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Applying species–energy theory to conservation: a case study for North American birds

Linda Bowers Phillips,[1,4] Andrew J. Hansen,[1] Curtis H. Flather,[2] and Jim Robison-Cox[3]

[1]*Department of Ecology, Montana State University, Bozeman, Montana 59715 USA*
[2]*USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado 80526-1891 USA*
[3]*Department of Math Sciences, Montana State University, Bozeman, Montana 59717 USA*

Abstract. Ecosystem energy is now recognized as a primary correlate and potential driver of global patterns of species richness. The increasingly well-tested species–energy relationship is now ripe for application to conservation, and recent advances in satellite technology make this more feasible. While the correlates for the species–energy relationship have been addressed many times previously, this study is among the first to apply species–energy theory to conservation. Our objectives were to: (1) determine the strongest model of bird richness across North America; (2) determine whether the slope of the best species–energy model varied with varying energy levels; and (3) identify the spatial patterns with similar or dissimilar slopes to draw inference for conservation. Model selection techniques were used to evaluate relationships between Moderate Resolution Imaging Spectroradiometer (MODIS) measures of ecosystem energy and species richness of native land birds using the USGS Breeding Bird Survey (BBS) data. Linear, polynomial, and break point regression techniques were used to evaluate the shape of the relationships with correction for spatial autocorrelation. Spatial analyses were used to determine regions where slopes of the relationship differed. We found that annual gross primary production (GPP) was the strongest correlate of richness (adjusted $R^2 = 0.55$), with a quadratic model being the strongest model. The negative slope of the model was confirmed significantly negative at the highest energy levels. This finding demonstrates that there are three different slopes to the species–energy relationship across the energy gradient of North America: positive, flat, and negative. If energy has a causal relationship with richness, then species–energy theory implies that energy causes richness to increase in low-energy areas, energy has little effect in intermediate-energy areas, and energy depresses richness in the highest-energy areas. This information provides a basis for potential applications for more effective conservation. For example, in low-energy areas, increased nutrients could improve vegetation productivity and increase species richness. In high-energy areas where competitive dominance of vegetation might reduce species richness, vegetation manipulation could increase species richness. These strategies will likely be most effective if tailored to the local energy gradient.

Key words: biodiversity; Breeding Bird Survey; conservation; gross primary production (GPP); Moderate Resolution Imaging Spectroradiometer (MODIS); normalized difference vegetation index (NDVI); North America; species–energy curves; species–energy theory.

Introduction

Ecosystem energy is well established as a primary correlate of global patterns of species richness (Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001, Hawkins et al. 2003). The species–energy relationship has been well tested among various taxonomic groups, spatial scales, and geographic locations and is now ripe for application to conservation (e.g., Verschuyl et al. 2008). For example, the relationship between richness and energy could be used in conjunction with satellite estimates of energy to predict species richness across landscapes in order to identify local areas of high richness that may be high priorities for conservation. In cases in which the relationship is causal, ecosystem energy and the means by which it influences species richness (e.g., vegetation structure) could be manipulated to achieve biodiversity objectives. If the relationship is nonlinear and the effect of energy on species richness differs among locations of low, intermediate, or high energy, then the effectiveness of conservation strategies could be improved by tailoring them to local energy conditions. Using the species–energy relationship as a context for managing biodiversity requires knowledge of the measures of energy that best explain species richness, the slope of function at different energy levels, and the geographic location of areas that differ in the slope of the relationship. The purpose of this paper is to evaluate the species–energy relationship for breeding land birds across the energy gradient of North America and to

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[4] E-mail: lphillips@montana.edu

draw initial implications for conservation. This research is among the first to attempt to apply knowledge from the species–energy relationship to conservation, and in doing so it utilizes the most recent advances in satellite data, the robust bird richness data of the USGS Breeding Bird Survey (BBS), and advanced statistical techniques to best quantify the nature and shape of the relationship. We restrict the analyses to BBS samples from locations of relatively low-intensity human land use because agriculture, home development, and other more intense land uses alter bird species richness through changing ecosystem energy and other means (Blair 1996, Marzluff 2001, Davies et al. 2007, Pidgeon et al. 2007). Hence, this paper seeks to quantify the relationship between natural ecosystem energy and native land bird species richness and draw conclusions for management.

Energy predictors of species richness

The most frequent measures of ecosystem energy that have been used in studies of the species–energy relationship involved radiant energy, primary productivity, or correlates of these such as water balance (Currie 1991, Hawkins et al. 2003). The quantification of these measures across regional to continental areas in species–energy studies has evolved with improving satellite and simulation technology. Initial studies used data from meteorological stations to quantify measures of climate including potential and actual evapotranspiration (Kerr 2001), ambient temperature (Turner et al. 1987, Acevedo and Currie 2003), precipitation (van Rensburg et al. 2002, Chown et al. 2003), and water balance (Hawkins et al. 2003). Measures of heat and water were thought to limit organisms directly and/or influence primary productivity and thus food availability.

The first generation of satellite-derived indices of plant productivity were used in species–energy studies through the 1990s. The normalized difference vegetation index (NDVI) was derived from advanced very high resolution radiometer (AVHRR) data as a correlate of primary production (Tucker and Sellers 1986, Chong et al. 1993, Sellers et al. 1994). The NDVI is a simple vegetation index based on the ratio of the near-infrared spectral band radiation. It has been shown to be significantly related to species richness of many taxonomic groups in many geographic regions and at many spatial scales (Whiteside and Harmsworth 1967, Abramsky and Rosenzweig 1984, Owen 1988, Hoffman et al. 1994, Kerr and Packer 1997, Hawkins et al. 2003, 2005). In the case of BBS data for breeding birds, the variation in species richness explained by the NDVI differed considerably among studies (14–51%; Currie 1991, Hurlbert and Haskell 2003, Evans and Gaston 2005). The NDVI is thought to be a strong predictor of species richness because it is a product of soils, climate, and topography, which might influence organisms indirectly, and an index of food availability for consumers.

The Moderate Resolution Imaging Spectroradiometer (MODIS), launched in 1999, represented a substantial improvement in our ability to represent global vegetation measures (Running et al. 2004, Zhao et al. 2005). In addition to NDVI, the MODIS energy products included an enhanced vegetation index (EVI) and gross and net primary productivity (GPP and NPP). The enhanced vegetation index is a variation on NDVI that includes coefficients to increase the clarity of the vegetation signal, minimizing noise from the atmosphere and soils. The GPP and NPP estimates are simulated based on spectral data, climate, land cover, and vegetation characteristics. Phillips et al. (2008) evaluated the four MODIS energy products and found that annual GPP explained more variation (54%) than the other products in breeding land bird species richness across North America, especially in places of sparse and dense vegetation, where the NDVI is known to have limitations.

Uncertainty remains in the temporal formulation of vegetation productivity that best explains bird species richness. Hurlbert and Haskell (2003) found for breeding birds across North America that NDVI for the bird breeding season (June) was a stronger predictor than annual NDVI. For breeding birds across Great Britain, Evans et al. (2005*a*) found the annual formulation of NDVI produced a slightly stronger model than the breeding season model. These are examples of the lack of consensus on aspects of the species–energy relationship that must be addressed before implications of the relationship can be applied to conservation management.

