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ENERGY AND LARGE-SCALE PATTERNS OF ANIMAL- AND PLANT-SPECIES RICHNESS

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Abstract.—Many hypotheses have been proposed to explain the great variation among regions in species richness. These were tested by first examining patterns of species richness of birds, mammals, amphibians, and reptiles in 336 quadrats covering North America. These patterns were then compared with the regional variation of 21 descriptors of the environment suggested by the hypotheses. I found that, in the four vertebrate classes studied, 80%–93% of the variability in species richness could be statistically explained by a monotonically increasing function of a single variable: annual potential evapotranspiration (PET). In contrast, tree richness is more closely related to actual evapotranspiration (AET). Both AET and PET appear to be measures of available environmental energy. The relationships between tree and vertebrate richness are strikingly poor. Species richness in particular orders and families of the Vertebrata is also closely related to PET, but not always monotonically, often resembling a replacement series along an environmental gradient. The present results are consistent with the hypothesis that environmentally available energy limits regional species richness. However, my observations are not completely consistent with earlier species-energy theory. The energy-richness relationship appears to depend on scale, and it is affected differently by variations in area and in areal energy flux.

One might paraphrase the fundamental question underlying Charles Darwin's most celebrated work as being: How did there come to be so many different kinds of organisms? The evident sequel to that question is: How did there come to be *this* many different kinds of organisms (May 1986)? In different words: Why, in a given environment, does one find n different species, not more or fewer, and why does n vary so greatly among environments?

Many hypotheses have been proposed to account for spatial variability in species richness (MacArthur 1965; Pianka 1966; Begon et al. 1990). These may be grouped under a number of headings, which are summarized in table 1 (this list is not exhaustive, but it includes the hypotheses thought to apply most generally). There is evidence (reviewed by Begon et al. [1990]) that most of these factors do indeed influence species richness, at least to some extent, on some spatial scales.

By far the greatest variability in species richness is that observed among geographical regions (e.g., Wallace 1878; Simpson 1964; Schall and Pianka 1978). Superimposed upon the regional variability is variability on the local scale —among and within habitats—which is usually of much smaller magnitude (see, e.g., Abramsky and Rosenzweig 1984; Cornell 1985; Askins et al. 1987). Species richnesses on these two spatial scales seem likely to be controlled by different

TABLE 1

FACTORS HYPOTHESIZED TO INFLUENCE SPECIES RICHNESS

Factor	Rationale
1. Climate	Benign conditions permit more species
2. Climatic variability	Stability permits specialization
3. Habitat heterogeneity	Physically or biologically complex habitats furnish more niches
4. History	More time permits more complete colonization and the evolution of new species
5. Energy	Richness is limited by the partitioning of energy among species
6. Competition	a. Competition favors reduced niche breadth
	b. Competitive exclusion eliminates species
7. Predation	Predation retards competitive exclusion
8. Disturbance	Moderate disturbance retards competitive exclusion

factors. Regional species pools exist, the sizes of which probably depend on factors that act on very large scales (e.g., climate); local subsets seem likely to be derived from the regional pool by local processes such as biotic interactions. This hypothesis suggests two separate questions: What factors determine the size of regional species pools, and what factors control the subsampling from the regional pool that establishes local pools?

The purpose of the present study is to investigate the hypotheses in table 1 with respect to the variation in species richness on the continental scale. Although in principle many factors may affect species richness, it is reasonable to inquire whether one factor, or a small number of factors, is responsible for most of the variation. Most of the hypotheses in table 1 predict that correlations will exist between observable characteristics of the environment and species richness. Even though correlations do not demonstrate causality, they do serve two useful functions. When a correlation predicted by a hypothesis is not observed, the hypothesis may be considered false. Furthermore, when a correlation predicted by a hypothesis is weaker than other observed correlations, one may conclude that a better hypothesis exists. In this study, I examine the correlations between the species richnesses of North American birds, mammals, amphibians, and reptiles and the characteristics of their environment suggested by the hypotheses in table 1, including the species richness of trees. I have not included Mexico and Central America in this analysis because species distributions in these areas do not yet appear to have been summarized in a useful manner.

METHODS

In general terms, the study was organized as follows. The North American continent was divided into 336 quadrats. The number of species of trees, birds, mammals, amphibians, and reptiles occurring in each quadrat was estimated from published sources. Similarly, 21 descriptors of the environment were determined for each quadrat. Statistical relationships among the variables were then sought. Details follow.

North America north of the Mexican border was divided into quadrats follow-ing lines of latitude and longitude: $2\frac{1}{2}° \times 2\frac{1}{2}°$ south of 50° N, and 5° (latitude) $\times 2\frac{1}{2}°$ (longitude) north of 50° N. This system yields quadrats with unequal areas but with boundaries that are easy to establish on maps of any projection (unlike equal-area quadrats, e.g., those of MacArthur and Wilson 1967). The land area within each quadrat was determined by planimetry and was used as a covari-ate in regression models. Offshore islands (e.g., Vancouver, Anticosti, New-foundland, the Florida Keys, the Canadian arctic islands, etc.) were excluded from this analysis.

The number of species of trees (any lignified plant growing to a height of at least 3 m anywhere in its geographical range; Little 1971) occurring in each quadrat was established by superimposing maps of the feral geographical distributions of the 620 tree species indigenous to North America (Little 1971; Elias 1980; Hosie 1980) and then tallying the number of species present in each quadrat. The species richness of mammals was established similarly from the range maps of Hall and Kelson (1959), and the richnesses of amphibians and reptiles from the maps of Stebbins (1966) and Conant (1975).

The richness of bird species was estimated from the already-compiled map presented by Cook (1969). The present system of quadrats was superimposed on Cook's map, and the maximum species density occurring anywhere in the quadrat was taken as the species richness. This procedure probably underestimated the true richness by a small amount.

Descriptors of the environment were also determined from published maps (International Map of the World 1912–; Climatic Atlas of the United States 1968; Prest 1969; USSR National Committee for the International Hydrological Decade 1977; Climatic Atlas of North and Central America 1979; National Atlas of Can-ada 1981). The effect of climatic severity (table 1, hypothesis 1) was investigated using the mean annual values of temperature, precipitation, potential evapotrans-piration (Budyko 1974), actual evapotranspiration, total solar radiation received at the earth's surface (MJ m^{-2} yr^{-1}), and elevation. Climatic variability (hypothe-sis 2) was represented by the difference between the mean January and July temperatures and levels of precipitation. Habitat heterogeneity (hypothesis 3) was described by the difference between maximum and minimum values within each quadrat of each of the variables above. The principal historical effect (hypothesis 4) that might have influenced species richness in North America was glaciation; I therefore considered whether or not a quadrat had been glaciated or inundated during the Wisconsin period (Prest 1969). The hypothesis that energy might deter-mine richness (hypothesis 5) was examined using mean annual solar radiation, potential and actual evapotranspiration, and annual primary productivity esti-mated from Lieth's (1975) model. The intensities of competition, predation, and disturbance (hypotheses 6–8) are difficult to assess on the large scale; they were therefore neglected. Finally, I considered whether or not a quadrat was on a seacoast or on a peninsula (Nova Scotia and Michigan were treated as penin-sulas).

