The Effect of Energy and Seasonality on Avian Species Richness and Community Composition

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ABSTRACT: We analyzed geographic patterns of richness in both the breeding and winter season in relation to a remotely sensed index of seasonal production (normalized difference vegetation index [NDVI]) and to measures of habitat heterogeneity at four different spatial resolutions. The relationship between avian richness and NDVI was consistent between seasons, suggesting that the way in which available energy is converted to bird species is similar at these ecologically distinct times of year. The number and proportion of migrant species in breeding communities also increased predictably with the degree of seasonality. The NDVI was a much better predictor of seasonal richness at finer spatial scales, whereas habitat heterogeneity best predicted richness at coarser spatial resolutions. While we find strong support for a positive relationship between available energy and species richness, seasonal NDVI explained at most 61% of the variation in richness. Seasonal NDVI and habitat heterogeneity together explain up to 69% of the variation in richness.

Keywords: species-energy theory, birds, species richness, productivity, habitat heterogeneity, scale.

The latitudinal gradient of species richness is one of the most fundamental geographic patterns of life on earth. Understanding the factors that regulate species richness and generate these broad pervasive patterns has become one of the most important challenges in contemporary ecology (Hutchinson 1959; Brown 1981, 1995; Wilson 1988; Ricklefs and Schluter 1993; Tilman and Downing 1994; Rosenzweig 1995). Productivity, area, climatic sta-

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bility, and evolutionary history are just a few of the factors proposed to influence species richness, but despite decades of research, there has been little consensus about the relative importance of these and other factors (Pianka 1966; Rohde 1992; Ricklefs and Schluter 1993; Brown 1995; Rosenzweig 1995). One reason for the lack of progress in eliminating competing hypotheses is that many of the climatic and ecological variables frequently used as predictors of richness are correlated with latitude and each other.

Birds offer a unique opportunity to evaluate the effects of productivity on species richness. Their ability to move long distances allows them to exploit ephemeral resources by responding to both spatial and temporal variation in environmental production. The phenomenon of migration and the consequent redistribution of bird species during a portion of the year presents a natural experiment through which we may disentangle the effects of productivity and latitude. While average annual productivity tends to decrease with latitude, the relationship between seasonal production and latitude is far more complex, particularly during the summer. Summer production exhibits no gradient with latitude ($r = 0.12$), and the spatial pattern is only very weakly correlated with the pattern of winter production in North America (fig. 1). Thus, by breaking down the relationship between productivity and richness seasonally, our study allows us to test productivity explicitly rather than some undefined correlate of latitude.

While some have suggested a hump-shaped relation between productivity and species richness (e.g., Tilman 1982; Rosenzweig and Abramsky 1993; Huston 1994), the prevailing trend at continental to global scales tends to be a continuously increasing function (Wright 1983; Currie 1991; Wright et al. 1993; Guegan et al. 1998; Waide et al. 1999; Chase and Leibold 2002). One of the most promising theoretical frameworks for understanding richness patterns is the species-energy theory (SET), which asserts that sites with greater available energy are able to support more individual organisms and, hence, more species (Connell and Orias 1964; Brown 1981, 1995; Wright 1983; Wright et al. 1993; see also Hubbell 2001). Various mechanisms have been proposed for species-energy theory. Increases
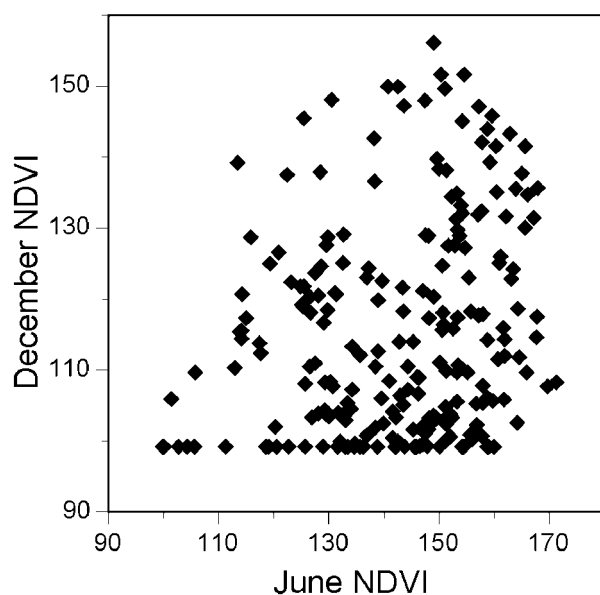
Figure 1: Relationship between June production and December production as estimated by the remotely sensed normalized difference vegetation index (see "Methods").

in abundance may come about directly from an increased resource supply (Connell and Orias 1964; Brown 1981; Wright 1983; Currie 1991), or increased temperature may reduce thermoregulatory loads and allow organisms to allocate more energy to growth and reproduction (Turner et al. 1988; Lennon et al. 2000). In either case, increased abundance has been hypothesized to lead to reduced extinction risk and a higher equilibrium number of species. Others have suggested that speciation rates also increase with various measures of available energy including temperature (Connell and Orias 1964; Allen et al. 2002). However, ecology still lacks a realistic theory and conclusive empirical evidence for the division of energy among individuals and species within ecological communities (Brown et al. 2001; Enquist and Niklas 2001; Haskell 2001; Enquist et al. 2002).

Debate over species-energy theory has taken two major trajectories, one disputing the general relationship between energy availability and species richness (Price 1991; Latham and Ricklefs 1993) and the other debating the mechanisms proposed by the SET (Enquist and Niklas 2001). While the causal mechanisms of the SET remain unproven, richness has been shown to increase over a broad range of spatial scales with various estimates of available energy, including actual and potential evapotranspiration rates, ambient temperature, solar radiation, rainfall, biomass, and net primary productivity (e.g., Pianka 1971; Brown and Davidson 1977; Brown 1981; Wright 1983; Currie and

Paquin 1987; Gentry 1988; Adams and Woodward 1989; Currie 1991; Blackburn and Gaston 1996; Guegan et al. 1998; Waide et al. 1999; Lennon et al. 2000; Rahbek and Graves 2001). Despite the increasing number of studies examining these relationships, however, many of the tests of the SET have been coarse. Studies of bird species richness, for example, have ignored the seasonal variation in available energy, correlating breeding season richness with an estimate of average annual productivity (Wright 1983; Currie 1991; Blackburn and Gaston 1996; Rahbek and Graves 2001). However, analyses that use average annual productivity may obscure the species-energy relationship for organisms that are known to track seasonal fluctuations in resources.

In this article, we examine changes in seasonal patterns of bird richness across North America with respect to seasonal estimates of environmental production, on the basis of a remotely sensed vegetation index. Species-energy theory predicts that seasonal variation in avian richness should reflect the underlying variation in available energy. The theory also yields predictions for the relative numbers of migrants and residents as a function of the seasonality regime. Our study is the first to explicitly examine seasonal and spatial variation in species richness in the same context: energy availability.

