Scratching the niche: A continental-scale evaluation of the productivity hypothesis in explaining geographic variation of bird diversity across 25 years

Dobson, LuAnna Lee

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UNIVERSITY OF CALIFORNIA,
IRVINE

Scratching the niche: A continental-scale evaluation of the productivity hypothesis in explaining geographic variation of bird diversity across 25 years

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

LuAnna Lee Dobson

Dissertation Committee:
Professor Bradford A. Hawkins, Chair
Distinguished Professor John C. Avise
Professor Nancy T. Burley
Professor Jennifer B. H. Martiny

2017

DEDICATION

To Christopher Alan James

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My sincere love and gratitude goes to my partner Stephen M. Hatosy for showing me the power of mutual respect and equality, and whose intellectual, emotional, and practical support has contributed vastly to my achievements thus far.

CURRICULUM VITAE

LuAnna L. Dobson
LDobson@uci.edu

1. EDUCATION

University of California, Irvine Irvine, CA
Ph.D. in Ecology and Evolutionary Biology 2017
Scratching the niche: A continental-scale evaluation of the productivity hypothesis in explaining geographic variation of bird diversity across 25 years

University of Redlands Redlands, CA
M.S. Geographic Information Systems 2010
Thesis: Missouri Ozark Forest Ecosystem Project: A GIS Analysis of Salamander Capture

Mt. San Jacinto College Menifee, CA
Certificate, Geographic Information Science 2009

Scripps College Claremont, CA
B.A. Environmental Science, Minor: Biology 2006

2. Research Publications

Published

3. Dobson, L.L., La Sorte, F.A., Manne, L.L., and Hawkins, B.A. 2015. The diversity and abundance of North American bird assemblages fail to track changing productivity. **Ecology** 96: 1105 – 1114.

2. Dobson, L.L. 2006. Desertification and the Water Cycle. Pages 107-117 *in* J.E. Morhardt, editor. Roberts Environmental Center 2006 Guide to Ecosystems Services Research. Roberts Environmental Center Press, Claremont, CA

1. Dobson, L.L. 2006. Water Pollution. Pages 161-176 *in* J.E. Morhardt, editor. Roberts Environmental Center 2006 Guide to Research in Natural Resources Management. Roberts Environmental Center Press, Claremont, CA

In Prep

Dobson, L.L., and Hawkins, B.A. 2016. Energy-scaled abundance responds randomly to interannual changes in primary productivity, violating the predictions of the productivity hypothesis. *In prep.*

Dobson, L.L., and Hawkins, B.A. 2016. Diversity without abundance: minimal support for predictions of the productivity hypothesis as a driver of the species richness of North American wintering bird assemblages. *In revision.*

Dobson, L.L., Hawkins, B.A. 2016. Raw richness outperforms effort-adjusted richness in estimating winter avian diversity in the Christmas Bird Count. *In revision.*

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3. TEACHING

University of California, Irvine Irvine, CA
Department of Ecology and Evolutionary Biology 2011-2017
Instructor of Record
Geographic Information Systems (GIS) for Environmental Science

Graduate Student Researcher
Developed curriculum for a new program titled Master in Conservation and Restoration Science including courses Restoration Ecology, Field Methods in Restoration, Conservation Biology, Technical Writing, Science Communication, Project Management, Advanced GIS, Remote Sensing, and Spatial Statistics

Teaching Assistant
Ornithology, Global Sustainability, Ecosystems to Organisms, Ecology and Evolutionary Biology, Horticulture, and Physiology Lab

Workshop Development and Implementation
TA Professional Development Program in 2014 and 2015, Time Management in Grading workshop, Active Learning workshop, and GIS for Ecology.

Mt. San Jacinto College, Department of Geosciences Menifee, CA
Associate Faculty 2010 - 2012
Courses taught include Introduction to GIS, Programming for GIS, GIS in Science Business and Government, and Cartography

Program Coordinator
Coordinated tutor hiring, Perkins grant funding, course scheduling, special events and programs, and interfacing with other offices and departments. Developed department, program, and course student learning outcomes. Developed and taught free Community GIS Workshops. Designed and taught day-long workshops including Spatial Statistics, Solar Analysis with GIS, and Programming for GIS.

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4. CONFERENCE PRESENTATIONS

International Biogeography Society Meeting Tucson, AZ
Poster Presentation 2017
Title: " Diversity without abundance: minimal support for predictions of the productivity hypothesis as a driver of the species richness of North American wintering bird assemblages."

International Biogeography Society Meeting Bayreuth, Germany
Poster Presentation 2015
Title: "The diversity and abundance of North American bird assemblages fail to track changing productivity."

Graduate Women in Science (OCGWIS) Spring Science Conference Irvine, CA
Oral Presentation, ***Best Talk Award*** 2015
Title: "The diversity and abundance of North American bird assemblages fail to track changing productivity."

Winter Ecology and Evolutionary Biology Graduate Student Seminar Irvine, CA
Oral Presentation 2015
Title: "Citizen Science: Doomed by varying effort?"

Evolution Meeting Raleigh, NC
Oral Presentation 2014
Title: "A reappraisal of the productivity hypothesis for North American bird assemblages".

Ecological Society of America 98th Annual Meeting Minneapolis, MN
Poster Presentation 2013
Title: ""Does plant productivity really influence the richness of bird assemblages? A re-appraisal of the energy-richness hypothesis for North America"

Winter Ecology and Evolutionary Biology Graduate Student Seminar Irvine, CA
Oral Presentation 2012
Title: "Does plant productivity really influence the richness of bird assemblages? A re-appraisal of the energy-richness hypothesis for North America"

5. PROFESSIONAL EXPERIENCE

Missouri Ozark Forest Ecosystem Project, MO Dept of Conservation Winona, MO
Reptile and Amphibian Research Technician 2008
Herpetofauna sampling and identification using pitfall and funnel trap arrays and hand captures. Transect-based plant surveys. Aquatic turtle survey. Goose and avian capture/recapture surveys.

Buck Island Sea Turtle Research Program, National Park Service St. Croix, U.S.V.I.s
Research Assistant 2007
Saturation tagging (inconel and PIT tags) and hatch success of critically endangered Hawksbill and Leatherback Sea Turtles, and threatened Green and Loggerhead Sea Turtles.

Audubon California's Starr Ranch Sanctuary Trabuco Canyon, CA
Riparian Invasive Species Control and Restoration Intern 2006
Effects of watering regimes on riparian restoration of native tree, shrub, and groundcover plant species. Riparian invasive species mapping using GPS and GIS, invasie species non-chemical control, bird mist-netting for MAPS and MAWS, and freshwater stream nutrient testing and soil invertebrate sampling.

Roberts Environmental Center Claremont, CA
Environmental Analyst 2006
Performed Pacific Sustainability Index reviews of Fortune Global 500 and Fortune 1000 Companies. Sectors included Motor Vehicles & Parts, Industrial & Farm Equipment, and Energy & Utility.

Firestone Center for Restoration Ecology at Pitzer College Dominical, Costa Rica
Research Assistant 2006
Conducted stream water sampling project comparing rainfall-induced nutrient and bacterial input in primary- versus secondary-growth rainforests. Participated in other assorted wildlife projects.

Moorinya National Park Annual Vertebrate Fauna Survey Qld, Australia
Fauna Survey Volunteer 2005
Performed trapping, mist-netting, point counts, and visual ID of assorted fauna.

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6. GRANTS & AWARDS

Research

First Place Talk Award, Orange County GWIS Conference	$150	2015
Morrison-Family Fellowship, University of Redlands	$64,000	2010

Teaching

Edward J. Steinhaus Teaching Award	$750	2016
Department of Education GAANN Fellowship	$14,000	2015
Teaching Learning & Technology Center Pedagogical Fellowship	$2,000	2015
Teaching Learning & Technology Center Pedagogical Fellowship	$2,000	2014
Center for Environmental Biology Teaching Award	$500	2014
Department of Education GAANN Fellowship	$46,000	2014
Department of Education GAANN Fellowship	$46,000	2013
Department of Education GAANN Fellowship	$46,000	2012

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7. SERVICE & OUTREACH

Sea & Sage Audubon Society and OC Society for Conservation Biology Irvine, CA
Conservation Lecture Series Invited Speaker 2015
Title: "Citizen science: Helping us understand the drivers of avian diversity in North America,"

University of California, Dept. of Ecology and Evolutionary Biology Irvine, CA
Graduate Student Panelist 2016
Shared my experience choosing, applying for, and carrying out graduate work with undergraduate students enrolled in senior seminar in Ecology and Evolutionary Biology

Interactive Equity Workshop Organizer 2014
Worked with the Office of Equal Opportunity and Diversity and the Title IX Officer to organize a workshop titled: "Grey-zone Harassment", addressing common instances of mild yet persistent and common harassment TAs face, with scripts and practice role-play for addressing these.

Center for Environmental Biology's Annual Ecological Workshop
Planning Committee 2014
Responsible for inviting speakers, created and managed RSVP platform, made all room and catering reservations at the Beckman Center of the National Academies of Sciences

Ecology Group Oral Presentation, Titled: "Gender Issues in Science" 2014

Graduate Student Invited Seminar Speaker Planning Committee 2014

Non-R1 Jobs Workshop Planning Committee 2014

Mt. San Jacinto College, Dept. of Geosciences Menifee, CA
GIS Day Coordinator and Presenter 2011
Title: " Missouri Ozark Forest Ecosystem Project; a GIS Analysis of Salamander Capture"

STEM Summer Bridge Program Coordinator, Faculty Panel, and Presenter 2011
Invited Lecture, Learning Resource Center (LRC) TA Training Event 2010
Title: "Women in Math and Science"

Free Friday GIS Community Workshops Coordinator and Instructor 2010

Invited Keynote Speaker, LRC faculty training event 2010
Title: "Women in Math and Science"

GIS Day Coordinator and Presenter 2010

GIS Day Presenter 2009
Talk title:"Coachella Valley Solar Farm Project"

ABSTRACT OF THE DISSERTATION

Scratching the niche: A continental-scale evaluation of the productivity hypothesis in explaining geographic variation of bird diversity across 25 years

By

LuAnna Lee Dobson

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2017

Professor Bradford A. Hawkins, Chair

Primary productivity and animal species richness are associated across spatial scales and extents. The productivity hypothesis had been credited for explaining these correlations by asserting that places with more energy fixed in the system by plants should support more individuals, whereby the community accumulates more species. Many have interpreted the spatial association between richness and productivity as support for the hypothesis. If true, bird richness should track productivity temporally, and there should be spatial and temporal relationships between productivity and both bird abundance and richness.

We tested these predictions in the breeding season and winter across space and time. Using a remotely-sensed primary productivity proxy (NDVI) and avian data from two large North American citizen science surveys, the Breeding Bird Survey (BBS) and Christmas Bird Count (CBC), we evaluated the response of avian richness and abundance to interannual changes in plant productivity across 25 years. In the breeding season we found positive spatial relationships between richness and NDVI each year, but when evaluated temporally no support for the hypothesis was found. Richness and NDVI were positively associated at only half

(49.3%) of BBS sites (mean $r^2 = 0.09$). Further, total abundance and productivity were unrelated.

Despite summer findings, it is possible that richness depends more on productivity in winter when birds are stressed by harsh conditions. Using CBC data we found that across several thousand communities the number of individuals was not spatially associated with productivity, providing no support for the productivity hypothesis.

In these and earlier tests of the hypothesis, trait-neutral partitioning of resources across individuals is assumed, though it may be more realistic that partitioning is in unequal shares. To test for energetic trait differences, we regressed total avian biomass at sites against NDVI and found that avian biomass is independent of productivity.

We conclude that primary productivity is unlikely the driver of bird diversity. Spatial relationships between productivity and bird richness may be spuriously arising via covariance between productivity and vegetation structural complexity, and the latter may be driving bird communities, consistent with the MacArthurs' classic hypothesis that the vertical profile of foliage drives bird species diversity.

CHAPTER 1

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

LUANNA L. DOBSON,[1,4] FRANK A. LA SORTE,[2] LISA L. MANNE,[3] AND BRADFORD A. HAWKINS[1]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, California, 92697 USA*

[2]*Cornell Laboratory of Ornithology, Cornell University, Ithaca, New York, 14850 USA*

[3]*Department of Ecology and Evolutionary Biology, College of Staten Island, Staten Island, New York, 10314 USA*

[4]*E-mail: ldobson@uci.edu*

ABSTRACT

Plant biomass/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 summer Normalized Difference Vegetation Index (NDVI) from 1982 – 2006 and the North American Breeding Bird Survey, we evaluated the response of avian richness and abundance to inter-annual changes in plant biomass/production. We found positive spatial relationships between richness and NDVI all 25 years. Temporally, however, richness and NDVI were positively associated at 1,579 survey sites and negatively associated at 1,627 sites (mean $r^2 = 0.09$). Further, total abundance and NDVI were unrelated spatially (r^2s 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/productivity and vegetation structural complexity, and the latter may be driving bird communities. This is consistent with the MacArthurs' 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

Running head: Productivity and bird diversity patterns

INTRODUCTION

Positive spatial correlations between species richness and plant biomass/productivity have been well documented for birds at numerous geographic grains and extents (Wright 1983, Hawkins et al. 2003, 2007, Hurlbert and Haskell 2003, Hurlbert 2004, Currie et al. 2004, Carnicer et al. 2007, Verschuyl et al. 2008, Phillips 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 with measures of energy have been found across numerous geographic areas. Such associations are predicted by species-energy theory, developed by Wright (1983) as a natural extension of species-area theory, who called it "a more general biogeographic theory". Species-energy theory posits that energy per unit area explains species richness more reliably than area alone. Wright found that the richness of flowering plants and birds 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).

Whereas 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 (Carnicer et al. 2007, Evans et al. 2006, Yee and Juliano 2007). It should be noted that under the productivity hypothesis, energy is defined by primary 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 while 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 co-vary 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 transferrable the results are to other taxonomic groups. Across an altitudinal gradient in Spain, Carnicer et al. (2007) found that the predictions of 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 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 rainforest 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 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 while 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 broad-scale 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/productivity, using a space-for-time substitution to infer that bird community size and structure are driven by productivity in time. Though 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 ben 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 inter-annual 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 inter-annual temporal changes in bird species richness and total bird abundance with respect to changes in plant biomass/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/productivity drives bird species richness through increased resources, then as vegetation biomass/productivity fluctuates temporally, richness and abundance should rise and fall accordingly.

MATERIALS AND METHODS

We used bird data from the BBS (www.pwrc.usgs.gov/bbs, accessed January, 2011), and normalized difference vegetation index (NDVI) data from NASA AVHRR for 1982 – 2006 (http://glcf.umd.edu/data/gimms, accessed June, 2012). 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-minute timed bird count within a 400-meter 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 8 years between 1982-2006, leaving 3,207 routes used in the analysis.

We used NDVI data from 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, Stegen et al. 2013, Siefert 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) (http://ivm.cr.usgs.gov/EROS_AVHRR_Greenness_composites.pdf). 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 bi-monthly NDVI datasets 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 mid-point and represented in the analysis as vector point data. At the coordinates of each BBS point, NDVI was extracted from the summer-averaged raster dataset. 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 - 2006 (25 regressions; linear regression of richness versus 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 (3,207 regressions) (linear regression of richness versus 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 versus NDVI and for species richness versus abundance. For the curve of richness versus 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 versus NDVI after introducing a 1-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 3,205 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. While 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 0.93 units, nearly double the temporal maximum. Further, temporal sampling effort is ≤ 25 years for each site, compared to approximately 3,200 sample sites each year. In our simulation, we iteratively generated subsamples of random sites from the spatial dataset 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 1,000 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 1.A), which makes this test conservative. The distribution of 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 co-varies with NDVI across North America, so as part of our evaluation we attempted to partition the effects of vegetation structure on avian richness versus primary biomass/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) (www.epa.gov/wed/pages/ecoregions.htm). 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 1.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 every year of the 25-year period (Figs 1.1, 1.2 and see Appendix 1.A), with annual coefficients of determination (r^2s) spanning

0.29 - 0.40. Thus, the spatial relationship between bird species richness and plant productivity/biomass has been consistent and reasonably stable for a quarter century. However, spatial relationships between species richness and total bird abundance, and abundance and NDVI, also expected under productivity hypothesis, were weak or absent (Fig. 1.2 and Appendix 1.A). For the spatial curves of richness vs. abundance, a linear function yielded r^2s spanning 0.04 - 0.16, a logarithmic function 0.08 - 0.28, and a power function .08 to 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/productivity through years, although abundance may be weakly tracking NDVI. Richness positively associated with NDVI at 1,579 (49%) survey sites and negatively associated at 1,627 (51%) sites (mean±SD slope = -0.66±52.64, indistinguishable from 0, $p = 0.479$, mean $r^2 = 0.09 \pm 0.12$) (Fig. 1.3). There were no spatial patterns in the distribution of temporal slopes across North America (Appendix 1.B, panels A,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 (mean slope = 68.81±1704.04, $p = 0.022$, mean $r^2 = 0.10 \pm 0.12$), with no spatial structure (Moran's *I* values across 22 distance classes again ranged from -0.01 to 0.01) (Appendix 1.B, panels C,D). Introducing a 1-year time lag in the abundance response to NDVI yielded similar results (mean 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, $p < 0.001$) (Fig. 1.3). When compared on a site-by-site basis, 76.3% of sites had a simulated slope that was greater than its observed temporal slope (mean of [simulated - observed] = 50.27±102.82) (Fig. 1.3). 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. 1.4). The remaining four had r^2 values closer to the continental value, ranging between 0.25 to 0.39. These four included all of the desert and semi-arid ecoregions: Warm Deserts, Cold Deserts, South-Central Semiarid Prairies, and West-Central Semiarid Prairies (Fig. 1.4). 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. 1.5). In every ecoregion, the distribution of spatially simulated slopes was significantly more positive than the temporal slopes within ecoregion (Fig. 1.4). 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 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/productivity is striking both statistically and spatially, with no indication at all that they are either directly or indirectly linked (see Figs 1.3 and Appendix 1.B). For example, at half of 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/productivity has generated no detectable non-random 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/productivity implies there is a variable that co-varies with NDVI spatially but not temporally. We propose that 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. 1.4). However, where these vegetation types have experienced warmer, drier weather over the past 25 years, NDVI likely 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/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 semi-arid regions the strength of the spatial relationship between richness and NDVI are 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. But we found no evidence for this, as bird species richness and average productivity/biomass at a site are independent through years at even the lowest NDVI levels (see Fig. 1.5). Alternatively, habitats classified as desert are actually highly variable in terms 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 1.B). We introduced the 1-year time lag in the potential response of birds to summer NDVI because it may be unreasonable to assume 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 productivity-limited. Spatial relationships between abundance and NDVI also ranged from absent to weak across years (see Fig. 1.2 and Appendix 1.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 the maximum spatial r^2 for the relationship between abundance and NDVI 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, but 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 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. While 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 co-varies 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/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, Verschuyl 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. While canopy height and variability are not the same as detailed survey-based measures like 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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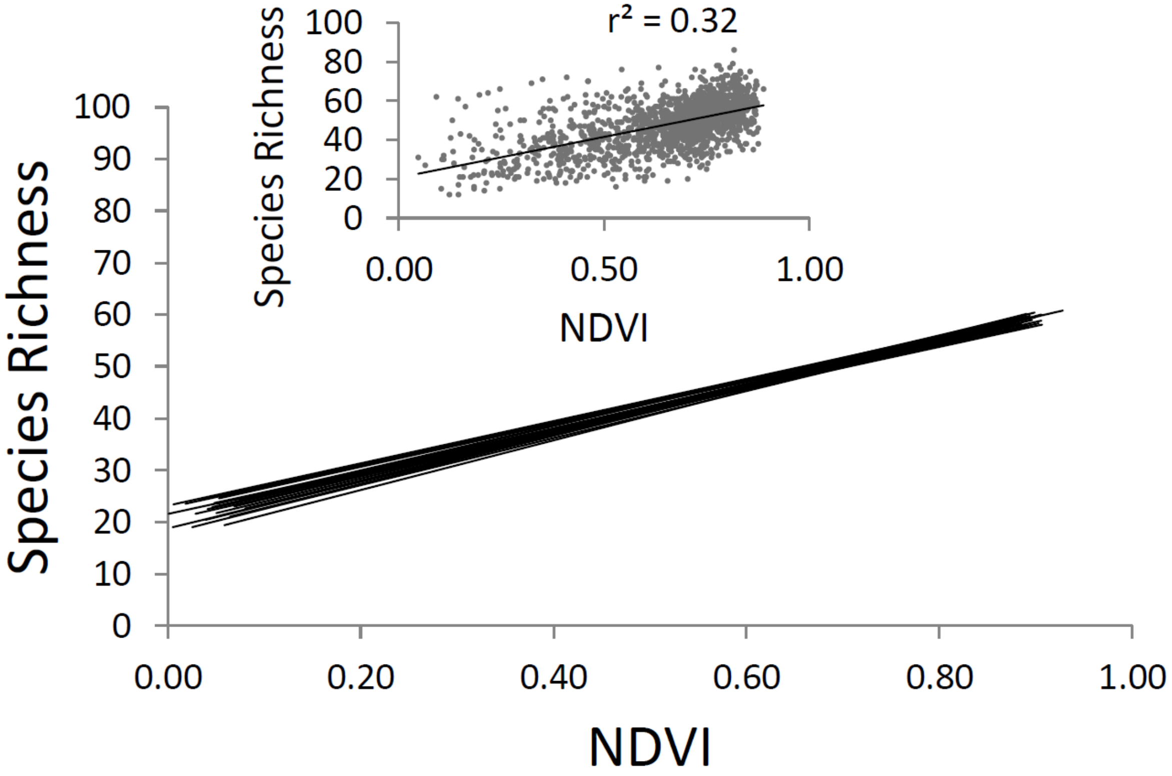

FIG. 1.1. Regression lines describing the annual spatial relationships between bird species richness and NDVI (Normalized Difference Vegetation Index) for 1982-2006. Inset shows the data for 1982. Slopes and r^2 values for each year are provided in Appendix 1.A.

