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The diversity and abundance of North American bird assemblages fail to track changing productivity

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Abstract. Plant biomass or productivity and the species richness of birds are associated across a range of spatial scales. Species–energy theory is generally assumed to explain these correlations. If true, bird richness should also track productivity temporally, and there should be spatial and temporal relationships between productivity and both bird abundance and bird richness. Using the summer normalized difference vegetation index (NDVI) for 1982–2006 and the North American Breeding Bird Survey, we evaluated the response of avian richness and abundance to interannual changes in plant biomass or productivity. We found positive spatial relationships between richness and NDVI for all 25 years. Temporally, however, richness and NDVI were positively associated at 1579 survey sites and negatively associated at 1627 sites (mean $r^2 = 0.09$). Further, total abundance and NDVI were unrelated spatially (r^2 values spanning <0.01 and 0.03) and weakly related temporally (mean $r^2 = 0.10$). We found no evidence that productivity drives bird richness beyond the spatial correlations, and neither prediction arising from species–energy theory was confirmed. Spatial relationships between productivity and bird richness may thus be largely spurious, arising via covariance between plant biomass or productivity and vegetation structural complexity, and the latter may be driving bird communities. This is consistent with the MacArthur’s classic hypothesis that the vertical profile of foliage drives bird species diversity.

Key words: bird species richness; Breeding Bird Survey; climate; community richness; diversity gradients, more individuals hypothesis; NDVI; productivity hypothesis; species–energy theory; species richness.

INTRODUCTION

Positive spatial correlations between species richness and plant biomass or productivity have been well documented for birds at numerous geographic grains and extents (Wright 1983, Hawkins et al. 2003, 2007, Hurlbert and Haskell 2003, Currie et al. 2004, Hurlbert 2004, Carnicer et al. 2007, Phillips et al. 2008, Verschuyf et al. 2008, Hurlbert and Jetz 2010, Hansen et al. 2011, Morales-Castilla et al. 2012, Cumming et al. 2013, Zhang et al. 2013). More broadly, positive spatial correlations between animal species richness and measures of energy have been found across numerous geographic areas. Such associations are predicted by species–energy theory, developed as a natural extension of species–area theory by Wright (1983), who called it “a more general biogeographic theory.” Species–energy theory posits that energy per unit area explains species richness more reliably than does area alone. Wright found that the richness of flowering plants and birds (see Plate 1) was well predicted by actual evapotranspiration (AET, a climate-based proxy of primary productivity)

on 36 islands of differing size. Subsequently, species–energy theory has been implicated in at least partially explaining the global diversity gradient (e.g., Hawkins et al. 2003, Turner and Hawkins 2004, Brown 2014).

Although the spatial correlation between species richness and energy is broadly accepted, the presumed mechanisms underlying it are less clear (Hawkins et al. 2003, 2007, Turner and Hawkins 2004, Evans et al. 2005, Evans et al. 2006, Brown 2014). One mechanism is the productivity hypothesis (also known as the “more individuals” hypothesis and the “energy–richness” hypothesis). The productivity hypothesis relies on community abundance (total number of individuals) translating energy into species richness, predicting that a more productive site can support more individuals, and by accumulating more individuals, the site also accumulates more species. Species accumulation could arise either from passive sampling, whereby more individuals colonizing from the regional species pool will result in more species in the local assemblage (Hubbell 2001, Hawkins et al. 2003, Hurlbert 2004, Evans et al. 2005, White and Hurlbert 2010), or more individuals can reflect larger population sizes for many species, reducing extinction rates (Evans et al. 2006, Carnicer et al. 2007, Yee and Juliano 2007). It should be noted that under the productivity hypothesis, energy is defined by primary

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production, as this is the realized energy in an ecological system. Other definitions of energy exist within the broader context of species–energy theory, including ambient energy as measured by temperature or potential evapotranspiration.

Observational approaches have yielded mixed but largely supportive evidence for the productivity hypothesis. Currie and Paquin (1987) found that AET explained 76% of the variance in tree species richness across North America, in apparent support of the productivity hypothesis. However, Pau et al. (2012) found that although woody plant species richness in Hawaii is correlated with NDVI (normalized difference vegetation index, another commonly used proxy of primary production), structural equation modeling showed no direct effect of NDVI on richness. The direct causal relationships within their model were with precipitation and vegetation structure, both of which covary with NDVI. This suggests that relationships between species richness and primary productivity are not always causal, but rather the result of colinearity with other variables. Given that this was a study of tree richness, it is unclear how transferable the results are to other taxonomic groups. Across an altitudinal gradient in Spain, Carnicer et al. (2007) found that the predictions of the productivity hypothesis for bird species richness were supported in low-productivity areas, but in high-productivity areas, species richness was not correlated with community size or productivity measures.

