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A plant economics spectrum of litter decomposition among coexisting fern species in a sub-tropical forest

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• **Background and Aims** The plant economics spectrum theory provides a useful framework to examine plant strategies by integrating the co-ordination of plant functional traits along a resource acquisition–conservation trade-off axis. Empirical evidence for this theory has been widely observed for seed plants (Spermatophyta). However, whether this theory can be applied to ferns (Pteridophyta), a ubiquitous and ancient group of vascular plants, has rarely been evaluated so far.
• **Methods** We measured 11 pairs of plant functional traits on leaves and fine roots (diameter <2 mm) on 12 coexisting fern species in a sub-tropical forest. Litterbags of leaves and roots were placed *in situ* and exposed for 586 d to measure decomposition rates. The variation of traits across species and the co-ordination among traits within and between plant organs were analysed. Finally, the influence of the traits on decomposition rates were explored.
• **Key Results** Most leaf and root traits displayed high cross-species variation, and were aligned along a major resource acquisition–conservation trade-off axis. Many fern traits co-varied between leaves and fine roots, suggesting co-ordinated responses between above- and below-ground organs. Decomposition rates of leaves were significantly higher than those of fine roots, but they were significantly and positively correlated. Finally, our results highlight that the decomposition of both leaves and roots was relatively well predicted by the leaf and root economics spectra.
• **Conclusions** Our results support the existence of an acquisition–conservation trade-off axis within ferns and indicate that traits have important 'afterlife' effects on fern litter decomposition. We conclude that the plant economics spectrum theory that is commonly observed across seed plants can be applied to ferns species, thereby extending the generality of this theory to this ancient plant lineage in our study site. Our study further suggests that the evolutionary and ecological basis for the relationships among key economics traits appears to be similar between ferns and seed plants. Future studies involving larger data sets will be required to confirm these findings across different biomes at larger spatial scales.

Key words: Above-ground–below-ground, plant functional traits, ecological strategy, plant economics spectrum, litter decomposition, ferns, plant–soil interactions.

INTRODUCTION

Functional traits are measurable plant characteristics that are shaped by long-term adaptation of plants to a wide range of biotic and abiotic factors (Violle *et al.*, 2007). Across large spatial scales or environmental gradients, plants generally vary widely in morphological and physiological traits as a response to different environmental conditions (Dolph and Dilcher, 1980; Reich *et al.*, 1999; Wright *et al.*, 2004, 2005; Liu *et al.*, 2010; Chen *et al.*, 2013; Roumet *et al.*, 2016), but plant traits can also vary substantially at the local scale or within the plant community (Ricklefs and Matthew, 1982; Wright *et al.*, 2004; Karst and Lechowicz, 2007; Hättenschwiler *et al.*, 2008; Comas and Eissenstat, 2009; Liu *et al.*, 2010). Furthermore, plant traits generally do not vary independently, but show broad

co-variation patterns among different traits (Reich *et al.*, 1999; Craine *et al.*, 2001; Díaz *et al.*, 2004; Wright *et al.*, 2004, 2007; Karst and Lechowicz, 2007; Osnas *et al.*, 2013; Prieto *et al.*, 2015; Roumet *et al.*, 2016; de la Riva *et al.*, 2016, 2018; Zhou *et al.*, 2018). For instance, the 'leaf economics spectrum' describes a suite of leaf traits that consistently co-vary along a single major axis and represents a resource acquisition–conservation trade-off (Reich *et al.*, 1999, 2014; Wright *et al.*, 2004, 2005, 2007; Freschet *et al.*, 2010; Bakker *et al.*, 2011). Species at the resource-acquisitive end of the spectrum tend to exhibit high photosynthesis rates, specific leaf area (SLA) and leaf nutrient concentrations, while species at the resource-conservative end of the spectrum tend to exhibit high lignin concentrations, dry matter contents (DMCs) or a high carbon (C) to nitrogen

(N) ratio (Wright *et al.*, 2004; Freschet *et al.*, 2010). For below-ground traits, recent studies have demonstrated that roots are subject to a resource economics spectrum similar to that described for leaves (Reich, 2014; Prieto *et al.*, 2015; Roumet *et al.*, 2016). Acquisitive plant species have higher specific root lengths (SRLs), N concentration and root respiration rates, while conservative plant species tend to exhibit higher root DMCs, C and lignin concentrations and lignin:N ratio (Roumet *et al.*, 2016; Prieto *et al.*, 2015).

Despite the increasing necessity to assess whether and how plant traits and ecological processes are co-ordinated between above- and below-ground organs, leaf and root trait spectra have commonly been studied separately from each other (e.g. Wright *et al.*, 2004; Bakker *et al.*, 2011; Prieto *et al.*, 2015; Roumet *et al.*, 2016; de la Riva *et al.*, 2018; Zhou *et al.*, 2018; Lin *et al.*, 2019; but see Freschet *et al.*, 2010; Perez-Ramos *et al.*, 2012; Reich, 2014; de la Riva *et al.*, 2016). Leaf and root traits are theoretically thought to be functionally co-ordinated to maximize the efficiency of acquiring and using limited resources (Reich, 2014). Yet, mixed results have been reported in the literature. For instance, SLA and its below-ground counterpart SRL have been found to be either positively correlated (Newman and Hart, 2006; Freschet *et al.*, 2010; Liu *et al.*, 2010), uncorrelated (Tjoelker *et al.*, 2005; Chen *et al.*, 2013; Kramer-Walter *et al.*, 2016; Bergmann *et al.*, 2017) or negatively correlated (Cheng *et al.*, 2016). Furthermore, many studies have reported that the variation in root traits was multi-dimensional rather than one-dimensional, as reported for leaf traits (Kong *et al.*, 2014, 2019; Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016; de la Riva *et al.*, 2018; Zhou *et al.*, 2018). Therefore, the generality and the extent to which the co-variation patters of economics traits can be extended to the whole-plant level still require additional studies.

