

INVITED SPECIAL ARTICLE

For the Special Issue: *Using and Navigating the Plant Tree of Life*

Are rates of species diversification and body size evolution coupled in the ferns?

Weston L. Testo¹ and Michael A. Sundue^{1,2}

Manuscript received 6 June 2017; revision accepted 9 November 2017.

¹ The Pringle Herbarium, University of Vermont, 27 Colchester Drive, Burlington, VT 05405, USA

² Author for correspondence (e-mail: michael.sundue@uvm.edu)

Citation: Testo, W. L., and M. A. Sundue. 2018. Are rates of species diversification and body size evolution coupled in the ferns? *American Journal of Botany* 105(3): 1–11.

doi:10.1002/ajb2.1044

PREMISE OF THE STUDY: Understanding the relationship between phenotypic evolution and lineage diversification is a central goal of evolutionary biology. To extend our understanding of the role morphological evolution plays in the diversification of plants, we examined the relationship between leaf size evolution and lineage diversification across ferns.

METHODS: We tested for an association between body size evolution and lineage diversification using a comparative phylogenetic approach that combined a time-calibrated phylogeny and leaf size data set for 2654 fern species. Rates of leaf size change and lineage diversification were estimated using BAMM, and rate correlations were performed for rates obtained for all families and individual species. Rates and patterns of rate–rate correlation were also analyzed separately for terrestrial and epiphytic taxa.

KEY RESULTS: We find no significant correlation between rates of leaf area change and lineage diversification, nor was there a difference in this pattern when growth habit is considered. Our results are consistent with the findings of an earlier study that reported decoupled rates of body size evolution and diversification in the Polypodiaceae, but conflict with a recent study that reported a positive correlation between body size evolution and lineage diversification rates in the tree fern family Cyatheaceae.

CONCLUSIONS: Our findings indicate that lineage diversification in ferns is largely decoupled from shifts in body size, in contrast to several other groups of organisms. Speciation in ferns appears to be primarily driven by hybridization and isolation along elevational gradients, rather than adaptive radiations featuring prominent morphological restructuring. The exceptional diversity of leaf morphologies in ferns appears to reflect a combination of ecophysiological constraints and adaptations that are not key innovations.

KEY WORDS adaptive radiation; BAMM; evolution; growth habit; leaf size; niche; phylogenetics; Polypodiaceae; species diversification.

Evolutionary biologists have long sought to understand the relationship between species diversification and morphological evolution (Osborn, 1902; Huxley, 1942; Mayr, 1970; Givnish and Sytsma, 2000; Gavrillets and Losos, 2009). Evolutionary theory predicts that rates of morphological evolution and diversification should often be correlated, particularly in cases where morphological innovation promotes ecological divergence, leading to speciation. Indeed,

rapid phenotypic divergence is a trademark of adaptive radiations (Darwin, 1859; Givnish and Sytsma, 2000; Schluter, 2000) and is a central tenet of the hypothesis of punctuated equilibrium (Gould and Eldredge, 1977). This association between phenotypic evolvability and rates of cladogenesis is evidenced prominently by adaptive radiations across the animal and plant kingdoms, such as those that have occurred among African cichlid fish (Kocher, 2004; Seehausen,

2006), Caribbean *Anolis* Daudin lizards (Losos, 2009), Galapagan finches (Sato et al., 2001; Grant and Grant, 2008), the Hawaiian silversword alliance (Baldwin, 1997; Baldwin and Sanderson, 1998), Hawaiian lobeliads (Givnish et al., 2009), and bromeliads (Benzing, 2000; Givnish et al., 2007, 2011, 2014). The opposite pattern is exemplified by “living fossils” such as coelacanths (Holder et al., 1999; Inoue et al., 2005), *Ginkgo* L. (Major, 1967; Royer et al., 2003), and horsetails (Des Marais et al., 2003)—lineages that are characterized by low extant species diversity and extreme morphological stasis across hundreds of millions of years.

Despite the existence of many groups that exhibit apparently coordinated morphological shifts and species proliferation, relatively few studies have explicitly examined the role of morphological evolution as a driver of lineage diversification. These studies have mostly focused on rates of body size evolution, presumably because body size is a metric that can be obtained from taxa across the tree of life and an organism's body size is a useful estimator of its niche (Wilson, 1975; Westoby et al., 2002; Ackerly 2009). Most studies examining the relationship between rates of body size change and lineage diversification (e.g., Moen and Wiens, 2009; Mahler et al., 2010; Slater et al., 2010; Sundue et al., 2015; Ramírez-Barahona et al., 2016; Rose et al., 2016) have focused on single groups that had undergone putative adaptive radiations; only a few (Harmon et al., 2003; Adams et al., 2009; Rabosky et al., 2013) have sought to characterize these patterns across multiple lineages. Results of these studies have been mixed, indicating that further study is needed to better understand the relationship between body size evolution and lineage diversification, especially in non-animal systems, for which comprehensive studies are lacking.

Here, we used a comparative phylogenetic approach to examine the relationship between rates of body size evolution and lineage diversification in the ferns. Ferns represent an excellent system for the study of body size evolution and diversification in plants for several reasons: (1) they exhibit a remarkable range of body sizes (Figs. 1, 2); (2) they comprise clades with varied evolutionary histories, including rapid recent (Sánchez-Baracaldo, 2004; Schneider et al., 2005; Sánchez-Baracaldo and Thomas, 2014) and ancient (Schneider et al., 2004a; Schuettpelz and Pryer, 2009; Rothfels et al., 2012) radiations, as well as depauperon lineages (Des Marais et al., 2003; Bomfleur et al., 2014) (Fig. 2); and (3) a densely sampled, time-calibrated phylogeny of the entire group has recently been published (Testo and Sundue, 2016). In addition, the two studies that have investigated body size evolution as a correlate of diversification in fern clades (Sundue et al., 2015; Ramírez-Barahona et al., 2016) reported conflicting results, highlighting the need for a study with broader taxonomic scope. Such is the goal of this work: to couple large phylogenetic and body size data sets to test for body-size–diversification relationships across the ferns, including comparisons of patterns among terrestrial and epiphytic species, which experience different pressures driving niche occupancy (Watkins and Cardelús, 2012). We hypothesize that rates of body size evolution and lineage diversification are positively correlated across the fern phylogeny because (1) leaf area is a strong predictor of ecological niche in ferns (Watkins et al., 2010; Creese et al., 2011), (2) leaf size and morphology varies prominently both within and across fern clades (Vasco et al., 2013), and (3) unlike leaves in woody angiosperms, the leaf is the primary functional organ in fern sporophytes, meaning that selective pressures should act strongly on leaf size and allow us to capture such effects with our analyses.

MATERIALS AND METHODS

Phylogeny

We used a large time-calibrated phylogeny that was recently published (Testo and Sundue, 2016) as a framework for this study. This phylogeny was chosen because it includes nearly 40% of extant fern diversity, it is time-calibrated with a robust sampling of 26 fossil taxa, and includes growth habit data for all taxa in the phylogeny. When originally constructed, this phylogeny had been checked to include only a single representative per species by checking against species checklists and lists of synonymy provided by the International Plant Names Index (IPNI.org), Tropicos (www.tropicos.org), and monographs. That phylogeny of 3973 fern species was pruned to remove taxa for which morphological data were not readily available, resulting in a tree of 2654 species that was used in this study. For use in some phylogenetic independent contrast analyses (PIC, see *Hypothesis testing* section), this tree was trimmed further to produce (1) a tree with one taxon per family, (2) a tree with only epiphytic taxa, and (3) a tree with only terrestrial taxa.