To determine the relationships between species richness and environment, I

first examined bivariate plots of richness and each environmental descriptor to determine whether the relationship was monotonic. I then calculated nonparametric correlations among the variables and identified the two or three variables most closely related to richness. Most of these relationships proved to be nonlinear and heteroscedastic. The richness data were therefore first transformed to the logarithm of the species number plus one to stabilize their variance. Nonlinear functions were then fitted to the data by iterative minimization of the residual sums of squares (routine CNLR in SPSS-X; SPSS 1988). In most cases, several models were tried for each pair of independent and dependent variables. The best predictor was taken as the relationship with the highest Pearson correlation coefficient, the least apparent lack of fit, and approximately homoscedastic residuals. Multiple regressions were then carried out using the nonlinear function as the first step.

RESULTS

Maps of the spatial distribution of species richness of trees, mammals, amphibians, and reptiles are shown in figure 1. These may be compared to analogous maps of Simpson (1964) and Kiester (1971). Generally, the maps in this figure are quite similar to those published earlier. I report systematically fewer species than does Simpson (1964), perhaps because I lumped all subspecies. The differences between the present maps and those of Simpson and Kiester also reflect the differing size and placement of quadrats in the various studies. These differences indicate the variability associated with the estimates of species richness.

Species richnesses of all the groups of organisms considered in this study vary strongly with latitude, as has been observed many times before (Wallace 1878; Simpson 1964; Cook 1969). The less expected observation is that the relationship is not monotonic for most of these well-studied groups of organisms (fig. 2). When the overall trend in these data is sought with LOWESS (locally weighted sums of squares, a regression technique designed to identify the underlying trend in a data set without a priori specification of a model; Cleveland 1979), bird and mammal richnesses show pronounced peaks at 44° N and 39° N, respectively, and amphibian richness peaks more gently at 34° N. Tree (fig. 3A) and reptile richness both decrease monotonically with latitude over the range studied. Mid-latitude peaks of species richness have been observed before in more restricted studies (birds of the East Coast of the United States, Rabenold 1979; ichneumonid wasps, Janzen 1981); it now appears that this phenomenon is quite general. This almost certainly reflects the fact that species richness is not determined by latitude per se; rather, it depends on other factors that co-vary imperfectly with latitude.

Tree-species richness and the factors related to it have been discussed earlier (Currie and Paquin 1987). I briefly review our findings for comparison with the results for animals below. Tree richness was found to be highly significantly correlated with most of the environmental descriptors studied here (Currie and Paquin 1987, table 1). Tree richness is strongly related to temperature, solar ra-

diation, and potential evapotranspiration (fig. 3*B;* all three relationships are similar), and it shows a weak relationship with precipitation (fig. 3*C*). The strongest correlation is observed with actual evapotranspiration (fig. 3*D*), which statistically explains 76% of the variability in tree richness (Currie and Paquin 1987). We have interpreted this correlation to be consistent with the hypothesis that energy limits regional tree-species richness (see also below).

The most obvious hypothesis to explain variation in animal-species richness is that it varies as a function of the richness of plants with which the animals are associated (MacArthur and MacArthur 1961). The relationships between the species richness of each class of terrestrial vertebrates and that of trees are shown in figure 4. Certainly, it would have been preferable to consider the species richness of all plants. Unfortunately, information on the distributions of plant species other than trees is incomplete. However, tree richness and the vascular plants as a whole probably co-vary closely (see the Discussion). I therefore assume that tree richness is a reasonable surrogate for total vascular-plant richness. It is apparent from figure 4 that only amphibian richness shows a clear monotonic relationship with tree richness. The other vertebrate classes are not functionally related to tree richness in any simple fashion, except in low-richness environments, where all groups co-vary closely.

The next most obvious hypothesis is that richness should be related to primary productivity (Wright 1983; Abramsky and Rosenzweig 1984; Owen 1988). I have estimated primary productivity from annual actual evapotranspiration using Lieth's (1975) model (Rosenzweig's [1968] model yields similar results). Its relationship to the richness of each vertebrate class is shown in figure 5. The scatter in the upper left corners of these plots represents quadrats in the southwestern United States, where vertebrate richness is quite high despite low primary productivity.

Highly significant nonparametric correlations are observed between vertebrate species richness and virtually all the climatic variables investigated in this study (table 2). This reflects the fact that all the climatic factors co-vary to greater or lesser degrees. The three strongest correlates of species richness of each of the vertebrate classes are annual potential evapotranspiration (PET), solar radiation, and mean annual temperature, often in that order. Richness also correlates with the within-quadrat and annual variability of environmental descriptors, but much less strongly so. The latter correlations probably result from the strong correlation of the mean and the variance of all environmental descriptors with each other. The common element in the three strongest correlates of richness is that they all reflect aspects of the regional energy balance.

The best parametric predictor of species richness for each of the vertebrate classes is PET (fig. 6; shown after logarithmic transformation of richness in order to stabilize its variance). In each case, richness appears to be a saturating function of PET (table 3). Bird richness increases linearly with PET up to 525 mm yr^{-1} and then remains constant. The richnesses of mammals, amphibians, and reptiles all increase according to an exponentially decelerating function (fig. 6). In all of these cases, PET alone explains at least 79% of the variability in species richness.
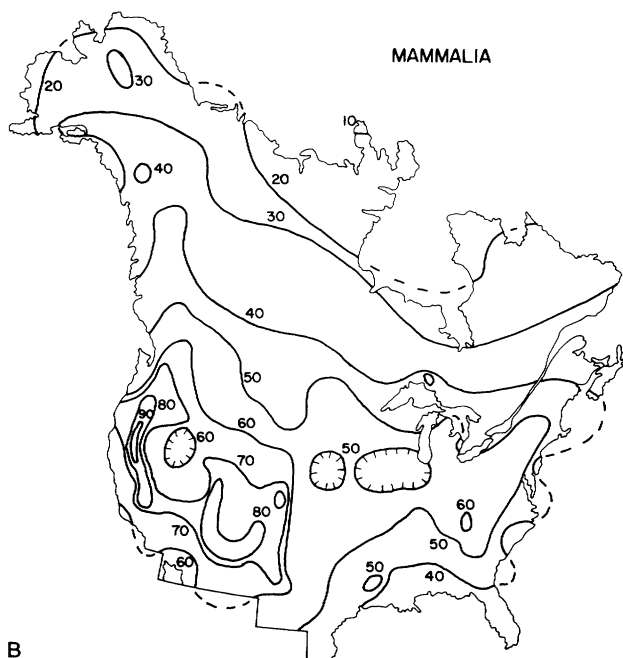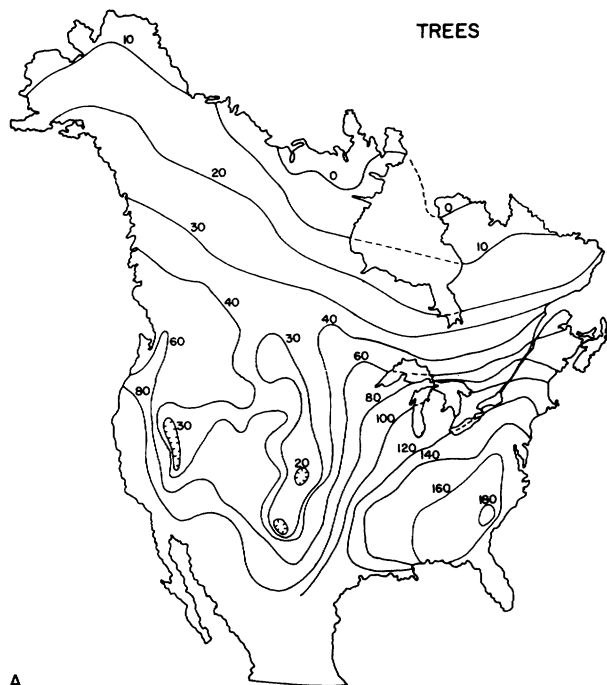
TREES

