

Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency

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Latham and Ricklefs observed statistically significant continent (region) effects in global comparisons of the species richness of forest trees. They argued that ecologists should entertain diversity hypotheses that include region-specific effects of history and geography on biological diversity. Francis and Currie rejected this approach, claiming that alternative hypotheses based on variation in local ecological conditions are more parsimonious. In response, we point out that the diversity of the earth's biota, whether examined at the local, regional, or global level, does have a history and is responsive to large-scale events and processes that have region-specific expression and influence the net rate of diversification. Francis and Currie state that historical explanations may not be proper hypotheses because they make no predictions about contemporary patterns. However, historical insights into the accumulation of diversity within regions do invite the development of testable, mechanistic hypotheses about how geography and climate influence rates of speciation and extinction. Diversification at the intersection of ecology and evolution presents biologists with both a formidable challenge and an exciting, but largely unexploited opportunity to further their understanding of biological communities at many scales of analysis.

Within a continent, the number of species of trees in large latitude-longitude blocks (macro-scale: 51000–100000 km²) in temperate regions is correlated with actual evapotranspiration (AET) (Currie and Paquin 1987, Adams and Woodward 1989, O'Brien 1993). AET bears a direct relation to annual aboveground plant growth (Rosenzweig 1968), and is commonly interpreted as an integrated measure of local ecological conditions that influence primary production (but see Rohde 1992). Latham and Ricklefs (1993a) compared meso-scale (10–10000 km²) temperate-zone tree species richness (diversity) within and between continents and found a strong relationship of diversity to AET within

continents, but also a significant “continent” (region) effect. In comparisons of temperate and tropical forests at a micro-scale (0.5–10 ha), no significant effect of AET was evident in an analysis of covariance (ANCOVA) that also included “tropical” versus “temperate” as a main effect.

Significant regional effects are consistent with hypotheses that link diversity to the unique history and geography of a region independently of local ecological conditions (Orians and Paine 1983, Schluter and Ricklefs 1993). Latham and Ricklefs argued that the research agenda for community ecology should include historical explanations for differences in diversity between similar habitats or climate zones in different regions. Contrasting temperate and tropical locations, they suggested that the latitudinal gradient in species diversity, as well as other relationships of diversity to ecology, could have partly historical origins (Ralph 1985, Farrell and Mitter 1993, Hoffman et al. 1994).

Recently, Francis and Currie (1998) questioned the fundamental message of Latham and Ricklefs that history and geography may leave an imprint on biological communities. The basic issue is one of local ecological equilibrium versus regional differentiation. With the rise of population biology in the 1960's (Kingsland 1985), ecologists first began to seek local, equilibrium explanations for patterns in species diversity (MacArthur 1965, Brown 1981, Ricklefs 1987). Most ecologists recognized that regional diversity responded to large-scale processes and events, including widespread extinction of taxa associated with late-Tertiary climate cooling in northern latitudes (Mai 1981, Delcourt and Delcourt 1987, Sauer 1988). However, they

also persuaded themselves that ecological communities could be isolated from variation in regional diversity. This required postulating local regulation of diversity through species interactions and adjustment of disparities between local and regional diversity through turnover of species between habitats (beta diversity) (MacArthur 1969, Cody 1975).

Complete local ecological determinism predicts coincident relationships between diversity and ecology in independently assembled communities. Increasing evidence for regional effects in comparisons of local diversity (e.g., Latham and Ricklefs 1993b, Ricklefs and Latham 1993, Schluter and Ricklefs 1993) is consistent with the idea that regional processes and historical events also may influence species richness, creating diversity "anomalies" among ecologically comparable environments.

Francis and Currie nevertheless dismissed Latham and Ricklefs's interpretation of patterns of tree diversity on several grounds, three of which seem crucial. First, they rightly pointed out that a significant regional effect does not necessarily reflect regional and historical contingency. Rather, such effects could arise from consistent differences in local ecology between regions, related, for example, to soil nutrients, that are not captured by such measured variables as AET. This provides a plausible alternative hypothesis that is amenable to testing by direct observation. Second, where AET and regional effects vary in parallel, Francis and Currie implied that ecological factors provide a stronger, more parsimonious explanation. In their words, "Unless it can be shown that observed patterns of richness are more closely related to some specific pattern predicted by an historical hypothesis than to contemporary factors, there is no scientific reason to prefer the historical hypothesis" (p. 601). Nor, we might add, is there any reason to prefer ecological hypotheses, especially when ecological factors are, like history, invoked as post hoc explanations. Third, Francis and Currie suggested that where Latham and Ricklefs failed to detect a statistical effect of AET on micro-scale species richness in an ANCOVA that included tropical versus temperate as a main effect, their statistical analysis lacked sufficient power.