Morphological data

We used mean leaf area as a body size proxy, following previous studies on plant size evolution (Ackerly, 2009; Sundue et al., 2015; Ramírez-Barahona et al., 2016). This metric is a particularly useful estimator of body size in the ferns, as fern stems are generally compact and/or subterranean and do not contribute significantly to the individual's occupation of physical space, as is the case for many seed plants. The clear exception are arborescent species (“tree ferns”); by using this metric, we undoubtedly underestimated functional body size of these taxa. Mean leaf and width measurements were obtained from descriptions in monographs and floras or from direct measurements of herbarium specimens. For taxa with fertile/sterile leaf dimorphism, measurements from sterile leaves were used. In some clades (e.g., *Psilotum* Sw., *Equisetum* L.) leaves are highly reduced; for these taxa, we used measurements of the photosynthetic portion of the stem instead of leaf area. Leaf area was calculated using the general formula for the area of an ellipse: Leaf area = $\pi \times (\frac{1}{2} \text{ leaf length}) \times (\frac{1}{2} \text{ leaf width})$.

Because a positive correlation between body size evolution and diversification rate was reported for the terrestrial tree fern family Cyatheaceae (Ramírez-Barahona et al., 2016) but not in the primarily epiphytic family Polypodiaceae (Sundue et al., 2015), we felt it was important to investigate the possibility of differing evolutionary patterns between terrestrial and epiphytic lineages. To do so, we obtained growth habit data for all taxa in our phylogeny from Testo and Sundue (2016). These data, along with our estimates of leaf area, are provided in Appendix S1 (see Supplemental Data with this article).

Rate estimation

Rates of diversification (speciation, extinction, and net diversification) and body size evolution were independently estimated using the program BAMM v.2.5.0 (Rabosky, 2014). BAMM uses a reverse-jump MCMC to evaluate a range of diversification regimes across a phylogeny and to estimate rates of diversification (or phenotypic evolution) across all branches in the tree. Diversification rates and body size evolution rates were estimated in independent



FIGURE 1. Diversity in leaf form and size among the ferns. (A) *Asplenium holophlebium* (Aspleniaceae), (B) *Sphaeropteris cuatrecasasii* (Cyatheaceae), (C) *Jamesonii goudotii* (Pteridaceae), (D) *Woodsia glabella* (Woodsiaceae), (E) *Pteris grandifolia* (Pteridaceae), (F) *Hemionitis palmata* (Pteridaceae), (G) *Stigmatopteris contracta* (Dryopteridaceae), (H) *Tomophyllum secundum* (Polypodiaceae), (I) *Sticherus flabellatus* (Gleicheniaceae), (J) *Schizaea pusilla* (Schizaeaceae), (K) *Elaphoglossum sartorii* (Dryopteridaceae). Photo credits: A–I, K, M. A. Sundue; J, F. Matos.

analyses; rate priors for both analyses were estimated using the getBAMMpriors function in the R package BAMMtools (Rabosky et al., 2014a, b), and incomplete taxon sampling was accounted for by incorporating a sampling file providing the proportion of species in each family that was included in our phylogeny, following the diversity estimates of the Pteridophyte Phylogeny Group (2016). For

each rate type, the MCMC analysis was run with four chains for 50 million generations and sampled every 25,000 generations, generating 1800 trees after 10% burn-in was discarded; effective sample sizes of likelihood and rate shift estimates were more than 400 for both analyses. The retained data were then used to calculate speciation, extinction, and net diversification rates for our diversification

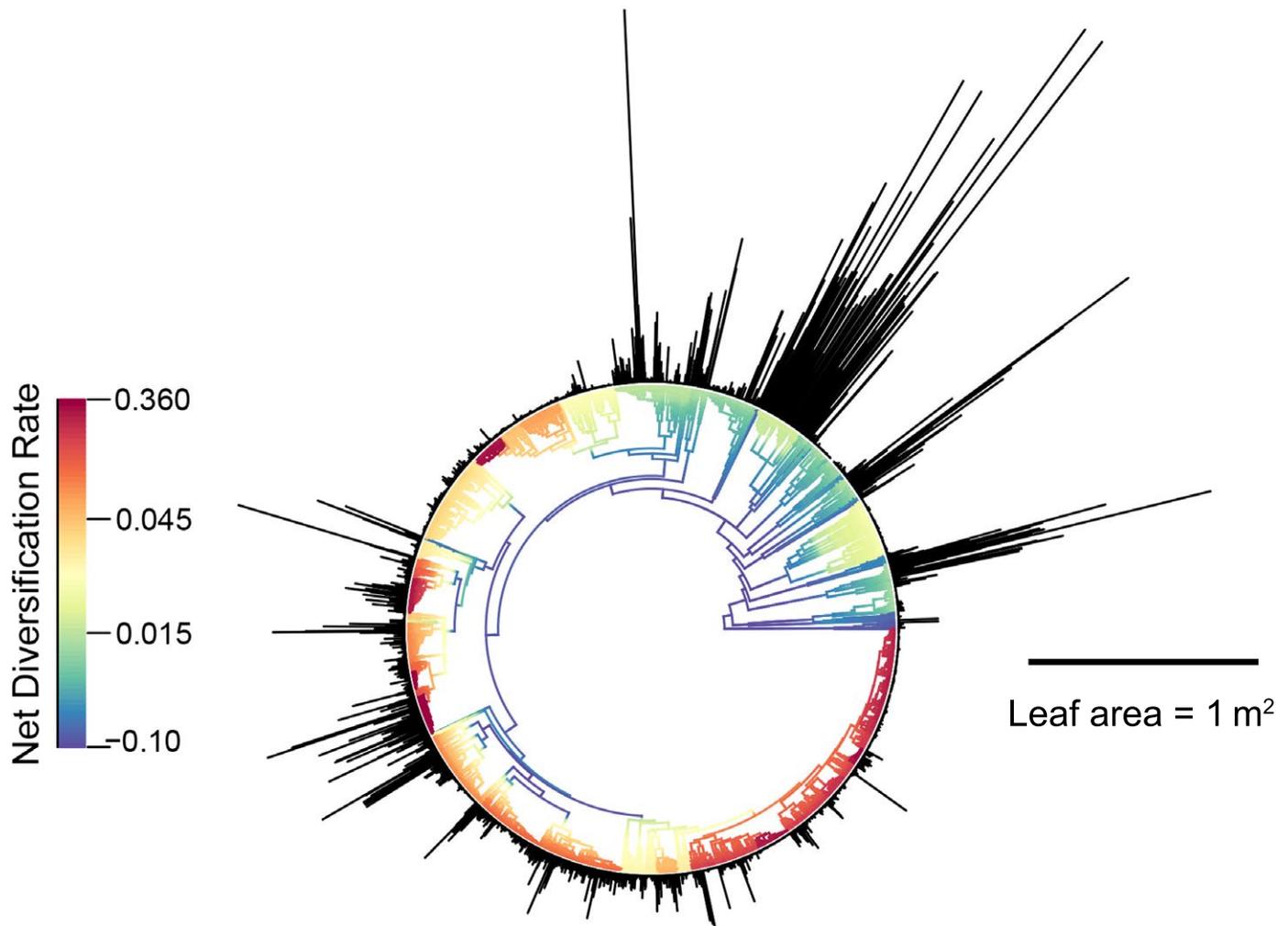


FIGURE 2. Net diversification rates and leaf area across the fern phylogeny. Branches are colored according to net diversification rates inferred from BAMM; bar lengths at tips depict mean leaf area.

rate analysis, and rates of leaf area change in our body size evolution analysis. Mean family-level rate values and tip-specific rate values were obtained using the functions `getCladeRates` and `getTipRates`, respectively. All rate data are provided in Appendix S1 (see Supplemental Data with this article).