The Model

Assuming a positive monotonic relationship between energy and species richness, we have developed a graphical model that depicts our expectations for the effects of seasonal variation in available production on species richness and the proportion of migrants in breeding communities (fig. 2). Within each of the two seasonally distinct bird communities, breeding and wintering, we expect species richness to be determined by the amount of resources available in that season. The influence of seasonality (the degree to which resources fluctuate predictably on an annual basis) on the proportion of migrants in the breeding community has been addressed qualitatively (MacArthur 1959; Herrera 1978; Rabenold 1979) but has not yet been rigorously tested. We assume that resident species can compensate only partially for seasonal pulses in production via functional and numerical responses (Holling 1959). Production not used by permanent resident species should be available to seasonal migrants. Therefore, we expect that resident species richness will be limited by the period of lowest production at a site, while migrant species richness will be determined by the magnitude of the seasonal pulse in production. The proportion of migrants in the breeding community is then determined by the ratio of winter to summer production. For example, two sites with approximately equal levels of energy available during
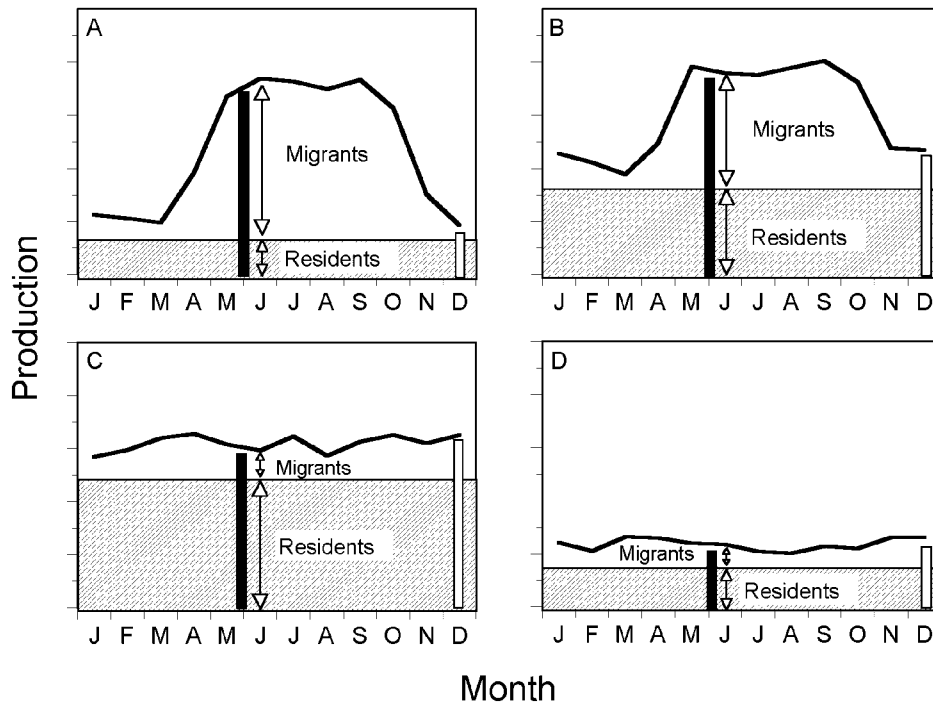
Figure 2: Patterns of seasonal variation in normalized difference vegetation index (*solid line*) for sites in (*A*) Ontario, (*B*) Virginia, (*C*) Georgia, and (*D*) Nevada, and the predicted levels of summer richness (*solid bars*), winter richness (*open bars*), number of residents, and number of migrants (*arrows*).

the breeding season would be expected to have the same summer richness. However, if one site experiences nearly constant production throughout the year (e.g., fig. 2*C*), it would be expected to have a much smaller proportion of migrants than would a site with a large summer peak in production (e.g., fig. 2*A*).

Using this framework, we have mapped the predictions from our model onto a production phase space with June production plotted against either December or minimum monthly production. In this phase space, the line of equality denotes aseasonal environments (fig. 3), while areas toward the lower right are extremely seasonal. We develop a graphical model that extends species-energy theory to make testable predictions about how spatial and temporal variation in productivity should impact avian richness and migratory guild composition. In general, species-energy theory predicts that richness is a monotonic positive function of available energy (Brown 1981; Wright 1983; Wright et al. 1993). Given the mobility of birds, we predict that the geographic pattern of avian richness during the breeding and winter seasons should reflect the underlying pattern of environmental productivity at the respective time of year. Specifically, (1) breeding season richness should be proportional to breeding season production (fig. 3*A*);

(2) winter richness should be proportional to winter production (fig. 3*B*); (3) the number of resident species should be proportional to the minimum monthly production experienced each year; (4) the number of migrant species should increase with the difference between summer and winter production (fig. 3*C*); and (5) the proportion of migrant species in the breeding community should increase as the ratio of summer to winter production increases (fig. 3*D*); conversely, the proportion of resident species in the breeding community should vary inversely with that ratio.

To determine the influence of scale on the observed relationships, we tested each of these predictions at four different spatial resolutions. In general, we expect an increase in the precision of the productivity-diversity relationship at finer spatial resolutions. The way in which energy is divided up among species should be more straightforward at the local scale, where habitat is more likely to be homogeneous and species are more likely to compete directly for the same pool of resources. At more regional scales, we expect two factors to weaken the relationship between productivity and richness. First, we expect the number of habitat types to increase with area, leading to an increase in richness via species turnover.
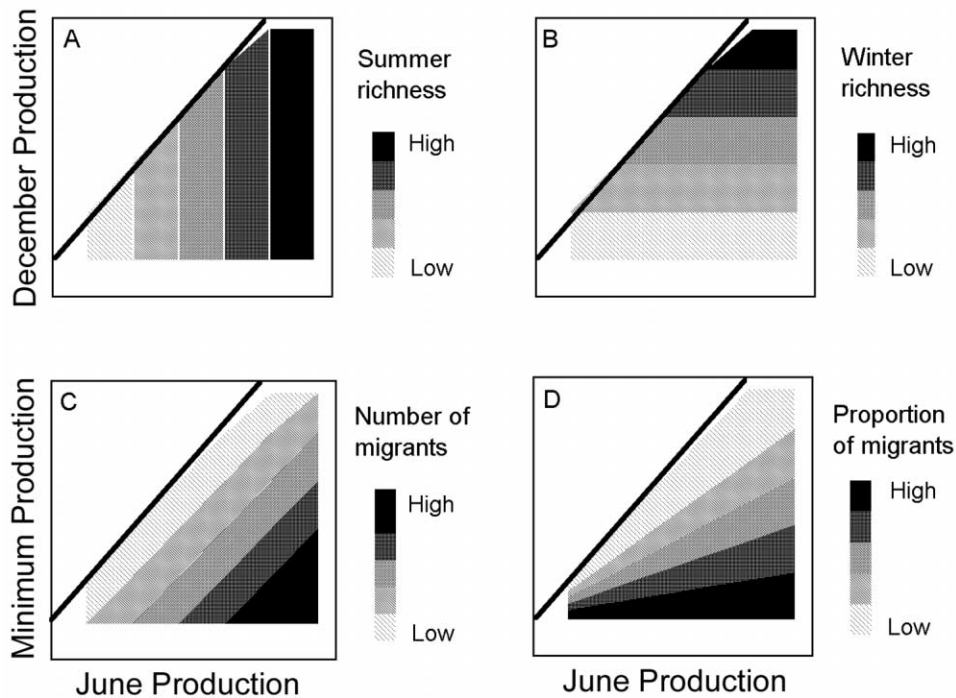
Figure 3: Expected variation of (*A*) summer richness, (*B*) winter richness, (*C*) number of migrants, and (*D*) percentage of migrants in the breeding community on production phase space (see text).

