

Contrasting environmental and regional effects on global pteridophyte and seed plant diversity

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Pteridophytes (ferns and fern-allies) represent the second-largest group of vascular plants, but their global biogeography remains poorly studied. Given their functional biology, pteridophytes are expected to show a more pronounced relation to water availability and a higher dispersal ability compared to seed plants. We test these assertions and document the global pattern of pteridophyte richness across 195 mainland and 106 island regions. Using non-spatial and spatial simple and multiple regression models, we analyze geographic trends in pteridophyte and seed plant richness as well as pteridophyte proportions in relation to environmental and regional variables. We find that pteridophyte and seed plant richness are geographically strongly correlated (all floras: $r = 0.68$, mainland: $r = 0.82$, island floras: $r = 0.77$), but that the proportions of pteridophytes in vascular plant floras vary considerably (0–70%). Islands (mean = 15.3%) have significantly higher proportions of pteridophytes than mainland regions (mean = 3.6%). While the relative proportions of pteridophytes on islands show a positive relationship with geographic isolation, proportions in mainland floras increase most strongly along gradients of water availability. Pteridophyte richness peaks in humid tropical mountainous regions and is lowest in deserts, arctic regions, and on remote oceanic islands. Regions with Mediterranean climate, outstanding extra-tropical centres of seed plant richness, are comparatively poor in pteridophytes. Overall, water-energy variables and topographical complexity are core predictors of both mainland pteridophyte and seed plant richness. Significant residual richness across biogeographic regions points to an important role of idiosyncratic regional effects. Although the same variables emerge as core predictors of pteridophyte and seed plant richness, water availability is clearly a much stronger constraint of pteridophyte richness. We discuss the different limitations of gametophytes and sporophytes that might have limited the ability of pteridophytes to extensively diversify under harsh environmental conditions. Our results point to an important role of taxon-specific functional traits in defining global richness gradients.

The disproportionately higher species richness of some places compared to others is among the most prominent, yet unresolved questions in biogeography and ecology. An increase of species richness from the poles to the equator known as the latitudinal diversity gradient has been documented for a variety of different groups of organisms (reviewed in Hillebrand 2004), and a growing number of studies document strong associations between regional species numbers and different climatic and other environmental variables (among many others: Currie and Paquin 1987, O'Brien 1993, 1998, Kerr and Packer 1997, Jetz and Rahbek 2002, Hawkins et al. 2003, Kreft and Jetz 2007, Field et al. 2008). Contemporary climatic factors, particularly ambient energy and water availability may constrain the number of individuals and thereby species that can coexist in a region or may limit the number of species that

are able to tolerate specific local conditions or might have prevented many clades to adapt to colder and drier climates (Wright 1983, O'Brien 1993, 1998, Mittelbach et al. 2001, Jetz and Rahbek 2002, Hawkins et al. 2003, Currie et al. 2004, Wiens and Donoghue 2004). Second, variation in the degree of topographic heterogeneity and associated spatial variability in climate may cause differences in richness through local species turnover (Ricklefs 1987, Kerr and Packer 1997). Finally, climate and habitat heterogeneity may drive regional differences in speciation rates (Qian and Ricklefs 2000, Ricklefs 2004). Alternative hypotheses emphasize the importance of the idiosyncratic biogeographic history of regions caused, e.g. by plate tectonics, mountain uplift, glacial extinction, and post-glacial dispersal (Ricklefs 1987, 2004, Jansson 2003, Wiens and Donoghue 2004, Fine and Ree 2006, Hughes and

Eastwood 2006, Jansson and Davies 2008). An intrinsic complication for understanding the specific role of historical and present factors arises from the fact that many attributes of past and modern environments important for species richness are strongly collinear (Endler 1982). Although there is little doubt that contemporary environmental conditions constrain regional species richness (Hawkins et al. 2003, Currie and Francis 2004, Field et al. 2008), it has been shown that the species richness of various groups of organisms responds differently to these gradients (Currie 1991, Jetz et al. 2009, Kissling et al. 2009). This suggests that further insights into the ecological and evolutionary drivers of cross-taxon differences in richness might contribute towards a more mechanistic understanding of richness gradients. Here, we use the global pteridophyte flora as a model and compare it to seed plants in order to investigate how contemporary environment interacts with taxon-specific ecological and evolutionary constraints in shaping the global distribution of species richness.

With an estimated 13 000 species (Smith et al. 2006), pteridophytes (ferns and fern allies, a paraphyletic group including monilophytes and lycophytes) form the second largest group within the estimated ca 320 000 vascular plant species (Prance 2001) and are at the base of the phylogeny of vascular plants (Pryer et al. 2001). With an age of ca 400 million yr, pteridophytes are considerably older than flowering plants and dominated landscapes during the Carboniferous and Permian (Niklas et al. 1983). In contrast to the common notion of extant pteridophyte diversity being a remnant of a very old diversification (Niklas et al. 1983), recent studies into the molecular evolution and phylogeny of pteridophytes (reviewed in Pryer et al. 2004, Smith et al. 2006) have revealed that the extant diversity of pteridophytes is a product of a rather recent diversification that paralleled the rise of angiosperms, which now dominate global landscapes (Schneider et al. 2004a). This has challenged traditional perspectives on the evolution and biogeography for pteridophytes. According to Schneider et al. (2004a), two evolutionary scenarios are invoked to explain the secondary diversification in pteridophytes: first, the rise of the angiosperms in the Cretaceous might have created habitats with greater structural complexity and new “niche space” in which various clades of pteridophytes could have diversified. Alternatively, major changes in the global environment (tectonic uplifts, changes in climate and CO₂ concentration) could have triggered the diversification of ferns.

