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Erratum

Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production

Linda B. Phillips [a,*], Andrew J. Hansen [a], Curtis H. Flather [b,1]

[a] Department of Ecology, Landscape Biodiversity Lab, Montana State University, Bozeman, MT 59717, United States
[b] USDA Forest Service, Rocky Mountain Research Station, Natural Resource Research Center, 2150-A Centre Avenue, Fort Collins, CO 80526-2098, United States

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ABSTRACT

Ecosystem energy has been shown to be a strong correlate with biological diversity at continental scales. Early efforts to characterize this association used the normalized difference vegetation index (NDVI) to represent ecosystem energy. While this spectral vegetation index covaries with measures of ecosystem energy such as net primary production, the covariation is known to degrade in areas of very low vegetation or in areas of dense forest. Two of the new vegetation products from the MODIS sensor, derived by integrating spectral reflectance, climate data, and land cover, are thought to better approximate primary productivity than NDVI. In this study, we determine if the new MODIS derived measures of primary production, gross primary productivity (GPP) and net primary productivity (NPP) better explain variation in bird richness than historically used NDVI. Moreover, we evaluate if the two productivity measures covary more strongly with bird diversity in those vegetation conditions where limitations of NDVI are well recognized.

Biodiversity was represented as native landbird species richness derived from the North American Breeding Bird Survey. Analyses included correlation analyses among predictor variables, and univariate regression analyses between each predictor variable and bird species richness. Analyses were done at two levels: for all BBS routes across natural landscapes in North America; and for routes in 10 vegetation classes stratified by vegetated cover along a gradient from bare ground to herbaceous cover to tree cover. We found that NDVI, GPP and NPP were highly correlated and explained similar variation in bird species richness when analyzed for all samples across North America. However, when samples were stratified by vegetated cover, strength of correlation between NDVI and both productivity measures was low for samples with bare ground and for dense forest. The NDVI also explained substantially less variation in bird species richness than the primary production in areas with more bare ground and in areas of dense forest. We conclude that MODIS productivity measures have higher utility in studies of the relationship of species richness and productivity and that MODIS GPP and NPP improve on NDVI, especially for studies with large variation in vegetated cover and density.

1. Introduction

Early biogeographers observed that the primary pattern in global biodiversity is a reduction in the number of species from the tropics to the poles (Fisher 1961; MacArthur 1972). Since then, numerous hypotheses have been proposed to explain the spatial patterns of species richness. While there is likely no single factor that explains species richness patterns, there is growing consensus that latitude is a surrogate and that much of the pattern can be explained by some measure of available energy (Wright, 1983; Gaston, 2000; Pimm & Brown, 2004). Many possible mechanisms have been proposed to explain how ecosystem energy might constrain species diversity (Willig et al 2003; Evans et al., 2005), including that energy influences rates of evolution (Rohde, 1997; Allen et al., 2002; Rohde, 1992; Evans and Gaston, 2005b; Hawkins et al., 2007), or that energy influences thermoregulatory load (Turner et al., 1987), or that energy limits the number of individuals in a population and thus influences extinction rates (Wright, 1983). Uncertainty in the precise causal mechanism of the species energy relationship and lack of continental-scale energy data has lead to uncertainty in how to best represent available energy.

Initial studies of species energy relationships used a number of climate variables to represent energy, including potential and actual evapotranspiration (Currie, 1991; Kerr, 2001; Hawkins, Porter, & Diniz-Fahlo, 2003), ambient temperature (Turner et al., 1987; Acevedo and Currie, 2003), precipitation (Van Rensburg et al., 2002; Chown et al., 2003), and water-energy balance (Hawkins, Field, et al., 2003). Spatially continuous energy data was usually generated by collecting empirical data and interpolating between points to create contour lines that represented a continuous surface (Currie and Paquin, 1987). Collectively, these studies found significant relationships between climate variables

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[*] Corresponding author. Tel.: +1 406 994 1614.
E-mail address: lphillips@montana.edu (L.B. Phillips).

[1] Tel.: +1 970 295 5021.

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and biodiversity. However, because the casual mechanism was not understood, these studies raised questions as to whether more complete measures of ecosystem energy, such as primary production, would better explain patterns of diversity (Hawkins, 2004).

In the last few decades, the utility of remote sensing technology to map ecosystem energy has increased substantially (Turner et al., 2003). Vegetation indices, such as the normalized difference vegetation index (NDVI), a strong correlate with photosynthesis and biomass, historically have been used as a surrogate for ecosystem productivity or general ecosystem energy. A new suite of satellite products have recently been developed that are thought to improve on NDVI by quantifying ecosystem primary production. These satellite-derived products use simulation models parameterized with spectral, climate, and land use data to estimate primary productivity, vegetation duration, and biomass (Running, 2002). The purpose of this paper is to evaluate the merits of the two productivity measures in the suite, GPP and NPP in predicting avian diversity compared to historically used NDVI.

1.1. Initial satellite-based measures of energy

Early use of satellite spectral data to generate measures of ecosystem energy focused prominently on NDVI. Mechanically, NDVI is a spectral transformation that describes the reaction of two electromagnetic bands (i.e., the absorption of the red and the reflectance of the near-infrared) to healthy green photosynthesizing vegetation. Functionally, the ratio of these bands has been found to covary with a number of vegetation characteristics including the fraction of photosynthetically active radiation (fPar) (Dye and Goward, 1993; Sellers et al., 1994), leaf area index (LAI) (Shabanov et al., 2005) and total green biomass (Chong et al., 1993; Sellers et al., 1994).

Many species energy studies used NDVI generated from the Advanced High Resolution Radiometer (AHVRR) to represent primary production, photosynthesis, ecosystem energy (Paruelo et al., 1997; Fraser, 1998; Baily et al., 2004; Evans et al., 2006) and NDVI has shown to be a strong correlate with biodiversity of many taxonomic groups (Whiteside & Harmsworth, 1967; Abramsky & Rosenzweig, 1984; Owen, 1988; Hoffman et al., 1994; Kerr & Packer, 1999; Hawkins, Porter, et al., 2003; Hawkins et al., 2005) in many geographic regions, and at many spatial scales. In our review, comparable studies of AVHRR NDVI and breeding bird species richness found statistically significant relationships with a wide range in variation explained (14–51%) (Currie, 1991; Hurlbert & Haskell, 2003; Evans & Gaston, 2005a).

The creation of NDVI revolutionized our ability to detect subtle differences in vegetation canopy and has been used extensively in many disciplines (Kerr & Ostrovsky, 2003). While NDVI is a useful measure of many vegetation properties and has many worthwhile applications, there are important limitations to using it as a surrogate for ecosystem energy across all vegetated surfaces (Goward et al., 1991). NDVI was developed to recognize subtle differences in agricultural field crops (Rouse et al., 1973) and yet has been applied across the gradient in vegetation cover from bare ground to dense grasslands and forests. It is well recognized that NDVI would be less accurate at representing productivity in places with some bare soil or dense vegetation (Huete, 1988). As the fraction of vegetation cover drops from 100% to 0%, NDVI becomes increasingly sensitive to soil properties (i.e., backscatter) and less representative of vegetation characteristics (Richardson & Wiegand, 1977; Gao et al., 2000). In dense vegetation, NDVI is unable to detect differences in vegetation canopy at the upper portion of NDVI values due to saturation effects (Box et al., 1989). Backscatter and saturation, and other forms of systematic error (Kerr & Ostrovsky, 2003), motivated remote sensing scientists to seek methods to better represent vegetation productivity across the gradient in vegetation cover.