Second, the average energy availability over a large region does not necessarily provide an accurate representation of the resource pool at any given location in that region. For example, if a region is made up of both high- and low-productivity habitats, the average energy availability across the region will be moderate, but species richness will likely be high since two different suites of species will be represented. A local survey is much more likely to fall within one habitat type, and thus the effect of adding species via enhanced habitat heterogeneity is minimized. Habitat heterogeneity has long been invoked as a mechanism maintaining bird diversity (MacArthur 1964; Cook 1969; Recher 1969; Roth 1976; Crowe and Crowe 1982; Blackburn and Gaston 1996; Bohning-Gaese 1997). For the reasons stated above, we also examine the importance of a landscape-scale measure of habitat heterogeneity for explaining the geographical variation in richness.

In conducting these analyses, we have made a number of assumptions on which the validity of the conclusions depends. First, estimates of species richness on the basis of survey data are a reasonable approximation of actual species richness, and survey data provide an accurate depiction of the migratory guild composition in an area. Both of the surveys whose data we employ are known to have a number of limitations (Bock and Root 1981; Bystrak

1981), but their standardized methodologies provide consistent estimates of species number and composition across the continent. Second, designations of migratory guild describe the seasonal composition of a community. We recognize that migratory behavior is variable among individuals, between years, and across a region, but we assume that the migratory status designation approximates the role that species fill within a community. Third, the remotely sensed vegetation index that we use is a reasonable estimate of environmental production, and it is correlated with the energy available to birds. Although the vegetation index has important limitations (see "Methods"), on a continental scale it appears to capture the important variation in primary production between seasons and regions. We assume that the amount of potential photosynthetic activity estimated by the vegetation index approximates the productivity of plant and animal foods on which birds forage. Fourth, remotely sensed vegetation index data for 1992–1993 are representative of the geographic pattern of productivity over the decade. For reasons of data availability, we have compared vegetation index data from 1992 to 1993 with bird survey data from 1997. Each data set was chosen independently to achieve the maximum coverage. Fifth, singly or in combination, any biases or errors in the data or in our assumptions will result in increased

residual variation. Errors should not create patterns where none exist, only obscure our ability to detect significant relationships.

Methods

Bird Data

We examined the geographic patterns of species richness of the North American terrestrial avifauna (species considered to be primarily marine or aquatic were excluded from analyses) in the winter and summer of 1997 using data from two continent-wide surveys, the North American Breeding Bird Survey (BBS) and the Audubon Christmas Bird Count (CBC). Both data sets are available online at http:// monitoring2.er.usgs.gov/bbs/ and http://www.nmt.edu/ ~shipman/z/cbc/, respectively. Each BBS survey is censused in May or June along a 39.2-km roadside route over which 50 3-min point counts are conducted at 800-m intervals (see Bystrak 1981 for details on methodology). After the elimination of routes for which data collection did not meet BBS quality standards, 2,494 BBS routes were available for analyses. Each CBC survey area consists of a 24-km-diameter circle (452 km²) in which all birds are enumerated on a single calendar day within 2 wk of Christmas (see Bock and Root 1981 for details). A total of 1,619 CBC circles were used to characterize the winter pattern of avian richness. The BBS and CBC survey areas provide extensive coverage of the contiguous United States and southern Canada.

Species richness patterns were examined at four different scales of spatial resolution. At the finest scale, the survey level, we used the richness of individual BBS routes or CBC circles. In addition, estimates of species richness were calculated for equal-area grid cells of three different sizes—20,000, 40,000, and 80,000 km²—across the continent. These grid cell sizes are hereafter referred to as small, medium, and large, respectively. For any given grid cell size, the number of surveys per cell varied considerably. Since species richness is a function of survey effort, we employed rarefaction (sensu Hurlbert 1971) to get the expected value of species richness over n randomly chosen surveys within a grid cell. The value of n for each of the different grid sizes was chosen such that the greatest number of grid cells could be used while still characterizing the richness of each cell on the basis of as many surveys as possible (table 1). The geographic patterns of species richness were not affected by the choice of n.

We used the migratory classifications of the Patuxent Wildlife Research Center (Laurel, Md.) to designate bird species as migrants or residents. The migrant category includes both Neotropical and short-distance migrants because both groups undergo seasonal movements to use ephemeral resources. Elsewhere, we are analyzing differences in patterns of richness and responses to environmental variables by the two classes of migrants (A. H. Hurlbert and J. P. Haskell, unpublished manuscript). Only 2% of species were unclassified, and they were excluded from analyses regarding migratory status.

Normalized Difference Vegetation Index

We used a remotely sensed vegetation index from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer satellite to assess seasonal changes in productivity. The normalized difference vegetation index (NDVI) is a measure of greenness calculated from reflectance in the near infrared and red portions of the electromagnetic spectrum. The NDVI has been shown to be correlated with total green biomass, leaf area index, and percent incident photosynthetically active radiation (Asrar et al. 1984; Chong et al. 1993; Sellers et al. 1994). Some of the constraints on NDVI are that the index saturates at very high levels of productivity (Box et al. 1989) and that it may be influenced by soil reflectance characteristics in regions with low vegetation cover (Huete 1989). Also, NDVI does not take into account the effect of temperature on the rate of photosynthesis. However, many studies have found that NDVI provides a reasonable estimate of net primary productivity (Chong et al. 1993; Goward et al. 1994; Hobbs 1995; Paruelo et al. 1997). We assume that NDVI is positively correlated with production of the food available to birds.

While raw NDVI values range from −1 to 1, the Earth Resources Observation Systems Data Center rescaled the index from 0 to 200, with values from 100 to 200 representing increasing greenness and values <100 indicating nonvegetated surfaces such as snow, water, or bare soil (Eidenshink and Faundeen 1994). In our data set, the lowest mean values of NDVI were around 96, but we set values lower than 99 to 99 to index zero production.