As with other rate-based comparative phylogenetic methods (Maddison and FitzJohn, 2015; Rabosky and Goldberg, 2015), the statistical behavior of the BAMM model and the validity of its estimates have been questioned. In particular, Moore *et al.* (2016) reported that the model's likelihood function is unreliable and that its prior estimation is problematic, following a series of analyses on simulated data. Rabosky *et al.* (2017) responded to this criticism, arguing that BAMM's behavior is not fundamentally flawed and that it provides reliable estimates of evolutionary rates when appropriate settings are used. To minimize the chances of erroneous rate estimation, we followed the guidelines for model selection and result interpretation provided by the authors of BAMM (Rabosky, 2014; Mitchell and Rabosky, 2017; Rabosky *et al.*, 2017); nonetheless, we are aware that evaluation of this method (and other comparative phylogenetic methods) is ongoing, and we advocate cautious interpretation of results.

Hypothesis testing

To examine the correlation between body size evolution and diversification rates, we performed PICs (Felsenstein, 1985) of log-transformed body size evolution rates against log-transformed diversification (speciation, extinction, and net diversification) rates in the R package `ape` (Paradis *et al.*, 2004). Data were partitioned in three ways: (1) mean rates for each family ("clade rates"), (2) species-specific rates for all taxa ("tip rates"), and (3) species-specific rates sorted by growth habit; separate PIC analyses were run on each of these data sets.

Rates of body size evolution and diversification of epiphytic versus terrestrial species were also compared by generating kernel density plots of the posterior distribution of rates across the MCMC run for each growth habit and comparing the distribution of rates of epiphytic and terrestrial species with a Mann-Whitney *U*-test, for which a null rate distribution was generated using a structured rate permutation implemented through the `traitdependentBAMM` function in `BAMMtools`.

To compare patterns of lineage diversification and body size evolution across a set of species-rich but ecologically diverse

clades, we conducted the same analyses described above on rates of net diversification and leaf area change for the following families: Cyatheaceae, Dryopteridaceae, Polypodiaceae, and Pteridaceae. These families were chosen because together they comprise nearly half of extant fern diversity, they represent several major fern clades (tree ferns, noncore Polypodiales, eupolypods), and include lineages that span the breadth of ecological diversity occupied by ferns (including aquatics, epiphytes, xerophytes, and arborescent taxa).

RESULTS

Net diversification rates varied across the phylogeny, but generally were highest among the Polypodiales and Cyatheales (Fig. 2, Appendix S1); both speciation and extinction rates tended to be highest in these groups, with some exceptions, such as the heterosporous water fern families Marsileaceae and Salviniaceae, which had high rates of both speciation and extinction. Leaf area

varied dramatically across families, from less than 1 cm² in some filmy ferns (Hymenophyllaceae) to nearly 10 m² in some tree ferns (Cyatheales) (Fig. 2). Rates of leaf size evolution were highest in the Marsileaceae and Salviniaceae and lowest in the Equisetaceae and the Rhachidosoraceae.

Rates of leaf size evolution and diversification rates were not significantly correlated (Table 1), neither when family rates or tip rates were considered, although the association between rates of net diversification and body size evolution was nearly significant, both when clade rates ($P = 0.076$) and tip rates ($P = 0.058$) were considered. When growth habit was factored into our analyses, we found no evidence of a significant difference in rates of diversification or body size evolution between terrestrial and epiphytic species (Fig. 3). Support for a correlation between body size evolution and diversification rates was not significant for either epiphytic or terrestrial taxa (Fig. 4), though a modest nonsignificant ($P = 0.073$) association was recovered between net diversification and body size evolution rates among terrestrial species.

