

PRODUCTIVITY AND HISTORY AS PREDICTORS OF THE LATITUDINAL DIVERSITY GRADIENT OF TERRESTRIAL BIRDS

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Abstract. The latitudinal diversity gradient is the largest scale, and longest known, pattern in ecology. We examined the applicability of three versions of the energy hypothesis, the habitat heterogeneity hypothesis, and historical contingency to the gradient of terrestrial birds. The productivity version of the energy hypothesis, tested using actual evapotranspiration, a water–energy variable closely associated with plant productivity, accounted for 72% of the variance in a model of global extent. An historical contingency model based on biogeographic region explained 58% of the variance. A combined climate–region model accounted for 78% of the variance, but 52% comprised the overlap between these effects. This suggests that further resolution of contemporary vs. historical processes at the global level will require the inclusion of phylogenetic information.

Regional-extent regression models suggest a latitudinal shift in constraints on diversity; measures of ambient energy (potential evapotranspiration and mean annual temperature) best predicted the diversity gradient at high latitudes, whereas water-related variables (actual evapotranspiration and annual rainfall) best predicted richness in low-latitude, high-energy regions. Intraregional spatial autocorrelation analysis confirmed that climatic models adequately describe geographic richness patterns at all but the smallest spatial scales resolved by the analysis. We conclude that the “water–energy dynamics” hypothesis, originally developed for plant diversity gradients, offers a parsimonious explanation for bird diversity patterns as well, presumably operating via plant productivity. However, more refined tests of historical factors are needed to fully resolve their influences on the gradient.

Key words: birds; energy hypothesis; habitat heterogeneity; historical contingency; latitudinal diversity gradient; productivity hypothesis; spatial autocorrelation; species richness; water–energy dynamics.

INTRODUCTION

Many hypotheses have been proposed to explain why there are more species toward the tropics (Pianka 1966, Huston 1979, 1994, Rohde 1992, Rosenzweig 1995), and new hypotheses continue to appear (e.g., Ritchie and Olff 1999, Colwell and Lees 2000, Dynesius and Jansson 2000). However, many of these hypotheses are circular, logically flawed, or not supported by the evidence, and attention has now focused on a much more restricted subset of plausible explanations. The climatically based “energy hypothesis,” in particular, has received a great deal of attention in the past 20 years. Ironically, the hypothesis that energy limits diversity represents the first ever proposed for the latitudinal diversity gradient (von Humboldt 1808).

For patterns of diversity at large extents, no other hypothesis has received the level of support found for climate, and variables associated with energy availability and climate have been linked to the diversity of

many groups of plants and animals (Terentev 1963, MacArthur 1975, Rabinovich and Rapoport 1975, Schall and Pianka 1977, 1978, Richerson and Lum 1980, Pianka and Schall 1981, Wright 1983, Currie and Paquin 1987, Turner et al. 1987, 1988, Adams and Woodward 1989, Currie 1991, O'Brien 1993, 1998, Oberdorff et al. 1995, Fraser and Currie 1996, Guégan et al. 1998, Kerr et al. 1998, Leathwick et al. 1998, O'Brien et al. 1998, 2000, Kerr and Currie 1999, Kerr and Packer 1999, Rutherford et al. 1999, Badgley and Fox 2000, Boone and Krohn 2000, Lennon et al. 2000, Balmford et al. 2001, Rahbek and Graves 2001, van Rensburg et al. 2002, Hawkins and Porter 2003). Thus, little doubt exists that climate influences large-scale patterns of species richness. Even so, number of critical issues related to continentally and globally extensive diversity gradients must be resolved before it can be concluded that climate, in general, and energy, in particular, represent the primary explanations for the patterns.

Although it is widely accepted that both energy and water drive plant diversity and form (Wright 1983, Currie and Paquin 1987, Adams and Woodward 1989, Stephenson 1990, O'Brien 1993, 1998, Leathwick et al. 1998), three versions of the energy hypothesis are relevant for animals. Wright (1983) envisaged energy op-

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erating by its capture and conversion into food. He predicted that plant diversity would be limited by solar energy tempered by water availability. For animals, diversity would then be limited by the production of food items needed (e.g., plant biomass for herbivores, herbivore biomass for predators). This is also referred to as the “productivity hypothesis” and represents the most widely studied version of the hypothesis (Huston 1994, Mittelbach et al. 2001).

The second form of the hypothesis (the “ambient energy hypothesis”) is founded on physiological requirements of organisms. Turner et al. (1987) argued that sunshine and temperature were primary determinants of butterfly diversity in Britain because adult activity levels depend on ambient temperature and on basking in direct sunlight. Presumably for similar reasons, hours of sunshine and average temperature were important predictors of reptile richness in the Iberian Peninsula, (Schall and Pianka 1977) and for lizards in North America (Schall and Pianka 1978). For terrestrial North American vertebrate groups Currie (1991) hypothesized that thermoregulatory needs explain why richness is more strongly correlated with annual potential evapotranspiration (PET), a measure of ambient or atmospheric energy (Thornwaite and Mather 1955) than with annual actual evapotranspiration (AET), a measure of energy–water balance closely associated with plant productivity (Rosenzweig 1968). Whether or not these thermoregulatory explanations are correct in detail, the mechanistic hypothesis that they address is very different from Wright’s (1983) definition. At its extreme, the ambient energy hypothesis is related to von Humboldt’s (1808) original hypothesis. This third energy hypothesis explicitly argues that many organisms are limited at higher latitudes by their inability to withstand winter temperatures (the “freezing tolerance” hypothesis).

Regarding the three energy hypotheses, the first issue requiring clarification is that analyses have found support for both the productivity and ambient energy versions of the hypothesis, possibly because workers have not always distinguished between them. Currie and his colleagues, who do distinguish the hypotheses, found that vertebrate richness in North America depends on ambient energy rather than on actual evapotranspiration (Currie 1991, Kerr et al. 1998). Similarly, Turner et al. (1987, 1988) found that temperature and hours of sunshine were the best predictors of British butterfly and bird richness, but they did not include any productivity-related variables, so it is not known if measures of food availability might be better predictors. In contrast, Guégan et al. (1998) found that net primary productivity was a strong predictor of fish diversity, but they did not include any measures of ambient energy.

A second issue is that different factors may operate at different latitudes. Currie (1991) found asymptotic relationships between North American vertebrate spe-

cies richness and potential evapotranspiration. Kerr and Packer (1997) reanalyzed Currie’s mammal data and demonstrated that although PET was a strong predictor of mammal richness when $PET < 1000$ mm/yr, range in elevation within grid cells (assumed to represent a measure of habitat heterogeneity) was the best predictor at greater PET levels. Because asymptotic or unimodal relationships between richness and energy measures are commonly found in studies encompassing large geographic areas (e.g., Currie and Paquin 1987, Currie 1991, Kerr et al. 1998, O’Brien et al. 1998, Rutherford et al. 1999), ambient energy is probably more critical in some latitudes than in others.

Third, there is reasonable evidence for additional hypotheses that are not based directly on energy or climate. For example, the habitat heterogeneity hypothesis states that areas of a given size that contain more types of habitats will support greater diversity. Rosenzweig (1995) provided several examples of this relationship and Kerr and Packer (1997) indirectly tested this hypothesis for mammals in the warmer parts of North America. Rahbek and Graves (2001) also argued that habitat heterogeneity (again measured as range in elevation) predicts bird diversity in northern South America, although they did not include any measures of productivity. Guégan et al. (1998) argued that global richness patterns or riverine fish species are best explained by a combination of net primary productivity and habitat diversity.