Shape of the relationship

The shape of the relationship of energy to biodiversity is the subject of a vast ecological literature (e.g., Wright 1983, Rosenzweig and Abramsky 1993, Huston 1994, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001, Whittaker and Heegaard 2003). Nearly all studies found a positive linear relationship between species richness and energy at lower levels of energy. At intermediate to high levels of energy, the relationship has been found to be positive linear, positive flattening, or unimodal where richness peaks at intermediate energy levels and decreases at high-energy levels (Fig. 1). Several hypotheses have been proposed to explain both the positive and negative shapes of the relationship, although it is fairly well accepted that different mechanisms apply in different geographic areas based on limiting factors of the particular ecosystem (Rosenzweig 1995). The most widely cited explanation for the positive relationship is the "More Individuals Hypothesis," which suggests that increasing energy decreases the probability of local extinctions by influencing organism abundances and populations sizes (Wright 1983, Srivastava and Lawton 1998). The most widely cited hypothesis explaining the negative slope of the relationship is the "Dominance Hypothesis," which suggests that at high energy levels, a few plant species are able to dominate and competitively

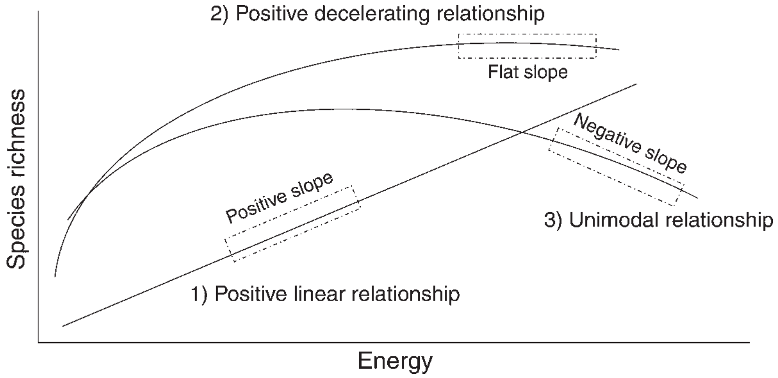

FIG. 1. To utilize knowledge of the species–energy relationship for conservation management, the nature of the relationship and knowledge of the shape of the curve are essential. If the nature of the relationship varies across an energy gradient, there could be up to three different energy influences on biodiversity: positive, flat (no influence), or negative.

exclude other species, resulting in lower vegetation structure and plant species richness and lower habitat and food diversity for higher trophic levels (Huston 1994).

Attempts to synthesize the results of species–energy studies among geographic locations, taxonomic groups, or spatial scales have not found strong generalities in the shape of the species–energy relationship. A review by Waide et al. (1999) found that at very broad spatial scales similar to those of our study, a positive linear relationship for animals was found more frequently, followed by a positive unimodal relationship. However, since then Mittelbach et al. (2001) performed a meta-analysis designed to be inclusive of all taxonomic groups, all spatial scales, and across community types. In this work, when analyzing animal species, positive linear and unimodal relationships were common, but at the broadest spatial scale, a unimodal relationship was more often found. There has been criticism of this review regarding inappropriate consideration of spatial scale, acceptable statistical parameters, lack of consideration of predictor variable limitations (Whittaker and Heegaard 2003), and general experimental design flaws (Gillman and Wright 2006). When statistical parameters were changed slightly (Whittaker and Heegaard 2003) and studies with flawed experimental design approaches were omitted (Gillman and Wright 2006), positive linear relationships were more prevalent at the broadest scales in most of the analyses in the Mittelbach et al. (2001) study. Additionally, and important to note, these studies assumed a unimodal relationship for all quadratic models that since then have been demonstrated to often be a positive decelerating relationship without the negative slope at highest values.

Among studies that looked specifically at bird richness and productivity surrogates, a positive linear or positive decelerating relationship was most common (Waide et al. 1999). Evans et al. (2005*a*) found a linear relationship between NDVI for breeding birds across Great Britain. Similarly, Hurlburt and Haskell (2003) found that the strongest relationship between NDVI and both breeding bird richness and wintering bird richness was linear. In contrast, a quadratic model best represented the relationship between MODIS GPP and breeding land bird richness across North America (Phillips et al. 2008). The shape of the species–energy relationship is highly relevant to applications to conservation because changes in slope in the relationship suggest changing underlying mechanisms (Fig. 1).

Geographic distribution of energy levels

Levels of ecosystem energy tend to be spatially contiguous across broad subregions of continents due to subcontinental- to continental-scale gradients in climate, topography, parent material, and other factors (Running et al. 2004). Thus, if the slope of the species–energy relationship varies across the energy gradient, it should be possible to identify geographic areas where the relationship has a positive slope, locations where the slope is flat, and/or locations where the slope is negative. The mechanisms by which energy influences species richness may differ among these locations, suggesting that effective conservation and management strategies may differ among locations of low, intermediate, and high ecosystem energy.

Application of the species–energy relationship to conservation

Maturation of our knowledge of the species–energy relationship provides a basis for applications to conservation and management. For example, knowledge of the mechanisms underlying the species–energy relationship may allow for manipulation of nutrients, vegetation structure, and/or disturbance regimes to favor higher levels of diversity in a given place. Additionally, the relationship could be used to extrapolate between field samples to more accurately predict the boundaries of places of high bird species richness to refine land allocation to protect biodiversity hotspots. These strategies will likely be most effective if tailored to the local energy gradient. In locations where the species–energy relationship has a positive linear slope, species richness may be limited by ecosystem energy. In these areas, specific locations of relatively high energy may be hotspots for biodiversity and merit protection (Hansen and Rotella 2002). Strategies such as nutrient enrichment may also increase diversity. In locations where the relationship function is flat, energy may not be limiting and management regarding energy would be less important. In areas that have a negative slope on the species–energy curve, species richness may be favored by manipulating vegetation to reduce competitive dominance of canopy plant species and increasing habitat and food heterogeneity (McWethy et al. 2009).

The goal of this paper is to determine the shape and strength of the strongest model of primary production and terrestrial breeding bird species richness across portions of North America with relatively low-intensity land use, in order to begin application of this knowledge to conservation management. Specific objectives are: (1) to determine which of the new productivity-based, satellite-based measures of ecosystem energy, temporal formulations, and shapes of relationships best explain variation in breeding land bird species richness across North America; (2) to determine whether the slope and sign of the best species–energy model varies significantly with energy level; and (3) if the slopes of the relationship are variable, to determine the geographic distribution of places with similar slopes and draw inferences for conservation and management.

Methods

The general approach involved quantifying the influence of energy on species richness for geographic areas relatively less impacted by humans, determining whether the slope of the relationships differed among levels of energy, and then identifying the geographic locations of samples with differing slopes. Because of current uncertainty in the strength of different energy predictors, temporal formulations, and shapes of relationships, we used information theoretic techniques (Burhnam and Anderson 1998) to evaluate competing models derived from the four MODIS primary productivity predictors (NDVI, EVI, GPP, NPP), two time periods (bird breeding season, annual), and four species–energy relationship functions (linear, break point, quadratic, spline). We used the coefficient of determination to evaluate the strength of the model independent of other models. For the best model, we tested for significance of differences of slopes between three energy intervals. Where the slope of the best species–energy model varied across the energy gradient, we identified locations across North America on each portion of the curve and described implications for conservation and management for each location.

Study area

The study area included the United States and Canada. This area represents a large range of habitat types and a broad gradient in ecosystem energy to explore the species–energy relationship (Waring et al. 2006, Phillips et al. 2008). The wide latitudinal range and large land area result in varying climates ranging from polar to tropical and desert to rainforest. Consequently the biomes of North America include desert, Mediterranean woodland, temperate grassland, temperate forest, boreal forest, and tundra (Molles 2002). The climate and vegetation of North America result in a wide gradient in GPP (1–19 g C/m^2; Turner et al. 2006).

Avian data

Native land bird species richness was derived from species count data collected by the USGS Breeding Bird Survey (BBS; Robbins et al. 1986). The BBS survey routes are 39.4 km linear routes that are randomly located along secondary roads throughout the United States and Canada. The BBS data has been collected every May or June since 1966 with a trained surveyor recording every species observed at 50 3-min point count locations spaced at 0.8-km intervals along the route. The survey begins soon after sunrise and observers record birds that are seen or heard within 400 m from the point stop. There are >4000 BBS routes that provide species counts and relative abundance data at the landscape scale (see Bystrak [1981] for methodology details).

