Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness

Roger Earl Latham and Robert E. Ricklefs

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Energy-diversity theory has gained currency as an explanation for global patterns of species richness. We examine the suggestion of Currie and Paquin (1987; Nature 329: 326–327) that variation in evapotranspiration – a function of moisture availability and temperature that is directly related to plant production – predicts tree species richness in global comparisons. We present contrary evidence: the number of tree species on 26 large (17–7 401 km²) areas of moist temperate forest show continental differences unrelated to geographical patterns in evapotranspiration. Tree species richness of 128 samples of ca 1 ha within moist-forest biomes of the world reveal patterns of variation among continents, and with latitude, that likewise cannot be attributed to geographical patterns in evapotranspiration. We suggest an alternative, scale-dependent interpretation of the relationship between evapotranspiration and tree species richness inferred by Currie and Paquin and others from regional samples. We propose historical explanations for the dissimilarity of tree species richness among similar biomes on different continents, and for the pervasive decrease in species richness with distance from the equator.

R. E. Latham and R. E. Ricklefs, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104-6018, USA (current address of REL: Dept of Geology, Univ. of Pennsylvania, Philadelphia, PA 19104-6316, USA).

Several authors have suggested that energy availability may constrain the numbers of species coexisting in communities (Hutchinson 1959, Connell and Orias 1964, MacArthur 1965, Richerson and Lum 1980, Brown 1981, Wright 1983, Currie and Paquin 1987, Turner et al. 1988, Adams and Woodward 1989, Brown and Maurer 1989, Currie 1991, Wright et al., in press). Stated simply, energy-diversity theory (called by some authors "species-energy" theory) argues that the more energy available, "the more organisms and hence, the more species the environment can support" (Brown 1981). Furthermore, greater biomass increases biological heterogeneity which, in turn, favors specialization and thereby promotes the coexistence of species.

Tests of the validity of the energy-diversity hypothesis have focused on the relationship of species richness to measures of energy available to the biological community (Brown 1981, Wright 1983, Currie and Paquin 1987, Turner et al. 1988, Adams and Woodward 1989, Currie 1991). Annual actual evapotranspiration (AET, expressed in mm), which is computed from temperature, precipitation and estimated soil water storage, accurately predicts primary (plant) productivity (Major 1963, Rosenzweig 1968, Lieth and Whittaker 1975). Currie and Paquin (1987) used range maps to count the numbers of tree species (maximum height ≥ 3 m) in North America in 336 contiguous sampling areas measuring 2.5° (latitude) × 5° north of 50°N latitude and 2.5° × 2.5° to the south. Species richness within these blocks correlated positively with AET ($r^2 = 0.71$, $P < 0.001$). The authors then tested the predictive power of a sigmoidal regression model based on the relationship between species richness and AET in North America. Although data from Ireland and Great Britain
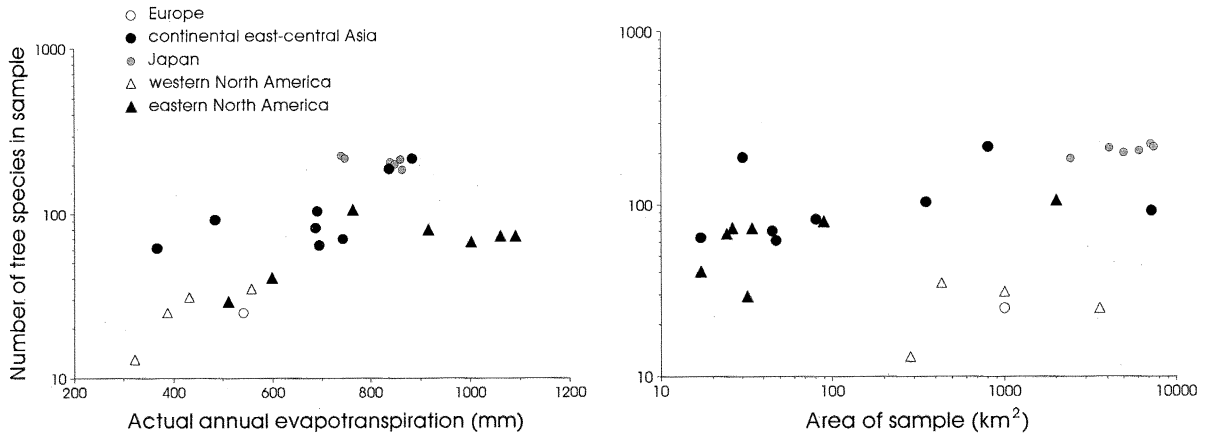
Fig. 1. Tree species in $10-10^4$ km^2 areas of moist temperate forest in Europe, Asia and North America, as a function of actual annual evapotranspiration (AET) and area (data from Table 1).

