Patterns of North American Fern and Lycophyte Richness at Three Taxonomic Levels

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ABSTRACT.—North American monilophyte (fern) and lycophyte richness patterns are examined at three taxonomic levels (species, genus, and family). We determine: (1) if fern richness patterns are associated with water and energy variables that are predicted by the productivity-diversity hypothesis and (2) whether the pattern or strength of the relationship varies with taxonomic level. We present species richness maps for individual families of ferns and lycophytes allowing us to identify taxa with unique distributional patterns and taxa with patterns comparable to ferns in general. To accomplish these goals, we use data from the Flora of North America project for continental North America north of Mexico plus Greenland. We construct 479 GIS fern species range maps and tabulate fern and lycophyte richness in a gridded map with 2500 km² squares. We perform regressions of fern richness on water and energy climate variables (with squares as data points) in order to identify which variables most influence fern richness. We find that fern richness correlates with water and energy variables in ways consistent with the productivity-diversity hypothesis. A multiple regression model that includes mean annual temperature (MAT) and annual rainfall (RAN) explains 78.1% of the variation in fern family richness. The relationship between fern family richness and climate is stronger than the relationship between fern species richness and climate.

KEY WORDS.—fern, lycophyte, GIS, richness, taxonomic richness, North America, productivity-diversity hypothesis

Scientists have long been aware of latitudinal richness patterns, where richness tends to decrease from low to high latitudes in a wide array of organisms (Wallace, 1878). Plants are believed to play a central role in governing broad latitudinal gradients in species richness (Kreft and Jetz, 2007; Kier et al., 2005; and references therein) because they constitute the primary trophic level and their physiological requirements are proximally affected by environmental factors related to climate, primarily water and energy availability (Currie and Paquin, 1987; Field et al., 2005; O’Brien, 1993; O’Brien, 2006). The important effect of climatic variables on richness is supported by recently developed empirical climate models in which factors related to water and energy availability are highly successful in predicting woody plant species richness (Field et al., 2005).

A number of similar hypotheses for plant latitudinal diversity gradients hold that gradients in productivity drive gradients in diversity, where higher productivity leads to greater diversity (Field et al., 2009; Hawkins et al., 2003),

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which we refer to as the productivity-diversity hypothesis. In this study we examine the relationship between climate and monilophyte (fern) richness at three taxonomic levels, in order to test the productivity-diversity hypothesis. We use the Smith et al., (2006) fern taxonomic classification system. First, we test a number of regression models that employ linear combinations of simple climate variables to determine whether these variables predict fern richness. We also test whether one particular richness-climate model, the interim general model I (IGM I), accurately predicts fern richness. We employ the IGM I because it successfully predicts richness gradients in other plant groups and it has a plausible theoretical basis (O’Brien, 2006).

A theoretical basis for linking the generation of plant diversity with climate factors is provided in water-energy dynamics theory (WED; O’Brien, 1998; O’Brien, 2006), which can be included among productivity-diversity hypotheses. WED states that plant biological activity is related to liquid water and energy availability, which foster higher productivity, and finally lead to greater biological richness. Climate factors associated with greater plant productivity also lead to greater rates of molecular evolution (see Rohde, 1992; Wright et al., 2003; Wright et al., 2006) or greater amounts of biological activity in general (generation time, faster growth, more individuals). Higher rates of molecular evolution lead to more population divergence (Martin and McKay, 2004), which eventually leads to greater numbers of species. The WED hypothesis is related to the evolutionary rates hypothesis (ERH) which predicts that diversity will be associated with conditions that cause higher rates of molecular evolution (Evans and Gaston, 2005). For plants, regions with higher (or optimal) temperatures and more liquid water are likely to be associated with higher rates of molecular evolution and higher rates of productivity.

