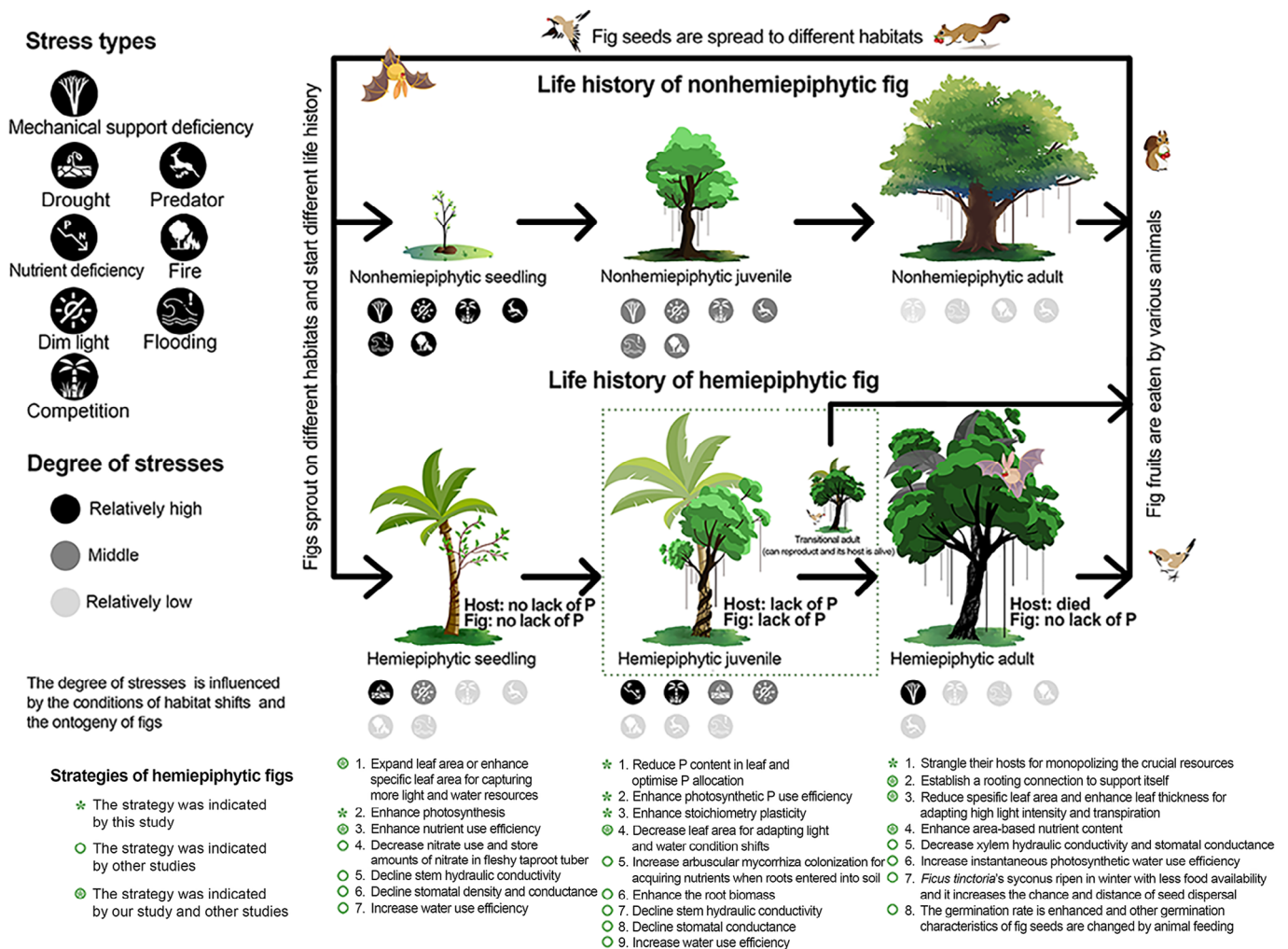
Fig. 7 Adaptive strategy of hemiepiphytic figs in changing habitats. These supplementary adaptive strategies of hemiepiphytic figs are reported by Putz & Holbrook (1989); Holbrook & Putz (1996); Schmidt & Tracey (2006); Guevara & Lopez (2007); Hao *et al.* (2010); Hao *et al.* (2011); Liu *et al.* (2014); and Chen *et al.* (2015).

Author contributions

Y-XM and W-YL conceived and designed the study. Y-XM collected and analysed data, and Y-XM and W-YL wrote the manuscript. RTC contributed substantially to the revision, LS, H-ZL and GW revised the manuscript and figures. G-YH and R-YM performed the P content analysis of most figs and palms in the XTBG. YW participated in the data analysis. S-ZM and YL participated in the field experiments.

Competing interests

None declared.

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Data availability

All data within the manuscript and the Supporting Information files of this study are available (please refer to Dataset S1 for details).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Leaf functional traits of *Ficus tinctoria* and oil palm in the common garden, and mass-based leaf P content of figs and palms on a global scale.

Fig. S1 Hemiepiphytic figs with different type host trees.

Fig. S2 The study site and material sampling.

Fig. S3 The correlation between crown diameter and diameter at breast height of nonhemiepiphytic *Ficus tinctoria*.

Fig. S4 Leaf C, N, K, Ca and Mg dynamics of hemiepiphytic and nonhemiepiphytic *Ficus tinctoria* and their host palms at different growth stages.

Fig. S5 The correlations between leaf P content and C, N, K content of *Ficus tinctoria* and their host palms.

Table S1 Differences in plant traits and substrate characteristics of hemiepiphytic and nonhemiepiphytic *Ficus tinctoria*.

Table S2 Trait syndromes of *Ficus tinctoria* and their responses to ecotype, ontogeny, their interactions, substrate C : (N : P) and substrate water content.

Table S3 Substrate available P content affected leaf P content of hemiepiphytic *Ficus tinctoria*.

Table S4 Trait plasticity of hemiepiphytic *Ficus tinctoria* at different growth stages.

Table S5 P-related traits and arbuscular mycorrhizal colonisation rate of hemiepiphytic figs during the different growth stages in the different study sites.

Notes S1 The mass-based leaf P content of figs from worldwide.

Notes S2 The mass-based leaf P content of palms from worldwide.

Notes S3 The mass-based leaf P content of dominate evergreen broad-leaved woody plants from local area (Xishuangbanna).

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