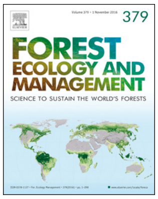
Forest Ecology and Management 435 (2019) 66–76

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Obligate to facultative shift of two epiphytic *Lepisorus* species during subtropical forest degradation: Insights from functional traits

Quan Chen[a,b,1], Hua-Zheng Lu[a,1], Wen-Yao Liu[a,*], Yi Wu[a,b], Liang Song[a], Su Li[a]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Keywords:
Epiphytic fern
Forest degradation
Functional traits
Facultative
Obligate
Plasticity

ABSTRACT

Epiphytic ferns are an important group of plants strongly affected by sudden changes in forest community composition and structure. However, a key gap persists in our understanding of their responses to forest degradation, specifically concerning the changes in species distributions and functional traits and their underlying mechanisms. Here, we investigated the vertical distribution of two *Lepisorus* species of a subtropical primary forest and its two-stage degraded forests in Southwest China, and measured 18 plant functional traits of individuals growing in terrestrial (i.e., on the ground) and 0.5–2.5 m epiphytic forest habitats. We found that the relative abundance of both species peaked at heights of approximately 8–16 m in the canopy of primary forest but at heights of 0–4 m on tree trunks in two degraded forests. Terrestrial individuals occurred only in secondary forests, and the relative abundance of these two species on lower tree trunk and forest ground increased with canopy openness within degraded forests. Principal component analysis of the epiphytes' functional traits and plasticity provided evidence for two suites of traits related to light acclimation and nutrient strategies. Furthermore, variation in both species' morphological and physiological traits revealed resource use trade-offs in response to forest degradation. Epiphytic individuals in primary forest had higher capacity for light capture while those in secondary forests had a higher photosynthetic capacity and resource-use efficiency. Within the same secondary forest, terrestrial individuals tended to acclimate to a low-light understory and were more efficient in their nutrient use than epiphytic conspecifics. Together, these results showed a shift of two obligate epiphytic ferns to be facultative in secondary forests, and underwent a downward shift in their microhabitat occupancy to lower tree trunks and understory soils in response to forest degradation. They could achieve this shift by adjusting their functional traits at an intraspecific level, which promoted rhizome extensions to find optimal habitats for persistence.

1. Introduction

Many tropical floras and montane cloud forests are characterized by prominent epiphytes (e.g., bryophytes, orchids, bromeliads, and ferns), a group which comprises ~9% of all known vascular plant species and function to maintain canopy diversity, carbon fluxes, forest hydrology, and nutrient cycling (Benzing, 2004; Nieder et al., 2001; Zotz, 2013; Zotz and Bader, 2009). As a key component of the epiphytic vascular flora, ferns represent 59% of all such species and they can be obligate or facultative according to their relationship with host trees (Benzing, 2004; Schellenberger Costa et al., 2018). Obligate epiphytes are known to root only on tree barks, while facultative ones can both grow on host trees and on the forest ground soil (de Freitas et al., 2003; Lu et al., 2015). Yet regional variation can exist in the degree of habitat fidelity within a vascular epiphytic species, so that while terrestrial in most of its natural range it is exclusively epiphytic in another region (Gomes-da-Silva and Costa, 2011). As to ferns, clonal integration contribute greatly to performance of facultative epiphytic ones, which is more important in epiphytic habitat than in terrestrial habitat (Lu et al., 2015). However, this pattern is not adequately explained solely by distinct growing conditions (e.g., light, water, and nutrients) between epiphytic and terrestrial habitats, leaving its underlying mechanism elusive (Watkins et al., 2006; Kluge et al., 2006).

Evolutionarily, the major diversification of epiphytism in ferns began in Cretaceous while burst in Cenozoic, mainly driven by ecological opportunistic response hypothesis and evolution of epiphytism

---

[*] Corresponding author.

E-mail addresses: chenquan@xtbg.ac.cn (Q. Chen), luhuazheng@xtbg.org.cn (H.-Z. Lu), liuwy@xtbg.ac.cn (W.-Y. Liu), wuyi@xtbg.ac.cn (Y. Wu), songliang@xtbg.ac.cn (L. Song), lis@xtbg.ac.cn (S. Li).

[1] These authors contributed equally to the article.

https://doi.org/10.1016/j.foreco.2018.12.037
Received 9 October 2018; Received in revised form 18 December 2018; Accepted 20 December 2018

(Schuettpelz and Pryer, 2009). The existence of leptosporangiatae ferns extended to as far back as the Devonian-Carboniferous, approximately 200 Ma before the evolution of angiosperms (Schuettpelz and Pryer, 2009; Brenner, 1996). Fossil records indicated that three major Leptosporangiatae radiation sequentially occurred in Carboniferous, late Paleozoic to early Mesozoic, and Cretaceous (Schuettpelz and Pryer, 2009; Zhang, 2012). However, the latest molecular phylogenetic evidence provided a fourth rapid radiation in Cenozoic, with the flourishing of epiphytes (Zhang, 2012). Extant ferns diversified in the third and fourth radiation, being coincident with the establishment and diversification of tropical forest dominated by flowering plants (Schneider et al., 2004a; Schuettpelz and Pryer, 2009). Polygrammoids, one of the four major clades for epiphytic ferns, was considered to diversify in Tertiary (Dubuisson et al., 2009). Concerning on whole polygrammoids, Schneider et al. (2004b) believed that numerous rapid radiations might have occurred and it was likely related to epiphytism acquisition. It seemed that leptosporangiatae ferns on Earth today were developed to be more capable to occupy the forest canopies (Smith et al., 2006; Schuettpelz and Pryer, 2009). However, we are still limited in understanding the evolution of epiphytism and the adaptation strategies of epiphytic ferns (Schneider et al., 2004b; Tsutsumi and Kato, 2006).

Ferns have two separate free-living generations, which includes a thin and delicate gametophyte considered as the first stage of establishment in a habitat (Watkins et al., 2007). Since obligate epiphytic ferns spend their entire lifetime on host trees, they are strongly affected by variation in plant community composition and structure resulting from forest degradation and habitat fragmentation (Benzing, 2004; Magrach et al., 2014; Watkins et al., 2007). The harsher and more heterogeneous environment of degraded forests might drive the exclusion of some species and influence the distribution of persisting ones (Bhaskar et al., 2014; Lavorel and Garnier, 2002). This pattern has been shown for other vascular epiphytes, and while we expect the same for ferns due to their habitat preference (Einzmann et al., 2015). Yet our understanding of the responses of epiphytic ferns to forest degradation remains poor; in particular, during this process, variability in both the fine-scale distribution pattern and functional traits are two aspects needing empirical study.

Over the last few decades, trait-based approaches have been widely used in field studies, ranging from the organismal level to that of ecosystems, to confirm plant adaptability (Ames et al., 2016; Violle et al., 2007). The current view is that vegetative biomass, reproductive output, and plant survival are all influenced by morphological, physiological, and phenological traits that operate from the cell to the whole plant level (Gutschick, 1999; Violle et al., 2007). Adaptation of specific traits, and diversity in trait combinations, allows for many epiphytic ferns to thrive in the unique environment of the forest canopy (Karasawa and Hijii, 2006; Lavorel and Garnier, 2002). Accordingly, in drastically changed environmental conditions, high plasticity and trade-offs in plant functional traits are likely to play a crucial role in enabling ferns to persist in their new environments (Zhu et al., 2016). To date, however, scant attention has been paid to epiphytic ferns due to logistical challenges in accessing the canopy where they occur. As fragile and vulnerable components of forest ecosystems, epiphytic ferns can show remarkable responses to variable environments in both vertical and horizontal ecological gradients (respectively, micro-environmental differences going from the forest floor to the top canopy, across distinct forest habitats corresponding to degradation stages) (Magrach et al., 2014; Saldaña et al., 2015; Petter et al., 2016). Therefore, trait-based research of this peculiar plant group can provide insights into ecological restoration and biodiversity conservation (Pywell et al., 2003).

To our knowledge, limited information exists on the degradation of epiphytic fern populations in the subtropics, while little is known of how their life history, distribution pattern, and functional traits vary during forest degradation. Working with the congeneric taxa in Polypodiaceae, which shows some of the most spectacular epiphytic specializations in subtropical montane forests in Ailao Mountains National Nature Reserve (NNR), Southwest China, will improve our understanding on diversification of epiphytic forms and strategies. Here, we focus on two *Lepisorus* species which are clustered as one clade in phylogeny (Wang et al., 2010). Both species are mainly epiphytes in primary forests yet colonize terrestrial and epiphytic habitats in NNR's secondary forests. This study aimed to answer three questions: (1) How does the vertical distribution and abundance of *Lepisorus* spp. vary in response to greater canopy openness during forest degradation? (2) Is functional trait variation related to the abundance of the fern species in contrasting light conditions and growth substrates (tree barks in epiphytic habitat versus understory soil in terrestrial habitat)? (3) Is there any notable difference in adaptation strategies of fern individuals from the primary and degraded forests?

2. Materials and methods

2.1. Study area and field survey

This study was conducted from June 5th, 2015 to August 25th, 2016, in subtropical montane moist evergreen broad-leaved forest in the core area (i.e., Xujiaba Region) of Ailao Mountains NNR, Southwest China (2400 m a.s.l.; 100°54′–101°01′E, 23°35′–24°44′N; Fig. 1A). The Ailao Mountains lie between the southern and northern subtropical forest formations, in a transition area with an annual mean temperature of 11.3 °C and mean annual rainfall of 1841 mm (Lu et al., 2015). Influenced by the southwest monsoon and exposed to frequent and intense wind and heavy fog events, the NNR's climate alternates between wet and dry conditions, with precipitation peaking in July through September followed by a dry season lasting from December to next March (Lu et al., 2015; Song et al., 2015). The suitable growing season for epiphytic ferns is from June to October.