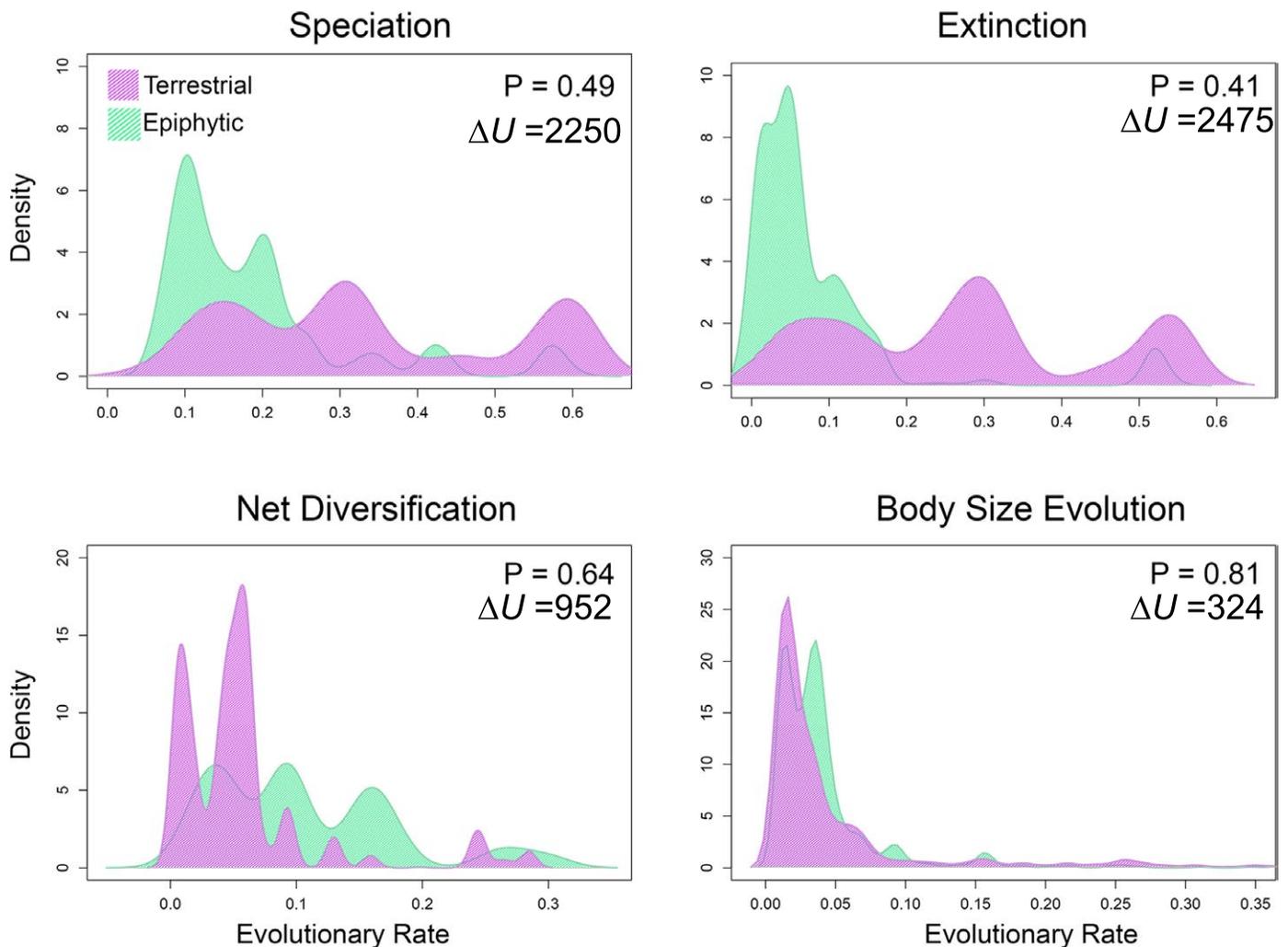


FIGURE 3. Comparison of evolutionary and morphological rates between terrestrial (purple) and epiphytic (green) fern taxa. Curves are kernel density plots depicting posterior probability distribution of absolute tip rates as estimated by BAMM. P -values are from Mann–Whitney U -tests (difference in mean U -scores given) of rate differences between terrestrial and epiphytic species, as implemented in BAMM.

TABLE 1. Results of phylogenetic independent contrasts of diversification and morphological evolution rates.

Comparison	Rate type	df	β	SE	t	P
Speciation~Morph	Clade	44	0.176	0.127	1.386	0.173
Speciation~Morph	Tip	2652	0.002	0.002	1.005	0.315
Extinction~Morph	Clade	44	0.085	0.152	0.570	0.572
Extinction~Morph	Tip	2652	< 0.001	0.003	0.001	0.992
Net Div~Morph	Clade	44	0.375	0.207	1.816	0.076
Net Div~Morph	Tip	2652	0.004	0.002	1.893	0.059
Speciation _{Epi} ~Morph	Tip	769	0.004	0.005	0.727	0.468
Extinction _{Epi} ~Morph	Tip	769	0.004	0.009	0.496	0.620
Net Div _{Epi} ~Morph	Tip	769	0.003	0.005	0.843	0.400
Speciation _{Terr} ~Morph	Tip	1881	0.002	0.002	1.047	0.295
Extinction _{Terr} ~Morph	Tip	1881	< 0.001	0.003	0.085	0.932
Net Div _{Terr} ~Morph	Tip	1881	0.005	0.003	1.79	0.073
Net Div _{Cyatheaaceae} ~Morph	Tip	80	< 0.001	< 0.001	0.303	0.763
Net Div _{Pteridaceae} ~Morph	Tip	407	0.003	0.004	0.665	0.506
Net Div _{Dryopteridaceae} ~Morph	Tip	475	< 0.001	0.003	0.023	0.981
Net Div _{Polypodiaceae} ~Morph	Tip	601	0.002	0.002	0.982	0.323

Notes: β , standardized coefficients; Div, divergence; Morph, morphological; subscript_{Epi}, epiphytic taxa; subscript_{Terr}, terrestrial taxa.

DISCUSSION

We find that rates of body size evolution and lineage diversification are decoupled across the fern phylogeny (Table 1); thus, we reject our hypothesis that these rates would be positively correlated. It is possible that methodological and/or biological artefacts could obscure any such relationship; we consider four possibilities here. First, it is known that both rates of morphological change and lineage diversification can be negatively correlated with clade age (Foote, 1997; Rabosky, 2009). If both phenomena were occurring among taxa included in our phylogeny, an artefactual, negative correlation between rates of leaf area change and diversification would be observed; however, if this time-scaling effect acted upon only one class of rates, it could act to cancel out a real positive relationship. We doubt such an effect is responsible for the observed lack of a relationship, given that the association between clade age and both speciation and morphological rates of families is weak and not significant (Appendix S1). A second possibility is that a large number of under-detected cryptic species could have a compounding effect on our results, as described by Rabosky et al. (2013) for ray-finned fishes. The potential problem is one stemming from taxonomic practice: if morphologically similar lineages are not recognized by taxonomists with the same frequency that morphologically disparate lineages are, diversity estimates will be disproportionately low for groups with high incidences of cryptic species. This bias would directly affect our analysis by impacting our estimates of clade-level taxon sampling, thus resulting in underestimation of lineage diversification rates and overestimation of body size evolution in morphological stable clades (i.e., those with low rates of body size evolution). A third, related, phenomenon is similarly difficult to assess: the effects hybrid speciation on patterns of morphological evolution. Because species formed through reticulate evolutionary processes are typically morphologically intermediate to their progenitors (rather than morphologically divergent from each other, as expected under divergent evolution), the high incidence of hybrid speciation in ferns may act to disrupt expected patterns of morphological evolution. Because of this intermediacy in leaf morphology (Barrington et al., 1989), reticulate evolution should act to depress rates of leaf area evolution, thereby generating a negative association between diversification and morphological rates. To

estimate the effect of this phenomenon on our data set, we tested for a correlation between rates of leaf area evolution and polyploid incidence across 25 clades for which such data were available (W. L. Testo and M. A. Sundue, unpublished data). We found no relationship ($R^2 = 0.01$), suggesting that there is no consistent relationship between frequency of reticulate evolution and patterns of leaf size evolution across our data set. Finally, our fourth concern relates to a fundamental limitation of our phylogenetic data set, namely, the use of a phylogeny derived from uniparentally inherited markers in a system where reticulate evolution is known to be widespread. In our phylogeny, species of hybrid origin are resolved with their maternal progenitor, thus incompletely representing their true evolutionary affinities and presenting a misleading pattern of leaf area evolution. While the effects of reticulate evolution on phylogenetic inference are well documented (Linder and Rieseberg, 2004; Huson and Bryant, 2006; Soltis et al., 2008; Marcussen et al., 2012), their impact on diversification analyses are largely unknown and potentially powerful (see Soltis et al., 2014). Further study incorporating phylogenies derived from biparentally inherited nuclear markers may help us better understand these effects; unfortunately, densely sampled nuclear phylogenies are lacking for ferns.

These potentially confounding factors notwithstanding, a likely explanation for the observed weak association of body size evolution and lineage diversification is simply that the primary mode(s) of speciation in ferns is unrelated to divergence in leaf area. Under several evolutionary scenarios, morphological evolution and lineage diversification should not be correlated. Non-adaptive radiations, for example, are characterized by periods of elevated diversification without appreciable corresponding functional divergence (Gittenberger, 1991). Among plants, such radiations are generally considered to be associated with highly dynamic climate and habitat conditions (Linder, 2008) and this appears to hold true for ferns, with montane forests playing a particularly important role (Moran, 1995; Kreft et al., 2010; Wang et al., 2012; Sundue et al., 2015; Kessler et al., 2016). Rapid diversification events linked to exploration of montane habitats, rather than shifts in morphology, have been suggested for several groups of ferns, including *Lepisorus* (J.Sm.) Ching (Wang et al., 2012); *Pleopeltis* Humb. & Bonpl. ex Willd. (Haufler et al., 2000), *Serpocaulon* A.R.Sm. (Kreier et al., 2008), and *Polystichum* Roth (McHenry and Barrington, 2014) and recently demonstrated

