

RESEARCH ARTICLE

Journal of
Biogeography

WILEY

More individuals or specialized niches? Distinguishing support for hypotheses explaining positive species–energy relationships

Grace J. Di Cecco¹ | Sara J. Snell Taylor¹ | Ethan P. White^{2,3} | Allen H. Hurlbert^{1,4} ¹Department of Biology, University of North Carolina, Chapel Hill, North Carolina, USA²Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA³Informatics Institute, University of Florida, Gainesville, Florida, USA⁴Environment, Ecology, and Energy Program, University of North Carolina, Chapel Hill, North Carolina, USA**Correspondence**

Grace J. Di Cecco, Department of Biology, University of North Carolina, Coker Hall CB #3280 120 South Road, Chapel Hill, NC 27599, USA.

Email: gdicecco@live.unc.edu**Handling Editor:** Lisa Manne**Abstract**

Aim: Positive productivity–richness relationships have been observed across taxa and ecosystems. We assessed support for two hypotheses explaining these relationships, the More Individuals Hypothesis (MIH) and the Niche Specialization Hypothesis (NSH) in two complementary datasets of avian communities in North America, the Breeding Bird Survey (BBS), which has been widely used to study productivity–richness relationships, and the Breeding Bird Census (BBC), which has been used rarely yet offers accurate population density estimates and more homogeneous landscapes, eliminating confounding variables that may make it more difficult to test predictions of the NSH and MIH in the BBS alone.

Location: Coterminous United States, 1988–2009.

Taxon: Birds.

Methods: We first evaluated the strength of productivity–richness relationships in the BBS and BBC, and tested predictions from the MIH and NSH in the two datasets by examining patterns in community abundance, productivity niche breadth and number of foraging guilds along a gradient of normalized difference vegetation index (a measure of vegetation productivity). We also implemented a null model to examine the contribution of sampling effects due to increasing species richness in explaining patterns in number of foraging guilds in both datasets.

Results: We found that the BBS had a much stronger productivity–richness relationship than the BBC, potentially as a result of increased landscape diversity with increasing productivity at BBS survey sites. Although the MIH and NSH may not be mutually exclusive, we found weaker support for the MIH in the BBC, and stronger support for the NSH in the BBC and BBS.

Main Conclusions: Researchers should consider the role of confounding variables such as landscape diversity and focus on developing direct measurements of food resources at macroecological scales to determine the relative importance of mechanisms driving productivity–richness relationships.

KEYWORDS

birds, Breeding Bird Census, Breeding Bird Survey, foraging guilds, productivity, species richness

1 | INTRODUCTION

The species–energy relationship, in which species richness increases with estimates of energy availability, is one of a few macroecological patterns that have been observed repeatedly across broad scales for many taxonomic groups (Currie, 1991; Evans et al., 2005; Hawkins et al., 2003; Wright, 1983). While many studies support this correlation across taxa, different hypotheses have been proposed to explain the causal link between energy availability and species richness, and there is not a clear consensus on the mechanism by which species–energy relationships operate (Evans et al., 2005; Storch et al., 2018).

In this paper, we examine two potential explanations for the empirically observed positive species–energy relationship in birds: the More Individuals Hypothesis (MIH) and the Niche Specialization Hypothesis (NSH; Bonn et al., 2004; Srivastava & Lawton, 1998). The MIH posits that increased energy availability increases the number of individuals that an area can support, which, in turn, results in a greater number of species that can be maintained above some viable population size (Hurlbert & Stegen, 2014; Storch et al., 2018). In contrast, the NSH proposes that as total energy availability increases, there is an increase in relatively rare resource types, which opens new niche positions (Abrams, 1995; Schoener, 1974). This increases the number of species that can be supported by increasing the number of niche specialist species. These two hypotheses are not mutually exclusive, and positive species–energy relationships may be driven by some combination of the two mechanisms (Hurlbert & Jetz, 2010). Importantly, for large clades of organisms like birds that are assessed over continental to global extents, energy availability is typically characterized by estimates of net primary productivity (Hurlbert & Jetz, 2010; Mönkkönen et al., 2006; Storch et al., 2018), and hereafter we use ‘energy availability’ and ‘productivity’ interchangeably.

