Research

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Rates of ecological divergence and body size evolution are correlated with species diversification in scaly tree ferns

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Variation in species richness across regions and between different groups of organisms is a major feature of evolution. Several factors have been proposed to explain these differences, including heterogeneity in the rates of species diversification and the age of clades. It has been frequently assumed that rapid rates of diversification are coupled to high rates of ecological and morphological evolution, leading to a prediction that remains poorly explored for most species: the positive association between ecological niche divergence, morphological evolution and species diversification. We combined a time-calibrated phylogeny with distribution, ecological and body size data for scaly tree ferns (Cyatheaceae) to test whether rates of species diversification are predicted by the rates at which clades have evolved distinct ecological niches and body sizes. We found that rates of species diversification are positively correlated with rates of ecological and morphological evolution, with rapidly diversifying clades also showing rapidly evolving ecological niches and body sizes. Our results show that rapid diversification of scaly tree ferns is associated with the evolution of species with comparable morphologies that diversified into similar, yet distinct, environments. This suggests parallel evolutionary pathways opening in different tropical regions whenever ecological and geographical opportunities arise. Accordingly, rates of ecological niche and body size evolution are relevant to explain the current patterns of species richness in this 'ancient' fern lineage across the tropics.

1. Introduction

Geographical variation in species richness among clades has been widely documented, but explaining the causes of these differences remains one major challenge in evolutionary biology [1–6]. In general, differences in species richness can be associated with heterogeneity in the rates of species diversification, but the drivers of such rate heterogeneity remain poorly explored for many groups of species. As exemplified by well-known radiations [7–11], high species diversity is often mirrored by high levels of eco-morphological variation, suggesting that species diversification is linked to evolutionary change [12–14]. However, little is known about the ubiquity of the coupling between ecological divergence, phenotypic evolution and species diversification.