The forests in this study area sustain diverse and abundant epiphytes (Lu et al., 2016; Song et al., 2011). Due to the anthropological disturbance in the last century, a landscape mosaic of primary montane forest and some secondary forests in different stages of succession was formed (Qiu et al., 1998; Yang et al., 2008). Thus, the NNR provides an ideal site to examine variation in the epiphytic fern communities of primary and secondary forests. To perform our work, we selected primary *Lithocarpus* forest (PLF), as well as *Lithocarpus* regrowth forest (LRF) and *Alnus nepalensis* secondary forest (ANSF) which represent well the two main phases of forest degradation that occurs in Ailao Mountains (Table 1; Figs. 1B–F; 2A). PLF accounts for nearly 80% of NNR (Qiu et al., 1998), and is characterized by fully closed forest canopy. The shaded and moist understory is dominated by *Sinarundinaria nitida*, with a coverage of 80% (Tang et al., 2007; Li, 2010). There are > 600 epiphytic species in PLF, including 114 ferns and lycophytes that are obligate or facultative (Li et al., 2014; Lu et al., 2015). LRF represents advanced succession after clear-cutting that occurred approximately 100 years ago (Young et al., 1992), with a canopy openness of 8% and densely distributed epiphytes (Lu et al., 2016; Xu and Liu, 2005). It represents the first stage of forest degradation of PLF, with little shrub and herbs (Li, 2010). By contrast, the ANSF had formed after frequent and repeated deforestation, burning, and grazing in primary broad-leaved forests during the 1950–1960s. But because its stands typically occur at NNR boundary, this secondary forest type is exposed to further grazing of domesticated animals, human foraging for non-timber forest products and fuel-wood, and unlawful deforestation; hence, it is best described as severely degraded forest of PLF (Li, 2010; Li et al., 2013). In ANSF, the shrub layer is dominated by *Rhododendron delavayi*, *Vaccinium sprengelii*, *Hypericum patulum*, etc., with a coverage of 30%; the herb layer consists of abundant species, with a coverage of 80% (Li, 2010).

To accurately determine the distribution and abundance of epiphytic and terrestrial individuals of ferns in these three forest types, an

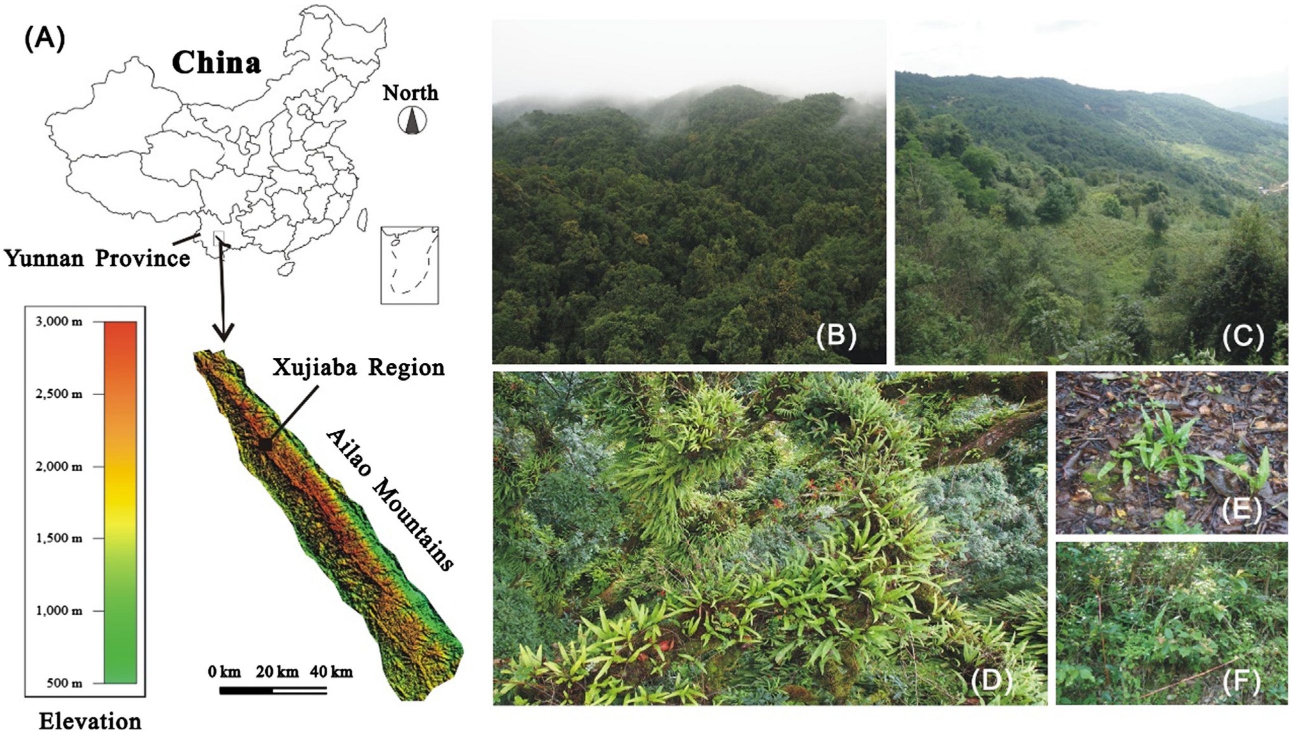


Fig. 1. Location of the study area (A) and photos of investigated forests and species (B–F). B: primary *Lithocarpus* forest (PLF) in the Ailao Mountains, Yunnan Province, Southwest China; C: secondary forests at the edge of the nature reserve; D: intertwining individuals of *Lepisorus scolopendrium* and *L. bicolor* in epiphytic habitat of PLF; E and F: co-occurring individuals of *L. scolopendrium* and *L. bicolor* respectively in terrestrial habitats of *Lithocarpus* regrowth forest (LRF) and *Alnus nepalensis* secondary forest (ANSF).

intensive field survey was conducted between June and July 2015. In PLF, many host canopy trees had fallen in a snowstorm in January 2015 and in the dry-wet season transition that followed (April-May 2015), providing an opportunity to study the vertical distribution of epiphytic ferns. In secondary forests, the trees are relatively shorter in height, so it was not difficult to access their canopy with an extended ladder or by free climbing them. We selected 49, 37 and 48 host trees which are representative of the forest respectively from three stands each in PLF, LRF, and ANSF. Each tree was divided into 2-m height segments: within each, for every live epiphytic fern found its species name and number of individuals were recorded. For the terrestrial ferns, considering on the scattered distribution of LRF with small patches, we set up three 30-m × 30-m plots in this forest type, while four same-sized plots each in PLF and ANSF. Each plots was divided into 2-m × 2-m quadrats. Fern species and individual numbers in every quadrat were also recorded. Relative abundance was calculated as (A_s/A_t)*100%, where A_s is the total count of a given species and A_t is the summed counts of all fern species in the study site.

2.2. Plant materials and experimental design

Lepisorus scolopendrium and *L. bicolor* (Polypodiaceae), two congeneric co-occurring deciduous epiphytic fern species, have rhizomes that branch and creep and are strongly attached to the substratum by clusters of thin and dark brown adventitious roots (Wang et al., 2010; Lu et al., 2016). Both species are clonal ferns that occupy similar habitats and present similar morphological and phenological characteristics (Wang et al., 2010). Normally, they sprout in late May, shedding their leaves in early November, but their rhizomes can persist for many years (Li et al., 2013). They dominate the canopy of primary forests of Ailaoshan NNR (Figs. 1D; 2A) (Xu and Liu, 2005). Moreover, many terrestrial individuals of both species occur also in secondary forests (Figs. 1E, F; 2A).

According to our preliminary observations on the abundances of the two *Lepisorus* species, we selected four, three, and four 30-m × 30-m plots 500 m apart, with a similar slope direction, in PLF, LRF, and ANSF, respectively. In each plot, to avoid sampling individuals that have intact ramets rooted lower on tree trunk bark in contact with the understory soil—we randomly selected 12 host trees with a DBH ≥ 20 cm and on each tagged one individual of *L. scolopendium* and *L. bicolor* that occurred within the 0.5–2.5-m trunk height. To sample the terrestrial (ground surface) habitat, three 2-m × 2-m quadrats (> 10 m apart) were set up in each plot in ANSF and LRF. In each quadrat, at least four individuals each of *L. scolopendium* and *L. bicolor* were embraced and tagged; if four were not present, another quadrat was added to ensure sufficient sample sizes. The morphological and physiological traits were measured on the same frond from each individual.

2.3. Data collection

Measuring annual rhizome growth: For all fern individuals, a tiny elastic string was circle-tied near the growing point of a tagged rhizome; the length from the now-advanced growing tip to the stationary string was measured in early July 2015 (i.e., mid growing season). One year later, the same length was measured again and subtracted the former one to determine the annual growth of rhizome (AGR).

Photosynthetic light response curve: On sunny days, photosynthetic light response curves of the two *Lepisorus* fern species were measured between 08:30 AM and 11:30 AM using a Li-6400 unit (LI-COR, Lincoln, USA), under a CO_2 concentration of 400 μmol·mol^{-1}. The PPFD (photosynthetic photon flux density) was set at 1600, 1400, 1200, 1000, 800, 600, 400, 300, 200, 100, 50, 30, and 0 μmol·m^{-2}·s^{-1}. Before this experiment, plants were exposed to 1000 μmol·m^{-2}·s^{-1} of photosynthetically active radiation (PAR) for > 15 min to let their stomata fully open. For each species, eight healthy and fully-expanded infertile fronds from epiphytic and terrestrial habitats in all forests were selected for the measurement. Light response curves were fitted using a non-

Table 1
Plant community structure of three subtropical forest types representing different degradation stages in the Ailao Mountains, SW China.