1.2. Latest generation of satellite-based energy measures

In 1999, the Terra satellite, supporting the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor, was launched to provide advances in capturing properties of the land surface including more comprehensive measures of vegetation production, vegetation duration, and vegetated cover (Running et al., 2004). The MODIS sensor is one of the few sensors with improved atmospheric correction and cloud screening (Cohen & Justice, 1999). The two MODIS datasets designed to represent primary production, GPP and NPP, are derived from the same spectral bands as NDVI, but they also incorporate information on land cover, climate, and vegetation characteristics to derive measures of above-ground gross and net primary production. The vegetation continuous fields (VCF) measures percent of plant lifeform at subpixel resolution and is intended to provide a continuous gradient from bare ground to forested cover, as an alternative to categorical land cover classifications (Hansen et al., 2003). An additional vegetation index is also included in the MODIS suite of products. The Enhanced Vegetation Index (EVI) is a slight derivation from NDVI as it includes one additional spectral band, but no other peripheral data. All of these products, NPP, GPP, VCF and EVI are designed to improve on NDVI by addressing the noted weaknesses in NDVI attributed to backscatter and saturation.

1.3. Ecosystem energy and bird species richness

Given the limitations inherent with NDVI, we predict that MODIS GPP and NPP more accurately represent actual primary production and will therefore have a stronger relationship with bird biodiversity in the lower and upper portions of the vegetation cover gradient (Fig. 1). Because NDVI limitations are not expected to manifest at intermediate levels of vegetation cover, we predict all measures of ecosystem energy to have similar patterns of covariation with bird diversity along the mid-domain of the vegetation gradient.

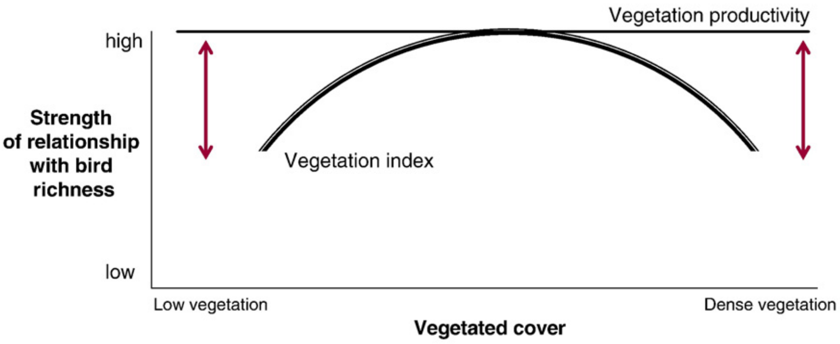

Fig. 1. Predicted relationships between bird species richness and two measures of ecosystem productivity (NDVI and MODIS productivity measures) across a gradient in vegetation cover. Due to limitations in NDVI in low vegetation (soil backscatter effects) and dense vegetation (saturation effects), we predict that the strength of the species/energy relationship between NDVI and primary production will be most different in these areas (red arrows).

Alternatively, since NDVI is the basis of the GPP and NPP algorithm, there might be significant data redundancy between the two. If there is significant data redundancy, NPP and GPP might not carry more information about ecosystem energy than NDVI, and we would expect that NDVI and the productivity measures would be highly correlated. This will limit the advantages of using productivity over NDVI for assessing species energy relationships.

Our goal for this study was to evaluate the relationship between bird richness and NDVI versus GPP and NPP products across North America. The specific questions were:

1) To what extent do GPP and NPP covary with NDVI and thus contain information redundant with NDVI?
2) Does GPP and/or NPP explain more variation in bird diversity than does NDVI?
3) Does GPP/NPP covary more strongly with bird diversity in those vegetation types where NDVI is known to have limitations (i.e., areas with high proportion of bare soil and areas with dense forest cover)?

2. Methods

Our general approach was to compare relationships between bird richness and MODIS products, NDVI, GPP and NPP, across a wide ranging gradient of vegetation cover. The goal was to determine if NPP and GPP had stronger relationships with bird species richness than the vegetation index, NDVI. To highlight if differences were a result of the NDVI limitations, the analyses were performed for all Breeding Bird Survey (BBS) routes, and then for routes in 10 classes stratified by vegetated cover across a gradient from bare ground to herbaceous cover and dense forest.

2.1. Predictor data

MODIS datasets were gathered from the Earth Observing System Data Gateway and were summarized as annual averages for the years 2000 through 2004 at a spatial resolution of 1 km. We used the 12 month average for all three predictor variables. There is not consensus on the best temporal measure of energy, as some studies have found annual measures stronger predictors (Wright 1983; Currie, 1991) and some found that seasonal measures of energy to be stronger predictors (Hurlbert & Haskell, 2003). In this study, we found that annual averages explained more variation in breeding bird species richness than breeding season averages (Phillips et al., in preparation). The NDVI is collected at 250 m spatial resolution, so we resampled NDVI to 1 km using nearest neighbor distance, to be the same spatial resolution as the 1-km resolution GPP and NPP data.

NDVI is created directly from reflective data collected from the MODIS sensor. Temporal composites are available at 16 day intervals, as best pixels (i.e. cloud free) are selected at this interval. NDVI is a normalized ratio of the near-infrared and red bands (Table 1).

The productivity products, GPP and NPP, represent above-ground productivity and were developed to represent the conversion of sunlight to organic material. GPP is created 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 adjusting the conversion efficiency estimate. This process concludes with an estimation of plant production daily, and is summarized to reflect the rate of primary production for an 8-day period (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. The NPP product 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. It is calculated by subtracting the estimated respiration costs that plants use for maintenance from the modeled GPP. Plant respiration varies with vegetation type, so LAI is used to estimate plant respiration. NPP is provided as an annual average, and is the most complex measure of energy availability of the MODIS suite of products.

Table 1
Description and details of MODIS data products used in this study

Scientific product	Spatial resolution before resampling (meters)	Method of calculation	References
Normalized difference vegetation index	250, 500, 1000	Near infrared − red/Near infrared + red	Huete et al. (2002)
Gross primary production	1000	MODIS land cover, LAI/fPar; non-MODIS min temp and VPD; estimate of PAR conversion efficiency	Running et al. (2004), Heinsch et al. (2003)
Net primary production	1000	MODIS land cover, LAI[a]/fPar[b]; non-MODIS minimum temperature and VPD[c]; estimate of PAR conversion efficiency — maintenance respiration estimates	Running et al. (2004), Heinsch et al. (2003)
Vegetation continuous fields	500	MODIS bands 1–7 to calculate proportional estimates for vegetative cover types: woody vegetation, herbaceous and bare ground	Hansen et al. (2003)
Land cover	1000	Algorithm including MODIS products: water mask, bands 1–7, EVI, snow cover, land surface temperature, VCF	Friedl et al. (2002)

[a] Leaf area index.
[b] Fraction of photosynthetically active radiation.
[c] Vapor pressure deficit.

Validation efforts for the MODIS products, including NPP and GPP measures, are complex and ongoing, and are done by comparing GPP measures at flux towers and plot-level measurement of NPP over the surrounding landscape and then 'scaling up' the results of these empirical observations to the 1-km spatial resolution (Morisette et al., 2003). Validation at nine sites distributed in a wide range of biome types globally suggests that NPP and GPP are representative of general trends in the magnitude of NPP and GPP associated with local climate and land use, but overestimate production in both low and highly productive areas (Turner et al., 2006). It is suggested that the error is a result of the 'scaling up' from fine scale data collection to the 1-km spatial resolution of the MODIS pixel.

MODIS EVI is a variation on NDVI that is collected and available at the same temporal and spatial resolution as NDVI. EVI includes a set of coefficients to increase the clarity of the vegetation signal, minimizing noise from the atmosphere and soils. EVI is intended to minimize operational noise in the vegetation signal by applying a soil background correction and an atmosphere resistance term. Both of these improvements to the EVI are intended to minimize soil backscatter and increase the signal sensitivity in high biomass regions addressing signal saturation. We briefly explore the utility of EVI in species energy relationship, yet the EVI comparison is not the focus of this paper.