Different expectations on the correlation among these three aspects of diversity result from varying mechanisms acting on diversification [3,12,13]. Adaptive radiation models assume that differences in diversification rates across clades are associated with the evolution of adaptive traits [7,13,15], such as life form [16–18] or ecological niche preferences [2,11,19]. Thus, adaptive models make a direct link between rates of species diversification and the rates of eco-morphological evolution among species. Alternatively, there are many instances where species diversification would not be correlated with phenotypic or ecological evolution [20,21]. In this case, species richness would be largely determined by other factors such as the age and distribution of lineages or environmental heterogeneity [10,22–25]. Several studies, especially in animals, that have directly addressed the coupling between
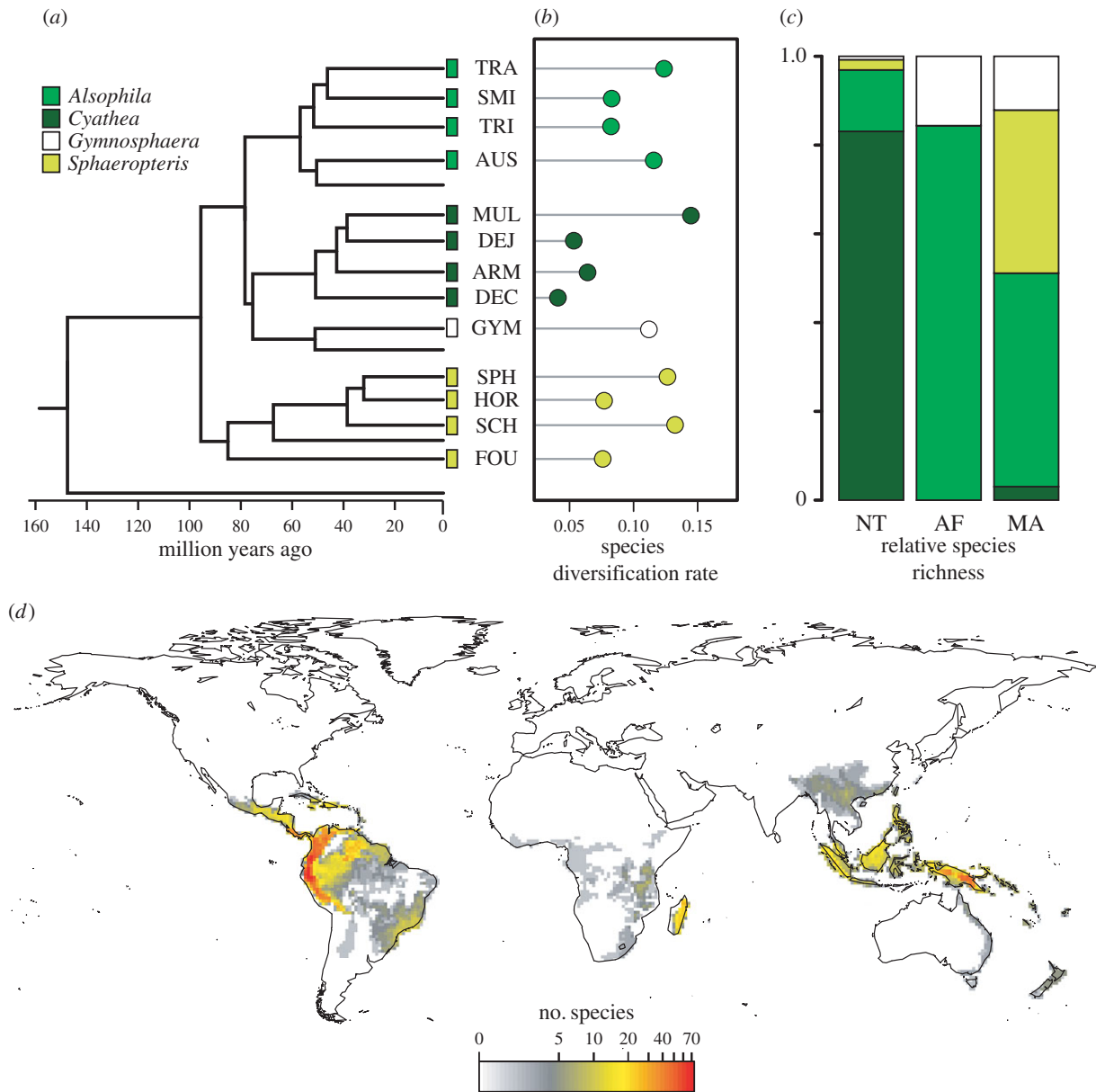
Figure 1. (a) Time-calibrated phylogeny showing the relationship between the 13 major clades of scaly tree ferns (Cyatheaceae). (b) Crown-group rates of net species diversification under a constant-rate model with no extinction for the 13 major clades depicted in the phylogenetic tree. (c) Relative species richness per genus across the three main tropical regions used in this study: Neotropics (NT), Africa (AF) and Malesia (MA). (d) Global map of species diversity estimated from the distribution of 521 species using a $1° \times 1°$ grid of the tropics. Clade names: 'Transatlantic' (TRA), 'Smithii' (SMI), 'Tripinnate' (TRI), 'Australis' (AUS), 'Multiflora' (MUL), 'Dejecta' (DEJ), 'Armata' (ARM), 'Decurrens' (DEC), 'Gymnosphaera' (GYM), 'Sphaeropteris' (SPH), 'Horrida' (HOR), 'Schizocaena' (SCH) and 'Fourneria' (FOU). (Online version in colour.)

species diversification and phenotypic evolution have obtained conflicting evidence (e.g. [2,17–20,26]). Thus, at present, we do not fully comprehend the relative effects of eco-morphological evolution on species diversification.