In response, we begin with the following general comment. It seems to us that data used to test a hypothesis must match the scale of the processes embodied by the hypothesis. To postulate that habitat productivity regulates local species richness implies that local conditions determine the outcome of local interactions between populations. Samples of species richness over large latitude-longitude blocks do not necessarily represent local species richness in habitats included within those blocks. For this to be true, habitat diversity and turnover of tree species between habitats would have to be independent of average AET, and this has not been verified. Thus, by this criterion alone, we

prefer micro-scale data on species richness to either meso- or, especially, macro-scale data.

It is also true, as Francis and Currie have pointed out, that correlated variation between independent variables obscures their separate statistical effects on dependent variables. However, as Francis and Currie showed in their Fig. 4, confirming Latham and Ricklefs's analysis, the continental effect in micro-scale comparisons including tropical and temperate locations is statistically stronger than the effect of AET. For example, in relating micro-scale species richness to a main effect of "tropical" versus "temperate" with AET as a covariate, correlated variation between AET and the temperate/tropical difference explained 68% of the variation in species richness. An additional 11% was uniquely related to differences between temperate and tropical localities independently of differences in AET, while less than 1% was uniquely related to variation in AET (that is, within climate zone). From a biological standpoint this says, at the least, that AET does not fully determine local species richness. In addition, differences uniquely associated with tropical and temperate latitudes, but which are independent of AET, are demonstrably important, as we discuss below. Because the largest component of variance cannot be ascribed unambiguously to either AET or to other differences between temperate and tropical regions, differences apart from AET (either historical or ecological in nature) may even predominate in their effects on diversity. In any case, the evidence to date does not allow us to reject this possibility. Furthermore, the observed diversity-AET correlation could arise through the influence of the physical environment on the net rate of diversification within a region. Thus, AET may influence regional/historical processes as well as local ecological processes that constrain species coexistence.

Concerning a relatively minor point, Francis and Currie suggested that Latham and Ricklefs failed to detect a within-continent effect of AET on species richness on the micro-scale because their analysis lacked statistical power owing to the narrow range of the independent variable in the samples from each climate zone. The range of variation in AET among either tropical or temperate sites included in the sample was 59 and 41%, respectively, of the total range in the combined sample. In a linear regression of Y (log of species richness) upon X (AET), that is, $Y = a + bX + \epsilon$, the model mean square related to the regression coefficient b varies in direct proportion to the range in X , but the error mean square related to ϵ is independent of the range in X . Thus, the F -ratio for a linear model varies in direct proportion to the range of variation in X . In the comparison of micro-scale sites reported by Latham and Ricklefs, the regression of the log of species richness on AET over the combined tropical and temperate sites had an F -ratio of 100.8 ($df = 1,46$, $P < 0.0001$, $R^2 = 0.69$). If the residuals were distributed homoge-

neously about the regression, reducing the range of values of AET to 41% of the combined range would still result in an F -ratio of 41, which is statistically significant ($P < 0.05$) with a sample size as small as 4 (or at the 0.001 level with $N = 8$). In fact, the F -ratio for the relationship of the log of species richness on AET was only 0.6 ($P = 0.43$, $R^2 = 0.02$, $N = 31$) within the tropics and only 4.1 ($P = 0.06$, $R^2 = 0.23$, $N = 16$) within temperate latitudes. Thus, Latham and Ricklefs' analysis had ample statistical power to detect a diversity-AET relationship within regions, had it been as strong as the relationship within the pooled regions, but failed to do so.

Clearly, there is a significant continent effect on species richness at macro- to micro-scales that is independent of variation in AET within temperate latitudes. Latham and Ricklefs (1993a; see also Latham and Ricklefs 1993b, Ricklefs and Latham 1993) as well as subsequent contributions, emphasized the possibility that historical and regional factors may have contributed to the regional effect. We have done so in part to balance the tendency of many ecologists, including Francis and Currie, to dismiss non-equilibrium explanations for ecological patterns. However, we have not advocated this viewpoint simply for the sake of argument. Although as-yet-unstated ecological hypotheses may close the gap between AET and regional diversity (see Wright et al. 1993), there are many reasons to believe that history, too, may leave its imprint on local ecology.

