Variability in Energy Influences Avian Distribution Patterns Across the USA

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ABSTRACT

Habitat transformations and climate change are among the most important drivers of biodiversity loss. Understanding the factors responsible for the unequal distribution of species richness is a major challenge in ecology. Using data from the North American Breeding Bird Survey to measure species richness and a change metric extracted from the MODerate resolution Imaging Spectroradiometer (MODIS), we examined the influence of energy variability on the geographic distribution of avian richness across the conterminous U.S. and in the different ecoregions, while controlling for energy availability. The analysis compared three groups of birds: all species, Neotropical migrants, and permanent residents. We found that interannual variability in available energy explained more than half of the observed variation in bird richness in some ecoregions. In particular, energy variability is

an important factor in explaining the patterns of overall bird richness and of permanent residents, in addition to energy availability. Our results showed a decrease in species richness with increasing energy variability and decreasing energy availability, suggesting that more species are found in more stable and more productive environments. However, not all ecoregions followed this pattern. The exceptions might reflect other biological factors and environmental conditions. With more ecoclimatic variability predicted for the future, this study provides insight into how energy variability influences the geographical patterns of species richness.

Key words: avian ecology; Breeding Bird Survey (BBS); MODIS; energy variability; biodiversity; richness patterns.

INTRODUCTION

Biological diversity is essential for the functioning of ecosystems. It is defined as the variability among

living organisms from all sources (Millennium Ecosystem Assessment 2005). Biodiversity is unevenly distributed on the Earth's surface. Understanding the factors that regulate its geographic variations is one of the great challenges in ecology (Ricklefs and Schluter 1993). Current ecological processes, including the spatial and temporal variability of ecosystem characteristics, may influence the spatial distribution of species.

The assumption that higher stability in ecosystem conditions allows for less population fluctuations and greater niche partitioning (Currie 1991), led to the hypothesis that stable ecosystems provide more opportunities for higher species diversity. By contrast, unpredictable and severe environmental conditions may have lower richness due to broader niches and higher chances of extinctions (Slobodkin and Sanders 1969; Pielou 1975). Effectively measuring energy stability has been a major challenge. Improved change metrics developed from wide field-of-view satellite data now allow measuring variations in vegetation activity at daily to decadal scales, and can be associated with climatic variability, anthropogenic perturbations, and other disturbances. The objective of this study was to understand how energy variability influences the observed spatial patterns in species richness.

In ecology, much emphasis has been placed on energy availability as the main factor in explaining the unequal global patterns of biodiversity (Rosenzweig 1995; Mittelbach and others 2001). The resulting species–energy relationships (SER) predict either a unimodal or a positive relationship between species richness and available energy, depending on the spatial scale at which observations are made as well as on the specific measure of energy (Mittelbach and others 2001; Gaston 2000). Furthermore, because a variety of hypotheses have been advanced to explain these SER (for example, specialization, population number and growth rates, and number of trophic levels; Srivastawa and Lawton 1998), no single mechanism can effectively explain all patterns of spatial variation in biodiversity studies (Gaston 2000).

Energy availability may only be a covariate of some other factors that are driving biodiversity. Historical factors, for example, have been shown to play a role in shaping today's spatial patterns of species richness (Fjeldsa and others 1997; Fjeldsa and Lovett 1997). As a result, more complex interactions between climate, vegetation, and species might also influence the observed richness patterns. The effects of land-cover conversions, such as deforestation, urbanization and cropland expansion, on biodiversity have been well documented (Blair 1996; Pimm and Raven 2000). However, terrestrial ecosystems also display large decadal, inter- and intra-annual variations in surface attributes without necessarily changing from one land-cover category to another (Lambin and others 2003). Hence, spatially explicit measurements of these land-cover modifications, which affect energy availability and variability, might improve our understanding of the observed

patterns in species richness (MacArthur 1972; Currie 1991).

A variety of equilibrium and non-equilibrium hypotheses have been formulated to explain the observed diversity patterns based on competition and disturbance frequency (Connell 1978). The first group of hypotheses assumes that communities return relatively quickly to their original state at equilibrium after they are disturbed, and that diversity patterns are largely the result of processes operating during the equilibrium phase (niche diversification hypothesis, circular network hypothesis, compensatory mortality hypothesis). The other group of hypotheses is based on the observation that a high frequency of perturbations may not allow species assemblages to reach an equilibrium state (intermediate disturbance hypothesis, equal chance hypothesis, gradual change hypothesis). Finally, at intermediate frequencies of disturbance (Connell 1978; Sousa 1979) diversity seems to be greatest, suggesting that both competition and disturbance explain biodiversity patterns (Huston 1979). If the frequency and intensity of ecosystem disturbances are closely related to the stability of these ecosystems, then the relationship between energy variability and species richness should be unimodal.

The potential of remote sensing to measure and monitor land surface attributes that affect biodiversity across broad habitats is well established. One common approach to measure energy availability, vegetation cover change, and habitat characteristics is the use of vegetation indices. Corrected for atmospheric and soil contamination, the Enhanced Vegetation Index (EVI) is very similar to the NDVI (Normalized Difference Vegetation Index) and has been shown to be related to chlorophyll activity, canopy structure and leaf area index (LAI) (Gao and others 2000; Huete and others 2002; Houborg and Soegaard 2004). The integration of the annual EVI profile (iEVI) provides an estimate of primary production (Prince 1991; Wang and others 2004). Because essential resources for animals (for example, food) are directly related to primary productivity, and hence to energy, the EVI can serve as a useful proxy for relating animal species to energy availability. However, vegetation indices can underestimate resources available in winter that are not directly related to winter foliage (Hurlbert and Haskell 2003).