Forest type	Canopy openness (%) (Li et al., 2013)	Canopy height (m) (Li, 2010)	Tree density (trees/ha) (Li et al., 2013)	Mean DBH (cm) (Li et al., 2013)	Dominant tree species (Young et al., 1992; Tang et al., 2007; Li et al., 2013)
Primary *Lithocarpus* forest (PLF)	6	18–25	1656	19	*Lithocarpus xylocarpus;Lithocarpus hancei;Castanopsis wattii;Schima noronhae;Stewartia pteropetiolata*
Lithocarpus regrowth forest (LRF)	8	8–15	1533	17	*Lithocarpus hancei;Vaccinium duclouxii*
Alnus nepalensis secondary forest (ANSF)	62	7–12	1577	12	*Alnus nepalensis*

rectangular hyperbola model, and the light saturation point (LSP), light compensation point (LCP), light-saturated photosynthetic rate per leaf area (A_a), light-saturated photosynthetic rate per leaf mass (A_m), photosynthetic nitrogen use efficiency (PNUE), and photosynthetic phosphorus use efficiency (PPUE) were calculated following the methods described by Zhu et al. (2016).

Chlorophyll content: We used a portable chlorophyll meter (SPAD-502, Konica Minolta Sensing, ING, Japan) to determine the relative chlorophyll content (SPAD value) of 12 epiphytic and terrestrial individuals respectively for each species in all forests. Three positions near the midrib of the frond were selected and their respective SPAD values determined and averaged as one measurement per plant. We converted this SPAD value into mass-based chlorophyll content (Chl_m), by using the equation proposed by Coste et al. (2010).

Frond morphology: Fully-expanded infertile fronds were used to measure fern frond morphological traits, namely frond length (FL), frond width (FW), specific frond area (SLA), frond thickness (LT), and stomatal density (SD). We measured FL, FW and LT for all tagged individuals. FL was the base-to-tip length of a frond measured with a tape. FW was the measured distance of two margin points at their widest position. The thickness of a frond at its base, middle, and top was first measured three times near the midrib with a digital Vernier caliper (Guanglu, China) and averaged as LT. A clear nail polish was applied to each frond sample and its stomata counted under a light microscope (Olympus, BH-2, Japan) to calculate the mean SD. Two impressions from the same frond piece were used per plant. We determined SLA and SD by using the same fronds in chlorophyll content measurement. From these fronds, between the midrib and frond margin a small piece of frond was cut out and was then digitally scanned (Epson Perfection V700 Photo) to obtain its sample area using the WinRHIZO system (Pro 2009b, Régent Instruments, Québec, Canada). These frond pieces were oven-dried at 60 °C for 72 h and then weighed to derive the SLA of each cutout piece.

Plant biomass and frond elemental analysis: After determining their photosynthetic light response curve and morphological traits, the whole plants of all tagged individuals were harvested and oven-dried at 60 °C for 72 h and weighed to obtain plant biomass (B). For each species, two individuals (also embraced in the above measurement) from epiphytic and terrestrial habitats of each plots in all forests were selected for the frond elemental analysis. Dried frond samples were then ground into fine powder and passed through a 60 mesh sieve. Mass-based frond nutrient concentrations (N_m and P_m) were analyzed in the Biogeochemical Laboratory of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences. To determine total N, a C/N analyzer was used (Vario MAX CN, Elementar Analysensysteme GmbH, Germany), while for total P the samples were first dispelled by HNO_3-$HClO_4$ and dissolved in HCl, and then determined using an inductively coupled plasma atomic-emission spectrometer (iCAP6300, Thermo Fisher Scientific, USA). Both N_m and P_m were divided by SLA to calculate area-based frond concentrations of nitrogen (N_a) and phosphorus (P_a).

2.4. *Microclimate measurement*

We used climate data loggers (Hobo U30, Onset Computer Corporation, USA) to record daily changes in relative humidity (RH) and air temperature (Ta); a quantum/foot-candle meter (Spectrum Technologies, Inc., USA) was used to record PAR between 27 July and 16 August 2016. In two plots of each forest type, the loggers were placed at 2-m height on the tree trunks and at 0 m on ground where the monitored ferns were growing.

2.5. *Data analysis*

To avoid neighbor resampling (and pseudoreplication), we averaged values of any adjacent two individuals as one measurement for FL, FW,

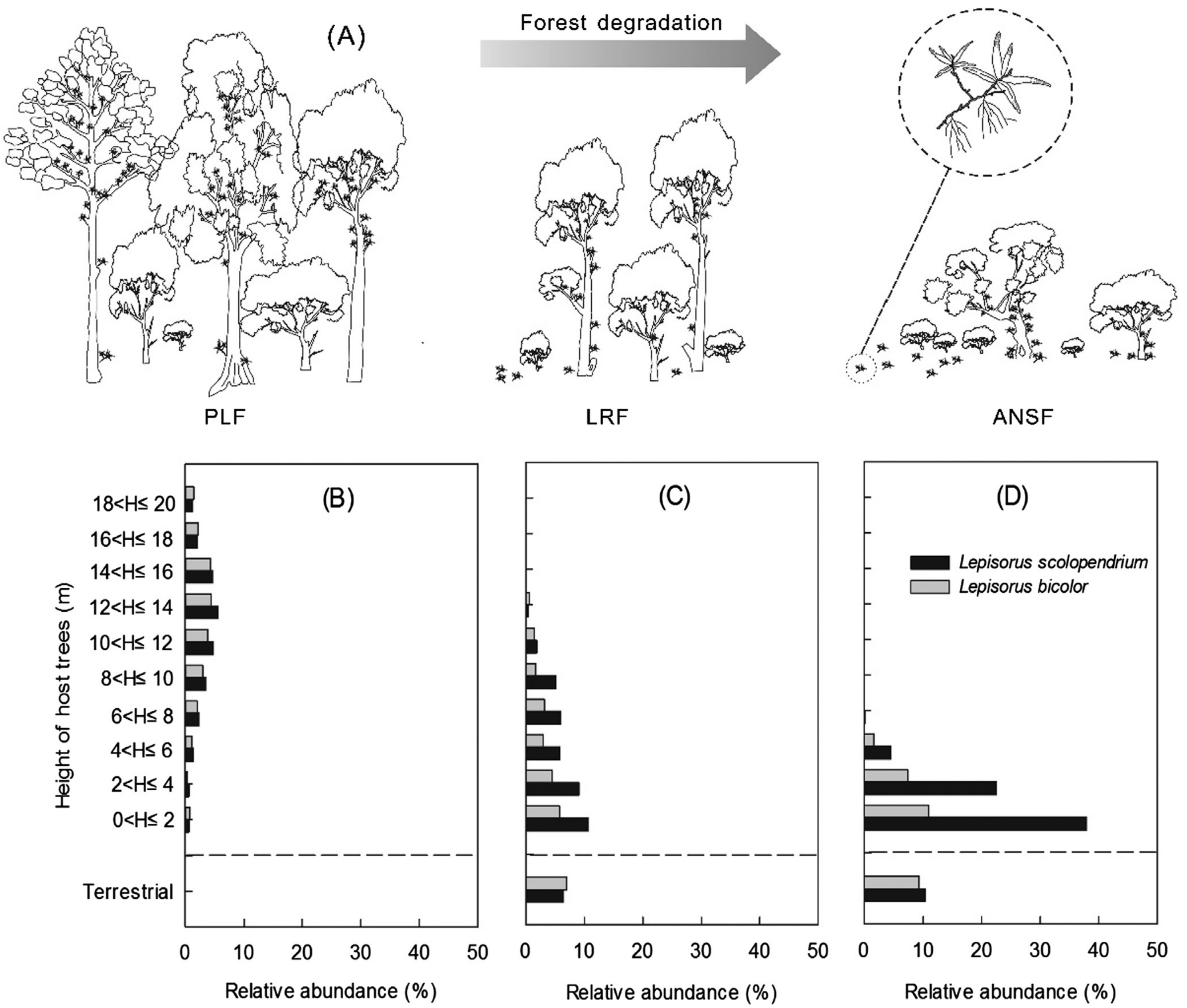


Fig. 2. Distribution pattern (A) and relative abundance (B–D) of two *Lepisorus* species in the primary and two degraded forests in the Ailao Mountains, Southwest China. B: primary *Lithocarpus* forest (PLF); C: *Lithocarpus* regrowth forest (LRF); D: *Alnus nepalensis* secondary forest (ANSF).

LT, AGR and B. For each plant functional trait, its trait plasticity was calculated following Fort et al. (2015). Variation in a trait value was represented as $T_S - T_{PLF}$, where T_S is the trait value of both species respectively from two secondary forests (LRF and ANSF), and T_{PLF} is the mean value of corresponding trait for these two species from primary forest (PLF). Thus, we calculated trait plasticity for each fern species in the two secondary forests as $([T_S - T_{PLF}]/T_{PLF}) * 100$. Two-way ANOVAs were performed to examine the effects of forest degradation stage (PLF, LRF, ANSF) and growth substrate (tree barks in epiphytic habitat vs. understory soil in terrestrial habitat) on each averaged functional trait of the two *Lepisorus* species. For trait data with a normal distribution, one-way ANOVA followed by post-hoc Tukey tests were run to determine significant differences across distinct habitats in forests with different degradation stages, while the Tamhane T2 test was applied for those traits lacking a normal distribution. Simple t tests were used to compare variation in a trait(s) between epiphytic and terrestrial individuals within the same forest. Data were standardized using the Z-score before a principle component analysis (PCA). All analyses were done using SPSS v19.0 software (SPSS Inc., Chicago, USA).

