Research Article

Functional traits: Adaption of ferns in forest

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Abstract Ferns that evolved from 400 million years ago show various functional traits and ecological strategies in extant species, over 80% of which belong to the youngest order Polypodiales. How the functional traits and strategies of ferns have changed during their evolutionary history remains unexplored. Here, we measured functional traits that are sensitive to environmental light and water availability in 345 fern species across fern phylogeny, and reconstructed their evolutionary histories. We found that ferns, mainly Polypodiales, have developed diversified functional traits in response to forest environments. Terrestrial species, especially Thelypteridaceae and Athyriaceae in eupolypods II, since the late Jurassic period, have shown decreased leaf mass per area (LMA) and area-based leaf nitrogen (Narea), but increased mass-based leaf nitrogen (Nmax) compared with early-derived polypods. Epiphytic species, mainly those in Polypodiaceae, have shown reductions in Nmax and individual leaf area (Area) since the late Cretaceous period. The adaption of functional traits of Polypodiales to forest environment may have played a crucial role in fern radiation since the late Jurassic period. Integrative analysis of functional traits, especially numerical ones, may shed new light on plant evolution.

Key words: epiphytic, evolutionary history, monilophyte, plant strategy, Polypodiales, terrestrial.

1 Introduction

Ferns (monilophytes) that have evolved from approximately 400 million years ago (Ma) (Lehtonen et al., 2017; Morris et al., 2018), have undergone dramatic climate changes and at least four mass extinction events (Elewa, 2008). However, with over 10,000 living species worldwide (PPG I, 2016), extant ferns form the largest group of spore-producing vascular plants on Earth. Fossil records show that early-derived ferns, including some tree-like species in Equisetales and Marattiales, were important components of palaeotropical wetland forests in the Carboniferous period (DiMichele & Phillips, 1994, 2002; Hibbett et al., 2016). Living ferns, which are mostly herbaceous plants in tropical and temperate forests, exhibit a marked diversity in ecological strategies ranging from xeric-adapted epiphytes in Polypodiaceae (Fig. 1A) to shade-tolerant terrestrial species in Thelypteridaceae (Fig. 1D) and from tree-like ferns in Cyatheaceae (Fig. 1I) to tiny filmy ferns in Hymenophyllaceae (Fig. 1L). Knowledge of the changes in the ecological strategy of ferns during their history is crucial for our understanding of plant evolution; to date, however, these changes have remained largely underexplored.

Previous research works on fern evolution have postulated that ferns diversified under angiosperm-dominated forests. By comparing the divergence time of ferns and angiosperms, Schneider et al. (2004) revealed that extant ferns are rarely evolutionary holdovers; most ferns, especially taxa in the order Polypodiales, did not diversify until the radiation of angiosperms in the Cretaceous. Ferns radiate because angiosperm-dominated forests can provide shade and epiphytic habitats. Schuettpelz & Pryer (2009) reconstructed a 400-taxon molecular fern phylogeny and reported the Cenozoic radiation of epiphytic ferns. Reconstruction of densely sampled and time-calibrated fern phylogenies (covering 3973 extant fern species in Testo & Sundue, 2016; 1116 in Lehtonen et al., 2017) generally confirmed that recent fern diversification happened mainly within the order Polypodiales. Taxa in Polypodiales diversified during the Cretaceous period, and radiated markedly in the Cenozoic period. Innovations, such as chlorophyllous spores and non-cordiform gametophytes, facilitate the diversification of epiphytic ferns (Watkins & Cardelus, 2012; Sundue et al., 2015). However, given that physical conditions, including light intensity, air temperature, water, and nutrient availability, change markedly from canopy to ground within a forest and from forest gap to edge (Ellsworth & Reich, 1993; Hubbell et al., 1999; Szaryszki & Anhuf, 2001), the functional traits of ferns in response to various microenvironments within forest communities have rarely been analyzed. How the functional traits of ferns changed when ferns no longer constructed forests and became mostly herbaceous understories or epiphytes in angiosperm-dominated forests remains unknown.
The “leaf economic spectrum” based mainly on seed plants shows that a combination of functional traits is closely related to plant strategy and environment (Westoby et al., 2002; Wright et al., 2004; Díaz et al., 2015). For example, plants enhance their leaf mass per area (LMA) and area-based leaf nitrogen (N_{area}) with increasing light intensity and water limitation from the ground to the canopy of forests but reduce their individual leaf area (Area) to optimize photosynthesis and reduce water usage (Ellsworth & Reich, 1993; Koch et al., 2004; Jin et al., 2014; Coble et al., 2017). By contrast,
increases in Area and decreases in LMA may help to capture light with a relatively low construction cost in shaded environments (Weischede et al., 2006); indeed, herbaceous plants show lower LMA but higher mass-based leaf nitrogen (Nmass) compared with woody species (Díaz et al., 2015). In comparison with open leaf venation, reticulated venation that provides network redundancy is important for damage resistance of plants (Price & Weitz, 2014). Compared with seed plants, ferns usually exhibit unique features such as low density in leaf venation and stomata (Zwieniecki & Boyce, 2014), passive stomatal regulation of leaf hydration, low water use efficiency and photosynthetic capacity (Brodribb & McAdam, 2011; Tosens et al., 2016), and red light-induced chloroplast movement (Kawai et al., 2003). Despite these differences, however, analyses of the foliar traits of 20 fern species in a temperate deciduous forest have revealed that correlations among traits in ferns are generally consistent with those in seed plants (Karst & Lechowicz, 2007). However, our knowledge of the functional traits of ferns across fern lineages in response to environment remains limited.