matched the North American pattern rather well, 7 of 8 points fell below the regression line (Wilcoxon matched-pair sign test, $P = 0.009$), indicating significantly lower species richness in the British Isles.

Currie and Paquin restricted their analysis to temperate North America and Europe. If their relationship can be generalized, it should predict diversity in moist-temperate forests of eastern Asia, which have long been known to support substantially higher numbers of tree species, at least on a regional basis, than forests in climatically similar areas in North America and Europe (Gray 1878). Eastern Asia's temperate forests embrace most of the total global diversity of temperate trees, whether measured by distributions of families (95% of the total northern hemisphere temperate tree flora), genera (87%) or species (63%) (Latham and Ricklefs, in press). Adams and Woodward (1989) attempted to test the global predictive power of the relationship between large-scale diversity and energy availability using methods similar to those of Currie and Paquin, but their Asian samples included only boreal Russian east Asia, insular Japan, and tropical and montane, insular Taiwan. Because continental Asian moist-temperate forests were not represented in their analysis, their conclusion that Asian and North American forests have similar diversity is unsupported.

Productivity and regional diversity in temperate and tropical forests

If energy-diversity theory has global validity, highly productive and diverse tropical forests and less diverse temperate forests should occupy different positions along a single energy-diversity regression line. Unfortunately, data from moist tropical regions are available only for much smaller sample areas than the contiguous

blocks used by Currie and Paquin and by Adams and Woodward. Some comparisons are nonetheless instructive (Table 1). Values predicted by Currie and Paquin's equation correspond moderately well to tree species richness in 11 large areas of relatively unaltered forest in North America where the flora has been well documented. This was to be expected since the equation is based on data from large blocks in North America. The Białowieża forest in eastern Poland-western Belorussia, which may be moist-temperate Europe's only remaining large old-growth forest tract (Faliński 1986), contains a lower percentage of the number of species predicted by Currie and Paquin's equation than any of the North American sites.

Two areas of moist tropical forest in Central and South America support greater species richness than predicted by Currie and Paquin's equation, even on 1 ha Amazonian study plots (Gentry 1988b), seven orders of magnitude smaller than Currie and Paquin's samples. The inability of Currie and Paquin's model to predict tree species richness of tropical samples arises in part from the low asymptote estimated from the North American data and the fact that values of AET for most regions of the humid tropics lie outside the range of temperate values. But the model also fails to predict the high species richness of large forest samples from mainland east-central Asia and Japan (Fig. 1), where AET values do not differ from those of the North American samples (Kruskall-Wallis $\chi_1^2 = 2.0$, $P = 0.16$, $N = 7$, 14).