These different mechanisms underlying the MIH and NSH yield four predictions that can be tested to distinguish support for the two explanations for positive productivity–richness relationships (detailed in Figure 1). As productivity increases, the MIH predicts that the total number of individuals that can be supported increases, resulting in an increased number of species. A key prediction of the MIH is then that community-wide abundance (summed over all species in the community) increases with productivity, while there is no direct expectation for such a relationship with the NSH (Prediction 1: Figure 1a). Controlling for the number of individuals in a community, the MIH predicts no further effect of productivity on species richness (Hurlbert, 2004). However, under the NSH, we would expect a positive relationship between number of species and productivity across communities even when controlling for the number of individuals (Prediction 2: Figure 1b).

The NSH assumes that as energy availability increases, new niches become available that are not present in lower productivity environments. For example, birds might experience new foraging substrates and canopy strata in high productivity forests compared to lower productivity grasslands and woodlands (Hurlbert & Jetz, 2010). Under the NSH, the addition of niche specialists at the high end of the productivity gradient results in a nested pattern of species occurrences in terms of the range of productivity

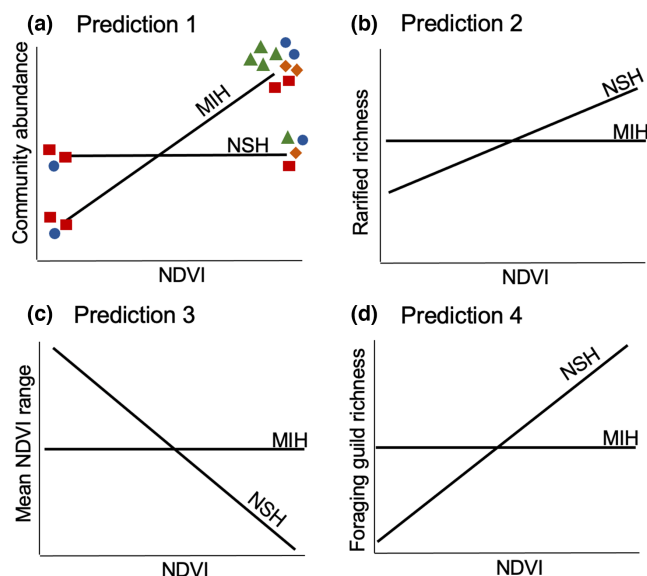


FIGURE 1 Graphical representations of hypotheses explaining positive relationships between species richness and productivity. (a) Prediction 1: As NDVI (a remotely sensed index of vegetation greenness used as a proxy for productivity) increases, the More Individuals Hypothesis (MIH) predicts that the number of individuals that can be supported increases, while the Niche Specialization Hypothesis (NSH) does not. (b) Prediction 2: As NDVI increases, the MIH predicts that the number of species when controlling for total abundance should not vary systematically, while the NSH predicts that it will increase with NDVI. (c) Prediction 3: The NSH predicts that species occurring at high niche position along the NDVI axis should have narrower NDVI ranges, since they specialize on resources only available at those niches. At low NDVI values, species present are expected to be generalists and have broader NDVI niches. As a result, as NDVI increases, the mean NDVI range across species that occur at that NDVI value is expected to decrease under the NSH, but not under the MIH. (d) Prediction 4: As NDVI increases, the NSH predicts that foraging guild richness (controlling for number of species; see text) should increase, while the MIH does not. NDVI, normalized difference vegetation index.

values species occur over (Bonn et al., 2004). At low productivity sites, species present will be more likely to be generalists with broad habitat niches such that we predict that as productivity increases the mean productivity range of species in a community will decrease (Prediction 3: Figure 1c), similar to patterns in geographical range size across latitudes described by Rapoport's Rule (Arita et al., 2005; Colwell & Hurtt, 1994). Under the NSH, we also predict that the number of foraging guilds in a community will increase with productivity even when accounting for increases in species richness (Prediction 4: Figure 1d).