Recent regional to continental-scale studies have provided key insights into the biogeography of pteridophytes. Aldasoro et al. (2004) found strong relationships between pteridophyte richness and humidity as well as with the distance to proposed glacial rainforest refugia in Sub-Saharan Africa. These findings are congruent with a study of pteridophytes in Ugandan rainforests where additionally strong controls by soil properties were found (Lwanga et al. 1998). Strong controls of diversity and composition by soil properties and micro-topography have also been found in Amazonian pteridophyte communities (Tuomisto and Poulsen 1996, 2000, Tuomisto et al. 2003). A strong effect of water availability on pteridophyte richness has been also demonstrated for the Australian flora (Bickford and Laffan

2006). Additionally, important insights also come from tropical elevational gradients consistently demonstrating peaks of pteridophyte diversity in mid-elevation montane forests at ca 1800–2400 m a.s.l. (Kessler 2000, Kessler et al. 2001, Hemp 2002, Bhattarai et al. 2004a, Kluge et al. 2006). Common explanations for this consistent pattern are maximal levels of humidity or a favourable combination of high humidity and mild temperatures (Kessler et al. 2001, Bhattarai et al. 2004b), while others have attributed mid-elevation peaks in richness to geometric constraints on range locations (Watkins et al. 2006). Together these results point to a strong effect of water availability on the broad-scale geographic distribution of pteridophyte richness. However, these studies mainly investigate tropical or subtropical pteridophyte floras not accounting for the full global spectrum of ambient energy, water availability, or habitat heterogeneity (Kerr and Packer 1997, Hawkins et al. 2003, Krefl and Jetz 2007). However, the global distribution of pteridophyte diversity and its relationship with environmental and regional factors remains unquantified.

In this paper, we analyze the global distribution of pteridophyte richness and relate it to abiotic variables. Our analyses are based on a comprehensive global data set of the diversity of pteridophytes and seed plants in 301 regional floras worldwide. A simple expectation about the geographic variation in pteridophyte richness might be that diversity patterns of pteridophytes and seed plants are largely indistinguishable either resulting from similar ecological responses to climatic constraints or from the similar timing of the relevant portions of pteridophyte and seed plant clades. This would then predict a strong correlation between pteridophytes and seed plants, similar proportions of pteridophytes in all floras worldwide (13 000 pteridophyte spp./320 000 vascular plant spp. \approx 4.1%), and consequently similar relationships between richness and environment in both groups. Such relationships could also be expected (all other things being equal) under a simplistic scenario of deep-time “evolutionary niche conservatism” (Wiens and Donoghue 2004), as both pteridophytes and seed plants originated under tropical humid conditions and additional adaptations were necessary for the colonization of and diversification in drier and colder habitats. However, pteridophytes and seed plants (gymnosperms and angiosperms) show major differences in their morphology, ecophysiology, and reproductive biology (Page 2002). Unlike seed plants, pteridophytes have two independent, free-living life stages, the haploid gametophyte and the diploid sporophyte. The free-living gametophytes are fertilized by motile spermatozooids that need a water film for movement. Another major difference is that pteridophytes have small, wind-dispersed diaspores and are not dependent on animal vectors for pollination and seed dispersal (Tryon 1970, 1986). Animal pollination and dispersal, on the other hand, are considered key innovations for an explosive diversification within angiosperms (Willis and McElwain 2002). All these differences are likely to have an influence on how pteridophytes and seed plants have responded to opportunities of diversifying into habitats with more extreme climatic conditions. This makes pteridophytes and seed plants suitable model groups to explore potential influences of taxon-specific ecological and life-history differences on the distribution of species

richness. In this study, we ask the following questions: 1) how is pteridophyte diversity distributed at a global scale? 2) What are core abiotic correlates of this pattern? 3) How does the relative proportion of pteridophytes in vascular plant floras vary geographically and along environmental gradients? 4) Given their stronger dependence on water, are pteridophytes greater in proportional richness in humid environments? 5) Given their different dispersal strategies, what is the difference in relative richness on islands compared to mainland regions and along gradients of isolation?

Methods

Diversity data

Complementary to a database that was assembled to estimate global patterns of overall vascular plant diversity and analyze its correlates (Barthlott et al. 1996, 2005, Kier et al. 2005, Mutke and Barthlott 2005, Krefl and Jetz 2007, Krefl et al. 2008), we collected information on species numbers of pteridophytes and seed plants for 301 geographic regions worldwide (195 mainland and 106 island floras; compare Fig. 1). The primary source for species numbers was the Checklist of world ferns (Hassler and Swale 2001, 2004) which includes ferns (i.e. monilophytes) as well as lycophytes. Additionally, floras, checklists, and compilations of species richness accounts were exploited

(compare Supplementary material Table S3). The data set covers a broad spectrum of abiotic conditions (Fig. 1). The number of seed plant species was derived by subtracting the number of pteridophyte species from the total number of vascular plant species.

Abiotic data

Boundaries of all geographic regions were digitalized in a geographic information system, and AREA (km²) as well as latitude and longitude of the centroid were calculated for each geographic unit. We analyzed a number of potential abiotic determinants of pteridophyte and seed plant richness, which have been shown to be strong predictors of overall vascular plant richness (Francis and Currie 2003, Hawkins et al. 2003, Krefl and Jetz 2007, Field et al. 2008). As climatic variables, we analyzed variables associated with ambient heat: mean annual temperature (°C; TMP), and potential evapotranspiration (mm yr⁻¹; PET); water availability: mean annual precipitation (mm yr⁻¹; PRE), number of days per year with precipitation >0.1 mm (n; WET); and integrative variables of water-energy dynamics: actual evapotranspiration (mm yr⁻¹; AET), and water balance (mm yr⁻¹; WTB). Mean values of climatic variables for all investigated geographic regions were derived from a global high-resolution climatology at 10' resolution (New et al. 2002). AET, PET, and WTB data were