The native tree floras of eight large forest remnants in China and Korea and six Japanese prefectures contain significantly greater tree species richness (by a factor of 1.9) than do the floras of similar climates in temperate eastern North America (Fig. 1). In an ANCOVA in which the logarithm of the sample area ($F_{1,17} = 33.4$, $P < 0.0001$, b = 0.138 ± 0.024) and AET ($F_{1,17} = 33.8$, $P < 0.0001$, b = 0.00073 ± 0.00013) were covariates, the logarithm of species richness differed significantly be-
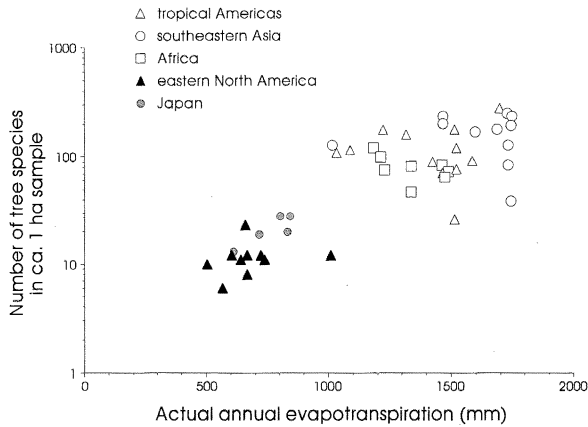
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Fig. 2. Semilogarithmic relationship between number of tree species and AET on ca 1 ha plots of uniform forest. We examined three compilations of tree species inventories – Richards (1952) and Whitmore (1984) for tropical forests and Braun (1950) for North American temperate forests – and more than 30 primary sources.* The minimum size criterion used for counting an individual as part of a sample varies widely among published reports. The most common criterion for published inventories of tree species in tropical forest stands, which tend to be recent and to be performed by biologists, is 10 cm dbh (stem diameter at breast height, 1.4 m). Criteria vary widely for published inventories of tree species in temperate forests: 2.5 cm (1 in), 5.1 (2), 7.6 (3), 10.2 (4), 15 (6) and 25 (10) recur in the literature. We used data collected in the tropics from sampling plots of 0.6 to 2 ha with dbh criteria of 9.7 to 15 cm. Because of the scarcity of comparable data from the temperate zone we relaxed the criteria for temperate samples, using data with minimum size criteria for counting an individual in a sample of 4 cm dbh (or 2 m height) to 25 cm dbh, and sampling areas of 0.5 to 10 ha. The temperate-zone data include only broad-leaved or mixed forests; boreal and other predominantly needle-leaved forests were excluded. Some studies reported the species composition of several (up to 50) stands within an area small enough to correspond to a single value of AET estimated from a nearby climate data station. We calculated the geometric means over all stands of number of tree species, number of individuals, and area sampled. Handled in this manner, our data set included 42 areas representing a total of 124 samples. The AET estimates are from the nearest weather station of similar elevation.

* Additional references: Anderson and Benson (1980), Ashton (1964), Aubréville (1938), Baur (1964; cited in Hall and Swaine 1981), Black et al. (1950), Brown (1941), Chittenden (1905), Cousens (1951), Curtis (1959), Davis and Richards (1933–1934), Foster and Hubbell (1990), Gentry (1988b), Hall and Swaine (1981), Hartshorn (1983), Kartawinata et al. (1981), Lutz (1930), Naka (1982), Nakashizuka and Numata (1982a), T. Nakashizuka (pers. comm.; sites described in Nakashizuka and Numata 1982b and Nakashizuka 1989), Nicholson (1965; cited in Austin and Greig-Smith 1968), Paijmans (1970), Potzger et al. (1942), Prance et al. (1976; cited in Anderson and Benson 1980), Proctor et al. (1983), Reed (1905), Reitsma (1988), Richards (1939), Schultz (1960; cited in Ashton 1964), Telford (1926; cited in Braun 1950), Vestal and Heermans (1945), White (1987), Whitmore (1974), Wyatt-Smith (1949), S. Yamamoto (pers. comm.), Zon (1904), Zon and Scholz (1929; cited in Braun 1950).

tween the Asian samples (geometric mean = 129 species) and eastern North American samples (69 species) ($F_{1,17} = 25.9$, $P < 0.0001$; overall ANCOVA, $F_{1,17} = 45$, $P < 0.0001$, $R^2 = 0.89$). Because AET was inversely related to latitude ($r = -0.82$, $P < 0.0001$) the two variables were interchangeable in this analysis, and neither made a unique contribution to the relationship with the other left in (Type III sums of squares, $P > 0.5$). We retained AET in the analysis because it has a more readily interpretable relationship to species richness.