A fourth unresolved problem is the extent to which “history” influences intercontinental diversity patterns. Some workers argue that contemporary climate is sufficient to account for most intercontinental variation (Adams and Woodward 1989, Oberdorff et al. 1997, Francis and Currie 1998, Guégan et al. 1998, O’Brien 1998), whereas others maintain that long-term historical differences based on differential speciation or extinction rates, coupled with dispersal limitation, are more important (Pianka 1989, Latham and Ricklefs 1993, McGlone 1996, Qian and Ricklefs 1999, 2000). Because all species have been generated in the past in specific locations, history must influence diversity patterns by logical necessity. However, at issue is the extent to which this historical signal has been lost due to dispersal in response to contemporary factors. Whittaker and Field (2000) have attempted to reconcile the opposing points of view, pointing out that unlike “historical contingency,” energy/climate provides a model for broadly predictable patterns of diversity, and thus represents the appropriate starting point for studying geographic variation in species richness, to which historical effects can be added when necessary.

In this paper we use terrestrial birds to evaluate these issues. Specifically, we evaluate the ability of three versions of the energy hypothesis (ambient energy, productivity, and freezing tolerance), the habitat heterogeneity hypothesis, and historical contingency, to account for geographic patterns in bird richness patterns

over five biogeographic regions. Our primary goals are to extend tests of the energy hypothesis using a diverse and well-known group of terrestrial animals and to evaluate the relative contributions of the various hypotheses to the overall diversity gradient. By comparing across six continents, we also investigate the inability of climatically based statistical models to account for intercontinental differences, thereby identifying a potential role for historical processes in the global bird diversity pattern.

METHODS

Bird species richness

In the Nearctic (Canada, the United States, and northern/central Mexico), the Neotropics (southern Mexico, northern Central America, and South America), the western and northern Palearctic (Europe, North Africa, the Middle East, and the republics of the former USSR), Australia, and the Afrotropics, geographic variation in bird species richness was measured by dividing each region into equal-area grid cells. Each cell was 220×220 km ($2^\circ \times 2^\circ$ at the equator), except for coastal cells and those surrounding major lakes, in which case adjacent cells were combined to obtain areas approximately equal in size to inland cells. Thus, area was held as constant as possible and was not included explicitly in the analysis. This grid represents an intermediate grain size compared to those generally used in large-extent studies of diversity gradients (e.g., Currie 1991, O'Brien 1993, Rahbek and Graves 2001). Offshore islands were excluded, except for Great Britain. After the grid system was modified for various map projections, it was overlaid onto enlarged range maps of terrestrially feeding birds taken from Howell and Webb (1995) and the National Geographic Society (1999) for the Nearctic and northern Neotropics; from Forshaw and Cooper (1977), Dunning (1987), Ridgley and Tudor (1989, 1994), Sibley and Monroe (1990), and del Hoyo et al. (1994) for South America; from Cramp and Simmons (1977, 1980, 1983), Cramp (1985, 1988, 1992), Cramp and Perrins (1993, 1994a, b), and Flint et al. (1984) for the Palearctic; from Simpson and Day (1984) for Australia; and from Brown et al. (1982), Urban et al. (1986, 1997), Fry et al. (1988, 2000), and Keith et al. (1992) for the Afrotropics. For the Afrotropical passerines not covered by the *Birds of Africa* series, we used maps from Hall and Moreau (1970), after updating them with more recent records from the sources listed in the series. Only native, breeding bird species that feed on terrestrial food were included in the study. We were unable to locate range maps for the birds of southern Central America, India, China, or southeast Asia, so these areas were excluded.

Environmental variables

We focused on seven variables, selected because they allow us to examine the five relevant hypotheses. Like

all analyses of global-extent gradients, we cannot test any hypothesis experimentally. However, if a particular variable accounts for very little of the variance in the geographic richness patterns, the hypothesis described by the variable is probably not a strong proximate explanation for the patterns. Also, a very large number of independent variables could conceivably be included in this analysis. However, we used parsimony, restricting the analysis to *likely* explanations. Further progress will not be made by attempting to correlate every possible aspect of the environment with diversity patterns.

The variables (with associated hypotheses in parentheses) are as follows.

1) Potential evapotranspiration (ambient energy). Both terrestrial vertebrate and invertebrate richness have been linked to PET in northern latitudes (Currie 1991, Kerr et al. 1998, Kerr and Packer 1999). Data are available online from the United Nations Environmental Program (UNEP)⁵ (see also Ahn and Tateishi 1994).

2) Actual evapotranspiration (productivity). Productivity is known to influence diversity gradients at a wide range of scales. Data are from the UNEP (available online;⁵ see also Tateishi and Ahn 1996).

3) Mean daily temperature in the coldest month (freezing). This examines von Humboldt's (1808) hypothesis. There have been few tests of this hypothesis for animals. Data were taken from the UNEP (see footnote 5) (see also Leemans and Cramer 1991).

4) Range in elevation (habitat heterogeneity). This tests patterns found for several groups (Richerson and Lum 1980, Kerr and Packer 1997, O'Brien et al. 2000, Rahbek and Graves 2001). Following these authors, we assume that range in elevation represents a proxy for habitat heterogeneity, although range in elevation and other measures of habitat diversity are not always strongly correlated (Kerr et al. 2001, Rahbek and Graves 2001). Maximum and minimum elevations within cells were estimated from regional maps compiled by the Polish Army Topographic Survey in the Pergamon World Atlas (Pergamon 1968).

5) Annual precipitation (water). Given that all of the biogeographic regions included in this study contain deserts, water availability may represent a critical limiting factor in at least some areas. Inclusion of precipitation also allowed us to evaluate the potential influence of water separately from the composite energy–water effects measured by actual evapotranspiration. Data were taken from the UNEP (see footnote 5).

6) Annual mean temperature (ambient energy). Annual and seasonal temperatures represent an alternative method of estimating energy input. We initially included four seasonal temperatures and annual mean temperature, in addition to temperature in the coldest month. However, due to strong positive colinearity among measures, we dropped the seasonal measure–

⁵ URL: <http://www.grid.unep.ch/data/grid/climate.html>

TABLE 1. Minimally adequate regional models of bird species richness.

Region	Model variables†	$R^2_{adj} \ddagger$	Species richness	$n\S$	Reduction in spatial autocorrelation (%)	
					Smallest distance	Largest distance
Nearctic	PET – PET ² + RELEV	0.559 (0.616)	662	376	36.4	83.1
Palearctic	AET – AET ² + PET – PET ²	0.709 (0.776)	502	606	48.8	62.0
Western	ANNT – ANNT ² + AET	0.853 (0.877)	325	197	89.4	86.1
Eastern	PET – PET ² + AET	0.724 (0.763)	428	409	42.9	88.5
Neotropics	AET	0.775 (0.832)	2894	389	63.6	90.5
Afrotropics	AET – AET ² + ANNT – ANNT ² + RELEV	0.546 (0.561)	1550	389	36.4	92.3
Australia	RAIN – RAIN ² + MINT – MINT ²	0.732 (0.785)	473	148	59.1	76.9

† The explanatory variables are: PET, potential evapotranspiration; RELEV, range in elevation; ANNT, annual mean temperature; AET, actual evapotranspiration; RAIN, annual precipitation; and MINT, mean temperature in the coldest month.

‡ The coefficients of determination (R^2_{adj}) have been adjusted for the number of variables in each model to make them comparable (parenthetical values are for models containing all six environmental variables).