Here, we examine the correlation between ecological niche divergence, body size variation and species diversification in the tree fern lineage (Cyatheales, *sensu* Smith *et al.* [27]), which is the second largest order of extant ferns, with approximately 700 species [27,28]. Among tree ferns, the scaly tree ferns (Cyatheaceae) represent an ideal system to investigate the relative roles of ecological and morphological evolution in the diversification of plant lineages for several reasons: (i) it is a highly diverse Pantropical fern family (approx. 630 species) with an exceptional concentration of species in the Neotropics and Malesia that mirrors global patterns of tropical diversity (figure 1); (ii) there are sharp geographical disparities in species numbers per genus across regions (figure 1; see

electronic supplementary material, table S1); (iii) although the family has a long evolutionary history dating back to the Cretaceous period [29], recent diversification has been associated with significant shifts in climatic niche preferences [30,31]; and (iv) species show a great deal of morphological variation, especially in terms of body size, from arborescent species reaching more than 15 m in height with leaves over 3 m long, to small herbaceous (trunkless) species with fronds less than 0.5 m long (e.g. [32–35]).

If increased species diversification rates (SDRs) in particular clades of scaly tree ferns have been facilitated by ecological or morphological evolution, then we predict that diversification would be tightly linked to the rates of ecological niche divergence and body size evolution. Thus, rapidly diversifying clades would be characterized by a high variation in species' body size and the occupation of a wide array of ecological niches. In this study, we address this

question by modelling ecological niche and body size evolution on a dated phylogeny for scaly tree ferns.

2. Material and methods

(a) Ecological data

To analyse ecological differences among scaly tree ferns, we compiled a world-wide list of species and obtained distribution data for 521 species (approx. 87%) from published systematic treatments (see electronic supplementary material, dataset S1). Ecological niche modelling was used to predict species' distributions in ecological space using the maximum entropy algorithm [36] for 351 species with more than three occurrence localities. Models were built from 12 climatic variables [37] and four topographic variables. For the remaining 170 species, we generated pseudo-presences around known occurrence localities by choosing neighbouring grid-cells with highly similar ecological conditions. Details of the modelling procedure are outlined in the electronic supplementary material.

The outlying mean index (OMI) [38] multivariate ordination was used to study the separation of species' niches in a multivariate ecological hyperspace. Basically, OMI estimates the deviation of a species' ecological niche from a reference centre representing the general environmental conditions encountered by the sampled community [38]. We performed OMI on a presence/absence matrix of species and a matrix of environmental conditions (see electronic supplementary material, Methods). We investigated differences in species' niche position among groups of species in the three tropical regions (i.e. Neotropics, Africa, Malesia) with a permutational multivariate analysis of variance [39] and also conducted an analysis of multivariate dispersions [40] to assess differences in ecological niche divergence among groups. This test measures the distance of individual trait values to the corresponding group's centroid and then compares the per-group mean distance values using an analysis of variance. The mean distance value of a group is a measure of trait dispersion, where high levels of dispersion among individuals within groups will result in higher mean distance values. Data processing and statistical analyses were handled in R [41].

(b) Morphological data

To examine body size variation between species, we gathered available data through species' descriptions for several morphological traits associated with overall body size (see electronic supplementary material, dataset S1). These represent the maximum observed trait values for each species, which decreases biases associated with the age of individuals. Statistical analyses were limited to trunk and lamina length, because the rest of traits showed a high proportion of missing data (e.g. more than 50% of species without data). We calculated a standardized body size index for 475 species (approx. 79%) from the product of trunk (m) and lamina length (cm): log(trunk length) + log(lamina length). This index is a measure of the overall size of plants, which has been shown to be ecologically important in scaly tree ferns [42,43]. We investigated differences in body size among groups of species in the three tropical regions using a permutational multivariate analysis of variance [39] and conducted an analysis of multivariate dispersions [40] to assess differences in body size variation between groups.