Francis and Currie stated that historical hypotheses are weak because they cannot be tested. The complement of this point of view is as follows: "Richness models such as that of Currie and Paquin (1987) make explicit quantitative predictions about richness in particular places. These predictions make the models eminently testable" (Francis and Currie: 601). This is true only in the sense that the predictions of such richness models are empirical generalizations, i.e., more species occur where it is warm and wet. They are, not the predictions of mechanistic models of the relationship between local diversity and local ecological conditions (McGlone 1996). Thus, they do not allow one to distinguish between local and regional models for variation in species diversity. Latham and Ricklefs (1993a) presented analyses that appeared to falsify one such "prediction" and stimulated Francis and Currie's response with respect to forest trees. However, even if the empirical generalization had been supported, hypotheses other than that of local ecological determination would be tenable.

Indeed, one plausible model of geographical variation in diversity features historical processes (Farrell and Mitter 1993, Latham and Ricklefs 1993a, b). It is generally agreed that angiosperms originated in the tropics (Raven and Axelrod 1974, Crane and Lidgard 1990), and that tolerance of freezing poses a major

physiological barrier to distribution. More than half the families of flowering plants are restricted to the tropics (Ricklefs and Renner 1994). Temperate trees are drawn disproportionately from more advanced clades of flowering plants compared to those of tropical areas (Ricklefs unpubl.). If occupation of cold-climate zones required the evolution of physiological mechanisms of cold tolerance, then one would expect a diversity gradient to be established between regions of origination (the tropics) and regions of subsequent colonization (temperate and boreal zones). Furthermore, temperate floras would in general be younger than tropical floras. A similar type of mechanism apparently controls plant diversity in mangrove habitats, which from the standpoint of energy comprise one of the most productive environments on earth. Invasion of mangrove habitats from adjacent terrestrial forests requires the evolution of physiological mechanisms for tolerating salt and anoxia in the root zone. The species-poor mangrove flora indicates that this evolutionary transition has occurred infrequently. However, it evidently has occurred more frequently in the Indo-West Pacific region, where there are four times as many genera and six times as many species of mangroves as in comparable environments in the Atlantic-Caribbean region (Ricklefs and Latham 1993).

What are historical explanations and how do we evaluate them? History is something that has happened. As such, it is more appropriate to reconstruct history than to develop hypotheses about the "effects" of history on contemporary patterns of diversity. This raises the fundamental issue, articulated by Francis and Currie, concerning whether historical explanations ever can be verified. How can we show that what we observe today reflects what has happened in the past? To answer this question, we first distinguish two kinds of history. The first includes the lasting effect of transient causes [large-scale disturbances such as mass extinctions (Kauffman and Fagerstrom 1993) and biotic interchange between regions (Vermeij 1991, Webb 1991)]. The second kind of history includes the accumulated effect of ongoing processes, as would occur if species were formed more readily in one region than another. Both kinds of history may be revealed by historical reconstruction. The second, especially, might also be amenable to hypothesis-testing approaches. Certainly the idea that some regions favor more rapid speciation might be "tested" by quantifying incipient stages of species production (e.g., isolated populations) in the contemporary biota.

Although historical processes and events are largely hidden from direct observation, we may gain insight into history by examination of the fossil record, comparative analysis (especially sister-taxon analysis), and phylogenetic reconstruction. For example, fossils show that the low regional diversity of forest trees in Europe and western North America resulted from extinction of

taxa throughout the latter half of the Tertiary. This historical process was associated with climate cooling and drying and with the absence of extensive refugia for temperate forests (Wolfe 1975, Mai 1981, Delcourt and Delcourt 1987, Sauer 1988, Latham and Ricklefs 1993b). Eastern North America apparently suffered no such loss. However, because of its isolation from European and eastern Asian centers of diversification of the temperate woody flora (Crane and Lidgard 1990, Lidgard and Crane 1990), eastern North America never achieved the diversity of eastern Asia and early Tertiary Europe (Latham and Ricklefs 1993b). Changes in diversity were probably forced by climate, in conjunction with the unique geographical positions of each region, but it is unlikely that regional diversity tracked an ecological equilibrium; certainly local diversity does not appear to do so at present (Latham and Ricklefs 1993a).