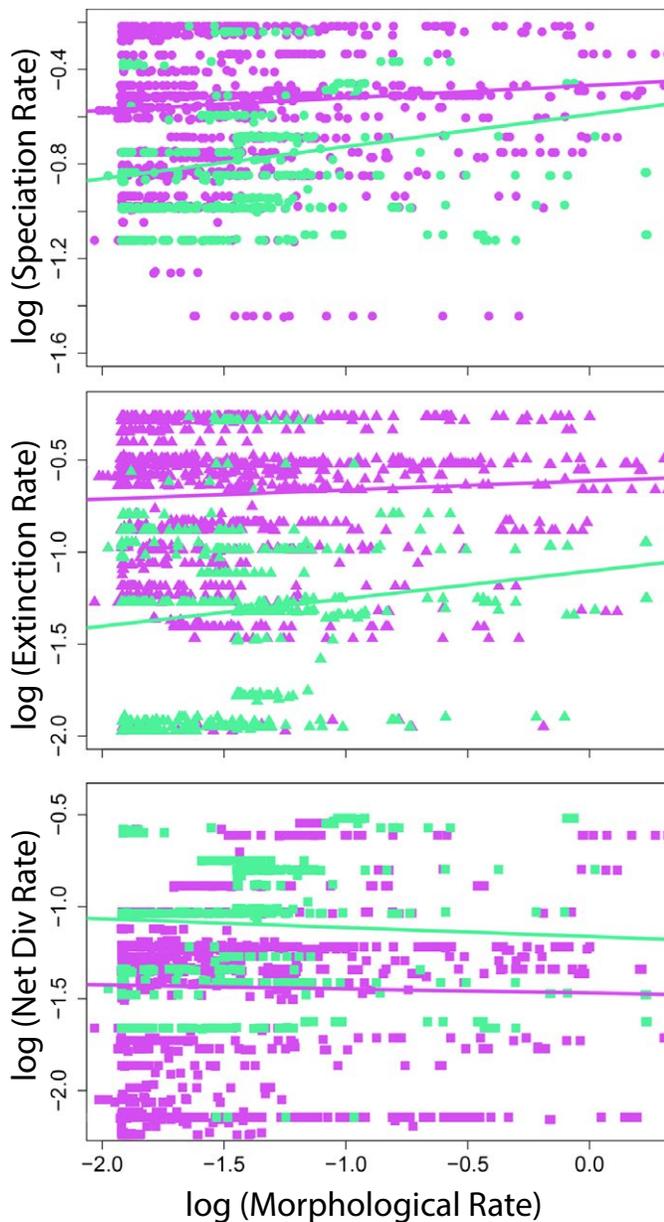


FIGURE 4. Scatter plots depicting correlation between evolutionary and morphological rates between terrestrial (purple) and epiphytic (green) fern taxa. Rates are mean tip rates inferred using BAMM, regression statistics are provided in Table 1; colored lines depict best-fit linear regressions. Div = diversification.

in the Polypodiaceae (Sundue et al., 2015). As proposed by Moran (1995, p. 360), “mountains have strongly influenced this group of plants by impeding migration and by promoting high species richness and endemism.” Though empirically testing this hypothesis across the ferns remains challenging (Kessler et al., 2016), the exceptional richness of numerous lineages of ferns in montane, tropical forests highlights the role of these habitats as centers of diversity. Clearly, successful diversification in these habitats does not require coordinated shifts in leaf size—families such as Aspleniaceae and Thelypteridaceae are among the most diverse fern families in montane forests, but rates of leaf size evolution are modest.

Contrary to our overall pattern of leaf evolution and lineage diversification, several groups have been hypothesized to have undergone rapid adaptive radiations involving shifts in leaf size, including *Jamesonia* Hook. & Grev. (Sánchez-Baracaldo, 2004; Sánchez-Baracaldo and Thomas, 2014), Madagascan Cyatheaceae (Janssen et al., 2008), and *Asplenium* L. in Hawaii (Schneider et al., 2005). Our results confirm these earlier reports and indicate that several other lineages exhibit the same pattern of rapid, coordinated morphological divergence and lineage diversification, including the *Diplazium dilatatum* Blume clade and *Polystichum* sects. *Hypopeltis* (Michx.) T. Moore and *Sorolepidium* Tagawa (Appendix S1). Further study is needed to determine if the latter two lineages have undergone adaptive radiations, though the *Diplazium dilatatum* group are a clade of exceptionally large-leaved species in a diverse lineage thought to have undergone a rapid radiation (Wei et al., 2013) and *Polystichum* sects. *Hypopeltis* and *Sorolepidium* both include highly reduced species that occupy extreme alpine habitats in eastern Asia (Liu et al., 2007). Thus, although rates of body size evolution and lineage diversification generally are not strongly correlated in the ferns, there appear to be at least some cases where morphological innovation is linked to exceptional evolutionary success.

It is important to keep in mind that elevated lineage diversification rates are not a requisite feature of adaptive radiations (Givnish, 2015). In these cases, where adaptive morphological divergence occurs in the absence of exceptional diversification, no correlation between rates of morphological change and diversification should be expected. Our data reveal several groups that correspond to this pattern, including the highly specialized epiphytic genera *Aglaomorpha* Schott and *Platycterium* Desv., the Hawaiian endemics *Adiantopsis* Gaudich. and *Sadleria* Kaulf., the neotropical xerophytic genus *Adiantopsis* Fée, and *Crepidomanes* C. Presl, a genus of filmy ferns that includes several dwarf species. All these genera are species-poor to modestly diverse (6–50 species) but comprise species that have adapted to a diverse array of ecological niches.

At a broader evolutionary scale, we also find no significant relationship between rates of leaf area change and diversification in four species-rich families that previously had been reported to have experienced rapid radiations: Cyatheaceae (Ramírez-Barahona et al., 2016), Dryopteridaceae (Labiak et al., 2014; McHenry and Barrington, 2014), Polypodiaceae (Schneider et al., 2004b; Schuettpelz and Pryer, 2009; Sundue et al., 2015), and Pteridaceae (Schuettpelz et al., 2007) (Table 1). Together, results for these four families indicate that body size evolution and diversification rates are weakly associated even within the most species-rich fern families, regardless of their respective ecologies and body plans.

The relationship between rates of body size evolution and diversification has been examined previously in two of these families: the Cyatheaceae (Ramírez-Barahona et al., 2016) and Polypodiaceae (Sundue et al., 2015). Our findings are consistent with those of Sundue et al. (2015), who reported no relationship between changes in leaf size and diversification rates in the Polypodiaceae, but conflict with those of Ramírez-Barahona et al. (2016), who reported a strong positive correlation between body size evolution and diversification rates in the Cyatheaceae. We believe the discrepancy between our findings and those of Ramírez-Barahona et al. (2016) possibly stems primarily from two methodological differences: choice of body size metric and method of diversification rate estimation. Whereas Ramírez-Barahona et al. (2016) used summed trunk and leaf lengths as a proxy for body size, we chose to analyze leaf area to facilitate co-analysis with non-arborescent taxa. While

these two metrics capture slightly different of niche space, our size estimates and those of Ramírez-Barahona et al. (2016) co-vary by clade; thus, we doubt they are responsible for the conflicting results between their study and ours. Instead, we suspect that differences in the estimation of diversification rate account for the conflicting results. Whereas we estimated diversification rates directly from the branch lengths of our time-calibrated phylogeny using a method that allows for rate heterogeneity across the phylogeny, Ramírez-Barahona et al. (2016) inferred diversification rates by simulating trees based on clade ages and species richness estimates under an assumption of constant diversification rates across time. Although this approach has been widely used in studies of lineage diversification, its central assumption of rate constancy across a clade through time is often inconsistent with observed patterns of clade species richness (Ricklefs, 2007; Rabosky, 2010) and has previously led to misleading estimation of correlated morphological evolution and lineage diversification (Rabosky and Adams, 2012).