Measuring energy stability using remote sensing is more difficult than measuring energy availability. Definitions of stability in ecology can be based on the system's dynamics (equilibrium stability, variability) or on the system's ability to respond to

change (resistance, resilience) (Pimm 1984). We measured variability, defined as the magnitude of change in a variable over time, to describe the stability of the available energy. A change metric based on the multitemporal change vector and using the EVI (Linderman and others 2005) was developed to quantify interannual variability in surface attributes by measuring changes due to differences in both phenology and annual vegetation activity.

Species richness is a valuable surrogate measure for many dimensions of biodiversity. It is calculated as the number of species in a given area. Many studies analyzing the different factors that determine species richness have relied on the distribution of avian communities. Due to extensive data and knowledge available on their distribution, birds offer an exceptional opportunity to evaluate the effects of energy variability on species richness. Because birds are more mobile than many terrestrial vertebrates, birds are able to track spatially and temporally fluctuating resources, thereby reacting rapidly to environmental changes. For instance, a recent study suggested that habitat perturbations in North America affected avian populations (Variela and Martinetto 2007). Patterns of breeding bird richness have been related with climate variables (H-Acevedo and Currie 2003) but the relationship between these patterns and the variability in climatic factors is not well understood.

The relationship between energy variability and species richness is likely to be different for resident and migratory bird species. In North America, resident species are exposed to conditions in the northern latitudes year-round, whereas migrants spend only part of the year on their breeding grounds and are thus exposed to the degradation of their wintering and breeding grounds, as well as the hazards encountered during their migration. Seasonality has been shown to influence the proportion of migrants in the breeding community (MacArthur 1959; Herrera 1978). There is also evidence of a relationship between seasonal vegetation production and the number of species present in an area during a given season (Hurlbert and Haskell 2003). As a result, the proportion of migrant species in the breeding community may be determined by the rate and timing of vegetation productivity. Currently, it appears that some resident bird species respond to annual measures of energy availability while migrants respond more strongly to seasonal measures of energy (Evans and others 2006). This suggests that resident and migrant species react differently to seasonal and annual variations in resource availability.

The aim of this study was to measure the influence of energy stability on the spatial distribution of bird species richness across North America, while controlling for energy availability. More specifically, we examined the following questions: (1) Does bird species richness increase with energy stability, when we control for energy availability? (2) Is the relationship between richness and energy stability different for resident species and species that migrate to the tropics during the winter period? (3) Is the relationship between species richness and energy variability influenced by the ecoregion where species breed?

MATERIALS AND METHODS

Avian Richness Across North America

Measures of avian species richness were derived from the annual North American Breeding Bird Survey (BBS; Sauer and others 2003). The BBS has been carried out since 1966 and is currently composed of approximately 3,000, 39.4-km routes across the United States and Canada. Skilled volunteer observers survey each route annually during the breeding season (May through June), carrying out 50, 3-min point counts per route at 0.8 km intervals. At each point count, the observer records all birds seen or heard within 0.4 km.

We used all acceptable BBS routes from 2000 to 2005 over the conterminous U.S. For each year, BBS personnel assigns whether the survey was carried out during an appropriate time window, under acceptable weather conditions, and by an experienced observer (Figure 1). For our analysis, we excluded surveys coded as unacceptable. In addition, we excluded bird species that were detected on fewer than 30 routes during the period of analysis, as well as numerous detections that were not identified to full species (for example, unidentified Empidonax, unidentified gull; Lepczyk and others 2008).

Analyses of the BBS data were carried out for three groups of birds: all species, Neotropical migrants, and permanent residents. Neotropical migrants are species that spend a portion of each year in the Neotropics (defined as south of the U.S.–Mexico border) and breed north of that line, in the temperate or cold zones. Permanent residents, in contrast, are species that are found in an area on a year round basis. Species included in each of these groups follow the definition used in the North American Breeding Bird Survey (Peterjohn and Sauer 1993). The reason for analyzing birds within groups is that species that share a
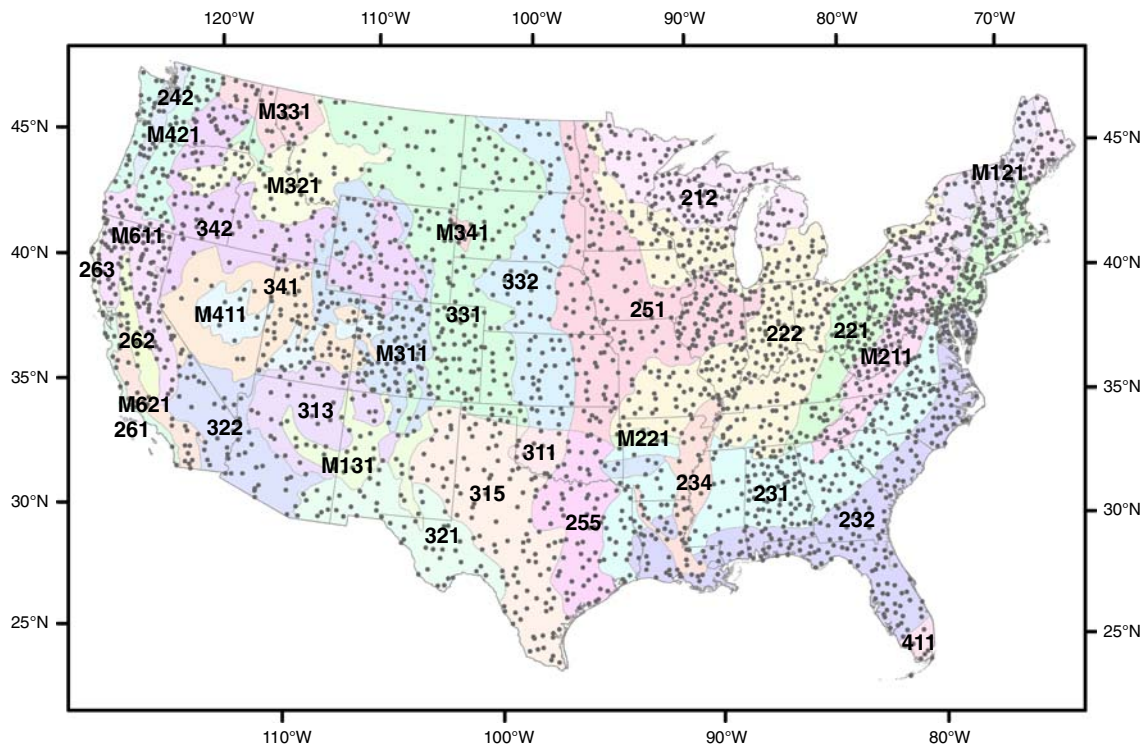
Figure 1. Bailey's provinces with the corresponding ecoregion numbers and the geographical distribution of the North American Breeding Bird Survey routes across the conterminous U.S. used in this study.