A

MAMMALIA

B

Fig. 1 (*above and facing page*).—Species richness in Canada and the United States: *A* (*upper*), of trees; *B* (*lower*), of mammals; *C* (*next page, upper*), of amphibians; *D* (*next page, lower*), of reptiles. Contours connect points with the same approximate number of species per quadrat. (Figure 1*A* is reprinted with permission from Currie and Paquin 1987, p. 326, fig. 1. Copyright © 1987 Macmillan Magazines.)

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AMPHIBIA

C

REPTILIA

D

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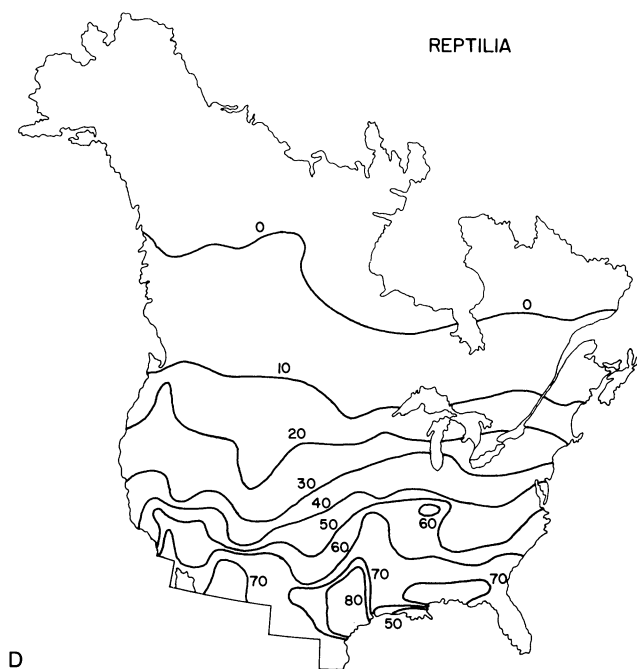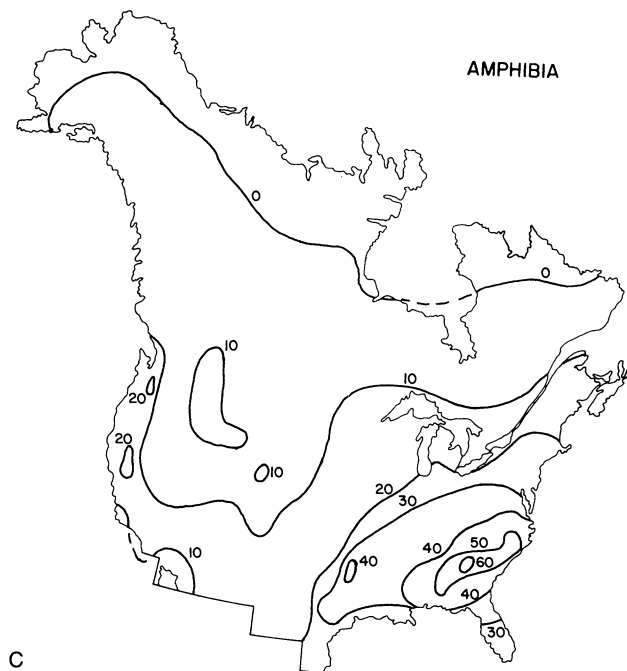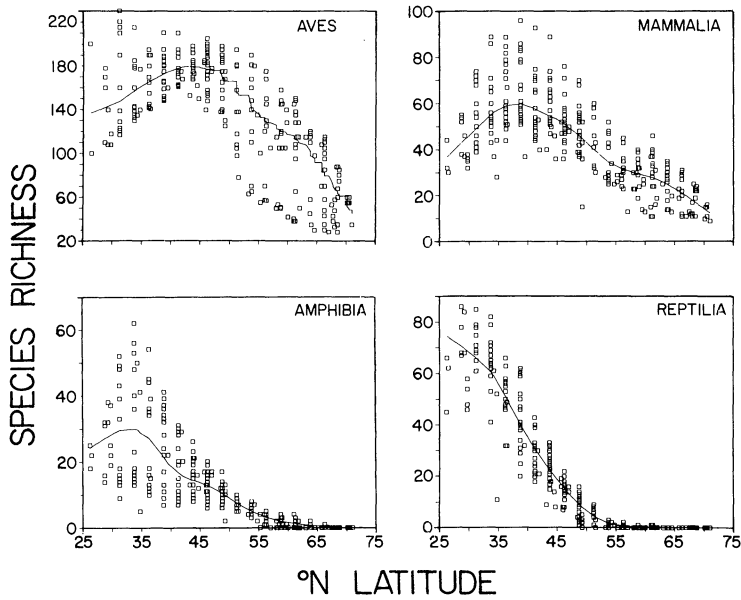
FIG. 2.—Species richness of birds, mammals, amphibians, and reptiles as they vary with latitude. The lines represent the underlying trend found by a LOWESS fit (Cleveland 1979) to the data. Most groups show a mid-latitude peak in richness.
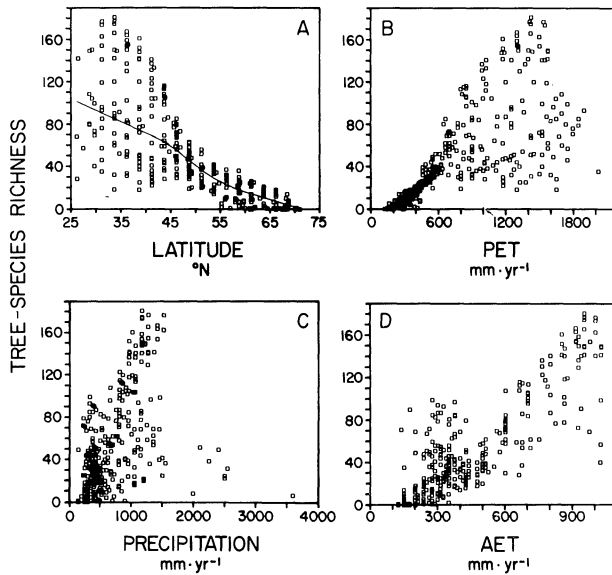
FIG. 3.—The species richness of trees as it varies with *A*, latitude; *B*, potential evapotranspiration (PET); *C*, precipitation; and *D*, actual evapotranspiration (AET). The relationship with AET is strongest. (Figure 3*D* is adapted from Currie and Paquin 1987, p. 327, fig. 2.)