Decomposition of plant tissues is an essential process in the biogeochemical cycles of C and nutrients (Garnier *et al.*, 2004; Bakker *et al.*, 2011; Zuo *et al.*, 2018). Most of the chemical and morphological traits of living plant tissues such as leaves persist upon death, and determine the quality of the litter produced (Santiago, 2007; Bakker *et al.*, 2011; Zukswert and Prescott, 2017). Therefore, chemical and morphological plant functional traits have commonly been used as good predictors of litter decomposition rates (Cornelissen and Thompson, 1997; Santiago, 2007; Cornwell *et al.*, 2008; Bakker *et al.*, 2011). For example, an increasing number of studies have demonstrated positive correlations between leaf decomposition rate and both leaf nutrient concentrations and SLA, or negative correlations with leaf DMC, lignin concentration and C:N ratio (Cornelissen and Thompson, 1997; Santiago, 2007; Cornwell *et al.*, 2008; Bakker *et al.*, 2011; Freschet *et al.*, 2012; de la Riva *et al.*, 2019). Furthermore, the trait syndromes from the leaf and root economics spectra are also commonly used as good indicators of litter decomposability (e.g. Bakker *et al.*, 2011; Freschet *et al.*, 2012; Reich, 2014; Roumet *et al.*, 2016; Zuo *et al.*, 2018; Lin *et al.*, 2019; de la Riva *et al.*, 2019). Species in the acquisitive side of the spectrum are generally associated with more rapid litter decomposition rates, while species associated with conservative strategies generally produce recalcitrant litters that are relatively hard to break down (Bakker *et al.*, 2011; Freschet *et al.*, 2012; Roumet *et al.*, 2016; de la Riva *et al.*, 2019). These results suggest that species' ecological strategies, indicated by the trait syndromes, may be useful to predict how changes in the plant community may alter ecosystem C storage and nutrient cycling (Santiago, 2007; Bakker *et al.*, 2011; Freschet *et al.*, 2012; Zuo *et al.*, 2018).

Ferns (Pteridophyta) are worldwide distributed vascular plants with >10 000 species (Page, 1979; Smith *et al.*, 2006; Kessler, 2010), and contribute significantly to ecosystem C and nutrient cycling (Marsh *et al.*, 2000; Richardson and Walker, 2010; Lyu *et al.*, 2019; Yang *et al.*, 2019). Ferns represent a distinct path in the evolution of vascular plants (Smith *et al.*, 2006) and, in comparison with seed plants (Spermatophyta), they are ecologically characterized by low vascular tissue development, leaf hydraulic conductance, photosynthesis capacity and nutrient concentrations (Brodribb *et al.*, 2005; Han *et al.*, 2005; Karst and Lechowicz, 2007; Sharpe *et al.*, 2010; Carriqui *et al.*, 2015; Tosens *et al.*, 2016). For example, maximum photosynthesis rates per unit area measured on a variety of fern species are mostly below 10 µmol CO_2 m^{-2} s^{-1} (Hollinger, 1987; Sessa and Givnish, 2014; Carriqui *et al.*, 2015; Tosens *et al.*, 2016), which is twice as low as the values (9.4–32.0 µmol CO_2 m^{-2} s^{-1}) found in seed plants (Wright *et al.*, 2004; Carriqui *et al.*, 2015). Similarly, Han *et al.* (2005) reported significantly lower leaf N (12.4 vs. 18.9 mg g^{-1}) and phosphorus (P; 0.81 vs. 1.22 mg g^{-1}) concentrations in ferns than in seed plants among 753 plant species. Despite these profound variations in trait values, trait co-variation patterns of ferns are generally consistent with those reported for seed plants (Karst and Lechowicz, 2007; Sessa and Givnish, 2014; Tosens *et al.*, 2016). For instance, area-based leaf N concentration is positively correlated with both leaf mass per unit area and maximum photosynthetic rate per unit area among 20 understorey fern species in a temperate deciduous forest (Karst and Lechowicz, 2007), and SLA is positively correlated with maximum photosynthetic rate per unit area among 11 eastern North American ferns of genus *Dryopteris* (Sessa and Givnish, 2014). These results suggest that relationships among the key economic traits may have been conserved throughout the evolution of vascular plants (Reich *et al.*, 2003). However, ferns are still relatively poorly represented in the current framework of resource economics spectrum theory. Indeed, in a meta-analysis describing the universal spectrum of leaf economics at the global scale, Wright *et al.* (2004) included 2021 vascular plant species, but only 13 fern species. Furthermore, only three fern species were included in the study assessing the existence of a 'whole-plant economics spectrum' across a wide range of sub-arctic plants (Freschet *et al.*, 2010). Therefore, the generality of the resource economic spectrum for fern species remains to be proven, and additional studies are necessary to assess whether trait variation within ferns is an important driver of key ecological processes such as decomposition rates.

In this study, we measured leaf and root functional traits and decomposition rates of 12 understorey coexisting fern species in a sub-tropical forest in China. Our main objective was to extract major dimensions of leaf and root trait variation, investigate how these major trait dimensions were related to each other and assess whether they were good predictors of litter decomposition. Because the conditions of light, nutrient availability and water vary strongly at the hectare scale in our study site (Yang *et al.*, 2001; Sun *et al.*, 2006; Wu *et al.*, 2019), we hypothesized that the variation in leaf and root traits of fern species should represent different resource use strategies along

a major resource acquisition–conservation trade-off axis (Fig. 1). This is because fern species are thought to be relatively well adapted to a wide range of biotic and abiotic conditions (Page, 1979), and may present a wide range of variation in their functional traits to cope with various environmental conditions (e.g. Karst and Lechowicz, 2007; Richardson and Walker, 2010; Sessa and Givnish, 2014). We also examined whether fern species with trait syndromes reflecting an acquisitive resource strategy would decompose faster than those with trait syndromes reflecting a conservative resource strategy. Specifically, we expected that species at the acquisitive end of the spectrum present high leaf and root nutrient concentrations, high SLA and SRL, and exhibit higher litter decomposition rates, whereas species at the conservative end of the spectrum are characterized by low nutrient concentrations, high DMC and lignin concentration, and exhibit low litter decomposition rate (Fig. 1).