3. Results

3.1. Differing microclimatic conditions among primary and secondary forests

During the growing season of epiphytic ferns, daily microclimate conditions fluctuated to a greater extent in LRF and ANSF than in PLF. Although in all forest types, PAR was higher in the canopy than on the forest floor, it increased with the opening of canopies during forest degradation, especially in severely degraded forest (Fig. S1A–C). The canopy Ta was slightly higher than forest floor Ta from 21:00 to 4:00 in both PLF and LRF, while little difference was found between these strata in ANSF at night. However, during daytime hours, PLF and ANSF had higher Ta in the canopy than forest floor, while LRF showed the opposite pattern (Fig. S1D–F). In contrast to PLF, during the daytime the RH was higher in the canopy than on the forest floor of LRF and throughout the day it stayed higher on forest floor than canopy of ANSF (Fig. S1G–I). Presumably, the higher daytime Ta and lower RH on the ground of LRF are ascribed to thin litter layer and sparse shrub layer, in which more sunlight can reach the ground and accelerate the water evaporation.

3.2. Variation in fern distribution and relative abundance during forest degradation

Our field survey revealed distinct distribution patterns of these two *Lepisorus* species in the primary and two degraded forests. In the non-degraded PLF, relative abundance of both species peaked at 8–16 m in the canopy, with no terrestrial individuals found in the understory (Fig. 2B). However, in secondary forests, their canopy openness was larger and more epiphytic individuals of *L. scolopendrium* and *L. bicolor* grew at lower height through the canopy, at approximately 0–4 m on tree trunks (Fig. 2C, D). At heights of 0–2 m, the relative abundance of epiphytic *L. scolopendrium* reached up to 37.85% in the ANSF (Fig. 2D). Moreover, terrestrial individuals occurred in LRF and ANSF, but in greater number in the more degraded forest, with average relative abundances that ranged from 6.70% in LRF to 9.80% in ANSF (Fig. 2C, D).

3.3. Responses of plant functional traits and their plasticity to forest degradation

Most of the fern traits were significantly affected by forest degradation, such as AGR, FL, FW, SD, Chl_m, A_a, A_m, among others (Table 2). Except for B, LT, SLA, N_m, and P_m, all other functional traits were influenced by the growth substrate ($P < 0.05$). Among all traits, only A_a, A_m, LSP, N_m, and P_m were apparently affected by the interaction of these two factors ($P < 0.05$).

Plant biomass of both fern species varied little under forest degradation, however, in LRF and ANSF the terrestrial individuals of *L. bicolor* had a higher plant biomass than their epiphytic counterparts (Fig. S2A). The AGR of both *L. scolopendrium* and *L. bicolor* in secondary forests were lower than that in primary forest, while higher in terrestrial individuals than their epiphytic conspecifics in ANSF (Fig. S2B). Following forest degradation, the FL, FW, SLA, and Chl_m tended to decrease, while LT and SD increased. Furthermore, some apparent differences were found between epiphytic and terrestrial individuals within the same forest type (Fig. S2C–H). Concerning the leaf photosynthetic-related and chemical traits, A_a, LSP, LCP, N_a, PNUE, and PPUE were all higher in the secondary forests than in primary forest, while N_m, P_m, and P_a were lower and A_m seemed uninfluenced by forest degradation (Fig. S3A–J). Moreover, P_m was reduced more sharply than N_m by forest degradation. Within the same secondary forest, for both fern species, their epiphytic individuals exhibited higher N_m and N_a in the LRF, and higher P_m and P_a in the ANSF than did terrestrial conspecifics (Fig. S3E–H). Conversely, photosynthetic nutrient-use efficiencies were generally higher in terrestrial individuals than in epiphytic ones (Fig. S3I, J).

Trait plasticity responses of two *Lepisorus* species to forest degradation were shown in Fig. 3. The positive values represent increases in trait values with forest degradation, whereas negative ones indicate trait values that decreased with forest degradation. Epiphytic individuals displayed trait plasticity that varied between −94.07% (B) and 282.39% (PPUE) in LRF; in more degraded forest (ANSF), their trait plasticity varied between −93.83% (B) and 588.23% (LSP). In ANSF, the plasticity of LT, SD, LSP, LCP, N_a etc. exceeded that in LRF, but this pattern was reversed for AGR, SLA, Chl_m, A_m, PNUE, PPUE etc. (Fig. 3A, B). Similarly, terrestrial individuals showed high trait plasticity, which varied between −91.83% (LCP) and 227.10% (B) in LRF yet more so in ANSF, to between −88.87% (B) and 460.41% (PPUE). Plasticity in LT, SD, A_a, A_m, LSP, LCP, N_a, PNUE etc. of the ferns in ANSF exceeded that of terrestrial individuals in LRF; by contrast, their plasticity in SLA, Chl_m, P_m etc. was lower in ANSF than in LRF (Fig. 3C, D).

3.4. Trait syndromes and their correlation with plant biomass and annual rhizome growth

In the PCA of 18 functional traits, its first and second axes respectively explained 26.77% and 20.75% of the total variance. The first axis loaded B, AGR, and SLA to the positive side while N_a to the negative side; the second axis loaded A_m, PNUE, and PPUE positively with just P_a on its negative part (Table S1; Fig. 4A). In the PCA for trait plasticity, 26.67% of its total variance was explained by the first while the second axis explained 22.52%. Plasticity of SLA and Chl_m was positively correlated with the first axis, while P_a exhibited a negative correlation; plasticity in A_a, A_m, SD and LT showed positive correlations with the second axis (Table S1; Fig. 4B).

Evidently, from the trait value PCA, epiphytic samples from PLF and terrestrial samples from LRF formed two distinct clusters along the positive side of the first axis, while the epiphytic and terrestrial samples of ANSF were distributed along the negative side. On the second axis, epiphytic individuals of PLF and ANSF were distributed along the

Table 2

Effects of forest degradation stage and growth substrate on plant functional traits of two *Lepisorus* species. Shown are F-values from a two-way crossed ANOVA for each variable.

Variable	Abbreviation	Degradation stage(DS)	Growth substrate (GS)	DS × GS
Plant biomass (g)	B	2.095	2.636	0.495
Annual growth amount of rhizome (cm)	AGR	17.978^{***}	18.539^{***}	3.565
Frond length (cm)	FL	33.945^{***}	27.742^{***}	1.684
Frond width (cm)	FW	20.840^{*}	5.770^{*}	2.623
Frond thickness (mm)	LT	11.509	0.079	1.834
Specific frond area ($cm^{-2} \cdot g^{-1}$) †	SLA	18.057^{***}	1.792	0.250
Stomatal density ($stomata \cdot mm^{-1}$)	SD	53.193^{***}	14.948^{***}	0.970
Chlorophyll content per mass ($mg \cdot g^{-1}$)	Chl_m	1.729^{***}	14.198^{***}	0.387
Area-based maximum photosynthetic rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)†	A_a	19.894^{*}	6.352^{*}	4.874^{*}
Mass-based maximum photosynthetic rate ($nmol \cdot g^{-1} \cdot s^{-1}$)†	A_m	14.514^{***}	17.188^{***}	29.378^{***}
Light saturation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$)†	LSP	20.117^{*}	6.628^{*}	70.330^{***}
Light compensation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	LCP	22.734^{*}	11.878^{***}	0.279
Mass-based total nitrogen concentration ($g \cdot kg^{-1}$)	N_m	16.776	0.236	9.030^{*}
Mass-based total phosphorus concentration ($g \cdot kg^{-1}$)	P_m	24.892	0.884	17.579^{***}
Area-based total nitrogen concentration ($g \cdot m^{-2}$)†	N_a	0.536^{*}	7.614^{*}	1.237
Area-based total phosphorus concentration ($g \cdot m^{-2}$)	P_a	21.582^{*}	7.248^{*}	1.498
Photosynthetic nitrogen use efficiency ($\mu mol \cdot mol^{-1} \cdot s^{-1}$)	PNUE	6.690^{*}	4.159^{*}	0.192
Photosynthetic phosphorus use efficiency ($mmol \cdot mol^{-1} \cdot s^{-1}$)†	PPUE	0.723^{*}	8.428^{*}	0.170

Trait data of both species were pooled for the analysis.

* significant at $P < 0.05$.

*** significant at $P < 0.001$.

† Log-transformed.