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FIG. 4.—Species richness of birds, mammals, amphibians, and reptiles as a function of tree-species richness.

FIG. 5.—The relationship between the species richness of birds, mammals, amphibians, and reptiles and primary productivity, estimated from actual evapotranspiration (based on Leith's [1975] model).

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TABLE 2

NONPARAMETRIC CORRELATIONS BETWEEN SPECIES RICHNESS AND CLIMATIC FACTORS IN NORTH AMERICA

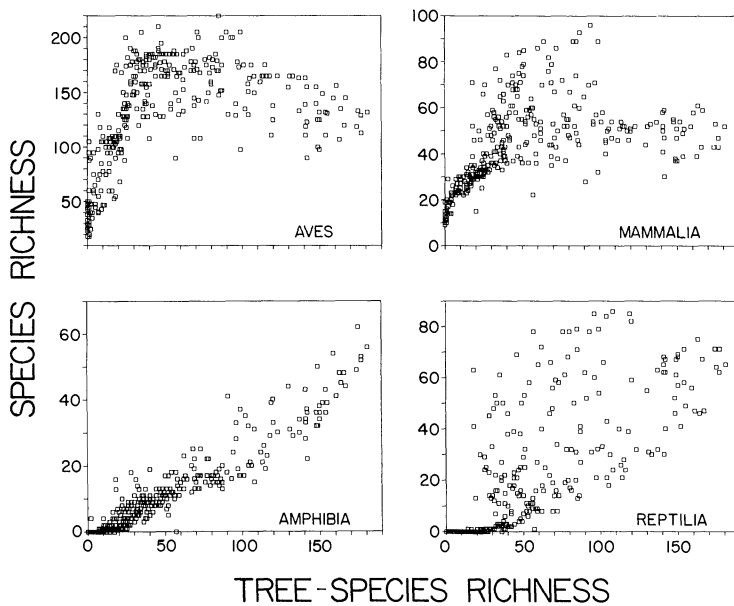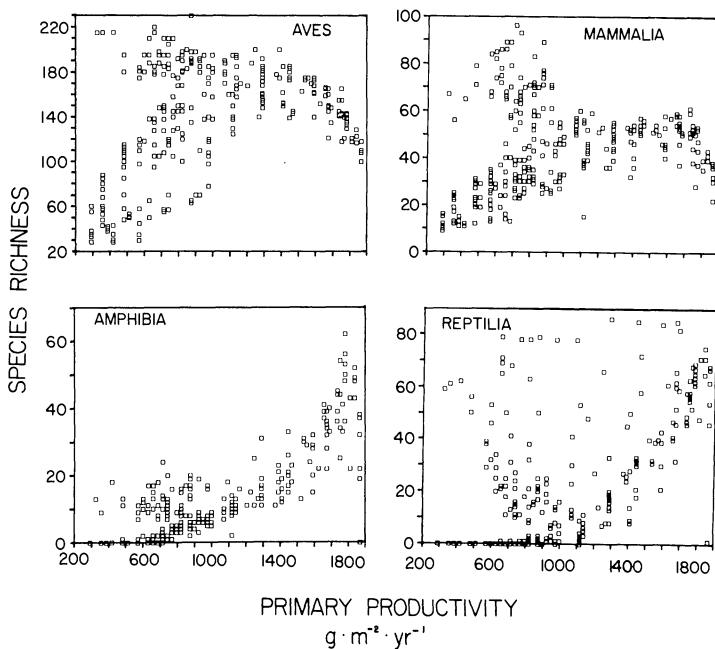| Measurement	Trees	Birds	Mammals	Amphibians	Reptiles	Vertebrates
Median within the quadrat of the annual mean:						
Temperature	.866	.612	.750	.893	.942	.930
AET	.790	.341	.413	.828	.677	.666
PET	.844	.689	.817	.865	.954	.954
Solar radiation	.756	.705	.818	.795	.914	.895
Precipitation	.598	NS	.189	.599	.345	.395
Range of variation within quadrat:						
Elevation	NS	.302	.354	NS	NS	NS
Precipitation	.199	NS	NS	NS	NS	NS
Solar radiation	.417	.415	.541	.433	.528	.530
Range of variation, January to July:						
Temperature	−.706	−.436	−.607	−.722	−.756	−.765
Precipitation	−.154	−.217	−.277	NS	NS	NS
Location:						
Latitude	−.853	−.601	−.754	−.889	−.953	−.935
Elevation	NS	.527	.525	NS	NS	NS
Coast (+/−)	−.267	−.451	−.471	−.230	−.272	−.342
Peninsula (+/−)	NS	−.226	−.219	NS	NS	−.155

NOTE.—Spearman rank correlations between species richness and climatic factors in 337 quadrats encompassing the continental United States and Canada. Vertebrates represent the sum of mammals (exclusive of bats), amphibians, and reptiles. AET and PET, the mean annual values of actual evapotranspiration and potential evapotranspiration. Coast (+/−) and peninsula (+/−) are dummy variables indicating whether or not quadrats are located on a coast or peninsula. NS, $P > .01$. All other correlations are significant at $P < .01$, and those where $|r_s| > 0.160$ are significant at $P < .001$.

Similar models may be constructed between species richness and temperature or solar radiation. These alternative models are shaped similarly, and they explain nearly as much variance as does PET.

The relationship with PET becomes even more striking when one combines the Reptilia and Amphibia with the nonvolant Mammalia (fig. 7; table 3). These three classes comprise the ground-dwelling representatives of the terrestrial Vertebrata, which I refer to here as nonvolant vertebrates. PET alone explains more than 91% of the variability in the species richness (log-transformed) of this group.