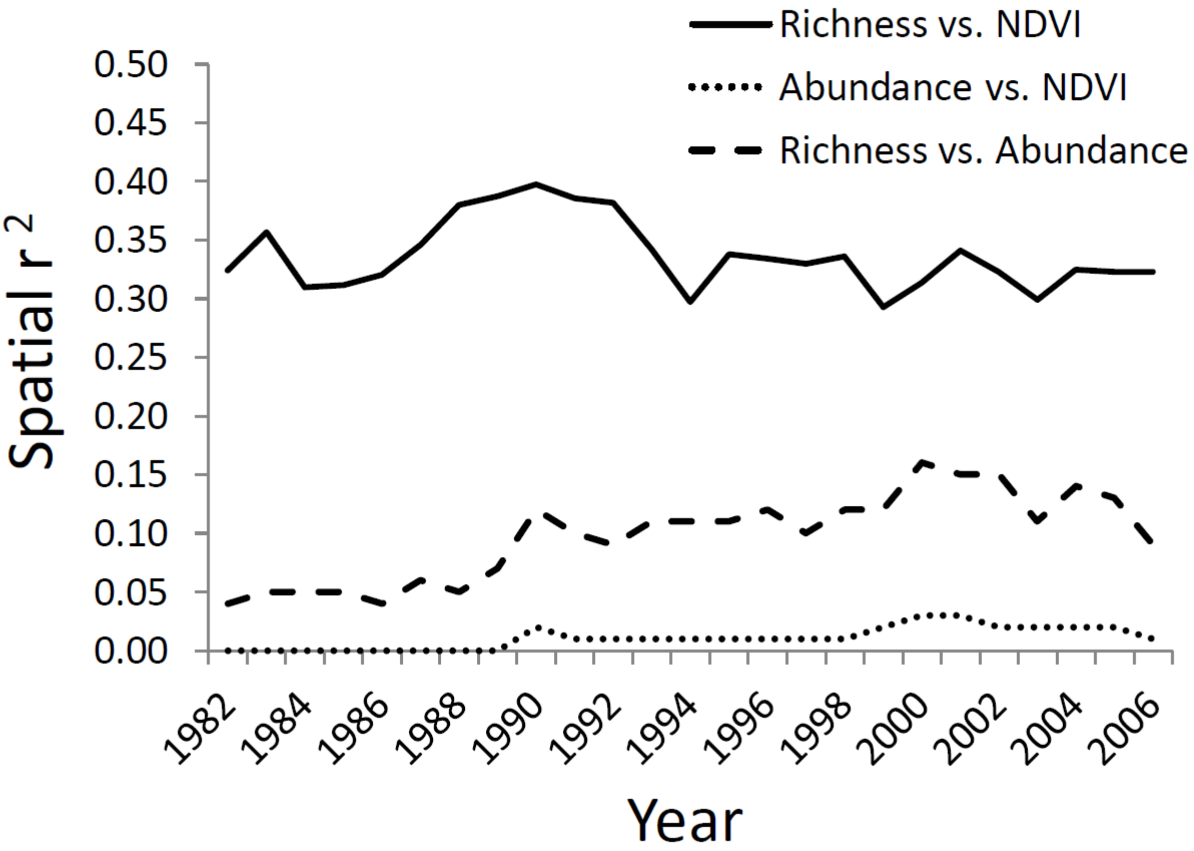

FIG. 1.2. Annual r^2s for spatial regressions of bird species richness vs. NDVI (Normalized Difference Vegetation Index), total bird abundance vs. NDVI, and species richness vs. abundance for 1982 to 2006. Richness vs. abundance was fit using a power function, while other relationships are linear fits.

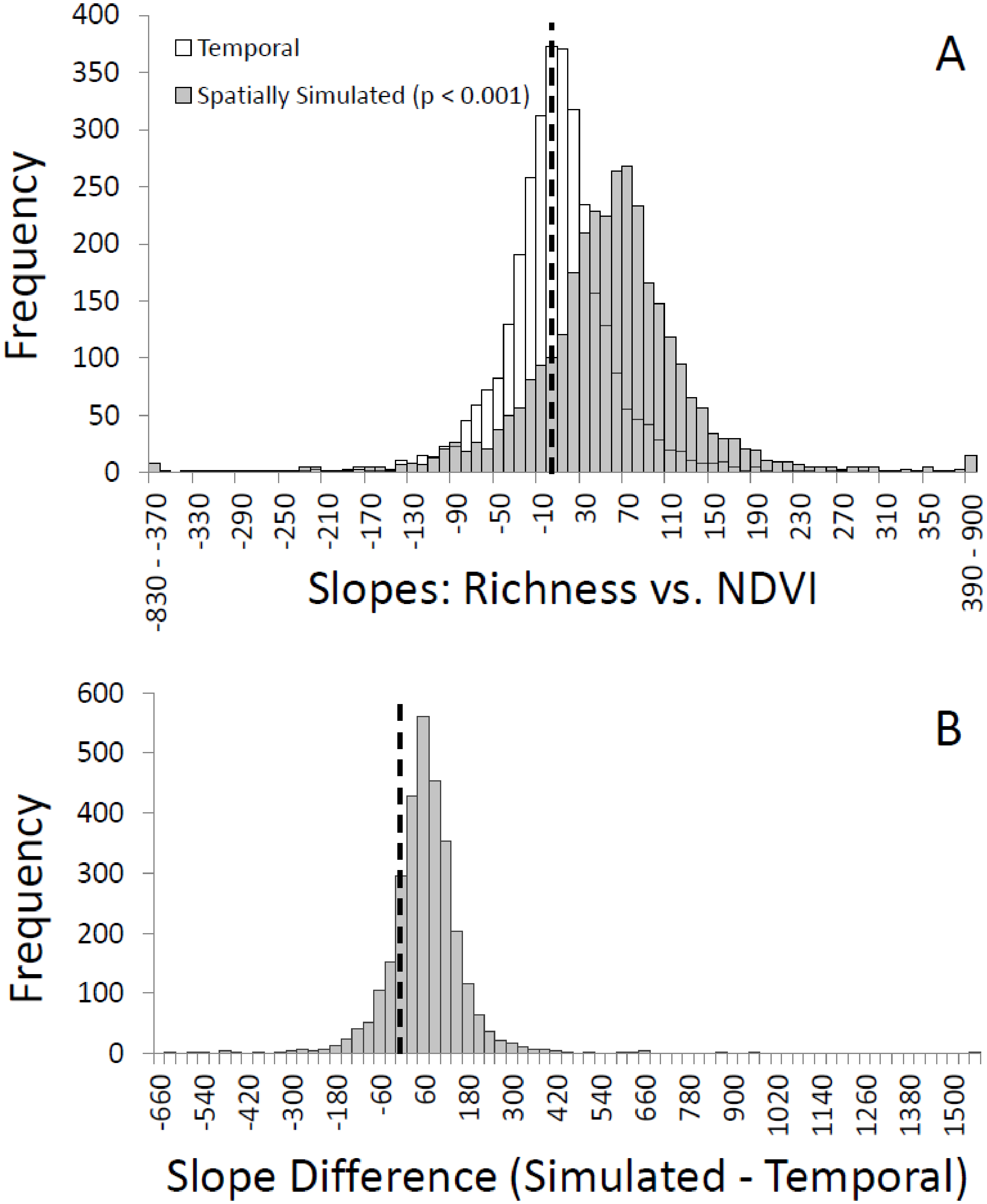

FIG. 1.3. (A) Histograms of temporal regression slopes of bird species richness vs. NDVI (Normalized Difference Vegetation Index). Temporal: the slopes of temporal regressions at each BBS site. Spatially Simulated: spatial slopes from a sub-sampling simulation constraining range

in NDVI and number of years sampled. P-value is from a t-test comparing the temporal and spatially simulated slope distributions. Dashed line denotes zero slope. (B) Histogram showing the site-by-site difference between the spatially-simulated slope and the temporal slope (Simulated Slope - Temporal Slope). Dashed line denotes zero difference.

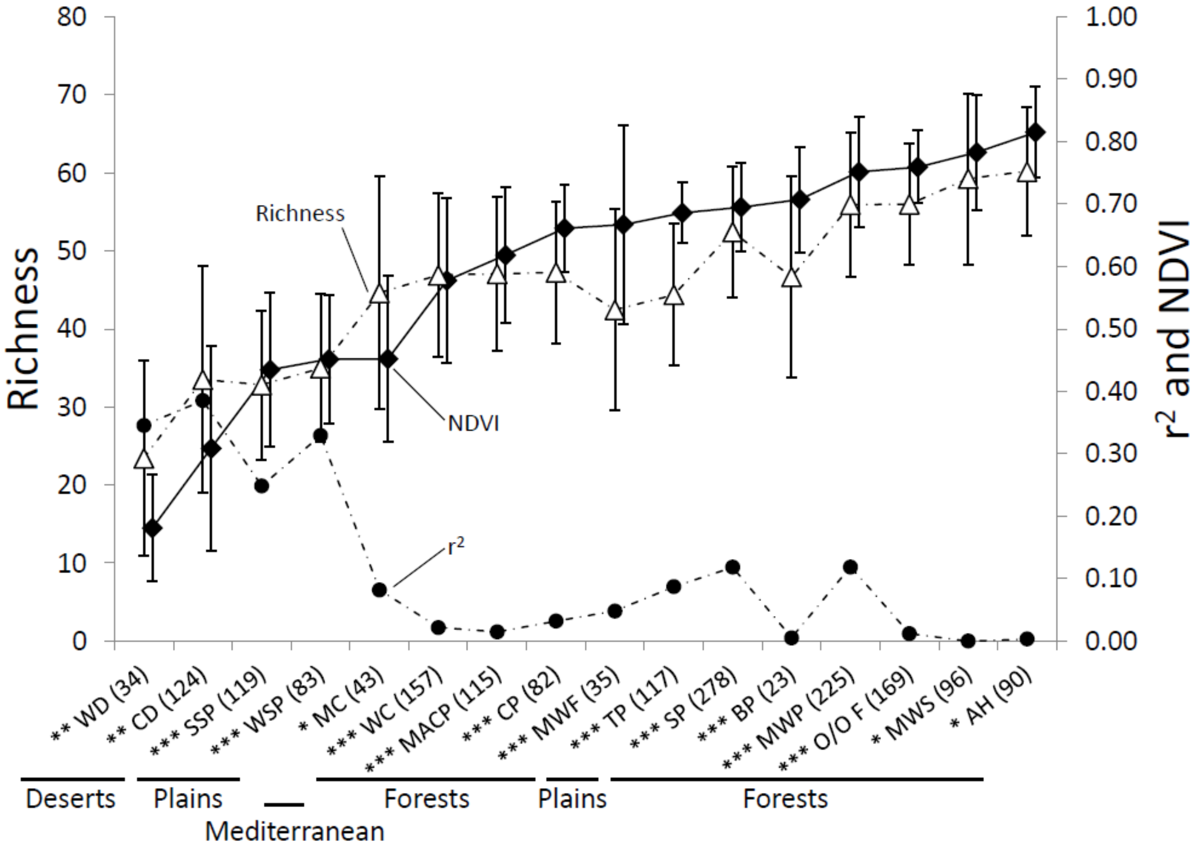

FIG. 1.4. Average species richness, average NDVI (Normalized Difference Vegetation Index), and spatial regression r^2 for richness vs. NDVI within North American ecoregions. Ecoregions are ranked from left to right in order of increasing average NDVI, with the number of sites found in that ecoregion in parentheses. Vertical bars represent 1 standard deviation. Asterisks below each ecoregion are significance levels derived from t-tests comparing temporal slopes with spatially simulated slopes segregated by ecoregion: p: * < 0.05, ** < 0.01, *** < 0.001. 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).

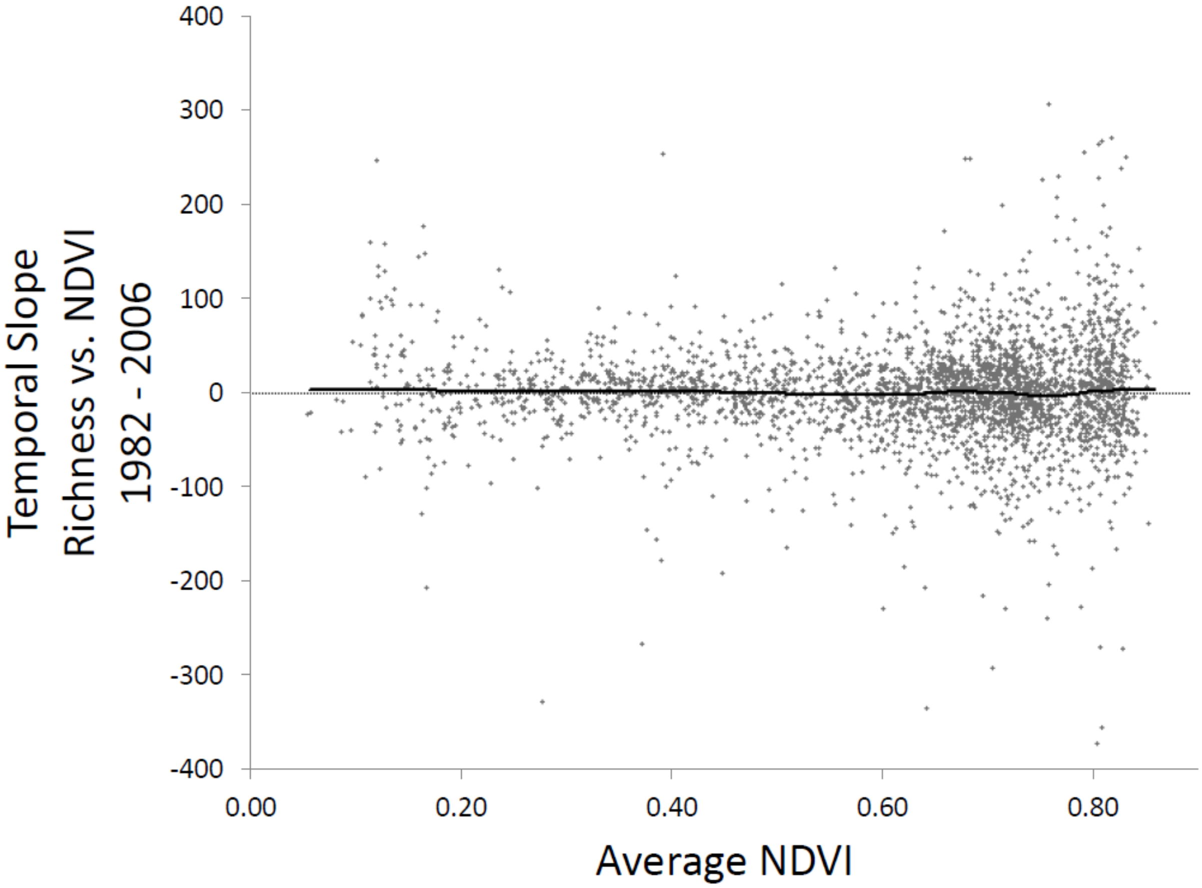

FIG. 1.5. Temporal regression slopes plotted against site-average NDVI (Normalized Difference Vegetation Index) at each BBS site from 1982 to 2006. Bold line is Lowess regression line.

SUPPLEMENTAL MATERIAL

APPENDIX 1.A

Table 1.A1. Spatial regression slope and r^2 values for each year from 1982 to 2006. Regressions were performed using a linear fit for richness vs. NDVI, abundance vs. NDVI, and log fit for richness vs. abundance.

	Richness vs. NDVI (linear)		Abundance vs. NDVI (linear)		Richness vs. Abundance (power function)	
Year	Slope	r^2	Slope	r^2	Slope	r^2
1982	41.35	0.32	23.66	0.00	0.20	0.08
1983	45.44	0.36	6.12	0.00	0.22	0.10
1984	41.81	0.31	-11.08	0.00	0.23	0.11
1985	40.37	0.31	0.22	0.00	0.24	0.12
1986	42.02	0.32	53.39	0.00	0.25	0.12
1987	44.86	0.35	88.76	0.00	0.29	0.15
1988	46.63	0.38	48.61	0.00	0.27	0.13
1989	46.33	0.39	92.57	0.00	0.31	0.19
1990	47.43	0.40	222.42	0.02	0.36	0.25
1991	47.96	0.39	212.27	0.01	0.35	0.22
1992	44.64	0.38	177.28	0.01	0.32	0.18
1993	45.47	0.34	173.89	0.01	0.37	0.24
1994	41.41	0.30	170.21	0.01	0.36	0.24
1995	44.92	0.34	196.59	0.01	0.37	0.23
1996	40.35	0.33	165.15	0.01	0.37	0.26
1997	41.48	0.33	162.25	0.01	0.35	0.23
1998	43.93	0.34	198.17	0.01	0.34	0.21
1999	40.71	0.29	249.99	0.02	0.34	0.23
2000	41.29	0.31	282.86	0.03	0.39	0.29
2001	42.92	0.34	297.14	0.03	0.38	0.27
2002	40.69	0.32	253.16	0.02	0.40	0.33
2003	40.29	0.30	242.33	0.02	0.36	0.26
2004	43.04	0.32	268.29	0.02	0.37	0.27
2005	43.70	0.32	225.01	0.02	0.37	0.26
2006	41.71	0.32	207.26	0.01	0.35	0.24
min:	33.36	0.32	-11.08	0.00	0.20	0.08
max:	47.82	0.42	297.14	0.03	0.40	0.33
mean:	39.85	0.37	160.26	0.01	0.33	0.21

APPENDIX 1.B

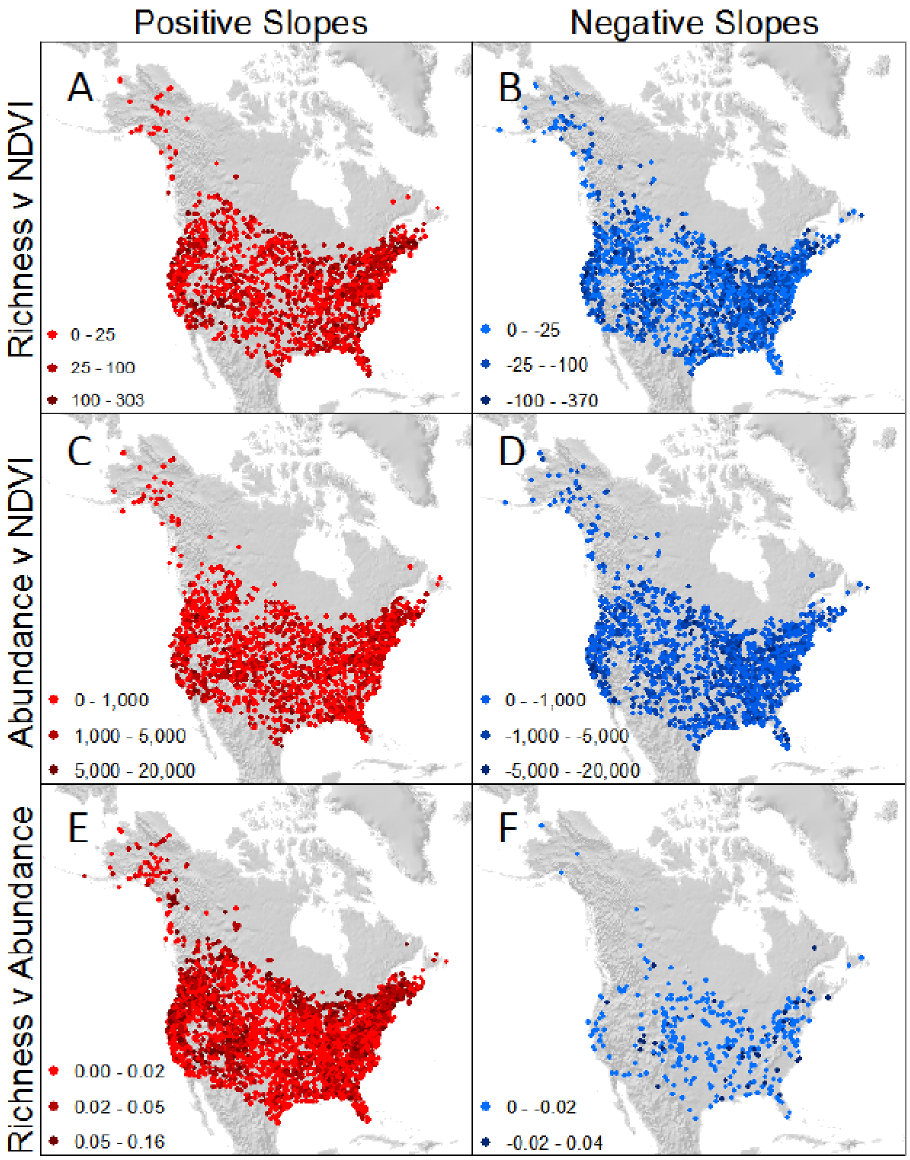

Fig. 1.B1. Maps showing geographic distributions of temporal regression slopes between (A, B) bird species richness and NDVI (Normalized Difference Vegetation Index), (C, D) total bird abundance and NDVI and (E, F) species richness and total abundance. Left panels show all sites with positive slopes, and right panels show all sites with negative slopes.

CHAPTER 2

Part I

Raw richness outperforms effort-adjusted richness in estimating winter avian diversity using the Christmas Bird Count

LUANNA L. DOBSON[1] AND BRADFORD A. HAWKINS

Department of Ecology and Evolutionary Biology, University of California, Irvine 92697

[1] Corresponding author: e-mail: ldobson@uci.edu

ABSTRACT

It has long been a subject of debate how best to leverage Christmas Bird Count (CBC) data to account for bias stemming from nonuniform sampling effort across sites. Using data from the years 1997 - 2007, we performed linear and log-transformed adjustments of species richness incorporating numbers of participants, parties, hours, and distances covered as well as a mathematical estimate which uses the ratio of singletons to doubletons to estimate richness (Chao1), and mapped the resultant spatial distributions of estimated richness. To assess these methods, we compared the richness patterns against the known spatial relationship between avian species richness and primary productivity. We regressed each richness estimate against the normalized difference vegetation index (NDVI, a proxy for primary productivity) with the assumption the richness estimate correlating most strongly with NDVI is likely to be the best estimate of true species richness. Regressions were calculated for every year in the time series and r^2s averaged across years. Unadjusted raw richness had the strongest relationship with

NDVI, with an average r^2 of 0.28 (SD ± 0.01). No linear effort-adjusted richness estimates were related to NDVI ($r^2 = <0.01 - 0.02$); log-transformed effort adjustments and Chao1 performed better ($r^2 = 0.07 - 0.27$) but none worked as well as raw richness. We recommend analyses of avian species richness using the Christmas Bird Count use raw richness and forgo accounting for differences in sampling intensity whose relationships with richness are very uncertain and almost certainly not linear.

INTRODUCTION

Many big questions in ecology are best investigated using long-term and broadscale datasets. Thanks to a handful of long-standing volunteer surveys, we have reservoirs of data documenting communities past and present that may give us a window into answering some of these questions. Some of the longest running and best known volunteer survey programs are avian, the Breeding Bird Survey (BBS) and the Christmas Bird Count (CBC). Because of its strict and consistent protocol, the BBS is perceived as a reliable data source and is widely used in analyses of avian diversity (Hurlbert and Haskell, 2003; Currie *et al.*, 2004; Hurlbert, 2004; La Sorte and McKinney, 2007; La Sorte *et al.*, 2009; White and Hurlbert, 2010; Mikkelson *et al.*, 2011; Davey *et al.*. 2012; McDonald *et al.*, 2012; Rittenhouse *et al.*, 2012; Coyle *et al.*, 2013; Culbert *et al.*, 2013; Stegen *et al.*, 2013; Boucher-Lalonde *et al.*, 2014; Goetz *et al.*, 2014; Karanth *et al.*, 2014; Pidgeon *et al.*, 2014; Distler *et al.*, 2015; Dobson *et al.*, 2015; Fristoe, 2015). By contrast, the CBC's usefulness has been criticized because of its lack of standardization, the consequences of which have been discussed at great length, along with varied recommendations for improvements (Stewart, 1954; Dunn *et al.*, 2005). Despite these concerns having been raised repeatedly, it remains a subject of debate how best to account for bias stemming from nonuniform sampling intensity across sites in the CBC.