We used BBS data for the years 2000–2004 to coincide with the years available for MODIS products. We explored models using routes with 1–5 years sampling effort and found no significant difference in the relationship with energy, so we included routes sampled for 1–5 years. Selection criteria for routes also included consideration of land use. Land use change has been shown to influence both bird diversity at landscape scales and satellite-derived vegetation measures (Flather and Sauer 1996, Hansen et al. 2001, McKinney 2002), and this land use effect could confound the relationship between richness and productivity. To minimize this human influence we subset routes into heavily human-dominated routes and less human-impacted routes. Land use was defined with the MODIS land cover product and the 17 classes in the International Geosphere-Biosphere Programme classification scheme (Friedl et al. 2002). Routes containing >50% of 1-km cells with land use classified as urban and "built up," cropland/natural vegetation mosaic, and cropland classes were excluded. For the routes included in this analysis (those with <50% more intense land use classes), we found that land use predictors (land use class, home density, human population density) did not contribute significantly to the relationship between bird species richness and GPP (A. J. Hansen et al., *unpublished manuscript*), thus justifying the criteria for inclusion of BBS routes.

We excluded aquatic, exotic, raptor, and nocturnal bird species. Aquatic species were excluded because they might be more strongly limited by hydrology than energy. Additionally we excluded BBS routes that were located within 10 km of the coast because they may be dominated by aquatic species and possibly reduced in richness by proximity to non-terrestrial areas. We also assumed that nonnative species may be more dependent upon human habitats and we omitted "partners in flight," species that are identified as nonnative to a particular bird conservation region. Raptorial and nocturnal birds are known to be inadequately sampled with BBS methods, so these families of birds were omitted.

The BBS data are known to have various biases (Link and Sauer 1998). Primary among these with regards to species richness are the roadside location of survey routes and the geographic bias in which routes are more densely located in more populated areas than more rural areas. Potential biases of the roadside survey are that habitats along roads are not representative of all habitats across the study area and that particular bird species avoid or are attracted to roads. Despite these biases, BBS data are often used for regional to continental bird monitoring because they are the most complete and accurate data available.

A source of error in using BBS data to derive species richness is the lack of complete detectability of species along a route. This results because all observers have some chance of missing species during counts and this chance is well known to differ among observers and routes (Boulinier et al. 1998). Nichols et al. (1998) developed a series of estimators based on capture–recapture theory to account for incomplete detection among species. We used the COMDYN software (Hines et al. 1999) to estimate route-level avian richness based on a closed population model that accounts for heterogeneity in species detection. The avian richness response variable used in our analysis was the mean of annual richness estimated for each year that a route was sampled in the 2000–2004 period.

To associate the BBS route to the 1-km raster satellite data, all raster cell values that overlay the digitized BBS route paths were summarized such that each BBS route had an average summary satellite product predictor value. This ~40-km footprint was the unit of analysis, and this summary across routes provided a species richness average associated with an average satellite product value for each BBS route, and each route was considered a sample.

Energy variables

The four MODIS predictor data sets were gathered from the NASA-operated Earth Observing System Data Gateway (*available online*).[5] These data included MODIS vegetation indices, NDVI and EVI, and productivity products, GPP and NPP. The vegetation indices, EVI and NDVI, are provided at finer resolution (250 and 500 m) and thus were resampled using the nearest neighbor sampling method to be compatible with the derived 1-km-resolution GPP and NPP data.

Gross primary production and NPP were developed to represent the conversion of sunlight to organic material. Gross primary production is determined by estimating photosynthetically active radiation (PAR) from reflective satellite data, modifying those values with MODIS land cover, estimating potential growth with modeled temperature and vapor pressures deficit climate data, and estimating the conversion efficiency (Running et al. 1999). This calculation does not account for the maintenance and respiration costs of plants, so does not represent actual energy available to birds. Net primary production represents plant production after maintenance and respiration costs have been subtracted, so should be a better representation of plant material available to birds than GPP. Net primary production is provided as an annual average and is the most complex measure of energy availability of the MODIS suite of products.

The two temporal measures were calculated by averaging the pixel values of the 16-day composites. The breeding season was defined as 15 May to 15 June as this is the range of time that the breeding bird data are collected. The annual average predictor values were summarized as annual mean for years 2000 through 2004. The exception to this is NPP, which is only represented in this work as an annual variable since respiration costs are not calculated daily or monthly.

Statistical analysis

To determine the best energy variable for predicting bird diversity (objective 1), we constructed 32 univariate multiple regression models. These included each of the four MODIS productivity predictors (NDVI, EVI, GPP, NPP) for two time periods (breeding season and annual). Four functions were used for each of these eight models to allow for increased variation in the shape and for identification of the best fit of regression lines. The linear model contained the energy variable. The quadratic model added the energy variable squared term. The quadratic model was used to test whether the relationship is curvilinear rather than linear. A quadratic, however, can force a symmetric curve both above and below a threshold value, even if the curve only fits the data on one side of the threshold. To decouple functions above or below threshold values, two additional models were considered. The break point and spline models allow relationships to change at predetermined energy values, or knot points. The break point model uses simple linear models between break points. General break point values were selected upon visual inspection of the scatterplot. Specific break points were selected after iterations of the regression relationship

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[5] ⟨http://nasadaacs.eos.nasa.gov⟩

and Akaike information criterion (AIC) values were considered. The specific break point values and intervals were 0–5.99, 6.0–11.99, and 12.0–19.0. All spline models reported were third-degree polynomial splines representing a cubic relationship between knots. We addressed nonconstant variance assumption (heteroscedasticity) by modeling the residual variance using the varPower function in R (R Foundation for Statistical Computing, Vienna, Austria).

All analyses were performed in R (version 2.3.1) and Spatial Analysis for Macroecology (SAM) (version 2.0) (Rangel et al. 2006). The 32 models were analyzed using ordinary least squares regression techniques. The AIC was the primary criterion for determining best models (see Burnham and Anderson 1998); it provides an estimate of the distance between the specified model and some full truth or reality. We used the difference in AIC values (ΔAIC) and Akaike weights of evidence (AIC weights) to assess relative model strength (Burnham and Anderson 1998). We interpreted the cumulative Akaike weights as relative probabilities of importance. However, AIC only provides a measure of model strength relative to other models being examined, but does not inform on the overall accuracy of the model. Hence, we used the coefficient of determination (R^2) as a measure of the degree to which the variation in the response variables was explained by the best model.

To determine the signs and slopes of the best model across the energy gradient (objective 2), simple linear regression models were performed independently across the three different intervals of the energy curve. Quadratic, break point, and spline models indicate a changing of slope across the range of values, but these methods do not necessary indicate a specific shape. As an example, a positive quadratic relationship can represent a unimodal curve that includes positive, flattening, and negative portions of the curve. Additionally, it can also indicate a positive decelerating (or flattening) of the curve. Therefore, to confirm the specific shape of the relationship between richness and energy, we split the best predictor variable into three equal-length intervals and performed simple linear regression on these intervals independently.

Slope and significance tests were important statistical output, so generalized least squares (GLS) models including the spatial structure of residuals were employed in addition to the ordinary least squares (OLS) regression models. These additional analyses were required since spatial autocorrelation of regression residuals violates the assumption of independent residual values and may inflate slope coefficients and significance values (Cressie 1991, Lennon 2000, Legendre et al. 2002). Semivariograms were used to look for spatial dependence (Pinheiro and Bates 2000). When spatial autocorrelation was found, the spatial structure was modeled and included in the models. When spatial autocorrelation was lacking, we concluded that after accounting for the predictors used in these models, the residuals from nearby routes were no more strongly correlated than those from distant routes as is commonly found in studies at such broad spatial scales (Hawkins et al. 2007). Conceptually, spatial autocorrelation inflates sample size by including samples that are similar due to proximity and are therefore not independent samples. While the effects of spatial autocorrelation at broad spatial scales with large sample sizes might be exaggerated (Hawkins et al. 2003) we applied both model types (OLS and GLS) to employ the most conservative approach to the analysis and to have greatest certainty in our resulting statistical output. For these first two objectives, the following standard regression protocol was followed. Regression techniques assume that residuals (error terms) are independent, normally distributed, and with constant variance. We inspected the normality of the residuals of the best models and found support for normality for species richness. Homogeneity of variance was tested and when rejected, observations were weighted with the "weightsvarPower" argument in R. "WeightsvarPower" models nonconstant variance when the variance increases or decreases with the mean of the response, allowing GLS to estimate the power that defines the relationship.