Potential evapotranspiration may be interpreted as a measure of integrated, crude, ambient energy. Operationally, it is the amount of water that evaporates from a saturated surface. It depends mainly on the amount of energy available to evaporate water and, to a lesser degree, on the relative humidity. The spatial variation in PET is closely related to latitude and to the variability in solar radiation (fig. 8A,B). The difference is that, although solar radiation is the direct radiant energy to which a region is exposed, much of this energy is redistributed on the earth's surface by reflection, counterradiation, and advection of air and water masses (Budyko 1974). PET (as well as temperature) integrates the regional energy balance. Particularly as estimated by Budyko's (1974) method (as it was in
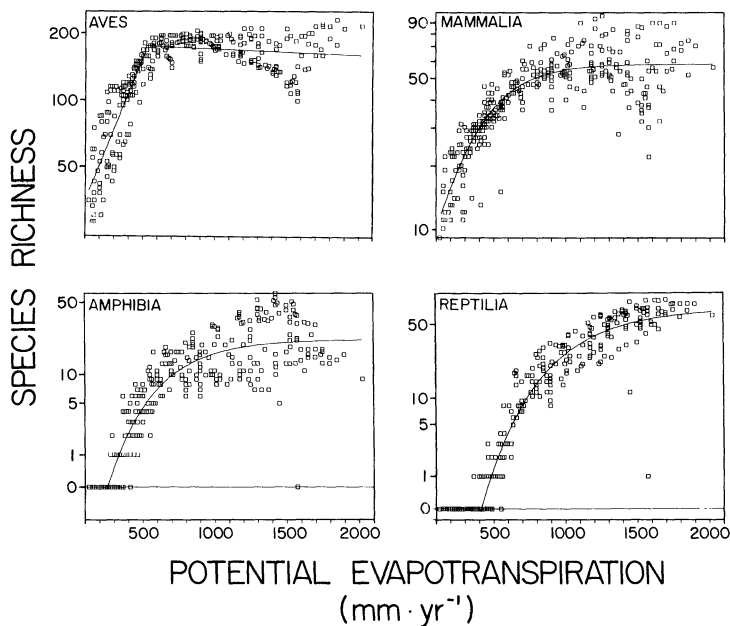
Fig. 6.—The relationships that predict the greatest portion of the variability in species richness (the logarithm of the number of species plus one) of birds, mammals, amphibians, and reptiles. In every case, annual potential evapotranspiration is the best predictor of richness. The striking negative outliers are quadrats on the coast of southern California and the Gulf of Mexico in which more than 95% of the area is ocean.

TABLE 3

UNIVARIATE MODELS PREDICTING SPECIES RICHNESS IN NORTH AMERICA AS FUNCTIONS
OF POTENTIAL EVAPOTRANSPIRATION

Group	Domain	Model	r^2
Birds	$PET < 525$ mm yr^{-1}	$1.40 + .00159\,PET$	
	$PET \geq 525$ mm yr^{-1}	$2.26 - .0000256\,PET$	.81
Mammals	All observations	$1.12[1.0 - \exp(-0.00348\,PET)] + .653$	.80
Amphibians	$PET \leq 200$ mm yr^{-1}	0	
	$PET > 200$ mm yr^{-1}	$3.07[1.0 - \exp(-0.00315\,PET)]$	.84
Reptiles	$PET < 400$ mm yr^{-1}	0	
	$PET \geq 400$ mm yr^{-1}	$5.21[1.0 - \exp(-0.00249\,PET)] - 3.347$	.93
Vertebrates	All observations	$1.49[1.0 - \exp(-0.00186\,PET)] + .746$	.92

NOTE.—These fitted models explain the highest portion of the variability in the logarithm of species richness (plus one). All are saturating functions of annual potential evapotranspiration (PET, mm yr^{-1}). Some of the models are biphasic: two separate models were fitted to the data above, and the data below, a stated value of PET. The slope of the relationship between PET and bird richness for $PET \geq 525$ is not significantly different from zero.
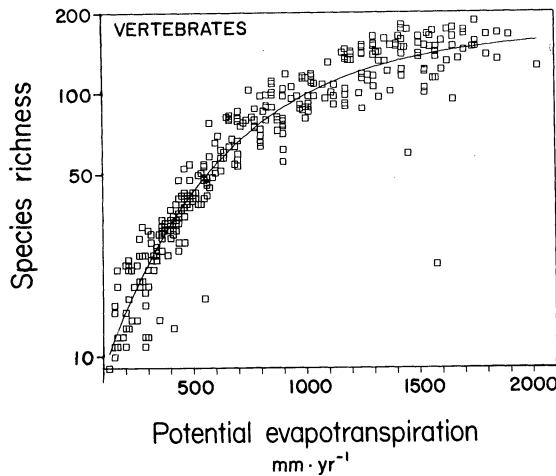
Fig. 7.—The relationship between species richness of nonvolant terrestrial vertebrates (i.e., mammals + amphibians + reptiles − bats) and annual potential evapotranspiration.

Fig. 8.—The relationships between (A) potential evapotranspiration (PET) and latitude and (B) PET and solar radiation. PET is determined mainly by solar radiation plus advective energy fluxes. Actual evapotranspiration (AET) reaches the limits set by available energy (C, PET) and available water (D, precipitation).

the data used in the present study; USSR National Committee for the International Hydrological Decade 1977), PET is estimated as a measure of the net atmospheric energy balance, independent of water availability. In contrast, actual evapotranspiration (AET) is t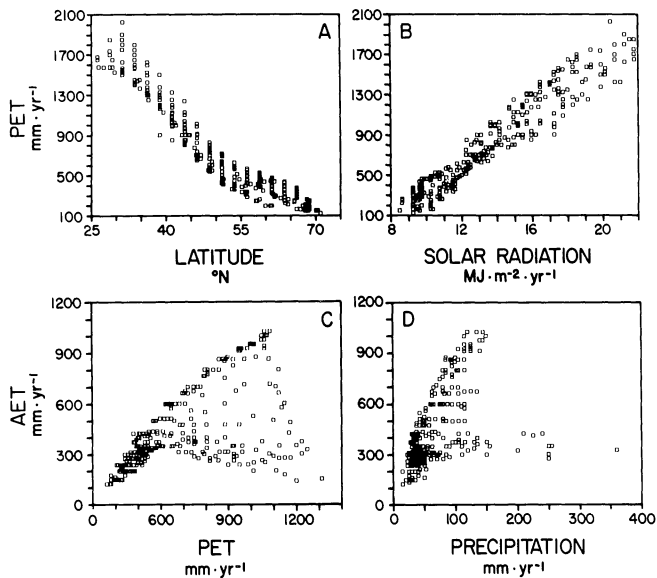he amount of water that actually evaporates or is transpired from an area. It represents the joint availability of energy and water (Budyko 1974), such that PET (fig. 8C) and precipitation (fig. 8D) both set upper limits on AET. Its variation with latitude (not shown) fills a triangular distribution similar to the mirror image of figure 8C.

The dependence of vertebrate richness on variables other than PET was addressed by calculating partial correlations, controlling for PET, and by examining the standardized regression coefficients (measures of the relative importance of each variable in the multiple regression) of full stepwise and backward multiple regressions. To do this, I created a surrogate variable f(PET) for each vertebrate class using the models in table 3. This variable was therefore linearly related to the logarithm of the number of species plus one. Multiple regressions were then carried out, including f(PET) as an independent variable. It would be pointless to present the full results, which typically involve 7–14 significant factors. Because the independent variables are highly correlated, the regression coefficients are difficult to interpret. However, two important points do emerge from the regressions.

First, the environmental data statistically account for nearly all the variability in regional species richness (adjusted $R^2 = 0.906$ for birds, 0.917 for mammals, 0.940 for amphibians, 0.969 for reptiles, and 0.953 for nonvolant vertebrates). Thus, considering only the physical habitat, with no explicit information concerning history, biotic interactions, disturbance, and so forth, one can statistically explain 91%–97% of the variability in regional species richness.