Despite the drastically different selective pressures acting on terrestrial versus epiphytic ferns, we found no evidence that growth habit affects the association between shifts in leaf area and diversification rates (Fig. 4, Table 1). Furthermore, rates of morphological evolution do not differ between terrestrial and epiphytic taxa (Fig. 3), suggesting that within-niche pressures on body size are similar, even though the abrupt downscaling of leaf size often associated with transitions to epiphytic growth occurs repeatedly across the phylogeny (Fig. 2). Thus, although body size appears to often change dramatically in association with shifts in growth habit, rates of morphological evolution subsequently stabilize in both terrestrial and epiphytic lineages, regardless of the pace of their diversification. Given this pattern, what explains the radiation of many fern lineages—both terrestrial and epiphytic—into a variety of distinct niches? Evidence from ecological and ecophysiological studies suggest that within-growth habit niche differentiation in ferns is driven in large part by functional innovations related to indument (Hevly, 1963; Kluge and Kessler, 2007), gametophyte functional ecology (Watkins et al., 2007), breeding systems (Tanaka et al., 2014; Sessa et al., 2016), and water relations (Hietz and Briones, 1998; Watkins et al., 2010; Pittermann et al., 2013; Testo and Watkins, 2013) among other factors. Thus, in most cases, key innovations driving niche differentiation among fern taxa appear to generally be unrelated to changes in leaf area.

CONCLUSIONS

Contrary to other groups, such as ray-finned fishes (Rabosky et al., 2013), plethodontid salamanders (Rabosky and Adams, 2012), and scinid lizards (Rabosky et al., 2014a, b), a consistent relationship between rates of body size evolution and lineage diversification is apparently absent among ferns. The possible factors contributing to the lack of a discernible correlation of morphological and diversification rates in ferns are complex and varied, but together present important insights into the accumulation of species richness in this prominent plant lineage. Unlike groups in which correlated morphological evolution and lineage proliferation have been shown to predominate, speciation in ferns appears to be driven primarily by a combination of geographic isolation (especially along elevational or edaphic gradients; Tryon, 1972; Barrington, 1993; Moran, 1995; Haufler et al., 2000; Kluge et al., 2006; Tuomisto, 2006; Watkins et al., 2006; Lehtonen et al., 2015; Sundue et al., 2015), hybridization (Barrington et al., 1989; Wood et al., 2009), and ecophysiological specialization

(Watkins et al., 2007; Watkins and Cardelús, 2012; Pittermann et al., 2013). None of these processes are intrinsically linked to changes in body size. Major changes in leaf area instead appear to be linked to shifts between terrestrial and epiphytic growth or between mesic and xeric habitats (Watkins et al., 2010; Creese et al., 2011); these transitions are significant at deep evolutionary timescales but ultimately uncommon across the fern phylogeny and rarely associated with individual speciation events (Schneider et al., 2004a; Schuettelpelz and Pryer, 2009; Testo and Sundue, 2014). Our study highlights the importance of using a densely and broadly sampled phylogeny as a framework for investigating macroevolutionary patterns across a variety of clades, rather than attempting to generalize findings based on the study of the radiation of a single group. It also provides a context for appreciating and understanding the exceptional diversity of leaf sizes in the ferns: as a marker of their collectively broad ecological amplitude, not a correlate of their rapid diversification.

ACKNOWLEDGEMENTS

We thank the organizers of this special issue, “Using and Navigating the Plant Tree of Life”, for inviting us to contribute this work, David Barrington for insightful conversations, and the editor and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. The Rolla and Alice Tryon Pteridophyte Library at the University of Vermont provided resources that were critical to the realization of this work.

DATA ACCESSIBILITY

The original phylogenetic tree file used in this study is available on TreeBASE at <http://purl.org/phylo/treebase/phylogs/study/TB2:S19934>. The list of taxa pruned from this tree is available in the online supplement.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

LITERATURE CITED

- Ackerly, D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences, USA* 106: 19699–19706.
- Adams, D. C., C. M. Berns, K. H. Kozak, and J. J. Wiens. 2009. Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society, B, Biological Sciences* 276: 2729–2738.
- Baldwin, B. 1997. Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. In T. J. Givnish and K. J. Sytsma [eds.], *Molecular evolution and adaptive radiation, 1840–1843*. Cambridge University Press, Cambridge, UK.
- Baldwin, B. G., and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences, USA* 95: 9402–9406.
- Barrington, D. S. 1993. Ecological and historical factors in fern biogeography. *Journal of Biogeography* 20: 275–279.