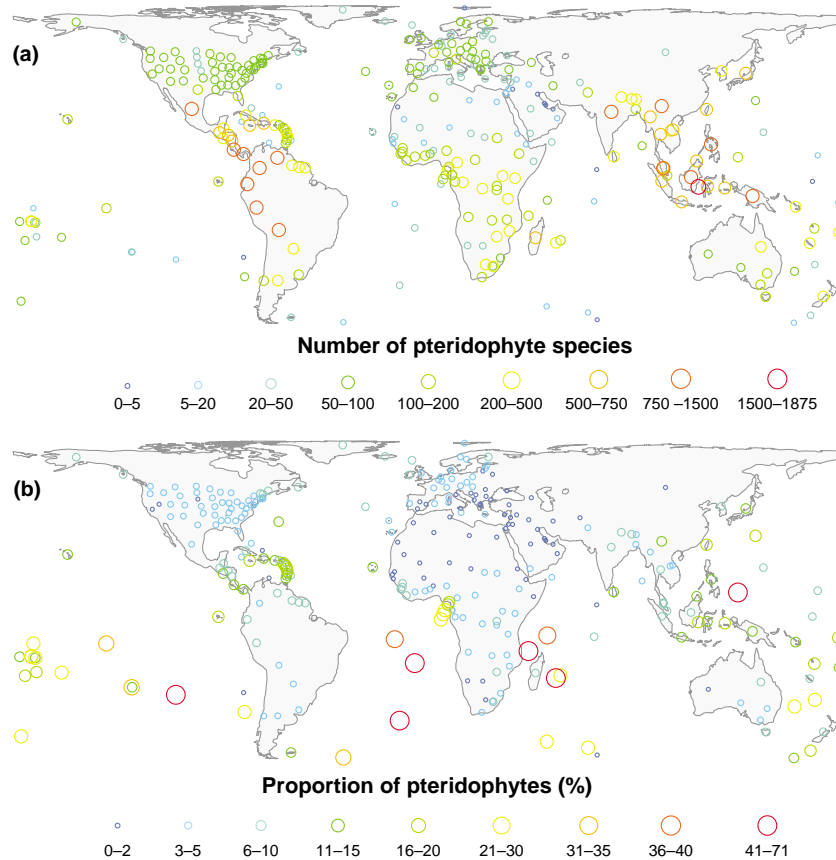


Figure 1. Spatial location of 301 floras analyzed in this study (195 mainland and 106 island floras). Circles represent mass centroids of each geographic unit. (a) Number of pteridophyte species per geographic unit, (b) relative proportion of pteridophytes in vascular plant floras.

obtained from a global database provided by UNEP-GRID at 0.5 degree resolution (Ahn and Tateishi 1994, Tateishi and Ahn 1996).

Two variables were investigated describing the heterogeneity of the landscape. First, as a proxy of ecosystem diversity (ECODIV), we counted the number of different ecosystems in each geographic unit from the GLC2000 global land cover data set at 30" resolution (European Commission Joint Research Centre 2002). Topographic diversity (TOPODIV) measured as elevational range (difference between maximum and minimum elevation) was derived from the GTOPO data set at a 30" resolution (USGS 1996). This measure encapsulates the diversity of landscapes within a region and additionally captures the potential for spatio-temporal climatic dynamics (Rahbek and Graves 2001, Jetz and Rahbek 2002). This measure is a strong correlate of overall vascular plant richness at broad geographic scales (Kreft and Jetz 2007). Each geographic region was further assigned to one major biome (Olson et al. 2001). The extraction of predictor variables across the boundaries of all geographic units was performed in ArcGIS/ArcINFO.

To account for potential regional effects and different biogeographic histories in our analyses, we investigated biogeographic realms (REALM) (compare Ricklefs et al. 2004, Kreft and Jetz 2007, Hortal et al. 2008, Qian 2008). Therefore, each geographic region was assigned to one of the following five biogeographic realms following the delineations of Olson et al. (2001): Afrotropics (AFT), Indo-Malaya (IND), Nearctic (NEA), Neotropics (NET), Palaearctic (PAA). Due to insufficient data points, Australia was not considered in this part of the analysis. Since most of the environmental variables were not available for small oceanic islands, we restricted these analyses to the mainland part of the data set. To test for a potential relationship between isolation and pteridophyte proportions, we calculated the Euclidean distance to the next continental land-mass for all islands assuming that continental floras are the main sources for island colonisations (Whittaker and Fernández-Palacios 2007). Dependent (species richness of pteridophyte and seed plants, pteridophyte proportions) and continuous independent variables were log₁₀-transformed for analysis to meet the assumption of normality of model residuals and to improve the linearity of models. Proportions are often analyzed using arcsine transformation (Sokal and Rohlf 1981), but in our data this did not improve the behaviour of model residuals and model fits.

Statistical analysis

We analyzed the association of pteridophyte and seed plant richness – both in absolute terms and as proportion of overall vascular plant richness – with environmental variables using single- and multi-predictor statistical models. Since the geographic units differed in size, regression analyses of species richness were performed including AREA as a covariate.

An inherent feature of macroecological data sets is the presence of spatial autocorrelation in the response variable (e.g. species richness), in predictor variables (e.g. climate, topography), and most importantly in model residuals

(Legendre 1993, Lennon 2000). Since spatial autocorrelation was present in our data, we confirmed our results from traditional Generalized Linear Models (GLMs) using Simultaneous Autoregressive models (SARs) of the “error-model” type which have been shown to represent a powerful statistical approach in dealing with spatial autocorrelation in macroecological data sets (Lichstein et al. 2002, Tognelli and Kelt 2004, Kreft and Jetz 2007, Kissling and Carl 2008). Since to date no theory-based selection procedure exists to choose among different SAR types in ecology, all three different types of SAR were evaluated (Lichstein et al. 2002, Kissling and Carl 2008). Model selection was based on model fit using Akaike information criterion (AIC) and on the reduction of spatial autocorrelation in model residuals (Kissling and Carl 2008). SARs of the “error model” type with a weighted neighbourhood structure and a lag-distance of 1500 km best accounted for the spatial structure in our data set. Spatial autocorrelation was evaluated using Moran’s I correlograms and global Moran’s I values. The goodness-of-fit of statistical models was assessed using AIC (Johnson and Omland 2004), a measure that evaluates the relative statistical support based on model fit and complexity. More complex models were given relatively more statistical support, if the ΔAIC was >2 . Additionally, we report r^2 -values, which for spatial models represent the non-spatial trend of the fitted model without including the spatial signal (Haining 1990). For SARs, these represent squared Pearson correlation coefficients between the non-spatial component of the SAR prediction and observed values. Statistical analyses were performed in R ver. 2.7 (R Development Core Team 2005) using the spdep library (Bivand 2006) for spatial analyses.

Results

Global distribution of pteridophyte richness

Pteridophytes occurred in almost all terrestrial habitats except for some parts of sandy deserts (most arid parts of the Arabian Peninsula), Antarctica, and some remote atolls (Fig. 1). Pteridophyte richness was highly unevenly distributed across the globe with a pronounced latitudinal gradient and peaked in tropical, humid regions containing complex topography (tropical Andes, Mesoamerica, Himalaya and south east Asia; Fig. 1b). Compared to other tropical regions, the African tropics showed only moderate levels of species richness. Lowest richness was encountered in hot and dry climates as well as in high arctic regions. There was also an apparent difference between the species richness of pteridophytes in mainland and island regions. Islands – and especially those of oceanic origin – were characterized by fewer pteridophyte species as compared to neighbouring mainland regions (Fig. 1b). Some large tropical land-bridge islands such as New Guinea, Borneo, and Sumatra, on the other hand, had very high species numbers and were among the globally most diverse regions in terms of pteridophyte richness.