Second, certain factors consistently emerge as important in these models. In stepwise or backward multiple regressions, f(PET) is retained as the most important predictor of species richness for all of the vertebrate classes (table 4). After controlling for PET, consistently strong partial correlations were observed with elevation and with actual evapotranspiration. These same variables also had among the highest standardized regression coefficients in the multiple regressions. However, the different vertebrate classes apparently respond differently to these variables: for a given level of PET, species richness is greater in mountainous areas for birds and mammals as well as for trees. However, it is reduced for amphibians and reptiles. Again holding PET constant, richness in birds and mammals is reduced where AET is higher (i.e., more species in drier areas), whereas it is enhanced in amphibians and reptiles. Thus, poikilotherms show the greatest species richness in high-energy, moist, low-elevation areas; homeotherms, in high-energy, dry, mountainous areas; and trees, in high-energy, moist, mountainous areas.

Other terms in the regression models are significant, albeit weak. They may do no more than correct for lack of fit in the stronger variables, or they may represent real effects. Two such variables that recur for all the vertebrate classes and for trees are reduced species richness on peninsulas and reduced richness in quadrats on the seacoast. Of the two, the coastal effect is much stronger. For all of these

TABLE 4

Other Factors Related to Species Richness: Partial Correlations after Controlling for Potential Evapotranspiration, and the Strongest Standardized Regression Coefficients in Multiple Regressions

Group and Factor	Partial r	Factor	SRG
Birds:			
AET	− .496	ƒ(PET)	.506
July precipitation	− .470	Elevation	.195
log (elevation)	.439	Area	.190
Mammals:			
log (elevation)	.613	ƒ(PET)	.720
AET	− .576	Elevation	.194
Elevation spatial variation	.564	PET spatial variation	.116
Amphibians:			
AET	.625	ƒ(PET)	.560
log (precipitation)	.472	AET	.291
Elevation	− .465	log (area)	.245
Reptiles:			
AET	.302	ƒ(PET)	.769
July temperature	.271	AET	.123
Elevation	− .269	January temperature	.121

NOTE.—A nonlinear function of potential evapotranspiration, ƒ(PET) (the models detailed in table 3), is the single variable most closely correlated with species richness in every case. The partial correlation coefficients (partial r) of the three most strongly correlated variables, after controlling for PET, are shown on the left. After a full stepwise multiple regression, the three factors with the largest standardized regression coefficients (SRG, a measure of the influence of the variable) are shown on the right. AET is actual evapotranspiration; spatial variability is measured as the difference between the minimum and the maximum values of a variable within a quadrat.

groups of organisms, reduced richness is particularly evident all along the Gulf of Mexico, somewhat less so along the southern Atlantic and Pacific coasts, and only slightly so in the North.

Finally, since quadrat area was not held constant, its effect on richness was explicitly examined. Area was never significantly correlated to richness by itself (e.g., for nonvolant vertebrates, $r_s = 0.09$; fig. 9). Land area within a quadrat did sometimes enter as one of the covariates in the multiple-regression models, but with a standardized regression coefficient much weaker than those of most other terms. Wright (1983) found that energy times area was the best predictor of species richness on islands where both latitude and island size varied widely. In the present study, PET times area was a much poorer predictor of richness than was energy alone (e.g., for nonvolant vertebrates, $r_s = 0.804$ vs. 0.950). Thus, the effect of area is much weaker than that of energy on this scale.

The relationships between PET and species richness for particular orders and families of the Vertebrata are sometimes strikingly different from those observed at the class (fig. 5) and subphylum (fig. 6) levels. The fits of LOWESS to the relationships between PET and species richness for each of the orders represented in the Mammalia, Amphibia, and Reptilia are shown in figure 10. At the class level, richness increases monotonically with PET. At the order level, the relationship often peaks. This is evident even more clearly at the level of the family (fig. 11, the families in the order Rodentia). Even at the level of the family,
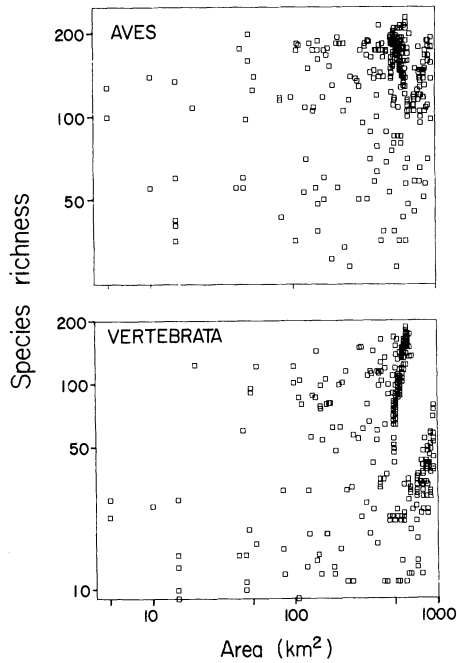
Fig. 9.—The relationship between species richness and quadrat area for birds and for terrestrial vertebrates (mammals + amphibians + reptiles − bats).

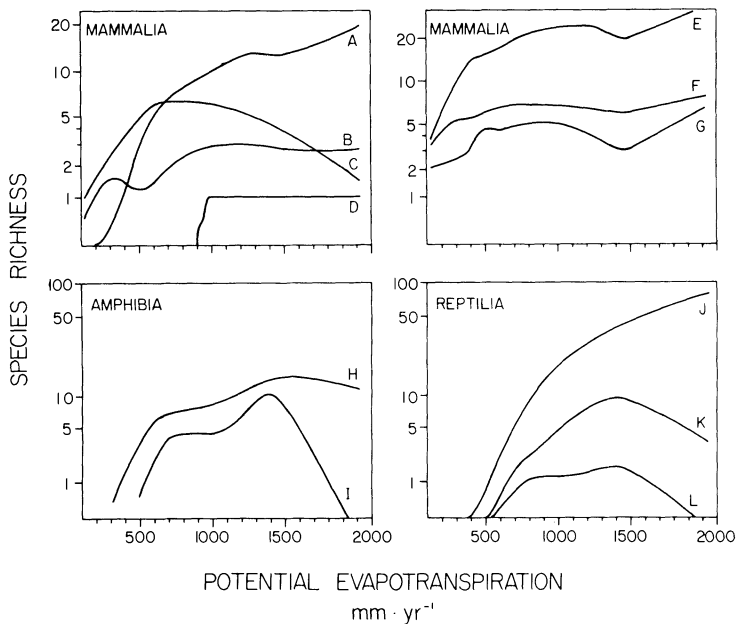Fig. 10.—The species richness of each of the orders of the terrestrial vertebrates as a function of the annual potential evapotranspiration. Only the LOWESS-smoothed curves are shown. Indications of the goodness of fit are given in table 5. Orders: A, Chiroptera; B, Lagomorpha; C, Insectivora; D, Marsupialia; E, Rodentia; F, Carnivora; G, Artiodactyla; H, Anura; I, Urodela; J, Chelonia; K, Squamata; L, Crocodylia.
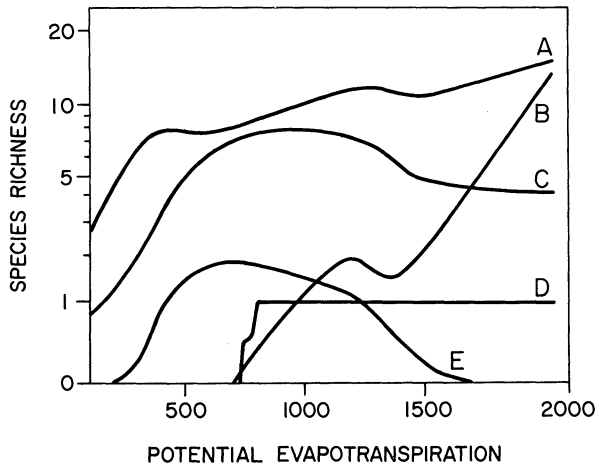
FIG. 11.—The species richness of the families of the order Rodentia as a function of annual potential evapotranspiration. Only the LOWESS-smoothed curves are shown. Indications of the goodness of fit are given in table 5. Families: A, Cricetidae; B, Heteromyidae; C, Sciuridae; D, Geomyidae; E, Zapodidae. Families in which all North American species are introduced (e.g., Muridae) and families having fewer than two species native to the United States and Canada (e.g., Castoridae) are not shown.