MATERIALS AND METHODS

Study site and species selection

Fieldwork was conducted in Jinyunshan National Nature Reserve (29°48'25"–29°51'53"N, 106°20'18"–106°24'42"E) in Chongqing, South-west China. This area is characterized by a sub-tropical monsoon climate, with a mean annual temperature of 13.6 °C and a mean annual precipitation of 1600 mm. The main vegetation in the reserve is an evergreen broad-leafed forest dominated by *Castanopsis fargesii* and *Machilus pingii*. Vegetation also includes plantations of *Pinus massoniana*, *Cunninghamia lanceolata* and *Phyllostachys pubescens*. Ferns are a major component of the understorey plant layer. For this study, we selected 12 common understorey fern species belonging to ten genera, namely *Diplazium hachijoense*, *Diplazium dilatatum*, *Dryopteris labordei*, *Dryopteris erythrosora*, *Athyrium delavayi*, *Woodwardia japonica*, *Pronephrium penangianum*, *Metathelypteris laxa*, *Odontosoria chinensis*, *Arachniodes chinensis*, *Osmunda japonica* and *Diplopterygium chinense*.

Leaf and root functional trait measurements

We focused on leaf and fine root (<2 mm in diameter) traits representative of the conservation–acquisition trade-off that was commonly used in previous studies (e.g. Freschet *et al.*, 2012; de la Riva *et al.*, 2018). Leaves or roots with obvious signs of damage (e.g. herbivory, galls and fungal attacks) were excluded. Morphological functional traits measured in this study included SLA, SRL and DMC. Chemical functional traits included C, N, P, cellulose and lignin concentrations, and pH (as proxy for cation contents; Cornelissen *et al.*, 2006). Element stoichiometry, i.e. C:N, C:P and N:P ratios, were calculated based on the C, N and P value for leaves and roots, respectively. All traits were measured on three independent samples per organ per species, and the mean of these three measurements was used in the data analysis.

Fresh leaf mass was measured within 1 h after harvest (sporangia were brushed off beforehand). Leaves were then scanned at 400 dpi using an Epson perfection V300 photo scanner. The images were processed using the ImageJ software to determine leaf area (Schneider *et al.*, 2012). After scanning, leaves were dried at 65 °C for 48 h and then weighed to determine their dry mass. Leaf DMC was calculated as the ratio of leaf dry mass to leaf fresh mass, and SLA was calculated as fresh leaf area divided by leaf dry mass. For root physical traits, full root systems were sealed in plastic bags and brought to the laboratory within 2 h after their harvest in the field. Roots were carefully washed under tap water. Fine roots with intact root branches were selected for the measurements of root traits. Root samples were soaked in distilled water, spread out to avoid any overlap and scanned at a resolution of 400 dpi using an Epson perfection V800 photo scanner equipped with a transmitted light source to avoid shadows. The resulting images were processed using the WinRHIZO software (Regent Instrument, Quebec, Canada) to determine total root length. After scanning, roots were removed from the distilled water, sponged carefully to remove all excess water and weighed to determine root fresh mass. Roots were then oven dried at 65 °C for 48 h and weighed to determine root dry mass. Root DMC was calculated as the ratio between root dry mass and root fresh mass, and SRL was calculated as the ratio between root length and root dry mass.

For the chemical analyses, dried leaf and root samples were ground into fine powder using a ball mill. The C concentration was measured by dry combustion using a solid module (Shimadzu SSM-5000, Japan) coupled with a TOC/TN analyser (Shimadzu TOC-L CPH, TNM-1, Japan). After digestion with concentrated H_2SO_4 and 30 % H_2O_2 (Jones, 2001), the N concentration was measured by using the TOC/TN analyser, and P concentration was determined spectrophotometrically by using the Mo–Sb colorimetric method. Cellulose and lignin concentrations were measured following the method as described in Graça *et al.* (2005). Following the method of Freschet *et al.* (2010), we shook leaf or root powder with deionized water for 1 h, and the pH of the suspension after centrifugation was measured using a pH meter.
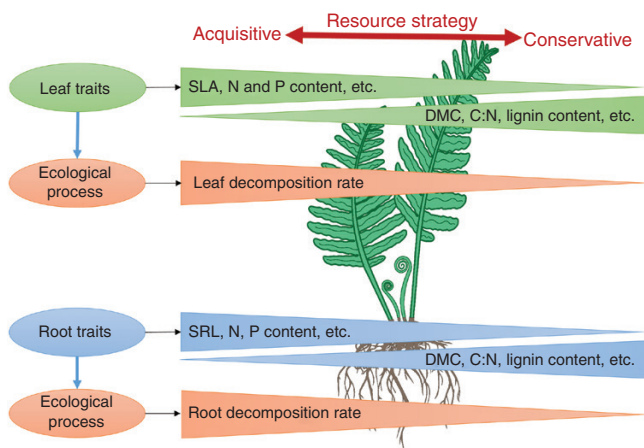

FIG. 1. Schematic diagram depicting the hypothetical leaf economics spectrum and root economics spectrum and their afterlife effects on litter decomposition within ferns. The variations in some key economic traits across the ecological axis of trade-off between acquisition and conservation are given. SLA, specific leaf area; SRL, specific root length; DMC, dry matter content; C, carbon; N, nitrogen; P, phosphorus.