To determine the geographic distribution of places of similar slope in the species–energy relationship (objective 3), we examined whether BBS routes of low, intermediate, and high GPP were randomly distributed among ecoregions. We used bird conservation regions to represent regions of ecological similarity since these delineations are designed to represent ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues (Rich et al. 2004). In cases in which bird conservation regions contained fewer than 20 BBS routes, adjacent regions with similar energy levels were merged. Chi-square analyses were used to determine whether the three energy classes occurred randomly among BBS routes in each region. Specifically, we tested whether frequency of the most common energy class in a region was greater than expected by chance relative to the second most common energy class. If the null hypothesis was rejected, we concluded that the most common energy class was significantly associated with that conservation region. Statistical significance was assumed for all tests with $P < 0.01$.

RESULTS

Of the 3476 BBS routes that had adequate richness data, a subset of 1383 met our criteria for analysis. These routes were sampled for one or more years, contained <50% human-dominated classified cells, and were >10 km from the coast.

Objective 1: best models among predictors, time periods, and statistical functions

The 32 models tested differed substantially in AIC values. Generally, the annual measures of energy and

TABLE 1. Statistical output of measures of ecosystem energy, temporal formulations (annual and breeding season [bs]), and shapes of relationships that best explain variation in breeding land bird species richness across North America.

Predictor variable	Time period	Model	Adjusted R^2	ΔAIC	AIC weights
GPP	annual	break point	0.55	0	0.9992
GPP	annual	spline	0.54	14.438	0.0007
GPP	annual	quadratic	0.53	21.182	<0.0007
NDVI	annual	quadratic	0.52	129.001	<0.0007
NDVI	annual	spline	0.52	149.708	<0.0007
NDVI	annual	break point	0.52	158.304	<0.0007
NPP	annual	spline	0.51	193.968	<0.0007
NPP	annual	quadratic	0.51	199.963	<0.0007
EVI	annual	quadratic	0.48	210.058	<0.0007
EVI	annual	spline	0.48	230.573	<0.0007
NPP	annual	break point	0.50	233.309	<0.0007
EVI	annual	break point	0.48	248.735	<0.0007
EVI	bs	quadratic	0.39	407.824	<0.0007
NDVI	bs	spline	0.46	408.277	<0.0007
NDVI	bs	break point	0.45	414.755	<0.0007
EVI	bs	break point	0.40	415.75	<0.0007
EVI	bs	spline	0.41	420.946	<0.0007
NDVI	bs	linear	0.43	422.087	<0.0007
NDVI	bs	quadratic	0.44	422.341	<0.0007
EVI	annual	linear	0.39	450.74	<0.0007
NDVI	annual	linear	0.42	452.413	<0.0007
EVI	bs	linear	0.36	455.747	<0.0007
GPP	bs	break point	0.39	473.844	<0.0007
GPP	bs	quadratic	0.39	479.184	<0.0007
GPP	bs	linear	0.38	479.379	<0.0007
GPP	bs	spline	0.39	481.073	<0.0007
GPP	annual	linear	0.39	491.112	<0.0007
NPP	annual	linear	0.40	509.461	<0.0007

Notes: Predictor variables are arranged from lowest to highest ΔAIC (Akaike's information criterion). Output also includes time period, model type, weighted AIC, and adjusted coefficient of determination. Predictor variable abbreviations are: GPP, gross primary production; NDVI, normalized difference vegetation index; NPP, net primary production; EVI, enhanced vegetation index.

curvilinear models produced the strongest models, breeding season and curvilinear models ranked next, breeding season and linear models were third in strength, and annual and linear models were weakest (Table 1). The strongest correlate with bird species richness was annual GPP, and the three highest ranking models were curvilinear models with annual GPP as the predictor variable. The annual GPP break point model best represented this relationship (adjusted $R^2 = 0.55$), with spline and polynomial models notably weaker ($\Delta\text{AIC} =$ 14.43 and 21.18, respectively). Annual NDVI was the second strongest predictor variable, again with the curvilinear models all being the strongest models (quadratic, spline, and break point $\Delta\text{AIC} = 129.0$, 149.7, 158.3, respectively). Annual NPP was the third strongest predictor variable with the spline and quadratic ranked seventh and eighth best models ($\Delta\text{AIC} =$ 193.9 and 199.9, respectively). Annual EVI was the weakest annual predictor, yet all best EVI models were curvilinear models and all annual EVI curvilinear models have similar model strength ($\Delta\text{AIC} = 210$, 230, 248, respectively).

Bird richness was much less strongly correlated to all four predictor variables when the breeding season energy metric was considered. The strongest breeding season predictor variables were the vegetation indices, with EVI and NDVI models stronger than all GPP breeding season models. These models were also curvilinear with quadratic, spline, and break point models all in best breeding season models.

The worst ranked models were NPP and GPP annual linear models ($\Delta\text{AIC} = 509.4$ and 491.1) and all GPP breeding season models ($\Delta\text{AIC} = 473.8$, 479.1, 479.3). Additionally, the linear models for all predictor variables with all time periods were consistently weaker than curvilinear models. Out of the 28 models, all linear models were ranked below 17 and all breeding season models were ranked below 12. On the contrary, the top-ranked 13 models were all annual and all curvilinear models.

Objective 2: slope and sign of the species–energy relationship across energy levels

When simple linear regression models were applied to the three equal interval classes of GPP, the slope of the relationship and the strength of the relationship varied across the GPP gradient (Table 2). Semivariograms indicated that spatial autocorrelation of residuals was present in models and that the spatial pattern of the residuals differed across the study area. To address this,

TABLE 2. Statistical output to determine the slope and sign of the species–energy relationship (SER) for each gross primary production (GPP) interval for both spatial and nonspatial linear models.

GPP interval (g C/m^2)	Model	Slope	P	AIC
0–5.99	nonspatial	0.078	<0.0001	−414.55
0–5.99	spatial	0.099	<0.0001	−1083.14
6–11.99	nonspatial	0.016	<0.0001	−980.82
6–11.99	spatial	0.004	0.241	−1083.14
12–18.76	nonspatial	−0.019	<0.0001	−725.92
12–18.76	spatial	−0.010	<0.0001	−734.05

Notes: Statistical output includes GPP interval, model type, regression slope, significance value, and Akaike information criterion (AIC).

we determined the spatial structure of residuals for each GPP interval using semivariograms and maximum likelihood tests. Generalized least squares models (GLMs) were then performed using the spatial structure of residuals for each individual interval.

The lowest GPP interval showed a positive, significant relationship ($P < 0.001$) with a slope of 0.099 (Fig. 2). The intermediate GPP interval had a nonsignificant slope ($P = 0.241$), indicating that the model did not differ significantly from flat. The slope of the highest GPP interval was significantly negative with a slope of –0.01. These results confirm that the quadratic relationship across the full energy gradient was unimodal rather than positive decelerating.

Objective 3: spatial distribution of BBS routes with similar slopes

The BBS routes within each of the three energy intervals were not distributed randomly across the study area (Fig. 3; BBS routes represented as points). Of the 21 bird conservation regions or combinations of regions analyzed, BBS routes of a particular energy level occurred more frequently than expected at random in 18 bird conservation regions (Table 3). The BBS routes in the low-energy interval in which the species–energy relationship was positive were prevalent in eight regions in the American Southwest, Rocky Mountains, Alaska, and northwestern Canada (blue routes in Fig. 3). The BBS routes in the intermediate-energy interval where the relationship was flat were significantly associated with six regions in the eastern U.S. Prairie, the northeast United States and maritime regions of Canada, the Great Lakes region, the Boreal Shield region of Canada, and portions of California (green routes in Fig. 3). The BBS routes in the highest energy class, where the relationship was negative, were significantly associated with four regions in the southeastern United States (red routes in Fig. 3). Ten routes in the Coast Ranges of the Pacific Northwest United States were in the high-energy class, although they did not statistically dominate the large Northern Pacific Rainforest region.