We used monthly composites of the 1-km-resolution NDVI data from April 1992 through March 1993 to calculate mean monthly values for each grid cell and for a spatial neighborhood around each BBS route and CBC survey. The neighborhood around each BBS route was a

Table 1: Number of bird surveys used to characterize each grid cell size by rarefaction

Grid cell size (km²)	BBS routes	CBC circles
20,000	3	1
40,000	5	2
80,000	9	4

Note: BBS = Breeding Bird Survey; CBC = Christmas Bird Count.

5 × 5-km square centered on the route's starting point coordinates. The neighborhood for each CBC survey was the 24-km-diameter circle corresponding exactly to the area surveyed for birds. Two measures of seasonality were calculated from the mean monthly NDVI values. First, the difference between June NDVI and the minimum monthly NDVI was taken as an absolute measure of the seasonal pulse of production during the breeding season. Second, the ratio of the seasonal pulse (June NDVI minus minimum monthly NDVI) to June NDVI was used to index the proportion of production in June relative to the least productive month. If NDVI in June is roughly equal to the minimum monthly NDVI, then the ratio is close to 0. If the minimum monthly NDVI is very low, then the value in June represents almost entirely new growth, and the ratio will be close to 1.

Environmental Heterogeneity

We used two measures of environmental heterogeneity as potential predictors of species richness. The first measure was elevational range, determined from a 1-km-resolution digital elevation model of North America. For every grid cell, we calculated the difference between maximum and minimum elevation. At the survey level, we calculated the elevational range within the spatial neighborhoods described in the previous section for individual BBS routes and CBC circles. The second measure of heterogeneity was the number of biomes encompassed within a grid cell using the Environmental Protection Agency's map of North American biotic communities (Reichenbacher et al. 1998). Number of biomes could not be calculated at the survey level.

Data Analysis

Empirical data suggest that the relationship between species richness and environmental productivity will be approximated by a positive linear relationship over the range of variation in bird communities in North America (Currie and Paquin 1987; Currie 1991; Waide et al. 1999). We used multivariate regression analyses to demonstrate the limitations of SET that are primarily a function of its univariate nature. While SET emphasizes the impact of available energy on species richness, most ecologists believe that other factors, such as heterogeneity, influence the ability of individuals to use primary productivity. Using multivariate regression, we determined the relative importance of these factors and the degree to which model fit improved with a small increase in model complexity. Complex multivariate and nonlinear analyses, however, are beyond the scope of the theory that we are testing in this article.

Species richness and the environmental variables we ex-

amined all exhibited spatial autocorrelation, which may affect parameter estimates and inflate Type I errors in traditional regression (Cressie 1993; Lennon 2000). To address this problem, we used a spatial linear model that takes into account covariance among neighboring data points. A conditional autoregressive approach allowed us to break down the dependent data into the trend explained by the independent variables, the spatial signal of the neighbors, and the residual variation. This approach allowed us to model and remove the spatial signal of autocorrelation among neighbors, leaving the spatially independent trend (Cressie 1993; Kaluzny et al. 1998). For the gridded data, spatial neighbors were defined as the eight cells immediately surrounding a focal cell. We used a neighborhood of radius 200 km for individual BBS routes (nine neighbors per route on average) and CBC circles (seven neighbors per circle); R^2 values were determined by plotting fitted against observed values.

Results

The geographic patterns of avian richness in North America varied markedly between seasons and closely matched the seasonal patterns of NDVI (fig. 4). During the breeding season, richness was greatest across the eastern U.S.-Canadian border, along the Appalachian Mountains, and in the northwestern United States, while richness was lowest throughout the Great Plains. During the winter, richness was greatest at southern latitudes and along the coasts. Seasonal richness was correlated with NDVI for the respective season, supporting predictions 1 and 2, although the relationship was stronger in the winter than in the summer (fig. 5A, 5B). Latitude alone explained very little of the variation in richness during the breeding season ($R^2 = 0.04$ using 20,000-km² grid cells), while the residuals of NDVI on latitude explained nearly 30% ($R^2 = 0.27$, $P < .0001$). Because BBS routes and CBC circles survey vastly different areas (25 km² vs. 452 km²) and employ different methodologies, species richness cannot be compared directly between them. However, richness values within each survey can be standardized by the maximum richness observed in that survey. The standardized values represent the fraction of maximum richness observed in that season and allow comparisons between seasons. Standardized values of richness for both seasons exhibit similar relationships with NDVI (fig. 5C). Thus, regardless of the season, the mean NDVI for an area allows one to predict the relative richness reasonably well ($R^2 = 0.61$, $P < .0001$). Also, seasonal NDVI was a much better predictor of seasonal richness than annual NDVI summed across the year (table 2).