Decomposition rates

We used the litterbag technique to quantify decomposition rates of fern leaves and roots. Because it is difficult to accurately determine the timing of death of fine roots in soil, we chose to use fresh materials for roots and leaves to measure decomposition rates according to Fujii *et al.* (2018). Leaves and roots from 20–50 well-developed mature individuals of each fern species were collected during October to November 2016. For each individual, we collected leaves manually and dug out roots to a depth of about 15 cm. Roots were then cleaned carefully under tap water to remove attached soil particles.

A 3 g aliquot of leaf and a 2 g aliquot of fine root were enclosed in 10×15 cm litterbags made from 25 µm mesh nylon netting. Litterbags were then placed in three forest sites distributed at a distance of 200–300 m. In total, 576 litterbags [12 species × 2 litter types (leaf or root) × 3 forest sites × 2 replicates each site × 4 harvests] were used in this study. On 25 January 2017, leaf litterbags were anchored onto the forest floor with plastic pins (natural litter was removed prior to litterbag placement). Root litterbags were buried below the soil surface to a depth of 5–10 cm. Two replicates (randomly chosen) per litter type per species were collected from each site at four sampling dates: 1 May 2017 (113 d), 24 July 2017 (198 d), 26 January 2018 (386 d) and 12 August 2018 (586 d). The remaining leaf and fine root litter was dried at 65 °C for 48 h and weighed.

Litter mass loss (%) was calculated as $(M_i - M_f)/M_i \times 100$, where M_i and M_f are initial and final litter dry mass, respectively. The decay constants (k values in units of year^{-1}) were calculated by fitting the first-order exponential decay function (Olson, 1963):

$$M_t = M_0 e^{kt}$$

where M_0 is the proportion of initial litter mass remaining at time 0 (constrained as 100 here) and M_t is the proportion of remaining litter mass at a certain time t, e is the base of the natural logarithm and k is the decay constant. For each litter sample, the k value was first calculated by using the data from each incubation site separately, and then averaged across the three sites. Finally, the half-life of decomposing material ($T_{1/2}$, years), i.e. the time needed to reach 50 % mass loss of each litter, was calculated as ln $(0.5)/k$ (Gosz *et al.*, 1973; Freschet *et al.*, 2012). Higher $T_{1/2}$ values correspond to slower decomposition rates, and vice versa.

Statistical analysis

Variation in the value of each trait was quantified by the coefficient of variation (CV). To assess whether functional traits were co-ordinated within organs, a principal components analysis (PCA) was carried out for traits of leaf and root, respectively. Due to the high proportion of variation explained by the first PCA axis, we used the species scores of the first PCA axis of each of the leaf and root PCAs as the proxy for the leaf and root economics spectrum. To test the co-ordination between above- and belowground organs, bivariate relationships between leaves and roots in matching pairs of traits, economic spectra

and decomposition rates were evaluated using standardized major axis (SMA) regressions (Warton *et al.*, 2012). Significant differences in decomposition rates between leaves and roots were tested using a linear mixed-effects model, with organ as fixed effect and species as random effect. Finally, simple linear regressions were used to test the influence of individual functional traits or the economics spectra (predictor variables) on the decomposition rates ($T_{1/2}$) of leaves and roots (response variables). To meet the assumption of normality, SLA, SRL and root $T_{1/2}$ were ln-transformed prior to data analysis. All statistical analyses were performed on the R Software version 3.4.1 (R Core Team, 2017) with the 'vegan', 'smatr' and 'lme4' R packages for the PCA, SMA and linear mixed-effects model, respectively.

RESULTS

Interspecific variation in traits

Many fern traits exhibited large cross-species variation among the 12 coexisting species (Table 1; Supplementary data Table S1). For the morphological traits, SRL had higher cross-species variation (CV = 65.6 %) than the analogous leaf trait SLA (CV = 40.5 %); DMC of leaf and root (CV <31.0 %) showed less variation than SRL and SLA (Table 1). For chemical traits, pH of leaf and root showed low variation (CV <9.0 %). Similarly both leaf and root C had very low variation (CV < 5.0%), whereas N and P showed much higher variation (CV = 12.0–45.4 %) than C, leading to a high variation in all C:N:P ratios (CV >34.0 %). The variation of leaf and root cellulose (CV approx. 20 %) was lower than the variation of lignin (CV >42.0 %) (Table 1).

Co-variation of traits within and across organs

The first three PCA axes accounted for 74.54 % of the overall variation in leaf traits, with the first PCA axis accounting for 47.91 % (Fig. 2A; Supplementary data Table S2). All leaf traits, except pH, cellulose and lignin concentrations, contributed substantially to the first PCA axis, as indicated by the high individual loadings (Fig. 2A; Supplementary data Table S2). Leaf lignin concentration contributed strongly to the second PCA axis, while leaf cellulose concentration contributed strongly to the third PCA axis (Fig. 2A; Supplementary data Table S2). For root traits, the first three PCA axes accounted for 82.97 % of the overall variation (Supplementary data Table S2). Root DMC, pH, C, P, cellulose concentrations and C:P ratio contributed substantially to the first PCA axis which accounted for 46.45 % of the overall variation (Fig. 2B; Supplementary data Table S2). Root N, C:N and N:P contributed substantially to the second PCA axis, while SRL contributed strongly to the third PCA axis (Supplementary data Table S2).