The interim general model (IGM I) is a climate model designed to predict plant richness based on the principles of WED theory (Field et al., 2005) taking the following form:

\[
\text{Richness} = \beta_1 \text{RAN} + \beta_2 \text{PETmin} - \beta_3 \text{PETmin}^2 + \beta_0
\]

Where PETmin is the minimum monthly potential evapotranspiration and RAN is annual rainfall. Before each term are empirically fitted coefficients. Rainfall is included to reflect that plants require the liquid form of water. PET (potential evapotranspiration) is an index of energy; its relationship with richness is expected to be nonlinear. WED predicts greatest richness where water and energy climate conditions are most favorable for plant productivity and biological activity, while the IGM provides a hypothesis for, and quantification of, what these conditions would be.

For many organisms, species richness correlates with water and energy variables in a similar way as taxonomic richness at higher levels. We know of no reason a priori why ferns would be unusual in this regard. Family richness, additionally, may serve as a proxy of species richness patterns (Balmford et al., 1996; Francis and Currie, 2003; Gaston and Blackburn, 1995; Qian and
Ricklefs, 2004) if for some reason doubt is placed on the completeness of species level data. To test whether richness-climate relationships are similar across taxonomic levels, all climate models are examined with respect to species, genus and family richness.

Ferns and lycophytes.—As separate clades of vascular plants, ferns and lycophytes may be compared to seed plants to assess the generality of richness patterns and richness-climate relationships. Ferns and lycophytes share with other plants the same basic requirements of water, light, and nutrients that have been shown to be key factors in determining plant species distribution (Hengeveld, 1990; Holdridge, 1947; O’Brien, 1998; Salisbury, 1926; Woodward, 1987) and, thus, we expect them to have similar richness-climate relationships as other plant groups. However, ferns and lycophytes differ from other plants in key morphological and life-history traits. First, ferns and lycophytes have a unique life cycle that includes external fertilization during the gametophytic stage, requiring environmental liquid water (Raven et al., 1992). This reliance on external water during reproduction may impose limitations on the geographic distribution of fern species and gradients in species richness (Given, 1993; and references therein), although the existence of xeric adapted ferns demonstrates that this limitation is surmountable. Ferns have evolved a variety of aridity adaptations (Hietz, 2010; Kessler and Siorak, 2007). However, a recent analysis of global pteridophyte (ferns and lycophytes) richness patterns by Kreft et al. (2010) found that, relative to seed plants, fern and lycophyte richness more strongly correlates with liquid water regimes. Fern and lycophyte richness dropped more rapidly than seed plant richness when moving toward drier climates.

Second, fern and lycophyte spores are readily dispersed over extremely long distances; thus their distributions are less likely to be limited by dispersal barriers and more likely to be limited by the ability to adapt and persist under climates outside their current range (Barrington, 1993). Fern and lycophyte species distribution could be expected to match the climatic conditions that allow a species to become established and persist, or at least more so than other groups. In examining fern and lycophyte distribution the effect of dispersal on distributional patterns can be evaluated by comparison with groups with more constrained dispersal (Barrington, 1993). In addition, fern richness patterns have been studied on several continents allowing us to compare our results to other regions of the world. Fern richness patterns (or pteridophyte richness patterns) have been studied at regional scales in Northeast Iberia (Pausas and Saez, 2000), Japan (Guo et al., 2003) and Argentina (Ponce et al., 2002); along elevational gradients (Bhattarai et al., 2004; Hemp, 2002; Watkins et al., 2006), and at continental scales including Africa (Aldasoro et al., 2004), Australia (Bickford and Laffan, 2006) and Europe (Birks, 1976). Kreft et al. (2010) analyzed patterns of global pteridophyte diversity.

The primary objective of this study is to characterize the geography of North American fern and lycophyte richness (north of Mexico). The second goal is to explore potential climatic controls of observed richness patterns. Ferns and
Lycophytes are mapped and analyzed separately and most analyses apply to ferns. In order to accomplish these goals we map geographical patterns of fern richness at family, genus, and species levels and compare these patterns to the patterns found in other groups of organisms. Second, we examine the relationships between richness and climate variables that are known to be related to plant productivity (Table 1; Stephenson, 1998) at the three taxonomic levels. Among the regression models tested is the interim general model I (IGM I; Field et al., 2005; here fitted with coefficients matched to fern richness). Third, we map and compare the species richness patterns of individual fern and lycophyte families. We identify taxa with unusual distributional patterns and taxa with patterns comparable to ferns in general.

