

Notes and Comments

Taxon Richness and Climate in Angiosperms: Is There a Globally Consistent Relationship That Precludes Region Effects?

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An important goal of ecology since the 1960s has been to explain spatial patterns of taxon richness, which is typically characterized at the scale of approximately 10^4 – 10^6 -km² sampling units (Pianka 1966; Rohde 1992; Rahbek and Graves 2001; Whittaker et al. 2001). Dozens of hypotheses have been proposed, but these encompass primarily three basic ideas. First, ecological hypotheses emphasize the influence of environmental conditions such as productivity, seasonality, and abiotic stress on the coexistence of species within communities of interacting populations (e.g., Wright 1983; Currie and Paquin 1987; Wright et al. 1993; Francis and Currie 1998). Second, landscape-level (mesoscale) hypotheses extend local hypotheses to include the effects of habitat heterogeneity on both local (Shmida and Wilson 1985; O'Brien 1998) and mesoscale taxonomic richness (Rahbek and Graves 2001; O'Brien et al. 2000), recognizing the turnover of taxa between habitats as a component of larger-scale taxon richness (Cody 1975, 1993). Third, regional/historical hypotheses recognize the contribution to diversity patterns of large-scale processes such as species production and adaptive radiation and unique events of earth history, including tectonic pro-

cesses, glaciation, and climate change (Ricklefs 1987). At a more local scale of square meters to hectares, ecologists generally agree that the constraining influence of environmental factors, including soil conditions, is more evident and that the influence of regional processes is farther removed (Grime 1973; Huston 1979; Tilman 1982; Grace 1999).

Ecological hypotheses for large-scale patterns have been supported primarily by correlations between taxon richness and local climate or other environmental conditions (Wright 1983; Currie and Paquin 1987; Adams and Woodward 1989; Currie 1991; Kerr and Currie 1999; Badgley and Fox 2000). Recently, Francis and Currie (2003, p. 523) asserted that statistical models relating angiosperm family richness to climate variables are “globally consistent and very strong and are independent of the diverse evolutionary histories and functional assemblages of plants in different parts of the world.” They go on to conclude that the “effects of other factors such as evolutionary history, postglacial dispersal, soil nutrients, topography, or other climatic variables either must be quite minor over broad scales (because there is little residual variation left to explain) or they must be strongly collinear with global patterns of climate.”

Mechanisms relating diversity to climate are mostly linked to the greater capacity of areas with higher energy flux or water availability to support individuals (Maurer 1990; O'Brien 1993; Wright et al. 1993; O'Brien et al. 2000) or to increased opportunities for specialization afforded species in highly productive, generally tropical, habitats (Klopfer 1959; Hall 1992; Kleidon and Mooney 2000). Historical hypotheses have garnered support from significant region effects on taxon diversity within comparable habitats or climate zones (Cody and Mooney 1978; Orians and Paine 1983; Latham and Ricklefs 1993*a*, 1993*b*; Ricklefs and Latham 1993; Schluter and Ricklefs 1993; Qian and Ricklefs 2000; Ricklefs et al. 2004).

The three types of hypotheses are not mutually exclusive, and we expect that their relative influence will vary with the size of the area being considered and the scale at

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which patterns in diversity are characterized (Huston 1999; Rahbek and Graves 2001; Whittaker et al. 2001). However, despite the growing literature on this topic, no consensus on global patterns of taxon richness at the megahectare (10^4 km²) and larger scales has emerged. It has been argued that regional processes and historic events influence taxon richness over and above its relationship to local environmental conditions (Ricklefs 1989; Latham and Ricklefs 1993*b*; Ricklefs et al. 1999). Currie and others largely reject history and minimize interregional differences in taxon richness (Currie and Paquin 1987; Currie 1991; Francis and Currie 1998), giving observed correlations between diversity and physical factors in the environment causal primacy and leaving little room for the influence of regional and historical factors (Whittaker and Field 2000). This issue is of critical importance in ecology because the different viewpoints argue for different, albeit complementary, research programs.