2.2. Biodiversity data

Native land bird species richness (USGS Patuxent Wildlife Research Center, 2006) was derived from species count data collected by the USGS Breeding Bird Survey (BBS) (Sauer et al., 2005). BBS survey routes are 39.4 km linear routes, randomly located along secondary roads throughout the US 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-minute point counts spaced at 0.8 km intervals along the route. The survey begins in the morning, recording birds that are seen or heard within 400 m from the point stop. There are >4000 BBS routes that provide species count 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. Routes that were sampled one or more years within this time period were included. Selection criteria for routes also included consideration of land use. Land use change has been shown to influence bird diversity at landscape scales (Flather, 1996; Hansen et al., 2002; 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 more natural vegetation routes. We selected routes that were less than 50% human land use class, defined with the MODIS land cover product and the 17 classes in the International Geosphere-Biosphere Programme classification scheme (Running et al., 1994). Routes containing greater than 50% of cells with land use classified as urban and built-up, cropland/natural vegetation mosaic, and cropland classes were excluded.

We excluded aquatic, exotic, raptor, and nocturnal 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 5 km of the coast because they are dominated by aquatic species. 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 & Sauer, 1998). Primary among these with regards to species richness are the roadside location of survey routes. Potential biases of the roadside survey are that habitats along roads are not representative all habitats across the study area and that particular bird species avoid or are attracted to roads. Despite this roadside bias, 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 the 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 use 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 estimates for each year that a route was run 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 predictor value. This summary across routes provided a species richness average associated with an predictor variable average for each BBS route, such that each route was considered a sample.

2.3. Assigning routes to classes of vegetation lifeform cover

Routes were assigned to vegetation classes based on percent vegetated cover by lifeform (bare, herbaceous, tree) from the MODIS VCF product (Hansen et al., 2003). The spatial resolution of these data was originally 500 m and was resampled, using the nearest neighbor transformation, to 1-km to be compatible with the other predictor datasets.

VCF is calculated using the red, near-infrared, and blue bands of the electromagnetic spectrum, and is intended to represent land cover as a continuous variable rather than classified as a limited number of land cover classes (Hansen et al., 2003). Each VCF pixel represents the percentage of the pixel (0–100%) occupied bare ground, herbaceous vegetation, and woody vegetation, as three discrete continuous variables (Schwarz et al., 2002). The accuracy of this layer has been evaluated in some areas using both field collected data and finer-

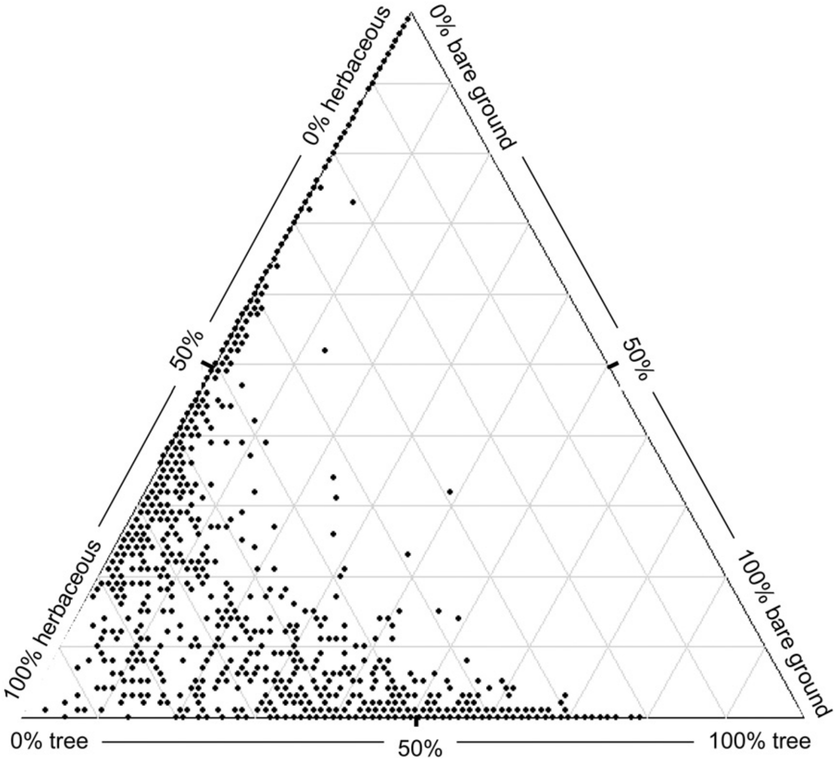

Fig. 2. Routes were classified across a 3-dimensional vegetation cover gradient, ranging from bare ground to herbaceous cover to tree cover. Routes consisting of cells with combinations of bare/herbaceous and herbaceous/tree were common. Routes with combinations of bare/tree did not exist (note bare/tree axis).

resolution satellite imagery and has shown mixed results. In the semi-arid southwest US region, VCF is shown in two separate studies to have a negative bias in estimating vegetated cover, with increasing underestimation of cover as vegetation increased (White et al., 2005), however in Britain VCF tended to overestimate tree cover (Disney & Lafont, 2004). Efforts to validate the accuracy of the VCF products are ongoing both empirical observations and finer-resolution remote sensing products (Hansen et al., 2003).

We created a three dimensional gradient with each axis representing a lifeform that enabled us to partition routes according to a vegetated surface class gradient (Fig. 2). Some routes were highly heterogeneous in vegetated cover. Our goal was to examine bird/energy relationships among BBS routes that were relatively homogeneous in vegetated cover along the route. Thus, we excluded routes that had a standard deviation of vegetated cover greater than 70% of maximum standard deviation for all routes.

The average values for vegetated cover along routes ranged from 0–100% bare, 0–93% herbaceous and 0–76% tree cover. Routes were classified into 10 life form classes with class definition varying slightly to insure adequate sample sizes. The minimum sample size per class was 46 routes and the maximum was 258 routes. We recognize that this is a large difference in sample sizes, however our focus was not on comparing models across vegetation cover classes, but rather on the explanatory power of predictors within cover classes. Thus unequal sample sizes across the vegetation cover gradient did not affect our evaluation of ecosystem energy measures.

When classifying the routes across the vegetated gradient of VCF, routes that were characterized by bare ground and herbaceous cover occurred more frequently ($n=1038$) than routes that were dominated by herbaceous and tree cover ($n=484$). Routes that were dominated by combinations of tree cover and bare ground did not occur, as non-vegetated lands and forest do not naturally occur within the size of a pixel. Analysis was therefore confined to the bare to herbaceous gradient and herbaceous to tree gradient.

2.4. Statistical analyses

To determine the degree of correlation and redundancy between NDVI, GPP and NPP (Objective 1), we examined the degree of correlation between the variables across all routes. The correlation coefficient will indicate similarity and the potential for the productivity measures to provide information regarding the richness–productivity relationship beyond NDVI. The degree of correlation between GPP, NPP, and NDVI, was subjectively compared using Pearson's correlation coefficient.

To determine if GPP and NPP provided more explanatory power than NDVI (Objective 2), bird species richness was regressed individually against the three predictor variables. Linear regression models were developed, using both linear and polynomial functions, and coefficient of determination, and statistical significance were reported.

To test the limitations of the NDVI across the vegetated surface gradient (Objective 3), correlation analyses and regression analyses were performed for routes in each of the 10 classes, stratified by the vegetated surface. The degree of correlation and best regression models were determined for each vegetated surface class with the same process and statistics previously described for the analysis of all routes.