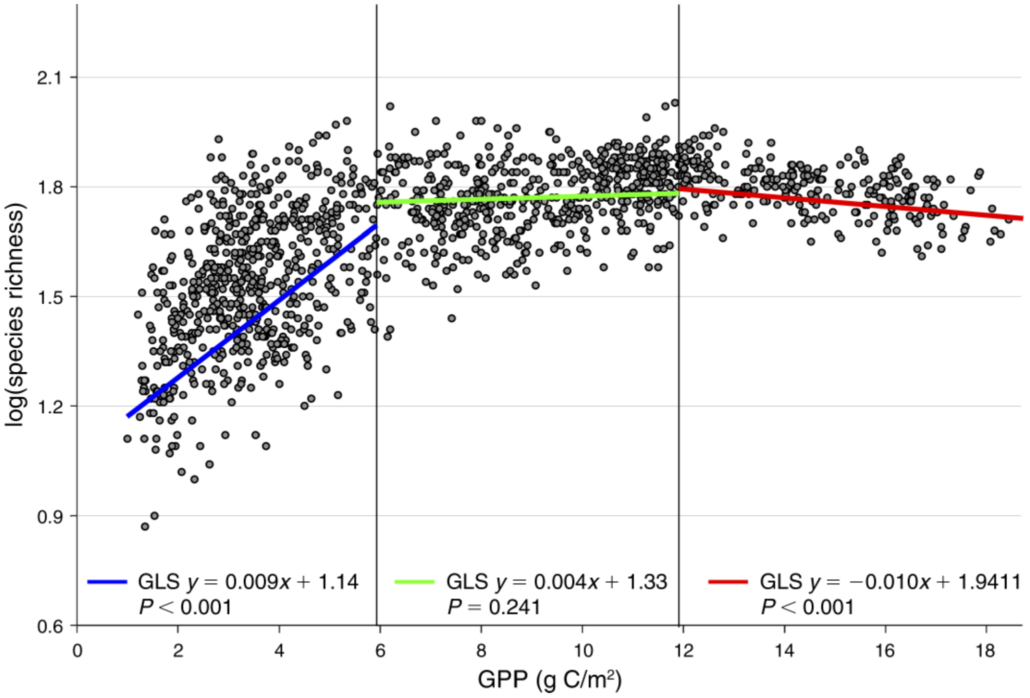

FIG. 2. Observed points and predicted generalized least squares (GLS) regression lines for log-transformed species richness in three intervals across the productivity gradient (gross primary production, GPP), with a positive slope in blue, a flat slope in green, and a negative slope in red.

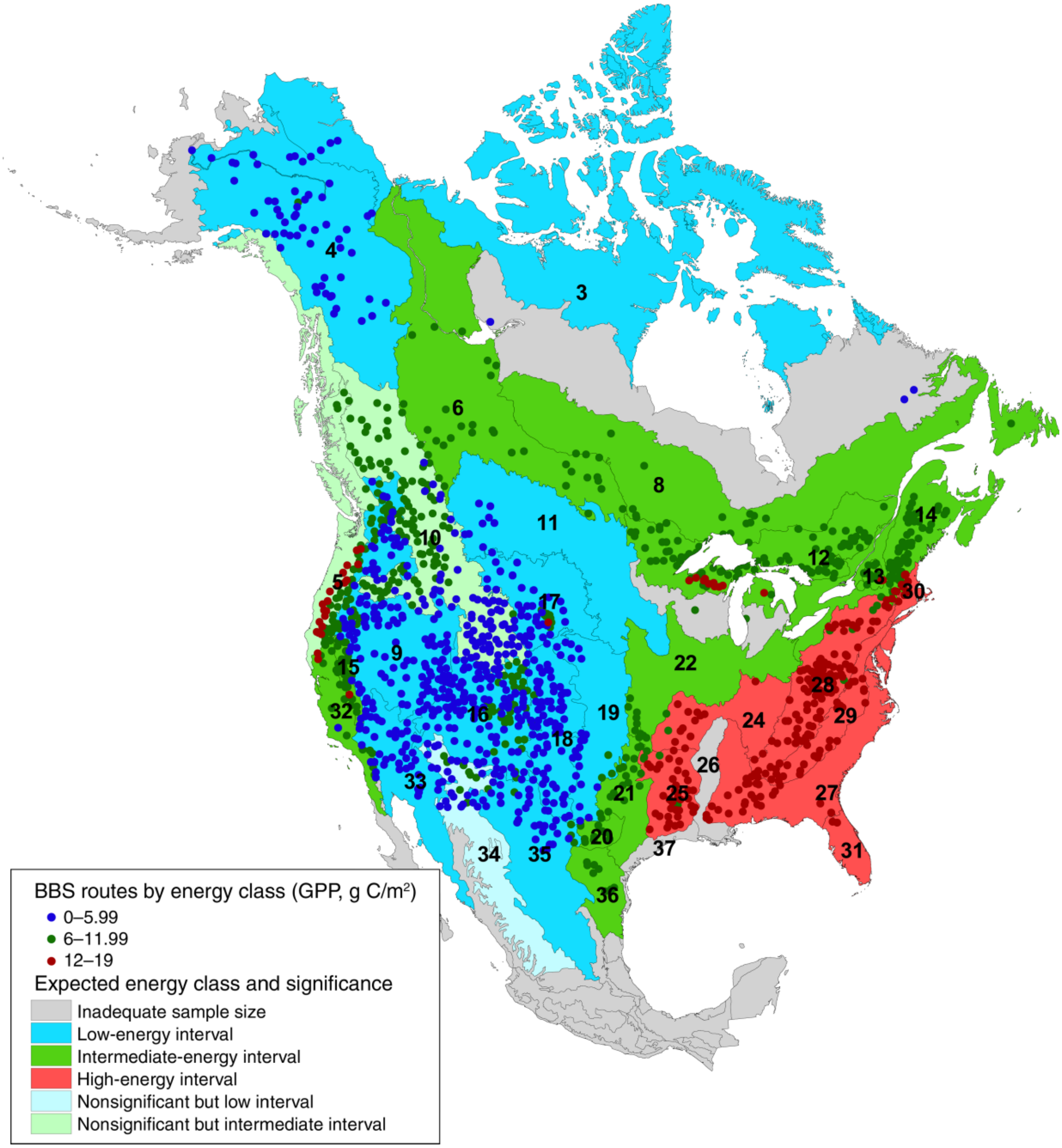

FIG. 3. The spatial pattern of Breeding Bird Survey (BBS) routes in the three gross primary production (GPP) intervals indicates that energy levels within bird conservation regions (BCRs) are not randomly distributed but rather have frequencies that are higher than expected in most regions. The conservation region colors indicate that energy classes were found significantly more frequently than expected if randomly distributed. The point colors coincide with the colors of regression lines in Fig. 2. Numbers within regions correspond to BCRs in Tables 3 and 4.

DISCUSSION

The primary goal of this paper was to utilize knowledge of the species–energy relationship for the conservation and management of biodiversity. We focused on breeding land birds across North America largely because of the unique data available through the USGS BBS. The BBS records abundances of bird species in the field annually at relatively fine spatial scales across the United States and Canada. These data allow estimation of bird species richness at a grain size similar to that available for the most recent satellite-based measures of primary productivity for the years that the satellite data have been collected. While the species–energy relationship has been the subject of vast research, greater certainty regarding the best predictor

TABLE 3. Results of the spatial analysis of the difference in the observed and expected frequency of finding Breeding Bird Survey (BBS) routes in specific energy intervals in bird conservation regions (BCRs).