The CBC, initiated in 1900 by the National Audubon Society, is commonly regarded as the first citizen science program anywhere. Although the CBC originated in North America, it has expanded through the years to include many other countries. The CBC is conducted in the winter, on one day in the weeks preceding or immediately following the Christmas holiday. In the CBC at each circle (The CBC name for a site) as many volunteer as are interested arrive at the start of the day and self-assemble into different sized parties. These groups meander away from the survey site's central meeting location to travel varying distances, performing a sight-and-sound survey as they go. Because of the casual nature of the CBC, the number of participants, parties, hours, mode of travel, and distance traveled can change at a site from year to year.

The primary source of hesitance to use CBC data for diversity research is the CBC's nonuniform sampling intensity across sites. No one has evaluated biases associated with nonuniform effort directly, leaving much uncertainty about the usefulness and reliability of this data. In animal surveys increased sampling intensity is expected to drive up both the number of species identified and species abundances, but it is unclear how sampling intensity should be measured, or what method should be used to account for it. Even Audubon says of its own program " ..considerable skepticism remains concerning the utility of CBC data for the purposes of trend estimation. [S]tatistical studies may be required before the use of CBC data reaches its full potential" (Sauer *et al.,* 1996a). These concerns have rendered research using CBC data relatively stagnant, despite the CBC offering unparalleled spatial and temporal scope documenting wintering bird assemblages. As a consequence our understanding of wintering avian diversity across North America remains extremely limited. Because the BBS is conducted in the summer during the breeding season and the CBC is conducted in the winter, it is also tempting to compare these surveys to identify seasonal patterns. Unfortunately, when comparing datasets when one is not standardized, it is challenging to know how robust any conclusions might be. Despite these limitations, encouraging patterns have managed to rise above the noise (Hurlbert and Haskell, 2003).

Of the workers who have used CBC data, most attempt to reconcile sampling limitations by adjusting avian data by some measure of data collection intensity. The CBC records assorted effort metrics (*see* methods below), with the hope that these data will allow researchers to account for differences in effort, although there is no consensus on which of these measures is most appropriate. Audubon uses a ‘party hour’ metric to linearly adjust species abundances (the number of individuals of a given species) when calculating population trends (Sauer *et al.*, 1996b) and cautiously recommends using the party hour with the caveat that " [t]he potential biases associated with these effort adjustments, or with other aspects of the analyses of CBC data, have never been the subject of thorough statistical review" (Sauer *et al.*, 1996a). Consistent with Audubon's recommendation, Meehan *et al.* (2004) identified a linear relationship between total assemblage abundance and party hour. However, Audubon makes no recommendation for adjusting for effort when estimating species richness at a site.

Approaches to control for effort in published studies using CBC data include none, on the grounds that it has not systematically changed through time and therefore is not expected to bias trends (Chao and Bunge, 2002; La Sorte and Jetz, 2012), whereas others do not specify if any adjustment was made for site effort, leaving one to assume raw richness was used (Hurlbert and Haskell, 2003; Distler *et al.*, 2015). Still others include a measure of effort as a model covariate rather than transforming raw richness, for example La Sorte *et al.* (2009) included log-transformed party hours as a covariate in their models. Advanced modeling techniques when accounting for varying effort have also been advocated (Link and Sauer, 1999), though these approaches appear not to have caught on broadly.

The availability of data from the CBC could be a boon to the avian macroecology community, but only if we can identify how best to account for differences in sampling intensity across time and space. Here, we aim to evaluate the relative accuracy of avian species richness estimates across North America when different methods of accounting for nonuniform sampling intensity are used. Specifically, our goal was to identify which effort metric, if any, is likely to be the most effective for estimating true avian species richness.

METHODS

Using avian richness data and the effort report from the Christmas Bird Count, we estimated richness across North America using six effort metrics to control for varying sampling intensity. CBC historical results were downloaded from the National Audubon Society (www.christmasbirdcount.org) for the years 1997 - 2007, used to calculate unadjusted raw species richness (defined as the total number of species identified) at each site in each year. Nonnative, marine, and nocturnal species were excluded. The CBC effort report reports the minimum and maximum number of parties (large parties at the start of the day typically fragment into multiple smaller parties by day's end), cumulative party hours, total number of field counters, cumulative distance traveled by all parties, and travel mode (car, snowshoe, boat, walking), although travel mode was not included in our analyses. Many sites report only some of the effort metrics, and not every site is sampled in each year. To ensure we were making fair comparisons across effort metrics, we included only those sites that were sampled every year between 1997 and 2007 and for which every effort metric was reported, yielding 1078 sites.

First, we used each effort metric to adjust species richness linearly by sampling intensity. To do so, we divided raw richness at a site by each effort metric, giving us richness per unit of effort. These estimates were calculated for each year in the time series and mapped using ArcGIS 10.2 (Esri, Redlands, California, U.S.A.). We then repeated the process using log-transformed measures of effort, again repeated for each year and mapped.

Finally, we calculated a mathematical richness estimate that is independent of the CBC effort metrics but attempts to control for variation in sample effort, Chao1 (Chao and Bunge, 2002). Chao1 uses the ratio of the number of singletons to doubletons (species with an abundance of just one individual, or two individuals, respectively) to estimate richness. The underlying principle is that early on in a sampling effort, there will be many singletons and few doubletons as each new record is likely to contribute a newly identified species to the pool. If a sample contains many singletons compared to doubletons, sampled richness is probably far less than the true richness of the site, and therefore the Chao1 estimate will be much higher than raw sampled richness. If there are far more doubletons compared to singletons, it is likely that nearly all species in the species pool have been sampled at least once, and the sampled richness approaches the true richness of the site. Chao1 richness estimates were mapped across North America for each year in the time series.

Because mapped distributions are difficult to compare quantitatively, as an additional test we compared the estimated richness patterns against a documented spatial relationship. Animal species richness has been demonstrated to correlate with primary productivity at a broad range of spatial extents and resolutions, for a great number of taxa, in many regions globally, predicating much of the literature in species-energy theory and the productivity hypothesis (Currie and Paquin, 1987; Hawkins *et al.,* 2003; Turner and Hawkins, 2004; Wright, 1983). Distributions of breeding season avian species richness are well-known to follow this trend, correlating spatially with measures of summer primary productivity (Wright, 1983; Hawkins *et al.,* 2003; Currie *et al.,* 2004; Hurlbert, 2004; Carnicer *et al.,* 2007; Phillips *et al.,* 2008; Verschuyl *et al.,* 2008; Hurlbert and Jetz, 2010; Hansen *et al.,* 2011; Morales-Castilla *et al.,* 2012; Cumming *et al.,* 2013; Zhang *et al.,* 2013; Dobson *et al.,* 2015). Less is known about the strength of the relationship between bird richness and primary productivity in winter, largely because work evaluating wintering avian richness is limited. One of the few studies looking at winter avian richness reported that wintering richness (derived from CBC data) and primary productivity are significantly spatially related ($r^2 = 0.25$) (Hurlbert and Haskell, 2003).

We regressed each richness estimate against primary productivity with the assumption whichever richness estimate correlates most strongly with primary productivity is likely to be the best estimate of true species richness. We used the normalized difference vegetation index (NDVI) as our measure of winter primary productivity. NDVI is a remotely sensed measure of greenness based on the spectral signature of light reflected from plant chlorophyll and is widely used proxy for primary productivity (Hurlbert and Haskell, 2003; Hawkins, 2004; Phillips *et al.,* 2008; Buono *et al.,* 2010; Pau *et al.,* 2012; Siefert *et al.,* 2013; Stegen *et al.,* 2013; Dobson *et al.,* 2015) . The index ranges from 0 (bare ground) to 1 (saturated greenness). NDVI has some limitations. Phillips *et al.* (2008) found NDVI performs poorly at the extreme ends of the index when there is either a lot of bare ground or in cases of very high primary productivity wherein greenness saturates. Despite these limitations, NDVI has nonetheless been demonstrated to be a strong proxy for primary productivity at broad spatial scales. Phillips *et al.* (2008) found that across varied habitats, NDVI is correlated with MODIS-derived primary productivity measures including gross primary productivity (GPP) (r =0.95) and net primary productivity (NPP) (r=0.91). Boelman *et al.* (2003) found that even in Tundra ecosystems NDVI was strongly related to above-ground biomass (r^2 = 0.84) and gross ecosystem production (r^2 = 0.75), concluding that "NDVI measurements may be a feasible means of monitoring [vegetation] changes." Given these findings and that the scale of analysis is continental and therefore spans a great range of primary productivity, we expect NDVI is a strong proxy. Additionally, NDVI has a practical advantage over more direct primary productivity measures like the MODIS-derived GPP and NPP variables used in Phillips *et al.* (2008). NOAA's AVHRR satellites have been continuously documenting NDVI since 1982, much earlier than any other remote sensed primary productivity measures (NASA's MODIS system was initiated in 2002). Thus NDVI permits time-series analyses that other measures of primary productivity cannot support.

We regressed each richness estimate, including raw richness, against an 18 y average January NDVI dataset. NDVI data were collected by the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer satellite system (Pinzon *et al.*, 2005; Tucker *et al.*, 2005) and downloaded from the Global Land Cover Facility (Tucker *et al.*, 2004). We repeated these regressions for every year in the time series and averaged the spatial r^2s across years. Finally, we performed pair-wise correlations between each richness estimate for each year.

To examine temporal trends in effort within the CBC, we averaged each effort metric across sites in each year, and these averages regressed against years.. Using the same method, we also examined trends in raw richness across time. To assess trends in the relationship between raw richness and NDVI across time, the strengths of the correlation (r^2) between raw richness and NDVI was regressed against years.

RESULTS

Raw species richness generated a diversity gradient that roughly corresponds to latitude across North America, as we might expect for bird species richness, whereas all maps of linear effort-adjusted richness estimates yielded no clear spatial patterns (Fig. 2.1.1). All linear effort-adjusted richness estimates yielded extremely low r^2 values when regressed against NDVI (mean r^2 ± SD: Field Counters <0.01 ± <0.01, Party Hours <0.01 ± <0.01, Max Parties 0.01 ± <0.01, Min Parties 0.01 ± <0.01, Kilometers 0.02 ± 0.02), whereas raw richness had a much higher average spatial regression r^2 of 0.28 (± 0.01) (Fig. 2.1.2).

Maps of log-transformed effort-adjusted richness estimates yielded clearer spatial gradients (Fig. 2.1.3) and performed better than linear adjustments when regressed against NDVI (mean r^2 ± SD: log[Min Parties] 0.07 ± 0.01, log[Max Parties] 0.15 ± 0.02, log[Field Counters] 0.18 ± 0.02, log[Party Hours] 0.23 ± 0.03, log[Kilometers] 0.27 ± 0.03) (Fig. 2.1.4). The Chao1 richness estimates yielded a clear spatial gradient and reasonably high average r^2 at 0.24 (± 0.01) (Figs. 2.1.3, 2.1.4).

Therefore, raw richness had the strongest relationship with NDVI, followed respectively by richness adjusted by log(Kilometers), the Chao1 estimate, and richness adjusted by log(Party Hours). Unsurprisingly, these richness estimates are each strongly correlated with one another, particularly the log(Kilometers) and Chao1 estimates (Table 2.1.1). Notably, assuming the link between birds and vegetation is real, none of the effort-correction methods performed better than raw richness.

Effort across the CBC is changing through time in interesting ways between 1997 to 2007. We regressed the average effort for each metric across all sites in each year against years and found the distance traveled and the minimum party number do not appear to be changing, though effort is increasing by 6.08 field counters, 2.83 maximum parties, and 2.05 party hours per decade. Raw richness is increasing through time as well by 2.75 species per decade. However, these changes do not appear to have any bearing on raw richness estimates, given that the strengths of the correlation (r^2) between richness and NDVI has not changed systematically through time (Fig. 2.1.5).

DISCUSSION

Maps of raw species richness look as would be expected, with higher bird richness in southern and coastal latitudes in the winter than in interior northern latitudes. In contrast none of the mapped richness estimates generated using linear effort-adjustments show biologically sensible patterns across the map, strongly suggesting that these effort-corrections obscure the richness signal that exists in raw richness. Log-transformed effort adjustments yield maps that look similar to what we might expect of bird species richness in the winter ─ notably the maps based on log (party hours) and log (kilometers) adjustments. The Chao1 richness estimate yields a clear gradient as well. These three best-performing corrected maps have patterns extremely similar to that of raw richness, raising the question of what benefit arises from making these adjustments.

When regressed against NDVI, raw richness outperforms all linear and log-transformed effort-adjusted species richness estimates. This result is surprising, as it undermines most assumptions of species accumulation across sample effort. These results suggest the species richness signal in North America is probably strong enough to override error introduced by nonstandardized sampling. In fact using a linear adjustment for effort erodes the richness signal fully. Dunn *et al.* (2005) noted "estimates from analyses based on birds per unit effort, which implicitly assumes a linear relationship between effort and counts, can sometimes be seriously biased — potentially even more than estimates based on counts unadjusted for effort." When applied to species richness, their suggestion that unadjusted estimates can be superior appears correct. That most other r^2s are near 0 demonstrates the weakness of those metrics at estimating species richness. We suspect the other traditional estimators have such low r^2s because they are poor analytical choices. They likely introduce so much noise that the spatial pattern of wintering bird species richness is eroded.

Of note is the r^2 of the statistical relationship between raw species richness and NDVI averages 0.28 in winter, which albeit not strikingly high is a value in-line with estimates found in the literature. As mentioned earlier Hurlbert and Haskell (2003) found an r^2 of 0.25 for the relationship between wintering bird richness and December NDVI. In the breeding season, Hurlbert (2004) demonstrated an r^2 of 0.30 for the relationship between breeding bird richness and NDVI in forest systems and 0.16 in grassland systems. Phillips *et al.* (2008) found linear relationships between breeding bird species richness and four different measures of primary productivity (NDVI, EVI, GPP, and NPP) with r's ranging from 0.36 - 040. Cumming *et al.* (2013) found four vegetation metrics (GPP, NPP, leaf area index, and NDVI) together explained 23% of variance in a model explaining breeding bird richness. Dobson *et al.* (2015) identified r^2s from 0.29 - 0.40 for breeding bird richness and summer NDVI in the years 1982 - 2006. Additionally, despite increasing average avian richness through time, the spatial relationship between winter raw richness and NDVI remains remarkably stable across years. Our findings are consistent with the result of Hurlbert and Haskell (2003) (*see also* White *et al.*, 2010) that the spatial relationship between bird species richness and primary productivity is stable across seasons.

Because the two estimates performing very similarly to raw richness (Chao1 and log[Kilometers]) are each so strongly correlated with raw richness (and with each other), it is reasonable to assume that these estimates add very limited information that raw richness does not already provide. Even though those estimates are strong performers, it is probably unnecessary to use them, as doing so simply adds complexity into a model with minimal unique contribution. It should be noted that these conclusions only apply to estimates of species richness at broad spatial scales. The role of sample effort when estimating species abundances, population trends, or estimates at finer spatial scales is still unknown, and likely matters more.

It remains to be seen if our unintuitive result holds for other broadscale animal surveys, or for different taxa, but for avian surveys expert opinion (J. C. Avise, pers. comm.) suggests despite the increasing popularity and participation in the Christmas Bird Count over time, there is a core population of expert birders that drive the survey, and their participation does not vary substantially from year to year. In line with this supposition is the fact, that in our time series, the number of field counters is going up but the number of parties at the beginning of the day is not, which could be explained by a stable core of experts that are accompanied by increasing numbers of participants in their associated parties each year. If so, this helps explain why accounting for effort does not improve richness estimates. The CBC reports total participation which may not be representative of the smaller group of expert participants making most data contributions. Conversely, Audubon warns that improvements in bird identification skill (thanks to better guides and optical equipment) might create a bias in the opposite direction, such that "analyses based on counts adjusted by party-hour may be positively biased as a consequence" (Sauer *et al.*, 1996a). Regardless of why it may be so, raw richness, unadjusted for effort, appears to be a strong estimator of true species richness. Consequently, we recommend analyses of avian species richness based on the Christmas Bird Count use raw richness that is unadjusted for differences in sampling intensity when analyzing patterns of diversity at the continental scale.

We argue work evaluating wintering avian richness has been stagnant because it is unknown how exactly to adjust for variation in sample effort when using CBC data. Few studies have evaluated the drivers of wintering bird species richness, despite the rich reservoir of assemblage data available from the CBC. We sought to identify the analytical processes that would elevate the CBC's usefulness to that of other projects like the BBS by evaluating the biases associated with effort. Our findings provide a common framework for working with CBC richness data. We hope workers will have more confidence performing analyses of species richness using the CBC data, leading to an improved understanding of wintering avian diversity.

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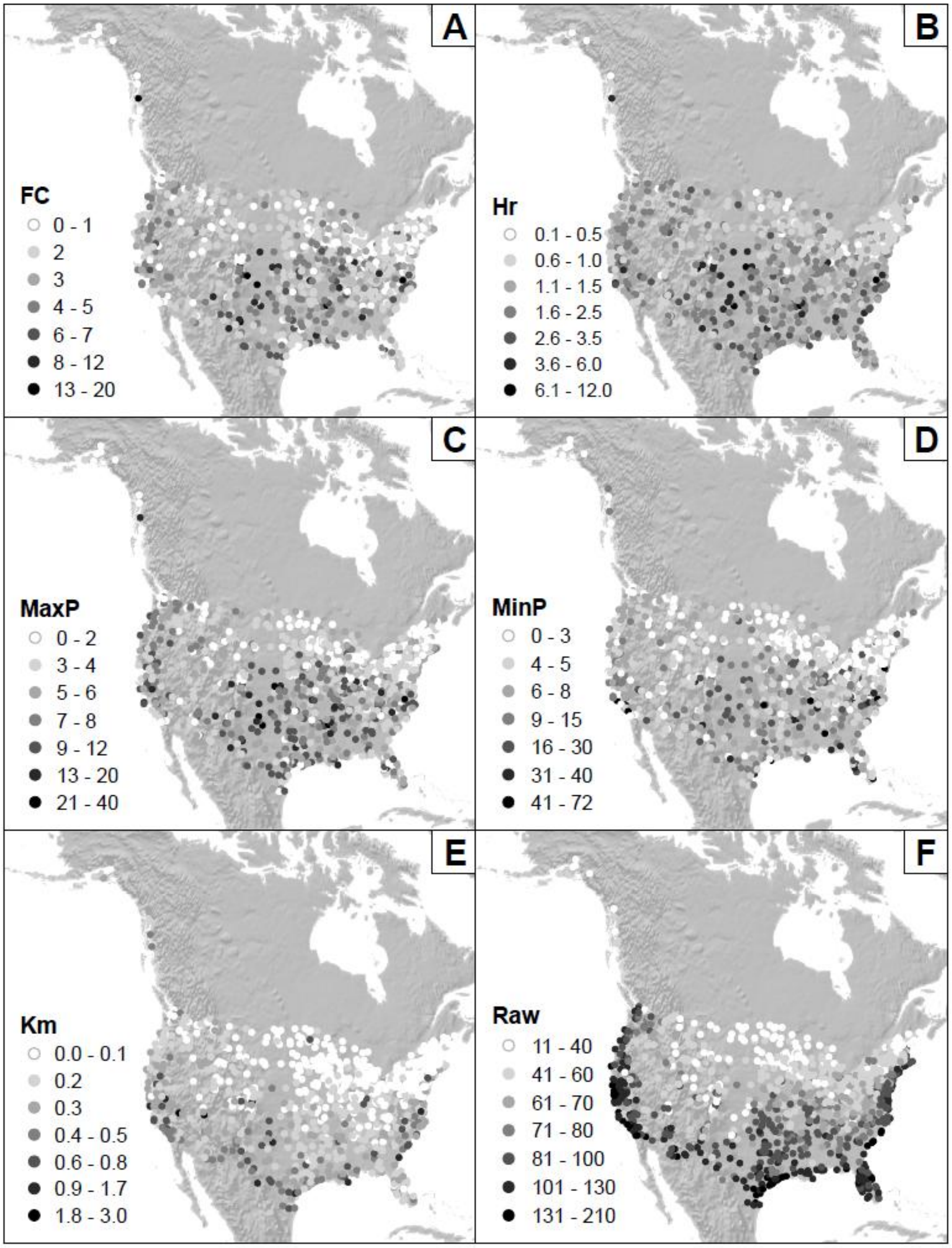

FIG. 2.1.1. Spatial distribution of avian species richness estimates in the Christmas Bird Count in 2007. Maps picture the distribution of raw species richness and richness linearly-adjusted by different effort metrics reported in the CBC's effort report. Spatial data were prepared for each year in the time series from 1997 - 2007, but only 2007 are shown here. The general patterns are

representative of each year. Maps are in order of strength of relationship with NDVI as reported in Figure 2.1.2. Richness estimates are the raw richness value divided by the following effort metrics: (**A**) FC, total field counters; (**B**) Hr, cumulative party hours; (**C**) MaxP, maximum party number; (**D**) MinP, minimum party number; (**E**) Km, cumulative kilometers traveled; and (**F**) Raw, raw richness without effort standardization.