- Barrington, D. S., C. H. Haufler, and C. R. Werth. 1989. Hybridization, reticulation, and species concepts in the ferns. *American Fern Journal* 79: 55–64.
- Benzing, D. H. 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge University Press, Cambridge, UK.
- Bomfleur, B., S. McLoughlin, and V. Vajda. 2014. Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. *Science* 343: 1376–1377.
- Creese, C., A. Lee, and L. Sack. 2011. Drivers of morphological diversity and distribution in the Hawaiian fern flora: trait associations with size, growth form, and environment. *American Journal of Botany* 98: 956–966.
- Darwin, C. 1859. On the origin of the species by natural selection. Murray, London, UK.
- Des Marais, D. L., A. R. Smith, D. M. Britton, and K. M. Pryer. 2003. Phylogenetic relationships and evolution of extant horsetails, Equisetum, based on chloroplast DNA sequence data (rbcL and trnL-F). *International Journal of Plant Sciences* 164: 737–751.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- Foote, M. 1997. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* 28: 129–152.
- Gavrilets, S., and J. B. Losos. 2009. Adaptive radiation: contrasting theory with data. *Science* 323: 732–737.
- Gittenberger, E. 1991. What about non-adaptive radiation? *Biological Journal of the Linnean Society* 43: 263–272.
- Givnish, T. J. 2015. Adaptive radiation versus ‘radiation’ and ‘explosive diversification’: why conceptual distinctions are fundamental to understanding evolution. *New Phytologist* 207: 297–303.
- Givnish, T. J., M. H. J. Barfuss, B. V. Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, et al. 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. *American Journal of Botany* 98: 872–895.
- Givnish, T. J., M. H. J. Barfuss, B. V. Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, et al. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution* 71: 55–78.
- Givnish, T. J., K. C. Millam, P. E. Berry, and K. J. Sytsma. 2007. Phylogeny, adaptive radiation, and historical biogeography of Bromeliaceae inferred from *ndhF* sequence data. *Aliso* 23: 3–26.
- Givnish, T. J., K. C. Millam, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, et al. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society, B, Biological Sciences* 276: 407–416.
- Givnish, T. J., and K. J. Sytsma. 2000. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge, UK.
- Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115–151.
- Grant, B. R., and P. R. Grant. 2008. Fission and fusion of Darwin’s finches populations. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 363: 2821–2829.
- Harmon, L. J., J. A. Schulte, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301: 961–964.
- Haufler, C. H., E. A. Hooper, and J. P. Therrien. 2000. Modes and mechanisms of speciation in pteridophytes: implications of contrasting patterns in ferns representing temperate and tropical habitats. *Plant Species Biology* 15: 223–236.
- Havly, R. H. 1963. Adaptations of cheilanthoid ferns to desert environments. *Journal of the Arizona Academy of Science* 2: 164–175.
- Hietz, P., and O. Briones. 1998. Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia* 114: 305–316.
- Holder, M. T., M. V. Erdmann, T. P. Wilcox, R. L. Caldwell, and D. M. Hillis. 1999. Two living species of coelacanths? *Proceedings of the National Academy of Sciences, USA* 96: 12616–12620.
- Huson, D. H., and D. Bryant. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23: 254–267.
- Huxley, J. 1942. Evolution. The modern synthesis. Allen & Unwin, London, UK. Available at <https://www.cabdirect.org/cabdirect/abstract/19432202794> [accessed 5 June 2017].
- Inoue, J. G., M. Miya, B. Venkatesh, and M. Nishida. 2005. The mitochondrial genome of Indonesian coelacanth *Latimeria menadoensis* (Sarcopterygii: Coelacanthiformes) and divergence time estimation between the two coelacanths. *Gene* 349: 227–235.
- Janssen, T., N. Bystrakova, F. Rakotondrainibe, D. Coomes, J.-N. Labat, and H. Schneider. 2008. Neoendemism in Madagascan scaly tree ferns results from recent, coincident diversification bursts. *Evolution* 62: 1876–1889.
- Kessler, M., D. N. Karger, and J. Kluge. 2016. Elevational diversity patterns as an example for evolutionary and ecological dynamics in ferns and lycophytes. *Journal of Systematics and Evolution* 54: 617–625.
- Kluge, J., and M. Kessler. 2007. Morphological characteristics of fern assemblages along an elevational gradient: patterns and causes. *Ecotropica* 13: 27–43.
- Kluge, J., M. Kessler, and R. R. Dunn. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography* 15: 358–371.
- Kocher, T. D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews Genetics* 5: 288–298.
- Kreft, H., W. Jetz, J. Mutke, and W. Barthlott. 2010. Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography* 33: 408–419.
- Kreier, H.-P., M. Rex, K. Weising, M. Kessler, A. R. Smith, and H. Schneider. 2008. Inferring the diversification of the epiphytic fern genus *Serpocaulon* (Polypodiaceae) in South America using chloroplast sequences and amplified fragment length polymorphisms. *Plant Systematics and Evolution* 274: 1.
- Labiak, P. H., M. Sundue, G. Rouhan, J. G. Hanks, J. T. Mickel, and R. C. Moran. 2014. Phylogeny and historical biogeography of the laestrosperid ferns (Dryopteridaceae). *American Journal of Botany* 101: 1207–1228.
- Lehtonen, S., M. M. Jones, G. Zuquim, J. Prado, and H. Tuomisto. 2015. Phylogenetic relatedness within Neotropical fern communities increases with soil fertility. *Global Ecology and Biogeography* 24: 695–705.
- Linder, C. R., and L. H. Rieseberg. 2004. Reconstructing patterns of reticulate evolution in plants. *American Journal of Botany* 91: 1700–1708.
- Linder, H. P. 2008. Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society, B, Biological Sciences* 363: 3097–3105.
- Liu, H., X. Zhang, Z. Chen, and Y. Qiu. 2007. Inclusion of the eastern Asia endemic genus *Sorolepidium* in *Polystichum* (Dryopteridaceae): evidence from the chloroplast *rbcL* gene and morphological characteristics. *Chinese Science Bulletin* 52: 631–638.
- Losos, J. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley, CA, USA.
- Maddison, W. P., and R. G. FitzJohn. 2015. The unsolved challenge to phylogenetic correlation tests for categorical characters. *Systematic Biology* 64: 127–136.
- Mahler, D. L., L. J. Revell, R. E. Glor, and J. B. Losos. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution* 64: 2731–2745.
- Major, R. T. 1967. The ginkgo, the most ancient living tree. *Science* 157: 1270–1273.
- Marcussen, T., K. S. Jakobsen, J. Danihelka, H. E. Ballard, K. Blaxland, A. K. Brysting, and B. Oxelman. 2012. Inferring species networks from gene trees in high-polyploid North American and Hawaiian violets (*Viola*, Violaceae). *Systematic Biology* 61: 107–126.
- Mayr, E. 1970. Populations, species, and evolution: an abridgment of animal species and evolution. Harvard University Press, Cambridge, MA, USA.
- McHenry, M. A., and D. S. Barrington. 2014. Phylogeny and biogeography of exindusiate Andean *Polystichum* (Dryopteridaceae). *American Journal of Botany* 101: 365–375.
- Mitchell, J. S., and D. L. Rabosky. 2017. Bayesian model selection with BAMM: effects of the model prior on the inferred number of diversification shifts. *Methods in Ecology and Evolution* 8: 37–46.
- Moen, D. S., and J. J. Wiens. 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). *Evolution* 63: 195–214.
- Moore, B. R., S. Höhna, M. R. May, B. Rannala, and J. P. Huelsenbeck. 2016. Critically evaluating the theory and performance of Bayesian analysis