common life history strategy may be affected similarly by environmental conditions. For each group, route level data were converted to a species richness estimate using COMDYN (Hines and others 1999). Raw counts underestimate species richness as species vary in detectability. COMDYN uses the jackknife estimator (Burnham and Overton 1979) to estimate species richness, and accounts for differences in detectability among species (for details, see Boulinier and others 1998a). The resulting estimated species richness was averaged for the 2000–2005 period and represents the measure of biodiversity used in the subsequent analysis.

Energy Variability

A land-cover change metric quantifying interannual variations in land surface conditions (Linderman and others 2005) was developed using the 1-km resolution, collection 4, Nadir Bi-directionally Adjusted Reflectance (NBAR) MOD43B4 product from the MODIS sensor aboard the Terra and Aqua platforms (Schaaf and others 2002) for the period from February 2000 to February 2006. The reflectance estimates from the NBAR data are 16-day composites, which are corrected for angular influences due to solar and viewing angle differences based on bi-direction inversion. Thus, a complete

annual profile consists of 23 composites. These reflectance estimates were converted to the EVI (Huete and others 2002), a spectral index very similar to the NDVI, designed to reduce atmospheric and soil background contamination. Given the erratic behavior of the EVI on snow-covered areas, it was replaced by the very similar Soil-Adjusted Vegetation Index (SAVI) (following Huete and others 2002) whenever the snow/ice flag was turned on in the quality assurance fields of the MODIS product. This flag was based on the normalized difference snow index. The SAVI is associated with a non-zero intercept of the vegetation index isolines to reduce soil background influences but does not use the blue band to reduce atmosphere contamination. It is thus less sensitive to snow.

The preprocessing steps prior to the change detection included the creation of a global mosaic of reflectance values, the calculation of EVI values, and temporal interpolation of pixels presenting unreliable BRDF correction and obvious noise, using a quadratic interpolation. The missing three composites from early 2000 were filled using the median value of the other years to provide a complete 6-year data set (2000–2005) with full growing seasons for each pixel. If more than three consecutive composites during a given year were influenced by clouds for one pixel then this given

year was excluded from our analysis for this pixel. Moreover, if for a given pixel, more than 2 years were excluded from the analysis then this pixel was masked and excluded completely from our analysis.

The variable characterizing available energy was then calculated by integrating EVI values on a yearly basis (iEVI, measured as $\sum_{j=1}^{23} \text{EVI}_j$). To measure energy variability we calculated the Sum of the absolute values of the Change Vector (SCV):

$$\text{SCV}(k) = \sum_{i=1}^{23} \left| I_i^k - I_i^{\text{ref}} \right|$$

where k is a given year (2000, 2001, ..., 2005), *ref* is the reference year, and I is the vegetation index value at each time step for the given year k (there are 23 16-day composites in a given year; Linderman and others 2005). The SCV measures all changes due to differences in phenology and total annual vegetation index (Figure 2). The detected changes have been associated with climate fluctuations, land use, and disturbances. To measure interannual change, each of the years was compared to a reference year, defined as the median value of the six yearly EVI values for each pixel. Furthermore, to calculate areas subjected to change, the SCV for a given pixel was normalized by the integrated vegetation index of the reference year for that pixel, thus providing an annual percent change relative to the median year:

$$\%\text{SCV} = \frac{\text{SCV}}{\sum_{i=1}^{23} I_i^{\text{ref}}}$$

The annual values of each variable, energy availability (iEVI) and variability (as measured by the %SCV), were then averaged for every pixel over the 2000–2005 period (Figure 3).
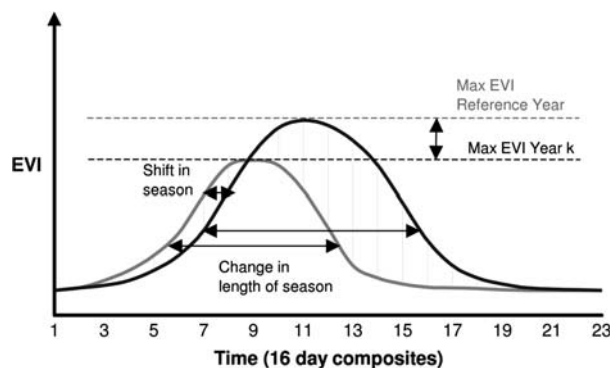

Figure 2. Interannual variability in land surface attributes, as measured by the SCV.

Finally, the center of the minimum bounding rectangle that encompassed the BBS route was used to locate a 19.7 km radius buffer (1/2 the length of a BBS route) to define approximately 1,200 km^2 landscapes (Pidgeon and others 2007) within which we evaluated the average energy availability and variability for each BBS route. Masked and water pixels were excluded from these spatial averages. This broad scale approach ensures that each route is centrally located within the 19.7 km buffer, despite variation in the BBS route paths and is consistent with previous BBS data analysis protocols (for example, Pidgeon and others 2007; Lepczyk and others 2008).