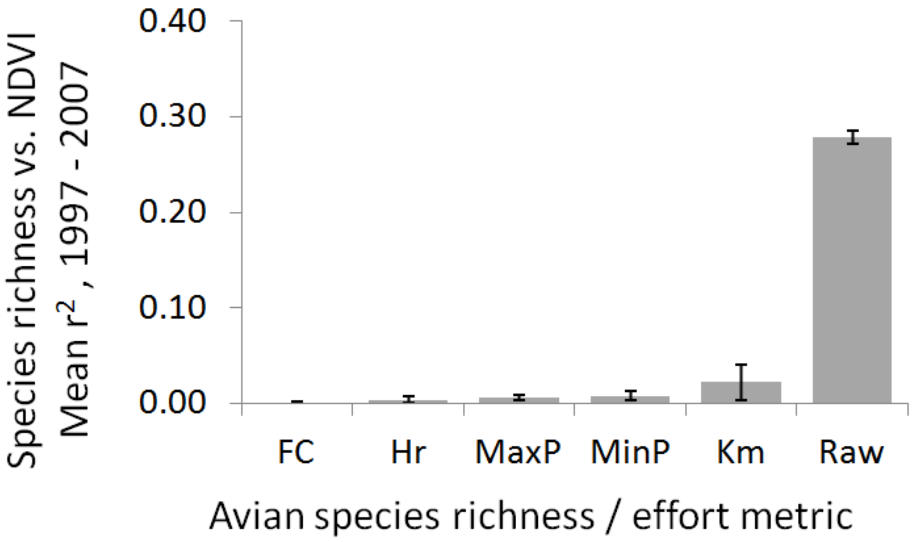

FIG. 2.1.2. Mean spatial regression r^2 for species richness estimates versus NDVI for 1,078 Christmas Bird Count sites averaged over 11 annual regressions across a time series 1997-2007. Error bars are 1 SD. Richness estimates are the raw richness value divided by the following effort metrics: FC, total field counters; Hr, cumulative party hours; MaxP, maximum party number; MinP, minimum party number; Km, cumulative kilometers traveled; and Raw, raw richness without effort standardization

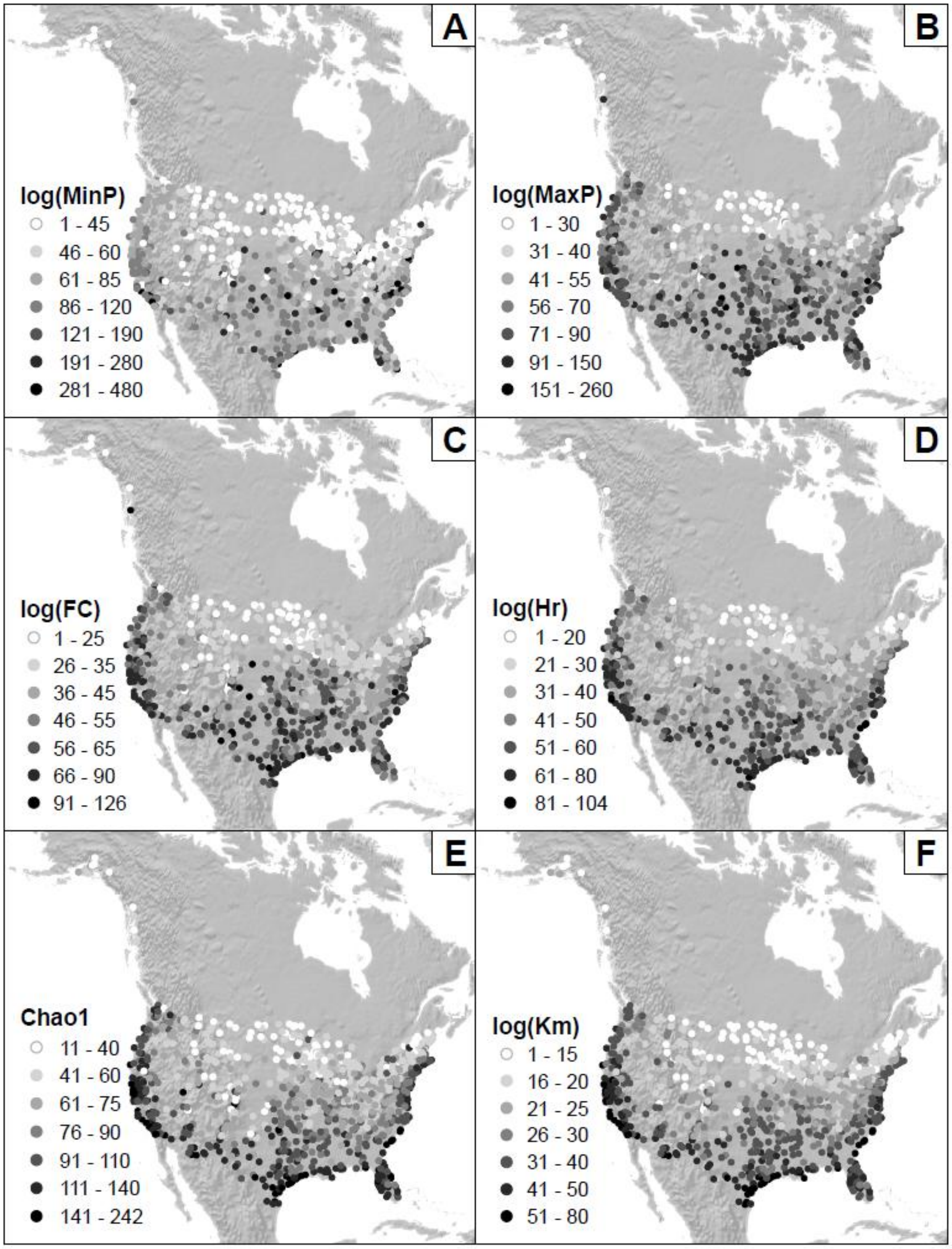

FIG. 2.1.3. Spatial distribution of avian species richness in the Christmas Bird Count in 2007. Maps picture the distribution of raw species richness adjusted by the log of different effort metrics reported in the CBC's effort report. Presentation as in Figure 2.1.1. Maps are in order of strength of relationship with NDVI as reported in Figure 2.1.4. Richness estimates are the raw

richness value divided by the following effort metrics: (**A**) log(MinP), log of minimum party number; (**B**) log(MaxP), log of maximum party number; (**C**) log(FC), log of total field counters; (**D**) log(Hr), log of cumulative party hours; (**E**) Chao1, Chao1 mathematical species richness estimate; and (**F**) log(Km), log of cumulative kilometers traveled

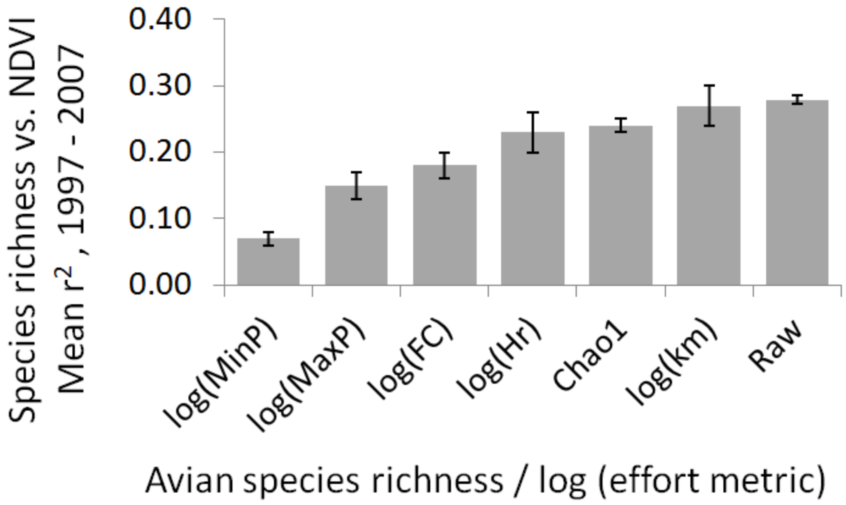

FIG. 2.1.4. Mean annual spatial regression r^2 for species richness estimates versus NDVI for 1,078 Christmas Bird Count sites. Error bars are 1 SD. Presentation as in Figure 2.1.2. Richness estimates are the raw richness value divided by the following effort metrics: log(MinP), log of minimum party number; log(MaxP), log of maximum party number; log(FC), log of total field counters; log(Hr), log of cumulative party hours; Chao1, Chao1 mathematical species richness estimate; log(Km), log of cumulative kilometers traveled; and Raw, raw richness without effort standardization

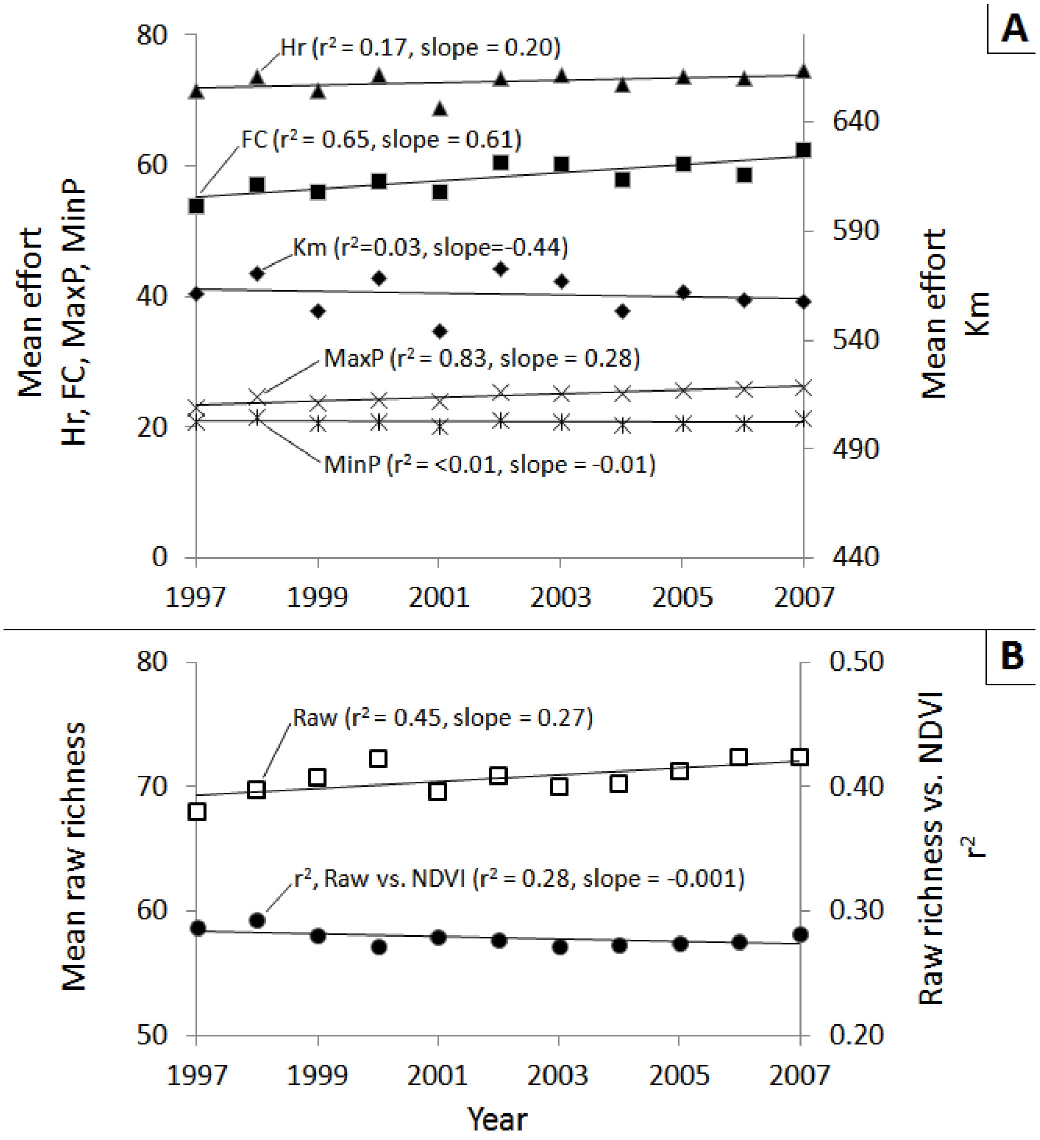

FIG. 2.1.5. (**A**) Average annual effort for each recorded effort metric across 1,078 Christmas Bird Count sites, regressed against years. Party hours (Hr), field counters (FC), maximum party number (MaxP), and minimum party number (MinP) are displayed on the primary axis, and kilometers traveled (Km) on the secondary axis. (**B**) Average annual raw richness across sites, regressed against years on the primary axis, and on the secondary axis the annual r^2 of the spatial relationship between raw richness and NDVI, regressed against years

TABLE 2.1.1. Pair-wise coefficients of determination (r^2) between all richness estimates, averaged across years 1997 - 2007, in order of strength of correlation with NDVI. Richness estimates are calculated using the raw richness values divided by the following effort metrics: FC, total field counters; Hr, cumulative party hours; MaxP, maximum party number; MinP, minimum party number; Km, cumulative kilometers traveled; log(), log-transformed effort metrics; Chao1, Chao1 mathematical species richness estimates; and Raw, raw richness, unadjusted for effort

	FC	Hr	MaxP	MinP	Km	log(MinP)	log(MaxP)	log(FC)	log(Hr)	Chao1	log(Km)	Rich
FC	1.00	0.51	0.70	0.20	0.11	0.11	0.32	0.34	0.08	0.00	0.01	0.00
Hr		1.00	0.63	0.21	0.31	0.13	0.31	0.19	0.19	0.00	0.05	0.00
MaxP			1.00	0.30	0.14	0.21	0.55	0.32	0.15	0.01	0.04	0.01
MinP				1.00	0.07	0.83	0.20	0.13	0.09	0.02	0.04	0.02
Km					1.00	0.07	0.13	0.11	0.16	0.04	0.18	0.04
log(MinP)						1.00	0.41	0.36	0.34	0.23	0.28	0.24
log(MaxP)							1.00	0.84	0.73	0.45	0.55	0.48
log(FC)								1.00	0.79	0.58	0.66	0.61
log(Hr)									1.00	0.75	0.89	0.80
Chao1										1.00	0.86	**0.95**
log(Km)											1.00	**0.91**
Rich												1.00

CHAPTER 2

Part II

Diversity without abundance: Minimal support for the productivity hypothesis in explaining species richness of North American wintering bird assemblages

LuAnna L. Dobson and Bradford A. Hawkins

ABSTRACT

It is well-documented that primary productivity and animal species richness are positively correlated for a variety of taxa across a wide range of spatial scales and extents. The productivity hypothesis had been credited for explaining these correlations by asserting that places with more energy fixed in the system by plants (i.e. high primary productivity) should support more individuals at higher trophic levels, whereby the community accumulates more species. For birds in particular, many observational studies have interpreted the spatial association between species richness and productivity as support for the hypothesis. It follows that when vegetation biomass increases or declines temporally, so should animal species richness. However, a recent study focused on the North American Breeding Bird Survey found that when evaluated temporally, the productivity hypothesis failed to explain interannual changes in breeding season avian richness. Even so, it is possible that avian richness has a stronger dependence on primary productivity in the winter months when birds are stressed by colder temperatures and food scarcity. Using community data from the Christmas Bird Count in North America from 1982 - 2002, we evaluated if wintering local avian richness tracks changing

primary productivity. By regressing avian species richness against winter NDVI (normalized difference vegetation index, a proxy for primary productivity) at each CBC site through years, we found that species richness weakly responds to interannual changes in NDVI. However, we found no support for the more individuals mechanism predicted by the hypothesis. Thus, the productivity hypothesis apparently explains none of the interannual variation in North American species richness of avian assemblages in summer and only a small fraction of the variation in winter.

INTRODUCTION

Primary productivity and avian species richness are positively correlated across a range of spatial scales and extents (Wright 1983, Hawkins et al. 2003a, 2007, Hurlbert and Haskell 2003, Hurlbert 2004, Currie et al. 2004, Carnicer et al. 2007, Verschuyl et al. 2008, Phillips et al. 2008, Hurlbert and Jetz 2010, Hansen et al. 2011, Morales-Castilla et al. 2012, Cumming et al. 2014, Zhang et al. 2013), and more broadly, the association between vegetation and richness has been identified for a variety of animal taxa (see e.g. Brown 2014 for discussion). The primary explanation for these relationships is the productivity hypothesis (also known as the more individuals hypothesis or the energy-richness hypothesis). The productivity hypothesis predicts that the amount of energy captured in a system via primary productivity directly limits the number of individuals that place can support by imposing a maximum capacity. As the community accumulates more individuals from the regional pool more species are also accumulated either via neutral processes (Hubbell 2001, Hawkins et al. 2003b, Hurlbert 2004, Evans et al. 2005, White and Hurlbert 2010) or via reduced extinction rates at high population sizes (Evans et al. 2006, Carnicer et al. 2007, Yee, D. A., Juliano 2007).

Despite the simple and compelling logic underlying the productivity hypothesis, and its broad apparent support from many observational studies, experimental manipulations have largely failed to bear out the predictions of the hypothesis (see Dobson et al. 2015 for a more thorough discussion of the literature). This disparity between results obtained via observation versus manipulation may be the product of differences in scale, but more likely suggests that observational approaches may be making unmerited assumptions of causality on the basis of spatial correlation. Progress resolving correlative vs. experimental approaches is difficult because broad-scale experimental manipulations of primary productivity are challenging and arguably unethical. A third approach, although still not as definitive as a controlled experiment over entire continents, can utilize a temporal analysis of response to change over time to strengthen claims of potential causality at broad geographic scales. Few observational studies have taken this third approach, most likely due to the lack of productivity and species richness data over long enough time spans. However, recently Dobson et al. (2015) used historical avian richness data from the North American Breeding Bird Survey across two and a half decades to test for a diversity response to changing summer primary productivity and found that species richness appears to respond randomly to changing productivity; a result consistent with most experimental manipulations. Furthermore, they found that avian community abundance was not spatially correlated with primary productivity, calling into question the primary mechanism by which energy is hypothesized to translate into species richness.

Despite this single analysis and result, birds are highly mobile organisms, with over half of North American species undertaking seasonal migrations to exploit winter primary productivity in warmer southern climates (Hurlbert and Haskell 2003, Gill 2007, Newton 2008). As mentioned above, primary productivity is hypothesized to impose a resource-based carrying capacity on the number of organisms a place can support, which assumes the organisms found there are limited by the energy available at that place. However, when organisms are highly mobile, and particularly when they undertake migration, individuals can supplement their energy use at one place with energy from other systems, thereby partially ameliorating the constraint imposed by energy availability at the focal place. Under this logic, it is possible that narrowing focus on fully resident, non-migrant species may generate better support for the productivity hypothesis. Populations of year-round resident species more closely reflect the coupled plant-animal systems envisaged by the productivity hypothesis.

Wintering avian communities in North America are primarily (though not entirely) composed of year-round resident species that overwinter in the same place in which they breed in spring and summer. It has already been confirmed that avian species richness in winter is correlated with primary productivity spatially much like in summer (Hurlbert and Haskell 2003). In this paper we test the simplest two predictions of the productivity hypothesis, that as winter primary productivity changes across years, both wintering species richness and total bird abundance should temporally track that change.

METHODS

Data collection

Species richness

Bird data was obtained from National Audubon's Christmas Bird Count (CBC) for each year in the time series 1982 - 2002 (National Audubon, 2010). The CBC is an annual volunteer-based survey wherein on a given calendar day volunteers perform sight and sound counts of species and their abundances within 24 km diameter circular sites. CBC count records and geographic coordinates for each site in North America were downloaded with permission from National Audubon. We compiled species richness and total community abundance (the total number of individuals of all species) for CBC sites across the United States for each year. Nocturnal, marine, accidental and exotic species were excluded, and sites that were sampled in fewer than 8 years were excluded, leaving 1,509 sites available for analysis. CBC site coordinates were used to map estimates of species richness. Mapping and spatial analysis were performed using ArcGIS 10.0.

CBC records contain many instances of identification to sub-species or race level. These were re-classified to species level. In cases where taxonomic designations have changed in the course of the time series, decisions were made on a case-by-case basis to maintain taxonomic consistency through the time series. In cases where two species have been merged into a single species, the new single species replaced old instances of the separate species. Where one species has been resolved into two distinct species, the original single species name replaced newer instances of the two. Common names were used for species richness counts, due to many blanks and spelling inconsistencies in the 'scientific name' field of CBC records. Inconsistencies in common name designations were corrected for consistency throughout the database (Table 2.2.A1).

There is debate in the literature about how best to control for variation in sample effort in CBC-based estimates of species richness. Between sites and within a site from year to year, sites vary in sample effort on the basis of volunteer participation and behavior. Dimensions of sample effort that vary include the number of volunteers that participate, how many groups these volunteers form, the duration of time each group searches, and the cumulative distance traveled by participants. Given classic predictions of species-area and species-time relationships, these variations in effort are generally expected to bias both species richness and community abundance measures at sites. However, a recent analysis concluded that raw richness, unadjusted for effort, is the best estimate of winter avian richness, and that attempting to control for sample effort seriously erodes estimates of richness (Dobson and Hawkins unpubl. ms). Since sample effort is uncontrolled during the survey, we also estimated actual richness at each site using the non-parametric estimator Chao1. However, we found that estimated actual richness and sample richness were very strongly correlated across sites (r = 0.95) (see Dobson and Hawkins unpubl. ms), so we used observed richness in all analyses.

Primary productivity

We used the normalized difference vegetation index (NDVI) as a proxy for primary productivity. NDVI is a remotely-sensed measure of vegetation greenness which is strongly correlated with both gross primary productivity and net primary productivity at broad spatial scales (Phillips et al. 2008), even in regions where vegetation is sparse (Boelman et al. 2003). NDVI is widely used as a proxy for primary productivity in macroecological studies (Hurlbert and Haskell 2003, Hawkins 2004, Phillips et al. 2008, Buono et al. 2010, Pau et al. 2012, Stegen et al. 2013, Siefert et al. 2013, Dobson et al. 2015).

The NDVI data product was generated and made available by the Global Inventory Modeling and Mapping Studies (GIMMS) 2.0 at the Global Land Cover Facility (GLCF) (Tucker et al. 2004), using remote sensed spectral data collected by the National Oceanic and Atmospheric Association's (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite system (Pinzon et al. 2005). The GIMMS NDVI data products for the summer months of June, July, and August were used in analyses of breeding season diversity reported by Dobson et al. (2015) which this study intends to complement, but the GLCF has taken the GIMMS NDVI data product offline indefinitely for maintenance. A reduced-resolution version of the GIMMS NDVI product was obtained online from the Oak Ridge National Laboratory (ORNL) archives at http://daac.ornl.gov (Hall et al. 2006, Tucker et al. 2010). The years used in our time series analysis were limited by NDVI data availability from ORNL archives and span 1982 - 2002.

Because Hawkins et al. (2004) found that seasonal productivity better predicts species richness than annual productivity in the breeding season, we averaged NDVI across November, December, and January at each site, the months that bracket the CBC survey which is typically performed in mid- to late-December. NOAA's AVHRR satellite system makes data collection sweeps twice monthly. We averaged NDVI values across sweeps within our target months, removing negative values and zeros that represent either data error or non-terrestrial targets. One limitation of NDVI as a proxy for primary productivity is its vulnerability to cloud cover (as are most remotely sensed metrics). In addition to the assorted data quality control algorithms applied by the GLCF to adjust for cloud cover and other types of error in their NDVI estimates, we assume that by averaging across all six sweeps from our target months that any remaining impact of cloud cover is substantially diluted (see Dobson and Hawkins unpubl. ms for a more detailed discussion of the limitations of NDVI and justifications for its use as a proxy). We extracted NDVI values at the coordinate midpoint of each CBC site for every year in the time series, associating a single average winter NDVI value for each site in each year.

Analyses

Spatial regression

For each year in the 21-year time series, we regressed richness vs. NDVI, abundance vs. NDVI, and richness vs. abundance across all 1,509 CBC sites. We fit these regressions with linear, logarithmic, and power functions, identifying the best-fit according to which function yielded the highest average r^2 across years. Regression statistics from each year were plotted against years to visualize trends through time in the strength of the spatial relationships between avian metrics and NDVI.

Temporal regression

To evaluate whether species richness has tracked interannual changes in primary productivity, species richness was regressed against NDVI across years within each site. One regression was performed for each CBC site, where N is the number of years the site was sampled in the time series, and each data point in the regression represents species richness and NDVI for that site in one year. We fit temporal regressions with the function demonstrated in the spatial analysis as best fit (in all cases, power functions), in addition to linear functions to make results comparable to the breeding season as analyzed in Dobson et al. (2015). To consider lag effects, we performed additional regressions with a 1-year lag introduced into the response of richness to NDVI, fit with linear and power functions. Temporal best-fit was determined on the basis of highest mean r^2 across sites.

Sites with positive temporal slopes indicate that richness is tracking changes in primary productivity at those sites as predicted by the productivity hypothesis. Negative slopes would indicate that as primary productivity changes, richness responds in the inverse direction. If site richness responds randomly to changing NDVI (our null hypothesis), we would expect roughly an equal number of positive and negative temporal slope values with a mean slope not significantly different from zero. Using temporal regression statistics from all sites, we generated a distribution of temporal regression slopes, and used a t-test to compare the observed temporal slope distribution to a mean of zero. Temporal regression statistics were also calculated at every site for the other relationships predicted under the productivity hypothesis including abundance vs. NDVI and richness vs. abundance, again comparing the distribution of slope values against a null of zero.