Testing these four predictions of the MIH and NSH at macroecological scales is complicated by biases that may confound inferences from continental-scale data sources. Support for productivity–richness relationships in birds has been assessed using range-map approaches (Currie, 1991) and survey-based approaches using presence and abundance data. The North American Breeding Bird Survey (BBS; Sauer et al., 2017) has been used widely to both document patterns in

**TABLE 1** Four predictions from the More-Individuals Hypothesis (MIH) and Niche Specialization Hypothesis (NSH) tested in the two complementary datasets used in this study—Breeding Bird Survey (BBS) and Breeding Bird Census (BBC) in North America

Relationship	Datasets tested	Predicted relationship	Justification
(1) Community abundance as a function of NDVI	BBC	MIH: Positive	As a proxy for resource availability, more individuals can be supported at high NDVI
		NSH: None	–
(2) Rarefied species richness (controlling for abundance) as a function of NDVI	BBC	MIH: None	There should be no additional effect of NDVI on richness above and beyond the effect on community abundance
		NSH: Positive	Species richness increases with NDVI for reasons independent of community abundance
(3) Average productivity range of species in a community as a function of NDVI	BBS	MIH: None	–
		NSH: Negative	At high NDVI, specialist species occurring only at high productivity will be added to communities
(4) Number of foraging guilds (controlling for species richness) as a function of NDVI	BBS, BBC	MIH: None	–
		NSH: Positive	More foraging niches will be available at high NDVI, facilitating the coexistence of more foraging guilds

Abbreviation: NDVI, normalized difference vegetation index.

productivity–richness relationships and to evaluate potential explanations (Dobson et al., 2015; Hurlbert, 2004; Hurlbert & Haskell, 2003). However, the nature of the BBS survey protocol (a single-visit roadside point count-based survey) may impact the ability to adequately test some of the assumptions and predictions of species–energy hypotheses that rely on precise population or community density estimates.

The extent to which the total number of birds observed reflects the total number of birds present on that route will depend on species' detectability which likely decreases along the productivity gradient itself (Hurlbert, 2004). More densely vegetated habitats may be more likely to obscure the visual and aural detection of individual birds, complicating inferences about geographical patterns of community abundance in this dataset. Additionally, at larger landscape scales, roadside forested areas of high productivity are more likely to be intermixed with habitats of very different structure (e.g. meadows, agriculture, areas of secondary growth) compared to lower productivity areas of desert, grassland or scrubland, and the presence of roads themselves may create forest edge habitats with their own distinct bird communities (Boulinier et al., 1998). Since landscape diversity has a well-known positive effect on avian diversity (Farwell et al., 2020; Tews et al., 2004), this may confound the interpretation of productivity–richness relationships in the BBS.

We examine the generality of the positive productivity–richness relationship observed in the BBS by comparing it to an alternative continent-wide bird dataset, the Breeding Bird Census (BBC; Marshall, 1991), which is based on spot mapping surveys in natural areas and does not suffer from these issues. One advantage of the BBC is that census areas tend to be in more homogeneous natural areas away from roads (Lowe & Desante, 2012; Marshall, 1991). Also, the census protocol involves territory mapping based on repeated visits over the course of the breeding season which generates more reliable estimates of population density (Robbins, 1970). Earlier work has used the BBC to document a positive productivity–richness relationship, but that work was restricted to forested sites only (Mönkkönen

et al., 2006). However, because the BBC dataset is less geographically extensive and with fewer sites, this dataset is less useful for characterizing range-wide properties of species such as niche breadth.

As a result of properties of the two datasets discussed above, we do not test all predictions in each dataset (Table 1). Predictions 1 and 2 require unbiased estimates of community abundance, and are therefore tested with the BBC dataset. Prediction 3 requires characterizing the productivity niche of each species across its breeding range, and so it is evaluated using the more geographically extensive BBS dataset. Finally, we test Prediction 4 regarding how the number of foraging guilds varies with productivity using both the BBC and the BBS. Our goal in this study is to provide a comprehensive examination of productivity–richness relationships using these two complementary macroecological datasets.