(c) Phylogenetic data

To date, current molecular data include less than 20% of extant diversity of scaly tree ferns [28–30]. Thus, we reviewed species' descriptions and available phylogenetic evidence [28–35] to identify major clades within the Cyatheaceae (figure 1; see electronic supplementary material, table S1). We recognized 13 major clades of scaly tree ferns, to which we were able to assign 537 species (approx. 89%). Tree fern taxonomy and classification have been problematic and marked by frequent changes in the number and definition of genera [28,34,35]. We adopted a morphological circumscription of clades that is very close to Holttum's [32] system of subgenera and sections within a universal *Cyathea*, which shows a surprising correspondence with phylogenetic evidence [28–30]. Although we acknowledge possible unnatural species' assignments, we believe this would represent a minor proportion of species.

To analyse phylogenetic relationships between clades, we constructed a phylogenetic tree using a *cpDNA* sequence dataset including 77 representative species for scaly tree ferns [30]. The times of lineage divergence for Cyatheaceae were estimated using the Bayesian Markov chain Monte Carlo approach implemented in BEAST 1.8.2 [44], using an uncorrelated lognormal clock model and four calibration points based on fossil evidence. Details of the divergence time estimation are outlined in the electronic supplementary material. We obtained a maximum clade credibility tree with mean divergence times and 95% posterior density intervals (see electronic supplementary material, figure S1).

(d) Species diversification, ecological divergence and body size evolution

For each clade, we used the mean divergence time and the number of assigned species (electronic supplementary material, table S1) to calculate net SDRs for crown and stem groups with the methods of moments approach [45]. We also estimated absolute rates of speciation (λ) and extinction (μ) for each clade using Nee *et al.*'s method [46] as implemented in the 'diversitree' package in R (see electronic supplementary material, Methods). We accounted for incomplete sampling in the phylogeny by incorporating a sampling fraction based on the number of species assigned to each clade.

We used a simulation approach [47,48] to explore the correlation between species diversification and rates of ecological and body size evolution. For each clade, we simulated 1000 trees under a constant-rate model of evolution [49,50] using the clade's size, SDR and mean age estimate. Estimation of SDRs and simulations were performed for crown and stem groups under two models with relative extinction rates (ε) of 0.0 and 0.9. The number of species used in simulations and details on the estimation of rates of evolution are outlined in electronic supplementary material. For each simulated clade-tree, we used the maximum-likelihood approach of O'Meara *et al.* [49] to fit a single-rate Brownian motion model of character evolution, which was used to estimate time-independent rates of ecological divergence (σ^2_{ECO}) and body size evolution (σ^2_{BODY}). Subsequently, we investigated the correlation between the estimated rates and species diversification using Kendall's non-parametric ranked correlation test (τ) and a phylogenetic generalized least-squares (PGLS) regression [51] to fit a nonlinear model with a correlation structure derived from clade relationships. We also used PGLS to fit a multiple regression model to test if σ^2_{ECO} and σ^2_{BODY} collectively explain more variation in SDRs than simple regression models. Models were compared using a log-likelihood ratio test with SDRs multiplied by 1000 to ensure negative log-likelihoods. Finally, we used PGLS to test the correlation between log-transformed species richness and the rates of evolution and species diversification. All simulations and statistical analyses were performed in R.