RESULTS

Spatial analysis

Winter avian species richness was positively correlated with NDVI in every year in the time series (Fig. 2.2.1). The average spatial r^2 across years was highest for the power function, spanning 0.23 - 0.38 (mean 0.31 ± SD 0.04), with little variation in fitted curves from year to year (Fig. 2.2.1). Linear and logarithmic fits yielded mean r^2s of 0.28 (± 0.03) and 0.29 (± 0.03), respectively (see Table 2.2.B1 for all spatial regression statistics for each year fit by linear, logarithmic, and power functions). When plotted across the 21 years, the relationship between richness and primary productivity in winter has been stable (Fig. 2.2.1).

The spatial relationship between abundance and NDVI was best fit by a power function as well, with a weak but stable relationship with NDVI across years (mean $r^2 = 0.15 \pm 0.03$) (Fig. 2.2.2). Richness and abundance were positively associated and well-fit by a power function (mean $r^2 = 0.60 \pm 0.03$), again with a stable spatial relationship from year to year (Fig. 2.2.2).

Temporal analysis

Species richness weakly tracked interannual changes in NDVI over time. Fitting linear vs. power functions to temporal regressions on average yielded similar relationship strengths, with identical mean r^2 and SD across sites (See Table 2.2.B2 for temporal regression statistics for all relationships and fit functions tested). Because applying a power function did not improve the fit, and to aid in comparison with breeding season analyses reported by Dobson et al. (2015) which were fit linearly, the linear fit results are presented here for the temporal relationship between richness and NDVI. The average strength of temporal regressions between species richness and NDVI at sites was very weak (mean $r^2 = 0.07 \pm 0.10$) (Fig. 2.2.3), but the slope distribution of these relationships was significantly different from zero (Fig. 2.2.4), with 59% of sites demonstrating positive temporal slopes. This winter result is in contrast to the breeding season results reported in Dobson et al. (2015), where the same analytical approach yielded a slope distribution not significantly different from zero (Fig. 2.2.4). Introducing a 1-year lag weakened the response of winter bird richness to changing NDVI to a marginally non-significant level (Fig. 2.2.4).

There was no evidence that abundance has tracked interannual changes in NDVI over time. The average temporal slope of abundance in response to NDVI was not significantly different from zero, regardless of fit function or introduction of a 1-year lag (Table 2.2.B2). However, richness tracked interannual changes in abundance with moderate relationship strength (linear: $r^2 = 0.26 \pm 0.21$; power: $r^2 = 0.30 \pm 0.23$) with temporal slope distributions significantly different from zero (linear and power fits: $p < 0.001$).

DISCUSSION

We expected species richness to be potentially coupled with primary productivity in winter, although it is not in summer (Dobson et al. 2015). This is what we found, although the winter relationship, albeit statistically detectable, appears quite weak. One explanation for this seasonal disparity may be that the richness of wintering avian assemblages is more sensitive to temporal changes in primary productivity than breeding season assemblages due to a much higher proportion of year-round residents. These winter residents are dependent on resources from that site year-round, experiencing the metabolic stress of harsher winter conditions and more limited food resources. But even if this is true, the productivity hypothesis explains a very small fraction of the variation in species richness interannually.

Moreover, there is no evidence that the response of species richness to changing primary productivity is driven by the proposed mechanism underlying the productivity hypothesis. Under the productivity hypothesis, energy fixed in the system by primary productivity is translated into species richness via species accumulation as a byproduct of accumulated abundance. However, in our analyses assemblage abundance appears not to track changing primary productivity at all. Therefore even though we found a weak temporal response of species richness to primary productivity, the predictions of the productivity hypothesis remain largely unsupported.

The lack of temporal support for the productivity hypothesis contrasts with apparent ample support for the hypothesis when its predictions are tested spatially. In our analyses, the strength of the spatial relationship between winter avian richness and primary productivity (average spatial $r^2 = 0.28 - 0.31$ depending on fit function, Table 2.2.B1) is only slightly less than the strength of the spatial relationship in the breeding season (mean $r^2 = 0.37$, Table 2.2.A1, Dobson et al. 2015), and is consistent with Hurlbert and Haskell (2003).

When interpreting broad-scale patterns of abundance in the CBC, it should be noted that, unlike species richness, the role of sampling bias in measures of community abundance is only beginning to be understood. Using the previously documented spatial relationship between richness and NDVI (Hulbert and Haskell 2003), Dobson and Hawkins (unpubl. ms) found that raw richness, unadjusted for differences in sample effort, surprisingly provides a good estimate of species richness across North America. This gives us confidence in CBC estimates of species richness. Unfortunately, no such known relationship exists for abundance, making an analysis of sampling bias very difficult. Without knowing more about how abundance should respond to sample effort, any analyses of raw abundance must be interpreted cautiously. We can conservatively claim that there is no evidence that raw abundance tracks changing primary productivity, and only weakly correlates spatially with primary productivity. This claim is consistent with the findings of Dobson et al. (2015) that summer assemblage abundance and primary productivity are not spatially related. That result was based on bird data from the Breeding Bird Survey whose sample effort is meticulously standardized therefore estimates of abundance are assumed more reliable. Regardless of confidence in the winter abundance result, the response of richness to changing productivity in winter is very weak. Taken in concert with its poor explanatory power for summer bird richness, the productivity hypothesis does not appear a strong candidate for explaining bird richness in any season.

In conclusion, despite the evidence that wintering avian species richness weakly tracks interannual changes in primary productivity, we failed to find unambiguous support for the productivity hypothesis in explaining avian diversity in North America. If the productivity hypothesis does not sufficiently explain temporal changes in the distribution of avian diversity, we must consider other possibilities. The productivity hypothesis is predicated on neutral processes, wherein high-productivity sites accumulate more individuals and thereby accumulate more species. Perhaps it is challenging to find support for the hypothesis because the drivers of avian diversity in North America are not neutral and/or because a reassessment of the logical assumptions underlying these processes is necessary. Firstly, one assumption under the productivity hypothesis is that primary productivity imposes a carrying capacity on the number of individuals in a community, but perhaps trait differences among bird species interact with that carrying capacity. For example, because birds vary in body size perhaps productivity limits the summed biomass of all individuals rather than the number of individuals. The second assumption that more individuals translate to more species, either via random species accumulation or via reduced extinction rates due to higher population sizes, may be flawed logic. While abundance and richness do appear to be spatially associated, we have found little evidence that more individuals in a community is temporally related to greater species richness in that community in either summer or winter.

That being said, the prolific spatial association of species richness and primary productivity cannot be so easily discounted, even if the neutral mechanisms of the productivity hypothesis fall short of explaining the association. One promising avenue for future analyses is to consider the role of energy-related trait differences between bird species that might influence their sensitivity to changes in primary productivity. If bird community abundance can be scaled to reflect differences in energetic needs of its occupants, we may be closer to resolving the mechanisms at play that result in an association between primary productivity and diversity that appear to operate outside of raw abundance. We offer this as one potential avenue for evaluating the observed link between animal diversity and vegetation.

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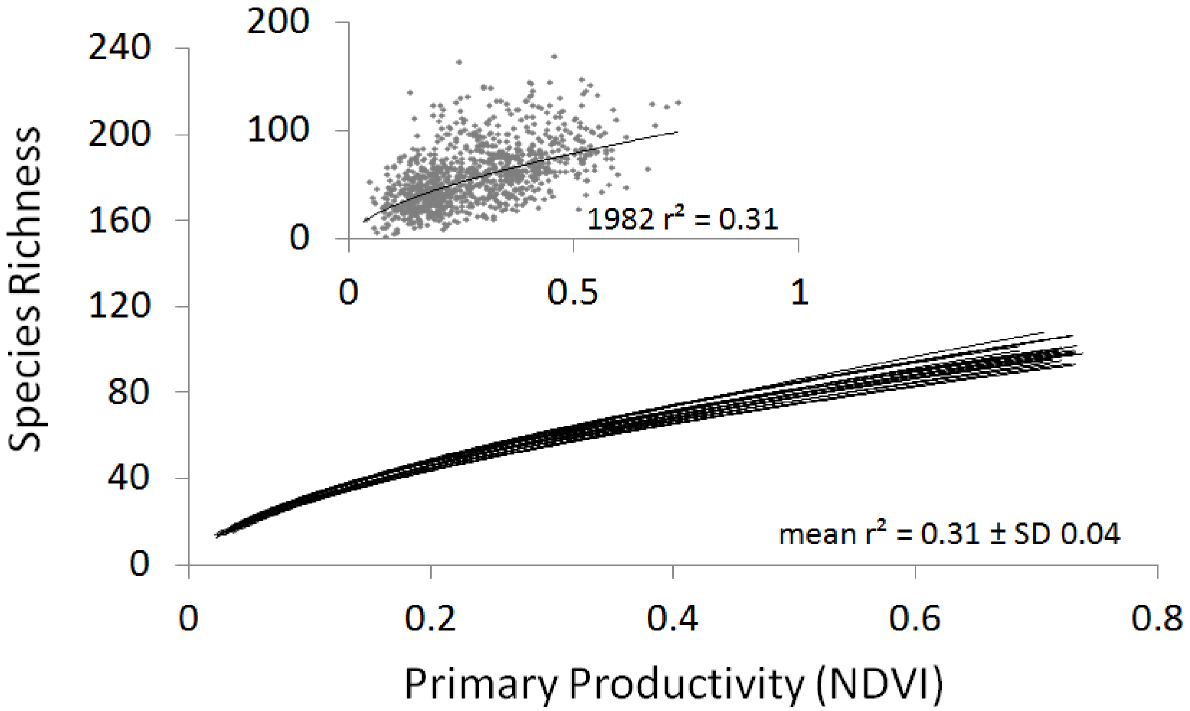

FIG. 2.2.1. Best-fit curves (power functions, see Table 2.2.B1) for the spatial relationship between species richness and Normalized Difference Vegetation Index (NDVI, a proxy for primary productivity) juxtaposed for each year in the time series from 1982 - 2002. The inset shows a scatterplot and regression curve for 1982, which is representative of other years in the time series.

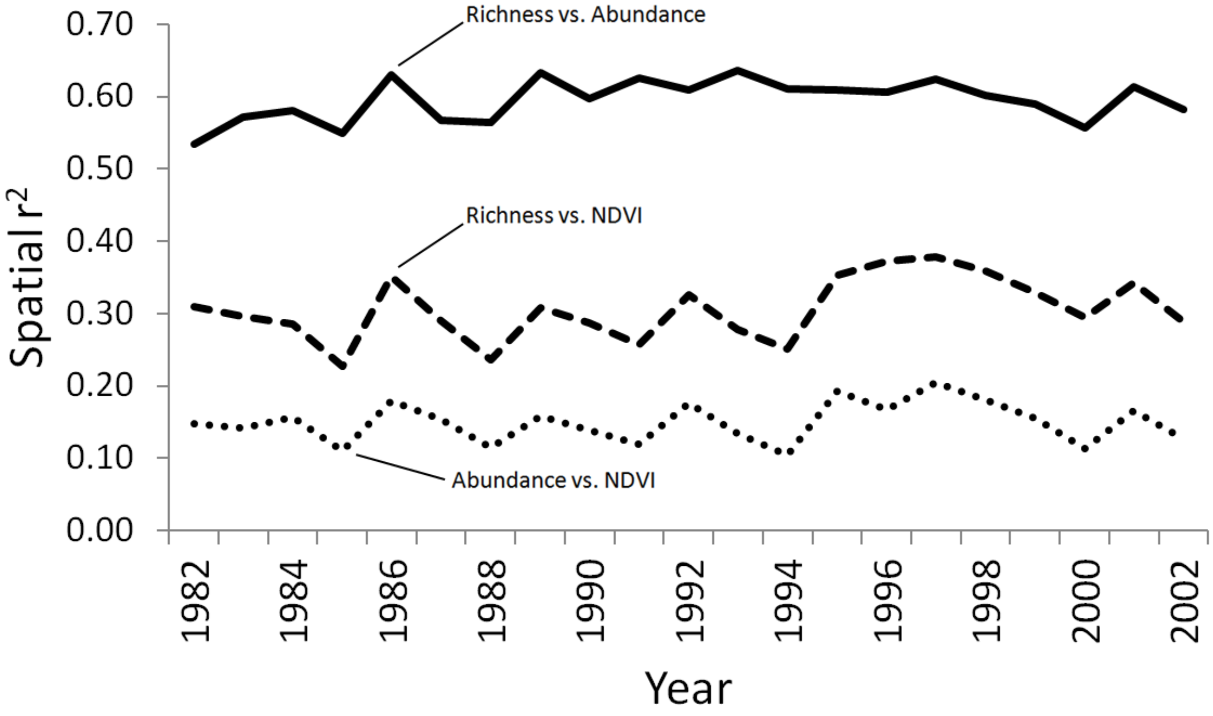

FIG. 2.2.2. Winter spatial regression r^2s for the relationships between avian species richness vs. avian community abundance , richness vs. NDVI, and abundance vs. NDVI, in each year from 1982 - 2002. Spatial regressions were fit with power functions (best fit, see Table 2.2.B1).

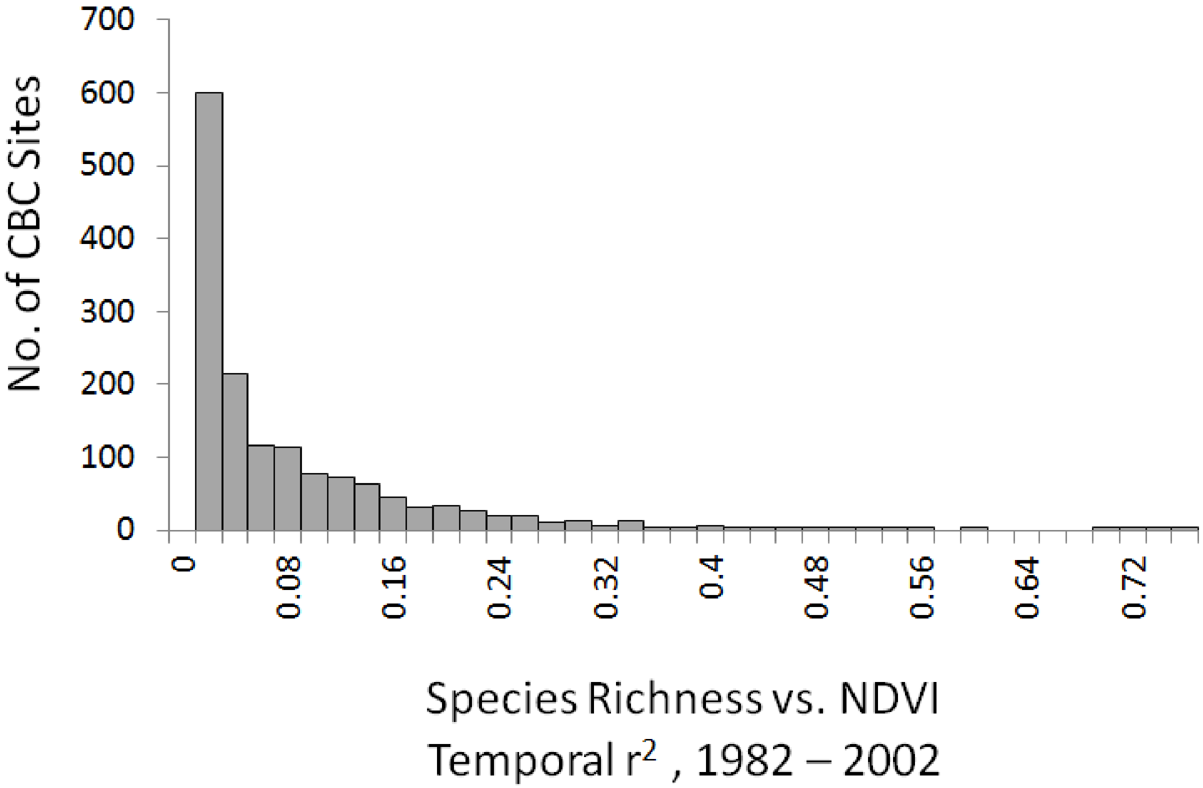

FIG. 2.2.3. Histogram of winter temporal regression r^2s for the relationship between avian species richness vs. NDVI across years 1982 - 2002. One regression was performed for each site, wherein each data point is the richness count and NDVI value for each year at that site. Temporal regressions were fit with linear functions (see Table 2.2.B2).

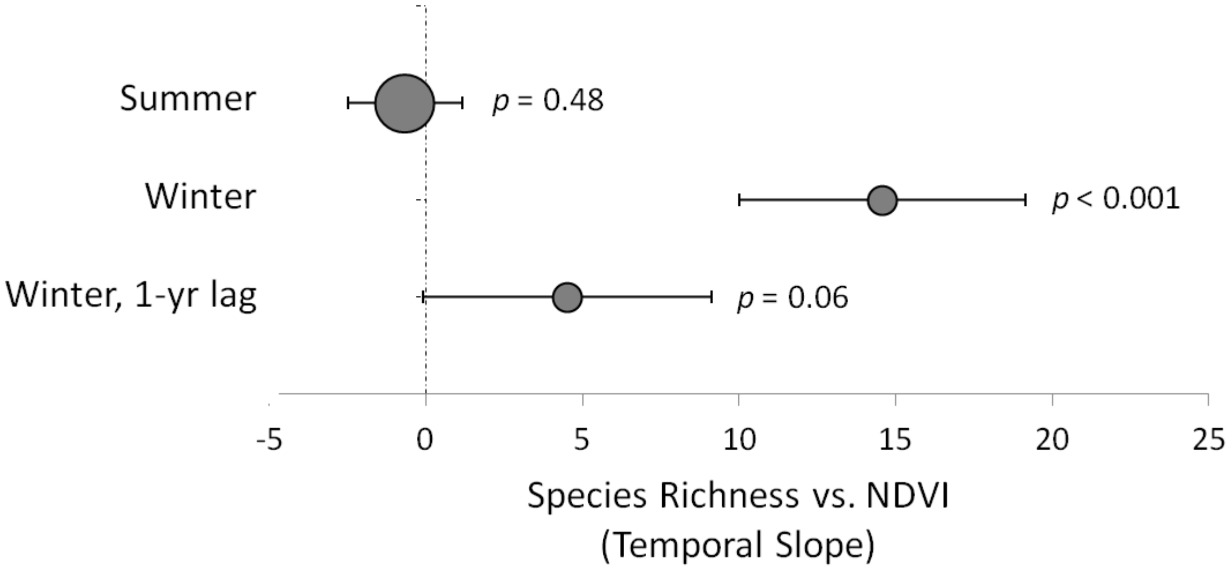

FIG. 2.2.4. Mean temporal regression slopes between avian species richness vs. NDVI for the winter time series 1982 - 2002, and summer time series 1982 - 2006 as reported by Dobson et al. (2015). Temporal regressions were performed as described in Fig. 2.2.3. Summer: mean temporal regression slope across 3,207 Breeding Bird Survey sites in North America for the time series 1982 - 2006; Winter: mean temporal regression slope across 1,509 Christmas Bird Count sites; Winter, 1-yr lag:, with a 1-year lag introduced in the response of species richness to NDVI. Temporal regressions statistics were generated with linear fits (Table 2.2.B2). Point size is relative to sample size for each series. Dashed line denotes zero slope. Whiskers are 95% confidence intervals. P-values calculated with t-tests comparing each distribution against zero.

SUPPLEMENTARY MATERIAL

Appendix 2.2.A

Table 2.2.A1. Christmas Bird Count species list with original entries and with name changes/corrections as analyzed. Species common names as analyzed are shown in the left column and the corresponding original CBC database entries are shown in the right column. This is the master species list, including species whose common names were unchanged.