Statistical Analysis

Simple and multiple linear regression models were used to describe the influence of energy availability (iEVI) and variability (%SCV) on species richness, first for all birds and then for Neotropical migrants and permanent residents separately. The models were constructed at a continental level, and for individual ecoregions, at the province level (Figure 1; Bailey 1995). To ensure robustness of our results, only ecoregions with more than 30 BBS routes were included in the analysis (23 ecoregions met this criterion). To assure a linear relationship between the variables we log$_{10}$ transformed iEVI. As only two explanatory variables were used to model species richness, no selection procedure was used for the multivariate models. We report the coefficients and statistical significance of each variable. Residual plots were checked for random distribution of unexplained variance as well as normality. We also checked for multicollinearity using the Variance Inflation Factor (VIF). Semi-variograms were used to test for spatial autocorrelation on all multivariate models, as it may affect parameter estimates and inflate Type I errors. If spatial autocorrelation was found in the residuals, then we used general linear models with a spatial exponential covariance structure to estimate the model coefficients.

RESULTS

Patterns in Species Diversity and in Energy Availability and Variability

The average estimated species richness across the conterminous U.S. was 37.4 species per BBS route (minimum = 3.8, maximum = 75.2). Richness patterns varied by groups, with Neotropical migrants and permanent resident species averaging
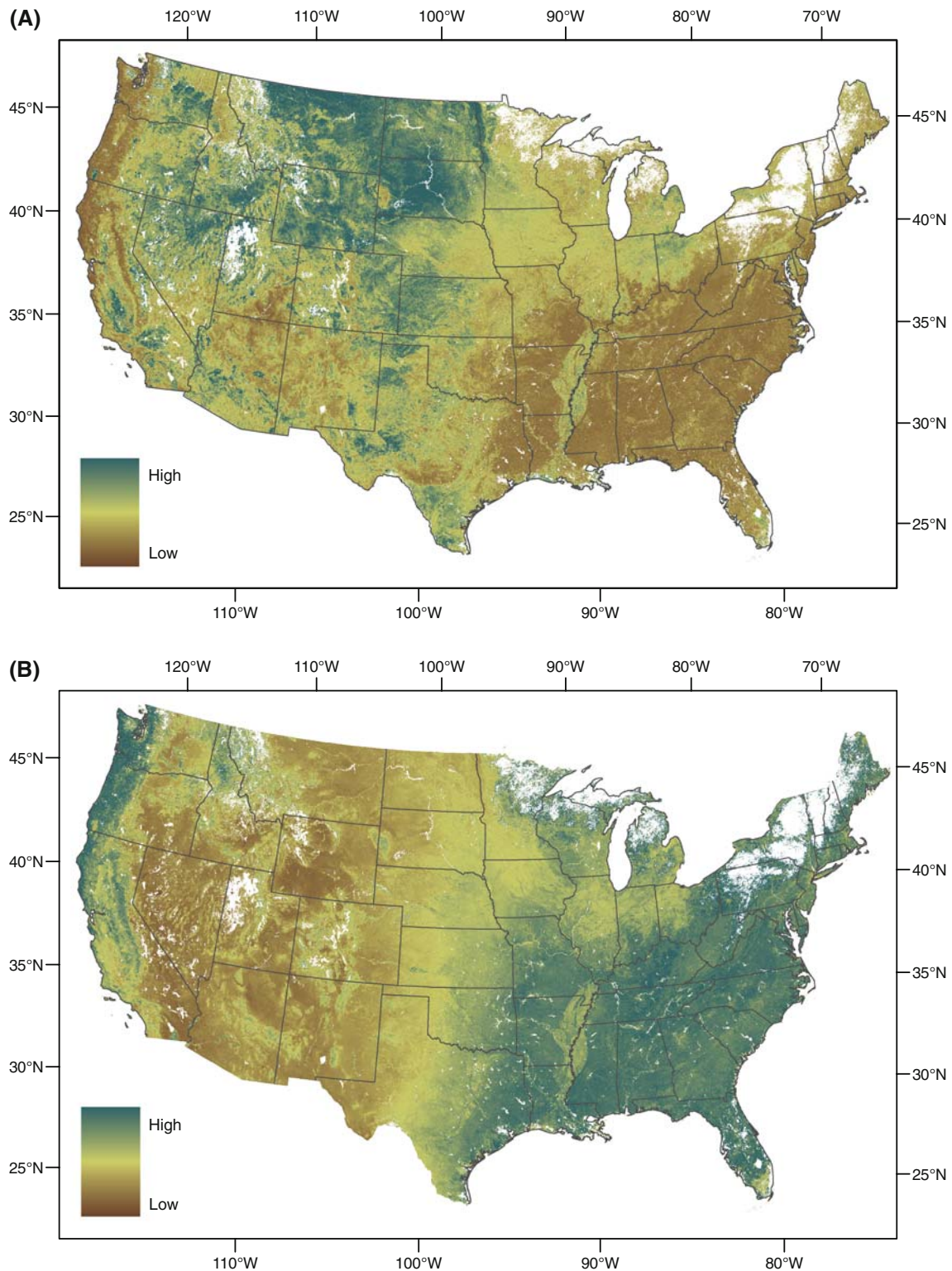
Figure 3. Geographical distribution of (**A**) energy variability, as measured by the Sum of the absolute value of the Change Vector (%SCV), and (**B**) energy availability as measured by the annual integrated Enhanced Vegetation Index (iEVI).