richness is usually still quite well correlated with PET (table 5), although the correlation is generally weaker and more variable at lower taxonomic levels. Thus, at the level of the order and the family, richness still varies closely with energy, but not in the monotonically increasing fashion shown at the class level.

<div align="center">DISCUSSION</div>

Species richness is undoubtedly influenced by many factors. There is evidence (reviewed by Begon et al. [1990]) that most of the processes listed in table 1 do influence species richness, at least locally under some circumstances. The present study sought to establish which factors are generally most important on the regional scale.

On this large scale, the strongest extant evidence indicates that richness depends on something about the regional environmental conditions and about the areas of the regions considered. Many earlier studies have also examined regional richness and the physical environmental conditions. Solar radiation, temperature, and precipitation, in particular, have been shown to correlate with the richness of particular groups of plants (Richerson and Lum 1980; Wright 1983) and animals (Schall and Pianka 1978; Wright 1983; Turner et al. 1987; Owen 1988). The common thread in these correlations between richness and environmental conditions appears to be energy.

The idea that energy may determine regional species richness was proposed by Hutchinson (1959) and developed by Connell and Orias (1964), Brown (1981), and Wright (1983). The basic argument is as follows. The abundance of terrestrial

TABLE 5

THE PERCENTAGE OF THE VARIANCE OF SPECIES RICHNESS EXPLAINED BY THE ANNUAL POTENTIAL
EVAPOTRANSPIRATION IN THE TERRESTRIAL VERTEBRATA AND EACH OF ITS CLASSES,
ORDERS, SUBORDERS, AND SELECTED FAMILIES

Taxonomic Aggregate	%	Taxonomic Aggregate	%
Vertebrata	92.5	Mammalia (*Cont'd*)	
Mammalia	81.1	Sciuromorpha	66.4
Chiroptera	92.5	Sciuridae	38.6
Phyllostomidae	34.1	Geomyidae	43.8
Vespertilionidae	92.2	Heteromyidae	48.0
Molossidae	61.9	Aves	83.4
Carnivora	34.3	Amphibia	92.5
Canidae	2.5	Anura	88.9
Ursidae	*	Bufonidae	72.6
Procyonidae	74.3	Ranidae	58.1
Mustelidae	64.6	Hylidae	78.5
Felidae	81.0	Urodela	58.5
Insectivora	64.5	Reptilia	95.5
Marsupialia	49.7	Crocodylia	45.4
Lagomorpha	49.7	Chelonia	95.1
Artiodactyla	31.5	Squamata	70.9
Rodentia	71.2	Lacertilia	91.2
Myomorpha	72.1	Ophidia	93.9
Cricetidae	61.8		
Muridae	*		
Zapodidae	68.9		

NOTE.—In each case, the percentage of variance explained is derived from the r^2 of a LOWESS fit to the data. These data indicate how well richness can be predicted from PET, regardless of the shape of the function. The sample size is 366 in each case; $P < .01$ for the percentage of variance explained is $\geq 1.5\%$.

* No correlation coefficient can be calculated because there was never more than one species per quadrat.

organisms, as a whole, must be limited by their supply of energy (Hairston et al. 1960), as evidenced by the fact that the accumulation of fixed energy by the biosphere is negligible in comparison with primary productivity (Hutchinson 1948). The finite amount of solar energy fixed on earth is partitioned among species in some fashion. Partitioning can go only so far: for a population to persist, it must have some minimum number of individuals. Each individual requires a certain amount of energy. Thus, a population requires some minimum amount of energy to persist. Partitioning of the available energy into species-sized parcels limits the number of populations that can share the energy in a particular region. If this hypothesis is true, then a measure of energy availability should allow one to predict the maximum number of species in a region.

Evidence consistent with the energy hypothesis now comes from several sources. The strongest evidence is probably Wright's (1983) observation regarding island floras and faunas. Species-area relationships on islands have typically been found in samples restricted to particular archipelagoes. Wright found that plant and animal richness on islands worldwide is related to the total energy received on the island (i.e., area × solar energy per area). He proposed that

MacArthur and Wilson's (1967) species-area relationship is a special case of a more general species-energy relationship.

The energy hypothesis predicts that, in regions of roughly equal area, energy flux per unit of area should be the prime determinant of species richness. In the case of plants, primary production represents realized energy capture. The best environmental correlate of primary productivity on the large scale is AET (Rosenzweig 1968; Lieth 1975). In a study parallel to this one (using the same predictor variables), North American tree-species richness was best predicted by AET (Currie and Paquin 1987). Similarly, Richerson and Lum (1980) related vascular-plant richness in California to temperature and precipitation (the two main elements in AET), and Wright (1983) related angiosperm richness on islands to AET. Together, these studies suggest that the richness of terrestrial higher plants in general is strongly related to capturable energy, as measured by AET.

For animals, the situation appears to be more complicated. Several hypotheses can be quickly eliminated on the basis of the results presented above. First, terrestrial vertebrate richness is less closely related to tree richness and plant productivity (as estimated from AET) than it is to PET, temperature, or solar radiation. It is unlikely that the poor relationship between vertebrate richness and productivity results from AET's being a poor predictor of primary productivity: vertebrate richness is maximal in the southwestern United States, where tree richness and productivity are both very low (Currie and Paquin 1987). It is also unlikely that vertebrate richness is related to the richness of some other group of plants, since the richness of all the vascular-plant groups examined to date correlates well with AET. One can also reject the hypothesis that annual variability of climate per se has any important effect on richness. Spatial variability and historical effects are both significantly, but only weakly, correlated with richness.