**Materials and Methods**

**Study system.**—The North American ferns and lycophytes are two divisions of vascular plants. Ferns and lycophytes together (pteridophytes) are a paraphyletic grouping, but each taxon alone is monophyletic (Pryer et al., 2004). The majority of species in this study are ferns (387 out of 479). Fern and lycophyte distribution data for this study derive from the Flora of North America Vol. 2 (FNA editorial committee, 1993). We used the more recent Smith et al., (2006) fern taxonomic classification system for reported analyses and maps instead of the FNA taxonomic classification system. Results are similar regardless which taxonomic system is chosen. The study region contains 23 families, 67 genera, and 387 species of ferns and 3 families, 9 genera, and 92 species of lycophytes. We treat the eighty-five hybrids, varieties, and subspecies as species in the same manner as Tryon (1972). The use of sub-specific designations in ferns allow pteridologists to provide information about their beliefs with respect to the amount of divergence between populations - certain populations can be designated as subspecies or varieties - putatively in different stages of divergence, which would otherwise
be considered separate species by some taxonomists (Tryon, 1969). It is common for fern taxonomists to use subspecific designations to distinguish similar but distinct non-intergrading taxa (Hickey et al., 1989; Yatskievych and Moran, 1989). Regardless, many of these types are geographical subspecies and so the species would not be counted twice in any one location. Richness patterns are largely unchanged when hybrids are excluded and subspecies or varieties are considered as single species.

Range maps.—We used published non-GIS fern range maps from the Flora of North America North of Mexico Vol. 2, Pteridophytes and Gymnosperms (FNA editorial committee, 1993) to produce geo-referenced range map polygons for GIS analysis. Image files were obtained online at http://www.fna.org/. The image files were used as a template on which to produce 479 polygon shape files in the ArcView 9.1 GIS software (Esri, 2005). The non-GIS range maps were produced by the author of each taxon treatment in the Flora by hand drawing shaded regions from herbarium records (see Flora of North America volume 2).

Richness maps.—All analyses were performed on a North American Lambert conformal conic projection with standard parallels at 20° and 60° latitude and the central meridian at 96°W. A polygon shapefile layer with a grid of 50 km × 50 km (2,500 km²) was created over North America using Hawth’s Analysis Tools for ArcGIS (Beyer, 2004) and used as a base-map. All maps were generated with this grid with a total of 8,760 squares. Regression analyses were applied to a sub-sample of this grid, 88 squares, in order to account for the effect of spatial autocorrelation on the regression results (described below). The Lambert conformal conic projection has low areal distortion in our region of analysis (Bolstad, 2005) and is not expected to affect the results.

Richness in each grid square was determined by summing the number of species range map polygons that overlapped each grid square. This was accomplished using Hawth’s tools polygon in polygon analysis (Beyer, 2004). The number of families and genera occurring in each grid square was tabulated similarly.

Climate variables and regression models.—The climate variables tested and their sources are listed in Table 1. Worldclim variables represent climate normals for the period 1950–2000 (Hijmans et al., 2005), while actual evapotranspiration (AET) and potential evapotranspiration (PET) are the normals from 1931–1960 (Leemans and Cramer, 1991). Annual Rainfall (RAN) is calculated as the sum of precipitation of months with a mean temperature greater than zero degrees Celsius. Worldclim climate maps were 2.5 minute resolution. Maps of climate variables were converted to vector point maps when necessary and summarized in each 2,500 km² grid square using a spatial join in Arcview 9.1 (Esri, 2005); the average value of the points in the climate layer in each grid square was then determined. Ordinary least-squares (OLS) regressions were performed between richness variables and climate variables with 2,500 km² grid squares forming the sample points. Regressions also were performed on an 88 square sub-sample of the total set of 8,760 squares to assess
spatial autocorrelation issues. Regression analyses were performed with the R statistical package (R core development team, 2009).