BCR	*N*	Expected	χ^2	*P*	Energy class
9	164	81.5	40.25	<0.001	low
16	150	75	38.51	<0.001	low
17	44	21.5	12.3	<0.001	low
33	43	21.5	43	<0.001	low
35	39	19.5	21.56	<0.001	low
11, 17	52	25.5	18.84	<0.001	low
18, 19	97	48.5	71.02	<0.001	low
3, 4	58	29	54.07	<0.001	low
34	27	13.5	3	<0.0001	low
14	75	32	64	<0.001	medium
15	28	13.5	16.33	<0.001	medium
12, 13	100	50	54.76	<0.001	medium
20, 21, 22, 36	44	22	40.09	<0.001	medium
6, 8	51	25.5	51	<0.001	medium
32	25	12	8.17	<0.01	medium
5	43	21	0.1	<0.0001	medium
10	163	81.5	1.04	<0.0001	medium
28	101	50.5	78.43	<0.001	high
24, 25	57	28.5	35.53	<0.001	high
27, 31	31	15.5	31	<0.001	high
29, 30	29	14.5	29	<0.001	high

Notes: *N* is the number of BBS routes. Numbered BCRs correspond to those shown in Fig. 3.

variables and nature of the relationship is necessary for applications to management. Thus, we used the USGS BBS data set, sophisticated modeling techniques that allow maximum freedom in model form, and the latest-generation satellite-based measures of primary productivity to identify the best relationship between energy and breeding land bird species richness. We then mapped places with similar slopes across North America and explored implications for conservation and management.

Evaluation of species–energy models

We found that GPP (best model $R^2 = 0.55$) explained more variation in bird species richness than the three other MODIS-derived measures of primary productivity (NDVI, EVI, NPP). This finding is consistent with our results from a related study (Phillips et al. 2008) that used a similar data set to evaluate the species–energy relationship across a gradient in vegetation life form and density. Gross primary production likely outperformed other measures in our study because it better predicts primary productivity in areas of sparse vegetation where spectral backscatter from bare ground results in NDVI underestimating productivity. Also, in areas of dense forest vegetation, NDVI becomes insensitive to vegetation canopy and NDVI values saturate so do not distinguish differences in productivity (Phillips et al. 2008). Theoretically, NPP should better explain bird species richness than GPP because it is a measure of new plant biomass produced, whereas GPP estimates potential energy before growth and maintenance costs are considered. Phillips et al. (2008) concluded that the strength of GPP over NPP could be explained by the error propagation or the intricacies in the NPP and GPP algorithms rather than an ecological explanation.

Unlike our results, EVI has elsewhere been shown to be more sensitive to biophysical vegetation properties by reducing the saturation effects in dense vegetation that are common with other indices (Huete et al. 2002). Nightingale et al. (2007) showed that EVI was a strong predictor of tree richness, with R^2 values ranging from 0.57 to 0.75. This work was performed with tree richness summarized over ecoregion-sized grain for the lower 48 United States (Nightingale et al. 2007). The EVI is possibly a weak predictor variable in this study because EVI is designed to increase the sensitivity of the signal in forested areas with high EVI values. This high EVI value range is the range of values that have little variation in richness. This might result in a weaker relationship between richness and energy by increasing the spread of EVI values in the area of the curve that has less variation in richness.

The relationships between vegetation productivity and bird species richness we found were stronger than previous studies using AVHRR-based NDVI. Hurlbert and Haskell (2003) used satellite data for 1992–1993 and BBS bird data for 1997 and evaluated only linear models. They found that variation in bird species richness explained by June NDVI was 41% and by annual NDVI was 34%. Hurlbert (2004) also used AVHRR NDVI data for June 1992 and BBS data for 2000. He found that linear and power functions explained 45–49% of the variation in the relationship. This stronger relationship than found by Hurlbert and Haskell (2003) for linear models may be due to the nonrandom selection of BBS routes. The Hurlburt analysis focused on differences in vegetation structure and selected desert and grassland BBS routes and deciduous forest routes. These samples may not have represented the full range of vegetation cover classes and emphasized the grassland and forest cover classes where Phillips et al. (2008) found the relationship was stronger. The stronger relationships we found with GPP ($R^2 = 0.55$) and NDVI ($R^2 = 0.52$) could be due to satellite product improvement, from a reduction in confounding factors such as using MODIS and BBS data from the same time periods, taking a five-year average of the satellite and bird data, and/or from excluding BBS routes with human land use or near coasts.

Our results are not comparable with many other NDVI-based studies (Currie 1991, Bonn et al. 2004, Evans et al. 2005*b*) because of differences in the spatial scale of analyses, since differences in summarizing analysis unit, spatial resolution, and map extent strongly influence results (Waide et al. 1999, Hawkins et al. 2003).

We found that the annual measures of energy and curvilinear functions produced strongest models for all four energy predictors. Hurlbert and Haskell (2003) suggested that breeding season energy is especially relevant to bird species richness because birds are highly mobile and migratory. They found that bird species richness during the breeding season was better explained by June NDVI than annual average NDVI and that bird species richness in winter was better explained by January NDVI than annual average NDVI. Their predictions regarding how annual NDVI phenology influences ratios of resident and migratory species were also supported.

The use of only linear models by Hurlbert and Haskell (2003), however, casts doubt on their conclusions. Like Hurlbert and Haskell, we found that linear NDVI models were stronger for the breeding season than for annual time periods. However, we also found that curvilinear models were substantially stronger than linear models and that annual curvilinear models were substantially stronger than breeding season curvilinear models.

The strength of the annual energy models over breeding season models suggests that breeding bird species richness is more influenced by annual available energy than breeding season energy. The temporal basis of the bird species–energy relationship is likely complex and is not well understood. Gross primary production likely influences both food availability for birds and habitat structure. The habitat structure available to birds during the breeding season could be developed at any time of the year. The foods available to breeding birds would seem to most likely reflect primary productivity during the bird breeding season. However, we know relatively little about how the availability of seeds, fruits, or herbivorous invertebrates to birds during the breeding season may be influenced by annual primary productivity. Hence, there is insufficient knowledge at present to provide an ecological explanation as to why annual energy predictors explain more variation in breeding bird richness than do breeding season energy predictors.

Additionally, the strength of the annual energy models over the breeding season models could be explained by an artifact of the data. L. B. Phillips and A. J. Hansen (*unpublished manuscript*) found that MODIS GPP is better able to represent primary production in highly productive areas than seasonal NDVI. MODIS GPP has a broader range of variation in dense forests where seasonal NDVI is most sensitive to signal saturation. This could contribute to the strength of GPP against seasonal NDVI measures.

Shape of the species–energy relationship

Our results indicate that the slope of the species–energy relationship varies significantly across the energy gradient. This is highlighted by considering that for all variables and all time periods, the best model is a break point regression model, the second best is the cubic spline model, and the third best is the quadratic model. Additionally, the top 17 models are these "slope variable" models, and the best model that does not vary across the gradient (18th best model) is a substantially weaker model.

While these results suggest that the slopes of the relationship are variable across the North American gradient of GPP, additional analyses are needed to confirm significantly different slopes. Polynomial regression models assume symmetry around an inflection point such that one side of the predicted line will mimic the other end of the predicted line. As a result, if the polynomial model is found the best model, the relationship could indeed be a unimodal relationship or it could be a positive to flattening relationship, referred to as positive decelerating (Mittelbach et al. 2001). This has historically been misrepresented by the polynomial function as a unimodal relationship.

We confirmed a unimodal relationship in this study by using break point and spline functions and determining the slopes of the relationships for each of three intervals of GPP. After controlling for the effect of spatial autocorrelation, the relationship is significantly positive at GPP values below 6 g C/m^2, significantly negative at GPP values above 16 g C/m^2, and the slope does not differ significantly from zero between GPP values of 6 and 16 g C/m^2 (Fig. 2). Thus, the results provide strong evidence that the best model for the bird relationship is unimodal, with richness increasing with GPP at lower GPP values and richness decreasing with GPP at the highest GPP values. Possible explanations for this unimodal relationship for breeding land birds across North America emerge when the spatial distributions of the three intervals of GPP are mapped across the study area.