3. Results

The phylogenetic tree agrees well with previous studies [29] and with the proposed morphological circumscriptions of
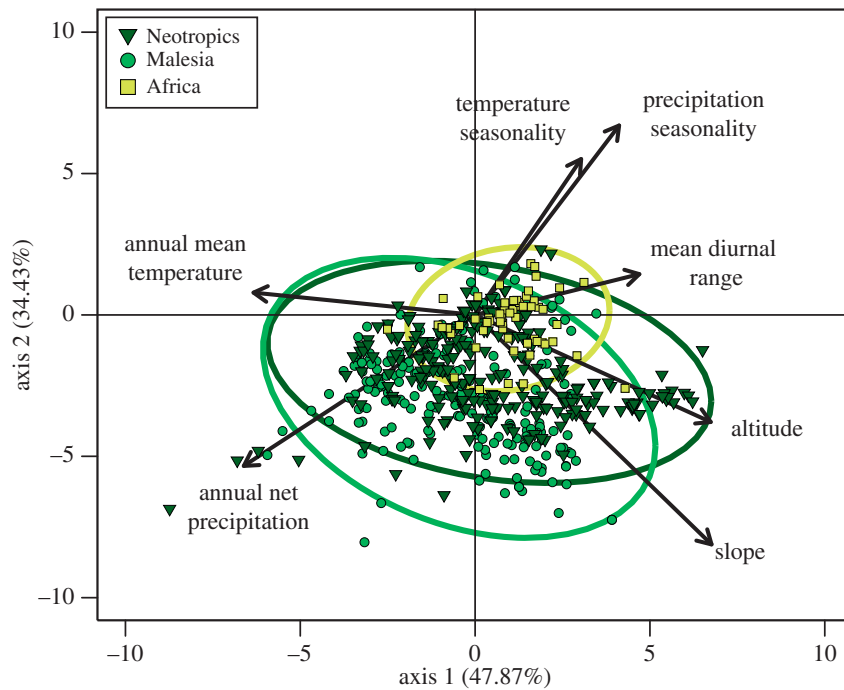
Figure 2. Species niche position for scaly tree ferns (Cyatheaceae) in an ecological hyperspace across the tropics. Colour marks represent the 521 species within the three main tropical regions used in this study. Rings correspond to the 95% confidence ellipses estimated using the mean species' niche position for each region. (Online version in colour.)

scaly tree ferns. Divergence time estimates for the maximum credibility tree were similar to previous estimates [29], only differing by a few million years. Overall, the crown-group age estimates for clades lay within the Palaeogene roughly around 50–30 Ma (electronic supplementary material, figure S1 and table S1). Despite the wide distribution of the four genera of scaly tree ferns, high-diversity clades within each genus are restricted to distinct geographical regions (e.g. the *Cyathea multiflora* clade in the Neotropics and *Schizocaena* in Malesia; electronic supplementary material, table S1). PGLS showed a positive correlation between the log-transformed species richness and SDRs for both crown and stem groups (regression slope p-values < 0.0001, d.f. = 13; electronic supplementary material, figure S2), supporting the idea that clades have increased in richness at very different rates. Regarding the relative roles of speciation and extinction, only three clades showed absolute extinction rates greater than zero (electronic supplementary material, table S2): *Sphaeropteris* clade ($\lambda = 0.277$, $\mu = 0.146$), *Alsophila australis* clade ($\lambda = 0.233$, $\mu = 0.098$) and *C. multiflora* clade ($\lambda = 0.176$, $\mu = 0.011$).

The ordination analysis on species' ecological niches showed significant levels of divergence in scaly tree ferns along two main environmental axes, explaining 47.87% and 34.43% of the total variance in species' niche position, respectively. The first axis was highly associated with altitude and temperature, whereas the second axis had a strong association with precipitation and seasonality (figure 2). We found significant differences in species' niche position ($F = 29.644$, d.f. = 464, $p = 0.001$) and species' ecological divergence between the three tropical regions ($F = 23.782$, d.f. = 464, $p < 0.0001$). Ecological divergence was higher for South American and Malesian species than for African species (figure 2). Accordingly, we also found significant differences in species' body size ($F = 8.192$, d.f. = 410, $p = 0.002$) and body size variation between regions ($F = 21.284$, d.f. = 410, $p < 0.0001$). Body size variation was higher for Neotropical species than for African and Malesian species. In turn, neither

ecological niche divergence nor body size variation show significant positive correlations with log-transformed species richness per clade (electronic supplementary material, figure S2), indicating that eco-morphological variation is not a function of species richness.