§ The number of cells in each sample grid.

|| The percentage reductions in the spatial autocorrelation (Moran's I) in the species richness data achieved by the environmental models in the smallest distance classes and the largest distance class in which significant spatial autocorrelation in the raw data was observed (see also Fig. 10). Due to limitations in the software, random samples of 360 cells were used to test for spatial autocorrelation in the larger regions.

ments from the analysis. Data were taken from the UNEP.⁵

7) Biogeographic region (historical contingency). Biogeographers have long distinguished regions based on the uniqueness of their faunas and floras, and we use biogeographic region here as a proxy for the evolutionary history of regional faunas. We note that this geographically based measure of history is somewhat crude and very coarse-grained compared to the other predictor variables, but the fact that biogeographic regions can be identified based on the taxonomic affinities of the biota indicates that major interregional barriers to dispersal exist and that region must contain a significant historical signal.

Analysis

The data were analyzed at both the global and regional extents. Both were initially analyzed using forward stepwise multiple regression to identify minimally adequate explanatory models. Because of spatial autocorrelation in the data and very high statistical power, automatic stepwise procedures were uninformative and a manual iterative stepwise procedure was used instead. At each step, we evaluated each variable based on the coefficient of determination, and stopped when the addition of a variable (including a quadratic term if the relationship was nonlinear) did not improve the model R^2 by $\geq 5\%$ (i.e., we used a $R^2 = 0.05$ criterion of “significance” rather than a $P = 0.05$ criterion). For completeness, we also generated models incorporating all environmental variables; see Table 1).

For the global analysis, we followed the multiple regression with a partial regression (Legendre 1993, Legendre and Legendre 1998) to partition the variance explained by environmental variables and history. The coefficient of determination for biogeographic region was obtained from a single-classification model II (ran-

dom effects) ANOVA. The coefficient of determination of a model combining both climate and region was also obtained using a generalized linear model, with region added as a dummy variable. By comparing the three coefficients of determination, it was possible to partition the independent effects of environmental variation, interregional differences, and the overlap between them.

We evaluated spatial autocorrelation and scale-dependent effects of climate on the diversity gradient by comparing the pattern of spatial autocorrelation in the original species richness data with that of the residuals of the minimally adequate environmental models (Diniz-Filho et al. 2002). Because it is not meaningful to measure spatial autocorrelation among land masses separated by thousands of kilometers of water, correlograms were generated for each biogeographic region separately, based on Moran's I coefficients calculated at 10 geographic distances, using SAAP 4.3 (Wartenberg 1989). For each region, we compared the Moran's I coefficients for the original species richness and those for the residuals of the regression models at the first and last significant distance classes. This allowed us to evaluate quantitatively how the environmental variables control for spatial structure in species richness across spatial scales. We also divided the Palearctic region into two parts for the regional analysis, based on the sources of information for the range maps. The maps for western Palearctic birds are very highly resolved, and European bird distributions are the best documented in the world, so separating this subregion allowed us to examine the possible influence of knowledge about bird ranges on the results.

RESULTS

Global

The minimally adequate environmental model across all regions included only actual evapotranspiration,

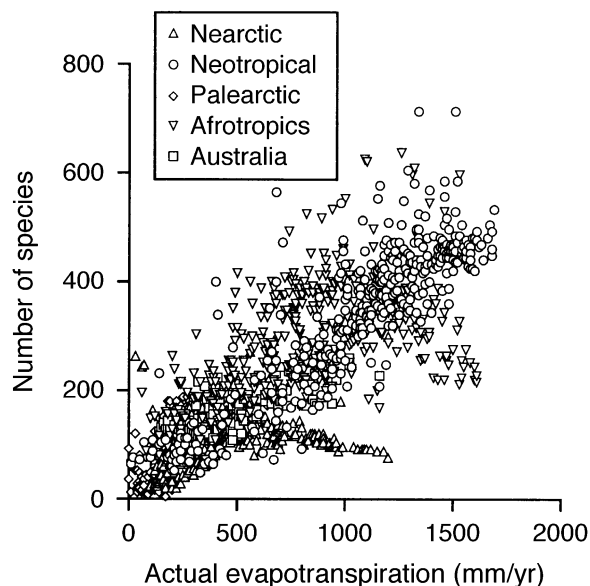


FIG. 1. The relationship between actual evapotranspiration and the species richness of terrestrial birds across five biogeographic regions. A simple regression model is highly significant ($y = 35.41 + 0.27x$, $P < 0.000001$, $n = 1908$).

which explained 72.4% of the variance in global bird species richness (Figs. 1 and 2). All five remaining environmental variables individually increased the coefficient of determination by $<2.5\%$, and a model with five variables explained 76.7% of the variance (annual temperature was not significant [$P = 0.39$], even in the face of inflated Type I error due to spatial autocorrelation). The separate historical model based on biogeographic region explained 58.2% of the global variance, 14% less than the water–energy (productivity) model. Partial regression indicated that covariance between climate and region make it impossible to fully isolate contemporary climate and historical processes on the latitudinal gradient when using species richness as the dependent variable (Fig. 2). Of the 26% of the variance to which independent effects could be attributed, climate accounted for 3.5 times more variance than did region. Thus, productivity is the most strongly supported hypothesis for the diversity gradient, with a secondary historical effect. No other hypothesis received any appreciable support at the global level.

Regional

Regional patterns of species richness are consistent with previously documented patterns. Variation in terrestrial bird richness in the Nearctic (Fig. 3) closely follows the pattern for terrestrial and aquatic birds documented by Cook (1969). In the east, richness peaks near the Great Lakes and drops to both the southeast and north. There is also a longitudinal component, resulting in moderately high richness in the Sierra Nevada, southern California, and Arizona, with richness further increasing south into Mexico.

Maximum richness in the Neotropics is found in the northern Andes, decreasing to the south and east (Fig. 4; see Rahbek and Graves 2001). Secondary peaks occur in northern Central America (Fig. 3), north-central Venezuela, and the southeast coast of Brazil (Fig. 4).

The Palearctic (Figs. 5 and 6) is characterized by a strong latitudinal gradient, with reversals in the desert areas of North Africa, the Middle East, and Kazakhstan. There are localized centers of diversity in the Balkans (Fig. 5), the Caucasus (Fig. 6), and the mountain ranges of south-central Asia (Fig. 6).

The Afrotropics are characterized by very high richness near Lake Victoria (Fig. 7), with a secondary peak at Mt. Cameron in the west (see Jetz and Rahbek 2001). Not unexpectedly, the fewest species occur in the Sahel, the Horn, and in the Namibian/Kalahari Deserts. More surprisingly, richness appears to be moderately low in the central Congo Basin.

As is typical of most plant and animal groups in Australia, bird richness is concentrated along the eastern coast, with virtually no latitudinal gradient (Fig. 8; see Pianka and Schall 1981).

The regional environmental models (Table 1) generate a more complex picture than the univariable global model. No two models are identical, but three of the four models focused on the northern temperate zone identify measures of ambient energy as the primary predictor of richness. There is an apparent inconsistency between the model for the entire Palearctic, which identifies actual evapotranspiration as the primary predictor, and the separate subregional models, which identify annual temperature and potential evapotranspiration as the primary predictors (Table 1). However, this reflects the fact that in cold climates AET is limited by energy input rather than precipitation, and values of AET cannot be greater than PET when PET is lower than rainfall (Stephenson 1990). Because PET is low over much of the Palearctic, PET and AET are nearly interchangeable as predictors of bird richness; AET and its quadratic term explain 59.6% of the variance, whereas PET and its quadratic term explain

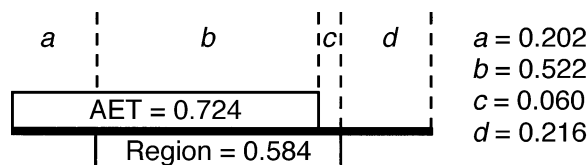


FIG. 2. Results of partial regression analyses using actual evapotranspiration (AET) and biogeographic region as predictors of worldwide patterns in bird richness. The unexplained variation (d) is $1 - R^2$ of a GLM including both AET and region, which corresponds to the portion $(a + b + c)$. The overlap between region and AET (b) is equal to $(a + b) + (b + c) - (a + b + c)$, where $(a + b)$ is the R^2 of the regression using AET, and $(b + c)$ is given by the R^2 of the ANOVA using biogeographic region. We can then partition variation explained by AET only (a) and biogeographic region only (c).