25.2 and 11.5 species per route, respectively. These patterns also varied by ecoregion (Table 1). High total avian richness was found in the mountainous Appalachian (ecoregion M211) and Adirondack (ecoregion M121) forests as well as in the north Midwestern Laurentian Mixed Forests (ecoregion

Table 1. Average Species Richness and Standard Deviation Across the Different Ecoregions Across the Conterminous U.S. for All Species, Neo-tropical Migrants and Permanent Residents

Ecoregion name	Ecoregion number	All species		Neotropical migrants		Permanent residents		%SCV		iEVI	
		Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
Laurentian Mixed Forest	212	47.3	9.0	36.5	7.3	9.8	3.1	0.10	0.01	91862	13876
Eastern Broadleaf Forest-Oceanic	221	43.9	9.2	31.1	8.0	12.4	2.0	0.08	0.02	89139	9428
Eastern Broadleaf Forest-Continental	222	42.3	9.2	29.7	7.5	12.1	2.7	0.10	0.03	77833	11861
South-Eastern Mixed Forest	231	44.5	7.7	30.0	6.3	14.0	2.2	0.05	0.01	90357	3708
Outer Coastal Plain Mixed Forest	232	39.6	8.7	25.0	8.0	14.1	2.4	0.07	0.02	88472	5402
Lower Mississippi Riverine Forest	234	39.7	7.2	26.1	5.5	12.8	2.0	0.10	0.03	79479	8799
Prairie Parkland-Temperate	251	37.2	9.2	25.2	6.5	11.2	3.8	0.12	0.03	63657	9581
Prairie Parkland-Subtropical	255	36.6	8.1	21.0	7.1	15.2	2.5	0.10	0.02	77192	7932
Colorado Plateau Semidesert	313	26.3	15.6	15.7	9.9	9.6	6.5	0.10	0.03	31595	8498
SW Plateau & Plains Dry Steppe	315	31.9	9.9	16.9	4.8	14.3	5.6	0.14	0.03	53935	13650
Chihuahuan Semidesert	321	33.8	10.6	16.8	6.0	16.3	4.9	0.12	0.03	35333	9047
American Semidesert & Desert	322	21.4	10.2	9.3	5.3	11.6	6.0	0.14	0.03	28057	9415
Great Plains-Palouse Dry Steppe	331	25.3	8.8	18.7	6.8	5.8	3.0	0.19	0.03	38893	7516
Great Plains Steppe	332	32.2	8.8	22.5	5.5	8.9	4.3	0.16	0.03	52802	7556
Intermountain Semidesert & Desert	341	21.8	11.3	14.2	8.2	6.4	3.5	0.15	0.05	30733	7079
Intermountain Semidesert	342	20.9	9.2	14.6	7.3	5.6	3.1	0.19	0.03	31363	9961
Adirondack New England Mixed Forest	M121	46.0	6.7	35.4	5.3	9.4	3.3	0.09	0.01	105454	8268
Central Appalachian Broadleaf Forest	M211	48.5	7.4	34.8	6.5	12.8	2.0	0.07	0.02	94141	8608
Cascade Mixed Forest	M421	34.3	8.7	22.2	6.2	11.3	3.6	0.10	0.04	74198	21432
Sierran Steppe-Mixed Forest	M611	39.6	9.5	22.3	5.1	16.1	5.8	0.09	0.04	67104	18047
Southern Rocky Mountain Steppe	M311	32.3	9.5	23.0	6.8	8.6	3.8	0.15	0.03	42943	7785
Middle Rocky Mountain Steppe	M321	32.1	9.2	22.5	6.7	8.9	4.0	0.16	0.04	48439	9289
Nevada-Utah Mountains	M411	33.2	15.5	23.1	12.2	8.7	4.1	0.14	0.02	36343	7700

The mean and standard deviation of energy variability (%SCV) and availability (iEVI) for each ecoregion are also included.

212). These ecoregions also corresponded to high richness in Neotropical migrants. By contrast, high richness in permanent residents was found in some dryer ecoregions such as the Chihuahuan Semi-desert (ecoregion 321) and the Sierran Steppe (ecoregion M611).

Energy variability (SCV) and availability ($\log_{10}$ (iEVI)) had a strong dynamic range across the USA (Figure 3). Vegetation was highly variable in the regions around the northern and southern central states as well as around Lake Erie. These regions also exhibited low energy availability.

Bivariate Models

Our models showed a moderate association between energy variability and bird species richness. At the continental scale, overall species richness declined with increasing %SCV values ($R^2 = 0.304$, coefficient = -139.46, $P < 0.0001$)—that is, the greatest number of species was found in more stable ecosystems (Figure 4). The relationship exhibited the same sign but was weaker for Neotropical migrants ($R^2 = 0.20$, coefficient = -90.53, $P < 0.0001$) and permanent residents ($R^2 = 0.26$, coefficient = -49.66, $P < 0.0001$). Consistent with the prediction of species–energy theory, species richness increased with increasing $\log_{10}$(iEVI) ($R^2 = 0.42$ for all species). However, energy availability explained less variation in permanent resident richness ($R^2 = 0.18$) than in Neotropical migrant richness ($R^2 = 0.37$).
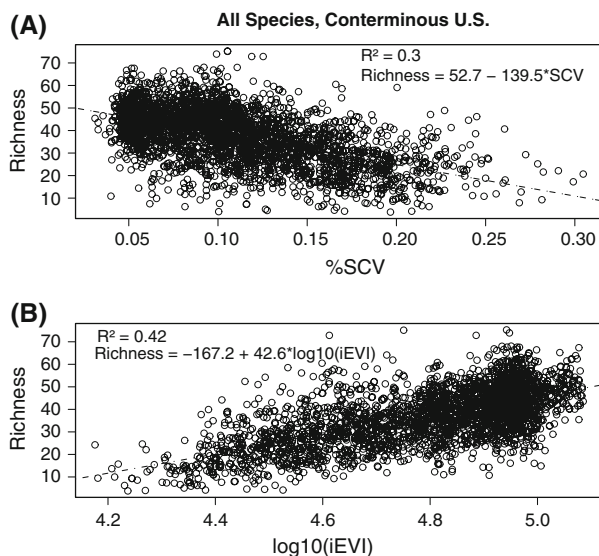

(A)
All Species, Conterminous U.S.
$R^2 = 0.3$
Richness = 52.7 – 139.5*SCV

(B)
$R^2 = 0.42$
Richness = –167.2 + 42.6*log10(iEVI)

Figure 4. Relationship between overall species richness and (**A**) energy variability (%SCV) and (**B**) energy availability ($\log_{10}$(iEVI)) across the USA.