Using tree simulations under a constant-rate model, we estimated rates of ecological and morphological evolution (σ^2_{ECO} and σ^2_{BODY}) and tested their correlation with SDRs. Correlation results were similar for crown and stem group estimates, and were not altered significantly by varying levels of relative extinction. Thus, we present here only the results obtained for the models with no extinction (figure 3 and table 1; for results with $\varepsilon = 0.9$, see electronic supplementary material, table S3). Kendall's test and PGLS showed a positive correlation between rates of evolution and SDRs, indicating that faster diversification rates are mirrored by faster rates of ecological and body size evolution. Although PGLS showed that σ^2_{ECO} and σ^2_{BODY} are positively correlated, this was strongly affected by the high rates estimated for the *C. multiflora* clade. Accordingly, excluding this clade from the analyses showed that σ^2_{ECO} and σ^2_{BODY} are uncorrelated (see electronic supplementary material, table S4). In this context, multiple regression and log-likelihood ratio tests indicated that σ^2_{ECO} and σ^2_{BODY} collectively explain more variation in SDRs than either simple regression model (table 1).

4. Discussion

Variation in species richness, ecology and morphology among lineages is a major feature of evolution [1,10,17,25,26,52]. While there are several reasons to expect a positive correlation between these three aspects of biodiversity, we initially expected species richness in scaly tree ferns to be a function of the age of clades due to their long evolutionary history [4,10,17]. Surprisingly, we found no such correlation, but instead discovered that species diversification across major
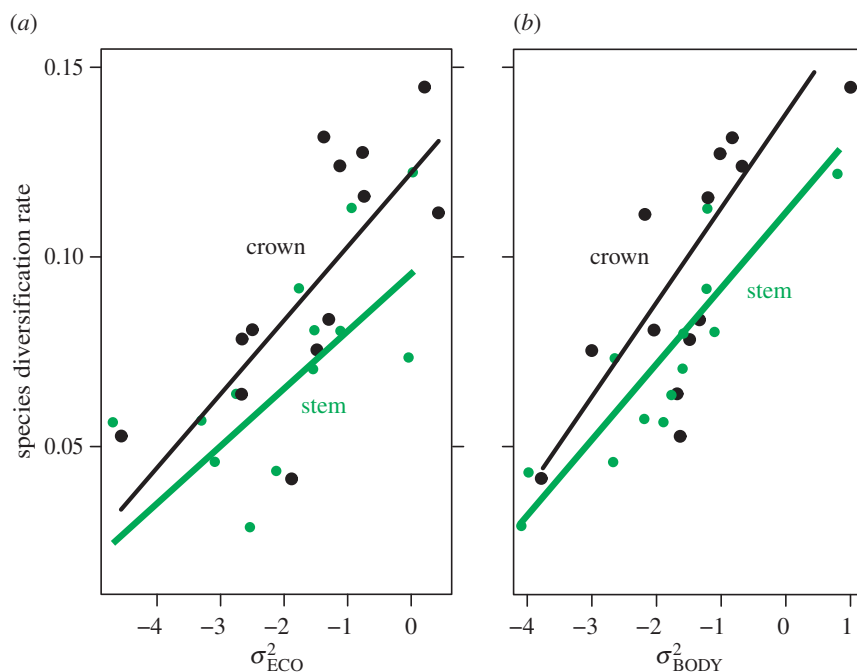
Figure 3. Rates of species diversification, ecological divergence and body size evolution in scaly tree ferns (Cyatheaceae). Correlation between species diversification rates and the logarithm of (*a*) rates of ecological divergence (σ^2_{ECO}) and (*b*) body size evolution (σ^2_{BODY}), using a constant-rate model with no extinction ($\varepsilon = 0.0$). Solid lines indicate the fitted phylogenetic generalized least-squares (PGLS) simple regression models for crown and stem group estimates. (Online version in colour.)