All other predictions of our species-energy model were also supported (table 2). The number of resident species
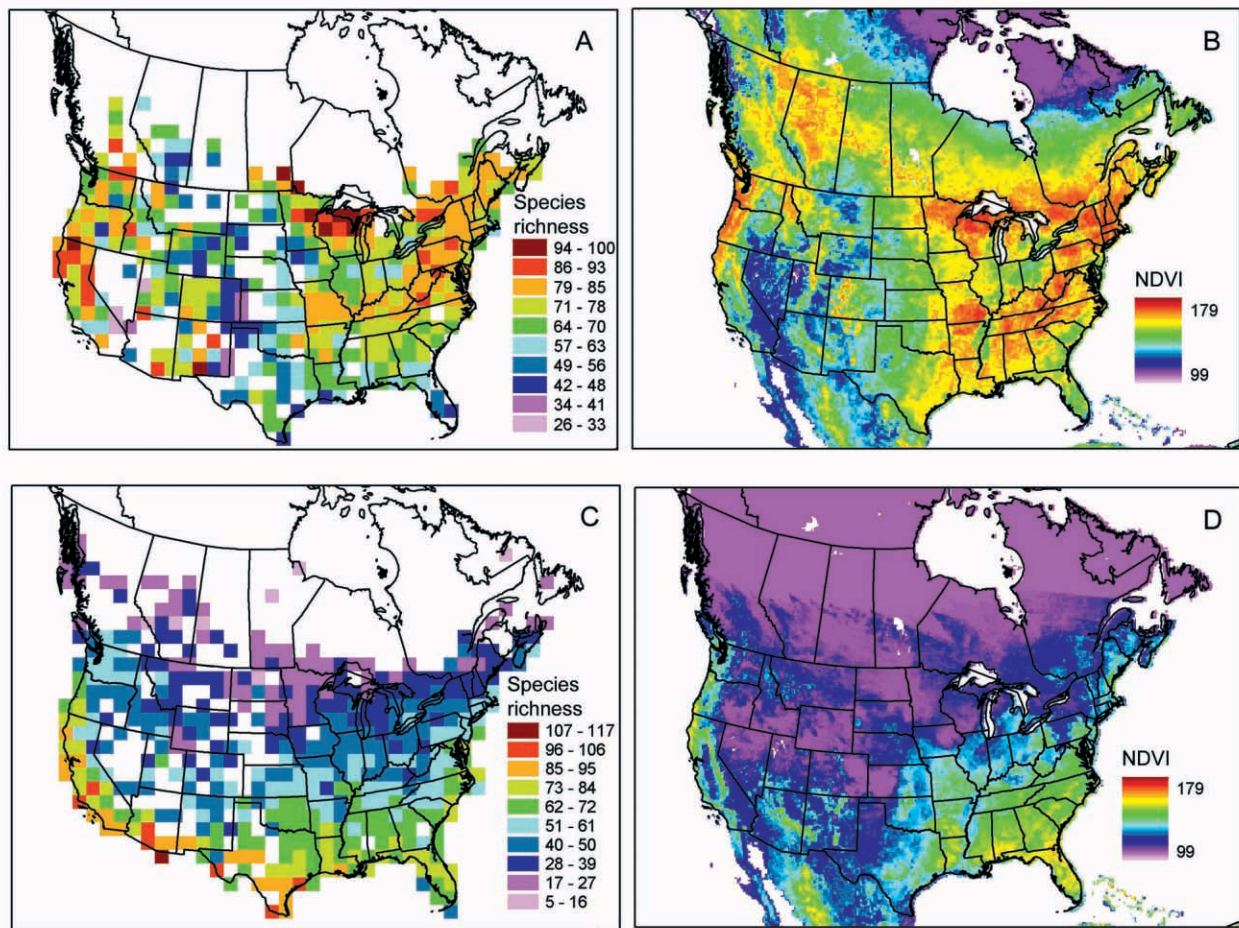
Figure 4: *A,* Summer pattern of species richness across North America on the basis of expected number of species over three randomly chosen Breeding Bird Survey routes per 20,000-km^2 grid cell. *B,* Spatial pattern of normalized difference vegetation index (NDVI) in June at 1-km resolution. *C,* Winter pattern of species richness across North America on the basis of expected number of species over one randomly chosen Christmas Bird Count circle per 20,000-km^2 grid cell. *D,* Spatial pattern of NDVI in December at 1-km resolution.

in breeding surveys was positively correlated with minimum monthly NDVI, the number of migrant species was positively correlated with the difference between June NDVI and minimum monthly NDVI, and the percentage of the community made up by migrants was positively correlated with the ratio of the seasonal pulse in NDVI to June NDVI (predictions 3, 4, and 5). A weak positive relationship was also observed between species richness in both seasons and the two measures of environmental heterogeneity.

Scale

The spatial resolution at which the data were examined influenced the strength of the relationships between species richness and environmental variables (fig. 6). While ele-

vational range best predicted species richness at the coarsest spatial resolution, NDVI was a better predictor at finer spatial resolutions. This general trend held for both summer and winter richness, except during the winter at the finest scale. Minimum monthly NDVI predicted the number of residents best at finer spatial resolutions, and the ratio of the seasonal pulse to June NDVI predicted the proportion of migrants in the community best at coarser resolutions (table 2).

Graphical Model

Predictions of our species-energy model are represented graphically in figure 2, where the dependent variable (summer richness, winter richness, number of migrants, and proportion migrants) is mapped onto NDVI space (June
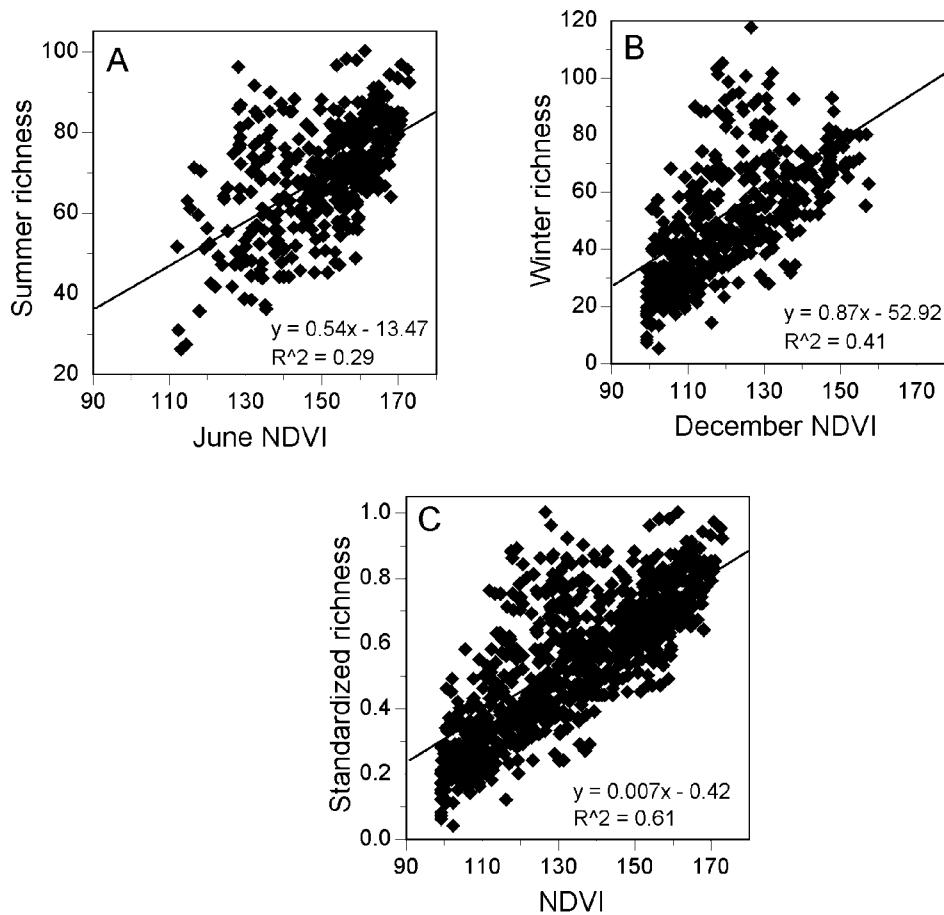
Figure 5: *A*, Relationship between breeding season species richness and June normalized difference vegetation index (NDVI) at the resolution of 20,000-km^2 grid cells. *B*, Relationship between winter species richness and December NDVI at the resolution of 20,000-km^2 grid cells. *C*, Relationship between standardized species richness (see text) and NDVI, including both summer and winter data.