Proportional richness of pteridophytes richness across islands, mainlands, and environments

In general, there was a strong positive relationship between pteridophyte richness and seed plant richness (all floras: $r=0.68$, mainland: $r=0.82$, island floras: $r=0.77$; all $p<0.001$; Fig. 2a, b). However, the relative proportions of pteridophytes varied considerably and ranged between 0 and 70% and differed strongly between mainland and islands floras (Fig. 1a, 2c). Islands had an average pteridophyte proportion of $15.3\% \pm 12.6$ (SD), whereas mainland regions had only $3.6\% \pm 2.5$ ($p \ll 0.001$; Mann-Whitney U test). On islands, the proportion of pteridophytes increased with geographic isolation ($r=0.41$, Fig. 2d).

The proportion of pteridophytes in mainland floras strongly co-varied with environmental gradients (Table 1, Fig. 3). Biome membership was a strong predictor of the relative proportion of pteridophytes and explained 53% of the variance (Table 1, compare Supplementary material Table S1 for SAR results, Fig. 3j). Highest proportions were found in montane biomes (mean = 8.0%) and tropical moist broad-leaf forests (mean = 6.8%), lowest proportions in arid biomes, like deserts (1.4%) and Mediterranean climate regions (2.1%) (Fig. 3j). The generally lower proportions of pteridophytes in more arid biomes was further evidenced by the strong positive relationship between pteridophyte proportion and variables representing water availability (Fig. 3, Table 1). Pteridophyte proportions were also significantly higher in regions with greater topographical complexity (Table 1, Fig. 3h). In a multi-predictor

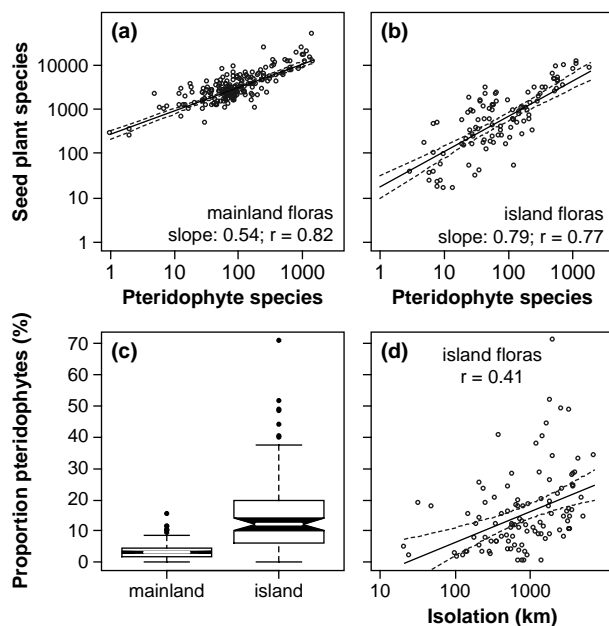


Figure 2. Relationship between the species richness of pteridophytes and seed plants of (a) mainland ($n=195$) and (b) island floras ($n=106$). (c) Box-and-whisker plots of pteridophyte proportions in mainland and island floras. Islands have significantly higher proportions ($p \ll 0.001$; Mann-Whitney U test). (d) Relationship between geographic isolation measured as distance to the nearest mainland (km) and proportions of pteridophytes in island floras. Linear fits with according correlation coefficients and 95%-confidence intervals are shown.

context, a model containing main effects of PET, PRE and TOPODIV had the highest relative support and together explained between 54 and 55% of the global variance in pteridophyte proportions in GLM and SAR, respectively (Table 2, Supplementary material Table S2).

Environmental predictors of mainland pteridophyte species richness

AREA had only a moderate effect on pteridophyte richness (Table 1). The slopes of the species–area relationship were very similar in both statistical approaches (GLM: 0.18 ± 0.05 , SAR: 0.17 ± 0.04) and comparable to previously reported values for plants (Rosenzweig 1995, Kier et al. 2005).

Both pteridophytes and seed plant richness patterns were strongly related to environmental conditions (Table 1). In pteridophytes, mean annual precipitation (PRE) was the strongest single-predictor (Table 1). Other terms representing water availability, single variables describing water-energy dynamics, or interaction terms between temperature and water-related variables also showed high or even slightly higher correlations with pteridophyte richness (Table 1). Variables representing only ambient energy either showed non-significant or minor effects on pteridophyte richness. Variables describing the heterogeneity of the landscape had significant positive yet weaker effects on pteridophyte richness (Table 1). High correlations were again observed with BIOME membership ($r^2=0.60$). REALM was a significant predictor of pteridophyte richness accounting for about half of the variance.

There were noteworthy differences in the effects of certain predictor variables or terms on the richness of pteridophytes and seed plants, respectively (Table 1). Most importantly, variables representing water availability and terms encapsulating both water and ambient energy had consistently stronger effects on pteridophyte than on seed plant richness. Terms representing ambient energy or heterogeneity in turn tended to be stronger predictors for seed plant richness. The effect of regional factors tended to be more pronounced in pteridophytes.

We continued to construct an ad-hoc statistical model of pteridophyte richness that incorporated AREA as a covariate. We then added terms from each of the categories ambient energy, water, and heterogeneity and tested all possible combination. In the context of a model including AREA and TOPODIV, the main effect terms of PET and WET were the strongest predictors of pteridophyte richness. Models of alternative combinations of the variables TEMP, PET, PRE, AET, or WTB, as well as models including interactions yielded lower statistical support. The resulting multi-predictor model including AREA, PET, WET, and TOPODIV accounted for 77% (GLM) and 78% (SAR) of the global variance in pteridophyte richness (Table 2, Supplementary material Table S2). Other variables as well as interaction terms failed to enter the model due to insufficient support based on AIC values.