We present the univariate regressions between each richness level and each climate variable (Table 1) with the highest R-squared values (Table 2). We also perform and present several multiple regressions (Table 2). We performed two, two-variable multiple regressions with the first regression using mean annual temperature (MAT) and AET and the second using MAT and RAN. Finally, we test the interim general model I (IGM I) on our fern richness data (equation above). The models presented in table 2 correspond closely with the best performing models based on Mallow’s CP (Mallow, 1973) and a best subsets regression, performed using variables from Table 1. AIC values for each regression model are provided. We report adjusted R-squared values throughout.

Biogeographical patterns are frequently explored with summary statistics without considering geographical pattern (Ruggiero and Hawkins, 2006). Here we present and discuss maps and explicitly evaluate model performances with respect to geography. Mapping residuals of richness-climate regression models allows us to identify specific regions and taxa responsible for model shortcomings, potentially identifying causal factors through spatial association.

Spatial autocorrelation.—In a spatial regression, if residuals are spatially autocorrelated this can potentially mean that the effective sample size is lower than the actual sample size (Fortin and Dale, 2005). As a result, we assess the impacts of spatial autocorrelation by calculating the effective sample size of our data set. Then we use a subsample of grid squares from our full data set (that is even smaller than the effective sample size) to evaluate the robustness of our results.

Equation 5.17 from Fortin and Dale, (2005) allows one to find the effective sample size of a spatial data set for a given spatial autocorrelation ρ between adjacent grid squares:

\[ n' \approx \frac{n(1-\rho)}{1+\rho} = n\Theta \]

Where n is the sample size, n’ is the effective sample size, and Θ is the approximate correction factor \( \Theta = (1-\rho)/(1+\rho) \). To find the effective sample size of our data set, we first calculated the autocorrelation coefficient ρ between the regression residuals of adjacent squares in a regression using all 8,760 squares. We used residuals from the regression model with fern family richness as a response and MAT, RAN, and Bio15 (precipitation seasonality) as predictors, mapped in Fig. 1D. For this model \( \rho = 0.8946 \) between adjacent squares. Plugging this value into equation 5.17 from Fortin and Dale (2005) yields an effective sample size \( n' = 487 \). We conservatively selected only 88 grid squares from our map using a hexagonal sampling grid with points spaced \( \sim 500 \) km apart (which is equivalent to a \( \rho = 0.98 \)). Using this conservative subsample, we perform standard OLS regressions in the same fashion as the 8,760 grid values. Equation coefficients and R-squared values were very similar whether we used the subsample, or the full dataset.
Table 2. Richness-climate regressions. Listed are seven models, three univariate, and four multiple regressions – one of which is the interim general model (IGM I). Each model was tested with species, genus, and family richness as response variables. R-squared, model AIC, and regression equation coefficients are listed for each model for each response variable.

<table>
<thead>
<tr>
<th>Model</th>
<th>Resp.</th>
<th>adj. R²</th>
<th>MAT</th>
<th>AET</th>
<th>RAN</th>
<th>PETmin</th>
<th>PETmin²</th>
<th>Bio15</th>
<th>Intercept</th>
<th>AIC</th>
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<td></td>
<td></td>
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<td>518.27</td>
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<td></td>
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<tr>
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<td>0.0114</td>
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<td></td>
<td></td>
<td>3.09</td>
<td>408.26</td>
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<td>0.0392</td>
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<td></td>
<td>10.26</td>
<td>708.67</td>
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<td></td>
<td>3.89</td>
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<tr>
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<td>534.91</td>
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<tr>
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<td>Spp.</td>
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<td></td>
<td>0.0314</td>
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<td></td>
<td></td>
<td></td>
<td>12.85</td>
<td>706.96</td>
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<td></td>
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<td></td>
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<td>0.15</td>
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<td>- PETmin²</td>
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<td>0.418</td>
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<td></td>
<td>12.39</td>
<td>707.33</td>
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<td></td>
<td>0.180</td>
<td>4.30e-3</td>
<td></td>
<td></td>
<td>-0.0413</td>
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<td>Bio15 or precip.</td>
<td>Gen.</td>
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<td>0.387</td>
<td>6.67e-3</td>
<td></td>
<td></td>
<td>-0.060*</td>
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<td>seasonality</td>
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<td>0.809</td>
<td>9.70e-3*</td>
<td></td>
<td></td>
<td>-0.21</td>
<td>31.55</td>
<td>678.93</td>
</tr>
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*bold P < 0.001; * P < 0.01.
FIG. 1. (A) Fern species richness. (B) Fern genus richness. (C) Fern family richness. Richness values are tabulated by counting numbers of species, genera, or families in 2500 km² grid squares. (D) Map of residuals of the regression of fern family richness on mean annual temperature (MAT), annual rainfall (RAN), and precipitation seasonality (Bio15). Projections are Lambert Conformal Conic. (E) Pteridophyte (ferns and lycophytes) species richness. (F) Lycophyte species richness. Color version of maps presented in this paper are available at: http://www.marcbogonovich.org/maps/ferns_lycophytes.html.
**Results**