Some observational studies have explored the effects of seasonal fluctuations in primary productivity on birds. In both the breeding season and winter, the spatial relationship between bird species richness and primary productivity is virtually unchanged (H-Acevedo and Currie 2003, Hurlbert and Haskell 2003), such that the spatial pattern in each season can be described by the same linear fit (White et al. 2010). The seasonal persistence of this spatial association between bird species richness and primary productivity cannot be attributed to individual species' range shifts, as evidenced by migratory species inhabiting different environmental space in the breeding season than they do in winter, lending support to what Boucher-Lalonde et al. (2014) term "top-down" hypotheses including species–area theory. Indeed, the migratory behavior of so many species of birds is likely to be driven by the seasonal fluctuation of productivity and food resources (Gill 2007, Newton 2008). These seasonal studies have consistently identified positive spatial relationships between species richness and primary productivity across seasons, in apparent support of the productivity hypothesis.

Experimental support for the productivity hypothesis is similarly mixed. For example, by manipulating productivity in tree holes colonized by aquatic insects, Srivastava and Lawton (1998) found that the predictions of the productivity hypothesis were supported when

reducing productivity, but not when increasing it. Further, by manipulating productivity, they successfully increased richness, but not the total abundance of individuals, in contrast to expectations under the productivity hypothesis. McGlynn et al. (2010) also failed to confirm the predictions of the productivity hypothesis when manipulating resource abundance for tropical rain forest litter ants. When they reduced productivity by removing resources, richness increased compared to the control, rather than decreasing as predicted. When resources were added, richness also increased, but more than that explained by increased abundance. In contrast, Yee and Juliano (2007) found support for the productivity hypothesis in tree hole microcosm experiments wherein they added or removed detritus.

The current evidence thus indicates that although observational studies appear to confirm predictions of the productivity hypothesis using spatial correlations, experimental work often fails to support those predictions. The obvious advantage of experimental approaches is the ability to measure temporal effects directly, but they are typically restricted to small spatial extents and quickly responding organisms. In direct contrast, limited data availability through time on richness and productivity has forced broadscale macroecological studies to use a space-for-time substitution. Contemporary climate change, however, is providing a natural experiment in which to test the effects of changing plant productivity on species richness across broad scales.

Net primary production is changing globally as a result of rapidly changing global climate (Nemani et al. 2003). If the relationship between bird richness and primary productivity is causal, we expect to see changes in richness as productivity shifts in response to climate change. To date, most tests of the productivity hypothesis as an explanation for bird species richness have been based on the spatial relationship between richness and biomass or productivity, using a space-for-time substitution to infer that bird community size and structure are driven by productivity in time. Although it appears true that substituting space for time is a viable assumption in many cases for predicting climate change effects on biodiversity (Blois and Williams 2013), some doubt has been raised over the reliability of this substitution for all taxonomic groups responding to contemporary climate change (La Sorte et al. 2009). To our knowledge, no workers have explored interannual variation in NDVI to confirm the validity of space-for-time substitutions in explaining species richness. For better or worse, climate has changed enough in the last 30 years that we can begin to analyze temporal relationships explicitly.

In this paper we use the North American Breeding Bird Survey (BBS) data to analyze interannual temporal changes in bird species richness and total bird abundance with respect to changes in plant biomass or productivity across the United States and Canada. If the

known spatial relationship is causal, we expect to see similar relationships temporally. The specific prediction we test is, if plant biomass or productivity drives bird species richness through increased resources, then as vegetation biomass or productivity fluctuates temporally, richness and abundance should rise and fall accordingly.

MATERIALS AND METHODS

We used bird data from the BBS (*available online*)⁵ and normalized difference vegetation index (NDVI) data from NASA AVHRR for 1982–2006 (*available online*).⁶ The BBS is an annual volunteer bird count conducted across the United States and Canada during the height of the bird breeding season, typically in June. Volunteers travel along 39.4-km survey routes, stopping at 0.8-km intervals to conduct a 3-min timed bird count within a 400 m radius based on sight and sound identification of individuals. We used these survey data to compile species richness and total abundance summed across species at each route for each year. We excluded marine, nocturnal, and exotic species and accidental sightings. The frequency with which a BBS route is surveyed depends on volunteer availability, so some routes are not surveyed every year. Many sites have also been added or abandoned since the survey began. We excluded routes that were surveyed fewer than eight years between 1982 and 2006, leaving 3207 routes used in the analysis.