After controlling for the above mentioned dissimilarities in area size and contemporary environmental conditions (Table 2), significant differences in residual species richness remained across the biogeographical realms (compare

Table 1. Single predictor non-spatial Generalized Linear Models (GLM) of pteridophyte proportions, pteridophyte species richness, and seed plant species richness for mainland floras. Pteridophyte proportions were $\log_{10}(x+1)$ -transformed. While there was no significant effect of AREA on pteridophyte proportions, richness models included AREA as a covariate to control for disparities in area size. Variable abbreviations: AREA – area size of the geographic unit in km^2 , TEMP – mean annual temperature, PET – potential evapotranspiration (mm yr^{-1}), PRE – mean annual precipitation (mm), WET – annual number of days with precipitation, AET – actual evapotranspiration (mm yr^{-1}), WTB – water balance (mm yr^{-1}), ECODIV – number of land cover classes (n), TOPODIV – elevational range (m), BIOME – biome membership, REALM – biogeographic realm. All continuous explanatory variables were \log_{10} -transformed.

Explanatory variables	Pteridophyte proportion			Pteridophyte richness			Seed plant richness		
	t	r^2	AIC	t	r^2	AIC	t	r^2	AIC
Null	–	–	–27	–	–	319	–	–	155
AREA	–1.61	0.01	–28	3.15	0.05	311	6.78	0.19	116
				Ambient energy					
TEMP	–1.39	0.01	–27	3.12	0.06	311	6.95	0.26	101
PET	0.15	0.00	–25	3.04	0.10	303	6.99	0.31	87
				Water					
PRE	14.22	0.52	–165	9.4	0.70	90	11.51	0.57	–3
WET	12.38	0.45	–139	7.73	0.54	175	9.83	0.43	53
				Water-energy					
AET	12.47	0.45	–140	7.72	0.66	116	10.91	0.57	–3
WTB	9.06	0.30	–94	5.88	0.36	236	8.71	0.34	79
TEMP \times PRE	–	0.53	–166	–	0.71	92	–	0.62	–22
TEMP \times WET	–	0.47	–144	–	0.67	115	–	0.67	–53
PET \times PRE	–	0.54	–172	–	0.72	83	–	0.64	–31
PET \times WET	–	0.49	–149	–	0.71	87	–	0.67	–50
				Heterogeneity					
TOPODIV	1.94	0.02	–29	0.37	0.20	281	3.45	0.38	68
ECODIV	0.52	0.00	–26	0.75	0.11	302	3.71	0.25	104
				Region					
BIOME	–	0.53	–147	–	0.60	170	–	0.61	2
REALM	–	0.42	–123	–	0.55	177	–	0.53	20

Fig. 4b). Including the variable REALM in the multi-predictor model of pteridophyte richness yielded considerably strong statistical support indicated by a sharp drop in AIC values (GLM: $\Delta\text{AIC} = 88$; SAR: $\Delta\text{AIC} = 82$) and explained an additional 8% of the variance. The Neotropical, Indomalayan, and Nearctic realm had significantly higher richness than expected from their current environment than Afrotropics and the Palaearctic realms (Fig. 4b, Tukey HSD test on ANOVA results).

Predicting global geographic trends

Model predictions across an equal area grid of ca $12\,000\text{ km}^2$ used the same environmental predictors and model coefficients obtained from the GLM. They illustrated the geographic interplay of the various predictors of pteridophyte proportions (Fig. 5a) and richness (Fig. 5b) as identified from the multivariate statistical modelling. Highest richness values were predicted for montane regions in the humid tropics: New Guinea, northern Andes, Borneo, or the Mesoamerican Isthmus. Lowest values were predicted for the most arid parts of deserts (Sahara, Arabian Peninsula, Thar Desert, and Taklamakan) as well as for high arctic tundra regions.

Discussion

The use of data derived from checklists and regional floras is not without problems, but given the lack of comprehensive

specimen data and range maps this represents the only source for global-scale macroecological analyses at present. One potential problem is that geographic units differ in size. While AREA had no significant effect on pteridophyte proportions, unsurprisingly AREA did have a significant effect on species numbers. However, this effect was comparatively weak for pteridophytes ($r^2 = 0.05$, GLM slope of the species–area relationship: 0.18), and moderate for seed plants ($r^2 = 0.19$, slope: 0.23). Environmental and regional variables, on the other hand, surfaced as much stronger predictors (Table 1). A second potential problem is that the global inventory of both pteridophyte and seed plant diversity is far from completed introducing the risk of biased results. It is reasonable to assume that there is a geographic trend in the completeness of floristic accounts. Temperate floras are most likely better documented than highly-diverse humid tropical ones. A more complete floristic inventory of the latter could even reinforce some of the relationships (namely the already strong correlations between richness and water-energy variables). On the other hand, we consider pteridophyte proportions to be rather robust towards incompleteness unless there is a severe geographic bias in the collection activity between pteridophytes compared to seed plants, with pteridophytes being systematically better collected in island floras, or relatively more under-collected in tropical regions. This said, we have no indication that this is actually the case. Inevitably, the data used stem from different time periods. The effect on our analyses is hard to evaluate, but an important impact would require differential effects on ferns