Species richness.—A coarse latitudinal pattern in fern species richness is observed with generally higher richness found at lower latitudes (Fig. 1A). Species richness centers occur in the southern half of the continent whereas species poor areas are found in the northern third. Species richness does not reach its peak in a single latitudinal band, nor is the pattern unimodal. Instead there are four richness peaks each with between 60–82 species (per grid square). These include two mid-latitude centers, one surrounding Washington state (herein Northwest), which reaches 62 species per square and another surrounding the Appalachians and the Great Lakes region (herein Northeast), which reaches 75 species per square. Two richness centers are identifiable farther south, one centered around Arizona and New Mexico (herein Southwest) reaching 70 species per square and a second, the highest richness peak, in Florida with 82 per square. The Northeastern richness center is the largest in geographical area, stretching from Nova Scotia and New England to the Great Lakes and extending south along the Appalachians. Richness poor regions include the Great Plains, the Canadian Arctic, and a richness trough between Florida and the northeast.

Lycophytes, like ferns, have species richness peaks in the U.S. northeast and northwest, though lycophyte richness and lycophyte richness peaks are comparably more northern, and the Great Plains is a species poor region for both groups. Unlike ferns, lycophytes lack species richness centers in Florida and the Southwest (Fig. 1F). The pattern of pteridophyte species richness is dominated by ferns, the larger constituent taxon (Fig. 1E).

Fern richness at higher taxonomic levels.—There are large differences in patterns of fern richness at the three taxonomic levels (Figs. 1A–C). Richness patterns observed at genus and family levels more closely approach a unimodal pattern than does species richness. The southwestern richness peak observed for species does not exist at the family level, and is much reduced at the genus level. Similarly, the rise in Northwestern species richness relative to surrounding areas is not as large at the family level. The Northeastern species richness center, observed at the species level, shifts south and is less pronounced at the family level and nearly merges with the Floridian richness peak. At the family level there is essentially a single richness center in the eastern United States, reaching its maximum in Florida, the subtropical region of the study area.

Richness-climate relationships.—Regressions between climate variables and fern species, genus, and family richness reveal interesting patterns (Table 2). The strongest relationships found are with fern family richness (with AET, $R^2 = 0.678$; MAT, $R^2 = 0.676$). The same climate variables explain substantially less variation in species richness (AET, $R^2 = 0.449$; MAT, $R^2 = 0.539$). Climate relationships are consistently stronger for fern family richness than genus richness. Most of our discussion below on richness-climate models concerns fern family richness.

As expected, multiple regressions incorporating two variables explain more variation in richness than single variable regressions. MAT and AET explain
77.6% and MAT and RAN explain 78.1% of the variation in fern family richness (Table 2; Fig. 2), roughly 10% more than any single variable. Warmer and wetter regions generally contain more fern families (Fig. 2a–b). Warmer regions that are also wet have slightly more families than regions that are warm but not as wet. Additionally, dry regions that are very cold have fewer families than similarly dry regions that are warmer.