Bivariate relationships revealed significant correlations between several trait pairs between leaves and roots (i.e. DMC, C, P and lignin concentrations, C:P and N:P ratios), but SLA and SRL, pH, N and cellulose concentrations and C:N ratio were

TABLE 1. *Summary of leaf and fine root traits of the 12 fern species measured in this study*

Trait (unit)	Leaf				Fine root			
	Mean	Min	Max	CV (%)	Mean	Min	Max	CV (%)
SLA ($cm^2 g^{-1}$)	305.33	164.44	632.48	40.5	–	–	–	–
SRL ($cm g^{-1}$)	–	–	–	–	232.45	77.26	622.01	65.6
DMC ($mg g^{-1}$)	286.15	122.52	402.27	27.0	324.76	156.88	522.33	30.8
pH	5.88	5.17	6.33	5.6	5.14	4.57	5.87	8.4
C ($mg g^{-1}$)	409.77	363.19	432.38	4.7	408.85	375.78	436.86	4.5
N ($mg g^{-1}$)	19.64	16.03	23.54	12.0	9.5	5.11	14.93	32.8
P ($mg g^{-1}$)	1.78	0.86	2.81	37.3	0.96	0.47	1.84	45.4
C:N	24.29	16.85	58.34	45.4	47.71	25.19	81.24	34.3
C:P	265.18	144.42	493.25	40.2	516.81	217.59	927.19	46.0
N:P	12.33	7.62	23.38	35.3	11.64	3.45	23.42	50.1
Cellulose ($mg g^{-1}$)	267.63	149.95	362.47	19.2	292.55	193.48	362.25	21.0
Lignin ($mg g^{-1}$)	69.75	16.70	143.44	57.5	224.48	92.50	353.70	42.3

The mean, minimum (Min), maximum (Max) values and coefficient of variation (CV) are given for each trait. Leaf and fine root trait values for each species can be found in Supplementary data Table S1.

SLA, specific leaf area; SRL, specific root length; DMC, dry matter content; C, carbon; N, nitrogen; P, phosphorus.
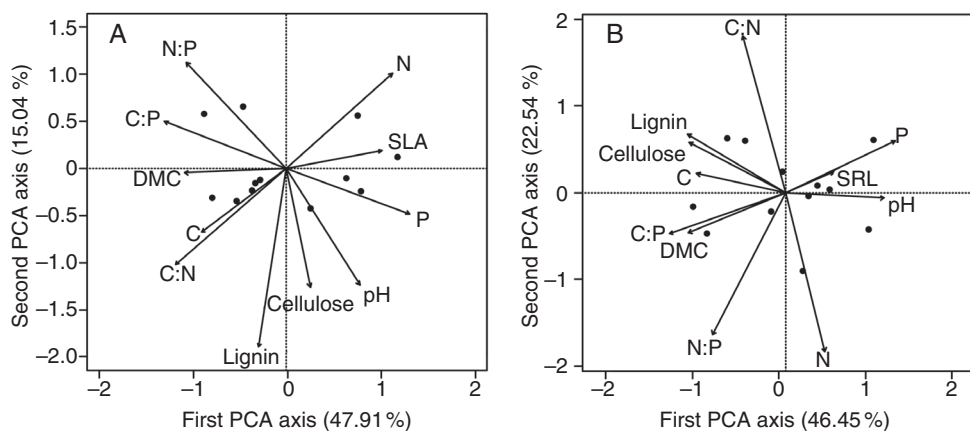

FIG. 2. Biplots of principal component analysis (PCA) on leaf (A) and root (B) functional traits. Points represent the 12 different fern species. SLA, specific leaf area; SRL, specific root length; DMC, dry matter content; C, carbon; N, nitrogen; P, phosphorus.

TABLE 2. *Bivariate relationships between matching pairs of leaf and root functional traits*

Leaf and root trait pairs	β	r^2	P-value
SLA–SRL	0.52	0.10	0.054
DMC	**0.75**	**0.41**	**<0.001**
pH	0.66	0.08	0.105
C	**1.14**	**0.44**	**<0.001**
N	0.98	0.03	0.312
P	**1.51**	**0.55**	**<0.001**
C:N	0.21	0.05	0.185
C:P	**0.42**	**0.73**	**<0.001**
N:P	**0.62**	**0.26**	**0.001**
Cellulose	0.59	0.06	0.140
Lignin	**0.41**	**0.14**	**0.026**

Relationships were tested using standardized major axis (SMA) regression. SLA and SRL were ln-transformed. Significant relationships are shown in bold ($P < 0.05$).

SLA, specific leaf area; SRL, specific root length; DMC, dry matter content; C, carbon; N, nitrogen; P, phosphorus.

not significantly correlated between leaves and roots (Table 2). Finally, the first PCA axes scores between leaves and roots were significantly and positively correlated (SMA regression: $r^2 = 0.78$, $P < 0.001$; Fig. 3A).

Decomposition rates of leaves and roots

After 586 d of decomposition, litter mass loss ranged from 10.5 to 73.1 %. First-order exponential decay curves for the entire decomposition experiment (0–586 d) fitted the decomposition data well (mean $r^2 = 0.91$; Supplementary data Table S3). The decay rates (k value) of fern leaves ranged from 0.984 $year^{-1}$ for *P. penangianum* to 0.369 $year^{-1}$ for *D. chinense*, which corresponds to a leaf $T_{1/2}$ of 0.70–1.88 years, respectively (Supplementary data Table S3). Fern roots decomposed significantly more slowly than leaves (mean k values = 0.667 ± 0.052 and 0.305 ± 0.060 $year^{-1}$ for leaves and roots, respectively; $P < 0.001$), with decay rates ranging from 0.585 $year^{-1}$ for *M. laxa* to 0.058 $year^{-1}$ for *A. chinensis*, corresponding to a root $T_{1/2}$ of 1.19–12.03 years (Supplementary

data Table S3). When considering all fern species, $T_{1/2}$ values of leaves and roots were significantly and positively correlated (SMA regression: $r^2 = 0.35$, $P = 0.047$; Fig. 3B).