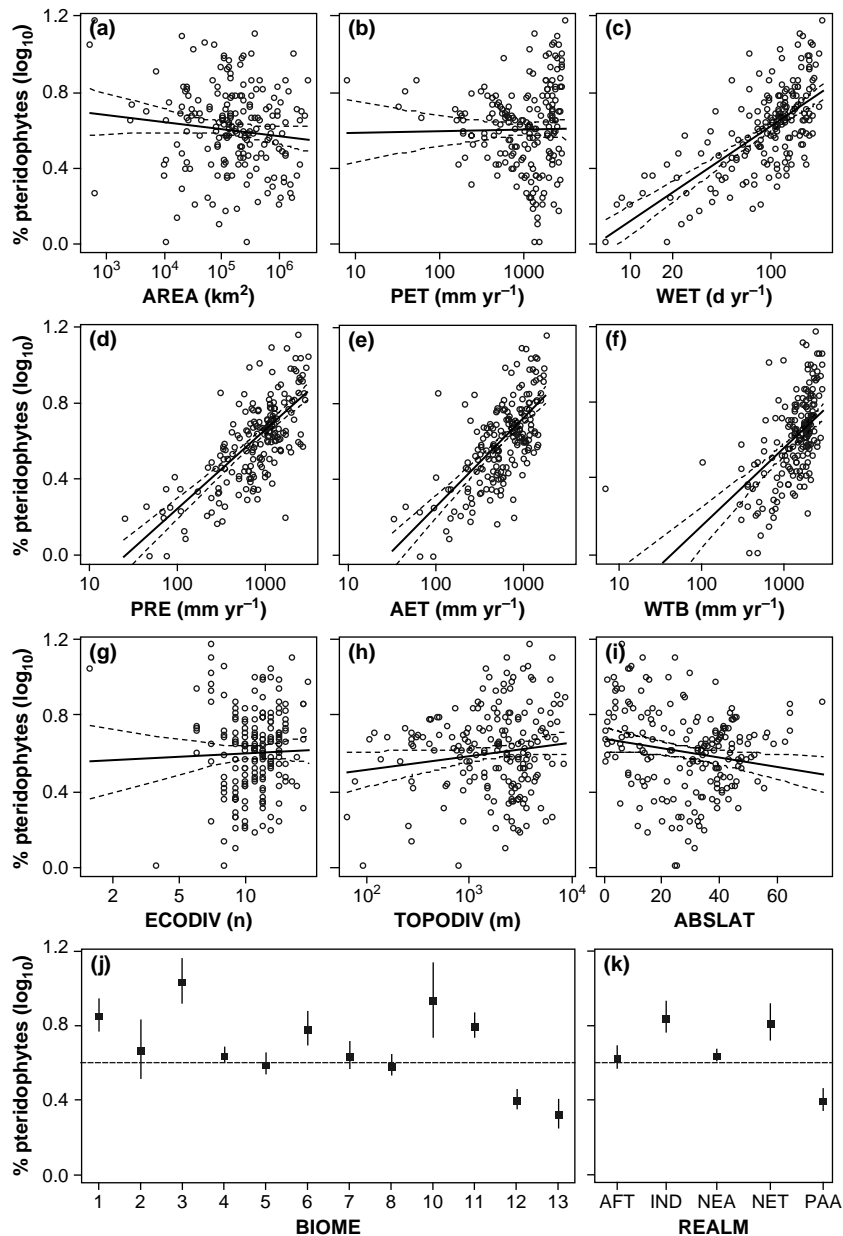


Figure 3. Single-predictor relationships between selected environmental variables and proportions of pteridophytes (y-axis; $\log_{10} x + 1$ -scale) for mainland floras. In (a) to (i) linear fits and 95%-confidence intervals are shown (a) AREA – area of the geographic unit (km^2), (b) PET – potential evapotranspiration (mm yr^{-1}), (c) WET – wet days per years (d yr^{-1}), (d) PRE – mean annual precipitation (mm yr^{-1}), (e) AET – actual evapotranspiration (mm yr^{-1}), (f) WTB – water balance (mm yr^{-1} ; $x + 1600$), (g) ECODIV – number of different ecosystems, (h) TOPODIV – maximum elevational range (m), (i) ABSLAT – absolute geographic latitude, (j) BIOME: 1 – tropical and subtropical moist broadleaf forests, 2 – tropical and subtropical dry broadleaf forests, 3 – tropical and subtropical coniferous forests, 4 – temperate broadleaf and mixed forests, 5 – temperate coniferous forests, 6 – boreal forests/taiga, 7 – tropical and subtropical grasslands, savannas, and shrublands, 8 – temperate grasslands, savannas, and shrublands, 9 – montane grasslands and shrublands, 10 – tundra, 11 – Mediterranean forests, woodlands and scrub, 12 – deserts and xeric shrublands. (k) REALM – biogeographic realms: AFT – Afrotropic, IND – Indomalaya, NEA – Nearctic, NET – Neotropic, PAA – Palearctic. Hatched lines in (j) and (k) mark the global mean.

and seed plants. To assess the completeness and whether there are differences between pteridophytes and seed plants, one could investigate the rates at which new species are added to checklists for available time-series of floristic accounts for the same region or based on specimen data. We consider this beyond the scope of our study and thus hypothesize that the data adequately reflect our current knowledge on diversity patterns in both groups.

At first glance, pteridophyte and seed plant richness show very similar geographic patterns. Pteridophytes exhibit a pronounced latitudinal diversity gradient with pteridophyte richness peaking in equatorial regions (Fig. 1a, 3f, 5b) – a pattern that is well supported for the majority of plant and animal groups (Humboldt 1808, Pianka 1966, Rohde 1992, Rosenzweig 1995, Hillebrand 2004, Mittelbach et al. 2007). Furthermore, pteridophyte richness varies

Table 2. Non-spatial Generalized Linear Models (GLM) multi-predictor environmental model of pteridophyte proportions and pteridophyte richness [$\log_{10}(x+1)$ transformed]. For variable descriptions and transformations, see Table 1 and Methods. The Akaike information criterion (AIC) for the null model containing only the intercept is -27 and 319 , respectively.

Explanatory variables	Pteridophyte proportions		Pteridophyte richness	
	Slope	t	Slope	t
(Intercept)	(-0.49)	-2.71^{**}	(-6.19)	-15.89^{***}
AREA	–	–	0.20	6.23^{***}
PET	-0.12	-2.12^*	1.02	10.42^{***}
PRE	0.42	14.69^{***}	–	–
WET	–	–	1.42	21.18^{***}
TOPODIV	0.07	2.92^{**}	0.34	7.51^{***}
AIC	-172		43	
Model r^2	0.54		0.77	
Moran's I	0.24		0.24	

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

systematically along gradients of climate and topography. Notably, the combination of PET and WET, which has been previously shown to be the strongest set of predictors for overall vascular plant richness in a previous study on a similar data set (Kreft and Jetz 2007), also emerged as the best variable combination to describe the water-energy-richness relationship for pteridophytes (Table 2). This is not surprising, since the availability of ambient heat and water represent ecophysiological constraints to plant life in general (O'Brien 2006) and is thus expected to affect both groups. Additionally, topographic heterogeneity facilitates the species richness of pteridophytes. These relationships and their geographic interplay are captured in the global richness predictions derived from the environmental model (Fig. 5b). Similar to vascular plants in general (Barthlott et al. 2005, Mutke and Barthlott 2005), centres of pteridophyte diversity are especially concentrated in tropical montane regions. Notably, the tropical Andes or the Indomalayan region – known centres for flowering plants (Barthlott et al. 2005, Mutke and Barthlott 2005) – also exhibit highest pteridophyte species numbers (Fig. 1a).