Sister-taxon comparison is another method of historical analysis. This method allows one to contrast the diversity of lineages having a common ancestor, hence equal age, but which have differed during their subsequent independent evolutionary history in such traits as morphology and distribution (Mitter et al. 1988, Farrell and Mitter 1993, Slowinski and Guyer 1993). Such comparisons of the floristic diversity of eastern Asia and North America among disjunct genera show that diversity differences occur primarily among woody plants, which evidently did not diversify, or suffered increased extinction, in North America compared to eastern Asia (Guo and Ricklefs unpubl.). The absence of a diversity discrepancy among herbaceous disjunct plants is more difficult to explain. It is evidently not tied to the relatively rapid diversification of advanced, largely herbaceous eudicots (Chase et al. 1993) in North America during the late Tertiary, when western North America, especially, experienced drying and increased vegetation heterogeneity related to mountain building (Wolfe 1969, Leopold and MacGinitie 1972, Wolfe 1978). The disjunct herbaceous taxa inhabit mostly wetlands and wooded sites. Such contrasts as that between woody and herbaceous taxa invite the development of both historical and ecological hypotheses, and also emphasize how poorly we understand the origin and regulation of patterns of taxonomic diversity.

Phylogenetic reconstruction of the origins of continental diversity also can provide insights into factors responsible for regional differences in diversity. We turn to birds for an example. The passerine (songbird) fauna of South America consists of an old South American radiation (parvorder Tyrannida), which produced 916 contemporary species, plus 14 additional clades derived from North American lineages at various times, several of which have undergone major radiations in South America, and which produced an additional 702 species. The passerine fauna of North America consists of 257 species in 23 clades, some of

them derived from South America, but none comprising a major North American radiation (Ricklefs unpubl., after Sibley and Ahlquist 1990). We can use genetic distance estimated by DNA-DNA hybridization (Sibley and Ahlquist 1990) as an index to relative age. In this case, genetic distance is expressed as the difference in melting points (temperature at 50% dissociation, ΔT_{H50}) between hybridized and selfed complementary strands of DNA. Accordingly, the base of the South American tyrannid radiation is at $\Delta T_{H50} = 13.8^\circ\text{C}$, and the exponential rate of subsequent diversification expressed as a function of ΔT_{H50} is $\log_e(916)/13.8 = 0.50^\circ\text{C}^{-1}$. Other South American clades began to diversify at an average genetic distance of $\Delta T_{H50} = 5.3^\circ\text{C}$, implying an average exponential rate of 0.61°C^{-1} . In comparison, North American clades of passerines (average $\Delta T_{H50} = 4.6^\circ\text{C}$) diversified at an average rate of 0.38°C^{-1} . Thus, the low diversity of passerine birds in North America is related to the relatively young age of the avifauna and slow net rate of diversification (speciation – extinction). Although net rate of diversification may have a local ecological component, it may also reflect geography and factors affecting rates of evolution and extinction.

So the influence of history is evident! But does history help us to understand geographical variation in local diversity? Perhaps the most important contemporary source of information about history would be the distribution of ages of taxa within regions or local communities. The potential strength of this information is measured by its ability to test hypotheses about diversity patterns. In particular, to the extent that biotas in areas with similar contemporary diversity have different age distributions, one could reject history as a plausible cause of this similarity.

The central issue addressed by Francis and Currie is spatial variation in taxonomic richness. Those who advocate local ecological determination of diversity should ask themselves whether ecological causes could explain three-fold differences in the local diversity of mangrove plants in comparable habitats in different regions. If historical explanations are tenable in this case, these individuals should also ask whether gradients in diversity that parallel gradients in ecological conditions might have historical explanations, as well. After all, different environments likely have had different histories.

The spatial and temporal dimensions of history and geography offer tremendous opportunities for ecologists to explore diversification at the intersection of ecology and evolution. Restricting ecological concepts to local interactions because they match a perception of local determinism, and to experimental studies because they are feasible, would be a tragic mistake. It would be equally wrong-headed to simply accept historical explanations for data that do not fit ecological models. What is needed is a broad-minded and scientifically rigorous integration of history and ecology.

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