In this study, we present the functional traits of 345 extant fern species across major fern lineages, compare these traits across fern habitats and with those of seed plants and reconstruct the evolutionary history of the functional traits of ferns. Ultimately, we aim to show how the functional traits of ferns have changed during their evolutionary history, focusing especially on how they respond to the forest environment. We predicted that:

1. In the aspect of functional traits such as LMA, Narea and Nmass, ferns respond to the environment consistently in the way seed plants respond. Extant ferns, mainly herbaceous plants growing on the forest floor, will show lower LMA and Narea but higher Nmass compared with seed plants in forests. Within ferns, terrestrial species will have lower LMA and Narea, but higher Nmass and Area compared with epiphytic species.

2. The functional traits of ferns during their evolutionary history will show diversification in response to the forest environment; fern lineages adapting to the forest floor will show decreased LMA and Narea but increased Nmass and Area, while epiphytic lineages adapting to the forest canopy, such as Polypodiaceae, will show enhanced LMA and Narea, but reduced Nmass and Area.

2 Material and Methods

2.1 Field sampling

With over 1900 fern species recorded in its territory (Lin et al., 2013; Yan et al., 2016), China probably has the richest fern species in the northern hemisphere; southeast China, in particular, is considered an ancient center of diversity (Lu et al., 2018). Field investigations were conducted during the growing seasons from 2014 to 2018 in tropical and subtropical forests from eastern to western China, including the provinces of Taiwan, Shanghai, Fujian, Zhejiang, Guangdong, Hunan, Yunnan and Xizang. The sampling area ranged from 22°36′N to 31°05′N in latitude, from 95°20′E to 121°28′E in longitude and from 7 m to 3871 m in altitude with climates ranging from 4.2 °C to 22.3 °C in mean annual temperature and from 788 mm to 2358 mm in annual precipitation. In the field, we sampled 950 sporophytes from 345 fern species identified according to the flora of China (Lin et al., 2013), which covers 87 genera, 28 families and 9 out of 11 orders in the PPG I system (PPG I, 2016) (Table S1). For each species except for a few rare ones, at least three individuals were collected as three samples; for each individual three or more fully expanded and healthy leaves were collected. All samples were collected with the permission of local nature reserves.