High correlations between species richness and contemporary environment, as found in the present study, have been interpreted as leaving little room for historical explanations (Francis and Currie 2003). However, this view disregards that climate history and thus rates of speciation,

extinction, and dispersal are broadly collinear with contemporary conditions (Endler 1982). This fact makes it extraordinarily difficult to disentangle the specific roles of past and modern conditions on global diversity gradients (Ricklefs 2004). The significant differences in residual richness across biogeographic regions (Fig. 4) demonstrate that an interpretation that is purely based on contemporary environmental determinism is not tenable. For instance, it has been long recognized that the Afrotropics are noticeably poor in pteridophyte species (Tryon 1986). Such cross-realm differences in pteridophyte diversity above and beyond contemporary climate are supported by our results. One plausible explanation for the lower diversity of the African pteridophyte flora might be that it has suffered disproportionately from extinctions during Pleistocene dry periods (Richards 1973, Tryon 1986), an interpretation that is congruent with the results from Aldasoro et al. (2004) who found pteridophyte richness to be higher in closer proximity to Pleistocene rainforest refugia. On a much longer time scale, African rainforests have also suffered greater area losses than the Neotropical or Indomalayan rainforests during the last 55 million yr which might have resulted in overall reduced possibilities for diversification and increased extinction rates (Fine and Ree 2006). Additionally, the smaller extent of humid tropical mountain systems in Africa might have resulted in lower speciation rates. Such historical processes are likely to have left prominent traces in the current distributions of pteridophytes and are important for a unified understanding and interpretation of their diversity patterns.

Comparison of our environment-based spatial prediction of pteridophyte richness (Fig. 5b) with expert-drawn (Barthlott et al. 2005) or modelled world maps of vascular plant richness (Kreft and Jetz 2007) revealed important differences between these two plant groups, despite the obvious similarities in their richness gradients. Notably, there was a much steeper increase of species densities of pteridophytes towards the equator compared to overall vascular plant and seed plant richness. In addition, looking at the proportions of pteridophytes in vascular plant floras, two pronounced trends surfaced: 1) compared to seed plants, pteridophytes are more diverse in tropical humid and mountainous regions and less diverse in arid regions and deserts (Fig. 3). 2) Pteridophytes are comparatively over-represented on islands (Fig. 2c). In the following, we

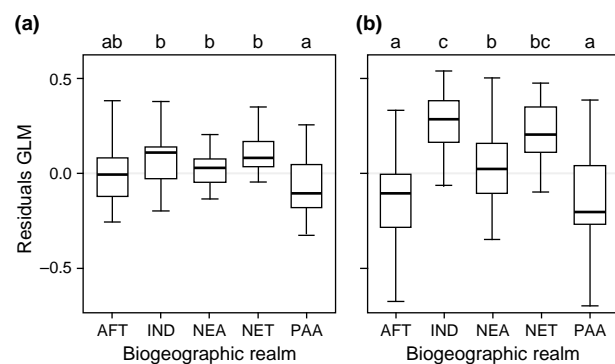


Figure 4. Box-and-whisker plots of the residual variation across biogeographic realms of (a) proportions of pteridophytes and (b) pteridophyte species richness after accounting for differences in contemporary environment (GLM models in Table 2). Characters indicate results from Tukey HSD tests on ANOVA results.

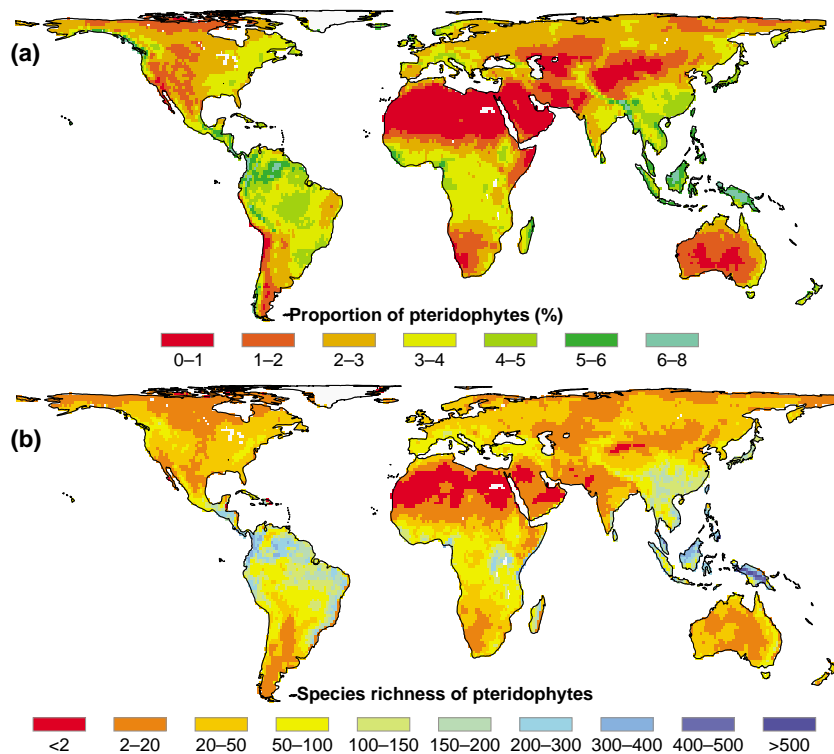


Figure 5. Environment-based spatial prediction of (a) proportions of pteridophytes (%) and (b) pteridophyte species richness. Predictions were derived from the multivariate GLM across an equal-area grid of ca 12 000 km² using the same environmental predictor variables and model parameters as in Table 2.

discuss why pteridophytes may have been less successful than seed plants in diversifying under arid conditions or more successful under tropical humid conditions and what makes pteridophytes so successful on islands compared to seed plants.