These simple multiple regressions incorporating one temperature variable and one liquid water variable slightly out-performed the IGM I ($R^2 = 0.781$ vs. 0.711 with family richness as the response variable). A best subsets regression on the variables included in Table 1, confirmed that the best two-variable model was simply MAT and RAN. The best three variable model included MAT, RAN, and precipitation seasonality (Bio15, Table 1), and explained 80.7% of the variation in fern family richness (Table 2). Again, as found for univariate regressions, the multiple regressions consistently explained more variation in family richness than species richness.

A map of the residuals of the regression of fern family richness as a function of MAT, RAN, and Bio15 (precipitation seasonality) illustrates regions where this regression model over-predicts and under-predicts family richness (Fig. 1D, presented are the residuals of the model using all 8,760 squares). There are more families along western North American coastal mountain ranges than predicted by this regression and fewer fern families in the mid-longitude Great Plains.
region of North America. There is some correspondence between positive residuals in this relationship and identified species richness peaks and negative residuals and species richness troughs (Fig. 1A and 1D).

**Family species richness patterns.**—Figs. 3–7 present maps of the 26 fern and lycophyte families of the study region. Families can be classified roughly by which of the four richness peaks correspond to their richness peak or peaks. Several families have one primary richness peak in Florida, such as the Thelypteridaceae, and the Polypodiaceae. Many families are barely in the study region, only appearing in Florida or surrounding areas with one or two species (e.g., Tectariaceae). Blechnaceae has a richness peak in Florida, but also has a small concentration of two species in the northwest. Several families have richness peaks in both northeast and northwest. The Pteridaceae has a large richness peak in the southwest.

**DISCUSSION**

**Climate models.**—The relative ranks in performance, based on R-squared values, of all richness-climate regressions that were tested are roughly the same whether the response variable was fern species, genus, or family richness (Table 2). However, all models have more explanatory power when applied to family richness. Much of our discussion on richness-climate models herein will concern explanatory models applied to fern family richness.

Richness at all taxonomic levels is positively correlated with water and temperature variables. Other continent-level studies of fern richness, in Africa (Aldasoro *et al.*, 2004) and Australia (Bickford and Laffan, 2006) reveal similar patterns, indicating the broad geographic universality of these relationships. The IGM I is not the most explanatory model. Instead, a simple two-variable linear model, including MAT and RAN, explains more variation in fern family richness (Table 2, Fig. 2b). More rainfall or higher average temperatures, however, may not always lead to higher fern richness. An optimum MAT might be expected instead, with extremely high MAT associated with lower fern family richness. However, within the geographical confines and conditions of the study region, the relationship appears linear (Fig. 2). Adding precipitation seasonality (Bio15) to the MAT and RAN model raised the model’s explanatory power to 80.7%. This is the best performing model in this study with the model explaining a surprisingly high percentage of variation considering that it does not incorporate spatial climatic variation within each 2,500 km$^2$ grid square.

There is further room for exploration of alternative fern richness-climate models. For example, the timing and duration of precipitation may matter for ferns as they lack deep root systems such as those possessed by many woody plants, and liquid water is essential for their reproduction. Incorporating terms for summer snow melt may account for some of the negative residuals observed along the wetter coastal ranges of North America (Fig. 1D). In addition, broad patterns may differ as more tropical regions are included in future studies.
FIGS. 3–7. Species richness maps of the 26 individual fern and lycophyte families. The lycophyte families are Isoetaceae (Fig. 4C), Lycopodiaceae (Fig. 4F), and Selaginellaceae (Fig. 6E). All other families are ferns (Monilophytes).
The equation for IGM I (Table 2) includes the minimum monthly potential evapotranspiration (PETmin). If PETmin of one month of the year is zero this term falls to zero, as does the PETmin² term. Thus, in many temperate regions, including much of our study region, the only term left in the IGM I is annual rainfall (RAN). Hawkins et al. (2007) tested an IGM model on temperate trees and found that the IGM predicted tree richness effectively ($R^2 = 0.651$) and that most of the explanatory power was derived from the rainfall term. Since much of our study region is temperate, our test of IGM represents another validation of this model’s predictive power in temperate systems and our results for family richness confirm its predictive power is high (71.1%). Though the fact that the MAT + RAN model performed better than IGM I shows that IGM I lacks climate terms that could further resolve variation in plant richness, or at least fern richness, in temperate regions even though the difference in performance between IGM I and the MAT + RAN model is relatively small (9.6%, Table 2).