NDVI vs. either December NDVI or minimum monthly NDVI). Points along the line of equality represent relatively aseasonal environments, while points in the lower right corner are highly seasonal. The observed data are in general accordance with the predictions (fig. 7). At the resolution of small (20,000 km^2) grid cells, summer richness increases with increasing June NDVI, independent of December NDVI (fig. 7*A*). Winter richness tends to increase with increasing December NDVI (fig. 7*B*), although the highest richness in this season is at intermediate December NDVI. These patterns are less clear at a coarser spatial resolution, suggesting that the effects of NDVI and environmental heterogeneity are scale dependent (fig. 7*A'*, 7*B'*). In the summer, richness is much higher than expected on the basis of NDVI alone in mountainous areas of the West, especially the Sierra Nevada. In the winter, richness is higher than would be predicted from NDVI across the southwestern United States. This may be due to conti-

nental geometry (e.g., Colwell and Hurtt 1994; Jetz and Rahbek 2001) and the occurrence of species whose wintering ranges are centered in Mexico but extend just into the southern United States.

The number of migrants increases in roughly parallel bands with increasing distance from the line of equality, suggesting that the difference in greenness between June and the month of minimum NDVI is a good predictor of how many species invade the community during the breeding season (fig. 7*C*, 7*C'*). Finally, migrants make up the smallest percentage of the community in the most aseasonal environments along the line of equality and make up the majority of the community (85%–95%) in the most seasonal environments along the bottom wedge (fig. 7*D*, 7*D'*). Interestingly, even in the most aseasonal environments, no BBS survey had fewer than 46% migrants, and no 80,000-km^2 grid cell had fewer than 55% migrants.

Table 2: Spatial linear regression results relating seasonal richness and migratory guild composition to normalized difference vegetation index (NDVI) and measures of habitat heterogeneity at four different spatial scales

Relationship	Large Slope	Large R^2	Medium Slope	Medium R^2	Small Slope	Small R^2	Survey Slope	Survey R^2
Summer richness versus:								
June NDVI	.51**	.01	.48***	.14	.54***	.29	.56***	.41
Annual NDVI	.02	.002	.04***	.06	.05***	.16	.05***	.34
Elevational range	.005*	.15	.006***	.07	.002	.003	.0002	7.5E−6
Number of biomes	2.02*	.10	3.01***	.05	−.74	.03	NA	NA
Winter richness versus:								
December NDVI	1.09***	.27	.96***	.32	.87***	.41	.72***	.25
Annual NDVI	.05	.01	.04*	.03	.04***	.08	.03***	.02
Elevational range	.0009	.04	−.0003	.01	−.0002	.0004	−.0009	.003
Number of biomes	2.52*	.18	3.19***	.14	1.42*	.05	NA	NA
Number of residents versus minimum NDVI	.21**	.12	.22***	.26	.23***	.34	.16***	.37
Number of migrants versus June minus minimum NDVI	.58***	.23	.46***	.29	.45***	.32	.36***	.27
Percent migrants versus seasonal pulse ratio[a]	.21***	.56	.21***	.55	.19***	.50	.20***	.43

Note: NA = not applicable.

[a] Ratio of the seasonal pulse (June NDVI minus minimum monthly NDVI) to June NDVI.

* $P < .01$.

** $P < .001$.

*** $P < .0001$.

Multiple Regressions

We conducted spatial multiple regressions (see "Methods") to see how much additional explanatory power was gained by adding variables characterizing environmental heterogeneity (table 3). June NDVI, elevational range, and the number of biomes together explained between 29% and 43% of the variation in breeding season richness, depending on the scale of analysis. December NDVI, elevational range, and number of biomes explained between 25% and 49% of the variation in winter richness. When data for both summer and winter richness are examined together using standardized values of richness, then NDVI, elevational range, and number of biomes are able to explain 57%–69% of the variation in the data.

Discussion

The empirical relationships between seasonal richness and seasonal production and between the degree of seasonality and the number and proportion of migrants in the breeding community are all consistent with species-energy theory. Birds use their mobility to track spatially and temporally fluctuating resources, even at continental and hemispheric scales. The fact that the relationship between richness and available energy is similar across seasons despite enormous changes in the geographic pattern of productivity suggests that bird species distribute themselves in the same way throughout the year in response to resource abundance and the presence of other species without regard to latitude. Thus, seasonal environmental production appears to determine the number of species that coexist in an area during a given season, and the rate and timing of that production determine the migratory guild composition of the breeding community. Not only have we confirmed the suggestions of both MacArthur (1959) and Herrera (1978) that the proportion of migrants varies with seasonality, but we have also incorporated the idea explicitly into species-energy theory, showing that it applies to species as well as to individuals.

Our analyses are clearly limited by our ability to measure accurately the energy available to birds. While NDVI, as a measure of greenness, provides a useful index, it is far from precise. For example, resources available in areas with harsh winters (e.g., seeds, dead arthropods) are not related to winter foliage and are undoubtedly underestimated. In such an environment, the resources available during the winter probably reflect, to some extent, production earlier in the year. Such a "storage effect" would predict higher winter richness in areas with greater summer production given equal levels of winter production (fig. 8). Our data provide no evidence for such a storage effect, and the tendency is in fact in the opposite direction: grid cells with similar December NDVI values tended to have higher winter richness when June NDVI was low (fig. 7B).

We have shown seasonality to be an important factor in determining both the number and proportion of migrants in a local breeding community. However, our model predicts that aseasonal environments should support al-
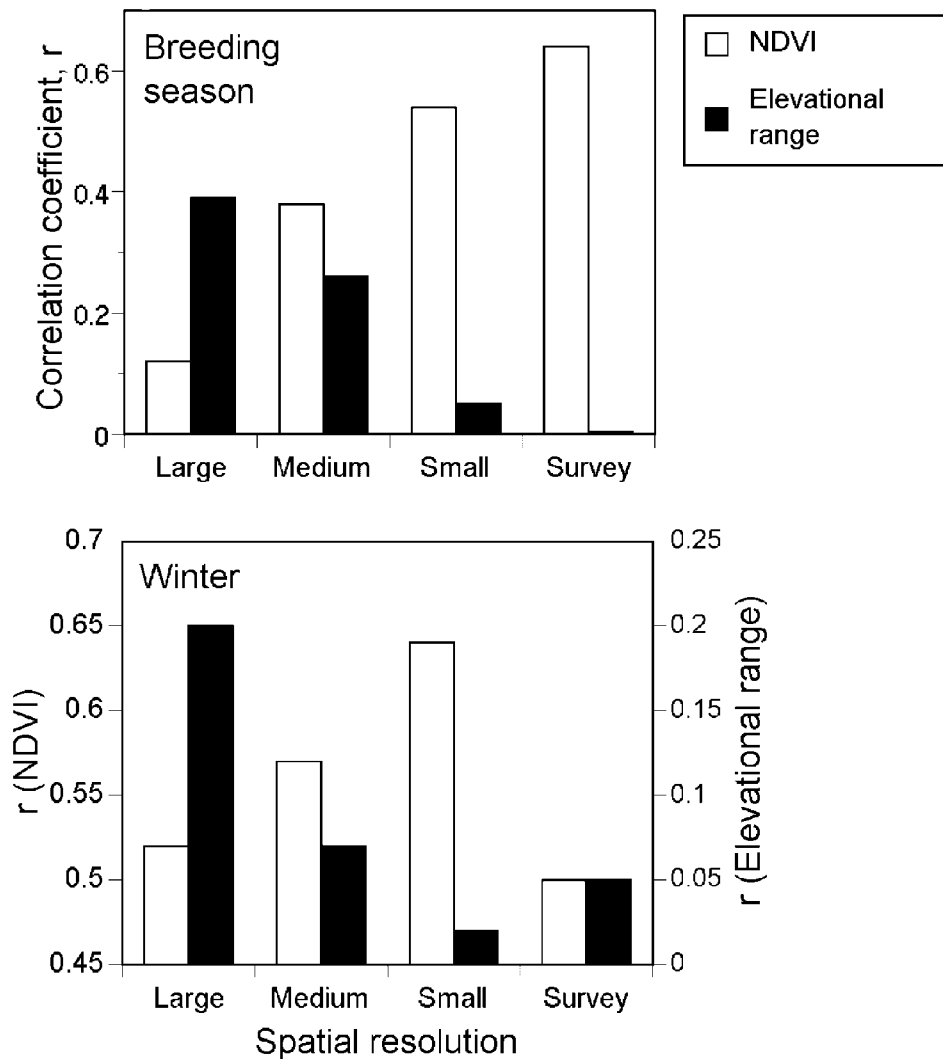
Figure 6: Relationship between the spatial resolution of the analysis and the correlation coefficient for relationships between species richness and normalized difference vegetation index and between species richness and elevational range in (*top*) June and (*bottom*) December.