The strong positive correlations between pteridophyte proportions and variables of water availability (Fig. 3, Table 1, 2) suggest that intrinsic traits related to water availability might disproportionately limit the ability of pteridophytes to persist or undergo extensive diversifications under arid conditions. Importantly, pteridophytes are not completely absent from most arid habitats; and some pteridophyte clades have independently evolved remarkable drought adaptations (Kessler and Siorak 2007). The range of drought adaptations includes desiccation tolerance, xeromorphism, dense pubescence, curling and shedding of leaves, dormancy, shortened gametophytic phase, or geophytic life style (Kornaś 1977, Nobel 1978, Given 1993). On the other hand, certain morphological and life-history strategies to cope with arid conditions common in flowering plants such as pronounced succulence, deep-rooted perennials, and annual life style are largely absent in pteridophytes. Additionally, most pteridophytes show only poorly controlled evaporative potential throughout most of their life-cycle thereby depending on soil-water availability and high air humidity (Page 2002). In arid environments, this often restricts pteridophytes to the most mesic microsites such as rocky crevices or below rock outcroppings (Nobel 1978). It has been frequently argued that the independent gametophyte stage of pteridophytes is also a disadvantageous trait in arid environments (Page 2002). Unlike seed plants, pteridophytes are not independent of

liquid water for fertilization, but require a water film for sexual fertilization by the free-swimming spermatozoids. Therefore, parallels to the amphibian life-cycle have been drawn (“return to the water to breed”; Page 1985, 2002). Consequently, pteridophytes are restricted to habitats where such conditions frequently occur or require special adaptations to tune the timing of spermatozoid release to periods of the year when conditions are favourable. Furthermore, the ecological potential of the gametophyte itself might be limited. The small gametophyte lacks vascular tissue, produces rhizoids instead of true roots, has poorly developed or non-existent cuticles, and little ability for internal water storage (Raghavan 1989). On the other hand, it has recently been shown that gametophytes of some species are remarkably desiccation-tolerant (Watkins et al. 2007), but how this generalizes across all extant pteridophytes is yet unknown.

Mediterranean climate regions (hot and arid summers, cool and humid winters) are well known extra-tropical centres of plant diversity (Cowling et al. 1996) and have a much higher plant diversity than expected from their latitudinal position or contemporary climate (Kreft and Jetz 2007). These same regions, however, are not outstanding diversity centres for pteridophytes (Fig. 3j). In addition to the constraints of harsh summer aridity, factors such as co-evolutionary processes between flowering plants and animal pollinators and seed dispersers discussed as potential drivers of the high Mediterranean flowering plant diversity (Cowling et al. 1996, Linder 2003) do not exist in pteridophytes.

Despite the environmental constraints in arid regions, the question why pteridophytes are disproportionately more

diverse in tropical regions is equally important. A main driver of the extraordinarily high species richness in tropical montane habitats is undoubtedly the pronounced tendency of pteridophytes towards an epiphytic life style (Benzing 1990). Approximately 20% of all pteridophyte species are epiphytes, twice as many as found in seed plants (Schuettelpelz and Pryer 2009). In some species-rich families like Hymenophyllaceae, Aspleniaceae, or Polypodiaceae the proportion of epiphytic species even ranges between 59 and 93% (Madison 1977, Kress 1986, Gentry and Dodson 1987). Tropical montane forests in turn are known as globally outstanding centres of epiphyte diversity (Gentry and Dodson 1987, Kreft et al. 2004, Küper et al. 2004). Furthermore, the bulge in epiphyte diversity in mid-elevation cloud forests has been primarily attributed to the high humidity and absence of temperature constraints, which both facilitate the richness of an epiphytic life style (Gentry and Dodson 1987). Epiphytic habit as an independently evolved key innovation has triggered an explosive radiation in many tropical fern clades (Schneider et al. 2004b, Schuettelpelz and Pryer 2009). Adaptive features for their great success as epiphytes include: 1) small, wind-dispersed diaspores, 2) independence from pollinators, 3) tendency of poikilohydry, 4) occurrence of xeric leaves, thick cuticles, succulent rhizomes, leaf scales and absorbing foliar trichomes, and 5) shade tolerance (Benzing 1987). The shift to more complexly structured canopies in angiosperm-dominated forests might have additionally triggered epiphytic pteridophyte diversification by niche differentiation (Schneider et al. 2004b). Additionally, many terrestrial pteridophyte species are low-light specialists (Page 2002). In combination with their tendency towards pronounced edaphic specialization (Tuomisto and Poulsen 1996, Tuomisto 2006), this might have led to extensive diversifications in dark habitats such as the forest floor of tropical montane and lowland forests leading to relatively lower competition for light and space with more light-demanding seed plant species.

Another striking difference between pteridophytes and seed plants emerges from the comparison of pteridophyte proportions in island and mainland floras. Island floras are generally characterized by lower species numbers than comparable mainland areas (Kreft et al. 2008) and this trend is also apparent for pteridophytes (Fig. 1a). The proportion of pteridophytes, however, is significantly higher on islands (Fig. 1b) and there is a globally positive relationship between the geographic isolation and pteridophyte proportions (Fig. 2d). This points to a greater colonization success in pteridophytes; and at least two life-history traits might explain this relationship: first, pteridophytes produce large numbers of small, airborne diaspores (20–60 µm; Tryon 1970) and are thus likely to have greater colonization rates than seed plants. It has been demonstrated that recurrent colonization events in pteridophytes are possible even over very long distances (Wagner 1995). Second, their independence of animal vectors for pollination and seed dispersal might provide pteridophytes a greater chance for establishing viable populations on newly colonized islands. Furthermore, it has been shown that speciation rates are generally higher for seed plants than for pteridophytes (Tryon 1970, Smith 1972). The higher diversification rates of seed plants in turn lead to a decrease

in pteridophyte proportions on islands and might thus partly compensate for the higher colonization rates of pteridophytes. The well-investigated vascular plant flora of New Zealand offers additional insights (McGlone et al. 2001). Here, pteridophytes and orchids, both characterized by dust-like diaspores but the latter depending on animal pollinators, are well-represented (McGlone et al. 2001). However, both groups have a significantly lower tendency towards endemism compared to other vascular plants (McGlone et al. 2001). This may suggest that there is a significant gene flow between island and mainland populations in some pteridophyte and orchid species. Relatively frequent long-distance dispersal events might thus be more important in the assembly of insular pteridophyte and orchid floras than animal interactions.

In summary, our results provide evidence that taxon-specific functional ecological and evolutionary constraints are reflected in the current distribution of species richness at broad geographic scales. Although similar environmental factors control the diversity patterns of pteridophytes and seed plants, our results suggest an important role for taxon-specific ecological and evolutionary limitations and advantages in defining global richness gradients.

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