When the one European and four western North American localities were included in an identical ANCOVA, AET made a significant contribution to variation in the logarithm of species richness ($F_{1,19} = 8.50$, $P = 0.0089$) even with latitude included ($F_{1,19} = 0.23$, $P = 0.61$). With latitude deleted from the analysis, the ANCOVA ($F_{5,20} = 60.2$, $P < 0.0001$, $R^2 = 0.94$, residual = 0.10) revealed species richness to depend significantly on both sample area ($F_{1,20} = 33.1$, $P < 0.0001$, b = 0.137 ± 0.024) and AET ($F_{1,20} = 38.5$, $P < 0.0001$, b = 0.00078 ± 0.00013), and to differ significantly between regions ($F_{3,20} = 33.6$, $P < 0.0001$): eastern Asia (least-squares geometric mean = 120 species) $\geq$ ($P < 0.0001$) eastern North America (63) > ($P = 0.014$, 0.011) western North America (36) = ($P = 0.425$) Europe (29).

Thus, as Currie and Paquin found, species richness was related to AET in these large samples, increasing by a factor of 1.2 for each 100 mm of AET, but species richness also differed by a factor of 1.9 between eastern Asia and eastern North America independently of AET. Indeed, the average AET for the large areas in eastern North America (849 mm) exceeded that in eastern Asia (734 mm). Furthermore, the Asian areas supported an average of 1.6 times the diversity predicted by Currie and Paquin's equation, in spite of their being one to three orders of magnitude smaller than the North American areas from which the equation was derived. Larger areas comparable to those considered by Currie and Paquin (51 000–100 000 km²) might harbor substantially more species than the smaller samples, owing to turnover of species between habitats within the larger areas. On a continent-wide basis, moist temperate forests in Asia harbor about three times as many species of trees as similar forests in North America (Latham and Ricklefs, in press).

Species richness in local forest plots

Species richness in large, ecologically heterogeneous areas reflects factors, such as habitat specialization, that do not directly pertain to testing the energy-diversity hypothesis. Local samples from small, homogeneous forest stands more appropriately match the scale of the processes assumed to be relevant, inasmuch as local

Table 1. Tree species richness in large forested areas.