Individual trait and trait syndrome as predictors of decomposition rates

Leaf $T_{1/2}$ increased with a decreasing C:P and N:P ratio; these ratios explained 50 % ($P = 0.01$) and 56 % ($P = 0.005$) of the variation in leaf $T_{1/2}$, respectively (Table 3). Surprisingly, leaf $T_{1/2}$ was not significantly correlated with any of the structure-related traits such as lignin or cellulose concentrations in leaves (Table 3). In contrast, root $T_{1/2}$ was predicted well by root lignin or cellulose concentrations. In particular, root lignin concentration was the most important trait affecting root decomposition, explaining 90 % ($P < 0.001$) of the variation in root $T_{1/2}$ (Table 3). Root $T_{1/2}$ was also significantly related to root C concentration, C:P ratio and pH, each parameter explaining around 50 % of the variation in root $T1/2$ (Table 3). Overall, fern roots with

low C, lignin and cellulose concentrations and a low C:P ratio tended to decompose faster, while roots with a low pH value tended to decompose more slowly (Table 3). The first PCA axis scores of leaves (representing the leaf economics spectrum) was a significant predictor of root $T_{1/2}$ ($r^2 = 0.37$, $P = 0.036$) but not leaf $T_{1/2}$ ($r^2 = 0.25$, $P = 0.098$), while the first PCA axis scores of roots (representing the root economics spectrum) was a significant predictor of both leaf $T_{1/2}$ ($r^2 = 0.40$, $P = 0.027$) and root $T_{1/2}$ ($r^2 = 0.74$, $P < 0.001$) (Fig. 4).

DISCUSSION

Trait variation and co-variation among coexisting ferns

In line with the high interspecific trait variation within a community reported previously in seed plants (Ricklefs and Matthew, 1982; Wright *et al.*, 2004; Hättenschwiler *et al.*, 2008; Comas and Eissenstat, 2009; Liu *et al.*, 2010), many traits showed remarkable cross-species variation among the 12 coexisting fern
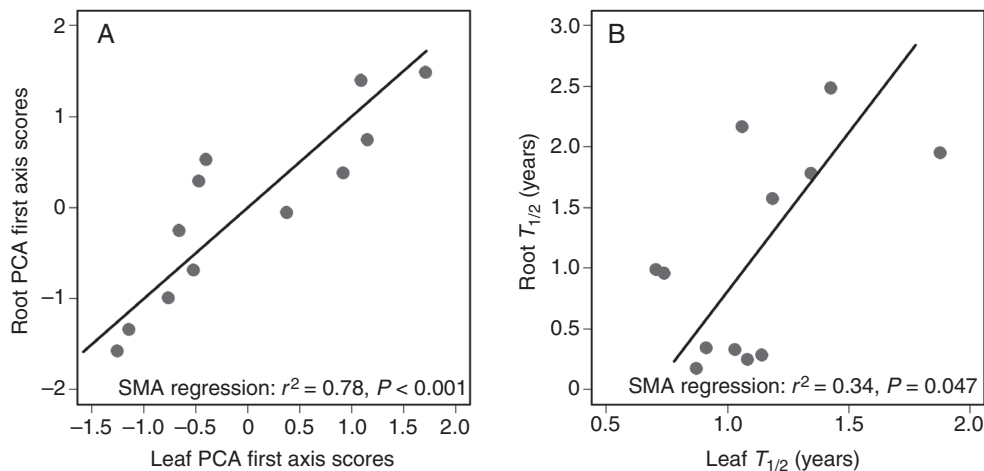

FIG. 3. Correlation between the first axes derived from PCA on leaf and root traits (A) and between decomposition half-lives ($T_{1/2}$) of fern leaves and roots (B). Regression lines were fitted using standardized major axis (SMA) regression. Root $T_{1/2}$ was ln-transformed.

TABLE 3. *Results of the single linear regression analyses with species' traits as predictor variables for interspecific variation in decomposition rates (decomposition half-life;* $T_{1/2}$*) of each fern organ*

Leaf traits	Leaf $T_{1/2}$ (years)				Root $T_{1/2}$ (years)		
	β	r^2	*P*-value	Root traits	β	r^2	*P*-value
SLA	−0.0005	0.04	0.527	SRL	−0.0012	0.05	0.503
DMC	0.0011	0.07	0.400	DMC	0.0039	0.21	0.131
C	0.0053	0.10	0.328	C	**0.0335**	**0.52**	**0.008**
N	−0.0208	0.03	0.583	N	−0.0915	0.11	0.285
P	−0.2639	0.29	0.070	P	−1.1128	0.33	0.051
C:N	0.0243	0.06	0.448	C:N	0.0181	0.12	0.267
C:P	**0.0022**	**0.50**	**0.010**	C:P	**0.0025**	**0.47**	**0.013**
N:P	**0.0573**	**0.56**	**0.005**	N:P	0.0534	0.14	0.239
pH	−0.2035	0.04	0.521	pH	**−1.3866**	**0.50**	**0.010**
Cellulose	0.0027	0.18	0.172	Cellulose	**0.0114**	**0.68**	**0.001**
Lignin	0.0017	0.04	0.514	Lignin	**0.0085**	**0.90**	**<0.001**

Root $T_{1/2}$ was ln-transformed. Significant relationships are shown in bold ($P < 0.05$).