We used NDVI data for 1982–2006 to approximate breeding season plant productivity each year. NDVI, a measure of “greenness,” is commonly used as a proxy for primary productivity (Hawkins 2004, Phillips et al. 2008, Buono et al. 2010, Pau et al. 2012, Siefert et al. 2013, Stegen et al. 2013) and is known to correlate spatially with North American bird species richness in both summer and winter (Hurlbert and Haskell 2003). NDVI ranges from 0 (bare ground) to 1 (saturated greenness); AVHRR data are *available online*.⁷ The time span included in this analysis was limited by availability of historical NDVI data for North America. Because summer NDVI is a stronger predictor of summer avian diversity than annual NDVI in North America (Hawkins 2004), we averaged bimonthly NDVI data sets of 8-km resolution for June, July, and August.

ArcGIS 10.0 was used for data processing and spatial analysis. BBS routes were reduced in dimension to their midpoint and were represented in the analysis as vector point data. At the coordinates of each BBS point, NDVI was extracted from the summer-averaged raster data set. This was repeated for each year in the time series.

The spatial relationship between species richness and NDVI was evaluated with linear regressions for each

year from 1982 to 2006 (25 regressions; linear regression of richness vs. NDVI across all sites within a year, repeated for each year). The temporal relationship between richness and NDVI was evaluated by regressing richness against NDVI at each site through time (3207 regressions) (linear regression of richness vs. NDVI through time at a given BBS site, repeated for each site). The temporal regressions provided linear parameters (slope and r^2) quantifying how bird richness changed with NDVI through time at each site. We mapped the temporal slopes of each site and generated a histogram of the distribution of slope values. The spatial and temporal analyses were repeated for abundance vs. NDVI and for species richness vs. abundance. For the curve of richness vs. abundance, we fit linear, logarithmic, and power functions, and selected the best fit as measured by r^2 . The temporal analysis was then repeated for abundance vs. NDVI after introducing a one-year time lag in the response to evaluate a possible time lag in responses.

Because the route data are observational and spatially structured, evaluations of statistical significance of regressions are complex and of doubtful utility (Burnham and Anderson 2002), but as a guide, the critical coefficient of determination (r^2) at $\alpha = 0.05$ for 3205 degrees of freedom is 0.008, the biological significance of which would be very limited. Because of this, we do not report P values for our temporal or spatial analyses, and instead only report regression parameters. The temporal regressions are affected by both spatial and temporal autocorrelation, but the unadjusted critical r^2 for $df = 23$ is 0.157. Although we contend that autocorrelation in the data is not a problem that needs correcting because the statistical significance of relationships is not biologically relevant (Hawkins 2012), it is potentially informative to examine patterns of spatial autocorrelation of our temporal regression parameters, which we did by calculating Moran's I at multiple scales.

We also performed a spatial simulation analysis to identify potential threshold effects in the temporal response of avian richness to NDVI (that is, the possibility that temporal changes in NDVI at a given site were too small compared to spatial turnover to generate a response by birds). Temporally, the range of NDVI within each site varied from 0.03 to 0.47. Spatially, NDVI ranged over 0.93 units, nearly double the temporal maximum. Further, temporal sampling effort is ≤ 25 years for each site, compared to ~ 3200 sample sites each year. In our simulation, we iteratively generated subsamples of random sites from the spatial data set with NDVI values that match the temporal set exactly and calculated a regression slope between richness and NDVI for the subsample. The subsample generation and analysis was iterated 1000 times for each site. A mean simulated slope could then be calculated for each site. We selected 1999 because that year had the weakest spatial relationship ($r^2 = 0.29$; see Appendix A), which makes this test conservative. The distribution of

⁵ www.pwrc.usgs.gov/bbs

⁶ <http://glcf.umd.edu/data/gimms>

⁷ http://ivm.cr.usgs.gov/EROS_AVHRR_Greenness_composites.pdf

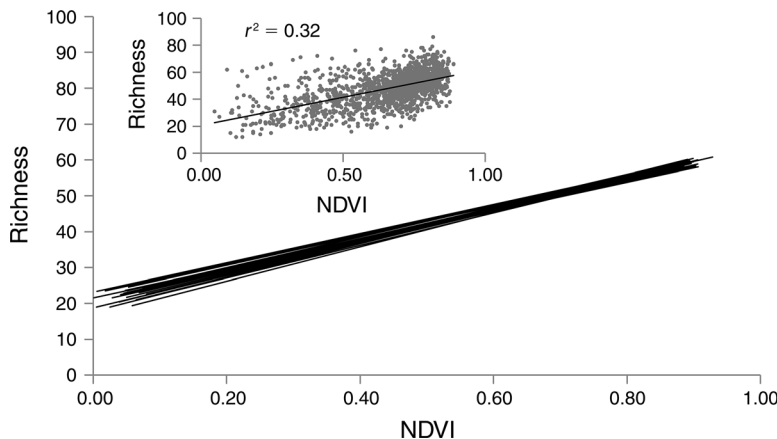


FIG. 1. Regression lines describing the annual spatial relationships between bird species richness (number of species) and NDVI (normalized difference vegetation index) for 1982–2006. The inset shows the data for 1982. Slopes and r^2 values for each year are provided in Appendix A. NDVI, a measure of “greenness,” is commonly used as a proxy for primary productivity, and ranges from 0 (bare ground) to 1 (saturated greenness).