	Area (km²)	Fraction*	AET (mm)[†]	Predicted[§]	Observed[¶]	%
Eastern North America						
Big Thicket (Texas, USA)[1]	34	$\frac{1}{1700}$	1061	151	73	54
Congaree Swamp (South Carolina, USA)[2]	89	$\frac{1}{710}$	915	131	80	61
Francis Beidler Forest (South Carolina, USA)[3]	24	$\frac{1}{2600}$	1001	144	68	47
Great Smoky Mountains (North Carolina/Tennessee, USA)[4]	2000	$\frac{1}{31}$	763	102	107	105
Huron Mountain (Michigan, USA)[5]	32	$\frac{1}{1700}$	510	54	29	54
San Felasco Hammock (Florida, USA)[6]	26	$\frac{1}{2600}$	1091	155	73	47
Tionesta Natural Area (Pennsylvania, USA)[7]	17	$\frac{1}{3500}$	599	70	41	59
Western North America						
Olympic Peninsula (Washington, USA)[8]	3600	$\frac{1}{14}$	388	36	25	69
Mt. Rainier National Park (Washington, USA)[8]	1000	$\frac{1}{50}$	432	42	31	74
Redwood National Park (California, USA)[9]	433	$\frac{1}{170}$	558	63	35	56
South Warner Wilderness (California, USA)[10]	286	$\frac{1}{250}$	322	29	13	45
Europe						
Białowieża Forest, (Belorussia and Poland)[11]	1000	$\frac{1}{91}$	541	59	25	42
Temperate eastern Asia						
Beihuashang-Xiaollongmen Forest (Beijing Shi, China)[12]	17	$\frac{1}{3500}$	695	89	64	72
Fukuoka Prefecture (Kyushu I., Japan)[13]	4963	$\frac{1}{13}$	848	119	203	171
Jigong Mountain (Henan, China)[14]	30	$\frac{1}{2200}$	836	117	190	162
Kochi Prefecture (Shikoku I., Japan)[15]	7104	$\frac{1}{9}$	740	98	226	231
Kumamoto Prefecture (Kyushu I., Japan)[16]	7401	$\frac{1}{9}$	746	99	217	219
Lichuan Xian (Hubei, China)[17]	800	$\frac{1}{80}$	883	125	217	174
Mt. Seolag (S. Korea)[18]	350	$\frac{1}{170}$	691	88	104	118
Nagasaki Prefecture (Kyushu I., Japan)[19]	4088	$\frac{1}{16}$	859	121	216	179
Pukhansan National Park (S. Korea)[20]	80	$\frac{1}{750}$	686	87	82	94
Saga Prefecture (Kyushu I., Japan)[21]	2439	$\frac{1}{26}$	862	121	186	154
Seonunsan Provincial Park (S. Korea)[22]	45	$\frac{1}{1400}$	743	98	70	71
Sonshang Forest (Hebei, China)[23]	47	$\frac{1}{1200}$	366	34	62	182
Taihang Mountains (Shanxi, China)[24]	7200	$\frac{1}{8}$	485	50	93	186
Yamaguchi Prefecture (Honshu I., Japan)[25]	6109	$\frac{1}{11}$	838	117	208	178
Tropical America						
Golfo Dulce (Costa Rica)[26]	6000	$\frac{1}{13}$	825–1501	114–179	433	242–380
Amazonia (Peru)[27]	1 ha	$< 10^{-6}$	1231–1760	167–183	155–283	90–155

* Fraction of the sampling area of Currie and Paquin's (1987) method: 2.5° latitude × 5° longitude (57000–100000 km²) north of 50°N and 2.5° × 2.5° (51000–71000 km²) to the south.
[†] Value of AET from climate data station nearest to sampling area, or geometric mean of data from multiple stations within sampling area (Thornthwaite 1964).
[§] Currie and Paquin's (1987) regression equation for tree species richness is R = 185.8 (1 + e$^{[3.09−0.00432(AET)]}$)$^{−1}$, which relates R to AET by a sigmoid curve with an inflection point (half of asymptotic value) at 715 mm AET and an upper asymptote (maximum richness) of 186 species.
[¶] Only native species of trees are included. Size criterion varies from study to study.
References: [1]National Park Service (1982; median of six samples); [2]Gaddy (1979); [3]Porcher (1981); [4]White (1982); [5]Simpson et al. (1990); [6]Dunn (1982); [7]Bjorkbom and Larson (1977); [8]J. F. Franklin (pers. comm.); [9]M. M. Hektner (pers. comm.); [10]Riegel and Schoolcraft (1990); [11]Faliński (1986); [12,14,23,24]Huo S. (unpubl.); [13]Amakawa (1975); [15]Yamanaka (1978); [16]Botanical Society of Kumamoto Prefecture (1969); [17]Chu and Cooper (1950), Hu (1980), Bartholomew et al. (1983); [18]Yim and Baik (1985); [19]Toyama (1980); [20]Lee and Yim (1989); [21]Baba (1981); [22]Kim et al. (1988); [25]Oka (1972); [26]Allen (1956; range from large tree species only to large and small tree species combined); [27]Gentry (1988b; range of six samples).

interactions among individuals of different species mediate the relationship of productivity to diversity.