Table 1. Relationship between net species diversification rates (SDRs) and the rates of ecological (σ^2_{ECO}) and body size evolution (σ^2_{BODY}) for major clades of scaly tree ferns (Cyatheaceae) under an evolutionary model with no relative extinction ($\varepsilon = 0.0$) (see electronic supplementary material, table S2 for coefficients under a model with $\varepsilon = 0.9$). Coefficients (*p*-values) are shown for Kendall's non-parametric (τ) test, the simple and multiple phylogenetic generalized least-square (PGLS, mPGLS) fitted models and the log-likelihood ratio test (χ^2) between PGLS nested models.

rate	fitted model	τ	PGLS slope	mPGLS slope	AIC	logLik	χ^2
crown group							
σ^2_{ECO}	logarithmic	0.564 (0.0087)	19.41 (0.0009)	17.15 (0.0005)	124.1	−59.05	16.25 (0.0001)
σ^2_{BODY}	logarithmic	0.667 (0.0019)	24.86 (0.0004)	12.60 (0.0011)	122.1	−58.22	14.59 (0.0001)
$\sigma^2_{ECO} + \sigma^2_{BODY}$					109.8	−50.92	
stem group							
σ^2_{ECO}	logarithmic	0.538 (0.0124)	15.18 (0.0011)	14.59 (0.0001)	119.3	−56.63	20.17 (0.0001)
σ^2_{BODY}	logarithmic	0.821 (0.0001)	20.05 (0.0009)	8.33 (0.002)	112.0	−53.02	12.94 (0.0003)
$\sigma^2_{ECO} + \sigma^2_{BODY}$					103.4	−46.55	

clades is closely linked to ecological niche divergence and body size evolution. Rapidly diversifying clades within scaly tree ferns are characterized by a higher variation in body sizes and the occupation of a wider array of ecological niches than slowly diversifying clades.

According to our results, the correlation between evolutionary rates and diversification is independent of phylogenetic relationships among clades (figure 3). This means that increased diversification rates coupled to high rates of evolution have appeared repeatedly within the Cyatheaceae, exemplified by *Cyathea* in South America [33–35] and *Sphaeropteris* in Malesia [32]. However, the same rates of diversification can be achieved with different combinations of absolute extinction and speciation rates [4,22,53]. Ideally, given a sufficient number of sampled species, absolute rates of extinction and speciation can be confidently estimated from a phylogeny [4,47,53]. We found some evidence of variation in extinction rates among three high-diversity clades (i.e. *Sphaeropteris*

clade, *A. australis* clade and *C. multiflora* clade), which suggests that increased diversification may be the result of different mechanisms affecting speciation and extinction [4,22,53]. Although the method we used incorporates information on missing species, most clades showed extinction rates equal to zero, which might be strongly affected by the uneven sampling of interior nodes for most clades [47]. Thus, we are not confident in establishing specific roles of extinction and speciation in generating the current patterns of diversity, and believe that a more densely sampled phylogeny would be needed to formally test hypotheses related to clade-specific speciation and extinction.

The association between species diversification and eco-morphological evolution we observed in scaly tree ferns is consistent with traditional views of evolutionary change leading to speciation [1,12,14,52]. Along these lines, the regression analyses we performed (figure 3 and table 1) support the hypothesis of both ecological and morphological

evolution as primary drivers of diversification in tropical ferns [21,54]. Several studies, especially in animals, have analysed the correlation between ecological or morphological variation and species diversification, but with inconsistent results [10,17,19,20,26,52]. This inconsistency suggests a varying role of ecologically mediated phenotypic evolution in the diversification of different animal lineages [26]. However, current evidence supports the view that the evolution of distinct life forms and ecological adaptations has promoted recent pulses of species diversification across major plant lineages, including bryophytes [55], ferns [16,56] and angiosperms [18]. Accordingly, the present results may partly explain why other tree fern families such as the Dicksoniaceae (approx. 30 species) [27], which appear to have less ecological and morphological variability than scaly tree ferns [57], have overwhelmingly lower species richness than Cyatheaceae.