most no migrants, whereas in reality, migrants make up approximately half of the breeding bird species in such environments. This discrepancy may exist in part because many of these aseasonal communities are invaded by a large number of wintering visitors; therefore, resident species are able to sequester only a fraction of the available energy during the winter season. It remains unclear why resident species do not use more of the year-round resources to the exclusion of visitors. Another possibility is that the relationship between NDVI and secondary production—that is, the production of bird food—is not the same between winter and summer. Regardless, the positive relationship between seasonality and the number and proportion of migrant species may allow us to predict the im-

pact of global climate change on bird communities (N. Lemoine and K. Böhning-Gaese, unpublished manuscript).

Most of our results show an increase in the precision of the relationship between environmental production and species richness with finer spatial and temporal resolution. Averaging over space and seasons weakens the species-energy relationship. This is an important point given the methodologies of many recent studies using data on birds to evaluate species-energy theory (Wright 1983; Currie 1991; Blackburn and Gaston 1996). These studies tend to examine the relationship between total breeding season richness and some estimate of mean annual energy (e.g., actual evapotranspiration, potential evapotranspiration, and net primary productivity). Such analyses ignore the
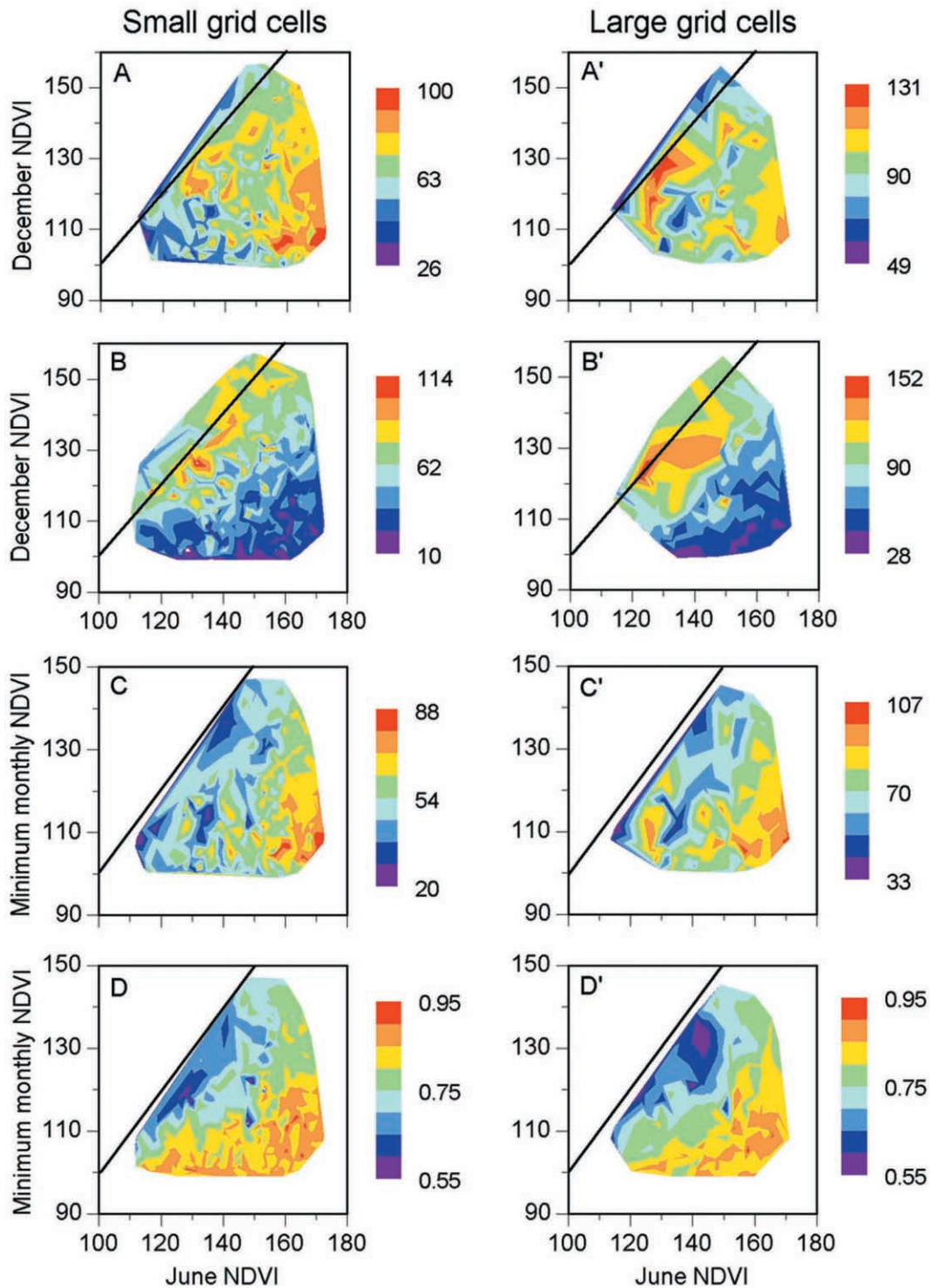
Figure 7: *A, A′*, Summer species richness plotted on normalized difference vegetation index (NDVI) space for small (20,000 km²) and large (80,000 km²) grid cells. *B, B′*, Winter species richness plotted on NDVI space for small and large grid cells. *C, C′*, Number of migrant species per grid cell plotted on NDVI space for small and large grid cells. *D, D′*, Percentage of migrant species in the community plotted on NDVI space for small and large grid cells.