Akaike's Information Criterion (AIC) was the primary criterion for determining best models (see Burnham & Anderson, 1998). AIC provides an estimate of the distance between the specified model and some full truth or reality. “Best” models are those that best approximate the true

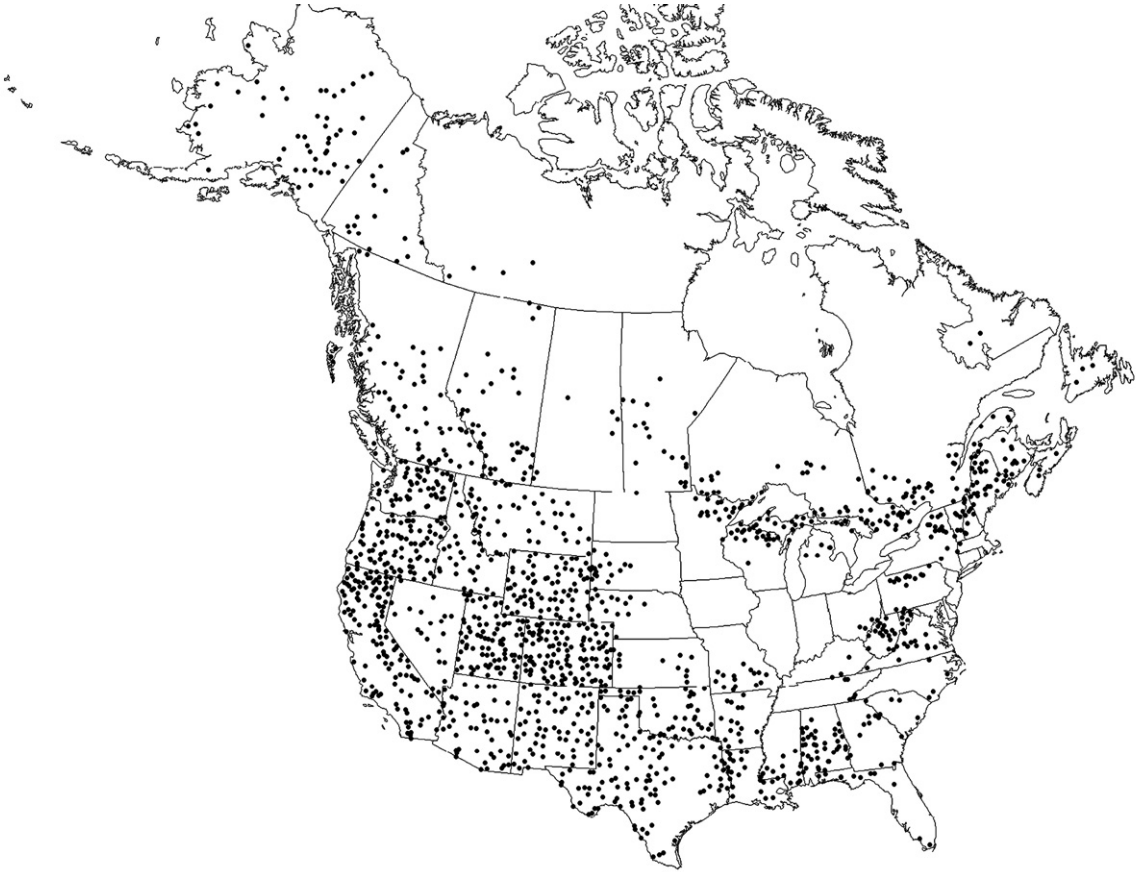

Fig. 3. The 1390 Breeding bird survey routes that were included in the analysis were distributed across North America.

model in a parsimonious manner. Thus AIC is useful for selecting from among several competing models. 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 how much variation in the response variables was explained by the best model.

Regression techniques assume that residuals (error terms) are independent, normally distributed, and with constant variance. Semi-variograms were used to look for spatial dependence, but showed little increase with distance (Pinheiro & Bates 2000). The lack of relationship indicates 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). Spatial correlation occurred at a scale finer than was measured with these data, or has been removed though use of these predictors. We inspected the normality of the residuals of the best models using and found the Normal Q–Q plots provided support for normality for species richness. Homogeneity of variance was confirmed with spread-location plots, which showed no trend in the absolute residuals over the fitted values. Statistical significance was assumed for tests with P values of <0.01.

Table 2

Statistical output for comparison of linear and polynomial univariate models of bird richness and the four MODIS predictor variables

Variable	Model	Adjusted r^2	AIC	ΔAIC	Model equation
NDVI	Linear	0.395	−1149.10	331.53	$1.35+0.69(X)$
NDVI	Polynomial	0.510	−1458.71	21.92	$0.99+2.71(X)-2.29(X^2)$
EVI	Linear	0.378	−1109.66	370.97	$1.34+1.29(X)$
EVI	Polynomial	0.492	−1389.97	90.66	$0.92+5.41(X)-8.40(X^2)$
GPP	Linear	0.363	−1077.33	403.30	$1.44+0.02(X)$
GPP	Polynomial	0.524	−1480.63	0.00	$1.22+0.098(X)-0.004(X^2)$
NPP	Linear	0.358	−1065.21	415.42	$1.39+0.05(X)$
NPP	Polynomial	0.504	−1424.80	55.83	$1.11+0.19(X)-0.01(X^2)$

3. Results

Of the 3476 total routes that had adequate richness data, a subset of 1390 routes met our criteria for analysis (Fig. 3). These routes were sampled for one or more years, contained less than 50% of cells classified as human-dominated land uses, were greater than 5-km from the coast, and cells constituted less than 70% of maximum standard deviation in VCF.

3.1. Objective 1: strength of correlation among predictor variables

When all 1390 routes are analyzed together, NDVI, GPP and NPP were all highly correlated. GPP and NPP were more strongly correlated with each other ($r=0.948$) than NDVI was with GPP ($r=0.946$) or slightly less, NPP ($r=0.914$). Scatterplots of the three variables showed that correlation was not consistent across all values (Fig. 4). The correlation between NDVI and GPP indicated a curvilinear relationship such that the correlation was less at the lower and higher values. This pattern would occur if NDVI was underestimating production in low and high values, or if GPP was estimating production in these values (Fig. 4, middle). The scatter of NDVI on NPP showed strong correlation in the lower values of each with increasing scatter as both NDVI and NPP values increased (Fig. 4, top). Interestingly, GPP and NPP were highly correlated in lower values, and increasingly less correlated as