At the province level, the relationship between interannual variability in energy (%SCV) and overall species richness was negative in 20 of 23 cases. This negative association was strongest in the Continental Eastern Broadleaf Forests (ecoregion 222), as well as the Subtropical Prairie Parkland (ecoregion 255), the Southern Rocky Mountain Steppes (ecoregion M311), and the Nevada-Utah Mountains (ecoregion M411) (R^2-values of 0.30, 0.23, 0.21, and 0.18, respectively). As expected, these relationships were negative, with the exception of the Colorado Plateau Semidesert (ecoregion 313, $R^2 = 0.15$), the American Semidesert and Desert (ecoregion 322, $R^2 = 0.07$), and the Central Appalachian Broadleaf Forest (ecoregion M211, $R^2 = 0.03$). Richness of permanent resident species and Neotropical migrants was strongly negatively related with energy variability in all ecoregions except the Colorado Plateau (ecoregion 313).

Multivariate Models

We examined the response of avian richness patterns to energy availability ($\log_{10}$(iEVI)) and variability (%SCV) in multivariate models. First, the presence of multicollinearity was investigated. A model using strongly related independent variables can produce misleading P-values as the variances of the estimated coefficients will be influenced by multicollinearity. Using the normalized SCV values, we still found some correlation between energy variability and availability (correlation coefficient $\rho = 0.72$). However, it is believed that correlation coefficients below 0.9 do not pose a problem and, as the VIF remained well below the critical value of 10 (VIF < 3; Neter and others 1996; Chatterjee and others 2000), no multicollinearity issues were found. Secondly, regarding spatial autocorrelation, semivariogram analysis revealed the presence of spatial autocorrelation only in the continental-scale models. At this continental level, we derived models both with and without a spatial covariance structure and found that coefficients varied just slightly (Table 2). For overall bird richness, the model explained over 43% of the variability at the scale of the conterminous U.S. When energy availability was controlled for in the model, the variability of energy was still a highly significant factor in explaining the patterns of bird richness for all species and for the permanent residents. In contrast, energy variability was not associated with patterns of Neotropical migrant richness.

At the ecoregion level (Table 3), a combination of both energy variability and availability explained

Table 2. Multivariate Regression Model Results at the Continental Scale for Which Spatial Autocorrelation was Present

	Uncorrected				Corrected for spatial autocorrelation			
	%SCV	*P*-value	$\log_{10}$(iEVI)	*P*-value	%SCV	*P*-value	$\log_{10}$(iEVI)	*P*-value
All species	−43	<0.0001	34	<0.0001	−53	<0.0001	38	<0.0001
Neotropical migrants	−2	0.59	31	<0.0001	−27	<0.0001	28	<0.0001
Permanent residents	−41	<0.0001	3	<0.0001	−20	<0.0001	9	<0.0001

Coefficients and significance for the uncorrected and correctly specified models are shown.

more than 51% of the variance in permanent resident species richness in the Great Plains Steppe (ecoregion 332). Contrary to the continental model, Neotropical migrant species showed statistically significant relationships with either one of the variables or a combination of both in most ecoregions. This was also the case for richness patterns of all species taken together. The ecoregions where the relationships were strongest for all three avian groups are the Eastern Broadleaf Forests (ecoregions 221 and 222), the Prairie Parkland (ecoregions 251 and 255), the Nevada-Utah Mountains (ecoregion M411), the Intermountain and Colorado Plateau Semideserts (ecoregions 342 and 313), and the Southwestern Plateau (ecoregion 315).

In some ecoregions there were unexpected relationships between species richness and energy variability or availability. For example, both overall bird species and Neotropical migrants in the Outer Coastal Plain Mixed Forest (ecoregion 232), the Subtropical Prairie Parkland (ecoregion 255), and the Central Appalachian Broadleaf Forests (ecoregion M211) had higher species richness in areas of lower energy availability. Equally surprising, permanent residents in the Sierran Steppe (ecoregion M611) exhibited greater richness in areas of greater energy variability.

DISCUSSION

Our results highlighted the importance of energy variability as a driver of species richness. This variability was quantified by the SCV (Sum of the absolute value of the Change Vector), which measures both changes in total vegetation activity and in seasonality. When controlling for energy availability, species richness was greatest in more stable ecosystems, similar to patterns of avian species richness in sub-Saharan Africa (Jetz and others 2004). In fact, interannual variability in vegetation productivity and energy availability explained more than half of the observed changes in bird

richness in some ecoregions. Note that energy availability interacts with variability, as densely vegetated areas are less likely to be affected by inconsistent rainfall patterns than more arid ecosystems. The dominant relationship we uncovered was a negative association between species richness and variability in vegetation productivity. In a few ecoregions, however, there was a positive association. For instance, in the Outer Coastal Plain Mixed Forest (ecoregion 232) there was a positive association, which may be due to the conversion of over 60% of the natural pine forest to densely stocked pine plantations, thereby simplifying both forest structure (Croker 1987; Walker 1991) and the avian community (Hunter and others 2001). Thus, areas of high variability in this ecoregion may be indicators of habitats that are now rare, including early successional, scrub-, shrub-, or grassland habitat conditions. On the other hand, in ecoregion M2611, which encompasses many altitudinal microhabitats when moving from the Sierran steppe through high elevation alpine meadow, we found that areas of high energy variability were associated with high permanent resident species richness. Although many of these residents do remain in the ecoregion, there is considerable altitudinal movement of the birds between summer and winter, which may account for high species richness in this guild. Finally, in the Subtropical Prairie Parkland (ecoregion 255), there are a relatively large number of generalist species with high physiological plasticity (Principle of Allocation; Levins 1968). Occurrence of a large number of generalist species accounts for high richness within the permanent resident guild in this ecoregion.