Relevant data are remarkably scarce. "Sample areas of ≥ 1 ha are needed to adequately measure tree species diversity" (Gentry and Dodson 1987: 149). Unfortunately, botanists most frequently sample trees by belt transects or within plots rarely more than 0.1 ha in area because of the time and effort required to exhaustively tabulate species. A circular 0.1 ha plot has a radius of less than 18 m, typically including only 20–70 post-sapling stage trees. The compilations of local tree species richness data with the largest sample sizes use 0.1 ha samples (e.g., Gentry 1988a). We maintain that they are inadequate from which to draw conclusions about global tree species richness patterns, particularly where local, within-habitat diversity exceeds the number of individual trees on such plots. Furthermore, lianas have commonly been lumped with trees in such samples (e.g., Gentry 1988a). Lianas comprise widely varying proportions of the plant species in tropical forest census data, often approaching or matching the number of tree species (Gentry and Dodson 1987), whereas they typically represent a trivial fraction of the species richness in temperate forests. Considering patterns of species richness of trees and lianas together could obscure the possible significance of the two growth forms' individual diversity patterns.

Few studies have produced tabulations of tree species for plots on the order of 1 ha in tropical and temperate undisturbed forests. Ironically, fewer samples at this scale exist for temperate undisturbed forests than for tropical forests, possibly because most of the former were altered or destroyed before scientific interest in species richness arose, or because species inventory in temperate forests provides a smaller payoff in new scientific knowledge. Unfortunately, 1 ha tree species tabulations have not, so far, been forthcoming from temperate, continental eastern Asia (Chen L., pers. comm.; Shen G., pers. comm.; Zhang J., pers. comm.).

Among 106 tropical and 22 temperate samples of 0.5–10 ha, representing 30 and 16 locations, tree species richness varied from 26–283 and from 6–28, respectively. Over the entire sample, species richness and AET were strongly related (Fig. 2). However, the contributions of AET and latitude to the relationship were roughly parallel, and the effects of these two independent variables cannot be distinguished statistically. In an ANCOVA, with tropical versus temperate as a main effect and AET as a covariate, the logarithm of species richness was independent of AET within latitude belts ($F_{1,44} = 1.9$, $P = 0.17$) but differed significantly between latitude belts ($F_{1,44} = 24$, $P < 0.0001$). Neither number of individuals nor area sampled was a significant effect in the model. Furthermore, within the tropical and temperate sets of localities AET does not explain variation in species richness when it is entered with plot area in a multiple regression (tropical: $F_{1,28} = 0.5$, $P = 0.48$; temperate: $F_{1,13} = 3.77$, $P = 0.074$).

Comparison of forest species richness among continents

In ANCOVAs of the small forest plot data (Fig. 2) with continent as the main effect, neither plot area nor AET was a significant covariate with diversity. In an ANOVA in which the dependent variable was the logarithm of species richness, 11 Asian areas had significantly more species of trees ($P < 0.05$; geometric mean $= 152$) than 8 African areas (79 species) by Tukey's honestly significant difference test (HSD); 12 tropical American areas were intermediate (108 species) and did not differ significantly from either of the other continents. The ANOVA results ($F_{2,28} = 3.7$, $P = 0.037$, $R^2 = 0.21$) and the lack of significance of AET entered as a covariate indicate that most variation occurs within continents, in response to factors other than AET.

Similarly, within temperate latitudes, tree species richness of 5 Japanese samples (21 species) significantly exceeded that of 11 eastern North American sites ($P < 0.01$; 11 species) by Tukey's HSD (overall ANOVA $F_{1,14} = 13.4$, $P = 0.0025$, $R^2 = 0.49$), despite the lack of significant differences between the two groups of samples in latitude (ANOVA $P = 0.12$; Wilcoxon rank sums test $P = 0.08$) or AET ($P = 0.22$; $P = 0.14$). For larger areas, also, temperate Asian forests clearly are more diverse than their counterparts in North America and Europe (Table 1; Wang 1961, Latham and Ricklefs, in press).