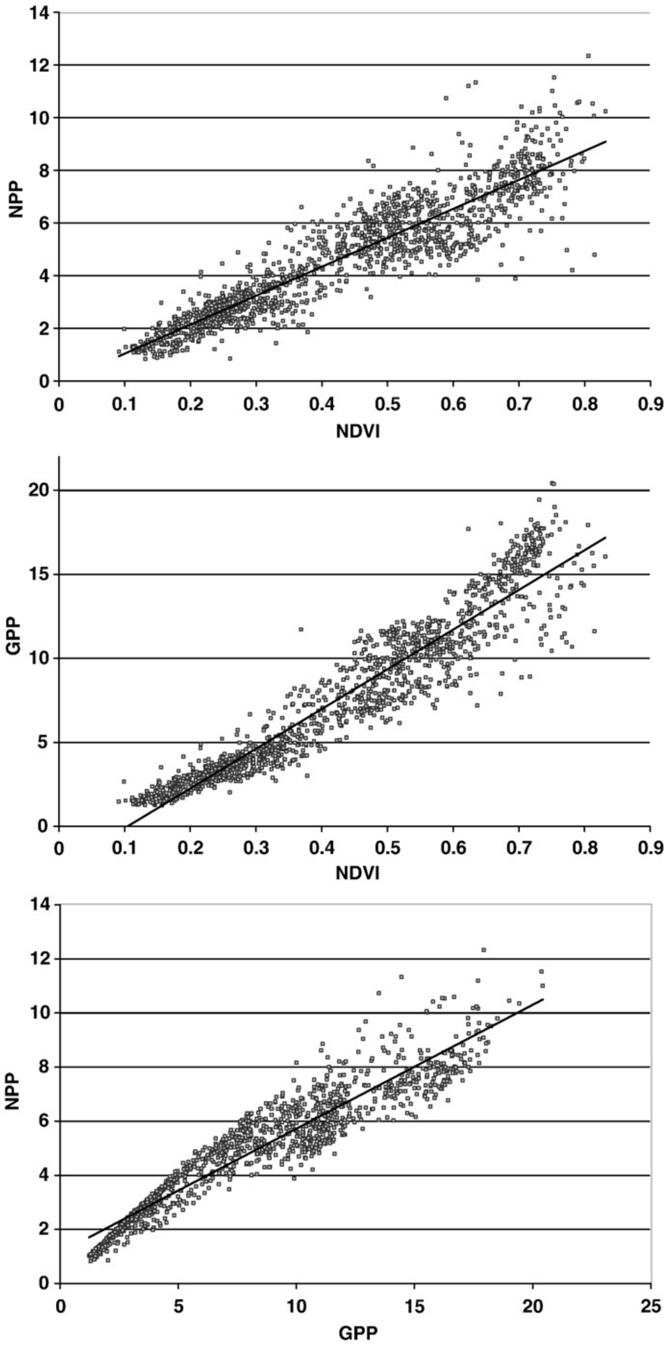

Fig. 4. Scatterplots showing the correlation between, NDVI/NPP and NDVI/GPP, and NPP/GPP (respectively from top to bottom).

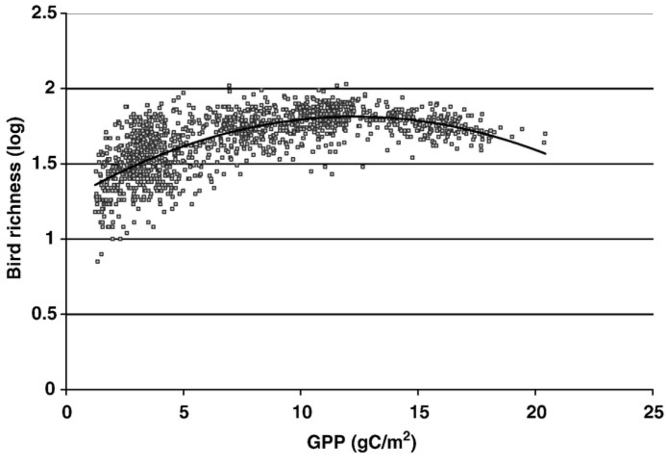

Fig. 5. Scatterplot and predicted quadratic line, showing the unimodal relationship between bird richness and GPP.

Table 3
Vegetation class number, class description, percent of each lifeform, sample size, and coefficient of determination (R^2) of the regression relationship between bird richness and each MODIS predictor variable, NDVI, GPP and NPP

Vegetated surface class	Vegetated surface description	Percent of cover	N	NDVI (R^2)	GPP (R^2)	NPP (R^2)
		%bare/%herbaceous/%tree				
1	Dominant bare ground	80–100/0–20/0–10	46	0.02	0.12	0.10
2	Bare/herbaceous	60–80/20–40/0–10	69	0.10	0.13	0.11
3	Herbaceous/bare	30–60/40–60/0–10	141	0.6	0.13	0.10
4	Herbaceous/bare	20–40/60–80/0–10	258	0.03	0.03	0.01
5	Dominant herbaceous	0–20/80–100/0–10	73	0.38	0.36	0.37
6	Dominant herbaceous	0–10/70–90/10–30	110	0.34	0.37	0.39
7	Herbaceous/tree	0–10/50–70/30–40	112	0.36	0.44	0.39
8	Herbaceous/tree	0–10/40–60/40–50	159	0.30	0.40	0.36
9	Tree/herbaceous	0–10/30–50/50–60	221	0.16	0.31	0.15
10	Dominant tree	0–10/30–40/60–70	201	0.11	0.24	0.05

values increased (Fig. 4, bottom). A systematic lack of correlation was also apparent in the lower values.

3.2. Objective 2: relationships between predictors and bird species richness

The regression analysis indicated that across all BBS routes the quadratic models for all variables were better than linear models (based on AIC). This pattern indicates that species richness increased with increasing values, then either flattens or decreases for middle and upper values, creating either a unimodal or positive decelerating relationship. The coefficient of determination did not differ greatly among the variables, however GPP had the strongest relationship with bird richness across all routes (R^2=0.52), with NDVI (R^2=0.51) and NPP (R^2=0.50) slightly less (Table 2 and Fig. 5).

3.3. Objective 3: variation in correlation and strength of relationship across vegetation classes

When routes were stratified across the vegetation cover gradient, there were substantial differences in the correlation and strength of the relationship between bird richness, NDVI and the productivity variables (Table 3).

NDVI was highly correlated with both GPP and NPP in herbaceous cover classes. However, in vegetation classes characterized by sparse and dense vegetated cover, NDVI and both GPP and NPP showed substantial lack of correlation, especially in classes characterized with partial bare ground cover (Fig. 6, lines and right axis). NPP was least correlated with NDVI in the three classes with least vegetated cover (r=0.14, 0.59, 0.63 respectively) and the most dense vegetated tree cover (r=0.73 and r=0.67 respectively). Interestingly, the two productivity measures, GPP and NPP, were highly correlated for all classes, with a pattern of slightly decreasing correlation as vegetated cover increased. NDVI and EVI were highly correlated for all classes and were slightly less correlated in the two classes dominated with bare ground and tree cover being (r=0.82 and r=0.72 respectively).

All three predictor variables showed similar trends in variation in the strength of the bird richness relationship when considering all 10 vegetated cover classes (Fig. 6, bars and left axis). The general trend was that all predictors explained more variation in the herbaceous classes, less in the lightly vegetated classes and large variation in the forested classes. However, as mentioned earlier, the coefficients of determination are not directly comparable among vegetation cover classes because of differences between classes in the ranges of variation in the predictor and response data and in the sample sizes. The explanatory power in the four vegetation classes that are characterized with bare ground and little herbaceous cover, showed a generally weak relationship with all predictors, ranging from R^2=0.02–0.0.13. Vegetation classes that were characterized by