simulated slopes was then compared with the distribution of temporal slopes using a t test. To make a site-by-site comparison, the difference between the simulated slope and temporal slope for each site was calculated. If the distribution of mean slopes resulting from the constrained spatial simulation was not different from the temporal slope distribution, it would suggest that a failure to find temporal relationships could be the result of insufficiently variable temporal NDVI sets. If the simulated slopes are more positive than the temporal slopes under these constraints, it would indicate a breakdown of the space-for-time substitution.

Vegetation structure undoubtedly covaries with NDVI across North America, so as part of our evaluation we attempted to partition the effects of vegetation structure on avian richness vs. primary biomass or productivity. Because we were unable to locate appropriate data quantifying vertical vegetation structure across the entire region, we classified the sites based on the ecoregion in which they occur, under the assumption that vegetation structure is relatively constant within an ecoregion through time, whereas NDVI is free to vary. We used Omernik’s Level II ecoregion definitions (Omernik 1987), which are available online.⁸ For this analysis, we used BBS survey data from 1990, the year with the strongest spatial relationship between richness and NDVI, with an r^2 of 0.40 (see Appendix A). Spatial regressions between species richness and NDVI were calculated within each ecoregion. Only those ecoregions that contained 25 or more sites were analyzed. If the strength of the continental spatial relationship between richness and NDVI is solely a consequence of the covariance of vegetation structure and NDVI, we would expect the relationship between richness and NDVI to be weak or absent within ecoregions. To explore the possibility that NDVI is a

stronger driver of diversity when productivity is more limiting, we correlated the temporal slope of each site for species richness and NDVI against its site mean NDVI. Finally, we segregated the distribution of spatially simulated slopes by ecoregion and compared these distributions to the distribution of temporal slopes within ecoregions.

RESULTS

Species richness and NDVI were spatially associated in every year of the 25-year period (Figs. 1 and 2; see Appendix A), with annual coefficients of determination (r^2 values) spanning 0.29–0.40. Thus, the spatial relationship between bird species richness and plant productivity or biomass has been consistent and reasonably stable for a quarter of a century. However, spatial relationships between species richness and total bird abundance, and between abundance and NDVI, also expected under productivity hypothesis, were weak or absent (Fig. 2; see Appendix A). For the spatial

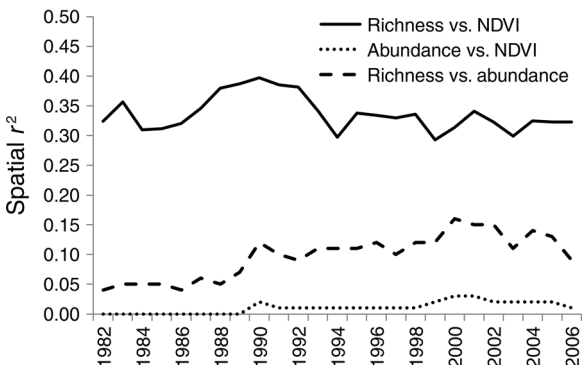


FIG. 2. Annual r^2 values for spatial regressions of bird species richness vs. NDVI, total bird abundance vs. NDVI, and species richness vs. abundance for 1982–2006. Richness vs. abundance was fit using a power function, whereas other relationships are linear fits.