Fern richness patterns.—North American ferns exhibit characteristics that are unusual among North American terrestrial organisms, both plant and animal. Ferns exhibit multiple species richness peaks in North America north of Mexico and two of these peaks are at mid-latitudes. Plants in general tend to display a more continuous decrease in species richness south to north (Currie and Paquin, 1987; Currie, 1991; Kreft and Jetz, 2007). Non-plant groups also exhibit more regular patterns. Amphibians have a species richness center in the Southern Appalachians, while reptiles show a relatively smooth decrease in richness south to north (Currie, 1991). Mammals are more like ferns, exhibiting irregular geographical richness patterns (Simpson, 1964). The multi-modality of fern species richness peaks may contribute to the low climate-species richness relationship relative to the family level relationship. Fern family richness patterns resemble the patterns seen in other groups more than fern species richness.
Surprisingly, fern family richness, followed by genus and then species richness, is most closely related to climate variables. These patterns differ from those found in other organisms, or in ferns from other regions, where R-squared values tend to decrease or stay the same from species to family richness levels. In a stepwise multiple regression including several climate variables, Aldasoro et al. (2004) found a decay in the strength of the relationship between climate and African fern richness from species to families ($R^2 = 0.676$, species; $0.654$, genus; $0.584$, family). Similarly, O’Brien et al. (1998) explained roughly 79% of the variation in Southern African woody plant species and genus richness using models including either two or three water and energy variables; but explained only 70–75% of the variation for families, depending on the model. These comparisons make the pattern reported here more puzzling.

The fact that family richness patterns are similar to those found in other regions and with other organisms, while species richness patterns are more unusual, suggests that species level patterns may emerge as an artifact of imperfect data at the species level. It is conceivable that fern species richness is not sufficiently well sampled to adequately describe fern species richness patterns, which might explain the weaker species richness-climate relationships. In contrast, the fern family richness pattern may be better understood because family distributions are relatively rapidly determined in the process of botanical exploration and can thus be used as a surrogate of species richness (Balmford et al., 1996). However, studies of botanical exploration challenge the interpretation that species richness may be insufficiently sampled in North America north of Mexico. Pteridologists can determine the pattern of species richness even before full sampling, even in regions as diverse as Bolivia (Soria-Auza and Kessler, 2008). The region of the U.S., Canada, and Greenland is probably more completely sampled than Bolivia, and has fewer ferns, providing confidence that the observed pattern of North American species richness is an adequate signal of the true pattern.

There are several other reasons why genus and family richness may be more strongly related to climate variables than is species richness in this study. First, characteristics that distinguish genera or families may mediate the impact climate has on the distribution of species more than traits that typically distinguish species. Many traits that distinguish fern species seem trivial as environmental adaptations (e.g., sori position on pinnae), while traits that distinguish genera include frond architecture and trophic type of the gametophyte. Second, families and genera may be more evolutionarily stable than species or, at least, less sensitive to short time-scale perturbations. Finally, the mid-latitude richness peaks might result from glacial processes, as the mid-latitude richness centers coincide with the glacial maximum. Glacial processes that promote speciation include recolonizations, founder effects, isolation, hybridization and polyploidization. Cold temperatures are known to foster polyploidization in plants (Otto and Whitton, 2000) and polyploidization is common among ferns (Wood et al., 2009). High fern richness could have been generated by these processes in the last glaciation or by accumulation over repeated cycles of glaciation.
Broader scales may put these patterns in perspective. Mexico has over 1,000 fern species (Mickel and Smith, 2004), more than twice as many as in the much larger, more northern study region. On a global scale, fern species richness patterns may be less unusual and species richness-climate relationships stronger, as temperate richness centers are swamped out by much larger richness centers closer to the Equator. Fern richness-climate regression models should be tested in future studies that incorporate larger areas and lower latitudes.