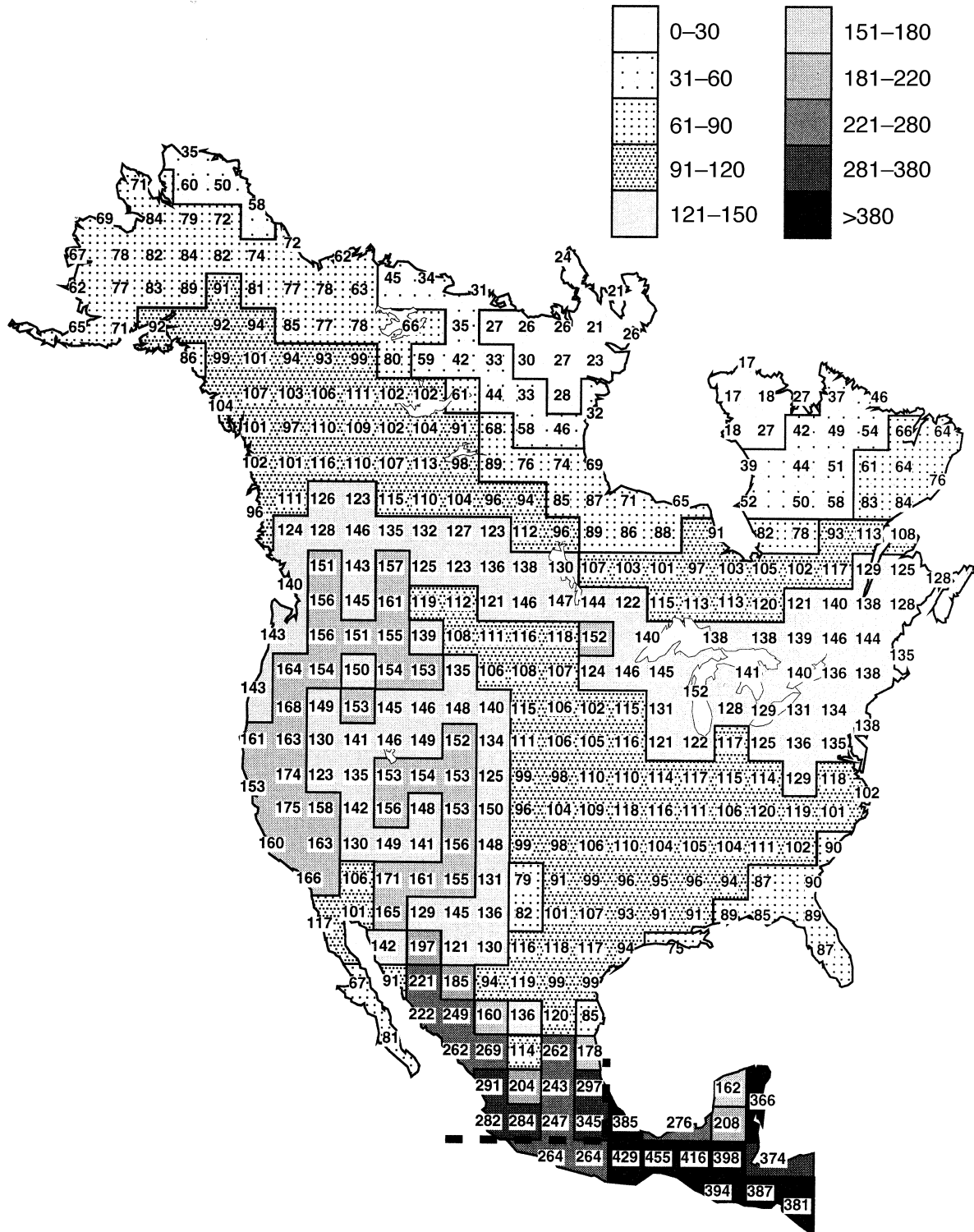


FIG. 3. Geographic variation in the richness of breeding terrestrial bird species in the Nearctic and northern Neotropics. The heavy dashed lines in southern Mexico distinguish cells classified as Nearctic and cells classified as Neotropical. Numbers represent the number of bird species in each cell.

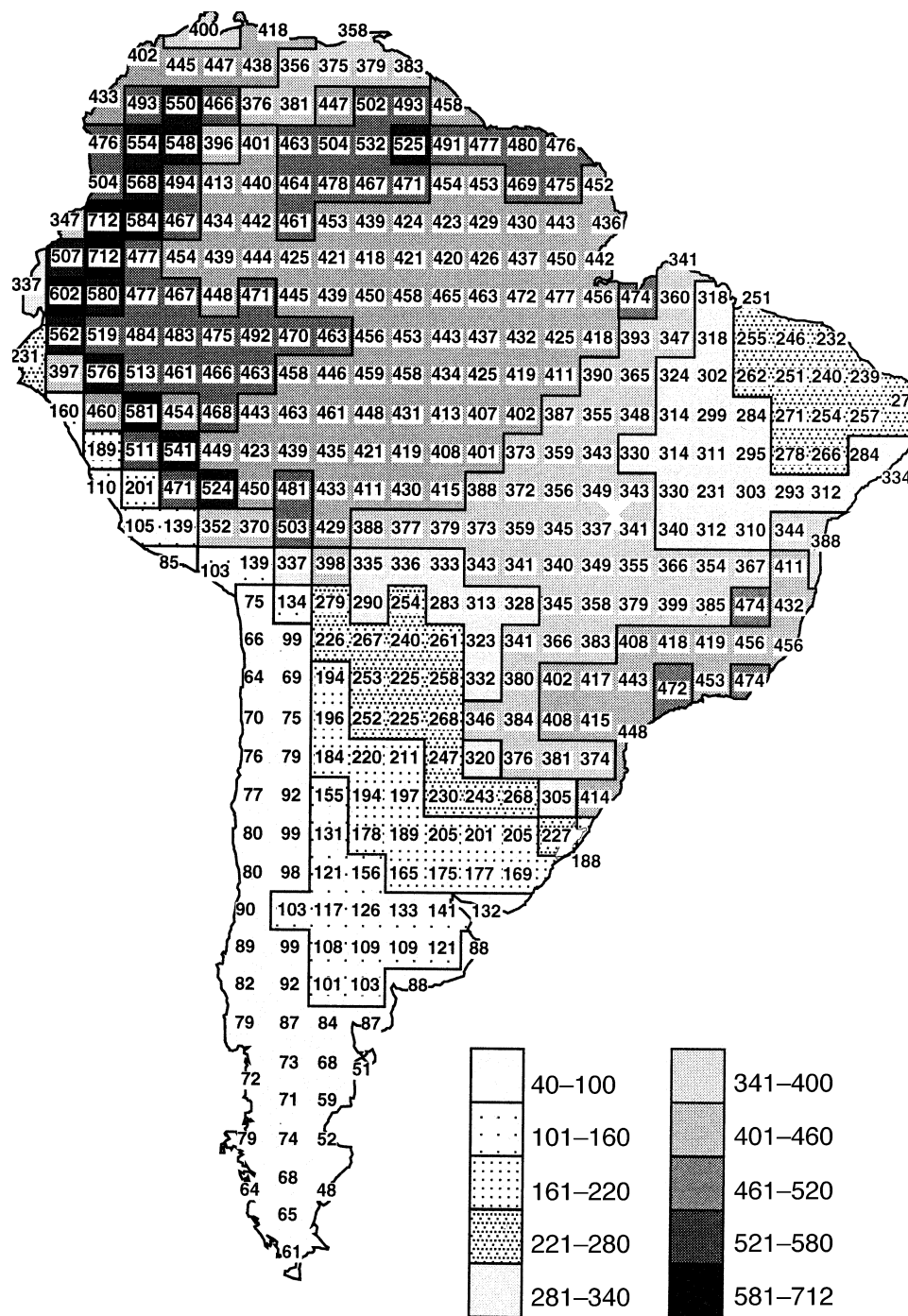


FIG. 4. Geographic variation in the richness of breeding terrestrial bird species in South America.