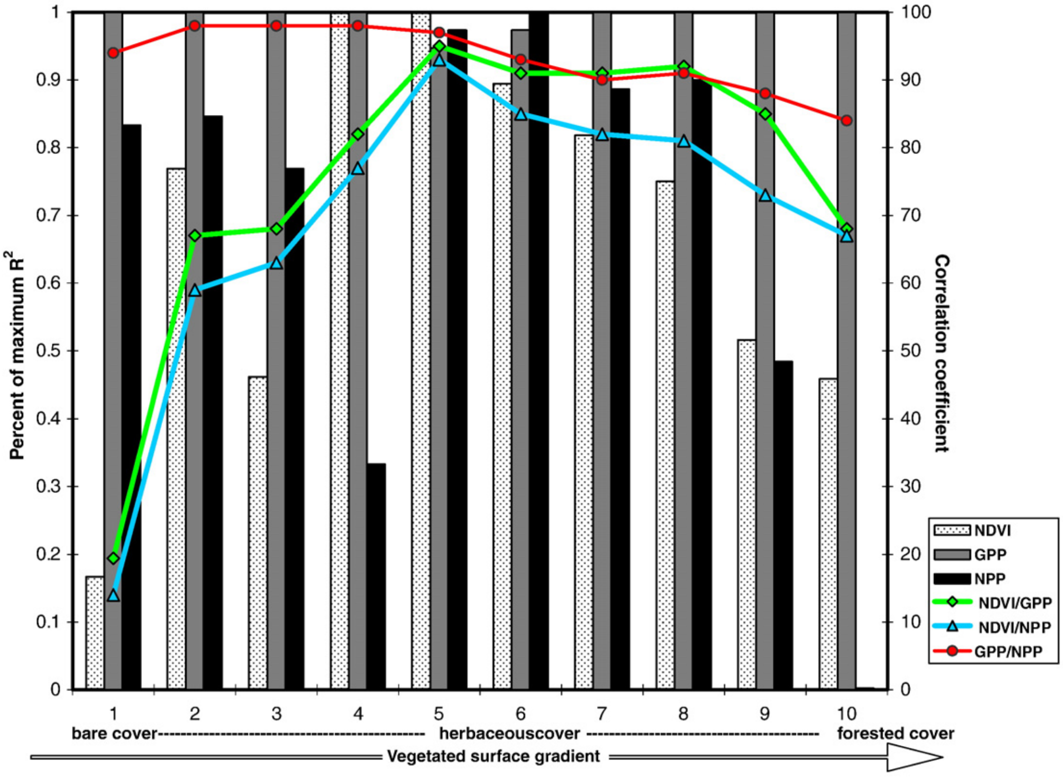

Fig. 6. NDVI and productivity are less correlated in bare ground and forested cover (line graph and right axis), and productivity is a stronger predictor of bird richness in these areas (bar graph and left axis). The bars in the histogram represent the percent of maximum coefficient of determination between bird richness and NDVI, GPP and NPP for the 10 vegetation classes (left axis). The line graph represents Pearson's correlation coefficient for NDVI/GPP, NDVI/NPP, and GPP/NPP.

dominant herbaceous cover had a stronger relationship with all four variables, ranging from R^2=0.28–0.43. Vegetation classes that had increasing tree cover were more variable in explanatory power, but all three predictor variables had a weaker relationship in these classes than the herbaceous dominated classes, and a stronger relationship than the bare ground/little herbaceous cover classes.

When we looked *within* each of the 10 vegetated cover classes and compared NDVI, GPP and NPP, there were substantial differences in strength of relationship with bird species richness (Fig. 6).

3.3.1. Bare ground to light herbaceous cover

In classes 1–3, characterized by bare ground and little herbaceous cover, both NPP and GPP had a stronger relationship with richness than with NDVI. GPP explained an average of 12.6%, NPP an average of 10.3%, and NDVI 6% in these three bare/herbaceous classes. In vegetation class 4, characterized by routes that are covered in slightly more herbaceous cover than bare ground, NDVI and GPP have equal strength, with NPP much weaker.

3.3.2. Herbaceous cover

In the vegetation classes 5 and 6, characterized by the highest amount of herbaceous (70–100% herbaceous) vegetation, NPP and NDVI had the strongest relationships, 38% and 36% respectively. These were the only two classes that GPP did not have the strongest relationship with richness. In vegetation classes 7 and 8, characterized by herbaceous cover and increasing tree cover, there was great variability in strength of relationship with each dataset. GPP was strongest in class 7, and NDVI was weakest in both of these classes. Vegetation class 7 additionally had the strongest relationship with GPP (R^2=0.44) than any other predictor variable in any other vegetation class. GPP explained 8% more than NDVI in this class.

3.3.3. Forest cover

The three most heavily vegetated classes, characterized by increasingly dominant tree cover and decreasing herbaceous vegetation (classes 8, 9 and 10), were highly variable in explanatory power among the three predictor variables. GPP was the strongest predictor in all three of these classes, ranging from 10 to 15% greater than NDVI. In the two most heavily forested vegetation classes (classes 9 and 10), GPP was consistently high, and NPP varied widely. NDVI was less than half of the explanatory power of GPP. NPP also explained less than half than GPP in vegetation class 9 and in the most heavily forested class had a negligible relationship with bird richness. These top two forested classes had the greatest absolute difference in explanatory power between the productivity product GPP and NDVI.

4. Discussion

The goal of this study was to evaluate if the new generation of satellite-derived measures of ecosystem productivity are more strongly correlated with bird species richness than the historically used NDVI. We found that NDVI and productivity measures were highly correlated across all BBS routes but showed large variations in degree of correlation when routes were stratified by vegetation cover class. Additionally, NDVI and the productivity measures were relatively similar in strength of regression relationship with bird richness across all routes, but showed large variations in relationship strength when routes were stratified by vegetation cover class. In areas of sparse and dense vegetation, where we suspected NDVI would be least representative of productivity, NPP and GPP substantially improved the strength of the richness–productivity relationship. The benefits of using GPP and NPP were not obvious until we accounted for the limitations of NDVI and compared correlation and strength of relationship in these areas. We conclude that MODIS productivity measures advance our ability to represent ecosystem production to address the species energy relationship at broad spatial scales.

4.1. Correlation of NDVI, GPP, and NPP among all vegetation cover classes

As we predicted, the degree of correlation between the three datasets was high.

GPP and NPP were more highly correlated than NDVI was with either. GPP is used to calculate an estimate of daily net photosynthesis (PSNnet) which is then summed across the year, for annual PSNnet. Plant costs for maintenance and growth respiration are estimated based on plant allometry, live wood mass and leaf area. The maintenance and growth expenditures are direct inputs into the NPP algorithm and are ultimately subtracted from GPP (Heinsch et al., 2003). Since GPP is the basis of the NPP calculation, we were not surprised to see a strong correlation between these datasets. However, since the algorithms used to create the GPP and NPP products are much more complex than the vegetation indices, incorporating climate, land cover and leaf area index information, error propagation through the modeling is likely.

Finally, there was strong correlation between the NDVI/GPP and NDVI/NPP. NDVI was nearly as highly correlated with GPP (r=0.94) and NPP (r=0.914) as with previously discussed EVI (0.964). When looking at the correlation across values, the scatterplots showed that in lower values NDVI was more strongly correlated with GPP and NPP in lower values was decreasingly correlated as values increased. Additionally, the correlation relationship between NDVI and GPP appeared to be somewhat curvilinear, such that NDVI underestimated production in the upper and lower values (Fig. 4, bottom). We suspected that the lower values contain pixels of bare ground and backscatter effects result in NDVI underestimating productivity here. In the upper values, we suspect that NDVI has saturated and it no longer sensitive to the subtle differences in vegetation canopy, and is not accounting for production under the forest canopy making GPP a better estimate of productivity in these denser forests.

Although EVI is not the focus of this paper, we noted that NDVI and EVI were the most highly correlated among the products and were highly correlated across all vegetation classes. This was expected because NDVI and EVI are the most similar in being derived entirely from spectral data. Unlike NDVI that is calculated as the ratio of the difference of the red and infrared electromagnetic bands, EVI additionally incorporates the blue band to address the backscatter and saturation limitations of NDVI (Huete et al., 2002). The addition of the blue band is designed to de-couple the atmosphere from the vegetation signal to gain more sensitivity to vegetation structural properties than to chlorophyll, resulting in a wider range of variation in denser forests. We predicted that this would result in less correlation with NDVI in the upper and in the lower values which could indicate that EVI is more sensitive than NDVI to vegetation in pixels with the combination of herbaceous cover and bare ground, that NDVI has not recognized as vegetation.

In previous work, EVI has been shown to be more sensitive to biophysical vegetation properties by reducing the saturation effects in dense vegetation that are common with other indices (Jiang et al., 2007). At high values, there was far less correlation between the two variables. This suggests that EVI has promise for greater sensitivity in the dense vegetation values that NDVI normally saturates. This greater spread in EVI values could represent the differentiation of subtle structural or canopy differences in the dense vegetation.

4.2. Species energy relationships across all vegetation cover classes

We found small differences in strength of relationship with bird species richness among NDVI, GPP and NPP across all vegetation cover classes. The coefficient of determination for quadratic models for the three predictor variables ranged from 0.504 to 0.524, with NPP weakest, then NDVI, and GPP strongest. Additionally, EVI had the weakest relationship of the four (R^2=0.492).