Explanations of species diversity patterns have focused on productivity, or more specifically, energy. Many different mechanisms have been proposed to explain these patterns, including the more-individuals hypothesis (MIH; Wright 1983; Currie and others 2004; Evans and others 2005), which postulates that more productive areas have

Table 3. Multiple Regression Models for Species Richness, in each Ecoregion (Bailey 1995), for (a) Overall Species Richness, (b) Neotropical Migrants, and (c) Permanent Residents

Ecoregion	Ecoregion number	n	AdjR^2	%SCV	P-value	$\log_{10}$(iEVI)	P-value
(a) Overall species richness							
Conterminous U.S.		2832	0.432	−43	***	34	***
Laurentian Mixed Forest	212	209	0				
Eastern Broadleaf Forest-Oceanic	221	204	0.305	−126	***	102	***
Eastern Broadleaf Forest-Continental	222	320	0.317	−90	***	37	***
South-Eastern Mixed Forest	231	198	0.084	−308	***	−16	0.63
Outer Coastal Plain Mixed Forest	232	239	0.191	−246	***	−150	***
Lower Mississippi Riverine Forest	234	34	0				
Prairie Parkland-Temperate	251	188	0.212	45	0.26	79	***
Prairie Parkland-Subtropical	255	58	0.295	−239	***	−57	*
Colorado Plateau Semidesert	313	39	0.499	90	0.23	94	***
SW Plateau & Plains Dry Steppe	315	103	0.434	−74	***	53	***
Chihuahuan Semidesert	321	49	0.118	−73	0.16	30	*
American Semidesert & Desert	322	48	0.142	65	0.26	29	*
Great Plains-Palouse Dry Steppe	331	183	0.103	−4	0.83	35	***
Great Plains Steppe	332	79	0.203	−45	0.17	54	***
Intermountain Semidesert & Desert	341	60	0.165	−55	‡	52	***
Intermountain Semidesert	342	121	0.315	−46	‡	34	***
Adirondack New England Mixed Forest	M121	63	0				
Central Appalachian Broadleaf Forest	M211	114	0.045	81	‡	32	‡
Cascade Mixed Forest	M421	59	0				
Sierran Steppe-Mixed Forest	M611	92	0.187	−200	***	−38	*
Southern Rocky Mountain Steppe	M311	102	0.195	−180	***	−8	0.52
Middle Rocky Mountain steppe	M321	56	0				
Nevada-Utah Mountains	M411	35	0.518	−188	*	104	***
(b) Neotropical migrants							
Conterminous U.S.		2832	0.367	−2	0.59	31	***
Laurentian Mixed Forest	212	209	0				
Eastern Broadleaf Forest-Oceanic	221	204	0.333	−116	***	93	***
Eastern Broadleaf Forest-Continental	222	320	0.229	−75	***	20	*
South-Eastern Mixed Forest	231	198	0.114	−299	***	−29	0.28
Outer Coastal Plain Mixed Forest	232	239	0.2	−221	***	−151	***
Lower Mississippi Riverine Forest	234	34	0				
Prairie Parkland-Temperate	251	188	0.09	65	*	49	***
Prairie Parkland-Subtropical	255	58	0.319	−217	***	−61	**
Colorado Plateau Semidesert	313	39	0.446	41	0.4	58	***
SW Plateau & Plains Dry Steppe	315	103	0.325	−61	***	16	***
Chihuahuan Semidesert	321	49	0.128	−16	0.59	22	**
American Semidesert & Desert	322	48	0				
Great Plains-Palouse Dry Steppe	331	183	0.07	19	0.21	25	***
Great Plains Steppe	332	79	0				
Intermountain Semidesert & Desert	341	60	0.118	−34	0.13	34	**
Intermountain Semidesert	342	121	0.226	−22	0.34	24	***
Adirondack New England Mixed Forest	M121	63	0				
Central Appalachian Broadleaf Forest	M211	114	0.077	89	*	34	*
Cascade Mixed Forest	M421	59	0				
Sierran Steppe-Mixed Forest	M611	92	0				
Southern Rocky Mountain Steppe	M311	102	0.136	−112	***	−7	0.52
Middle Rocky Mountain steppe	M321	56	0.072	8	0.79	28	*
Nevada-Utah Mountains	M411	35	0.445	−139	‡	77	***
(c) Permanent residents							
Conterminous U.S.		2832	0.271	−41	***	3	***
Laurentian Mixed Forest	212	209	0.047	27	‡	12	***