Ecological and morphological evolution in the Cyatheaceae may play a key role during the diversification process, allowing for persistence and coexistence of species by reducing competition by character displacement and ecological niche partitioning [12,14,17,52,58]. This does not mean all speciation would be adaptive, as other factors such as spatio-temporal environmental instability [23,24] may have a significant contribution to the observed patterns of species diversity. However, ecological niche partitioning is supported by field observations of altitudinal segregation among closely related tree fern species (e.g. [32–35,58]). Furthermore, body size variation appears to be ecologically important in scaly tree ferns, particularly regarding competition for light availability in closed-forest environments [32,42,43]. Indeed, our analyses suggest that radical body size evolution has been recurrent during the evolutionary history of scaly tree ferns, occurring multiple times in different clades, but not in all of them. At the very least, drastic morphological changes have occurred independently in all four genera. One notable example is the evolution of small and trunkless species in both Neotropical *Cyathea* and Malesian *Sphaeropteris* [32–35].

However, it would be difficult to estimate the number of instances of body size changes with the current phylogenetic data. In this context, traits (ecological or morphological) within clades might evolve towards different stationary optima due to varying selection regimes, and thus the correct estimation of evolutionary rates would not be straightforward [1,3,26,48]. Although the primary advantage of using rates of evolution is that these are time-independent [17,50], assuming constant rates of diversification within clades is probably a gross oversimplification [3,17,22]. The exploration of more complex models of trait evolution in scaly tree ferns, ideally with a complete time-calibrated phylogeny, might identify specific branches within clades where rate shifts have occurred [21,59], which would allow us to ascertain the direction of causality between ecological divergence, morphological change and species diversification.

As discussed for other ferns, such as polypods [16] and filmy ferns [56], it is tempting to establish a link between the diversification of scaly tree ferns and the emergence and dominance of angiosperms. The timing of scaly tree fern diversification and its association with eco-morphological evolution is consistent with a scenario of adaptive diversification driven by the rise of angiosperm-dominated rainforests. It has been generally accepted that ecological complexity in forest ecosystems increased with the evolution of angiosperms, ultimately leading to increased diversification in several groups of plants (e.g. [16,21,30,55,60]). More precisely, the rise of angiosperms probably had a major impact on tropical diversity by increasing local and regional precipitation levels [61]. The present analyses are consistent with this scenario (figure 2), showing that the vast majority of scaly tree ferns have preferentially diversified in regions with high precipitation levels and low seasonality [31]. Under this scenario, the incremental increase in rainfall within angiosperm-dominated forests would have had a positive impact on the diversification of scaly tree ferns by allowing for an expansion of available ecological niches [16,55,61].

Our results support the view that diversification of scaly tree ferns is associated with the evolution of similar ecological niches in different clades [31]. As observed in other plant groups [9,18,62], species with comparable morphologies have diversified into similar, yet distinct, environments (figure 2). This suggests a common driver of species diversification, with parallel evolutionary pathways opening whenever ecological and geographical opportunities arise. Nevertheless, the uneven distribution of species diversity within genera across the three main tropical regions (figure 1) is evidence of unequal species diversification across regions. These independent events of diversification, together with the long evolutionary history of scaly tree fern genera [29], fit well with the 'episodic' species turnover model of Koenen *et al.* [62], in which recent species radiations have stemmed from an 'ancient' stock of high-level taxa. For example, scaly tree ferns in *Alsophila* and *Gymnosphaera*, both with crown-group ages *ca* 50 Ma, were able to invade Madagascar during the recent establishment of modern tropical rainforests during the Miocene (*ca* 23–5 Ma), and subsequently were subjected to a rapid diversification of species [30]. We propose similar likely scenarios for South American and Malesian species, in which geological events [8] and environmental changes [25] have triggered separate yet simultaneous bursts of diversification across different genera [18,54,62].

Many studies have suggested that several groups of plants and animals have accelerated speciation rates in tropical mountains [4,6,8,10,23,25,30]. Ecological and geographical factors have led to the invasion of 'new' ecological space that, facilitated by morphological innovations, has been followed by a dramatic burst in species diversification [5,9,13–15,18]. Our analyses demonstrate that ecological niche divergence and body size evolution are relevant to explain species richness in scaly tree ferns. To our knowledge, this is the first study in plants to formally test the link between species' ecological niches, body size variation and species diversification.

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