Common name (modified)	Common name (CBC original)
Abert's Towhee	Abert's Towhee
Acadian Flycatcher	Acadian Flycatcher
Acorn Woodpecker	Acorn Woodpecker
Allen's Hummingbird	Allen's Hummingbird
Altamira Oriole	Altamira Oriole
American Avocet	American Avocet
American Bittern	American Bittern
American Black Duck	American Black Duck
American Coot	American Coot
American Crow	American Crow
American Dipper	American Dipper
American Golden-Plover	American Golden-Plover
American Goldfinch	American Goldfinch
American Kestrel	American Kestrel
American Oystercatcher	American Oystercatcher
American Pipit	American Pipit
American Redstart	American Redstart
American Robin	American Robin
American Three-toed Woodpecker	American Three-toed Woodpecker
American Three-toed Woodpecker	Three-toed Woodpecker
American Tree Sparrow	American Tree Sparrow
American Tree Sparrow	Tree Sparrow
American Wigeon	American Wigeon
American Woodcock	American Woodcock
Anna's Hummingbird	Anna's Hummingbird
Aplomado Falcon	Aplomado Falcon
Arizona Woodpecker	Arizona Woodpecker
Ash-throated Flycatcher	Ash-throated Flycatcher
Audubon's Oriole	Audubon's Oriole
Bachman's Sparrow	Bachman's Sparrow
Bahama Mockingbird	Bahama Mockingbird
Baird's Sandpiper	Baird's Sandpiper
Baird's Sparrow	Baird's Sparrow

Bald Eagle	American Bald Eagle
Bald Eagle	Bald Eagle
Baltimore Oriole	Baltimore Oriole
Bananaquit	Bananaquit
Band-tailed Pigeon	Band-tailed Pigeon
Bank Swallow	Bank Swallow
Barn Swallow	Barn Swallow
Barrow's Goldeneye	Barrow's Goldeneye
Bar-tailed Godwit	Bar-tailed Godwit
Bay-breasted Warbler	Bay-breasted Warbler
Bell's Vireo	Bell's Vireo
Belted Kingfisher	Belted Kingfisher
Bendire's Thrasher	Bendire's Thrasher
Bewick's Wren	Bewick's Wren
Bewick's Wren	Western Bewick's Wren
Black Oystercatcher	Black Oystercatcher
Black Phoebe	Black Phoebe
Black Rail	Black Rail
Black Rosy-Finch	Black Rosy-Finch
Black Scoter	Black Scoter
Black Turnstone	Black Turnstone
Black Vulture	Black Vulture
Black-and-white Warbler	Black-and-white Warbler
Black-backed Woodpecker	Black-backed Woodpecker
Black-bellied Plover	Black-bellied Plover
Black-bellied Whistling-Duck	Black-bellied Whistling-Duck
Black-billed Cuckoo	Black-billed Cuckoo
Black-billed Magpie	Black-billed Magpie
Blackburnian Warbler	Blackburnian Warbler
Black-capped Chickadee	Black-capped Chickadee
Black-capped Vireo	Black-capped Vireo
Black-chinned Hummingbird	Black-chinned Hummingbird
Black-chinned Sparrow	Black-chinned Sparrow
Black-crested Titmouse	Black-crested Titmouse
Black-crowned Night-Heron	Black-crowned Night-Heron
Black-headed Grosbeak	Black-headed Grosbeak
Black-necked Stilt	Black-necked Stilt
Blackpoll Warbler	Blackpoll Warbler
Black-tailed Gnatcatcher	(melanura) Black-tailed Gnatcatcher
Black-tailed Gnatcatcher	Black-tailed Gnatcatcher
Black-tailed Gnatcatcher	Californica Black-tailed Gnatcatcher
Black-throated Blue Warbler	Black-throated Blue Warbler
Black-throated Gray Warbler	Black-throated Gray Warbler
Black-throated Green Warbler	Black-throated Green Warbler
Black-throated Sparrow	Black-throated Sparrow
Blue Grosbeak	Blue Grosbeak
Blue Grouse	Blue Grouse
Blue Jay	Blue Jay
Blue Mockingbird	Blue Mockingbird

Blue-gray Gnatcatcher	Blue-gray Gnatcatcher
Blue-headed Vireo	Blue-headed Vireo
Blue-headed Vireo	Eastern Solitary Vireo
Blue-throated Hummingbird	Blue-throated Hummingbird
Blue-winged Teal	Blue-winged Teal
Blue-winged Warbler	Blue-winged Warbler
Boat-tailed Grackle	Boat-tailed Grackle
Bobolink	Bobolink
Bohemian Waxwing	Bohemian Waxwing
Boreal Chickadee	Boreal Chickadee
Botteri's Sparrow	Botteri's Sparrow
Brant	Black Brant
Brant	Brant
Brant	Brant (hrota)
Brant	Brant (nigricans)
Brant	White-bellied Brant
Brewer's Blackbird	Brewer's Blackbird
Brewer's Sparrow	Brewer's Sparrow
Bridled Titmouse	Bridled Titmouse
Broad-billed Hummingbird	Broad-billed Hummingbird
Broad-tailed Hummingbird	Broad-tailed Hummingbird
Broad-winged Hawk	Broad-winged Hawk
Bronzed Cowbird	Bronzed Cowbird
Brown Creeper	Brown Creeper
Brown Jay	Brown Jay
Brown Thrasher	Brown Thrasher
Brown Towhee	Brown Towhee
Brown-capped Rosy-Finch	Brown-capped Rosy-Finch
Brown-crested Flycatcher	Brown-crested Flycatcher
Brown-headed Cowbird	Brown-headed Cowbird
Brown-headed Nuthatch	Brown-headed Nuthatch
Buff-bellied Hummingbird	Buff-bellied Hummingbird
Buff-breasted Sandpiper	Buff-breasted Sandpiper
Bufflehead	Bufflehead
Bullock's Oriole	Bullock's Oriole
Bushtit	Black-eared Bushtit
Bushtit	Bushtit
Cackling Goose	Cackling Canada Goose
Cackling Goose	Cackling Goose
Cackling Goose	Hutchins's Goose
Cackling Goose	Richardson's Canada Goose
Cactus Wren	Cactus Wren
California Condor	California Condor
California Gnatcatcher	California Gnatcatcher
California Quail	California Quail
California Thrasher	California Thrasher
California Towhee	California Towhee
Calliope Hummingbird	Calliope Hummingbird
Canada Goose	(Aleutian) Canada Goose

Canada Goose	(large forms) Canada Goose
Canada Goose	Canada Goose
Canada Goose	Canada Goose (small races)
Canada Goose	Common Canada Goose
Canada Goose	Lesser Canada Goose
Canada Warbler	Canada Warbler
Canvasback	Canvasback
Canyon Towhee	Canyon Towhee
Canyon Wren	Canyon Wren
Cape May Warbler	Cape May Warbler
Carolina Chickadee	Carolina Chickadee
Carolina Wren	Carolina Wren
Cassin's Finch	Cassin's Finch
Cassin's Kingbird	Cassin's Kingbird
Cassin's Sparrow	Cassin's Sparrow
Cassin's Vireo	Cassin's Vireo
Cave Swallow	Cave Swallow
Cedar Waxwing	Cedar Waxwing
Cerulean Warbler	Cerulean Warbler
Chestnut-backed Chickadee	Chestnut-backed Chickadee
Chestnut-collared Longspur	Chestnut-collared Longspur
Chestnut-sided Warbler	Chestnut-sided Warbler
Chihuahuan Raven	Chihuahuan Raven
Chimney Swift	Chimney Swift
Chipping Sparrow	Chipping Sparrow
Chuck-will's-widow	Chuck-will's-widow
Cinnamon Teal	Cinnamon Teal
Clapper Rail	(Western) Clapper Rail
Clapper Rail	(Yuma) Clapper Rail
Clapper Rail	Clapper Rail
Clark's Grebe	Clark's Grebe
Clark's Nutcracker	Clark's Nutcracker
Clay-colored Sparrow	Clay-colored Sparrow
Cliff Swallow	Cliff Swallow
Common Black-Hawk	Common Black-Hawk
Common Gallinule	Common Gallinule
Common Goldeneye	Common Goldeneye
Common Grackle	Common Grackle
Common Ground-Dove	Common Ground-Dove
Common Merganser	Common Merganser
Common Moorhen	Common Moorhen
Common Nighthawk	Common Nighthawk
Common Pauraque	Common Pauraque
Common Pauraque	Pauraque
Common Poorwill	Common Poorwill
Common Raven	Common Raven
Common Redpoll	(flammea) Common Redpoll
Common Redpoll	(rostrata) Common Redpoll
Common Redpoll	Common Redpoll

Common Yellowthroat	Common Yellowthroat
Connecticut Warbler	Connecticut Warbler
Cooper's Hawk	Cooper's Hawk
Cordilleran Flycatcher	Cordilleran Flycatcher
Costa's Hummingbird	Costa's Hummingbird
Couch's Kingbird	Couch's Kingbird
Crested Caracara	Crested Caracara
Crissal Thrasher	Crissal Thrasher
Curve-billed Thrasher	Curve-billed Thrasher
Dark-eyed Junco	Dark-eyed (White-winged) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed caniceps) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed dorsalis x caniceps) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed x Oregon) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed x Pink-sided) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed x Slate-colored) Junco
Dark-eyed Junco	Dark-eyed (Gray-headed) Junco
Dark-eyed Junco	Dark-eyed (Oregon x Slate-colored) Junco
Dark-eyed Junco	Dark-eyed (Oregon) Junco
Dark-eyed Junco	Dark-eyed (Pink-sided) Junco
Dark-eyed Junco	Dark-eyed (Red-backed) Junco
Dark-eyed Junco	Dark-eyed (Slate-colored) Junco
Dark-eyed Junco	Dark-eyed Cassiar Junco
Dark-eyed Junco	Dark-eyed Junco
Dark-eyed Junco	Northern Slate-colored Junco
Dickcissel	Dickcissel
Downy Woodpecker	Downy Woodpecker
Dunlin	Dunlin
Dusky Flycatcher	Dusky Flycatcher
Dusky Grouse	Dusky Grouse
Dusky-capped Flycatcher	Dusky-capped Flycatcher
Eared Grebe	American Eared Grebe
Eared Grebe	Eared Grebe
Eastern Bluebird	Eastern Bluebird
Eastern Kingbird	Eastern Kingbird
Eastern Meadowlark	Eastern Meadowlark
Eastern Phoebe	Eastern Phoebe
Eastern Towhee	Eastern Rufous-sided Towhee
Eastern Towhee	Eastern Towhee
Eastern Wood-Pewee	Eastern Wood-Pewee
Elegant Trogon	Elegant Trogon
Emperor Goose	Emperor Goose
Evening Grosbeak	Evening Grosbeak
Ferruginous Hawk	Ferruginous Hawk
Field Sparrow	Eastern Field Sparrow
Field Sparrow	Field Sparrow
Fish Crow	Fish Crow
Five-striped Sparrow	Five-striped Sparrow
Florida Scrub-Jay	Florida Scrub-Jay
Fox Sparrow	(Red) Fox Sparrow

Fox Sparrow	(Slate-colored) Fox Sparrow
Fox Sparrow	(Sooty) Fox Sparrow
Fox Sparrow	(Thick-billed) Fox Sparrow
Fox Sparrow	(Western) Fox Sparrow
Fox Sparrow	Eastern Fox Sparrow
Fox Sparrow	Fox Sparrow
Fox Sparrow	Sooty Fox Sparrow
Fulvous Whistling-Duck	Fulvous Whistling-Duck
Gadwall	Gadwall
Gambel's Quail	Gambel's Quail
Gila Woodpecker	Gila Woodpecker
Gilded Flicker	Gilded Flicker
Glossy Ibis	Glossy Ibis
Golden Eagle	Golden Eagle
Golden-cheeked Warbler	Golden-cheeked Warbler
Golden-crowned Kinglet	Golden-crowned Kinglet
Golden-crowned Sparrow	Golden-crowned Sparrow
Golden-fronted Woodpecker	Golden-fronted Woodpecker
Golden-winged Warbler	Golden-winged Warbler
Grace's Warbler	Grace's Warbler
Grasshopper Sparrow	Grasshopper Sparrow
Gray Catbird	Gray Catbird
Gray Flycatcher	Gray Flycatcher
Gray Hawk	Gray Hawk
Gray Jay	Gray Jay
Gray Kingbird	Gray Kingbird
Gray Vireo	Gray Vireo
Gray-cheeked Thrush	Gray-cheeked Thrush
Gray-crowned Rosy-Finch	Gray-crowned Rosy-Finch
Gray-crowned Rosy-Finch	Hepburn's Rosy Finch
Great Blue Heron	(white phase) Great Blue Heron
Great Blue Heron	Great Blue (Wurdemann's) Heron
Great Blue Heron	Great Blue Heron
Great Blue Heron	Great Blue Heron (Blue form)
Great Blue Heron	Great Blue Heron (White form)
Great Blue Heron	white heron
Great Crested Flycatcher	Great Crested Flycatcher
Great Egret	Great Egret
Great Kiskadee	Great Kiskadee
Greater Pewee	Greater Pewee
Greater Prairie-Chicken	Attwater's Greater Prairie-Chicken
Greater Prairie-Chicken	Greater Prairie-Chicken
Greater Roadrunner	Greater Roadrunner
Greater Roadrunner	Roadrunner
Greater Sage-Grouse	Greater Sage-Grouse
Greater Scaup	Greater Scaup
Greater White-fronted Goose	Greater White-fronted Goose
Greater White-fronted Goose	White-fronted Goose
Greater Yellowlegs	Greater Yellowlegs

Great-tailed Grackle	Great-tailed Grackle
Green Heron	Green Heron
Green Heron	Little Green Heron
Green Jay	Green Jay
Green Kingfisher	Green Kingfisher
Green-tailed Towhee	Green-tailed Towhee
Green-winged teal	(American x Eurasian) Green-winged teal
Green-winged Teal	American Green-winged Teal
Green-winged Teal	Eurasian Green-winged Teal
Green-winged Teal	Green-winged Teal
Groove-billed Ani	Groove-billed Ani
Gunnison Sage-Grouse	Gunnison Sage-Grouse
Gyrfalcon	Gray Gyrfalcon
Gyrfalcon	Gyrfalcon
Hairy Woodpecker	Hairy Woodpecker
Hammond's Flycatcher	Hammond's Flycatcher
Harlequin Duck	Harlequin Duck
Harris's Hawk	Harris's Hawk
Harris's Sparrow	Harris's Sparrow
Henslow's Sparrow	Henslow's Sparrow
Hepatic Tanager	Hepatic Tanager
Hermit Thrush	Hermit Thrush
Hermit Warbler	Hermit Warbler
Hoary Redpoll	Hoary Redpoll
Hooded Merganser	Hooded Merganser
Hooded Oriole	Hooded Oriole
Hooded Warbler	Hooded Warbler
Hook-billed Kite	Hook-billed Kite
Horned Grebe	Horned Grebe
Horned Lark	Horned Lark
House Finch	House Finch
House Wren	Brown-throated Wren
House Wren	Eastern House Wren
House Wren	House Wren
Hudsonian Godwit	Hudsonian Godwit
Hutton's Vireo	Hutton's Vireo
Inca Dove	Inca Dove
Indigo Bunting	Indigo Bunting
Juniper Titmouse	Juniper Titmouse
Kentucky Warbler	Kentucky Warbler
Killdeer	Killdeer
King Rail	King Rail
Ladder-backed Woodpecker	Ladder-backed Woodpecker
Lapland Longspur	Lapland Longspur
Lark Bunting	Lark Bunting
Lark Sparrow	Lark Sparrow
Lawrence's Goldfinch	Lawrence's Goldfinch
Lazuli Bunting	Lazuli Bunting
Le Conte's Sparrow	Le Conte's Sparrow

Le Conte's Thrasher	Le Conte's Thrasher
Least Bittern	Least Bittern
Least Flycatcher	Least Flycatcher
Least Grebe	Least Grebe
Least Sandpiper	Least Sandpiper
Lesser Golden-Plover	Lesser Golden-Plover
Lesser Goldfinch	Lesser Goldfinch
Lesser Nighthawk	Lesser Nighthawk
Lesser Prairie-Chicken	Lesser Prairie-Chicken
Lesser Scaup	Lesser Scaup
Lesser Yellowlegs	Lesser Yellowlegs
Lewis's Woodpecker	Lewis's Woodpecker
Limpkin	Limpkin
Lincoln's Sparrow	Eastern Lincoln Sparrow
Lincoln's Sparrow	Lincoln's Sparrow
Little Blue Heron	Little Blue Heron
Loggerhead Shrike	Loggerhead Shrike
Long-billed Curlew	Long-billed Curlew
Long-billed Dowitcher	Long-billed Dowitcher
Long-billed Thrasher	Long-billed Thrasher
Long-tailed Duck	Long-tailed Duck
Long-tailed Duck	Oldsquaw
Louisiana Waterthrush	Louisiana Waterthrush
Lucy's Warbler	Lucy's Warbler
MacGillivray's Warbler	MacGillivray's Warbler
Magnificent Hummingbird	Magnificent Hummingbird
Magnolia Warbler	Magnolia Warbler
Mallard	Mallard
Mangrove Cuckoo	Mangrove Cuckoo
Marbled Godwit	Marbled Godwit
Marsh Wren	Long-billed Marsh Wren
Marsh Wren	Marsh Wren
McCown's Longspur	McCown's Longspur
McKay's Bunting	McKay's Bunting
Merlin	Merlin
Mexican Chickadee	Mexican Chickadee
Mexican Jay	Gray-breasted Jay
Mexican Jay	Mexican Jay
Mississippi Kite	Mississippi Kite
Montezuma Quail	Montezuma Quail
Mottled Duck	Mottled Duck
Mountain Bluebird	Mountain Bluebird
Mountain Chickadee	Mountain Chickadee
Mountain Plover	Mountain Plover
Mountain Quail	Mountain Quail
Mourning Dove	Mourning Dove
Mourning Warbler	Mourning Warbler
Nashville Warbler	Nashville Warbler
Nelson's Sharp-tailed Sparrow	Nelson's Sparrow

Northern Beardless-Tyrannulet	Northern Beardless-Tyrannulet
Northern Bobwhite	Bobwhite
Northern Bobwhite	Northern Bobwhite
Northern Cardinal	Northern Cardinal
Northern Flicker	Northern (Red-shafted x Yellow-shafted) Flicker
Northern Flicker	Northern (Red-shafted) Flicker
Northern Flicker	Northern (Yellow-shafted) Flicker
Northern Flicker	Northern Flicker
Northern Goshawk	Northern Goshawk
Northern Harrier	Marsh Hawk
Northern Harrier	Northern Harrier
Northern Mockingbird	Northern Mockingbird
Northern Oriole	Northern Oriole
Northern Parula	Northern Parula
Northern Pintail	Northern Pintail
Northern Pintail	Pintail
Northern Rough-winged Swallow	Northern Rough-winged Swallow
Northern Rough-winged Swallow	Rough-winged Swallow
Northern Shoveler	Northern Shoveler
Northern Shrike	Northern Shrike
Northern Waterthrush	Northern Waterthrush
Northern Wheatear	Northern Wheatear
Northwestern Crow	Northwestern Crow
Nuttall's Woodpecker	Nuttall's Woodpecker
Oak Titmouse	Oak Titmouse
Olive Sparrow	Olive Sparrow
Olive Warbler	Olive Warbler
Olive-sided Flycatcher	Olive-sided Flycatcher
Orange-crowned Warbler	Orange-crowned Warbler
Orchard Oriole	Orchard Oriole
Osprey	American Osprey
Osprey	Osprey
Ovenbird	Ovenbird
Pacific Golden-Plover	Pacific Golden-Plover
Pacific-slope Flycatcher	Pacific-slope Flycatcher
Painted Bunting	Painted Bunting
Painted Redstart	Painted Redstart
Palm Warbler	(Yellow) Palm Warbler
Palm Warbler	Palm Warbler
Palm Warbler	Western Palm Warbler
Pectoral Sandpiper	Pectoral Sandpiper
Peregrine Falcon	Peregrine Falcon
Phainopepla	Phainopepla
Philadelphia Vireo	Philadelphia Vireo
Pied-billed Grebe	Pied-billed Grebe
Pileated Woodpecker	Pileated Woodpecker
Pine Grosbeak	Pine Grosbeak
Pine Siskin	Pine Siskin
Pine Warbler	Pine Warbler

Pinyon Jay	Pinyon Jay
Piping Plover	Piping Plover
Plain Chachalaca	Plain Chachalaca
Plain Titmouse	Plain Titmouse
Plumbeous Vireo	Plumbeous Vireo
Prairie Falcon	Prairie Falcon
Prairie Warbler	Prairie Warbler
Prothonotary Warbler	Prothonotary Warbler
Purple Finch	Purple Finch
Purple Gallinule	Purple Gallinule
Purple Martin	Purple Martin
Purple Sandpiper	Purple Sandpiper
Pygmy Nuthatch	Pygmy Nuthatch
Pyrrhuloxia	Pyrrhuloxia
Red Crossbill	Red Crossbill
Red Knot	Red Knot
Red Phalarope	Red Phalarope
Red-bellied Woodpecker	Red-bellied Woodpecker
Red-billed Pigeon	Red-billed Pigeon
Red-breasted Merganser	Red-breasted Merganser
Red-breasted Nuthatch	Red-breasted Nuthatch
Red-breasted Sapsucker	Red-breasted Sapsucker
Red-cockaded Woodpecker	Red-cockaded Woodpecker
Reddish Egret	Reddish Egret
Reddish Egret	white morph Reddish Egret
Red-eyed Vireo	Red-eyed Vireo
Redhead	Redhead
Red-headed Woodpecker	Red-headed Woodpecker
Red-naped Sapsucker	Red-naped Sapsucker
Red-necked Grebe	Red-necked Grebe
Red-necked Phalarope	Red-necked Phalarope
Red-shouldered Hawk	Northern Red-shouldered Hawk
Red-shouldered Hawk	Red-shouldered Hawk
Red-tailed Hawk	(Western) Red-tailed Hawk
Red-tailed Hawk	Eastern Red-tailed Hawk
Red-tailed Hawk	Fuertes's Hawk
Red-tailed Hawk	Harlan's Hawk
Red-tailed Hawk	Krider's Hawk
Red-tailed Hawk	Red-tailed Hawk
Red-throated Pipit	Red-throated Pipit
Red-winged Blackbird	Eastern Red-winged Blackbird
Red-winged Blackbird	Red-winged Blackbird
Ringed Kingfisher	Ringed Kingfisher
Ring-necked Duck	Ring-necked Duck
Rock Sandpiper	Rock Sandpiper
Rock Wren	Rock Wren
Roseate Spoonbill	Roseate Spoonbill
Rose-breasted Grosbeak	Rose-breasted Grosbeak
Rose-throated Becard	Rose-throated Becard

Ross's Goose	blue morph Ross's Goose
Ross's Goose	Ross's Goose
Rough-legged Hawk	Rough-legged Hawk
Ruby-crowned Kinglet	Ruby-crowned Kinglet
Ruby-throated Hummingbird	Ruby-throated Hummingbird
Ruddy Duck	Ruddy Duck
Ruddy Ground-Dove	Ruddy Ground-Dove
Ruddy Turnstone	Ruddy Turnstone
Ruffed Grouse	Ruffed Grouse
Rufous Hummingbird	Rufous Hummingbird
Rufous-crowned Sparrow	Rufous-crowned Sparrow
Rufous-sided Towhee	Rufous-sided Towhee
Rufous-winged Sparrow	Rufous-winged Sparrow
Rusty Blackbird	Rusty Blackbird
Sage Sparrow	Sage Sparrow
Sage Thrasher	Sage Thrasher
Saltmarsh Sparrow	Saltmarsh Sparrow
Sanderling	Sanderling
Sandhill Crane	Sandhill Crane
Savannah Sparrow	(Savannah) Savannah Sparrow
Savannah Sparrow	Nevada Savannah Sparrow
Savannah Sparrow	Savannah (Belding's) Sparrow
Savannah Sparrow	Savannah (Ipswich) Sparrow
Savannah Sparrow	Savannah (Large-billed) Sparrow
Savannah Sparrow	Savannah Sparrow
Savannah Sparrow	Western Savannah Sparrow
Say's Phoebe	Say's Phoebe
Scaled Quail	Scaled Quail
Scarlet Tanager	Scarlet Tanager
Scissor-tailed Flycatcher	Scissor-tailed Flycatcher
Scott's Oriole	Scott's Oriole
Seaside Sparrow	Seaside Sparrow
Sedge Wren	Sedge Wren
Semipalmated Plover	Semipalmated Plover
Semipalmated Sandpiper	Semipalmated Sandpiper
Sharp-shinned Hawk	Sharp-shinned Hawk
Sharp-tailed Grouse	Sharp-tailed Grouse
Shiny Cowbird	Shiny Cowbird
Short-billed Dowitcher	Short-billed Dowitcher
Short-tailed Hawk	Short-tailed Hawk
Smith's Longspur	Smith's Longspur
Smooth-billed Ani	Smooth-billed Ani
Snail Kite	Snail Kite
Snow Bunting	Snow Bunting
Snow Goose	Greater Snow Goose
Snow Goose	Snow Goose
Snow Goose	Snow Goose (blue form)
Snow Goose	Snow Goose (blue-white intergrade)
Snow Goose	Snow Goose (white form)

Snowy Egret	Snowy Egret
Snowy Owl	Snowy Owl
Snowy Plover	Snowy Plover
Solitary Sandpiper	Solitary Sandpiper
Solitary Vireo	Solitary Vireo
Song Sparrow	Song Sparrow
Sooty Grouse	Sooty Grouse
Sora	Sora
Spot-breasted Oriole	Spot-breasted Oriole
Spotted Sandpiper	Spotted Sandpiper
Spotted Towhee	Spotted Towhee
Sprague's Pipit	Sprague's Pipit
Spruce Grouse	Spruce Grouse
Steller's Jay	Steller's Jay
Stilt Sandpiper	Stilt Sandpiper
Summer Tanager	Summer Tanager
Surf Scoter	Surf Scoter
Surfbird	Surfbird
Swainson's Hawk	Swainson's Hawk
Swainson's Thrush	Swainson's Thrush
Swainson's Warbler	Swainson's Warbler
Swallow-tailed Kite	American Swallow-tailed Kite
Swallow-tailed Kite	Swallow-tailed Kite
Swamp Sparrow	Swamp Sparrow
Tennessee Warbler	Tennessee Warbler
Thick-billed Kingbird	Thick-billed Kingbird
Townsend's Solitaire	Townsend's Solitaire
Townsend's Warbler	Townsend's Warbler
Tree Swallow	Tree Swallow
Tricolored Blackbird	Tricolored Blackbird
Tricolored Heron	Louisiana Heron
Tricolored Heron	Tricolored Heron
Tropical Kingbird	Tropical Kingbird
Tropical Parula	Tropical Parula
Trumpeter Swan	Trumpeter Swan
Tufted Titmouse	Tufted (Tufted) Titmouse
Tufted Titmouse	Tufted Titmouse
Tundra Swan	Bewick's Swan
Tundra Swan	Tundra Swan
Tundra Swan	Whistling Swan
Turkey Vulture	Turkey Vulture
Upland Sandpiper	Upland Sandpiper
Varied Bunting	Varied Bunting
Varied Thrush	Varied Thrush
Vaux's Swift	Vaux's Swift
Veery	Veery
Verdin	Verdin
Vermilion Flycatcher	Vermilion Flycatcher
Vesper Sparrow	Vesper Sparrow