⁸ www.epa.gov/wed/pages/ecoregions.htm

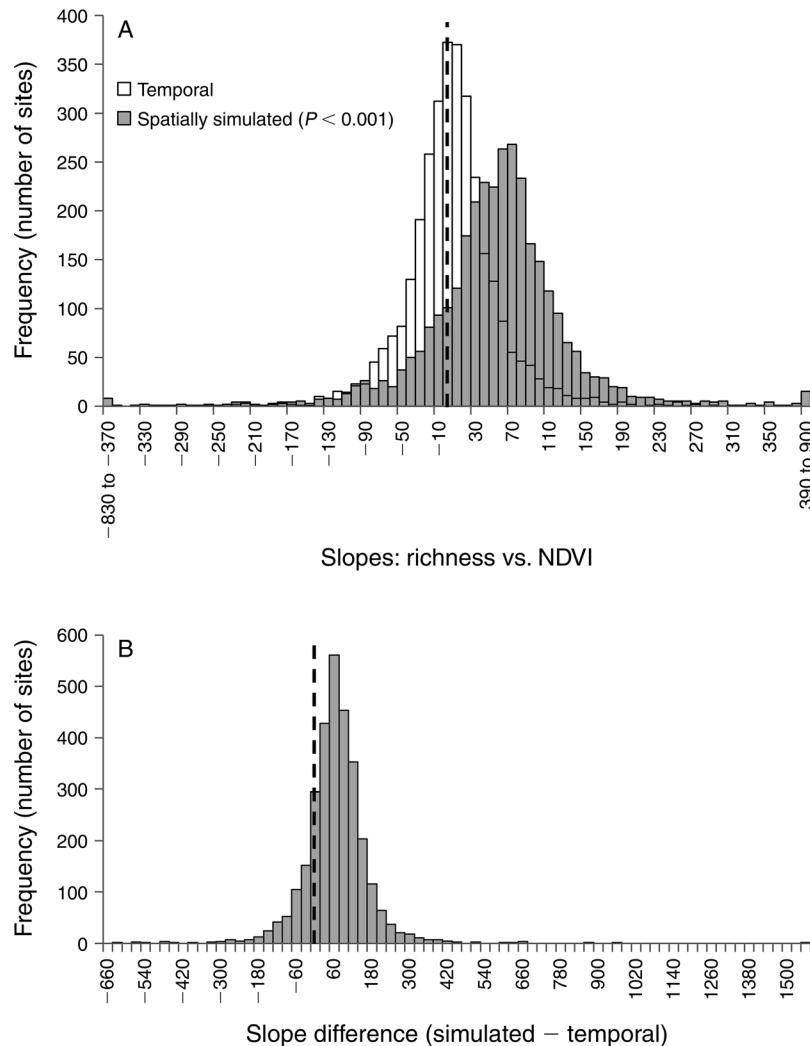


FIG. 3. (A) Histograms of temporal and spatial regression slopes of bird species richness vs. NDVI. In the key, temporal refers to the slopes of temporal regressions at each BBS site; spatially simulated refers to spatial slopes from a subsampling simulation (the means of each site's unique set of simulations) constraining range in NDVI and number of years sampled. The P value is from a t test comparing the temporal and spatially simulated slope distributions. The dashed vertical line denotes zero slope. (B) Histogram showing the site-by-site difference between the spatially simulated slope and the observed temporal slope. The dashed vertical line denotes zero difference.

curves of richness vs. abundance, a linear function yielded r^2 values spanning 0.04–0.16, a logarithmic function 0.08–0.28, and a power function 0.08–0.33. In every year, the power function outperformed the logarithmic function; therefore, we report the results of the power function in subsequent results. Although a weak relationship between species richness and total bird abundance was found, with the association becoming slightly stronger over time, abundance and NDVI were spatially independent over the entire 25-year period.

In contrast to the spatial associations of species richness and NDVI, we found no evidence that bird richness has tracked changing biomass or productivity through the years, although abundance may be weakly

tracking NDVI. Richness positively associated with NDVI at 1579 (49%) survey sites and negatively associated with NDVI at 1627 (51%) sites (mean \pm SD slope = -0.66 ± 52.64 , indistinguishable from 0; $P = 0.479$, mean \pm SD $r^2 = 0.09 \pm 0.12$) (Fig. 3). There were no spatial patterns in the distribution of temporal slopes across North America (Appendix B: Fig. B1, panels A and B); Moran's I values across a spatial correlogram with 22 distance classes ranged from -0.01 to 0.01 , indicating no spatial structure in the slopes at any scale. Total abundance and NDVI are weakly associated temporally (slope = 68.81 ± 1704.04 , $P = 0.022$, $r^2 = 0.10 \pm 0.12$), with no spatial structure (Moran's I values across 22 distance classes again ranged from -0.01 to 0.01) (Appendix B: Fig. B1, panels C, D). Introducing a