Francis and Currie's (2003) most recent analysis was based on global patterns in angiosperm (flowering plant) family richness within grid squares of approximately 3.5×10^4 km² (2° latitude span) compiled from family range maps by Heywood (1993). Climate variables were reduced to a smaller number of indices representing heat and water deficit. Our comments address aspects of the data themselves, the analysis of the data, and the interpretation of the results. We suggest that analyses of family-level diversity in large (approximately 200 × 200-km) grid squares over a spectrum of climates supporting vegetation ranging from bare desert to tropical rainforest do not test regional effects adequately (Whittaker et al. 2001); that the results presented by Francis and Currie indeed reveal unanalyzed region effects; and that taxon richness–climate correlations do not preclude evolutionary processes as causative mechanisms (Latham and Ricklefs 1993*b*).

The Data

The Use of Family Richness as a Stand-In for Diversity at the Species Level

Families of plants show less endemism with respect to large geographic regions than do species (Gleason and Cronquist 1964; Good 1974), and so analyses based on the presence or absence of families within large grid squares are less likely than those based on species to demonstrate regional effects. For example, in Latham and Ricklefs's (1993*a*) comparison of the tree flora of temperate eastern Asia (729 species in 177 genera in 67 families) with that of eastern North America (253 species in 90 genera in 46 families), few or no species were held in common, but 20 genera occurred in both regions, as did 40 families.

Although species and family richness are generally related among samples (e.g., Williams and Gaston 1994), enough scatter exists to obscure considerable variation in species richness (Balmford et al. 1996). In extreme comparisons, one area might have more families of plants than another but fewer species. For example, the native angiosperm floras of Florida and California, as reported in the literature (e.g., Hickman 1993; Wunderlin 1998) and published electronic databases (e.g., Kartesz 1999; CalFlora 2000; Wunderlin and Hansen 2003), with nomenclature standardized following Kartesz (1999), reveal fewer species in Florida (2,654 vs. 5,100) but more families (173 vs. 146).

Francis and Currie (2003) compared their data for family richness with the global species richness map produced by Barthlott et al. (1996) and found a coefficient of determination of $r^2 = 0.76$ in a logarithmic regression. Barthlott et al. (1996) produced a global contour map of 10 plant species diversity ranges based on species richness in 1,400 floras extrapolated downward semilogarithmically to a 10^4 -km² reference area where needed. Owing to heterogeneous geographical sampling, many of the contour lines were extrapolated on the basis of vegetation and climate zones.

In a comparison among 10 regional tree floras in temperate and tropical latitudes (19–93 families, 68–4,648 species), species richness increased as approximately the square of family richness (logarithmic regression slope 2.19 ± 0.36), with 83% of the variation in species richness related to variation in family richness (Latham and Ricklefs 1993*a*; R. E. Ricklefs, unpublished analyses). Nonetheless, the range of the deviations from the log species–log family regression was equivalent to a factor of 6.9, and the average deviation from the regression was equivalent to a factor of 1.5. Although these deviations are not large compared with the nearly two orders of magnitude range of species richness among the 10 floras, they are potentially substantial when comparing floras between regions of similar climate.

Finally, most families of plants arose before the mid-Tertiary, and many were present before the end of the Cretaceous (Ricklefs and Renner 1994; Magallon and Sanderson 2001; Wikström et al. 2001). Restricting patterns to family-level taxa eliminates tens of millions of years of history from floras. Because families originated so long ago, their distributions across regions reflect, in part, an ancient geography that is inappropriate for testing hypotheses about regional effects in the modern world.

The Quality of the Data

Francis and Currie (2003) calculated angiosperm family richness in each of 4,394 equal-area grid squares (2° lat-

itudinal span) from range maps taken from Heywood (1993). They further combined squares to tabulate angiosperm family richness at coarser scales of resolution: 4°, 6°, 8°, and 10° latitudinal spans. The classification system of Heywood followed Stebbins (1974), who in turn followed chiefly the system of Cronquist (1968). Stebbins (1974, p. 355) tabulated 347 families of angiosperms, but Heywood (1993) provided geographical distribution maps for only 306. Moreover, family concepts are fluid because family-level taxa are arbitrary, and molecular phylogenetic studies are continually refining relationships leading to the reorganization of taxa at many levels. Currently accepted taxonomic schemes recognize more than 450 families (e.g., 490 in Thorne 2001; 592 in Takhtajan 1997; 454 in APG II 2003). Many of the smaller families created recently or not depicted among the maps of Heywood (1993) have restricted distributions in single phytogeographic regions. The absence of these families from a database might bias analyses against revealing region effects.