Diversity and scale of sampling

The discrepancy between our analysis and that of Currie and Paquin lies in the different scales of the two studies and in their geographical scope. Currie and Paquin tabulated numbers of tree species in large geographical areas encompassing all of North America. In their study, the relationship between species richness and AET at a regional scale arose primarily from the fact that more species of trees occur in mesic forest habitats of east-central North America than in tundra, boreal and montane needle-leaf forests, grasslands and deserts in the north and west. We hypothesize that low tree species richness at low values of AET (less than 300–500 mm) in Currie and Paquin's and Adams and Woodward's temperate, mid-latitude samples reflects the confinement of trees to restricted mesic habitats, such as river courses, in regions that are generally too dry for trees. As moisture (and thus, AET) increases, the proportional area and variety of forested habitats in 51 000–100 000 km² samples increases, producing a corresponding increase in tree species richness. We propose a different explanation for low tree species richness in the Currie-Paquin and Adams-Woodward taiga or boreal forest samples, which we will discuss later.

The energy-diversity theory links supposed equilibrium species numbers to a resource limitation. A link between resource limitation and species' presence or absence depends on the sum of interactions, such as competition for food or space, among individual members of populations. Thus, we believe that local assemblages of species provide more appropriate tests of the theory's predictions than do regional lists.

Our compiled ca 1 ha samples were restricted to broad-leaved forest habitats. In spite of a two-fold variation in AET among these samples in North America (502–1 013 mm) and somewhat narrower ranges on other continents, AET had no significant influence on number of tree species, particularly when differences between continents were factored out statistically (AET: $F_{1,12} = 2.3$, $P = 0.15$). The same was true of the tropical samples, among which AET varied from 1 015–1 748 mm ($F_{1,26} = 0.35$, $P = 0.56$).

We believe that the Currie-Paquin and Adams-Woodward relationships reflect the dependence of tall, woody, broad-leaved plants on certain minimum conditions of temperature and moisture. Furthermore, the relationship may follow from the predominantly tropical and subtropical origins of the temperate flora. If temperature and moisture tolerances are, to some degree, clade-specific, then the distribution of species within a region will reflect the climatic conditions under which the clades evolved. Thus, Currie and Paquin's analysis may represent the geographical sorting out of a flora in relation to its historical origins. If the origins were primarily tropical, then areas with higher temperature and moisture (thus, greater AET) would likely harbor more species because of historical and biogeographical considerations. Assuming broad-leaved trees were mainly tropical in origin, then they crossed a major evolutionary barrier – frost tolerance – relatively recently as frost-influenced climates arose in the middle Tertiary and spread southward across the mid-latitudes. The clades that acquired frost tolerance would have radiated and diversified but, assuming similar production rates of new tree species in tropical and temperate forests, tree species richness would continue to show a geographical pattern of decrease with greater departure of conditions from those of moist tropical habitats. Boreal climates have presented more complex evolutionary barriers against entry by broad-leaved tree clades than cool-temperate climates, which in turn have posed more resistance than warm-temperate climates. Thus, the low tree species richness of the Currie-Paquin and Adams-Woodward boreal forest sampling blocks may reflect the evolutionary history of broad-leaved trees and the relative newness of continental arctic climates. This hypothesis predicts that biogeographical distribution and phylogenetic history should be related. For example, one would expect a nonrandom distribution of taxonomic groups among climatically differentiated subregions within a continent, reflecting clade-specific tolerances of ecological conditions.