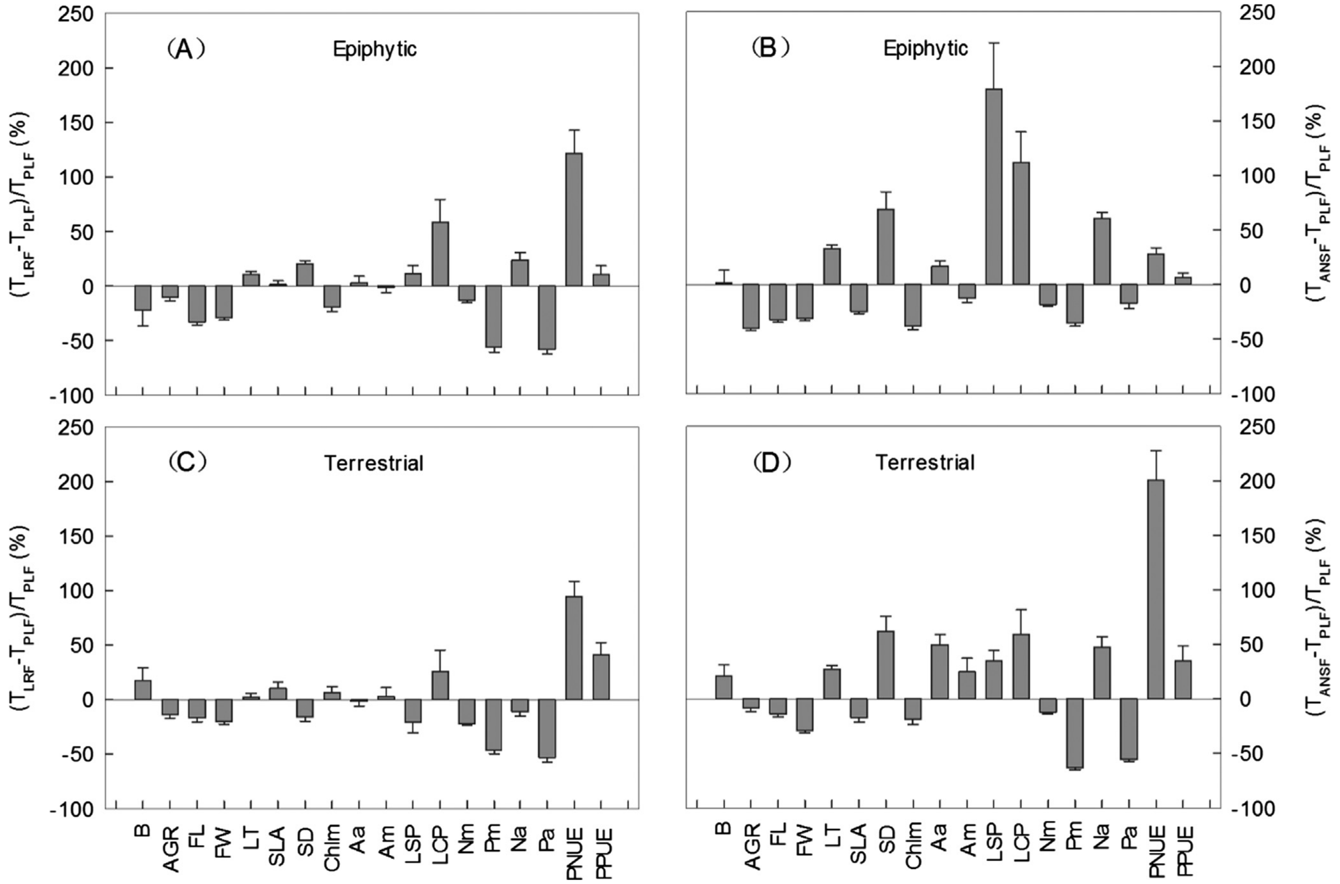


Fig. 3. Responses of 18 averaged plant functional traits to forest degradation in two fern species. (A) and (C): trait plasticity in epiphytic and terrestrial habitats of LRF; (B) and (D): trait plasticity in epiphytic and terrestrial habitats of ANSF. Trait plasticity data of both species were pooled for the analysis. Bars represent mean ± SE. Trait codes are defined in Table 2. n = 24–48 for B, AGR, FL, FW, LT, SLA, SD and Chl_m, while n = 12–16 for the remainder traits.

negative side; interestingly, epiphytic samples of LRF clustered with some terrestrial samples of ANSF on the positive side of the second axis (Fig. 4C). Similarly, in the score plots from the trait plasticity PCA, though most of the epiphytic and terrestrial samples from secondary forests were well differentiated by the first and second axis, several terrestrial samples from ANSF and some epiphytic ones from LRF clustered together on the positive side of the first axis (Fig. 4D).

Among all functional traits, only a few of them (Chl_m, A_a, LCP, N_m and P_a) were found significantly correlated with plant biomass, whereas other traits exhibited weak correlations. Contrastingly, many of the traits had significant correlations with AGR: FL, FW, SLA and P_m were positively associated with AGR, while LT, SD, A_a, LCP, P_a and PNUE were negatively associated (Table 3). The plasticity of A_a was positively correlated with plant biomass, while others had negligible associations with plant biomass. However, positive associations with AGR were found for the plasticity in FL, SLA and PPUE whereas distinctly negative correlations were found for LT, SD, LSP, P_m, N_a, and P_a plasticity (Table 3).

4. Discussion

4.1. Shift in ferns' epiphytic lifestyles and the role of forest degradation

Based on the relative abundance of the two *Lepisorus* species, a clear and distinct vertical distribution pattern was found across the different degradation stages of forests in the Ailao Mountains. Our results showed that relative abundance of these two species peaked in the upper canopies of the primary forest. However, the two secondary forest types had narrower distribution ranges (0–14 m and 0–6 m in height respectively for LRF and ANSF vs. 0–20 m for PLF) and their more open canopies augmented the ferns' relative abundance there in the 0–2-m height stratum and terrestrial habitat (Fig. 2A–D). Although characteristics of host trees somewhat affected the diversity and abundance of vascular epiphytes (Moran et al., 2003), most other studies showed lack of significant host-tree preference for epiphytic ferns (Kluge et al., 2006; Watkins et al., 2006; Cardelús and Mack, 2010). Neverthless, heterogeneity of microenvironments and plant community structure across forest stages went along with a shift in distribution of both *Lepisorus* species (Einzmann et al., 2015; Sillett and Bailey, 2003; Paciencia and Prado, 2005). Probably, both considerations contributed to the observed distribution patterns.

Firstly, a more open canopy conspicuously changes key environmental conditions, such as Ta, RH, and especially PAR, which temporarily favors the ferns and other plants in the lower canopy strata and understory (Saldaña et al., 2015). In PLF, besides the presence of a thick litter layer and dense *Sinarundinaria nitida* populations in the understory which hinder the fern growth, the low PAR through the mostly closed canopy may limit the colonization of sun plants in terrestrial habitat, and to some extents contribute to the absence of terrestrial individuals and low relative abundance of epiphytes at the base of tree trunks (Johnson et al., 2000; Watkins et al., 2007). In canopy-opened ANSF, more sunlight passing through them was partly impeded by dense shrubs, which kept the understory cooler and wetter (Bohlman et al., 1995). In this way, enough light and water availability could ensure the early establishment and survival of gametophytes and ramets (Lu et al., 2016; Watkins et al., 2007). Our field work corroborate this by recording more gametophytes and sexual reproductive offsprings on tree trunks in ANSF. The increasing relative abundance of both 0–4-m trunk-inhabiting and terrestrial individuals of these two species indicate their successful establishment in more light-exposed

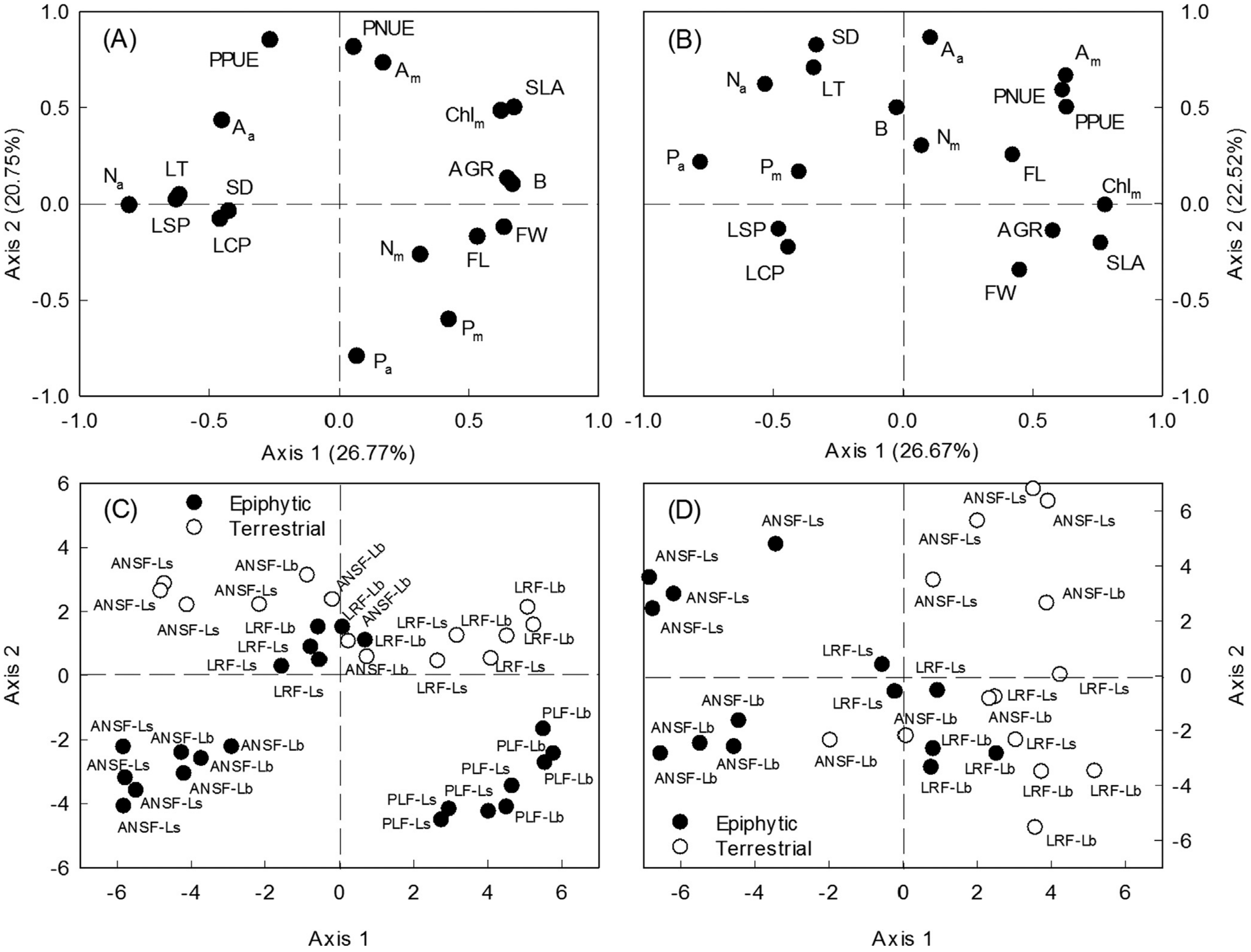


Fig. 4. Principal component analysis (PCA) for 18 functional traits of epiphytic and terrestrial individuals of two *Lepisorus* ferns in primary *Lithocarpus* forest (PLF), *Lithocarpus* regrowth forest (LRF), and *Alnus nepalensis* secondary forest (ANSF). A and C: Trait value coordinates on PCA components 1 and 2. B and D: Trait plasticity coordinates on PCA components 1 and 2. The symbols are labeled with their forest type-species code. Ls: *Lepisorus scolopendrium*; Lb: *Lepisorus bicolor*.