55.5%. Thus, the regional and subregional models are not as incongruent as they might appear, and the difference between the Palearctic models may be based on structural problems arising from collinearity among predictor variables rather than on biologically meaningful differences.

In contrast to the northern temperate zone, regional models in the warmer parts of the world identified wa-

ter-related variables as the primary predictors (Table 1): AET in the Neotropics and Afrotropics, and annual rainfall in Australia. Temperature-related variables also entered into the Afrotropical and Australia models, but in a secondary role.

A major difference between the global and regional models is the presence of nonlinear predictors in six of the seven regional models (Fig. 9). This is partic-

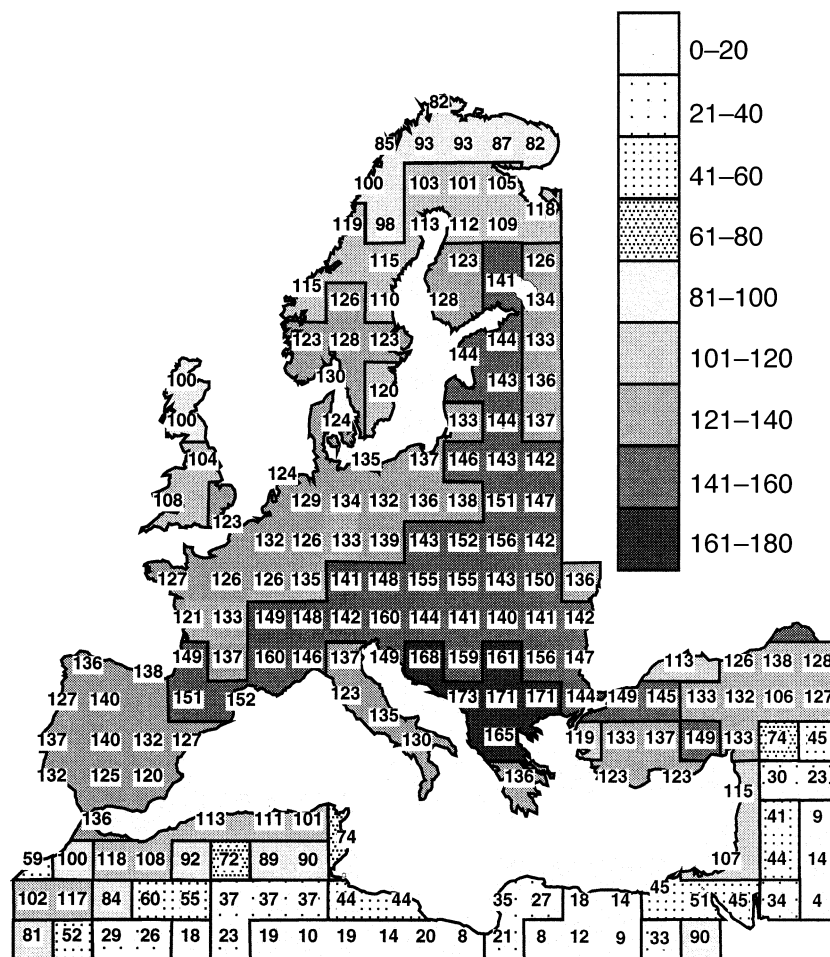


FIG. 5. Geographic variation in the richness of bird species in the western Palearctic region.

ularly apparent in the Nearctic and Palearctic models, in which ambient energy variables are positively associated with richness at low energy levels (Fig. 9a–c), have no relationship with richness at intermediate levels (Fig. 9a–c), and have a negative relationship with richness at very high levels (Fig. 9c). Nonlinear relationships between water variables and richness are also apparent in the Afrotropics (Fig. 9e) and Australia (Fig. 9f). Thus, at continental extents, linear associations of climate with richness are the exception rather than the rule. However, when comparing the global and regional models, as when comparing across regional models, it is important to note that relationships are sensitive to the range of values in both independent and dependent variables, and some of the differences among models simply reflect the fact that climate is much more variable at the global extent than within any single biogeographic region.

Richness patterns within regions are positively spatially autocorrelated at distances up to ~2000 km (Fig. 10). In most regions, the correlograms show a clinal spatial structure, with a monotonic decrease of Moran's

I with increasing spatial distances. In the Afrotropics, there is no spatial structure at large distances, indicating a more "patchy" spatial pattern in species richness. In the western Palearctic, there is a slight reversal in the pattern at large distances, indicating similar (low) species richness in northern Europe and northern Africa. Even so, the region-specific environmental models removed most of the spatial autocorrelation at the larger distance classes, irrespective of its structure (Table 1, Fig. 10). This indicates that at moderate to large spatial scales, climate accounts for species richness patterns very well. Although climate also reduced the amount of spatial autocorrelation by 33–90% in the smallest distance classes (Table 1), the Moran's I remained significantly positive ($P < 0.05$) in six of the seven regional analyses, indicating that factors not included in the analysis are contributing to the patterns of species richness at the smallest spatial scales resolved by our analyses.

The analysis of the western Palearctic also suggests that water and energy may predict bird species richness even better than indicated by the models for the other