2.2 Measurement of functional traits

For each sampled individuals, we measured four numeric leaf functional traits, including LMA, Narea, Nmass, and Area (Pérez-Harguindeguy et al., 2013), and recorded three categorical traits, including growth form, leaf venation type, and leaf type. Each sample, with single leaf petioles or compound leaf rachis removed, was scanned using an image scanner (LIDE10, Canon, Japan). Projected leaf area (cm²) of each sample was measured using the WinFOLIA system (Regent, Canada). Leaves were oven dried for at least 48 h at 60 °C to a constant weight, and the leaf dry mass was weighed to the nearest milligram. For each sample, LMA (g/m²) was calculated as the leaf dry mass divided by the projected area; Nmass (mg/g) was measured using an elemental analyzer (Elementar, Germany); Narea (mg/m²) was calculated as Nmass × LMA. The growth form (terrestrial, lithophyte, or epiphytic), leaf type (single or compound), and leaf venation type (open, semireticulate or reticulate) were also recorded (Table S1). The traits data at species level were averaged from all the sampled individuals within the species accordingly (Fig. 2; Table S2).

2.3 Reconstruction of the fern phylogeny

Research on fern evolution has yielded a relatively robust phylogeny at the family and genus levels (Rothfels et al., 2015; PPG I, 2016; Testo & Sundue, 2016; Lehtonen et al., 2017; Shen et al., 2018). The topology covering all 345 sampled fern species in this study was reconstructed based mainly on the molecular phylogeny inferred from four plastid genes (atpA, atpB, rbcl, and rps4) of 1116 species in 223 genera in Lehtonen et al. (2017) with reference to recent molecular phylogenies within families, such as Dryopteridaceae (Zhang et al., 2012), Polypodiaceae (Liu, 2016), Pteridaceae (Zhang et al., 2015a), and Thelypteridaceae (He & Zhang, 2012). This topology is consistent with the backbone phylogeny of fern-based transcriptome sequences (Shen et al., 2018) and former fern phylogenies (Schruppelz & Pryer, 2009; Rothfels et al., 2015; Testo & Sundue, 2016). To resolve polytomies within genera to dichotomies, we downloaded the sequences of the rbcl gene from NCBI (https://www.ncbi.nlm.nih.gov) and constructed Maximum Likelihood trees using MEGA (version 6.06) software (Tamura et al., 2013). The branch lengths of the phylogeny were then calculated using the “bladji” module in Phylocom (version 4.2) (Webb et al., 2008) with the ages of root or internal nodes representing genera or higher taxa fixed as that of the corresponding nodes in the phylogeny of Lehtonen et al. (2017) (Fig. 2; Data S1).
2.4 Statistical analysis

To determine the general characteristic of ferns and confirm that the combination of functional traits in certain adaption strategies in ferns were consistent with that in seed plants, we compared functional traits between ferns and seed plants (Fig. 3; Table S3). Traits data of seed plants representing 807 species were compiled from the published literature (Wright et al., 2004; Jin et al., 2014) and confined within forest biomes. We also analyzed, by Pearson correlation, the correlation of phylogenetic independent contrasts of leaf traits in ferns (Table 1) and compared functional traits among different growth forms within ferns using Tukey’s honest significant difference (HSD; Table 2).

To reveal the divergence of ecological strategy in ferns, we estimated the status of leaf traits for each ancient node in fern phylogeny by applying the “ace” (ancestral state estimation) function with the “Maximum Likelihood” method in the “ape” package (Cunningham et al., 1998; Paradis, 2012). The evolutionary history of each numeric trait in ferns was reconstructed (Fig. 4). The estimated ancestral

Fig. 2. Patterns of the leaf functional traits of 345 fern species in the context of phylogeny. Heat map showing the scaled values of LMA, Narea, Nmass, and Area for each species determined by using \((X_i - \min(X))/(\max(X) - \min(X))\) after the raw data were log\(\text{10}\) () transformed. Growth form, venation type, and leaf type are shown as different colors. Traits for each species were averaged from individuals. The geologic periods were defined in accordance with the International Chronostratigraphic Chart (v2018.08) (www.stratigraphy.org).
states of leaf traits among five major fern groups, namely early-derived ferns, early-derived polypods, eupolypods II, Dryopteridaceae, and Polypodiaceae (Fig. 5), were also compared using Tukey’s HSD. All statistical analyses were performed using the R package (version 3.6.0) (R Core Team, 2018).