Table 3
Correlations (Spearman's rho value) of plant biomass (B) and annual growth of rhizome (AGR) with other functional traits according to trait values and trait plasticity.

Trait	Trait value		Trait plasticity	
	B	AGR	B	AGR
FL	0.068	0.334**	0.120	0.217**
FW	−0.045	0.372**	−0.129	0.115
LT	0.023	−0.374**	0.069	−0.218**
SLA	−0.085	0.271**	−0.078	0.226*
SD	−0.007	−0.310**	−0.016	−0.261*
Chl_m	−0.320**	0.116	0.034	0.200
A_a	0.300**	−0.266**	0.274*	−0.229
A_m	0.147	0.068	0.149	0.082
LSP	0.172	0.029	−0.070	−0.433**
LCP	0.438**	−0.419**	−0.221	−0.204
N_m	0.522**	−0.133	0.094	0.115
P_m	−0.046	0.293*	0.066	−0.302*
N_a	0.101	0.150	0.060	−0.519**
P_a	0.463**	−0.558**	0.193	−0.463**
PNUE	0.173	−0.303**	0.134	0.050
PPUE	0.096	0.029	0.075	0.323*

* $P < 0.05$.
** $P < 0.01$. Trait codes are defined in Table 2.

epiphytic and terrestrial habitats.

Secondly, from a multi-species dominated PLF to a single-species dominated ANSF (Table 1), the decreased number and size of host trees provide less suitable niche space and substantial resources for epiphytic ferns in the upper canopies (Bohlman et al., 1995; Paciencia and Prado, 2005). In addition, less diverse and abundant epiphytic bryophytes in secondary forests might also have led to reductions in *Lepisorus* ferns: bryophytes are excellent water interceptors, inadvertently conserving it for the fertilization of established and mature fern gametophytes, though they compete with ferns in earlier life stages of gametophytes (Mizuno et al., 2015; Song et al., 2011). Conversely, lower positions of tree trunks and forest ground should have relatively abundant and stable humus, with more sunlight resulting from canopy opening benefiting the germination of fern spore banks, thus forming new colonies for these two *Lepisorus* ferns (Ramírez-Trejo et al., 2004; Ranal, 2004). In this way, an environment-driven downward distribution of these two species from the upper canopy to understory during forest degradation was shaped.

With respect to these two clonal fern species, resource sharing by their rhizomes enabled individuals to grow under heterogeneous environments and to withstand abiotic stresses (Lu et al., 2016); this also implies individuals were in a better position to flourish and grow on the understory soil of the open-canopy secondary forests (especially ANSF). Yet terrestrial individuals undergo a contrasting dilemma, given the high light damage to plant tissues, competition from shrub-layer species

(Fig. 1F) and more disturbance by herbivores in the understories (Watkins et al., 2007; Zotz, 2016). It seemed that the understory acted as a temporary refuge for epiphytic ferns. Thus, we predict that these terrestrial individuals might gradually vanish with forest succession, leaving only the epiphytic ones distributed as they are in the PLF (Zotz and Bader, 2009). This seemed to fall into the trajectory of evolutionary history of fern radiation that ferns evolved from open landscapes to understory, and some of them entered the canopy for a variety of reasons mentioned above.

4.2. Functional traits in response to changed light and growth substrates during forest degradation

Sampling within 0.5–2.5 m tree trunks for epiphytic individuals across primary and degraded forests falls in strict horizontal ecological gradients for the study. Meanwhile, lower tree trunks, which get close to the ground and represent a zone with frequent propagule exchanges between epiphytic and terrestrial plants, are ideal for the study of shift in epiphytic lifestyles and the responsible functional traits. In our study, some plant functional traits were found to vary strongly between epiphytic and terrestrial habitats within the same forest or across primary and degraded forests (Figs. S2A–H, S3A–J). Our results showed that both *Lepisorus* species displayed the conspicuous characteristics of sun plants—i.e., high LCP and LSP, with 30–70 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 890–2200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively—and exhibited high trait plasticity as they thrived in a better lit habitat (Fig. 3A–D). This result suggests that variation in many functional traits became larger in degraded forest, which is consistent with findings of ferns grown under different light conditions (e.g., Medeiros et al., 2017). Indirectly, our results could reflect a high light acclimation capacity and varied nutrient strategies of two *Lepisorus* species in response to forest degradation (Callaway et al., 2003; Magyar et al., 2007).

Our results confirmed enhanced trait plasticity in response to light variation during forest degradation, and revealed the effects of light variation on the photosynthetic behavior of two *Lepisorus* species. Light-mediated variation of trait plasticity also points to their intimate relationship with light acclimation strategies in plants. For example, terrestrial individuals had higher plasticity in FL, FW, and SLA than did epiphytic ones in LRF and ANSF, which might enable ferns to capture more light under weak and very fluctuating light conditions (Johnson et al., 2000; Li et al., 2008). In addition, the plasticity of SLA in the LRF was higher than that in ANSF for both groups of epiphytic and terrestrial individuals. This result is consistent with two other ferns studied by Larcher et al. (2013) and Kessler et al. (2007). Besides, thicker fronds could improve the light use efficiency and alleviate high-light stress in degraded forests, though this might result in a reduction of Chl_m due to the dilution by denser mesophyll tissues (Wright et al., 2001). Since we found photosynthesis-related traits, such as SD, A_a, LSP, and LCP, were significantly higher in secondary forests, this suggested open-canopy inhabiting individuals had a greater photosynthetic capacity than those in shaded habitats. A few other studies have also shown that changes in A_a, LSP, and LCP allowed fern species from incompletely light-exposed secondary forests to more efficiently utilize a higher light resource (Hietz and Briones, 2001; Sessa and Givnish, 2014; Zhu et al., 2016). This was well shown in our study, in that both fern species displayed similar increases in their photosynthetic capacity with greater available light to them.

Different growth substrates generated via forest degradation could also affect the nutrient characteristics and nutrient-use efficiency of the two *Lepisorus* species (Querejeta et al., 2018). Our results confirmed that nutrient-related traits were also plastic in response to forest degradation, with decreases in N_m and P_m but increases in PNUE and PPUE. Specifically, P_m and P_a exhibited more sharped reductions after forest degradation compared with N_m and N_a. These results agree with the current knowledge of vascular epiphytes being often subjected to P limitation or co-limitation by N and P (Wanek and Zotz, 2011). However, the unexpected and interesting result in our study was that epiphytic individuals in secondary forests showed higher frond nutrient concentrations than terrestrial conspecifics (especially N_m and N_a in LRF, and P_m and P_a in ANSF). This might be ascribed to higher N content of canopy soil in Ailao Mountain, since aged rotten barks as well as organic matter intercepted by rough barks of host trees contributed to nutrient supplementation of epiphytes (Cardelús and Mack, 2010; Wang et al., 2008). Accordingly, both fern species showed higher photosynthetic nutrient-use efficiency, especially PNUE and PPUE in ANSF, which had been severely degraded from PLF of Ailao Mountains. These findings are consistent with those of Zhu et al. (2016), who reported higher photosynthetic capacity and greater nutrient use efficiency in ferns from disturbed forests than those from natural forests. This nutrient strategy might alleviate sudden nutrient deficits, especially phosphorus limitation in the secondary forests.

Notably, our PCAs of measured functional traits and their plasticity also provided evidence for two suites of traits related to light acquisition and nutrient strategies. Although the first and second axes together explained only 47.52% and 49.19% of the total variance, respectively, for functional traits and trait plasticity, plant samples from PLF were separately clustered with those from secondary forests (Fig. 4). This outcome could be ascribed to multi-dimensional effects of forest degradation, which is mirrored intuitively by apparent differences in forest structure and microenvironmental conditions between primary and degraded forests (Magrach et al., 2014; Saldaña et al., 2015). A separation of plant samples implies different response to varied habitats. For example, the separation of PLF and ANSF by the first axis of functional trait PCA is attributed to contrasting variations in B, AGR, SLA and N_a; similarly, A_m, P_a, PNUE and PPUE are responsible for the cluster of all terrestrial samples on the positive side, while epiphytic samples of PLF and ANSF on the negative side along the second axis. For ANSF, its strongly fluctuating microenvironment and dense shrub layer amplified the deviation between epiphytic and terrestrial habitat suitability for the two fern species. Higher trait plasticity and resource use efficiency reflected distinct acclimation and competition capacity in the terrestrial individuals, causing the divergence of epiphytic and terrestrial individuals seen in the PCA.