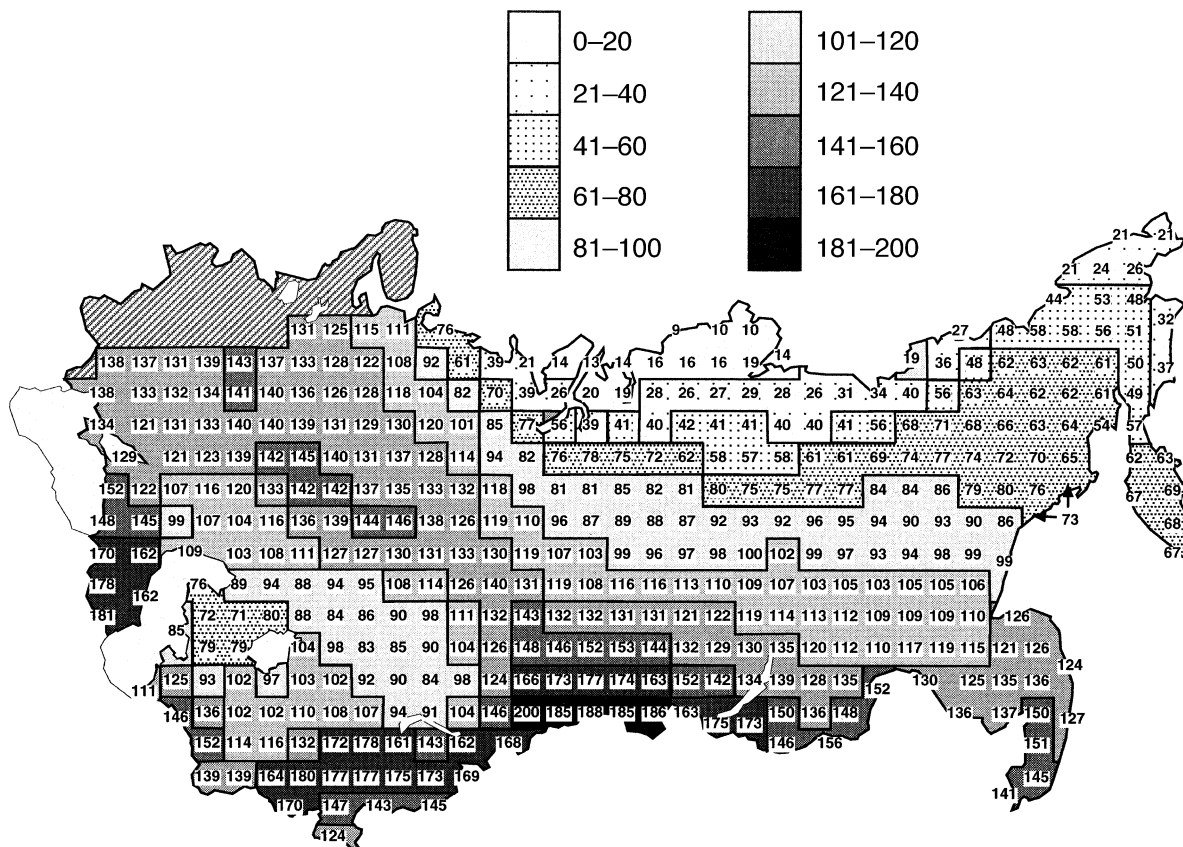


FIG. 6. Geographic variation in the richness of bird species in the former USSR. The hatched area in the upper left represents an area classified as the western Palearctic.

regions. This was our best-fitting model in terms of both high explanatory power of the climatic model and the reduction in autocorrelation structure in residuals (Table 1), and Europe also represents the area for which bird geographic ranges are best known and the maps are most finely resolved. Thus, the relatively poorer fits of environmental models and the residual spatial autocorrelation in other regions could partially reflect error due to less accurate or more coarsely resolved range maps.

DISCUSSION

Our analysis identifies contemporary levels of energy and water availability as strong predictors of the latitudinal diversity gradient. Thus, the energy hypothesis, in the broad sense, receives support as a primary explanation for the global gradient for terrestrial birds. At the global extent, the productivity version of the energy hypothesis, in particular, receives a strong level of support. However, the regional models support earlier work indicating that limits to diversity vary latitudinally. Ambient energy is limiting in the far north where it is likely to be in short supply (e.g., Kerr and Packer 1997), but in the subtropics and tropics, where a lack of energy inputs is almost certainly not an issue

(rather, too much energy may be a problem), water becomes the primary limiting factor (e.g., O'Brien et al. 1998). Thus, whether ambient energy or productivity limits diversity depends on which part of the world is concerned and on the overall water-energy input. In any case, being able to explain almost 75% of the variance in richness across six continents with a single climatic variable represents a strong argument for the power of contemporary climate to account for the latitudinal diversity gradient.

In both the Nearctic and the Palearctic, bird diversity gradients are congruent with those of a wide range of taxa, supporting the idea that ambient energy is the ultimate limiting factor for most terrestrial organisms above $\sim 50^\circ$ N (Turner et al. 1987, 1988, Currie 1991, Kerr et al. 1998, Kerr and Packer 1999, Lennon et al. 2000). However, despite growing evidence that energy input is strongly associated with numbers of species in the north, the underlying mechanism for the association is unclear. Cold temperatures and low-energy inputs presumably place thermoregulatory stress on local organisms, although this has seldom been tested with respect to latitudinal diversity gradients. Lennon et al. (2000) attempted to disentangle direct and indirect effects of temperature on the bird diversity gradient in

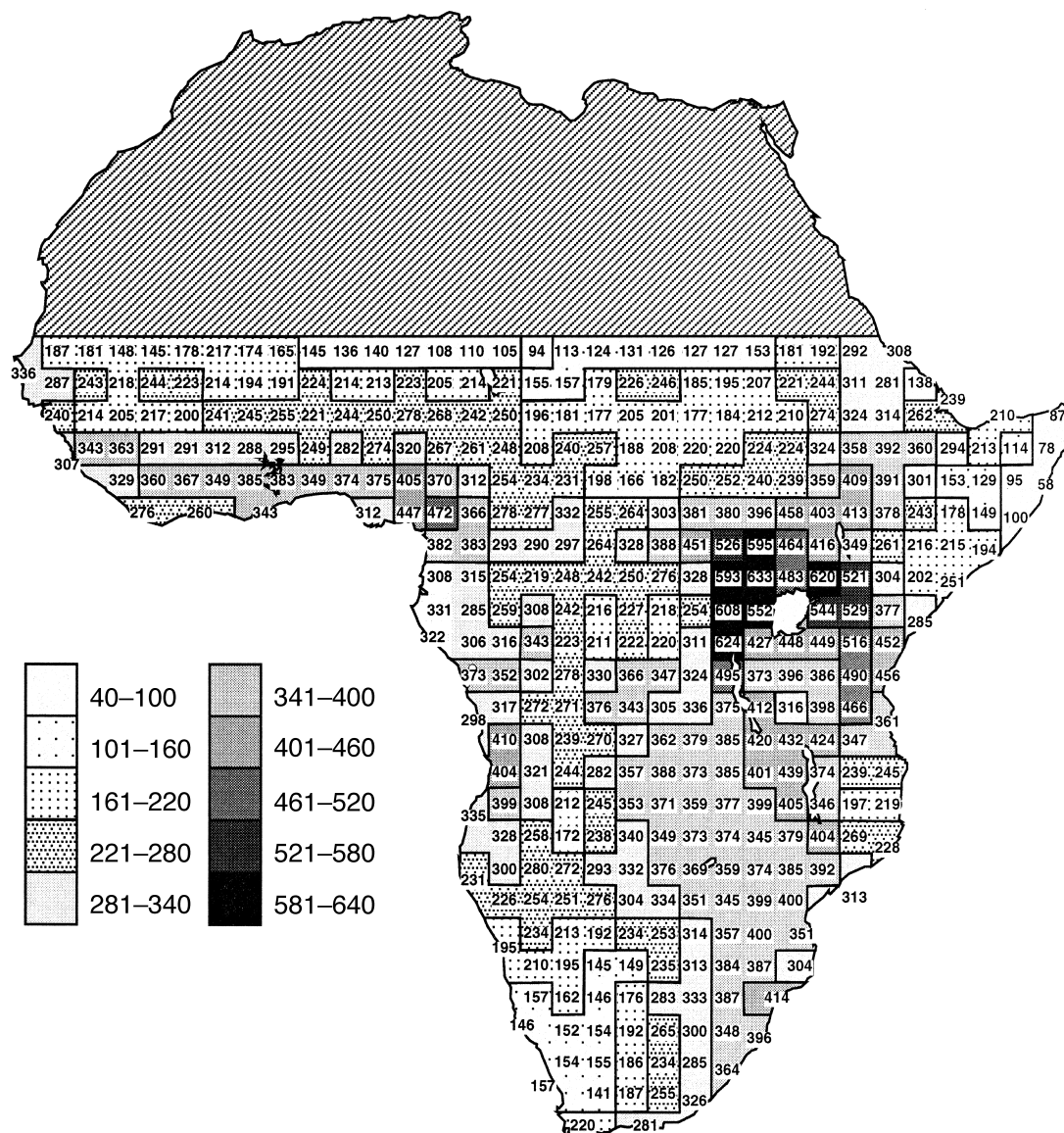


FIG. 7. Geographic variation in the richness of bird species in the Afrotropics. The hatched area represents the part of Africa generally considered to be part of the Palearctic region.