Table 1 Pearson correlations among the phylogenetic independent contrasts (pic) of four-leaf traits across 345 fern species

|         | pic.LMA | pic.Narea | pic.Nmass | pic.Area |
|---------|---------|-----------|-----------|----------|
| pic.LMA | 1.000   | 0.000     | 0.000     | 0.000    |
| pic.Narea | 0.779 | 1.000     | 0.000     | 0.000    |
| pic.Nmass | -0.312 | 0.353     | 1.000     | 0.002    |
| pic.Area | -0.318 | -0.204    | 0.166     | 1.000    |

Correlation coefficients are shown in the lower left corner, P-values are shown in the upper right corner. All leaf traits were log_{10}() transformed before pic analysis.

Fig. 3. Comparison of leaf functional traits between ferns and seed plants. A, B, Correlations of leaf N_{mass}, N_{area} with LMA in ferns and seed plants, with standard major axis shown respectively for ferns and seed plants (for N_{mass} vs. LMA) or in common (for N_{area} vs. LMA). C, Violin plots and comparison of leaf traits between ferns and seed plants. ***Indicates a significant difference (P < 0.001) between ferns and seed plants calculated using analysis of variance (ANOVA). Trait data from 345 fern species and 807 species of seed plants were used here.

3 Results

3.1 Functional traits across the fern phylogeny

In total, four numeric leaf traits and three categorical traits of 345 fern species are presented along with their phylogeny (Fig. 2). Functional traits varied considerably across the fern phylogeny. Among the 345 fern species, LMA ranged from 13.46 to 363.08 (g/m²); N_{area} ranged from 321.4 to 4864.1 (mg/m²); N_{mass} ranged from 5.50 to 53.33 (mg/g); and Area varied from 1.17 to 17338 (cm²). Among the sampled ferns, 62.0% of the species were terrestrial, and 96.3% and 82.7% had compound leaves and open venation, respectively. Within the Polypodiaceae group, 87.7% of the ferns were epiphytic,
and 86.0% and 96.5% had single leaves and reticulated venation, respectively.

3.2 Fern traits compared with seed plants and among growth forms

The LMA of ferns positively correlated with $N_{\text{area}}$ ($P < 0.001$) but negatively correlated with $N_{\text{mass}}$ or Area ($P < 0.001$), which is congruent with that in seed plants (Table 1; Fig. 3). Compared with seed plants, ferns exhibited 42.4% lower LMA and 24.1% lower $N_{\text{area}}$ but 31.8% higher $N_{\text{mass}}$ ($P < 0.001$; Fig. 3). On average, terrestrial ferns showed 35.4% lower LMA but 34.9% higher $N_{\text{mass}}$ and 6.8-fold higher Area ($P < 0.001$) compared with epiphytic species, excluding filmy ferns (Table 2).

3.3 Divergence of functional traits in ferns during their evolutionary history

The reconstructed evolutionary history of each leaf trait (Fig. 4) showed that the divergence of leaf traits in ferns began ap-
proximately 177 Ma during the Jurassic period, expanded in the Cretaceous and extended dramatically in the Cenozoic. The diversification of functional traits within Polypodiales, which greatly extended their range, occurred mainly in eupolypods II and the Polypodiaceae group. Compared with early-derived polypods, eupolypods II showed significantly reduced LMA and Narea but marked enhanced Nmass ($P < 0.05$). The Polypodiaceae group exhibited greatly reduced Nmass and Area ($P < 0.01$) and high levels of LMA and Narea. Functional traits in early-derived polypods and the Dryopteridaceae group were relatively moderate.

3.4 Divergence of functional traits among five major fern families

By comparing leaf traits among five major fern families from Polypodiales (Fig. 5), we found that Thelypteridaceae and Athyriaceae, which belong to eupolypods II, had lower LMA compared with families belonging to Dryopteridaceae and Polypodiaceae in eupolypods I ($P < 0.05$). Moreover, Polypodiaceae had higher LMA and Narea but lower Nmass and Area compared with Thelypteridaceae and Athyriaceae ($P < 0.05$). The traits of Pteridaceae within early-derived polypods were relatively moderate.