Spatial pattern of the species–energy relationship

The BBS routes within similar energy ranges and similar slope on species–energy curves tend to be located

TABLE 4. Descriptions of bird conservation regions (BCRs), identified by number, name, and biome type (Rich et al. 2004).

BCR	Associated regions	Biome type
9	Great Basin	sagebrush and sage, juniper woodlands, and ponderosa pine on higher slopes
16	Southern Rockies/Colorado Plateau	vegetation bands due to elevation; conifer with aspen at upper, juniper woodlands at lower elevation
33	Sonoran and Mohave Deserts	cacti, slow-growing grasses, desert shrubs
35	Chihuahuan Desert	arid grasslands and shrublands with oak–juniper woodlands and conifers at higher elevations
11, 17	Badlands and prairies	mixed-grass prairie
18, 19	Shortgrass and mixed-grass prairie	shortgrass and mixed-grass prairies with savannah-like habitat to the east
3, 4	Northwest forest/Arctic plains and mountains	forest, shrub, and graminoids in northwest region; coastal tundra with continuous permafrost and drier uplands in northern region
34	Sierra Madre Occidental	complex topography with oak–pine, pine, and fir forests, with semiarid scrubs on slopes
14	Atlantic northern forest	nutrient-poor soils support spruce–fir at higher sites and northern hardwoods elsewhere
15	Sierra Nevada	ponderosa pine (west) and lodgepole pine and fir (east) at lower elevations; spruce and alpine tundra at higher elevations
12, 13	Boreal hardwoods and lower Great Lakes Plain	nutrient-poor soils support northern hardwoods and conifer forests; lakeshore and wetland habitats surround waters
20, 21, 22, 36	Prairie–forest transition and tallgrass prairie	tallgrass prairie in northern region; shrubs, mesquite, juniper, and oak savannah in area dividing Great Plains and eastern forests
6, 8	Boreal Taiga and Boreal Softwood Shield	U-shaped region with seacoasts to east, dense conifer forests in north and west, and broadleaf forests in south
32	Coastal California	mixed chaparral
5	Northern Pacific rainforest	forest dominated by western hemock and sitka spruce in north and Douglas-fir and redwood in south, broadleaf forests in valleys
10	Northern Rockies	vegetation dominated by elevation gradient, from grassland valleys to Douglas-fir and lodgepole pine, and subalpine fir higher
28	Appalachian Mountains	oak–hickory and other deciduous forests, grassland and agriculture at lower elevations
24, 25	Central hardwoods and West Gulf Coastal Plain	Ozark Mountains just west of Mississippi river, oak–hickory forests to pine forests with short- and longleaf pines farther south
27, 31	Southeastern Coastal Plain and Peninsular Florida	coastal areas include swamps and marshes, interior forests dominated by longleaf, slash, and loblolly pine forests
29, 30	Piedmont and mid-Atlantic Coast	transition between Appalachians and Coastal Plain, dominated by pine and mixed hardwoods

in distinct geographic regions (Fig. 3). This study is the first, to our knowledge, to map the spatial locations of observations on different portions of the species–energy curve. Examination of these spatial patterns promotes discussion of the biophysical setting of each interval and of hypotheses of possible mechanisms linking primary production and breeding land bird species richness.

The nine bird conservation regions associated with the low GPP interval include two large geographic regions that represent (1) the southwest deserts north to the badlands and short-grass prairies and (2) portions of Alaska and northern Canada (blues in Fig. 3 and bird conservation region descriptions in Table 4). Primary productivity is constrained in the Southwest and High Plains regions primarily by moisture limitation and in the subarctic region by cold temperatures (Nemani et al. 2003).

This lowest interval of GPP values contains the largest spread of bird richness values, with species richness ranging from 7 to 94 species across the interval of GPP 0–5.99. The two distinct differences in limiting factors (i.e., water in southwest and temperature in northwest) likely contribute to the large variation in richness and the large residuals in the relationship. This variation contributes to the low GPP interval having the weakest statistical relationship between richness and energy in this area, even though the slope is the steepest.

Bird species richness is positively related to GPP in these regions possibly because increased GPP allows more complex habitat structure and/or increased seeds, fruits, invertebrates, and other foods. Alternatively, GPP may be correlated with climate (Avecedo and Currie 2003, Currie et al. 2004), which includes cold temperatures in the north (Root 1988) and heat and lack of surface water in the southwest (Hernandez-Acevedo and Currie 2003). The positive slope in these regions is similar to previous studies that have most often found that richness across many taxonomic groups is limited by moisture availability and is highly variable across space in this region with subtle differences in microclimates (Webb et al. 1983).

There are numerous mechanisms that have been suggested to describe the positive and decelerating relationships in species richness and energy. For most of these, there have been studies that find both support and lack of support for each mechanism (see Evans et al. [2007] for a review of nine of these mechanisms). A thorough discussion of the underlying mechanism for the positive linear relationship is beyond the scope of this paper. However, since all of the mechanisms suggested to drive the positive slope of the relationship suggest that with increasing ecosystem energy there are larger numbers of individuals (larger populations), recommended management scenarios that favor richness do not require a more specific understanding of the mechanism.

The intermediate GPP interval supports the highest bird diversity and is spatially the least contiguous region of the three intervals (Fig. 3, greens). The 12 bird conservation regions associated with the intermediate GPP interval include eight regions in the Northeast United States and southern Canada and west to the Rocky Mountains, three in Midwest to the Gulf Coast area, and two in California.

The bird conservation regions from New England to the Canadian Rockies have strongly continental and seasonal climates characterized by long cold winters and short warm summers. The Sierra Nevada and coastal California regions have a Mediterranean climate, and the area from eastern Oklahoma south to central Texas is characterized as a prairie ecosystem, with continental subhumid climate.

The species–energy relationship for this interval has a nonsignificant, slightly positive slope. The lack of relationship in this region suggests that energy is not limiting or depressing richness, but rather has little effect. This change in slope from the regions in the low-GPP interval to those in the intermediate-energy interval is consistent with the concept that the factors that limit species richness vary spatially and supports other work that finds a positive decelerating relationship. Several studies have found that the strongest correlates with species richness vary among subcontinental to continental areas (Kerr 2001, Acevedo and Currie 2003, Hawkins et al. 2003). Verschuyl et al. (2008) examined five landscapes in the Pacific and inland Northwest United States that spanned the low to high GPP intervals. Using bird data derived from point counts (rather than BBS routes), they found a unimodal relationship between indices of primary productivity and bird species richness. They also found that energy explained more of the total variation in bird species richness in low-energy landscapes and vegetation structural complexity explained more of the total variation in intermediate to high GPP landscapes.

The seven bird conservation regions in the highest GPP interval all had negative slopes and were all located in the southeastern United States. These included the southeast U.S. Piedmont and coastal plain extending north into the Appalachian highlands. This region has a moderate maritime climate with marked high humidity, lack of seasonality, and extensive growing season.

Several BBS routes in the Coast Range of Washington, Oregon, and northern California also were in this high GPP interval with a negative species–energy slope. These routes are within the North Pacific Rainforest region. The BBS routes in the eastern and northern portions of this region were in the intermediate GPP class, thus no energy class dominated the entire region (Fig. 3, light green). The Coast Range area has a relatively long growing season and moderate maritime climate.