4.3. Resource use trade-offs and ecological implications

Shifts in light and nutrient availability might positively or negatively feed backs on morphological and physiological traits and their plasticity, resulting in light- and nutrient-mediated ecological strategies of two *Lepisorus* ferns (Kim et al., 2014; Magyar et al., 2007; Saldaña et al., 2015). We demonstrated here that forest degradation induced variation in key morphological (decrease of FL, FW, SLA, N_m, P_m) and physiological traits (increase of A_a, LSP, LCP, PNUE, PPUE) across the primary and two degraded forests. The results indicated that intraspecific trade-offs in resource strategies were driven by different resource availabilities, as these would enable plants to capture more resources and persist in the community (Querejeta et al., 2018). Accordingly, epiphytic individuals in primary forest had higher capacity for light capture while those in secondary forests had a higher photosynthetic capacity and resource use efficiency (Wanek and Zotz, 2011). Within both LRF and ANSF, terrestrial individuals tended to acclimate to the low-light understory and were more efficient in their nutrient use than were epiphytic conspecifics (Ripullone et al., 2003; Wright et al., 2005).

In our study, evidence was found for correlated functional traits of the two *Lepisorus* species, which combined as trait syndromes and varied in coordinated manner via plastic adjustments in whole plant response to subtle and univocal changes in the environment. Various combinations and trade-offs of functional traits can enhance overall plant performance in multi-dimensional and highly heterogeneous resource space (Carins Murphy et al., 2014). We found that the rapid response of functional traits to forest degradation adjusted the annual growth of rhizomes—positive or negative correlations of some functional traits and their plasticity with AGR—rather than the plant biomass (Chau et al., 2013). In addition, rhizome lengthening dynamics in these two species, of shoot tip growth accompanied by the old base end dying off, enabled whole plant movement. Therefore, higher AGR of terrestrial individuals in secondary forests (especially in ANSF) implies that ferns are apt to seek out new optimal habitats after forest degradation, rather than colonize the immediate surrounding area through accumulated plant biomass.

5. Conclusions

In summary, our study revealed clear patterns not only in the vertical distribution of epiphytic plants but also their functional traits and their plasticity during forest degradation. Both obligate *Lepisorus* species shifted to be facultative in secondary forests and inhabited a narrower vertical distribution range than primary forest, and their relative abundance in the 0–2-m segment and terrestrial (ground surface) habitat increased with canopy openness during forest degradation. Their high plasticity and combination of functional traits enabled these two species to be phenotypically adaptive in primary and degraded forests, confirming that epiphytic individuals in primary forest had higher capacity for light capture while those in secondary forests had a higher photosynthetic capacity and resource-use efficiency. Within the same secondary forest, terrestrial individuals tended to acclimate to a low-light understory and were more efficient in their nutrient use than epiphytic conspecifics. These findings demonstrate that, in response to forest degradation the two canopy-dwelling ferns tended to occupy the lower tree trunk and understory ground, by the intraspecific adjustment of key functional traits to promote rhizome growth and expansion in search of suitable habitat.

6. Declarations of interest

None.

Funding

This work was funded by the National Natural Science Foundation of China (No. 31770496, 41471050, U1133605, 31872685); the Biodiversity Conservation Strategy Program of Chinese Academy of Sciences, China (No. ZSSD-016) and CAS 135 Program, China (No. 2017XTBG-T01, 2017XTBG-F03).

Acknowledgement

We thank Wenzheng Yang and Dawen Li for their assistance with the field experiment, Drs. Xi Chen and Peili Fu for technical support using the LI-6400. Ms. Fu Yun et al. in the Biogeochemistry Laboratory of Xishuangbanna Tropical Botanical Garden, CAS are particularly thanked for their assistance with chemical analysis of fern samples. We would also like to thank the management authority of the Ailao Mountains National Nature Reserve and Ailaoshan Station for Subtropical Forest Ecosystem Studies for granting us research permissions and facilitating this study. We are also grateful to two anonymous reviewers for their constructive comments on the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.12.037.

References

Ames, G.M., Anderson, S.M., Wright, J.P., 2016. Multiple environmental drivers structure plant traits at the community level in a pyrogenic ecosystem. Funct. Ecol. 30, 789–798.

Benzing, D.H., 2004. Vascular Epiphytes. In: Lowman, M., Rinker, H. (Eds.), Forest Canopies. Elsevier Academic Press, Berlington, pp. 175–211.

Bhaskar, R., Dawson, T.E., Balvanera, P., 2014. Community assembly and functional diversity along succession post-management. Funct. Ecol. 28, 1256–1265.

Bohlman, S.A., Matelson, T.J., Nadkarni, N.M., 1995. Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest, Costa Rica. Biotropica 27, 13–19.

Brenner, G.J., 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. In: Taylor, D.W., Hickey, L.J. (Eds.), Flowering Plant Origin, Evolution and Phylogeny. Springer, Boston, MA.

Cardelús, C.L., Mack, M.C., 2010. The nutrient status of epiphytes and their host trees along an elevational gradient in Costa Rica. Plant Ecol. 207, 25–37.

Callaway, R.M., Pennings, S.C., Richards, C.L., 2003. Phenotypic plasticity and interactions among plants. Ecology 84, 1115–1128.

Carins Murphy, M.R., Jordan, G.J., Brodribb, T.J., 2014. Acclimation to humidity modifies the link between leaf size and the density of veins and stomata. Plant, Cell Environ. 37, 124–131.

Chau, M., Reyes, W., Ranker, T., 2013. Ecological factors influencing growth of the endangered Hawaiian fern *Marsilea villosa* (Marsileaceae) and implications for conservation management. Am. J. Bot. 100, 1532–1543.

Coste, S., Baraloto, C., Leroy, C., Marcon, É., Renaud, A., Richardson, A.D., Roggy, J.C., Schimann, H., Uddling, J., Hérault, B., 2010. Assessing foliar chlorophyll contents with the SPAD-502 chlorophyll meter: a calibration test with thirteen tree species of tropical rainforest in French Guiana. Ann. For. Res. 67, 607.

de Freitas, C.A., Scarano, F.R., Biesboer, D.D., 2003. Morphological variation in two facultative epiphytic bromeliads growing on the floor of a swamp forest. Biotropica 35, 546–550.

Dubuisson, J.-Y., Schneider, H., Hennequin, S., 2009. Epiphytism in ferns: diversity and history. C. R. Biol. 332, 120–128.

Einzmann, H.J.R., Beyschlag, J., Hofhansl, F., Wanek, W., Zotz, G., 2015. Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. Aob Plants 7, plu073.

Fort, F., Cruz, P., Catrice, O., Delbrut, A., Luzarreta, M., Stroia, C., Jouany, C., 2015. Root functional trait syndromes and plasticity drive the ability of grassland Fabaceae to tolerate water and phosphorus shortage. Environ. Exp. Bot. 110, 62–72.

Gomes-da-Silva, J., Costa, A.F.D., 2011. A taxonomic revision of *Vriesea corcovadensis* group (Bromeliaceae: Tillandsioideae) with description of two new species. Syst. Bot. 36, 291–309.

Gutschick, V.P., 1999. Biotic and abiotic consequences of differences in leaf structure. New Phytol. 143, 3–18.

Hietz, P., Briones, O., 2001. Photosynthesis, chlorophyll fluorescence and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Plant Biol. 3, 279–287.

Johnson, G.N., Rumsey, F.J., Headley, A.D., Sheffield, E., 2000. Adaptations to extreme low light in the fern *Trichomanes speciosum*. New Phytol. 148, 423–431.

Karasawa, S., Hijii, N., 2006. Determinants of litter accumulation and the abundance of litter-associated microarthropods in bird's nest ferns (*Asplenium nidus* complex) in the forest of Yambaru on Okinawa Island, southern Japan. J. For. Res. 11, 313–318.

Kessler, M., Siorak, Y., Wunderlich, M., Wegner, C., 2007. Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. Funct. Plant Biol. 34, 963–971.

Kim, H.R., Shin, J.H., Jeong, H.M., You, Y.H., 2014. Effects of environmental factors on the growth response of above- and below-ground parts of *Mankyua chejuense*, endangered endemic plant to Jeju province, in Korea. J. Ecol. Environ. 37, 61–67.

Kluge, J., Kessler, M., Dunn, R.R., 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Global Ecol. Biogeogr. 15, 358–371.

Larcher, L., Boeger, M.R.T., Soffiatti, P., Da Silveira, T.I., 2013. Leaf architecture of terrestrial and epiphytic ferns from an Araucaria forest in southern Brazil. Botany 91, 768–773.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.

Li, L., Bueckert, R.A., Gan, Y., Warkentin, T., 2008. Light interception and radiation use efficiency of fern- and unifoliate-leaf chickpea cultivars. Can. J. Plant Sci. 88, 1025–1034.

Li, S., Liu, W.Y., Li, D.W., 2013. Bole epiphytic lichens as potential indicators of environmental change in subtropical forest ecosystems in southwest China. Ecol. Indicators 29, 93–104.

Li, S., Liu, W.Y., Li, D.W., Li, Z.X., Song, L., Chen, K., Fu, Y., 2014. Slower rates of litter decomposition of dominant epiphytes in the canopy than on the forest floor in a subtropical montane forest, southwest China. Soil Biol. Biochem. 70, 211–220.

Li, X.S., 2010. Regeneration of Different Vegetation Types and Controlling Measures of Degraded Mountainous Area at Xujiaba, Ailao Mountains, SW China. Ph.D. Dissertation. University of Chinese Academy of Sciences, Beijing.