4 Discussion

4.1 Environmental response of functional traits in ferns

In order to assess the effects of climate on fern leaf traits, we carried out analysis of variance of four numeric functional traits of 345 fern species across forests using data from 950 individuals (Fig. S1). We found that climatic factors, including mean annual temperature, annual precipitation, and relative humidity, explained in full approximately 4.1%–19.9% of the traits variation, while growth form explained 13.3% of variance in LMA, 5.4% in Narea, 8.3% in Nmass, and 37.8% in Area. This result suggested that adaption of fern traits to microenvironments within local forests may play an important role in fern evolution.

In addition, functional traits of ferns, such as LMA, Narea, Nmass, and Area, showed significant trade-offs across species.
As LMA increased across fern species, N_area tended to increase; while N_mass and Area showed a decreasing trend (Table 1; Fig. 3). Consistent with our first prediction, ferns generally had lower LMA and N_area but higher N_mass compared with seed plants in forests. This result is consistent with the pattern of herbaceous plants having lower LMA and N_area but higher N_mass compared with woody species (Reich et al., 1997; Díaz et al., 2015). We also found that terrestrial ferns tended to have lower LMA but higher N_mass, and Area compared with epiphytic ferns. The divergence of functional traits between growth forms has also been reported in Orchidaceae (Zhang et al., 2015b). Compared with terrestrial Cymbidium species on the forest floor, their epiphytic relatives have higher LMA and greater drought tolerance, which enables them to cope with the limited and irregular water supply of canopy habitats. The phenomenon that plants under low-light environments tend to show enhanced Area but reduced LMA, and which helps to optimize photosynthesis within Trifolium repens (Leguminosae) (Weischede et al., 2006), was also observed across fern species. The relatively low LMA, large Area, and open venation of terrestrial ferns may help them to capture light at a relative low cost of construction per unit area on the shaded and moist forest floor. By contrast, the high LMA, small Area, and reticulated venation of epiphytic ferns may help them to survive in the exposed and xeric forest canopy.

4.2 Functional traits diverge among fern lineages during adaption to forest

Our second assumption that ferns, especially Polypodiales, would show diversification of functional traits in response to forest during history was also supported. The reconstructed evolutionary history of functional traits in ferns showed that the divergence of fern traits has occurred mainly in Polypodiales since the late Jurassic period (Fig. 4). This divergence is highly congruent with the departure of eupolypods I and eupolypods II (shown in Fig. 2) and in recent fern phylogenies (Testo & Sundue, 2016; Lehtonen et al., 2017). Lineages within Polypodiales differed in changes of functional traits during their evolutionary history (Figs. 4, 5). Eupolypods II, including Thelypteridaceae and Athyriaceae, showed generally reduced LMA, enhanced N_mass, low N_area, and high Area among groups. This finding demonstrated the adaption of this group to shaded and moist forest floors in general. The Polypodiales group has shown enhanced LMA, but reduced N_mass and Area, since the late Cretaceous period. Grassulaceae acid metabolism, which helps to reduce evaporation in drought environments, has been reported in many epiphytic ferns from Polypodiales (Microsorum, Polypodium, Platycerium, Pyrrosia) (Holtum & Winter, 1999; Sayed, 2001) and a few early-derived epiphytic polypods (Haplopteris/Vittaria) (Minardi et al., 2014). These phenomena suggested that epiphytic ferns have adjusted their morphological traits and physiological processes in adaption to exposed and xeric forest canopies. Compared with eupolypods II and the Polypodiales group, early-derived polypods and the Dryopteridaceae group showed moderate functional traits with no clear trends during evolution (Figs. 2, 4), and indicated an ecological strategy to adapt to open and to semiopen terrestrial habitats. During our field work, we noted that Pteridaceae, which is the largest family in early-derived polypods, covered various marked growth forms, including terrestrial, epiphytic, lithophytic, and aquatic, and occupied various habitats including forest edges, tree trunks, rock crevices, and exposed wetlands. Dryopteridaceae, the largest fern family belonging to eupolypods I, occupied various habitats from forest gaps to edges to alpine rock crevices.