- of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences, USA* 113: 9569–9574.
- Moran, R. C. 1995. The importance of mountains to pteridophytes, with emphasis on Neotropical montane forests. In S. P. Churchill, H. Balslev, E. Forero, and J. Luteyn [eds.], *Biodiversity and conservation of montane forests*, 359–363. New York Botanical Garden Press, Bronx, NY, USA.
- Osborn, H. F. 1902. The law of adaptive radiation. *American Naturalist* 36: 353–363.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289–290.
- Pittermann, J., C. B. Brodersen, and J. J. Watkins. 2013. The physiological resilience of fern sporophytes and gametophytes: advances in water relations offer new insights into an old lineage. *Frontiers in Plant Science* 4: 285.
- Pteridophyte Phylogeny Group. 2016. A community-derived classification for extant lycophytes and ferns: PPG I. *Journal of Systematics and Evolution* 54: 563–603.
- Rabosky, D. L. 2009. Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters* 12: 735–743.
- Rabosky, D. L. 2010. Primary controls on species richness in higher taxa. *Systematic Biology* 59: 634–645.
- Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLOS ONE* 9: e89543.
- Rabosky, D. L., and D. C. Adams. 2012. Rates of morphological evolution are correlated with species richness in salamanders. *Evolution* 66: 1807–1818.
- Rabosky, D. L., S. C. Donnellan, M. Grundler, and I. J. Lovette. 2014a. Analysis and visualization of complex macroevolutionary dynamics: an example from Australian scincid lizards. *Systematic Biology* 63: 610–627.
- Rabosky, D. L., M. Grundler, C. Anderson, P. Title, J. J. Shi, J. W. Brown, H. Huang, and J. G. Larson. 2014b. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution* 5: 701–707.
- Rabosky, D. L., and E. E. Goldberg. 2015. Model inadequacy and mistaken inferences of trait-dependent speciation. *Systematic Biology* 64: 340–355.
- Rabosky, D. L., J. S. Mitchell, and J. Chang. 2017. Is BAMM flawed? Theoretical and practical concerns in the analysis of multi-rate diversification models. *Systematic Biology* 66: 477–498.
- Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications* 4: 1958.
- Ramírez-Barahona, S., J. Barrera-Redondo, and L. E. Eguiarte. 2016. Rates of ecological divergence and body size evolution are correlated with species diversification in scaly tree ferns. *Proceedings of the Royal Society, B, Biological Sciences* 283: 20161098.
- Ricklefs, R. E. 2007. Estimating diversification rates from phylogenetic information. *Trends in Ecology & Evolution* 22: 601–610.
- Rose, J. P., R. Kriebel, and K. J. Sytsma. 2016. Shape analysis of moss (Bryophyta) sporophytes: insights into land plant evolution. *American Journal of Botany* 103: 652–662.
- Rothfels, C. J., A. Larsson, L.-Y. Kuo, P. Korall, W.-L. Chiou, and K. M. Pryer. 2012. Overcoming deep roots, fast rates, and short internodes to resolve the ancient rapid radiation of eupolypod II ferns. *Systematic Biology* 61: 490–509.
- Royer, D. L., L. J. Hickey, and S. L. Wing. 2003. Ecological conservatism in the “living fossil” Ginkgo. *Paleobiology* 29: 84–104.
- Sánchez-Baracaldo, P. 2004. Phylogenetics and biogeography of the neotropical fern genera *Jamesonia* and *Eriosorus* (Pteridaceae). *American Journal of Botany* 91: 274–284.
- Sánchez-Baracaldo, P., and G. H. Thomas. 2014. Adaptation and convergent evolution within the *Jamesonia-Eriosorus* complex in high-elevation biodiverse Andean hotspots. *PLOS ONE* 9: e110618.
- Sato, A., H. Tichy, C. O’Hugin, P.R. Grant, B.R. Grant, and J. Klein. 2001. On the origin of Darwin’s finches. *Molecular Biology and Evolution* 18: 299–311.
- Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford, UK.
- Schneider, H., T. A. Ranker, S. J. Russell, R. Cranfill, J. M. O. Geiger, R. Aguraitua, K. R. Wood, et al. 2005. Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proceedings of the Royal Society, B, Biological Sciences* 272: 455–460.
- Schneider, H., E. Schuettelpelz, K. M. Pryer, R. Cranfill, S. Magallón, and R. Lupia. 2004a. Ferns diversified in the shadow of angiosperms. *Nature* 428: 553–557.
- Schneider, H., A. R. Smith, R. Cranfill, T. J. Hildebrand, C. H. Haufler, and T. A. Ranker. 2004b. Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molecular Phylogenetics and Evolution* 31: 1041–1063.
- Schuettelpelz, E., and K. M. Pryer. 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. *Proceedings of the National Academy of Sciences, USA* 106: 11200–11205.
- Schuettelpelz, E., H. Schneider, L. Huiet, M. D. Windham, and K. M. Pryer. 2007. A molecular phylogeny of the fern family Pteridaceae: assessing overall relationships and the affinities of previously unsampled genera. *Molecular Phylogenetics and Evolution* 44: 1172–1185.
- Seehausen, O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society, B, Biological Sciences* 273: 1987–1998.
- Sessa, E. B., W. L. Testo, and J. E. Watkins. 2016. On the widespread capacity for, and functional significance of, extreme inbreeding in ferns. *New Phytologist* 211: 1108–1119.
- Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010. Diversity versus disparity and the radiation of modern cetaceans. *Proceedings of the Royal Society, B, Biological Sciences* 277: 3097–3104.
- Soltis, D. E., E. V. Mavrodiev, J. J. Doyle, J. Rauscher, and P. S. Soltis. 2008. ITS and ETS sequence data and phylogeny reconstruction in allopolyploids and hybrids. *Systematic Botany* 33: 7–20.
- Soltis, D.E., M.C. Segovia-Salcedo, I. Jordon-Thaden, L. Majure, N.M. Miles, E.V. Mavrodiev, W. Mei, et al. 2014. Are polyploids really evolutionary dead-ends (again)? A critical reappraisal of Mayrose et al. (2011). *New Phytologist* 202: 1105–1117.
- Sundue, M. A., W. L. Testo, and T. A. Ranker. 2015. Morphological innovation, ecological opportunity, and the radiation of a major vascular epiphyte lineage. *Evolution* 69: 2482–2495.
- Tanaka, T., Y. Isaka, M. Hattori, and T. Sato. 2014. Ecological and phylogenetic approaches for diversification of apogamous ferns in Japan. *Plant Systematics and Evolution* 300: 2041–2050.
- Testo, W., and M. Sundue. 2014. Primary hemiepiphytism in *Colysis ampla* (Polypodiaceae) provides new insight into the evolution of growth habit in ferns. *International Journal of Plant Sciences* 175: 526–536.
- Testo, W., and M. Sundue. 2016. A 4000-species dataset provides new insight into the evolution of ferns. *Molecular Phylogenetics and Evolution* 105: 200–211.
- Testo, W. L., and J. E. Watkins. 2013. Understanding mechanisms of rarity in pteridophytes: competition and climate change threaten the rare fern *Asplenium scolopendrium* var. *americanum* (Aspleniaceae). *American Journal of Botany* 100: 2261–2270.
- Tryon, R. 1972. Endemic areas and geographic speciation in tropical American ferns. *Biotropica* 4: 121–131.
- Tuomisto, H. 2006. Edaphic niche differentiation among *Polybotrya* ferns in western Amazonia: implications for coexistence and speciation. *Ecography* 29: 273–284.
- Vasco, A., R. C. Moran, and B. A. Ambrose. 2013. The evolution, morphology, and development of fern leaves. *Frontiers in Plant Science* 4: 345.
- Wang, L., H. Schneider, X.-C. Zhang, and Q.-P. Xiang. 2012. The rise of the Himalaya enforced the diversification of SE Asian ferns by altering the monsoon regimes. *BMC Plant Biology* 12: 210.
- Watkins, J. E. Jr., and C. L. Cardelús. 2012. Ferns in an angiosperm world: Cretaceous radiation into the epiphytic niche and diversification on the forest floor. *International Journal of Plant Sciences* 173: 695–710.
- Watkins, J. E. Jr., C. Cardelús, R. K. Colwell, and R. C. Moran. 2006. Species richness and distribution of ferns along an elevational gradient in Costa Rica. *American Journal of Botany* 93: 73–83.

- Watkins, J. E., N. M. Holbrook, and M. A. Zwieniecki. 2010. Hydraulic properties of fern sporophytes: Consequences for ecological and evolutionary diversification. *American Journal of Botany* 97: 2007–2019.
- Watkins, J. E., M. C. Mack, T. R. Sinclair, and S. S. Mulkey. 2007. Ecological and evolutionary consequences of desiccation tolerance in tropical fern gametophytes. *New Phytologist* 176: 708–717.
- Wei, R., H. Schneider, and X.-C. Zhang. 2013. Toward a new circumscription of the twinsonus-fern genus *Diplazium* (Athriaceae): a molecular phylogeny with morphological implications and infrageneric taxonomy. *Taxon* 62: 441–457.
- Westoby, M., D. Falster, A. Moles, P. Veski, and I. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- Wilson, D. S. 1975. The adequacy of body size as a niche difference. *American Naturalist* 109: 769–784.
- Wood, T. E., N. Takebayashi, M. S. Barker, I. Mayrose, P. B. Greenspoon, and L. H. Rieseberg. 2009. The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences* 106: 13875–13879.