Table 3.   continued

Ecoregion	Ecoregion number	n	AdjR^2	%SCV	P-value	$\log_{10}$(iEVI)	P-value
Eastern Broadleaf Forest-Oceanic	221	204	0				
Eastern Broadleaf Forest-Continental	222	320	0.371	−14	*	18	***
South-Eastern Mixed Forest	231	198	0				
Outer Coastal Plain Mixed Forest	232	239	0				
Lower Mississippi Riverine Forest	234	34	0				
Prairie Parkland-Temperate	251	188	0.426	−15	0.29	32	***
Prairie Parkland-Subtropical	255	58	0				
Colorado Plateau Semidesert	313	39	0.46	51	0.11	35	***
SW Plateau & Plains Dry Steppe	315	103	0.455	−14	0.22	33	***
Chihuahuan Semidesert	321	49	0.11	−55	*	6	0.33
American Semidesert & Desert	322	48	0.171	27	0.42	20	**
Great Plains-Palouse Dry Steppe	331	183	0.289	−30	***	11	***
Great Plains Steppe	332	79	0.512	−30	*	41	***
Intermountain Semidesert & Desert	341	60	0.18	−20	*	16	***
Intermountain Semidesert	342	121	0.311	−11	0.24	11	***
Adirondack New England Mixed Forest	M121	63	0				
Central Appalachian Broadleaf Forest	M211	114	0				
Cascade Mixed Forest	M421	59	0.045	−40	*	−9	0.15
Sierran Steppe-Mixed Forest	M611	92	0.267	−164	***	−38	***
Southern Rocky Mountain Steppe	M311	102	0.203	−64	***	1	0.78
Middle Rocky Mountain steppe	M321	56	0.164	−43	*	3	0.63
Nevada-Utah Mountains	M411	35	0.407	−35	0.18	26	***

*Coefficients and their significance (P-value) of energy availability ($\log_{10}$(iEVI)) and variability (%SCV), and the adjusted R^2 (AdjR^2) are reported; 'n' represents the number of BBS routes in each ecoregion. The following significance codes are used: *** (<0.001), ** (<0.01), * (<0.05), and ‡ (<0.1).*

more individuals and therefore more species. Our results support previous findings and predominantly show a positive relationship between primary production and species richness. However, we also found negative correlations in some ecoregions, suggesting that bird response to increasing productivity is influenced by other biological factors and/or environmental conditions. Previous studies have found that, in addition to productivity, habitat structure (Hurlbert 2004), topographic relief, ecosystem diversity, and historical events are important factors in the distribution of species, particularly those with narrow ranges (Jetz and others 2004; Rahbek and others 2007). Interactions of productivity, habitat structure, and topographic relief are likely strongly involved in driving the nature of the diversity–energy relationship for birds in different ecoregions. Our results suggest that the relationship between species richness and energy availability is context specific and depends on the ecoregion, and the life history and behavioral traits of the species involved.

Partitioning the avian community by group provided more insights on how energy availability and variability affect species with different migratory strategies. Neotropical migratory birds are affected by contemporary events on the North American breeding grounds as well as events happening during migration and/or on their tropical wintering grounds (Donovan and Flather 2002), and by past adaptation to dominant habitat types in these areas, whereas permanent resident species are exposed to conditions in the northern latitudes year-round. Our study showed that energy availability at the continental level explained less variance for permanent residents than for Neotropical migrant species. This contradicts previous results that suggested that annual energy metrics were better predictors of avian richness for resident species than for Neotropical migrants (Evans and others 2006). This may be due to differences in the original bird data or to the geographic context of the study as our results for the different groups vary at the ecoregion level.

In our models, about half of the variability in species richness remained unexplained. Species richness patterns are shaped not only by current and recent climatic and vegetation patterns, but also, to some degree, by infectious diseases (LaDeau and others 2007), invasive species (Mooney and Cleland 2001), habitat fragmentation (Donovan and Flather 2002), and human activities (Pidgeon and others 2007; Lepczyk and others 2008). Additionally, species richness patterns are a legacy of

past species movement, geography, and evolutionary and coevolutionary relationships (Fjeldsa and others 1997; Quian and Ricklefs 1999; Francis and Currie 2003; Jetz and others 2004; Rahbek and others 2007; Storch and others 2006). Global and regional patterns in species diversity are also linked to paleoecological stability and predictability in climatic factors (Andrewarthe and Birch 1954; MacArthur 1972; Fjeldsa and others 1999).

Our study of the United States is the first of its kind to demonstrate the role of energy variability in explaining species richness patterns at higher latitudes with a seasonal climate. Macroecological studies have suggested that aggregates of narrowly endemic species in the tropics may be related to long-term persistence of evolutionary lineages in stable local environments within montane areas, but this seems mainly to be the case close to the equator (Fjeldsa and others 1999).

Given the plethora of past and present selective pressures influencing individual species ranges, which in combination determine species richness, precise prediction of richness patterns is not possible from remote sensing alone. Thus, although the period of study of this analysis is too short to account for such long-term change, historical climatic variations are likely an additional confounding factor in the stability–diversity relationship as studied here. However, our remote-sensing based results lend credence to the hypothesis that stable and predictable environments are important conditions for the occurrence of high species diversity (Fjeldsa and others 1997).

Although our work demonstrated an important relationship between energy variability and species richness patterns, it also indicates future avenues of research to consider. For instance, because environmental correlates differ between widespread (that is, cosmopolitan) and range-restricted (that is, endemic) species (Rahbek and others 2007), it might be fruitful to investigate how stability relates to the geographic distribution of species. Similarly, considering that forest birds in fragmented landscapes show more temporal variability (Boulinier and others 1998b), future studies would benefit from examining the interrelationships between the variability of bird communities, energy availability and variability, and landscape structure. Finally, it is important to understand how energy availability and variability relate to individual species abundances across broad geographic ranges.

One outcome of global climate change is the likely increase in extreme events such as droughts, floods and heat waves, with relatively small mean climate changes (IPCC 2007). Such patterns will heighten interannual variability in vegetation productivity in some areas and may thus impact species richness. Habitat loss and climate change are already among the most important drivers of biodiversity loss (Sala and others 2000; Thomas and others 2004). Understanding how energy variability regulates the spatial distribution of species richness is thus key information for effective conservation efforts and policy.

We have demonstrated that interannual variability in vegetation productivity contributes to explaining the spatial distribution of species diversity and that the positive species–energy relationship is weaker when viewed at the level of ecoregions. With changing climate patterns, and ecosystem conditions predicted to be more variable, more research is needed to understand the biological processes linking ecosystem perturbations to biodiversity, to prevent local population extinctions.

ACKNOWLEDGMENTS

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