Early-derived ferns are highly diverse in terms of functional traits and ecological strategy according to the functional traits of extant species (Fig. 1) and estimation of ancient nodes (Fig. 4). This group covered epiphytic filmy ferns, which are markedly low in LMA and N_area to adapt to highly moist and shaded environments, and large tree ferns from Marattiales and Cyatheales, which typically have large compound leaves to adapt to warm and humid climates in the tropics. A few genera in this group, such as Ophioglossum, Christensenia, and Dipteris, already had reticulated venation types, which form redundant networks important for hydraulic security, and is universal in dicotyledonous plants (Price & Weltz, 2014). Moreover, the diversification dynamics of ferns (Testo & Sundue, 2016; Lehtonen et al., 2017) showed that none of the 10 orders of early-derived ferns had markedly enhanced their diversity within the recent 100 Ma. We confirmed that, although early-derived ferns are diverse in traits and strategies, they are mostly evolutionary holdovers. Taking the extinct fossil ferns into consideration, the diversity, habitats, and ecological strategies of early-derived ferns may have been greatly reduced due to factors such as mass extinction events, climate change, and competitive exclusion by angiosperms.

The reconstructed history of functional traits in ferns (Fig. 4) showed that the diversification of traits in ferns, especially for terrestrial groups, began in the late Jurassic period. This observed diversification occurred earlier compared with fern radiation since the Cretaceous period (Schneider et al., 2004; Schuettpelz & Pryer, 2009). Due to these finding, we applied a renewed divergence time estimation based on both molecular sequences and abundant fossil information from comprehensive species and that yielded the more ancient origins of ferns at approximately 400 Ma and Polypodiales at approximately 249 Ma (Testo & Sundue, 2016; Lehtonen et al., 2017; Morris et al., 2018). According to the latest research, major radiation of angiosperms occurred in the Jurassic and early Cretaceous periods (Barba-Montoya et al., 2018; Li et al., 2019) and finally dominated the terrestrial ecosystem at 90 Ma in the late Cretaceous period (Lidgard & Crane, 1988; Lupia et al., 1999). In other words, radiation may have occurred simultaneously in ferns and angiosperms in the late Jurassic period. Atmospheric moisture, which contributes to local rainfall and air humidity, can be recharged by evapotranspiration through the advanced vascular system of angiosperm-dominated forests (Boyce et al., 2010; Ellison et al., 2017). Therefore, angiosperm-dominated forests are especially important for epiphytic and terrestrial ferns. Correspondingly, the functional traits of terrestrial and epiphytic ferns evolved intensively over the late Cretaceous and Cenozoic period when angiosperms dominated the terrestrial ecosystem.

Our research revealed, for the first time, the evolution of plant functional traits and ecological strategy in ferns over a
broad scale of time and phylogeny. By analyzing the functional traits of 345 extant fern species in the context of their phylogeny, we found that: (i) the divergence of the functional traits of Polypodiaceae to adapt to different habitats within forests matched well with fern radiation since the late Jurassic period. Moreover, (ii) Polypodiaceae lineages showed evolved functional traits in efforts to adapt to different habitats. For example, eupolypods II revealed traits to adapt to the shaded, moist forest floor; the Polypodiaceae group revealed traits to adapt to the exposed, xeric, and nutrient poor forest canopy; and early derived polypods and the Dryopteridaceae group revealed traits to adapt to open and semiopen habitats. We suggest that adaption to various habitats within forests, especially angiosperm-dominated ones, may have driven the recent radiation of ferns since the late Jurassic period. Further integrative analysis of the functional traits of extant species using phylogenetic methods may shed light on the hidden history of plant evolution.

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Conflict of Interest

The authors declare no conflicting interests.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12669/suppinfo:

Table S1. Functional traits of 950 individuals of 345 fern species.

Table S2. Functional traits of 345 fern species in Fig. 2.

Table S3. Functional traits of ferns and seed plants in Fig 3.

Data S1. Time-calibrated phylogeny of 345 fern species in Fig. 2.

Fig. S1. Variation of four functional traits of ferns explained by three climatic factors and growth form.