Great Britain by matching seasonal diversity patterns with seasonal energy measures; they found no direct link between temperature and numbers of bird species. They concluded that although temperature represents a major determinant of bird species richness, it is probably not due to thermoregulatory stresses and the actual mechanism responsible remains unknown. We lack data to examine this pattern more critically, other than noting that the association between bird diversity and energy is unlikely to be due to direct effects of freezing, in which case we would have found strong positive associations between mean temperature in the coldest month and bird richness in our models. (Because this variable did not represent the best predictor of bird richness in either northern region, we reject von Hum-

boldt's freezing hypothesis as a primary explanation.) We also note that a plausible alternative is that the energy inputs that are limiting at high latitudes operate indirectly via the influence of energy on plant productivity.

In the warm parts of the world, water becomes the strongest correlate of bird richness. However, the relationship between water and terrestrial birds may have different underlying causes in Australia and over most of the Afrotropics or the Neotropics. Annual precipitation is the strongest predictor of bird richness in the former, suggesting a direct link between birds and water, whereas AET is the best predictor in the latter two regions, suggesting that the link operates indirectly via the influence of water on plant productivity. It is pos-

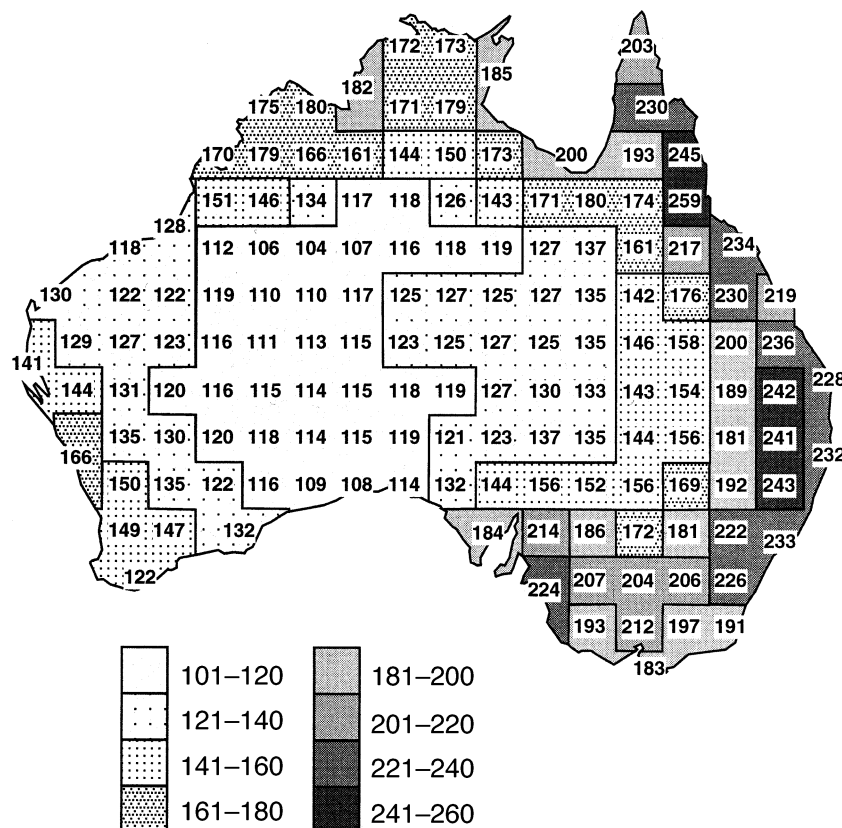


FIG. 8. Geographic variation in the richness of bird species in Australia.

sible that this difference reflects model instability arising from strong collinearity between rainfall and AET in the tropics. But if real, it is likely that this regional difference reflects the fact that Australia is the driest continent; the median precipitation value in Australia is 359 mm/yr, far less than the 937 mm/yr in Afro-tropical cells and 1432 mm/yr in the Neotropics. We are not the first to find that water is an important correlate of bird diversity in tropical and southern subtropical regions (Pianka and Schall 1981, Rahbek and Graves 2001). Thus, although data for the Oriental tropics are currently unavailable, it is becoming clear that water represents a major determinant of animal diversity patterns in the high-energy tropics and subtropics. On the other hand, as in all large-scale studies using climatic variables, an important caveat is that although AET is strongly associated with plant production, we cannot determine if the relationship between bird richness and AET is indirect (operating via food availability) or direct (operating via heat stress and the availability of free-standing water).

Consistent with the arguments of Whittaker and Field (2000), the historical signal on the global gradient appears to be largely masked by contemporary climatic variables. However, the partial regression indicates that the covariation between region and water-energy is so strong that most variation in richness cannot be inde-

pendently attributed to either factor. We doubt that further progress can be made without explicit evolutionary data. Kerr and Currie (1999) used cladistically based phylogenies for cicindelid (tiger) beetles and three families of freshwater fishes to determine whether climate or intracontinental evolutionary history best described richness patterns in North America. They found that measures of the evolutionary advancement of faunas in grid cells explained less variance than did PET (40–43% vs. 56–87%), and similar to our global model, found that history explained only an additional 1–6% of the variance in richness after fitting climate models. However, their analysis was restricted to a single biogeographic region, and the ability of phylogenetically based measures of faunal age and evolutionary development to account for intercontinental differences in richness remains untested. The strongest barriers to dispersal must exist between biogeographic regions, so quantitative measures of speciation patterns, as estimated by regional phylogenies, are essential to further partition the influence of historical and contemporary factors on the diversity gradient for birds.

The shape of the diversity-productivity relationship has been the subject of much discussion (recently reviewed by Mittelbach et al. 2001). However, at the global extent, the relationship for birds is clearly linear, with no evidence of a unimodal or hump-shaped re-

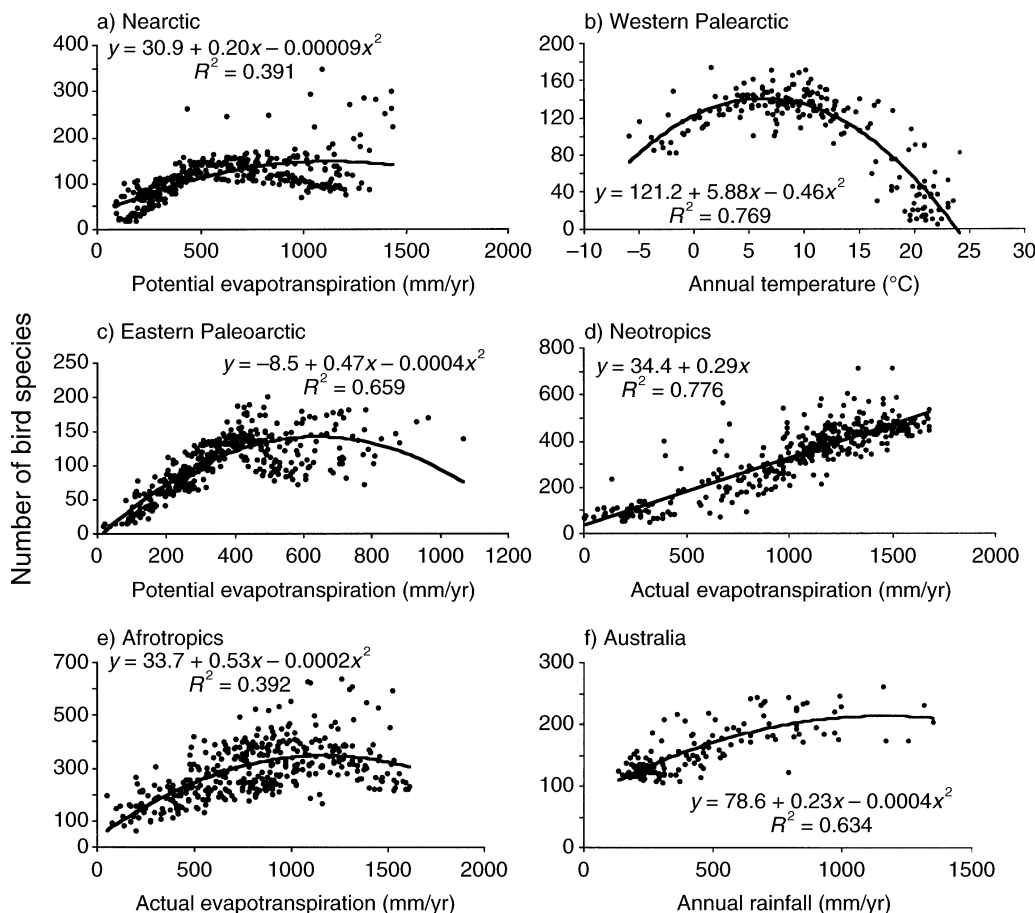


FIG. 9. Relationships between richness and the primary explanatory variables in the regional regression models (see Table 1).