Rather, the best predictor of vertebrate-species richness is consistently PET, but other regional energy variables (temperature and solar radiation) are nearly as good. Earlier studies reporting correlations between animal richness and environment have also found temperature, sunshine, or solar radiation to be the variables most closely related to the richness of animal groups (Schall and Pianka 1978; Turner et al. 1987; these studies did not consider PET). Wright (1983) related bird richness on islands to primary productivity (estimated from AET). Although bird richness in this study also correlated with AET ($r_s = 0.341$, $P < .001$; fig. 4), it was better correlated with PET ($r_s = 0.689$, $P < .001$; fig. 5). Moreover, a reanalysis of Wright's data has shown that PET is better related to richness than is AET (J. L. Wylie and D. J. Currie, unpublished manuscript). In addition, PET is consistently the best predictor of species richness in temperate regions on other continents (D. J. Currie and H. Lee, unpublished manuscript). All the extant evidence shows vertebrate richness to be closely related to ambient-energy levels.

Why should vertebrate richness be better related to crude atmospheric energy than to primary productivity? One possible explanation is that the energy available to vertebrates is better characterized by atmospheric energy than by food energy. Ectotherms regulate their body temperature by directly absorbing heat from their environment, and the metabolic costs to homeotherms decrease with

increasing ambient temperature (to the species' upper critical temperature; Randolph 1973; Hainsworth 1981). A second explanation is suggested by a comparison of PET and AET. PET and AET rise together so long as water is not limiting; otherwise, PET is greater than AET (fig. 8). When PET rises above AET, animal richness continues increasing, whereas plant richness does not. It is possible that these environments offer energy sources (niches?) unrelated to local primary productivity. It would be interesting to examine vertebrate richness divided into dietary categories—herbivores, insectivores, detritivores, and so on—to determine whether particular categories of animals are correlated with AET and others with PET. In any case, it is evident that total vertebrate richness apparently depends on total regional energy, not just on primary productivity.

Area has also often been shown to correlate strongly with species richness on the regional scale. The area effect is most evident in studies of archipelagoes and other locales where area varies widely while other environmental conditions are reasonably homogeneous (Connor and McCoy 1979). In the present work, the area effect was discernible but weak. This probably reflects the fact that area varied by less than a factor of two for most of the quadrats, whereas PET and AET varied widely. Area and energy both undoubtedly affect regional richness; the strength of the correlations between richness and area or energy depend strongly on their ranges of variability.

In Wright's (1983) species-energy model, richness on islands is hypothesized to depend on area times the areal energy flux (i.e., AET, PET, or primary production). Energy flux per unit of area and area itself are therefore postulated to affect richness proportionally. A doubling of either area or energy should lead to the same increase in richness. A new study (J. L. Wylie and D. J. Currie, unpublished manuscript) shows that this assumption is not true, either in Wright's data or in data from a set of land-bridge islands. Rather, energy has been found to have a much stronger effect on richness. The same effect is evident here. The shape of the energy-richness relationship differs from that of the area-richness relationship, and the regression coefficients are very different. This explains why energy times area is a much poorer predictor of richness than is energy alone. The species-energy model proposed by Wright (1983) is a clear improvement over the species-area model (MacArthur and Wilson 1967), but it fails to account for the different effects of area and energy on richness.

The effect of glacial history was barely discernible in the present data. Moreover, energy-richness patterns in Europe and Australia are consistent with those observed here (D. J. Currie and H. Lee, unpublished manuscript). It is certainly true that historical factors can affect the distributions of species (e.g., the postglacial recolonization of northern Europe and North America) and that richness can be affected on short time scales. My data suggest that tree and vertebrate richness can reach the limits set by energy in something less than 14,000 yr (the time since the end of the last glaciation). Historical effects on regional richness could be evident elsewhere on earth, but the evidence suggests that these effects are not long lasting.

There are at least two further difficulties with the species-energy hypothesis. First, in at least some productive, high-biomass environments, such as *Spartina*

or *Typha* marshes, richness is apparently very low (Al-Mufti et al. 1977; Grime 1979; Day et al. 1988). In Tilman's (1982) proposed model of resource competition in a heterogeneous environment, species richness should be a peaked function of available resources. This peaked relationship has been observed for both plants and animals (Al-Mufti et al. 1977; Tilman 1982; Abramsky and Rosenzweig 1984; Day et al. 1988; Owen 1988), and it appears to be inconsistent with the simple energy hypothesis.

Second, the energy hypothesis is logically incomplete (D. Tilman, personal communication). The hypothesis explains why richness cannot increase indefinitely, but it does not explain why richness should tend toward the maximum set by available energy. Why doesn't a small number of species monopolize the available energy? Tilman (1982) confronted essentially the same problem in his models of resource competition: Why are there no superspecies that are superior competitors for all resources? MacArthur and Wilson (1967) and Wright (1983) postulated that a balance between immigration and extinction causes richness to approach its theoretical maximum. Tilman suggested that, in a heterogeneous environment, selection should favor specialists for particular resources and that specialists outcompete generalists. However, Bonner (1988, chap. 5) argued that natural selection leads to increased richness: organisms that avoid competition or predation by some evolutionary innovation are selectively favored. Any of these explanations is plausible, but for continental biota, there is little evidence to support any of them. Indeed, the evidence cited in the preceding paragraph suggests that richness does not always tend toward its possible maximum.

The solution to this paradox appears to have something to do with scale. Tilman's (1982) model is consistent with local variations in richness as functions of local variation in productivity or standing crop (see, e.g., Al-Mufti et al. 1977; Tilman 1982; Abramsky and Rosenzweig 1984; Day et al. 1988; Owen 1988). Other studies on the local scale have correlated richness with local habitat diversity, disturbance, and so forth (MacArthur and MacArthur 1961; Connell 1978; Bailey 1988). In contrast, regional richness increases monotonically with climatic variation in energy (figs. 6, 7; Richerson and Lum 1980; Wright 1983; Currie and Paquin 1987). In other words, small-scale patterns of species richness have been related to factors that act on the small scale and that are variable on the small scale; regional patterns of richness have been related to factors that show pronounced large-scale variation. Arnold's (1972) study relating the richness of reptilian predators to the richness of their prey may appear to be an exception. However, although Arnold's samples represented local richness, they were drawn from widely scattered locations. His correlations between predator and prey richness may be due to the covariation of the two with energy. The fact that richness varies with energy differently on large and small spatial scales suggests that different mechanisms act at the two scales. Large-scale patterns might simply represent the summed effects of many local interactions. Alternatively, regional patterns may be observed if local species interactions are highly constrained by regional variation in energy. However, it is also possible that processes operating at the regional level may determine the size of the species pools from which local inter-

actions select species. The almost total lack of residual variation seems to suggest that richness may respond in a simple, direct way to total available energy.

Finally, it is interesting that the richnesses of some orders and families have distributions that peak as a function of energy, and others increase monotonically (figs. 8, 9). Peaked patterns have usually been interpreted as supporting Tilman's (1982) model of competition in heterogeneous habitats (Tilman 1982; Abramsky and Rosenzweig 1984; Owen 1988). In the case of the present data, it seems unlikely that competition could account for patterns on such a large scale. Several alternative explanations are possible. Particular families and orders have differing physiological tolerances for given environmental conditions. The peaked pattern may simply reflect partitioning of an energy gradient among families. Alternatively, random spatial concentration of families might also lead to this pattern. Thus peaked relationships between richness and energy, even locally, must be interpreted with caution. They may result from competition, or they may result from other large-scale phenomena.

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