Violet-crowned Hummingbird	Violet-crowned Hummingbird
Violet-green Swallow	Violet-green Swallow
Virginia Rail	Virginia Rail
Virginia's Warbler	Virginia's Warbler
Wandering Tattler	Wandering Tattler
Warbling Vireo	Warbling Vireo
Western Bluebird	Western Bluebird
Western Flycatcher	Western Flycatcher
Western Grebe	Western (Western) Grebe
Western Grebe	Western Grebe
Western Kingbird	Western Kingbird
Western Meadowlark	Western Meadowlark
Western Sandpiper	Western Sandpiper
Western Scrub-Jay	Western Scrub-Jay
Western Tanager	Western Tanager
Western Wood-Pewee	Western Wood-Pewee
Whimbrel	Whimbrel
Whip-poor-will	Whip-poor-will
White Ibis	White Ibis
White Wagtail	Black-backed Wagtail
White Wagtail	White Wagtail
White-breasted Nuthatch	Northern White-breasted Nuthatch
White-breasted Nuthatch	White-breasted Nuthatch
White-collared Seedeater	White-collared Seedeater
White-crowned Pigeon	White-crowned Pigeon
White-crowned Sparrow	Gambel's White-crowned Sparrow
White-crowned Sparrow	Western White-crowned Sparrow
White-crowned Sparrow	White-crowned Sparrow
White-eyed Vireo	White-eyed Vireo
White-faced Ibis	White-faced Ibis
White-headed Woodpecker	White-headed Woodpecker
White-rumped Sandpiper	White-rumped Sandpiper
White-tailed Hawk	White-tailed Hawk
White-tailed Kite	White-tailed Kite
White-tailed Ptarmigan	White-tailed Ptarmigan
White-throated Sparrow	White-throated Sparrow
White-throated Swift	White-throated Swift
White-tipped Dove	White-tipped Dove
White-winged Crossbill	White-winged Crossbill
White-winged Dove	White-winged Dove
White-winged Scoter	White-winged Scoter
Whooping Crane	Whooping Crane
Wild Turkey	Eastern Wild Turkey
Wild Turkey	Turkey
Wild Turkey	Wild Turkey
Willet	Willet
Williamson's Sapsucker	Williamson's Sapsucker
Willow Flycatcher	Willow Flycatcher
Willow Ptarmigan	Willow Ptarmigan

Wilson's Phalarope	Wilson's Phalarope
Wilson's Plover	Wilson's Plover
Wilson's Snipe	Wilson's Snipe
Wilson's Warbler	Wilson's Warbler
Winter Wren	Winter Wren
Wood Duck	Wood Duck
Wood Stork	Wood Stork
Wood Thrush	Wood Thrush
Worm-eating Warbler	Worm-eating Warbler
Wrentit	Wrentit
Yellow Rail	Yellow Rail
Yellow Warbler	Yellow Warbler
Yellow-bellied Flycatcher	Yellow-bellied Flycatcher
Yellow-bellied Sapsucker	(Yellow-bellied) Yellow-bellied Sapsucker
Yellow-bellied Sapsucker	Yellow-bellied Sapsucker
Yellow-billed Cuckoo	Yellow-billed Cuckoo
Yellow-billed Magpie	Yellow-billed Magpie
Yellow-breasted Chat	Yellow-breasted Chat
Yellow-crowned Night-Heron	Yellow-crowned Night-Heron
Yellow-eyed Junco	Yellow-eyed Junco
Yellow-headed Blackbird	Yellow-headed Blackbird
Yellow-rumped Warbler	Yellow-rumped (Audubon's) Warbler
Yellow-rumped Warbler	Yellow-rumped (Audubon's-Myrtle Intergrade) Warbler
Yellow-rumped Warbler	Yellow-rumped (Myrtle) Warbler
Yellow-rumped Warbler	Yellow-rumped Warbler
Yellow-throated Vireo	Yellow-throated Vireo
Yellow-throated Warbler	Yellow-throated Warbler
Zone-tailed Hawk	Zone-tailed Hawk

Appendix 2.2.B

Table 2.2.B1. Spatial regression statistics (slope and r^2) for the relationships between species richness vs. NDVI, abundance vs. NDVI, and richness vs. abundance, each fit with linear, logarithmic, and power functions for each year in the time series.

	Species richness vs. NDVI						Abundance vs. NDVI						Richness vs. Abundance					
	Linear		Logarithmic		Power		Linear		Log		Power		Linear		Log		Power	
Year	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq
1982	117.73	0.29	0.95	0.29	0.59	0.31	245896.55	0.01	1.79	0.13	1.14	0.15	0.00	0.01	0.00	0.01	0.26	0.53
1983	122.08	0.28	1.00	0.29	0.60	0.30	685315.83	0.01	1.99	0.13	1.22	0.14	0.00	0.01	0.00	0.00	0.26	0.57
1984	124.15	0.29	0.98	0.28	0.58	0.28	800683.07	0.00	1.90	0.15	1.13	0.16	0.00	0.00	0.00	0.00	0.29	0.58
1985	121.28	0.24	0.94	0.24	0.57	0.23	1035892.37	0.00	1.80	0.11	1.12	0.11	0.00	0.00	0.00	0.00	0.26	0.55
1986	119.56	0.33	0.96	0.33	0.59	0.35	477127.21	0.00	1.79	0.16	1.11	0.18	0.00	0.01	0.00	0.00	0.30	0.63
1987	119.50	0.27	0.95	0.28	0.60	0.29	1869541.51	0.01	1.97	0.15	1.27	0.15	0.00	0.00	0.00	0.00	0.26	0.57
1988	115.34	0.23	0.91	0.24	0.57	0.24	1646604.44	0.00	1.70	0.11	1.11	0.11	0.00	0.00	0.00	0.00	0.27	0.56
1989	110.16	0.26	0.95	0.29	0.58	0.31	30040.73	0.05	1.54	0.14	0.99	0.16	0.00	0.35	0.00	0.25	0.33	0.63
1990	117.58	0.26	0.95	0.28	0.60	0.29	816263.58	0.00	1.64	0.13	1.08	0.14	0.00	0.00	0.00	0.00	0.30	0.60
1991	108.81	0.22	0.91	0.25	0.58	0.26	134078.77	0.01	1.54	0.11	1.00	0.12	0.00	0.01	0.00	0.01	0.31	0.63
1992	124.51	0.30	1.00	0.31	0.60	0.33	271034.65	0.01	1.91	0.17	1.16	0.18	0.00	0.01	0.00	0.01	0.30	0.61
1993	126.73	0.28	1.00	0.28	0.57	0.28	135262.26	0.01	1.70	0.12	1.01	0.13	0.00	0.02	0.00	0.01	0.32	0.64
1994	137.15	0.25	1.06	0.24	0.67	0.25	749223.34	0.01	1.77	0.10	1.14	0.10	0.00	0.01	0.00	0.01	0.30	0.61
1995	122.83	0.30	1.00	0.33	0.62	0.35	151141.26	0.01	1.88	0.17	1.21	0.19	0.00	0.02	0.00	0.01	0.30	0.61
1996	129.64	0.33	1.01	0.34	0.61	0.37	144157.57	0.00	1.70	0.14	1.06	0.17	0.00	0.02	0.00	0.01	0.30	0.61
1997	120.25	0.31	0.97	0.34	0.56	0.38	110210.88	0.01	1.77	0.17	1.07	0.21	0.00	0.02	0.00	0.02	0.31	0.62
1998	126.32	0.33	0.98	0.34	0.60	0.36	78707.42	0.01	1.77	0.16	1.13	0.18	0.00	0.04	0.00	0.03	0.29	0.60
1999	127.13	0.28	0.98	0.30	0.60	0.33	133705.46	0.01	1.73	0.13	1.09	0.16	0.00	0.03	0.00	0.02	0.29	0.59
2000	116.02	0.25	0.89	0.27	0.59	0.29	171604.34	0.00	1.43	0.09	1.01	0.11	0.00	0.02	0.00	0.01	0.27	0.56
2001	127.62	0.32	0.97	0.32	0.61	0.34	135145.88	0.01	1.67	0.14	1.09	0.17	0.00	0.01	0.00	0.01	0.31	0.61
2002	109.90	0.25	0.86	0.27	0.57	0.29	67687.12	0.02	1.46	0.11	1.00	0.13	0.00	0.07	0.00	0.05	0.29	0.58
Mean:	121.16	0.28	0.96	0.29	0.59	0.31	470920.20	0.01	1.74	0.13	1.10	0.15	0.00	0.03	0.00	0.02	0.29	0.60
SD:	6.99	0.03	0.04	0.03	0.02	0.04	524010.66	0.01	0.15	0.02	0.08	0.03	0.00	0.07	0.00	0.05	0.02	0.03

Table 2.2.B2. Mean temporal regression statistics (slope and r^2) for the relationships between species richness vs. NDVI, abundance vs. NDVI, and richness vs. abundance for 1,509 CBC sites, each fit with linear and power functions, and 1-year lags where indicated. p-values were calculated using one-sample t-tests comparing the distribution of temporal slope values against a zero slope null model.

	Richness vs. NDVI								Abundance vs. NDVI								Richness vs. Abundance			
	linear		linear (lag)		power		power (lag)		linear		linear (lag)		power		power (lag)		linear		power	
	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq	slope	rsq
mean	14.57	0.07	4.51	0.08	0.06	0.07	0.02	0.08	-369127.02	0.08	-364915.95	0.07	0.09	0.08	0.11	0.07	0.00	0.26	0.14	0.30
SD	90.54	0.10	91.29	0.10	0.40	0.10	0.45	0.10	11750067.19	0.10	14991004.14	0.10	2.46	0.10	2.27	0.10	0.00	0.21	0.11	0.23
p	<0.001		0.06		<0.001		0.16		0.22		0.34		0.17		0.06		<0.001		<0.001	

CHAPTER 3

A broad-scale test of the productivity hypothesis using energy-scaled avian abundance shows independence from primary productivity across 25 years of change

LuAnna L. Dobson[*]*, Bradford A. Hawkins.*

ABSTRACT

The productivity hypothesis postulates primary productivity drives species richness because places with greater primary production can support more individuals, and thereby accumulate more species. However, in a recent broad-scale test of the productivity hypothesis for North American birds across 25 years, the number of individuals was not spatially associated with primary productivity across several thousand communities. Traditionally, tests of the productivity hypothesis have assumed trait-neutral partitioning of resources across individuals in the community. It may be more realistic that partitioning is in unequal shares, and therefore we propose a refinement to the predictions of the hypothesis: an accounting of energetic trait differences. To test this refinement, we scaled abundance estimates by body size and trophic level, traits that may feasibly describe the energy burden an individual places on its community. We predicted that as primary productivity changes temporally, total community biomass should respond to that change. Further, individuals at higher trophic levels should be more sensitive to change. Using abundance estimates, average species body sizes, and feeding guild data, we calculated the total avian biomass annually at 3,207 Breeding Bird Survey sites, subdivided by trophic level. We then regressed biomass against primary productivity spatially and temporally,

both overall and for each trophic level. Avian biomass was unrelated to primary productivity in neither space nor time, overall (spatial mean $r^2 = 0.004$; temporal mean $r^2 = 0.08$) or at any trophic level (herbivores/omnivores spatial mean $r^2 = 0.008$; temporal mean $r^2 = 0.09$; carnivores spatial mean $r^2 = 0.001$; temporal mean $r^2 = 0.08$). Because neither raw abundance nor energy-scaled abundance are related to primary productivity, we conclude that primary production is unlikely to be the driver of bird diversity, and that we should look to alternative hypotheses to explain geographic variation in diversity.

INTRODUCTION

Some of the oldest questions in Ecology ask why places host the number of species they do, why this number varies markedly across space, and how that number changes through time. For example, the global diversity gradient, a prolific geographic pattern of high diversity at low latitudes decreasing toward the poles, has stimulated curiosity since the 1700s. Among the many potential influences on diversity patterns, energy has consistently risen to the fore as an environmental factor that correlates positively with species richness (Currie and Paquin 1987, Hawkins et al. 2003, Hurlbert 2004, Currie et al. 2004, Evans et al. 2005, Pau et al. 2012, Brown 2014). This relationship is sufficiently prolific that it has generated a theory known as species-energy theory (Wright 1983). In short, species-energy theory is an extension of species-area theory, which claims that we can improve predictions of island diversity if we account for differences in energy captured through primary production. Empirically, Wright (1983) found that primary production explains 70 to 80% of variation in species number on 36 islands worldwide for angiosperms and land and freshwater birds. Subsequently, predictions of species-energy theory have been confirmed spatially for a variety of taxa at numerous geographic grains and extents, most notably for birds (Wright 1983, Hawkins et al. 2003, 2007, Hurlbert and

Haskell 2003, Hurlbert 2004, Currie et al. 2004, Carnicer et al. 2007, Verschuyl et al. 2008, Phillips et al. 2008, Hurlbert and Jetz 2010, Hansen et al. 2011, Morales-Castilla et al. 2012, Cumming et al. 2013, Zhang et al. 2013, Dobson et al. 2015), and species-energy theory has been implicated in at least partially explaining the global diversity gradient (Turner and Hawkins 2004, Brown 2014).

Different definitions for 'energy' exist within species-energy theory, including measures of ambient energy such as temperature or potential evapotranspiration (Currie 1991, Hawkins et al. 2003) or realized energy such as actual evapotranspiration or primary productivity (Currie and Paquin 1987), each with slightly different hypothetical predictions and varying levels of support depending on the group in question (Currie 1991, Evans et al. 2005). In this work, we will focus on one of these hypotheses: the productivity hypothesis, which defines energy as primary production (also known as the more individuals hypothesis).

The productivity hypothesis posits that plant productivity imposes an energetic carrying capacity on the number of individuals a place can support. When a place supports more individuals, species are thereby accumulated either via neutral mechanisms like passive sampling from the regional species pool (Hubbell 2001, Hawkins et al. 2003, Hurlbert 2004, Evans et al. 2005, White and Hurlbert 2010), or through increased population sizes, which depress extinction (Evans et al. 2006, Carnicer et al. 2007, Yee, D. A., Juliano 2007). From this general claim, we can make three simple predictions about spatial relationships between primary productivity and the diversity of animal communities: 1) places with more primary production contain more individuals, 2) places with more individuals are home to more species, and as an indirect effect of these first two predictions, 3) places with greater primary production are home to more species. Further, in the temporal context, we can predict that as primary productivity changes through time, both the number of individuals and the number of species should rise or decline accordingly.

Most tests of the productivity hypothesis at the macro scale have evaluated prediction 3, assuming that if supported, it follows logically that predictions 1 and 2 must also be true. This approach is due, in part, to the relatively limited availability of abundance data needed to test predictions 1 and 2 compared with widely available species richness data (thanks largely to range maps) for testing prediction 3. Further, most of these tests have evaluated the spatial associations in absence of temporal tests, again because of the relatively limited availability of temporal data compared with that of spatial data. Though the first and second predictions have scarcely been tested at the macro scale, some local-scale manipulative experiments have done so. Interestingly, the small body of work where primary productivity has been experimentally manipulated, the findings tend not to support predictions 1 and 2 of the productivity hypothesis (Srivastava and Lawton 1998, Currie et al. 2004, Carnicer et al. 2007, McGlynn et al. 2010).

Dobson et al. (2015) represents one of the first studies measuring a temporal response of abundance to changing primary productivity at the macro scale, including a direct temporal test of prediction 1 of the productivity hypothesis. By using climate variability as a natural experiment through which primary productivity was manipulated, and using a longitudinal avian citizen science survey as a source of temporal data, Dobson et al. (2015) evaluated the response of both abundance and species richness to 25 years of change. Dobson et al. (2015) found that the total number of individuals in North American bird communities was unrelated to primary production in either space or time, a finding consistent with experimental tests. But before claiming that the productivity hypothesis does not explain the geographic patterning of species diversity through the number of individuals, we propose one further test of its predictions.

Here we propose a small refinement of prediction 1: trait differences between species. The productivity hypothesis has generally been tested in a trait-neutral format. Trait-neutral tests of the productivity hypothesis, like those performed in Dobson et al (2015), assume that community members of different species are equal in their use of local plant resources. However, it is more realistic to assume partitioning of resources across the community is likely to be in unequal shares, and that the share of productivity required to support an individual's place in the community varies depending on its traits. Here we adjust abundance estimates to account for two traits that should describe the energy burden an individual places on its community: body size and trophic level.

Specifically, we hypothesize that local primary productivity imposes a carrying capacity on energy-scaled abundance, here measured as community biomass. If true, we predict that as primary productivity changes temporally, total community biomass should respond to that change. Further, we predict that those species who are secondary consumers or above in a trophic chain should be more sensitive to changing primary productivity because of energy loss across trophic levels. Using two and a half decades of North American avian community data from the Breeding Bird Survey (BBS) and remotely-sensed measures of vegetation 'greenness', we analyzed the temporal response of avian community biomass to changing primary productivity.

METHODS

Using abundance estimates, average species body sizes, and feeding guild data we calculated the total avian biomass annually at each BBS site, distinguished by trophic level. We then regressed these biomass estimates against a proxy for primary productivity spatially and temporally across all birds and for each trophic level.

Extent and resolution

All species of birds identified by BBS volunteers in the United States and Canada, excluding nocturnal, marine, exotic, and vagrant species, were recorded for a total of 396 species. The temporal extent spans from 1982 to 2006 with an annual temporal resolution. The spatial extent includes the continental United States and southern Canada, with a spatial resolution defined by BBS route length of 39.4 km, for which the route midpoint was used for all analyses.

Bird Diversity and Primary Productivity

For inclusion sites had to be surveyed at least 8 years within the 25-year time series, resulting in 3,207 sites. Primary production was estimated by the normalized difference vegetation index (NDVI). The NDVI data product was generated and made available by the Global Inventory Modeling and Mapping Studies (GIMMS) 2.0 at the Global Land Cover Facility (GLCF) (Tucker et al. 2004), using remotely sensed spectral data collected by the National Oceanic and Atmospheric Association's (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite system (Pinzon et al. 2005). NDVI is widely used as proxy for primary productivity in macroecological studies (Hurlbert and Haskell 2003, Hawkins 2004, Phillips et al. 2008, Buono et al. 2010, Pau et al. 2012, Stegen et al. 2013, Siefert et al. 2013, Dobson et al. 2015). NDVI estimates vegetation 'greenness' using the spectral signature of light reflected from plant chlorophyll, ranging from 0 (bare ground) to 1 (saturated greenness). NDVI is strongly correlated with both gross primary productivity (r = 0.95) and net primary productivity (r = 0.91) at broad spatial scales (Phillips et al. 2008), and performs well even in regions where vegetation is sparse (Boelman et al. 2003). Additionally, NDVI has a practical advantage over more direct primary productivity measures like the MODIS-derived gross and net primary productivity. NOAA's AVHRR satellites have been continuously documenting NDVI since 1982, much earlier than any other remotely-sensed primary productivity measures (NASA's MODIS system was initiated in 2002). Thus NDVI permits multi-decadal time series analyses that other measures of primary productivity cannot support. The time window of 1982 to 2006 reflects data availability for the AVHRR-derived NDVI data product.

Analysis

BBS count data were used to estimate the abundance of each species at BBS sites for each year of the time series. Using bird body size taken from the Handbook of Birds (http://www.hbw.com), the average body size of each species was multiplied across the site-species abundance matrix, generating a biomass estimate for each species. Biomass was initially summed across species at each site each year. Biomass was then subdivided according to the trophic classifications of species, defined as trophic 1 (herbivore or omnivore) and trophic 2 (carnivore) biomass.

Species were assigned to trophic level depending on their primary feeding guild as reported in Cornell Lab of Ornithology's online bird guide (https://www.allaboutbirds.org). Trophic level classifications were based on breeding season dietary behavior (summer through late fall). Because we expect secondary consumers to require a greater allocation of resources than primary consumers, we made this test conservative by setting a very strict threshold of secondary consumption for what constitutes a Trophic Level 2 species. If a species' diet contains at least 5% vegetation, that species was classed as trophic level 1 (referred to as 'trophic 1'). If a species' diet contains less than 5% vegetation (i.e. more than 95% of the diet is secondary or higher consumption), it was classed a trophic level 2 species ('trophic 2'). Avian biomass for all species and subdivided by trophic level were mapped across North America. Average biomass across the time series was interpolated using a Krigging function in ArcGIS 10.

Primary productivity for each year in the time series was defined as average NDVI of June, July and August . We extracted the summer-average NDVI at the coordinate midpoint of each BBS site in each year of the time series.

To test the predictions of the productivity hypothesis, first we spatially regressed estimates of avian body mass against NDVI for each year of the time series. To identify a possible trend through time in the strength of the spatial relationship between biomass and productivity, the resultant spatial regression statistics were plotted against the years of the time series.

To evaluate a response in community biomass to changing primary productivity through time, community biomass was temporally regressed against NDVI. A positive slope indicates a temporal response of bird biomass to primary productivity. A negative slope or slope of zero indicates no support for the hypothesis. The slopes of these temporal regressions were mapped across North America to identify any spatial patterning or lack thereof in the response of biomass to changing primary productivity.

In a preliminary analysis we also included a measure of reproductive effort, expecting that production of reproductive mass contributes to the energetic burden an individual places on community resources. However, we found that the independent contribution of reproductive effort contributed little not already captured by body size. Our approach comprised estimates of annual reproductive mass (# of eggs per clutch * number of clutchers per year * hatchling mass) using species-averages for these traits taken from An Age Database, via TraitBank, an initiative of Encyclopedia of Life (http://eol.org/traitbank). These data were available for fewer than half of the species in the BBS data. For those species which data was available, we correlated each species' reproductive mass with adult body size, and found that these metrics are strongly correlated (r = 0.91) (Fig. 2.2.S1). As a second test of the independence of information reproductive mass contributes, we correlated site biomass estimates based on species' adult mass alone versus adult mass plus reproductive mass, and found these two metrics to be strongly correlated (r = 0.95) (Fig. 2.2.S2). Given the extreme collinearity of reproductive mass with body size, the fact that community biomass estimates did not change appreciably when reproductive mass was included, and that reproductive mass data is only available for a subset of species, we excluded reproductive mass in our estimates of community biomass and rely on adult body size alone.