SLA, specific leaf area; SRL, specific root length; DMC, dry matter content; C, carbon; N, nitrogen; P, phosphorus.
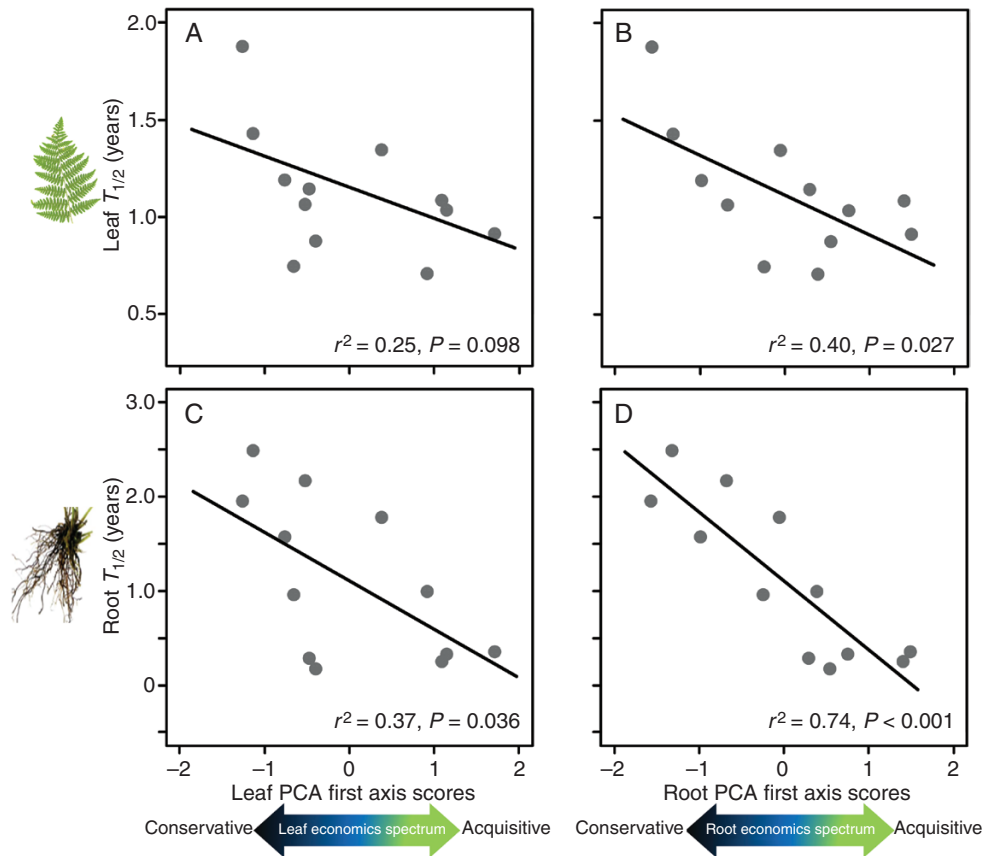
FIG. 4. Influences of the principal component analyses (PCA) first axis score representing the economics spectrum on decomposition half-lives ($T_{1/2}$) of fern leaves and roots. Root $T_{1/2}$ was ln-transformed.

species (Table 1; Supplementary data Table S1). This can be explained by the heterogeneity in microhabitats because our study site is located in an area with a relatively important variability in topographic reliefs and hence differ in soil fertility, light and water conditions (Yang *et al.*, 2001; Sun *et al.*, 2006; Wu *et al.*, 2019). Such variability in environmental conditions may favour the existence of different resource-use strategies, thereby explaining why different ferns species vary in their main morphological and physiological traits.

As expected by the plant economics spectrum theory (Wright *et al.*, 2004; Freschet *et al.*, 2010; Reich, 2014), many traits varied in opposite directions among the 12 coexisting fern species (e.g. SLA and nutrient concentrations vs. DMC and C:N:P ratios). Accordingly, in agreement with our hypothesis, different species were relatively well segregated along the first PCA axis, for each plant organ considered (Fig. 2). Fern species found at the positive side of the first PCA axis presented traits linked to resource acquisition, i.e. with high SLA and leaf N and P concentrations, and high root pH and P concentration (Wright *et al.*, 2004; Freschet *et al.*, 2010). Fern species located at the negative side of the first PCA axis presented a rather conservative resource-using strategy, i.e. with high leaf DMC, C concentration and C:N:P ratios, along with high root DMC, C:P ratio, C, cellulose and lignin concentrations (Wright *et al.*, 2004; Freschet *et al.*, 2010). These results are in line with previous studies on seed plants (Bakker *et al.*, 2011; Roumet

et al., 2016; de la Riva *et al.*, 2018), and highlight that, although ferns and seed plants obviously differ in their morphological, physiological traits and evaluation (Page, 1979; Brodribb *et al.*, 2005; Han *et al.*, 2005; Karst and Lechowicz, 2007; Sharpe *et al.*, 2010; Carriqui *et al.*, 2015; Tosens *et al.*, 2016), the co-variation patterns of key economics functional traits do not depend on the specific plant group. This further suggests that the evolutionary and ecological basis for the relationships among these key economics traits appear to be similar between ferns and seed plants.

We also found that plant trait variation is co-ordinated between above- and below-ground organs (Table 2; Fig. 3A). Indeed, most traits representative of the resource acquisitive strategy were clearly segregated from traits representative of the resource conservation strategy along the first PCA axis, based on either leaf or root traits. Functionally, this indicates that acquisitive plant species with large and thin leaves, high evaporative demand and high photosynthetic rates also require acquisitive roots to ensure enough water and nutrient supply to maintain high growth rates (Eissenstat, 2002.; Fort *et al.*, 2013; Reich, 2014). Conversely, conservative plant species with small and thick leaves and slow growth rates invest more in structural C compounds and have lower photosynthetic rates and nutrient demands. Therefore, we conclude that the co-ordination between above- and below-ground organs allows for an optimization of the resource-use strategy at the whole-plant level.

However, we also found that some key trait pairs were not significantly correlated between leaves and roots, such as the SLA–SRL and N concentrations (Table 2). This suggests that the extrapolation from above- to below-ground organs requires some caution (Freschet *et al.*, 2010; Reich, 2014), especially given that some root traits are decoupled from the variation in leaf traits across various plant species (Weemstra *et al.*, 2016; Bergmann *et al.*, 2017).