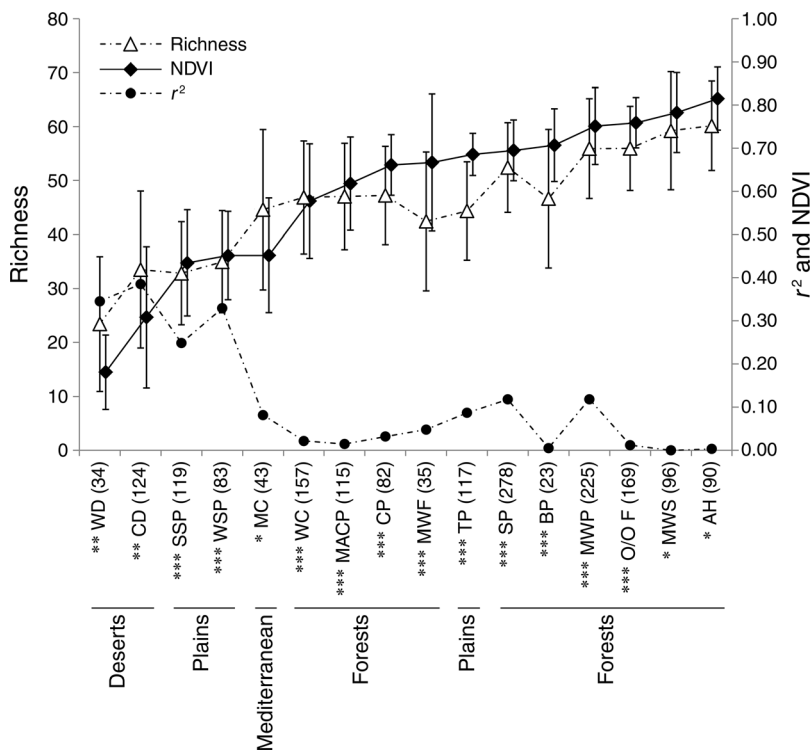


FIG. 4. Species richness (mean \pm SD), NDVI (mean \pm SD), and spatial regression r^2 for richness vs. NDVI within North American ecoregions. Ecoregions are ranked from left to right in order of increasing average NDVI, with the number of sites found in that ecoregion in parentheses. Asterisks below each ecoregion are significance levels derived from t tests comparing found slopes with spatially simulated slopes segregated by ecoregion. Ecoregion codes are: WD, Warm Deserts (North American Deserts); CD, Cold Deserts (North American Deserts); SSP, South-Central Semiarid Prairies (Great Plains); WSP, West-Central Semiarid Prairies (Great Plains); MC, Mediterranean California (Mediterranean California); WC, Western Cordillera (Northwestern Forested Mountains); MACP, Mississippi Alluvial and Southeast USA Coastal Plains (Eastern Temperate Forests); CP, Central USA Plains (Eastern Temperate Forests); MWF, Marine West Coast Forest (Marine West Coast Forest); TP, Temperate Prairies (Great Plains); SP, Southeastern USA Plains (Eastern Temperate Forests); BP, Boreal Plain (Northern Forests); MWP, Mixed Wood Plains (Eastern Temperate Forests); O/O F, Ozark/Ouachita-Appalachian Forests (Eastern Temperate Forests); MWS, Mixed Wood Shield (Northern Forests); AH, Atlantic Highlands (Northern Forests).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

one-year time lag in the abundance response to NDVI yielded similar results (slope = 66.32 ± 1750.63 , $P = 0.03$).

We found no threshold effects in the temporal response of species richness to changing NDVI. The distribution of spatially simulated slopes was significantly more positive than the distribution of temporal slopes (49.14 ± 89.82 , $P < 0.001$; see Fig. 3). When compared on a site-by-site basis, 76.3% of sites had a simulated slope that was greater than its observed temporal slope ([simulated - observed] = 50.27 ± 102.82 , mean \pm SD) (Fig. 3B). Thus, the lack of temporal relationships is unlikely to be because NDVI is insufficiently variable to detect a signal.

When spatial regressions were calculated within ecoregions, the spatial relationships were weaker than for the continent overall. In 1990, for which the continental-scale $r^2 = 0.40$, within-ecoregion r^2 values were below 0.12 in 12 of 16 ecoregions (Fig. 4). The remaining four had r^2 values closer to the continental value, ranging between 0.25 and 0.39. These four

included all of the desert and semiarid ecoregions: Warm Deserts, Cold Deserts, South-Central Semiarid Prairies, and West-Central Semiarid Prairies (Fig. 4). Spatial r^2 values declined in ecoregions as average ecoregion NDVI increased (consecutively, temperate prairies, plains, forests, and highlands). However, there was no relationship between mean site NDVI and that site's temporal r^2 (Fig. 5). In every ecoregion, the distribution of spatially simulated slopes was significantly more positive than the temporal slopes within ecoregion (Fig. 4). Thus, although spatial relationships between richness and productivity were stronger in low-productivity ecoregions, temporal relationships between richness and productivity are not stronger at sites with low productivity.