Table 3: Results of spatial multiple regressions correlating normalized difference vegetation index (NDVI), elevational range, and number of biomes with seasonal species richness at various temporal and spatial scales

Scale	Regression parameters				Model R^2
	Intercept	NDVI	Elevational range	Number of biomes	
Survey:					
Summer	−35.854	.558***	.0012	NA	.40
Winter	−37.168	.722***	.0025	NA	.25
Small grid:					
Summer	−21.078	.584***	.0031***	−.229	.36
Winter	−56.382	.863***	.0002	1.499*	.46
Seasonal[a]	−46.959	.741***	.0016*	.767*	.65
Annual[b]	−12.995	.049***	.0030**	−.564	.22
Medium grid:					
Summer	−28.947	.646***	.0045**	2.314**	.43
Winter	−45.453	.852***	−.0035	4.092***	.49
Seasonal[a]	−44.644	.717***	.0009	2.652***	.69
Annual[b]	−10.303	.048***	.0046*	1.710*	.22
Large grid:					
Summer	−12.984	.646***	.0025	3.300	.29
Winter	−55.296	1.071***	−.0029	3.482*	.45
Seasonal[a]	−30.438	.642***	−.0004	2.206***	.57
Annual[b]	34.663	.031	.0032	1.391	.16

Note: NA = not applicable.

[a] Dependent variable is the standardized seasonal richness regardless of season (see text).

[b] Dependent variable is summer richness, and the NDVI variable is the annual sum of monthly NDVI values.

* $P < .01$.

** $P < .001$.

*** $P < .0001$.

fact that avian richness tracks seasonal fluctuations in resource availability.

In addition to the temporal averaging of available energy, spatial averaging of either richness or productivity data also weakened the species-energy relationship. Blackburn and Gaston (1996) examine species richness and net primary productivity at the scale of 611,000-km^2 grid cells. Our analyses show that even at spatial resolutions as coarse as 80,000 km^2, the relationship between richness and available energy is substantially weaker than at finer scales. At coarser spatial resolutions, our measure of habitat heterogeneity becomes increasingly important for predicting species richness. Over large areas, available energy is divided up among species that specialize on different habitat types, while available energy influences how many species occur in each habitat type. Our data suggest that the processes that regulate richness and their relative importance are scale dependent, but we do not have an independent explanation for our observations.

Spatial and temporal aggregation of richness data often occurs when the presence of a species within a grid cell is determined from range maps rather than from actual survey data (e.g., Cook 1969; Currie 1991; Blackburn and

Gaston 1996). For large-scale macroecological studies, range maps are often the best or only source of data on species distributions. However, it is important to recognize the potential limitations of using range map data. Because of habitat selection, two species whose ranges overlap extensively may coexist in local communities only infrequently, or the overlapping range may be partitioned between them on a seasonal basis. Thus, for characterizing the number of species that actually coexist and share a pool of local resources at a given time, survey data are far more accurate. The advantage of the BBS and CBC surveys is that they provide a snapshot of actual species coexistence in avian communities across the continent. While range map–derived richness values are undoubtedly correlated with survey-derived richness, the functional form of the relationship is unknown (e.g., Huston 1999). This distinction may become important when we begin to probe the actual mechanisms of species-energy theory and how a given quantity of energy is partitioned among species.

Our analyses provide strong evidence that energy is not the only factor that regulates avian richness. Habitat heterogeneity, measured by either elevational range or the number of distinct biomes present within a grid cell, adds
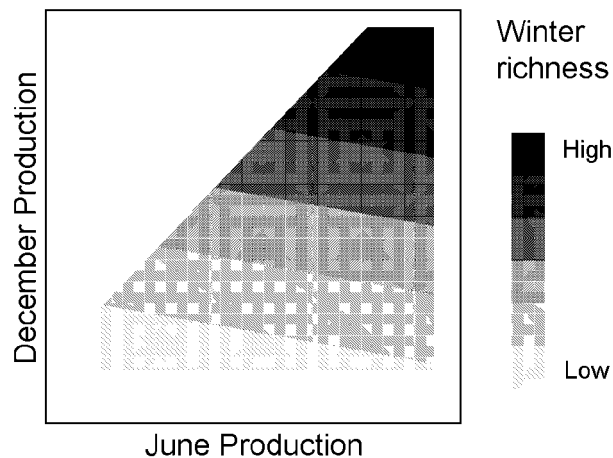
Figure 8: Expected variation of winter species richness on production phase space when the ability of an environment to support species in the winter is partially dependent on production in the summer via a storage effect (see text).

substantial explanatory power, especially at coarser spatial scales. Our conclusions regarding how scale affects the suitability of energy and heterogeneity as predictors of species richness are consistent with those of other recent work. Rahbek and Graves (2001) found that precipitation was a good predictor of avian richness in South America at finer resolutions while topographic heterogeneity explained more of the variance at coarser resolutions. About 30 hypotheses have been put forward to explain geographical patterns of species richness (see Pianka 1966; Mac-Arthur 1972; Rohde 1992; Brown 1995; Rosenzweig 1995), and all of them have empirical support to varying degrees. The fact that different correlates of richness are often identified at different scales of analysis (Ricklefs and Schluter 1993; Bohning-Gaese 1997; Huston 1999; Waide et al. 1999) has further complicated the search for primary regulating factors. The interaction of many different variables and processes at multiple scales makes the untangling of richness patterns a complex issue. The key will be to distill the factors that act universally from those that appear to be idiosyncratic. Species-energy theory provides a framework for understanding species richness patterns that is potentially universal in application.

While we have demonstrated that available energy and habitat heterogeneity together can explain the majority of the variation in avian richness across North America, we still lack an understanding of the underlying mechanisms. Species-energy theory assumes that energy is converted into individuals and that the number of species may be related to the number of individuals, but these links may not exist or have not been conclusively demonstrated (En-

quist and Niklas 2001; Hubbell 2001). Ecology still lacks a theory describing how and why energy is partitioned among species and individuals. Many theoretical models of diversity predict either complete competitive exclusion (e.g., Gause 1934; Park 1948) or infinite species richness (Tilman 1994; Kinzig et al. 1999) and fail to solve the "middle number problem" of real world biological diversity. Several recent studies provide suggestive evidence that a consistent set of energetic division rules operate at a locale through time, but the specifics remain unclear (Brown 1995; Rosenzweig 1995; Brown et al. 2001; Haskell 2001; Parody et al. 2001; J. P. Haskell and A. H. Hurlbert, unpublished manuscript). As ecologists develop a more complete understanding of the roles of resource supply and partitioning, it will become possible to develop a comprehensive framework of the processes that regulate the generation and maintenance of diversity.

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