Lu, H.Z., Liu, W.Y., Yu, F.H., Song, L., Xu, X.L., Wu, C.S., Zheng, Y.L., Li, Y.P., Gong, H.D., Chen, K., Li, S., Chen, X., Qi, J.H., Lu, S.G., 2015. Higher clonal integration in the facultative epiphytic fern *Selliguea griffithiana* growing in the forest canopy compared with the forest understory. Ann. Bot. 116, 113–122.

Lu, H.Z., Song, L., Liu, W.Y., Xu, X.L., Hu, Y.H., Shi, X.M., Li, S., Ma, W.Z., Chang, Y.F., Fan, Z.X., Lu, S.G., Wu, Y., Yu, F.H., 2016. Survival and growth of epiphytic ferns depend on resource sharing. Front. Plant Sci. 7, 416.

Magrach, A., Rodríguez-Pérez, J., Campbell, M., Laurance, W.F., 2014. Edge effects shape the spatial distribution of lianas and epiphytic ferns in Australian tropical rain forest fragments. Appl. Veg. Sci. 17, 754–764.

Magyar, G., Kun, A., Oborny, B., Stuefer, J.F., 2007. Importance of plasticity and decision-

making strategies for plant resource acquisition in spatio-temporally variable environments. New Phytol. 174, 182–193.
Medeiros, J.C.C., Silva, J.C.F., Teodoro, G.S., Coelho, F.D.F., 2017. Effects of shade on individual ramet growth and on clonal growth of the aquatic fern *Salvinia auriculata* (Salviniaceae). Am. Fern J. 107, 21–29.
Mizuno, T., Momohara, A., Okitsu, S., 2015. The effects of bryophyte communities on the establishment and survival of an epiphytic fern. Folia Geobot. 50, 331–337.
Moran, R.C., 2003. Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. Biotropica 35, 48–56.
Nieder, J., Prosperi, J., Michaloud, G., 2001. Epiphytes and their contribution to canopy diversity. Plant Ecol. 153, 51–63.
Paciencia, M.L.B., Prado, J., 2005. Effects of forest fragmentation on pteridophyte diversity in a tropical rain forest in Brazil. Plant Ecol. 180, 87–104.
Petter, G., Wagner, K., Wanek, W., Delgado, E.J.S., Zotz, G., Cabral, J.S., Kreft, H., 2016. Functional leaf traits of vascular epiphytes: vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. Funct. Ecol. 30, 188–198.
Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L.I.Z., Walker, K.J., Rothery, P., 2003. Plant traits as predictors of performance in ecological restoration. J. Appl. Ecol. 40, 65–77.
Qiu, X.Z., Xie, S.C., Liu, W.Y., 1998. Study on the Forest Ecosystem in Ailao Mountains, Yunnan. Yunnan Sciences and Technology Press, Kunming China (in Chinese with English summary).
Querejeta, J.I., Prieto, I., Torres, P., Campoy, M., Alguacil, M.M., Roldán, A., 2018. Water-spender strategy is linked to higher leaf nutrient concentrations across plant species colonizing a dry and nutrient-poor epiphytic habitat. Environ. Exp. Bot. 153, 302–310.
Ramírez-Trejo, M.D.R., Pérez-García, B., Orozco-Segovia, A., 2004. Analysis of fern spore banks from the soil of three vegetation types in the central region of Mexico. Am. J. Bot. 91, 682–688.
Ranal, M.A., 2004. Bark spore bank of ferns in a gallery forest of the ecological station of Panga, Uberlândia-MG. Brazil. Am. Fern J. 94, 57–69.
Ripullone, F., Grassi, G., Lauteri, M., Borghetti, M., 2003. Photosynthesis–nitrogen relationships: interpretation of different patterns between *Pseudotsuga menziesii* and *Populus* × *euroamericana* in a mini-stand experiment. Tree Physiol. 23, 137–144.
Saldaña, A., Parra, M.J., Flores-Bavestrello, A., Corcuera, L.J., Bravo, L.A., 2015. Effects of forest successional status on microenvironmental conditions, diversity, and distribution of filmy fern species in a temperate rainforest. Plant Species Biol. 29, 253–262.
Schellenberger Costa, D., Zotz, G., Hemp, A., Kleyer, M., 2018. Trait patterns of epiphytes compared to other plant life-forms along a tropical elevation gradient. Funct. Ecol. 32, 2073–2084.
Schneider, H.E., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallón, S., Lupia, R., 2004a. Ferns diversified in the shadow of angiosperms. Nature 428, 553–557.
Schneider, H.E., Smith, A.R., Cranfill, R., Hildebrand, T.J., Haufler, C.H., Ranker, T.A., 2004b. Unrevealing the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. Mol. Phylogenet. Evol. 31, 1041–1063.
Schuettpelz, E., Pryer, K.M., 2009. Evidence for a cenozoic radiation of ferns in an angiosperm-dominated canopy. Proc. Natl. Acad. Sci. USA 106, 11200–11205.
Sessa, E.B., Givnish, T.J., 2014. Leaf form and photosynthetic physiology of *Dryopteris* species distributed along light gradients in eastern North America. Funct. Ecol. 28, 108–123.
Sillett, S., Bailey, M., 2003. Effects of tree crown structure on biomass of the epiphytic fern *Polypodium acouleri* (Polypodiaceae) in redwood forests. Am. J. Bot. 90, 255–261.
Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. Taxon 55, 705–731.
Song, L., Liu, W.Y., Ma, W.Z., Tan, Z.H., 2011. Bole epiphytic bryophytes on *Lithocarpus xylocarpus* (Kurz) Markgr. in the Ailao Mountains, SW China. Ecol. Res. 26, 351–363.
Song, L., Zhang, Y.J., Chen, X., Li, S., Lu, H.Z., Wu, C.S., Tan, Z.H., Liu, W.Y., Shi, X.M., 2015. Water relations and gas exchange of fan bryophytes and their adaptations to microhabitats in an Asian subtropical montane cloud forest. J. Plant Res. 128, 573–584.
Tang, C.Q., Li, T., Zhu, X., 2007. Structure and regeneration dynamics of three subtropical midmontane moist evergreen broad-leaved forests in southwestern China, with special reference to bamboo in the forest understories. Can. J. For. Res. 37, 2701–2714.
Tsutsumi, C., Kato, M., 2006. Evolution of epiphytes in davalliaceae and related ferns. Bot. J. Linn. Soc. 151, 495–510.
Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892.
Wanek, W., Zotz, G., 2011. Are vascular epiphytes nitrogen or phosphorus limited? A study of plant N-15 fractionation and foliar N: P stoichiometry with the tank bromeliad *Vriesea sanguinolent*a. New Phytol. 192, 462–470.
Wang, G.S., Liu, W.Y., Fu, Y., Yang, G.P., 2008. Comparison of physical and chemical properties and microbial biomass and enzyme activities of humus from canopy and forest floor in a montane moist evergreen broad-leaved forest in Ailao Mts, Yunnan. Acta Ecol. Sin. 28, 1328–1336 (in Chinese with English summary).
Wang, L., Qi, X.P., Xiang, Q.P., Heinrichs, J., Schneider, H., Zhang, X.C., 2010. Phylogeny of the Paleotropical fern genus *Lepisorus* (Polypodiaceae, Polypodiopsida) inferred from four chloroplast DNA regions. Mol. Phylogenet. Evol. 54, 211–225.
Watkins, J.E., Cardelús, C., Colwell, R.K., Moran, R.C., 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. Am. J. Bot. 93, 73–83.
Watkins, J.E., Mack, M., Mulkey, S., 2007. Gametophyte ecology and demography of epiphytic and terrestrial tropical ferns. Am. J. Bot. 94, 701–708.
Wright, I.J., Reich, P.B., Westoby, M., 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high-and low-rainfall and high- and low-nutrient habitats. Funct. Ecol. 15, 423–434.
Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., 2005. Modulation of leaf economic traits and trait relationships by climate. Global Ecol. Biogeogr. 14, 411–421.
Xu, H.Q., Liu, W.Y., 2005. Species diversity and distribution of epiphytes in the montane moist evergreen broad-leaved forest in Ailao Mountain, Yunnan. Biodiv. Sci. 13, 137–147 (in Chinese with English summary).
Yang, L.P., Liu, W.Y., Ma, W.Z., 2008. Woody debris stocks in different secondary and primary forests in the subtropical Ailao Mountains, Southwest China. Ecol. Res. 23, 805–812.
Young, S.S., Carpenter, C., Wang, Z.J., 1992. A study of the structure and composition of an old growth and secondary broad-leaved forest in the Ailao Mountains of Yunnan, China. Mount. Res. Develop. 12, 269–284.
Zhang, X.C., 2012. Lycopods and Ferns of China. Peking University Press, Beijing.
Zhu, S.D., Li, R.H., Song, J., He, P.C., Liu, H., Berninger, F., Ye, Q., 2016. Different leaf cost-benefit strategies of ferns distributed in contrasting light habitats of sub-tropical forests. Ann. Bot. 117, 497–506.
Zotz, G., 2013. The systematic distribution of vascular epiphytes – a critical update. Bot. J. Linn. Soc. 171, 453–481.
Zotz, G., 2016. Plants on Plants – The Biology of Vascular Epiphytes. Springer International Publishing, Switzerland.
Zotz, G., Bader, M.Y., 2009. Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. In: Lüttge, U., Beyschlag, W., Büdel, B., Francis, D. (Eds.), Progress in Botany. Springer, Berlin Heidelberg, pp. 147–170.