DISCUSSION

We confirmed the spatial relationship between route-level bird species richness and NDVI, but found no evidence that they are associated through years; that is, the space-for-time substitution for the richness of North

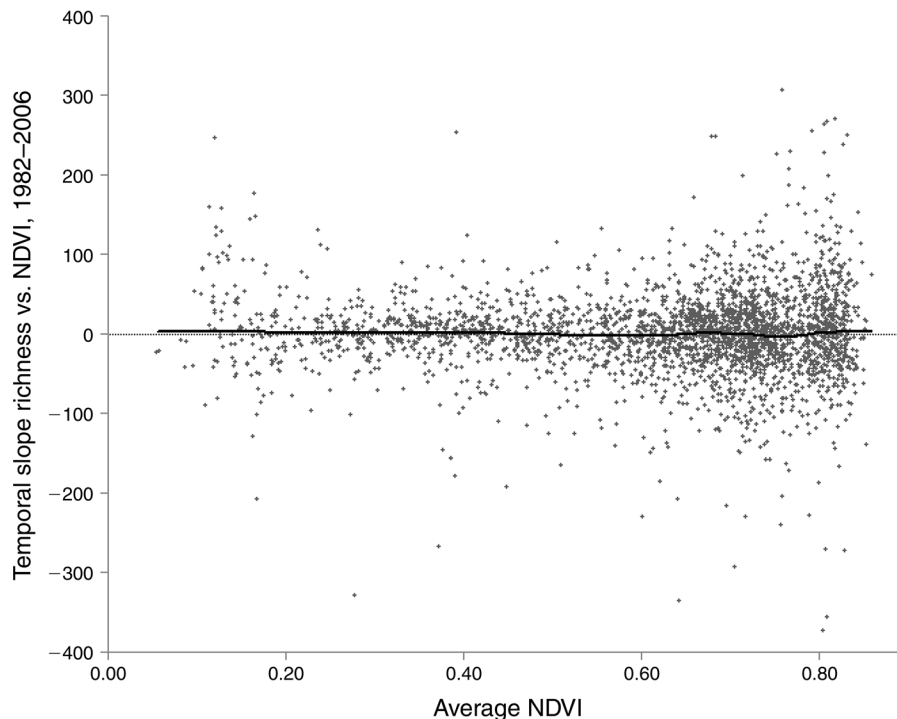


FIG. 5. Temporal regression slopes plotted against site-average NDVI at each BBS site for 1982–2006. The heavy line is the Lowest regression line.

American bird communities does not appear to be valid within the time span of the data. In fact, the absence of a temporal relationship between bird richness and plant biomass or productivity is striking both statistically and spatially, with no indication at all that they are either directly or indirectly linked (see Fig. 3 and Appendix B). For example, at half of the sites where NDVI has declined, bird species richness also declined (albeit weakly in most cases), and at the other half of these sites, species richness has increased. NDVI and bird richness appear to behave as independent random variables with respect to each other.

We were unable to find any evidence consistent with the possibility that NDVI has not varied sufficiently over the past quarter century to force a response by birds. It must be true that if local NDVI were to drop to 0, bird communities would collapse, but given the presence of some vegetation at all of the BBS sites, annual variation in NDVI amounting to one-quarter to one-half of the possible range in biomass or productivity has generated no detectable nonrandom response in bird species richness. This is in contrast to the spatial relationship, which remains even when spatial NDVI values are constrained to the temporal set.

The breakdown of the space-for-time substitution for the relationship between bird species richness and plant biomass or productivity implies that there is a variable that covaries with NDVI spatially but not temporally. We propose that this variable is vertical vegetation structural complexity, referred to as vertical foliage

height diversity by MacArthur and MacArthur (1961) and shown empirically by them to correlate strongly with bird species diversity. For example, forest is obviously structurally more complex than grassland and generally has higher NDVI (see Fig. 4). However, where these vegetation types have experienced warmer, drier weather over the past 25 years, NDVI probably declined, whereas structural complexity should be unaffected. In the absence of ecosystem collapse due to climatic change, a forest remains a forest, even if it becomes lower productivity forest with declining NDVI.

Indirect support of the vegetation structural complexity hypothesis is found within ecoregions. The spatial relationship between richness and biomass or productivity, despite being moderately strong across all ecoregions, tends to break down when general vegetation structure is held relatively constant. On the other hand, it is potentially revealing that although this applies to regions with moderate to large amounts of vegetation, in deserts and semiarid regions the strength of the spatial relationship between richness and NDVI is comparable to the continental relationship. This invites speculation, and we can think of two plausible explanations. First, productivity may drive bird community dynamics when vegetation is scarce. However, we found no evidence for this, because bird species richness and average productivity or biomass at a site are independent through the years at even the lowest NDVI levels (see Fig. 5). Alternatively, habitats classified as desert are actually highly variable in terms



PLATE 1. A Sooty Fox Sparrow in Oregon (USA) in the spring. Photo credit: L. L. Manne.

of the complexity of vegetation. This could generate a within-region link between vegetation and birds because a wide range of conditions ranging from nearly bare sand to diverse Sonoran Desert are lumped into the Warm Desert ecoregion.