A potentially more serious problem with the data used by Francis and Currie (2003) is that the range maps of Heywood (1993) are reproduced at a small size, and many have errors even at the 10° grid scale. An examination of the maps for families distributed in eastern Asia and/or North America, which are well known floristically and familiar to us, revealed no fewer than 20 families whose distribution ranges had discrepancies by as much as 10° in latitude. For example, *Cercidiphyllaceae* were incorrectly mapped by Heywood (1993) as occurring in northeastern China, the Russian Far East (including Sakhalin Island), Korea, and Japan, but this family is not distributed in these areas except for Japan. On mainland Asia, the family is restricted to subtropical and warm temperate areas in southern China (Kuan 1979; Wu and Raven 2001). The error in the northern limit of the distribution range of this family on mainland Asia by Heywood (1993) is more than 15°, which corresponds to an error of about 12°–15°C in mean annual temperature (Domrös and Peng 1988). Similar errors in range maps by Heywood occur in many other families, including those whose global distributions are well known (e.g., *Fagaceae*, *Leguminosae*, and *Rosaceae*). Details of some of these discrepancies are reported in the appendix in the online edition of the *American Naturalist*.

Assessment of the Statistical Effect of Region

One approach to evaluating variation in taxon richness between regions is to include region as a main effect in an ANCOVA in which environmental variables of interest are entered as covariates. For example, among tree floras

in regions of temperate forest (area = 17–7,401 km², i.e., smaller than the 3.5 × 10⁴ km² used by Francis and Currie [2003]), Latham and Ricklefs (1993b) found that region uniquely accounted for about 30% of the sums of squares in the logarithm of species number in an ANCOVA with the logarithm of area and AET as covariates. Differences in intercepts between regions were as large as 0.61 log₁₀ units, which is a factor of 4.1 (eastern Asia vs. Europe), and 0.28 log₁₀ units (a factor of almost 2) between eastern Asia and eastern North America, the sources of the largest number of samples.

Francis and Currie (2003) calculated predicted family richness within each of six biogeographic regions from the richness-climate regression for the five other regions and then compared the observed and predicted values for all the regions together. Their figure 5 shows a strong relationship between predicted and observed values, although the coefficients of determination within regions were as low as 0.43 for statistical models based on both temperature and potential evapotranspiration (PET). Furthermore, the calculation of predicted values for each region from models parameterized by data from all the other regions combined obscures differences between regions. Even so, it is clear from the regression lines superimposed on Francis and Currie's (2003) figure 5 that the observed versus predicted relationships varied substantially among regions in some cases. For example, observed family richness in the Oriental region appears to be higher relative to predicted than in the Neotropical and Ethiopian regions, as does that in the Palearctic compared to the Nearctic, by a factor of at least 1.5 and probably even more compared to Australia.

Francis and Currie (2003, p. 528) recognized, but also minimized, these differences: "After statistically accounting for climate, small systematic differences in richness among regions do remain. These differences account for an additional 3%–6% of the variance in family richness among regions." Francis and Currie (2003, p. 528) concluded that their most important result is "a globally consistent relationship between angiosperm richness and climate. Richness varies with climate within nearly every phytogeographic province and biome in very similar ways. Moreover, the richness of a given area can be predicted quite well using climate-richness models developed with data from other parts of the world, without the need to postulate other special circumstances for particular regions."

Part of our disagreement over the interpretation of regional effects is a matter of perspective. Looking at the same data, Francis and Currie (2003) find that strong diversity-environment relationships leave little room for region effects, whereas we are impressed by differences between regions on the order of a factor of 1.5. Predicted

family richness in Francis and Currie's (2003) figure 5 varies from fewer than 10 to almost 200 families, a factor of 20. Supposing that the variance on a log scale is roughly proportional to the square of the common log of a factor of 10 ($= 1$), then 3%–6% of this variance would be 0.03–0.06, the square root of which is 0.173–0.245, equivalent to a factor of 1.5–1.8. This is consistent with differences between regression lines in Francis and Currie's (2003) figure 5. Thus, our perceptions of the data are basically compatible, as Francis and Currie likely would have found had they explicitly evaluated region effects statistically.