Further observations.—The proportion of the continental fern flora found in highly diverse regions differs among taxonomic levels. The highest fern species richness is found in regions around Florida followed by the northeast. They contain 82 and 75 species, respectively, or \( \sim 20\% \) of the continental pool of 387 species. The percentages increase with taxonomic level. The highest concentrations of genera and families occur in Florida, with 42 genera, or 62.7\% of the continental pool of 67 genera, and 21 families, or 91.3\% of the pool of 23 families. Together with the climate relationships, this suggests that most fern families are tropical or subtropical in origin with differential expansion (of families) into temperate regions. This can be thought of as a climatic filtering of families toward regions of lower rainfall and temperature. This pattern is consistent with the out of the tropics hypothesis (OTT) articulated by Jablonski (1993) and Jablonski et al., (2006) to explain the evolutionary construction of the latitudinal diversity gradient. However, this pattern is also consistent with the tropical conservatism hypothesis (TCH; Wiens and Donoghue, 2004).

The species richness patterns of individual fern and lycophyte families may provide clues about overall fern and lycophyte richness patterns. The Southwest species richness center (Fig. 1A) is largely composed of species from one family, the Pteridaceae (42 out of 70; Fig. 6B); many of which are triploids. This pattern has been recognized before (Tryon, 1969). On the other hand the Northeast richness center appears to be the result of high numbers of species from several families including the Dryopteridaceae, Osmundaceae, and Ophioglossaceae among others. Together these observations suggest that multiple explanations may be required to explain fern species richness patterns, but also suggests that the northeast and northwest richness peaks are a general phenomenon and not the result of one or two aberrant fern families. Interestingly, two lycophyte families, which are only distantly related to ferns, have richness peaks corresponding to the northeast and northwest fern richness peaks. Other than the Pteridaceae, only the lycophyte family Selaginellaceae (Fig. 6E) reaches its peak richness in the southwest.

Other groups including mammals and other plants (trees) have lower richness in Florida than in surrounding areas (Currie and Paquin, 1987; Simpson, 1964). This pattern has been hypothesized to result from the so-called peninsular effect, related to island biogeography theory (Taylor and Regal, 1978; but see Jenkins and Rhine, 2008). Peninsulas share spatial properties with islands, namely separation and distance from continental species pools. Therefore, like islands, peninsulas are expected to have fewer
species than is typical for the environment due to limitations on dispersal of appropriate lineages into the peninsular regions. In contrast, ferns actually experience a high richness peak in Florida. Few Florida fern species are endemic and most also exist in the West Indies or South America, with fewer affinities to the Mexican fern flora. One explanation for the pronounced fern richness center in Florida may involve ferns’ long-range dispersal capacity (Spurr, 1941). Other geographical patterns of ferns are consistent with this hypothesis. The vascular plant floras of isolated oceanic islands tend to have higher percentages of pteridophytes than the mainland (Kref et al., 2010; Tryon 1970). The observed high species richness of ferns and low species richness of other groups in Florida is consistent with the interpretation that ferns are less limited by barriers to dispersal than other groups.

**Conclusion.**—North American ferns have unusual mid-latitude species richness peaks, while family richness patterns are more comparable to those reported for species in other organisms. The fern species richness peaks occur in diverse climates, with different composition and numbers of higher taxa, suggesting that there may be more than one explanation required to understand fern species richness patterns. In contrast, fern family richness is strongly correlated with a small number of climate variables, suggesting a parsimonious explanation is sufficient to explain family richness patterns.

The best regression model included three variables – mean annual temperature, annual rainfall, and precipitation seasonality – and explained 80.7% of the variation in fern family richness. The result that fern richness, particularly at the family level, is strongly related to water and energy variables supports the most general prediction of the productivity-diversity hypothesis. More work is needed to explore and evaluate alternative fern richness-climate models.

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**Literature Cited**