It is unclear why EVI, with its strong correlation to NDVI and improved formulation to better handle soil backscatter and canopy saturation issues (Huete et al., 2002) did not have at least as strong a relationship to bird species richness than NDVI. Also, contrary to expectation, NPP, which is designed to represent production of new vegetation biomass, was more weakly related to bird species richness (R^2=0.504) than GPP (R^2=0.524).

Similar to many other species energy studies at the continental spatial scale, we found that positive polynomial models have the strongest richness–energy relationships with NDVI, GPP and NPP. There is substantial lack of consensus on the nature of the species energy relationship that is demonstrated with two recent exhaustive reviews of the literature. A review conducted in 1999 found that for animals at very broad spatial scales similar to that of our study, a positive linear relationship was found more frequently, followed by a positive unimodal relationship (Waide et al., 1999). 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, unimodal was more often found. There has been heavy criticism of this review regarding inappropriate consideration of spatial scale, acceptable statistical parameters, lack of consideration of predictor variable limitations (Whittaker & Heegaard, 2003) and general experimental design flaws (Gillman and Shane, 2006). It was demonstrated (Whittaker and Heegaard, 2003) that when statistical parameters were changed slightly, or studies with flawed experimental design approaches were omitted (Gillman and Shane, 2006), that positive linear relationships were more prevalent at the broadest scales in most of the analyses in the Mittelbach et al. study. These two studies illustrate the interest and lack of consensus on the topic. For those studies that looked specifically at bird richness and productivity surrogates, again a positive linear relationship was most common, followed by a positive polynomial relationship (Waide et al., 1999). Seasonal and annual measures of energy were used for these studies (Hurlbert and Haskell 2003; Evans et al., 2005). In a similar ongoing study, we found positive and quadratic relationships with richness for all seasonal measures of energy, however these models had substantially weaker relationships than models using annual averages (Phillips et al., in preparation).

The relationships between MODIS products and bird species richness found here were stronger than in previous AVHRR-based NDVI-bird studies. The most comparable study is Hurlbert and Haskell (2003). They used monthly composites of AVHRR NDVI for at 12 month period during 1992 and 1993 and used the June average (representing the breeding season) and the annual average as predictor variables. Bird data were from the 2494 BBS routes that met data quality standards for the year 1997. They found for analyses at the spatial scale of BBS routes that the variation in bird species richness explained by June NDVI was 41% and by annual NDVI was 34%. Our findings of 50% and 53% of the variation in bird species richness explained by annual MODIS NDVI and GPP may be due to the improvements in MODIS over AVHRR data and in our methods of analysis. There have been many changes in the MODIS imagery that have likely improved the quality of data from previous sensors. AVHRR data was constrained with relatively poor spatial co-registration of images, crude atmospheric correction, calibration problems, and less-than-ideal cloud screening (Tan & Friedl, 2005). The MODIS sensor improves on the severity of these issues to increase the quality of the spectral signal. Additionally, the MODIS sensor collects a greater range of spectral signals at a higher radiometric resolution for better signal quality. The temporal resolution is also increased to global coverage every 2 days.

Also, some confounding factors may have been reduced in our analyses by using MODIS and BBS data from the same time periods, taking a 5-year average of the satellite and bird data, and excluding BBS routes with more intense land use or near coasts.

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) 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 we found the relationship was stronger. Our results are not comparable with many other NDVI-based studies (Currie, 1991; Bonn et al., 2004; Evans & Gaston, 2005a) because of differences in spatial scale of analyses, since differences in summarizing analysis unit, spatial resolution and map extent strongly influence results (Waide et al., 1999; Hawkins, Porter, et al., 2003, Evans et al., 2008).

4.3. Correlation and species energy relationships among vegetated cover classes

This study is the first to examine the richness–productivity relationship across the gradient of vegetation life forms and cover classes, and the first to compare NDVI to MODIS productivity measures. The results revealed that both the correlations among the MODIS products and their regression relationships with bird species richness varied considerably among vegetation cover classes. Importantly, in vegetation classes where NDVI and production was weakly correlated, the productivity measures were substantially stronger predictors of richness (Fig. 6).

NDVI was most weakly correlated with GPP and NPP, in the vegetation classes dominated by bare ground and was weakly correlated with GPP and NPP in the two classes with the highest tree cover than in intermediate vegetation cover classes dominated by herbaceous vegetation (lines in Fig. 6). As mentioned above, we suspect this results from the backscatter from bare soil and saturation effects in dense forest canopy that limit the ability of simple vegetation indices to adequate reflect productivity in these environments. In vegetation classes consisting of heavy bare ground, the NDVI value varied which GPP indicated little change. In vegetation classes of dense forest, the GPP values increased, while the NDVI values remained the same (Fig. 7). Both of these patterns would be found if NDVI had systematic error due to backscatter and signal saturation.

The productivity measures, especially GPP, explained considerably more variation in bird species richness than NDVI in these same classes (Table 3 and bars in Fig. 6). In bare to herbaceous classes, GPP explained 6% more variation than NDVI. In herbaceous dominated classes, GPP explained an average of 31.6% and NDVI average of 19%. Surprisingly, GPP also explained more variation in richness than NPP in 8 of the 10 classes. In the two classes that NPP was strongest, it had only 1 and 2% greater explanatory power and these were the herbaceous cover classes.

NDVI explained more variation in richness than EVI in 7 of the 10 vegetation classes. EVI was not the strongest predictor in any vegetation class, and was among the weakest in the classes characterized by dominant tree cover.

The pattern of GPP consistently explaining more variation in richness than NPP was perplexing. NPP is intended to represent organic material present in the form of vegetation. As a result we predicted that NPP would have the strongest relationship with species richness both for all routes and when stratified according to vegetative cover. We suspected that GPP would also have a strong relationship with bird richness, but would be inferior to NPP because it does not directly represent actual available energy but rather potential energy before growth and maintenance costs are considered. As discussed previously, NPP does not perform as strongly as GPP for all routes or when routes are stratified by vegetative cover.

A possible explanation for the discrepancy between GPP and NPP in explanatory power relates to error propagation resulting from the NPP algorithm being the most complex calculation of all MODIS datasets. The fact that the largest differences in explanatory power of GPP and NPP are in the heavily forested classes, suggests that there could be error in the transformation of daily PSNnet to annual NPP from an inaccurate estimation of respiration and maintenance costs for woody plants. The