Establishment of global diversity patterns

The absence of correlations between local-scale species richness and AET within broad latitudinal belts, and the divergence of species richness between continents in comparable climatic zones, leads us to question whether the general relationship between diversity and latitude is related to biological productivity, or any other local factor. To be sure, a relationship between diversity and AET within areas could be obscured by the maintenance of species within some habitats by migration of individuals from habitats having greater species richness (Shmida and Wilson 1985, Pulliam 1988, Stevens 1989). Furthermore, the diversity "anomalies" between continents are small (a factor of 2 in this study) compared to latitudinal differences in diversity (a factor of 10). But migration among habitats, which tends to obscure local ecological determinism, and global diversity anomalies, which reflect the unique histories and geographical positions of each region, underscore the importance of regional processes influencing the diversity of the local ecological community (Ricklefs 1987).

These processes might include global variation in Pliocene and Quaternary extinctions owing to singular events and circumstances that are idiosyncratic to particular areas of land. The fossil record reveals the disappearance of many contemporary eastern Asian and North American tree genera from Europe beginning in the Pliocene (van der Hammen et al. 1971). The amount of land at various latitudes and the nature of barriers to movement of populations during worldwide climatic fluctuations differ greatly among the continents and across geologic time (Sauer 1988). These geographic variables could have potently affected the sizes of forest refugia during glacial maxima and the degree of connectedness between temperate forests and species-rich tropical forests (Butzer 1974, Prance 1982, Delcourt and Delcourt 1987, Sauer 1988). Fossil floras reveal, however, that Asian mid-latitude forests have had considerably higher numbers of tree genera than those of North America and Europe since long before late-Tertiary global cooling (Latham and Ricklefs, in press).

On a global scale, latitudinal patterns in tree diversity may reflect very long-term evolutionary and geographical processes coinciding with most of the history of angiosperm evolution. The decrease in tree diversity with increasing latitude occurs primarily at the taxonomic level of the family (Ricklefs 1989), and thus reflects diversification that for the most part predates the middle Tertiary. If broad-leaved trees were predominantly tropical in origin and required major evolutionary change to invade temperate (generally frost-influenced) regions, and if clades produced species more or less independently of latitude, then diversity would accumulate in tropical regions owing to age and number of old taxa (Farrell et al. 1992, Latham and Ricklefs, in press).

This "time" hypothesis is itself quite old and has

resurfaced many times in the history of the debate over patterns of diversity (Willis 1922, Anderson 1974, Knoll 1986). Recent difficulty with the idea has its origin in a general disbelief that community diversity could fail to achieve a local ecological equilibrium (Ricklefs 1987). However, the plausibility of the time hypothesis is bolstered by at least three lines of evidence. First, species richness varies dramatically among geographically separate areas of certain ecosystem types, for example, mediterranean scrub (Shmida 1981) and mangrove (Ricklefs and Latham, in press). Second, accumulating evidence points to long-term evolutionary conservatism of ecologically important traits (Jablonski 1987, Vermeij 1987, Ricklefs and Latham 1992). Finally, angiosperm diversity in local fossil floras has increased steadily through the Cretaceous and Tertiary (Knoll 1986).

Patterns of species diversity, both among and within regions, reflect processes that occur at many scales. The patterns embody ecological interactions that limit the coexistence of species locally, factors that determine habitat selection and geographical range (Cody 1985, Brown and Maurer 1989), and regional processes of species production and migration (Ricklefs 1987). The number of species inhabiting an entire contiguous biome limits regional species pools, from which samples at the scales of landscape, habitat and patch are drawn. Thus, historical effects on continent-scale diversity may be expressed at several scales.

Comparative data compiled to evaluate hypotheses must match the scale of sampling to the scale of the processes that underlie the hypothesis. Predictions of the energy-diversity hypothesis must be compared to patterns of diversity in the small areas in which individuals compete for resources. The virtual absence of comparative data at the local scale from temperate and subtropical, continental eastern Asia points to the need to test further the prediction, from energy-diversity theory, of convergence in species richness between areas of similar climate or productivity. Diversity patterns at continental or global scales that cannot be explained by geographical patterns in local ecological conditions illustrate the need for a broader range of hypotheses. These should incorporate a hierarchy of mechanisms at the many scales of ecological systems.

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