The immediate or lagged temporal response of bird abundance to NDVI was weak (see Appendix B). We introduced the one-year time lag in the potential response of birds to summer NDVI because it may be unreasonable to assume that bird abundance will respond instantaneously to the current year's conditions, but the response continued to be weak. If anything, the response was slightly weakened compared to the model with no lag. This weak response suggests that total bird abundance is not limited by productivity. Spatial relationships between abundance and NDVI also ranged from absent to weak across years (see Fig. 2 and Appendix A), further undermining the hypothesis that bird richness responds to plant productivity in the manner assumed under the productivity hypothesis.

The failure of abundance to track changing NDVI, or to correlate spatially with NDVI, must be interpreted with caution. Detection likelihood of birds decreases with increasing NDVI, which can bias abundance lower in high-NDVI habitats (Hurlbert 2004, Pacifici et al. 2008). A truly positive abundance–NDVI relationship may appear flat. Indeed, Evans et al. (2006) found

stronger abundance–NDVI relationships using Resident Bird Counts that are less likely to incorporate this detection bias than the sight and sound detection methods relied upon in the BBS. Given that, for the relationship between abundance and NDVI, the maximum spatial r^2 was 0.03, and on average was <0.01 , this bias would have to be pronounced to disguise a true relationship with enough strength to be biologically meaningful. However, we cannot rule out the possibility. Finally, it should be noted that we used raw abundance summed over all bird species, irrespective of their body size and trophic level. A much more detailed analysis of abundance that more accurately measures the energy needs of birds could provide more insights into how community-level bird abundances are associated with productivity in time and space.

Our failure to find a temporal signal in species richness linked to NDVI does not indicate that birds are not responding to changing productivity at all. There is mounting evidence that community assemblages are shifting toward spatial homogenization due to the spread and dominance of the most common species (La Sorte and Boecklen 2005, La Sorte and McKinney 2007, Bühler and Roth 2011, Coyle et al. 2013) and the increasing dominance of generalist species at the expense of rarer specialists (Davey et al. 2012). These may well be due in part to the changing climate and gradual

decrease in productivity, although the common and generalist species that are responding are often those species that thrive in human-altered environments. Indeed, in North American agricultural and urban environments, species richness and temporal turnover of avian species compositions have declined, both across the annual cycle and across years (La Sorte et al. 2014), despite high productivity in agricultural environments. Irrespective, we cannot conclude that plant productivity has no influence on birds; indeed, that is difficult to believe. On the other hand, it does not appear to drive community species richness and total avian abundance across North America. Although we did confirm the spatial relationship between species richness and productivity, none of the other predictions associated with the productivity hypothesis were supported. Despite what would seem to be compelling logic that plant productivity *should* drive animal diversity across broad scales, we cannot find any evidence that it does.

Returning to the most likely alternative hypothesis for how vegetation influences bird communities (MacArthur and MacArthur 1961), given that NDVI covaries spatially with vegetation structure (Boelman et al. 2011), it is not surprising that a spatial correlation between NDVI and species richness emerges. Moreover, there is independent support for the notion that vegetation structure at least partially underlies relationships between bird species richness and plant productivity or biomass. Comparing relationships predicted by the productivity hypothesis in high-productivity sites (forests) with low-productivity sites (grasslands), Hurlbert (2004) found that despite positive correlations between NDVI and richness in a subset of the BBS survey data, richness rises with increasing habitat complexity in a way that outpaces that explained by increases in abundance. Also, Verschuyt et al. (2008) found that the slope of the relationship between structural complexity and bird species richness is greater in energy-limited locations, concluding that in low-energy environments, vegetation structural complexity is more important than when productivity is high. In forests, vegetation structure has been shown to positively influence bird species richness (Jankowski et al. 2013, Zhang et al. 2013), and Culbert et al. (2013) recently found that vertical vegetation structure, as measured by canopy height and canopy height variability, predicts avian richness. Although canopy height and variability are not the same as detailed survey-based measures such as foliage height diversity (MacArthur and MacArthur 1961), it is probably telling that these simple measures of vegetation complexity nonetheless have explanatory power. Based on the evidence to date, we conclude that MacArthur and MacArthur's (1961) classic explanation for bird community diversity is the strongest contender for explaining the link between plants and birds, and the widely accepted hypothesis that plant productivity drives bird community size and structure merits further scrutiny.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-0057.1.sm>