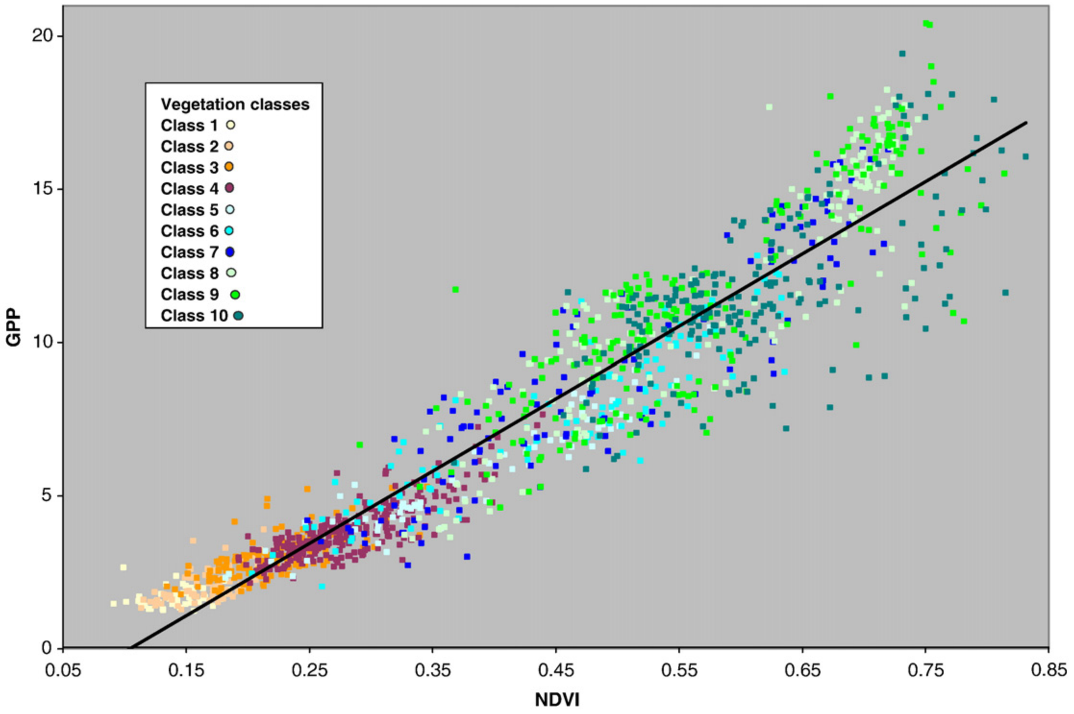

Fig. 7. Scatterplot of NDVI and GPP across the vegetated surface. The colors indicate vegetation classes, from bare ground to herbaceous cover to forested cover.

estimation of plant respiration has been shown to vary widely with temperature, species, and lifeform. If respiration costs were over or underestimated, we could see the largest discrepancy in forests areas due to their woody content. NPP relies on estimates of LAI, land cover classification, and estimation of maintenance respiration costs of plants. Since there are so many modeled and theoretical inputs to this algorithm, there is the greatest potential for error propagation in this final dataset.

Additionally, validation of these products is difficult because of scaling issues, as empirical primary production data is not feasible across a square kilometer (Morisette et al., 2006). However, one study found that NPP and GPP provided consistent measures across many biomes, and that both overestimated production in low productivity sites and underestimated at high productivity sites (Turner et al., 2006).

These results suggest that as previous work has demonstrated, species richness has a strong relationship with available energy, and GPP is the superior measure of available energy for birds over the historically used NDVI, and MODIS NPP. This is especially true in areas where NDVI and GPP are least correlated (Fig. 6), such as in areas of little vegetated cover to herbaceous cover (classes 1–3), and areas with herbaceous to increasing tree cover (classes 8–10) (Fig. 7). The

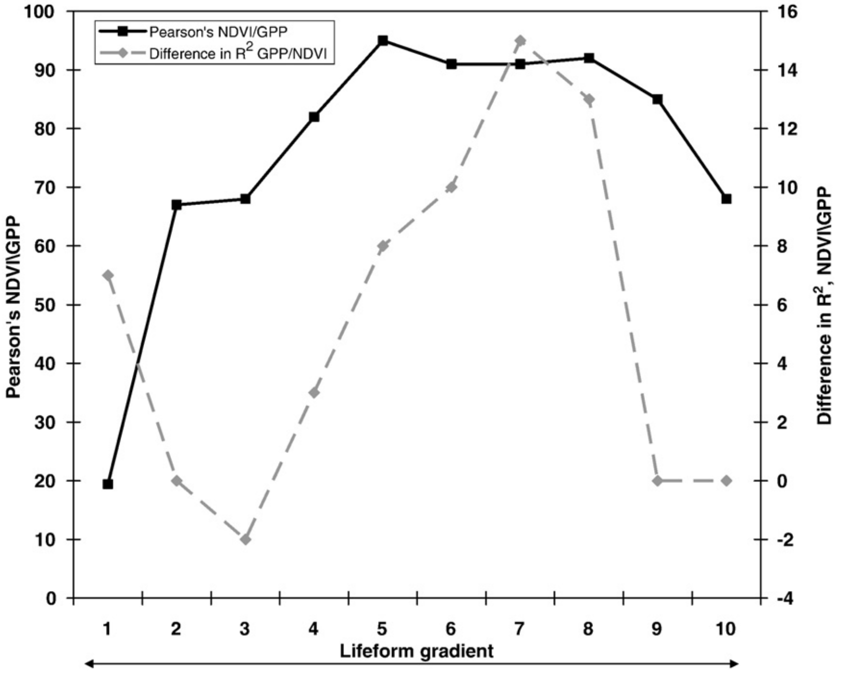

Fig. 8. GPP and NDVI were least correlated in the bare and tree portions of the vegetated gradient (left axis). GPP had greater explanatory power in these portions of the gradient (right axis).

correlation in these classes appears that NDVI underestimates productivity in these classes systematically. As we suggested in our conceptual model (Fig. 1), this analysis supports that in areas that have little vegetation cover and areas of dense forest cover, the correlation between NDVI and GPP is least and the explanatory power of GPP is greatest (Fig. 8). These results support our initial predictions, except that we expected NPP to have the greatest explanatory power.

When looking at the general regression results for NDVI, GPP and NPP across all vegetated classes, the relationship with richness was much stronger for herbaceous dominated vegetation classes 5–8, than for the classes characterized with more bare ground or with more tree cover. The coefficients of determination are not comparable between vegetation classes because regression analyses are heavily influenced by differences in the range of variation between both response and predictor variables. Fig. 6 illustrates that there is little variation in GPP in bare/herbaceous classes (1–3) and much more range of variation in GPP in herbaceous/tree vegetation (4–10) classes.

4.4. Limitations and confounding issues

This study was designed to analyze the correlations between bird richness and the predictor datasets generated from the MODIS sensor. 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 datasets cause the variations in diversity, but rather suggest 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 (Hawkins, pers comm). This difference in the range of variation of energy predictor variables among vegetation classes should be a consideration in understanding the differing results among studies of species/energy relationships.

The differences in the spatial resolution of the response and predictor data are less than ideal. The diversity data is available at the 39.2 km linear route level and the satellite predictor data is available at the 1-km resolution. The merging of these two data formats requires averaging of predictor data values for approximately 40 cells. The BBS cover a relatively large area, many habitat types and great variation in an environmental gradient, thus making the average predictor value less than ideal. We attempted to minimize this limitation by excluding routes with high variation in vegetated cover. This is more important issue for routes that are highly heterogeneous in vegetation cover/type than homogeneous routes.

This study does not allow the comparison of the strength of relationship between vegetation cover classes because the sample sizes are not equal and because regression techniques are sensitive to restricted variance. Sample sizes are not equal because of the differences in BBS geographic representation as BBS routes are much more common and dense in the more population areas of the US than the areas of lower energy and lower population (Lawler & O'Conner, 1994). Additionally, like other forms of correlation, it is not acceptable to compare correlation coefficients when samples are different in independent variables or dependent variables due to differences in variances of the variables such that some might have less variation to be explained. Phillips et al. (in prep) address the issue of differences in explanatory power.

These results only represent the relationship between the predictor datasets and the BBS collected bird richness data. Relationships with other taxonomic groups cannot be predicted since biodiversity hotspots are not the same for varying taxonomic groups (Williams et al., 1996). Additionally, richness was calculated for BBS routes that were sampled from 1 to 5 years. It would be ideal to have a larger time period that 1 year, but the MODIS data only became available in 1999 and we chose to include routes that were sampled during the same time period as the predictor data was collected.

4.5. Implications

This work indicates that the new MODIS vegetation products covary more strongly with species richness than NDVI, which may indicate that they are better representations of primary production. While many studies have previously used NDVI to look at the relationship of biodiversity measures and satellite products, none have examined the differences in the utility of using indices versus more complex products across a vegetated surface gradient. Our results indicate that using the GPP product provides stronger statistical relationships, and promote greater understanding of important species energy patterns. This is especially true in areas with low vegetated cover and dense vegetated cover. Additional work is needed to determine if the differences in relationship for all variables could be a result of error in the calculation of production in areas of less vegetation of dense vegetation.

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