Ecologists need to decide whether the region effect, which appears to be prevalent in comparative studies when environments are matched or accounted for as covariates (Schluter and Ricklefs 1993), is trivial or substantial enough to warrant consideration. It is not helpful to contrast ecological and historical hypotheses as alternatives because their mechanisms clearly can interact at many scales. Ecologists must also recognize that diversity–environment correlations can have historical origins (the “collinearity” that Francis and Currie [2003] mention), as we discuss below. In our view, it is premature for ecologists to reject, as Francis and Currie (2003, p. 534) have provisionally, the hypothesis that “differing evolutionary histories are responsible for contemporary gradients of richness.”

Interpretation of Diversity–Climate Relationships

The regression of diversity on climate raises two separate issues with respect to its interpretation: the origin of the unexplained (residual) variation and the cause of the explained variation, which is allied with the problem of collinearity. With respect to the first issue, the coefficients of determination in Francis and Currie's (2003; their table 3) diversity–climate models within phytogeographic provinces (0.42–0.94) leave open the possibility that other factors, including regional or historical influences and also unmeasured environmental variables, may be acting. In this context, it is important that ecologists test region effects explicitly in large-scale comparisons of diversity.

With respect to the second issue, correlations between taxonomic diversity and climate can have historical (evolutionary) as well as local (ecological) causes (Farrell et al. 1992; Latham and Ricklefs 1993*b*). Clades evolve and diversify from an ancestral ecological zone (e.g., Crane and Lidgard 1989). One expects the diversity of each clade to be greatest in its ancestral zone and to be more recent and more limited in other ecological zones to which members have to adapt over evolutionary time (Ricklefs and Schluter 1993). For example, angiosperms are thought to have originated in tropical regions (Takhtajan 1969; Raven and

Axelrod 1974; Lidgard and Crane 1990), and tolerance of freezing poses a major barrier for many angiosperm lineages against invasion of areas with low temperatures (Sakai and Larcher 1987). Thus, a taxon richness–climate relationship in angiosperms may reflect evolutionary processes.

Supporting an historical basis for a taxon richness–climate relationship is the fact that many monophyletic groups occur predominately in zones of low diversity to which they are adapted. For example, the angiosperm families Salicaceae, Betulaceae, Cactaceae, and Fagaceae have their centers of diversity in temperate, boreal, or arid subtropical regions that are otherwise taxon poor compared with the wet tropics (e.g., Qian 1998). Presumably, these lineages evolved primarily under the conditions in which they are presently most diverse; moreover, the relationship between taxon richness and climate for each of them would not parallel the overall relationship identified by Francis and Currie (2003). Of course, the origin of a flora need not override constraining effects of local interactions on local species coexistence. However, it is also not possible to reject, with the information and analyses at hand, a totally historical explanation for global patterns of taxonomic richness.

Francis and Currie's (2003, p. 523) conclusion that statistical models relating angiosperm family richness to climate variables are “globally consistent and very strong and are independent of the diverse evolutionary histories and functional assemblages of plants in different parts of the world” overstates the case for local, ecological control over taxonomic richness. Beyond accepting more broadly the legitimacy of historical hypotheses, ecologists likely can increase their understanding of patterns in diversity through global comparative studies of local-scale taxonomic richness (Huston 1999) accompanied by detailed ecological data (e.g., the 50-ha plots administered by the Center for Tropical Forest Science; Condit 1995), phylogenetic studies of the origins of local associations of organisms within the regional pool (McPeck and Brown 2000; Webb 2000; Webb et al. 2002), and appraisals of shifts to new ecological zones within regional phylogenies (e.g., Brown et al. 2000). It may be pointless to formulate hypotheses and devise tests that can reject either local or regional mechanisms for the origin and maintenance of local and regional diversity because both types of processes likely operate. However, serious consideration of a historical perspective should stimulate research into ecological and geographic mechanisms that promote diversification and that link local and regional patterns of taxonomic diversity (e.g., Cardillo 1999; Qian and Ricklefs 2000; Morris 2003; Stephens and Wiens 2003).

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