RESULTS

On average, avian biomass is low in the southwestern deserts, high throughout the midwest, southwest coastal areas, the south, and the southeast coast (Fig. 3.1). Average biomass across the time series was slightly lower for trophic 1 species (27,836 g ± SD 19,369) than for trophic 2 species (32,769 g ± 29,052).

Across years, the average linear spatial r^2 between and community biomass and NDVI was 0.004 for all species, 0.008 for trophic 1 species, and 0.001 for trophic 2 species (Fig. 3.2). The slopes of these spatial relationships are largely negative (Fig. 3.2). For reference, the average spatial r^2 between raw community abundance (total number of bird individuals) and NDVI for this same time series and season was 0.01 (Dobson et al. 2015). Scaling abundance by body size thus weakened the relationship between abundance and productivity as compared with raw abundance.

Given the very weak spatial relationship, it is perhaps unsurprising that bird biomass did not respond to changing primary productivity temporally. On average, the mean temporal r^2 across sites between bird biomass and primary productivity was 0.08 ± SD 0.11 for all species, 0.09 ± 0.12 for trophic 1 species, and 0.08 ± 0.11 for trophic 2 species. The average temporal slopes were all weakly negative (all species: -12.6 thousand ± 233.6 k, trophic 1: -2.8 k ± 128.2 k, trophic 2: -9.8 k ± 175.4 k) (Fig. 3.3). When the slopes of these temporal regressions are mapped, no clear spatial structure emerges, suggesting that the strength of the relationship does not vary regionally (Fig. 3.3).

DISCUSSION

Breeding season abundance is not correlated with primary productivity whether analyzed as raw number of individuals (Dobson et al. 2015), energetically-scaled to biomass, nor biomass by trophic level. Indeed, scaling community abundance by body size reduced the already weak spatial relationship between raw abundance and primary productivity. We cannot envisage what further refinement in the data could uncover a relationship between abundance and primary productivity in support of the predictions of the productivity hypothesis. Despite the positive spatial correlation between species richness and primary productivity (Wright 1983, Hawkins and Porter 2003a, Hurlbert 2004, Currie et al. 2004, Carnicer et al. 2007, Verschuyl et al. 2008, Phillips et al. 2008, Hurlbert and Jetz 2010, Hansen et al. 2011, Morales-Castilla et al. 2012, Cumming et al. 2013, Zhang et al. 2013, Brown 2014, Dobson et al. 2015), if no relationship can be found between primary productivity and community abundance, primary productivity cannot be the driver of species diversity through the mechanisms predicted by the productivity hypothesis. Surprisingly, productivity does not appear to impose a limit on the total number of individuals in a community or on the biomass of that community, for the spatial and temporal data at our disposal.

One potential reason we found no associations between primary productivity and community biomass is that birds are highly mobile organisms. Perhaps the productivity hypothesis is not appropriately applied to organisms that can disperse in response to shifting productivity supply, and perhaps a broad-scale analysis of animals that are less mobile might find that the productivity hypothesis better predicts abundance than it appears to in birds.

We are unsure why neither total abundance nor body-size weighted abundance track interannual changes in primary productivity. It is highly likely that the primary reason that so many birds exhibit migratory behavior is to allow them to take advantage of seasonal flushes of primary productivity. This is supported by the finding that in both summer and winter, the spatial relationship between richness and primary productivity remains similar (White and Hurlbert 2010, Dobson et al. 2015). Further, spatial relationships between bird richness and climatic variables are stable across summer and winter seasons (H-Acevedo and Currie 2003). These pieces of evidence together would suggest that bird individuals accumulate at sites with higher primary productivity. If we extend this rationale, the species should occupy the entire geography that provides the appropriate niche and should move around seasonally to continue to enjoy that same niche as it shifts geographically.

However, the climate space inhabited by an individual species is not necessarily constant across seasons. Boucher-Lalonde et al. (2014) found that migratory species do not track environmental niches (environment defined as temperature & the Enhanced Vegetation Index).

When birds migrate, the new range does not match the environment of the old range. Interestingly, the environment of one season is typically nested in the other, but birds do not fully realize the environmental tolerance demonstrated by the other season. This means that though richness tracks seasonal changes in temperature and productivity, individual species do not. This would appear to be in support of top-down hypotheses like the productivity hypothesis, which suggest productivity controls richness by imposing a kind of carrying capacity. Despite this, the mechanistic link relied on in the hypothesis- the positive relationship between primary productivity and abundance- is not supported (Dobson et al. 2015, Seoane et al. 2016).

There is one piece of evidence that demonstrates a dependence of bird abundance on vegetation, but the analyses demonstrating this relationship are based on models of single-species abundance as opposed to the community-wide abundance implicated in the productivity hypothesis. Specifically, Cumming et al. (2013) found that for Canadian songbirds, while climate was the strongest predictor of species abundances for most species, the independent contribution of remotely-sensed vegetation metrics was 23%, with 14% of this coming from primary productivity measures. This suggests that perhaps some species abundances track changing primary productivity while others do not. Regardless, in the context of productivity hypothesis, it is the number of individuals writ large in the community that is predicted to translate energy into greater species richness.

The productivity hypothesis may be predicated on an inappropriate conception of the role of resources in supporting diversity. Generally, we describe primary productivity as imposing a carrying capacity for number of individuals, so we are implicating vegetation as the foundation of a trophic web and thus as a food source, directly or indirectly. However, vegetation is not only a food source, but also provides nesting space, mating space, foraging space, and shelter from predators and harsh environments. We consider it likely that these ecological functions outweigh the value of vegetation as food. There is some evidence for this. For instance, avian frugivorous species are not more strongly correlated with fleshy-fruited tree richness than non-fleshy-fruited tree richness, providing no evidence for resource-consumer interactions in driving bird diversity (Kissling et al. 2008). Nor is the species richness of butterfly specialists strongly correlated with the richness of their host species (Hawkins and Porter 2003b). If food resources were the drivers of animal diversity through vegetation, these links should be easier to find.

In light of our findings, we suggest that niche space influences the number of species at a place, likely in large part controlled by the habitat's vertical vegetation structural complexity as proposed by MacArthur and MacArthur (1961). This hypothesis resolves seemingly inconsistent results by explaining how primary productivity may be related to species richness in a way that circumvents controls via population sizes. Vertical structural complexity of vegetation is correlated with primary productivity (Boelman et al. 2011); thus if vegetation structure and species richness are related, correlations can emerge spuriously between productivity and richness. However, testing this prediction at the macro scale is challenging, because of the sparse availability of data on vegetation structural complexity. This should change as data processing algorithms are developed to infer structural complexity from current vegetation indices, and/or technologies are deployed that permit data collection of vegetation structural data directly. Some progress has been made using heterogeneity of remotely-sensed vegetation metrics to serve as proxy for structural complexity, and in these cases have provided evidence for the important role of niche space in driving species richness (Culbert et al. 2013, Zhang et al. 2013, Seoane et al. 2016).

The failure of the productivity hypothesis to explain bird diversity across North America has important consequences for planning and land management for the preservation of animal diversity. It is important to understand whether primary productivity or vegetation structural complexity supports species richness, because there are community compositional changes that can occur which increase productivity while decreasing structural complexity, such as land-use changes or plant species invasions (Pau et al. 2012). If structural complexity drives species richness, high production at the expense of rich and complex habitat will not maintain species diversity. Land use changes may pose the far greater danger to diversity than climate change-induced reductions in primary productivity.

The optimist may find a hopeful message in these results. It is possible that bird diversity will be spared in the face of hotter, drier climates predicted to reduce primary productivity across the landscape (Nemani et al. 2003) if we can protect the complexity of vegetative habitats, at least in the short term. Long-term, if climate change simplifies the structural complexity of vegetated habitats, bird diversity may truly suffer.

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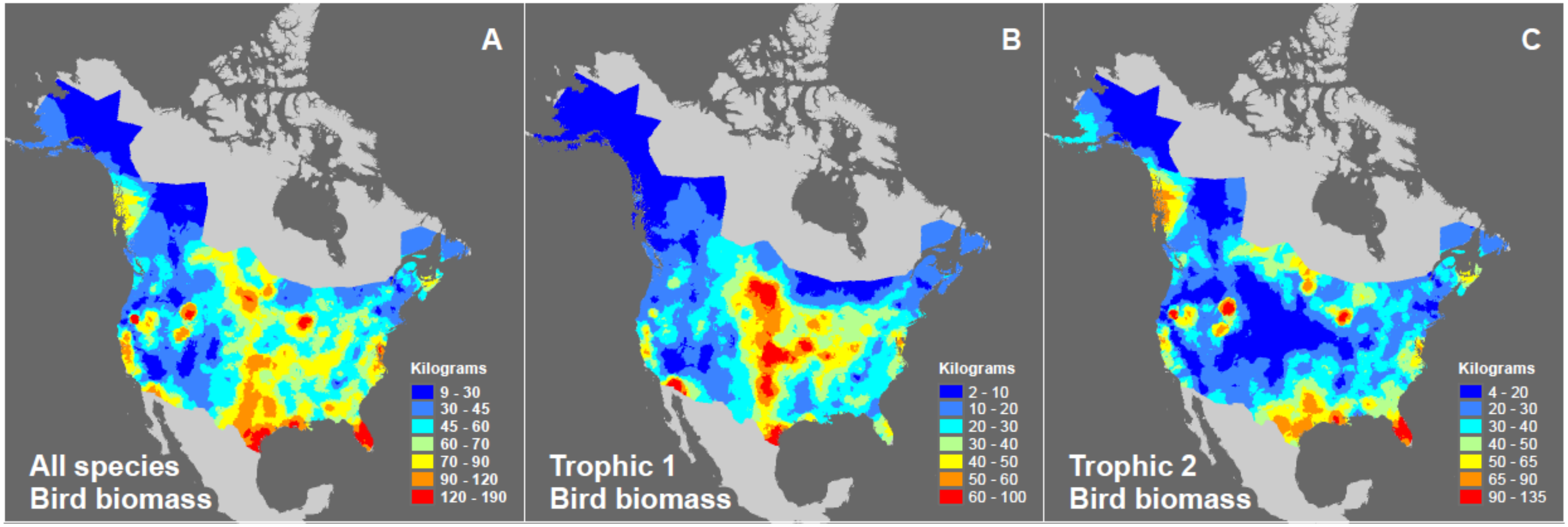


FIG 3.1. North American bird biomass in the breeding season, averaged across years 1982 - 2006. Biomass estimates were interpolated from Breeding Bird Survey sites using ArcGIS's Krigging interpolator function. Panels represent the summed biomass of individuals from A: all species included in analyses; B: species classified as trophic level 1; and C: species classified as trophic level 2. Reported biomass values are in kilograms, where blue represents the least biomass and red the most biomass.

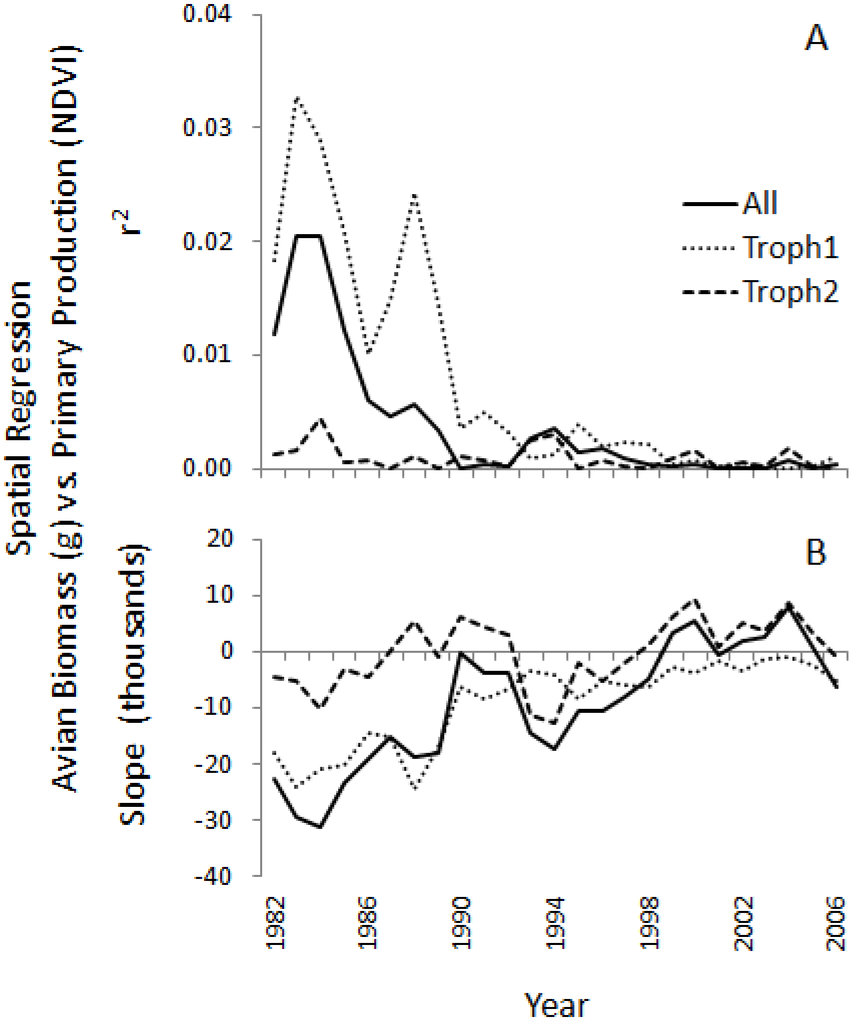


FIG. 3.2. Regression statistics from the annual spatial relationship between avian biomass (g) and primary productivity (NDVI) plotted against years 1982 - 2006. Spatial regressions based on all species are shown in solid line, trophic 1 species with a dotted line, and trophic 2 species with a dashed line. Row A: r^2 values from spatial regression repeated each year; row B: Slope values from spatial regression repeated each year, reported in thousands.

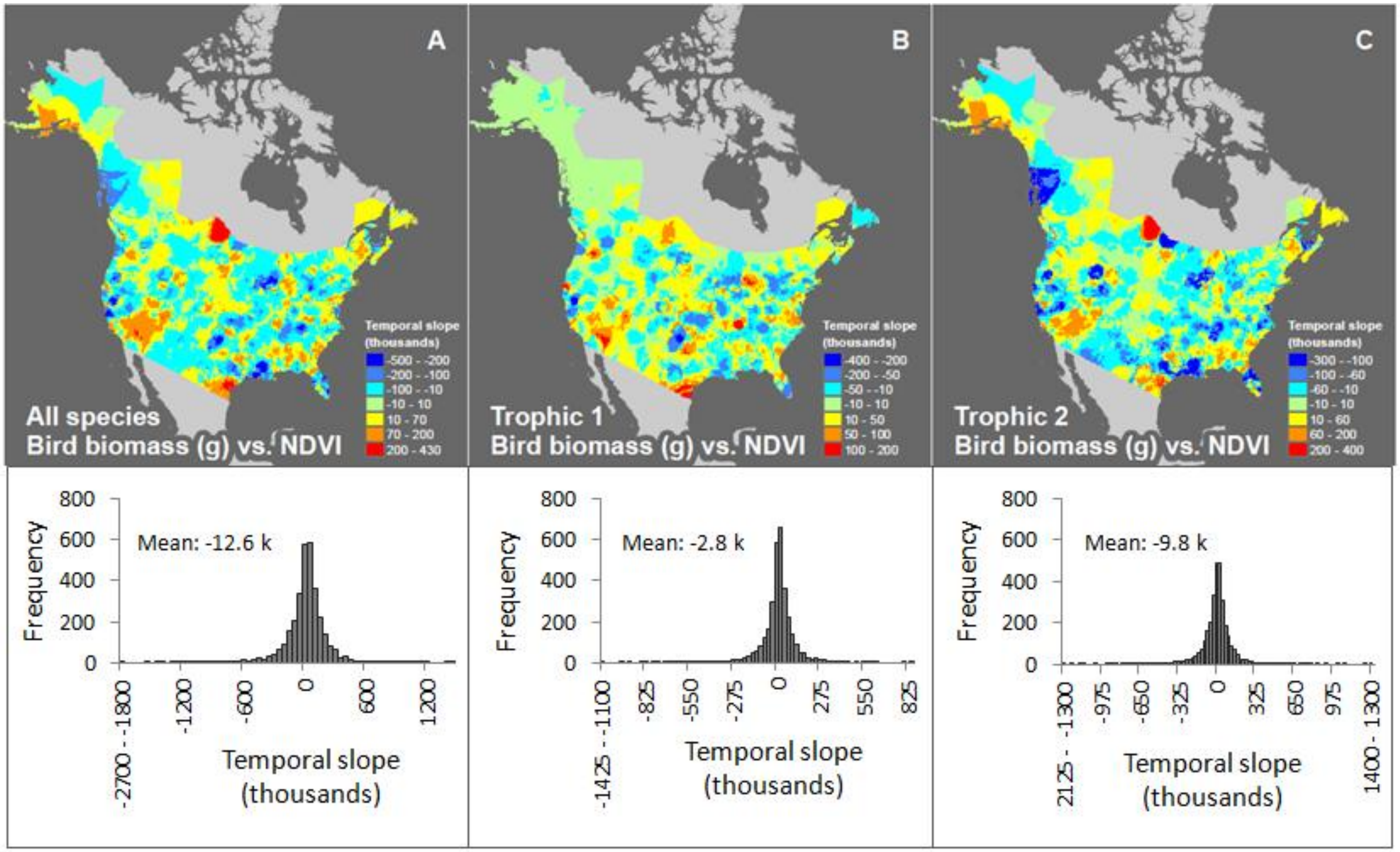
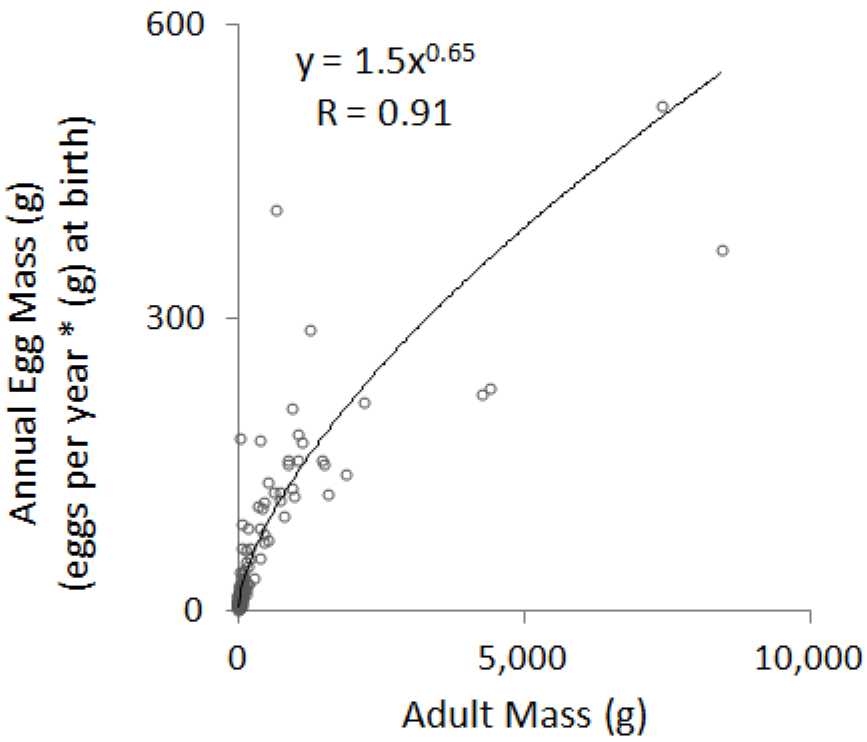


FIG. 3.3. Slope values of temporal regressions of bird biomass (g) versus primary productivity (NDVI) at Breeding Bird Survey sites from 1982 - 2006, interpolated using ArcGIS's Krigging function. Panel A represents regression slopes using biomass summed across all species; B: biomass from trophic 1 species only; C: biomass from trophic 2 species only. Slope values are reported in thousands.

SUPPLEMENTAL MATERIAL

Appendix 3.A.

Analyses of the contribution of reproductive mass to estimates of avian biomass across North America from 1982 - 2006. The first analysis correlates reproductive mass with adult body mass across the species analyzed in this work (Figure 3.A1). The second analysis correlates estimated biomass across BBS sites using only adult mass versus adult mass plus reproductive mass (Figure 3.A2).



3.A1. A scatterplot showing the correlation between annual egg mass and adult body mass of North American bird species. Each data point represents one species.

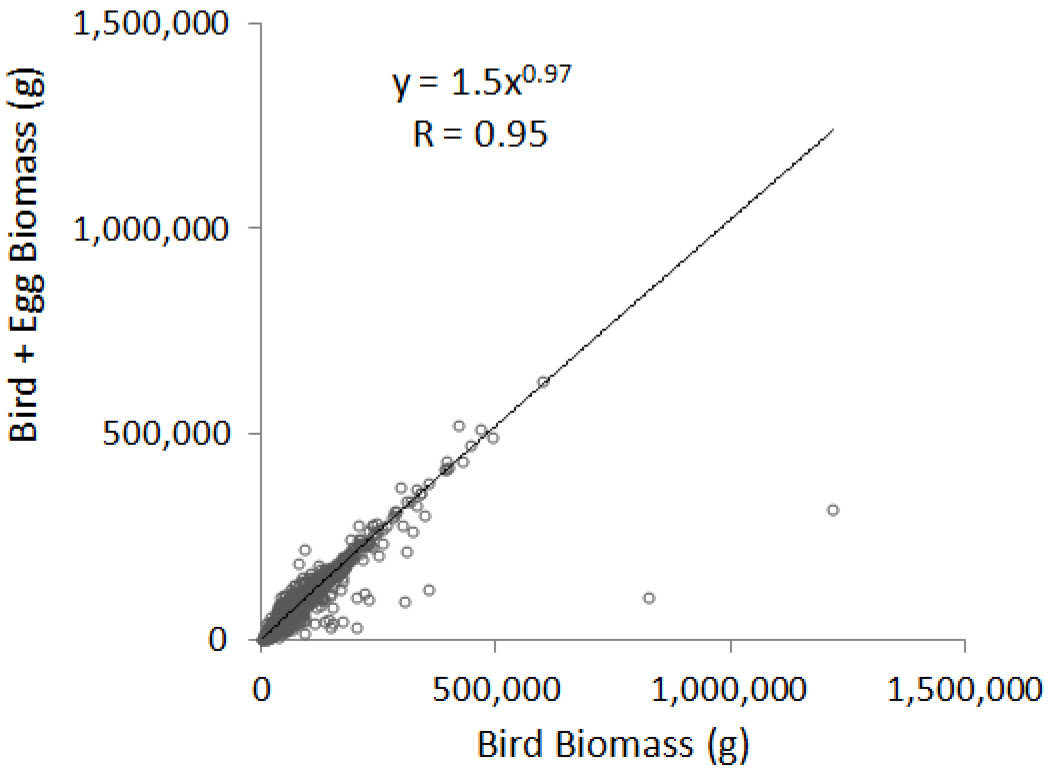


FIG. 3.A2. A scatterplot showing the correlation across Breeding Bird Survey sites between total community avian biomass estimated using species body size data alone (x-axis) versus adult mass plus reproductive mass (y-axis). Each data point represents the biomass estimates at one site, with 3,207 sites included.