This GPP interval of highest values had the least variation and the strongest regression relationship. The significant negative relationship suggests that energy may be depressing richness in these areas. There have been numerous mechanisms suggested to explain the negative portion of the species–energy relationship, but there are few that apply to broadscale studies (Evans et al. 2007). The Dominance Hypothesis is the most widely accepted mechanism to account for the negative effect of productivity on species richness. This has been demonstrated as competitive dominance by canopy tree species (Huston 1979, 1994, Rosenzweig and Abramsky 1993). The potential for competitive dominance is thought to be greater in productive environments because of a total increase in competition for all resources (Grime 1977), competition for light based on the scaling of the organism (Newman 1973, Tilman and Pacala 1993), or a change in population dynamics that leads to more rapid competitive exclusion (Huston 1979). In the absence of disturbance, high productivity may result in high overstory canopy coverage and leaf area concentrated in the upper forest strata. This may reduce light levels lower in the canopy and reduce structural complexity, tree and shrub species diversity (Swenson and Waring 2006), and resulting habitats and foods for bird species that specialize in niches lower in the canopy (Verschuyl et al. 2008). In support of this hypothesis, McWethy et al. (2009) found in one region of the Pacific Northwest that late seral forests in a high-energy landscape had higher canopy closure and less variation in canopy closure than a lower productivity forest. Bird species diversity was negatively associated with canopy closure in the more productive landscape.

We speculate that the relationship between ecosystem energy and species richness at higher energy levels is mediated by other factors such as disturbance regimes. Huston's (1979, 1994) Dynamic Equilibrium Hypothesis purports that species richness increases with disturbance in highly productive environments. The suggested mechanism is that competitive dominance is more pronounced in productive environments and that disturbance breaks this competitive dominance, frees resources, and allows rapid recovery of post-disturbance communities and increased levels of diversity. Support for this hypothesis comes from Proulx and Mazumder (1998), Petraitis et al. (1989), Davis et al. (1988), and Sousa (1979). Additionally, McWethy et al. (2009) found in the Pacific Northwest United States that bird richness increased with increasing levels of disturbance in the landscape within highly productive forests, whereas bird richness decreased with increasing disturbance in the surrounding landscape within less produc-

TABLE 5. Framework for managing biodiversity based on species–energy theory.

Conservation category	Low energy	Medium energy	High energy
Conservation zones	protect high-energy places	protect more natural areas	protect low-energy places
Disturbance	use fire, flooding, logging judiciously in hotspots	similar to "descending"	use disturbance to break competitive dominance; use shifting mosaic harvest pattern; maintain structural complexity
Sensitive species	focus on the numerous species with large home ranges and low population sizes due to energy limitations		focus on the numerous forest interior species
Landscape pattern	maintain connectivity due to migrations		manage for patch size and edge
Protected area size	larger areas required	smaller areas may be adequate	smaller areas may be adequate

tive forests. Examination of disturbance regimes and forest structure in the more productive regions of the world are needed to test the hypothesis that the downturn in species richness in the southeastern United States, the Pacific Northwest United States, and the Congo in Africa (Balmford et al. 2001, Hawkins et al. 2003) are due to the interaction of productivity and disturbance.

Limitations

This study was designed to analyze the correlations between bird richness and the energy predictor data sets generated from the MODIS sensor and apply knowledge of the species–energy relationship to conservation management. Correlation studies are useful in recognizing patterns but do not imply causation. The design of this study is limited in its ability to infer that the predictor data sets cause the variations in diversity, but rather suggests that there is a relationship between the response and predictor data.

While the range of variation within North America is large, this work does not include the full range of variation in primary production or in vegetated cover types. Future research, including similar analyses with even greater range of variation (i.e., tropical forests) would provide additional insight into the richness–productivity relationship, especially regarding variations in strength and slope (B. Hawkins, *personal communication*).

The BBS routes are not completely randomly distributed so are subject to a geographic bias. Geographic representation is not equal as BBS routes are much more common and dense in the more populated areas of the United States than in the areas of lower energy and lower population (Lawler et al. 2004).

These results only represent the relationship between the predictor data sets and the BBS-collected bird richness data. Relationships with other taxonomic groups cannot be predicted since biodiversity patterns are not the same for varying taxonomic groups (Williams et al. 1996). Additionally, richness was calculated for BBS routes that were sampled from one to five years. It would be ideal to have a time period longer than one year, but the MODIS data only became available in 1999 and we chose to include routes that were sampled during the same time period in which the predictor data were collected.

Conservation implications

The vast body of literature on the species–energy relationship suggests that population sizes, species home range sizes, abundances of species guilds, population response to disturbance, competitive interactions, and species richness all may vary with ecosystem energy. These factors are highly relevant to sustaining biodiversity (Molles 2002), yet application of the relationships to conservation and management is embryonic.

The results of this and related studies suggest a framework for managing biodiversity that is based on energy intervals of the species–energy relationship. To the extent that species richness shows a flattening or unimodal relationship with energy (Fig. 1), we suggest that ecosystems low, intermediate, and high in energy have different ecological properties and therefore merit different management strategies. The framework provides for tailoring management to local ecosystems according to where they are located both on the species–energy curve and where they are located geographically (Table 5, Fig. 3) to most effectively achieve biodiversity objectives.

In ecosystems in which energy is relatively low and the slope of the relationship is positive, localized places high in energy should support relatively high species richness. Such biodiversity "hotspots" often occupy a relatively small proportion of the land area in low-energy systems and may be critically important for maintaining population viability across the landscape (Hansen and Rotella 2002). Prioritizing such locations for conservation can be a cost-effective means of achieving biodiversity objectives in such landscapes. Disturbance such as logging and grazing should be permitted judiciously in low-energy systems because ecosystem recovery may be slow due to unfavorable abiotic conditions and low rates of productivity (Huston 1994, McWethy et al. 2009). Species with low population sizes and large home ranges are expected in relatively low-energy ecosystems (Harestad and Bunnell 1979). Relatively large protected areas management for connectivity across the landscape may be required to sustain such species.

In ecosystems in which energy is relatively high and the slope of the species–energy relationship is negative, low-energy places may be localized biodiversity hotspots and benefit from allocation as conservation zones. Because species richness may be depressed by dominance of overstory vegetation, use of logging, grazing, and prescribed fire may be effective in breaking competitive dominance and releasing early- and mid-seral species. The more favorable abiotic conditions and faster primary productivity should allow faster population and community recovery following disturbance. If energy is relatively high over much of the landscape, then a shifting mosaic pattern of disturbance will be effective in maintaining the full suite of seral stages (Loehle et al. 2006, Verschuyl et al. 2008). Vegetation structure is known to explain more variation in species richness relative to primary productivity in higher-energy systems (Verschuyl et al. 2008), hence maintenance of within-stand structural complexity will be required for many species. Species with small populations and large home ranges are less likely in these systems, thus protected areas can be smaller. However, relatively more species are likely to specialize on particular seral stages and on patch edges or interiors (McWethy et al. 2009). Hence, balancing early- and late-seral conditions and distribution of habitat edges and patch sizes is especially important.

Ecosystems that are intermediate in energy may be continental-scale hotspots for species richness and thus important in continental-scale conservation plans. Management of disturbances such as logging, grazing, and prescribed fire should be intermediate of those recommended for low- and high-energy areas. Human densities are often very high in these ecosystems (Balmford et al. 2001), and human activities may depress biodiversity below the biophysical potential (Gaston and Blackburn 2000). Thus protecting places that are least impacted by human land use may contribute highly to conservation. Where human activities are depressing biodiversity below the natural potential, public education and restoration efforts may be especially effective.

Our analysis was done across North America to identify the subcontinental areas with increasing, flat, or decreasing species–energy relationships to allow conservation strategies to be tailored to regional conditions. For conservation applications at the scale of large watersheds or ecoregions, we recommend that regional species–energy analyses be conducted using the methods described in this paper. We have done so across the Greater Yellowstone Ecosystem, USA, and mapped bird species richness at a 1-km grain size, explaining 70% of the variation in "hold-back" data sets (Jones et al. 2009). This finer scale approach can be used to identify local hotspots for species richness and as a basis for guiding local land use (Gude et al. 2007).

For analyses done at regional levels, the effects of human land use should be considered. The biophysical potential for supporting species richness (e.g., based on energy) is likely altered by more intense land uses. Knowledge of both biophysical potential and modifications due to land use provide a sound basis for developing local management strategies.

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