relationship. Even so, it is also clear that deviations from the general pattern occur in both the Afrotropical and Nearctic regions (Fig. 1). The relatively low richness levels in the most productive parts of Africa are in the center of the Congo Basin (see Fig. 7), and it is possible that this represents under-recording; this is historically a very difficult region in which to work, and bird richness may be greater there than currently documented. In contrast, the low richness in the most productive parts of North America (Fig. 1) cannot be due to recorder bias. Geographically, this reflects the drop in richness in the eastern United States from the Great Lakes area to the southeast (see Fig. 3). Measures of productivity are also poor predictors of mammal and reptile richness in North America (Currie 1991), so there may be a general breakdown in the productivity–richness relationship in this biogeographic region. None of the variables in our analysis can account for this pattern, so the basis for this anomaly remains unknown. A second anomaly in North America is reflected by very high richness levels in the Nearctic–Neotropical transition zone of central Mexico (see Fig. 3), which generate diversity levels far greater than ex-

pected based on PET levels (see Fig. 10a) and greatly reduce the R^2 of our environmental model. Presumably, this reflects a localized “historical” effect generated by the dispersal of large numbers of Neotropical bird species into the southern Nearctic.

A major stumbling block with respect to the productivity hypothesis has been the lack of a mechanism linking plant production with animal diversity. Although it is universally accepted that highly productive areas should support larger numbers of individuals, it has been unclear how more individuals can be linked to more species. However, a linking mechanism recently has been proposed as part of the Unified Neutral Theory (Hubbell 2001). This ecological drift model argues explicitly that “the number of new species arising per unit time is a function of the total number of individuals in the metacommunity, not the number of pre-existing species” (Hubbell 2001:236, italics in the original). The theory thus predicts that more productive areas will accumulate more species over time as a consequence of supporting more individuals. Although the underlying assumptions of this controversial theory require additional validation, it is no longer the case that

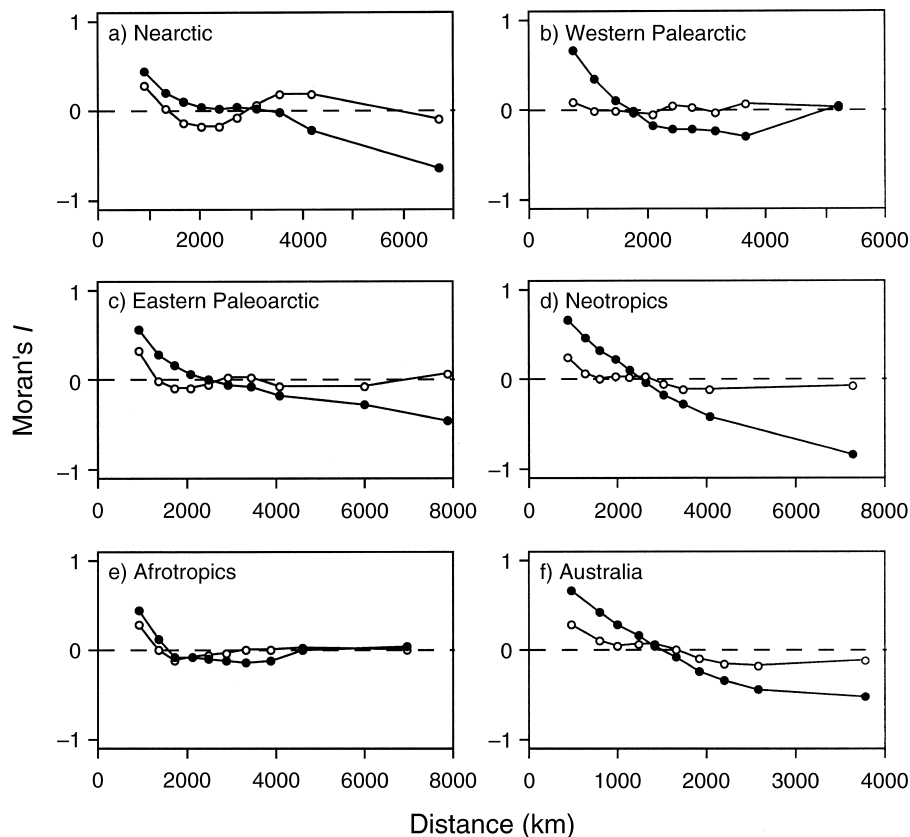


FIG. 10. Correlograms for original species richness (solid circles) and residuals (open circles) of the most parsimonious environmental model for each region (see Table 1). Moran's I values were computed using irregular distance class intervals, defined by optimizing the number of pairs of cells within each class, such that standard errors of all Moran's I across a correlogram were directly comparable.

the productivity hypothesis lacks a potential mechanistic explanation.

The methodological issue of spatial autocorrelation has recently become an important component of analyses of diversity gradients, and we used a spatial analysis here as an exploratory technique to describe spatial structures and evaluate scale-dependent effects of the climatic variables on species richness (see Koenig 1999, Badgley and Fox 2000, van Rensburg et al. 2002). As expected, we found strong spatial structures in all continents across a range of spatial scales, reflecting either gradients or patchy spatial structures in species richness. However, autocorrelation analyses of the residuals of the fitted regression models indicated that, at moderate to large spatial scales, climate is sufficient to account for almost all of the spatial structure of the species richness patterns, except perhaps for North America. On the other hand, because the climatic factors analyzed here vary continuously in geographic space, whereas almost all species have ranges that extend across numerous cells in our grid system, it follows that these factors cannot fully explain variation in richness at smaller scales, as indicated by their in-

ability to remove all positive autocorrelation in the residuals of the fitted models in the smallest distance classes. Similar results were recently found by Badgley and Fox (2000) for North American mammals. Finally, our results are consistent with the widely held idea that different factors affect diversity patterns at different spatial scales (e.g., Willis and Whittaker 2002).

In sum, our analysis indicates that the productivity version of the energy hypothesis is a strong predictor of global-extent geographical variation in the species richness of terrestrial birds. Further, the latitudinal shift in explanatory processes from ambient energy in the far north to water toward the tropics is broadly consistent with the "water-energy dynamics" hypothesis of plant diversity developed by O'Brien (1993, 1998). Although birds are not plants, and we might expect their diversity patterns to be influenced by different environmental variables, the major pattern predicted by the hypothesis is what we find: bird diversity drops as ambient energy becomes low, whereas when energy is high, diversity decreases with decreasing water. This hypothesis offers a parsimonious explanation for diversity gradients of both plants and a major group of

animals, and thus represents a potential unifying hypothesis for terrestrial diversity gradients. The extent to which this is true remains to be seen.

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