Interestingly, some important leaf or root traits were not completely aligned along the leaf or root economics spectra. For example, leaf lignin concentration, a C-related trait that is commonly associated with a resource conservation strategy, was relatively independent from the leaf economics spectrum in ferns (Fig. 2A; Supplementary data Table S2). This may be because lignin may also reflect the plant resistance to pathogens or herbivores (Johnson *et al.*, 2009; War *et al.*, 2012). Similarly, SRL, root N concentration and root C:N ratio, which are the most common root traits used to characterize root economics strategy (e.g. Fort *et al.*, 2013; Roumet *et al.*, 2016), were relatively independent from the root economics spectrum (Fig. 2B; Supplementary data Table S2). This may be because roots also play other pivotal roles such as physical anchoring and resource storage (Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016). Overall, these findings suggest that the economic spectra among the 12 coexisting ferns are multidimensional rather than one-dimensional, probably because plant traits can respond to other independent and ecologically important dimensions, such as resistance against grazing, tolerance to stress, resource storage or support functions (War *et al.*, 2012; Kramer-Walter *et al.*, 2016; Chauvin *et al.*, 2018). These results are in line with previous studies on grasses and trees that reported a multidimensional pattern of plant economics spectra, particularly for root traits (Kong *et al.*, 2015, 2019; Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016; de la Riva *et al.*, 2018; Zhou *et al.*, 2018; Lin *et al.*, 2019).

Plant economics spectrum predicts leaf and root decomposition rates

In line with previous studies on litter decomposition across various ecosystems (Vivanco and Austin, 2006; Wang *et al.*, 2010; Birouste *et al.*, 2012; Freschet *et al.*, 2012; Fujii *et al.*, 2016), we found that fern leaves decomposed at faster rates than roots. This is due to the fact that fern roots are poorer in nutrients and structurally more recalcitrant than leaves (e.g. high C:N:P ratios and lignin concentrations) (Table 1). Furthermore, we found that traits predicting decomposition rates differed between leaves and roots (Table 3). Decomposition of fern leaves was strongly determined by their stoichiometry, i.e. C:P and N:P ratios (Table 3). This can be explained by a strong P limitation in our study system, especially because tropical and subtropical soils are thought to be P deficient and thus limit the activities of microbial decomposers (Fanin *et al.*, 2013, 2015). In contrast to leaves, decomposition rates of fern roots were more limited by the forms of C compounds (especially the lignin concentration) rather than by N or P availability (Table 3). These results reinforce the idea that the decomposition of energy-rich substrates (fern leaves) are mainly limited by

nutrient imbalance, whereas recalcitrant substrates (fern roots) are mainly limited by the availability of labile C compounds (Güsewell and Verhoeven, 2006; Fanin *et al.*, 2016, 2017; de la Riva *et al.*, 2019). This further indicates that plant traits may differ in their predictive power on litter decomposition processes according to the plant organ considered (Wang *et al.*, 2010; Jackson *et al.*, 2013; Ma *et al.*, 2016; Zuo *et al.*, 2018).

Our decomposition experiment also showed that the decomposition rates of leaves and roots were positively correlated, i.e. fern species with rapid leaf decay rates presented rapid root decay rates (Fig. 3B). Our results also indicate that leaf and root economic spectra were good predictors of interspecific variation in decomposition rates especially for root decomposition (Bakker *et al.*, 2011; Freschet *et al.*, 2012; de la Riva *et al.*, 2019), with the acquisitive fern species generally decomposing faster than the conservative fern species (Fig. 4). These results are in accordance with the plant economics framework in which 'fast' leaves match 'fast' roots and 'slow' leaves match 'slow' roots (Freschet *et al.*, 2012; Reich, 2014). Furthermore, our results are in line with previous experimental studies and meta-analyses on trees and grasses that reported co-ordination in decomposability between leaves and other plant organs such as roots (Wang *et al.*, 2010; Birouste *et al.*, 2012; Freschet *et al.*, 2012, 2013; Fujii *et al.*, 2016). This further supports the idea that the dynamics of organic matter observed between coexisting plant species above-ground are probably paralleled below-ground, and thus that it is possible to predict decomposability of other organs from the decomposition rate of leaves, also in fern species (Birouste *et al.*, 2012; Freschet *et al.*, 2012, 2013). However, in contrast to our results, Hobbie *et al.* (2010) found no correlation in decomposition rates between roots and leaves among 11 temperate trees after 510 d. Further, Ma *et al.* (2016) observed that decomposition rates between leaves and roots were strongly linked during the first 3 months of decomposition, but they were unrelated in the subsequent 12 months. These contrasting results highlight that the relationship between leaf and root decomposition rates may depend on substrate quality or decomposition stage, and more efforts will be necessary to elucidate the (de)coupling between leaf and root traits and their afterlife effects during the decomposition process.

Conclusions

In studies dealing with the trait-based approach at the community level, ferns are commonly not included in the analysis for unconvincing reasons. Our study reveals how above- and below-ground plant traits and litter decomposition processes are linked across 12 coexisting fern species in a sub-tropical forest. We showed that the plant economics spectrum theory (commonly observed across seed plants) can also be applied to these fern species, but further studies including more species and across different sites are needed before any generalization can be made at larger spatial scales. The relatively similar trends in the relationships among above- and below-ground traits and their afterlife effects on decomposition suggest that fern species can fit relatively well into a broader vascular plant economic spectrum (e.g. Reich, 2014). The inclusion of more

fern functional traits in databases thus appears to be a priority to better predict decomposition rates across large scales, especially because ferns are rich in diversity and cover a wide geographical area from tropical to boreal ecosystems (Page, 1979; Smith *et al.*, 2006; Kessler, 2010). Furthermore, our results highlight that changes in fern communities caused by anthropogenic disturbance or other environmental factors may have important consequences on C and nutrient cycling through changes in plant functional traits and afterlife effects during the decomposition process. This also underscores the necessity for plant community conservation as a major policy priority for maintaining biogeochemical cycling in sub-tropical forests.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: summary of leaf and root functional trait values of the 12 coexisting fern species. Table S2: loadings of functional traits on the first three axes of the principal components analysis for leaf and root traits. Table S3: summary of decomposition rates of the 12 coexisting fern species.

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