In this study, we make use of the strengths of both the BBS and BBC datasets to investigate first whether there are positive richness–productivity relationships. We test our four predictions of the MIH and NSH to examine the degree of support for each of these hypotheses in the two datasets, and also examine how biases in environmental variables such as landscape productivity (a proxy for food resources) and land cover diversity (a proxy for niche availability) in either dataset may impact evaluation of the mechanisms underlying positive richness–productivity relationships. The results highlight the importance of integrating insights from multiple sources of information in disentangling the processes driving macroecological patterns.

2 | MATERIALS AND METHODS

2.1 | Data sources

We used bird community data from two sources: the North American BBS (Sauer et al., 2017) and BBC (Lowe & Desante, 2012). The BBS takes place annually across the United States and Canada during the

breeding season at over 4100 roadside routes. Trained volunteers survey each route once, typically in June, and record all individuals seen or heard within a 400-m radius at fifty 3-min point counts evenly spaced along each 40-km route. For this project, we used BBS routes occurring in the coterminous US that were surveyed continuously from 2000 to 2004 and which were between 38 and 42 km according to their detailed route path data (https://www.mbr-pwrc.usgs.gov/bbs/geographic_information/GIS_shapefiles_2012.html). For species in the BBS, we calculated abundance at a survey location as the sum of counts from 2000 to 2004 and community richness as the total number of species observed across those study years as in McGill (2003).

We determined the land cover composition within a 1-km buffer of each survey route using the National Land Cover Database version 2001 dataset (Homer et al., 2004) and removed any survey routes with over 50% agricultural land cover. Areas of high agricultural land cover may have high remotely sensed estimates of productivity (see below) comparable to that of forested sites, but this high productivity does not necessarily translate to increased energy available to bird communities because agricultural productivity is extracted for human use (Figure S1). Our dataset comprised 1135 BBS routes that fit these criteria (Figure 2).

We also obtained bird community data from the BBC, an ongoing long-term spot-mapping protocol. BBC surveys record the number and position of territories established by singing males, breeding pairs, and visitor species seen and heard. Experienced volunteers walk the entire area of a variable-sized plot (typically between 10 and 40 ha) on 8–12 days spread throughout the breeding season to exhaustively map the territories at each site, spending 10–12 min/ha for forested plots and 4–5 min/ha in open

habitats (Marshall, 1991). BBC plots are typically found in natural reserve areas. We used data for 393 census plots in the coterminous US and Ontario, Canada (Figure 2). We used the most recent survey at each BBC location, with survey dates ranging from 1988 to 2009 (Engstrom, 1989, 1990; Gardali & Lowe, 2007, 2009; Heath et al., 2006; Lowe, 1993, 1994, 1995, 1996; Lowe & Desante, 2012; Marshall, 1991, 1992; White et al., 2021). In the BBC survey protocol, number of established territories for each breeder species is recorded to the nearest 0.5 territory, while territories where less than 25% of the territory occurs in the BBC survey plot are denoted with a + symbol in the BBC dataset (Marshall, 1991). We converted any territories below 25% area to 0.25 and multiplied all territory numbers by four to preserve the relative abundance of territories per species at each site but have whole numbers necessary for individual-based rarefaction.

We examined richness patterns only for diurnal land birds, excluding waterbirds, shorebirds, nocturnal birds and birds of prey which are not representatively sampled by the BBS or BBC survey protocols (Butcher et al., 1987). Species without established territories, referred to as visitor species in the BBC dataset, were removed from the BBC dataset. Analogously, we removed species occurrences in the BBS if they occurred in only one out of 5 years at a particular survey route, as low temporal occupancy has been assumed to reflect 'transient' status (Snell Taylor et al., 2018). Based on sensitivity tests performed in Coyle et al. (2013), our results are likely to be robust to our threshold for transients. Our BBS analyses included 358 species and the BBC analyses included 260 species. We also obtained detailed foraging guild classifications based on diet and foraging strategy for each species in our analysis (González-Salazar et al., 2014).

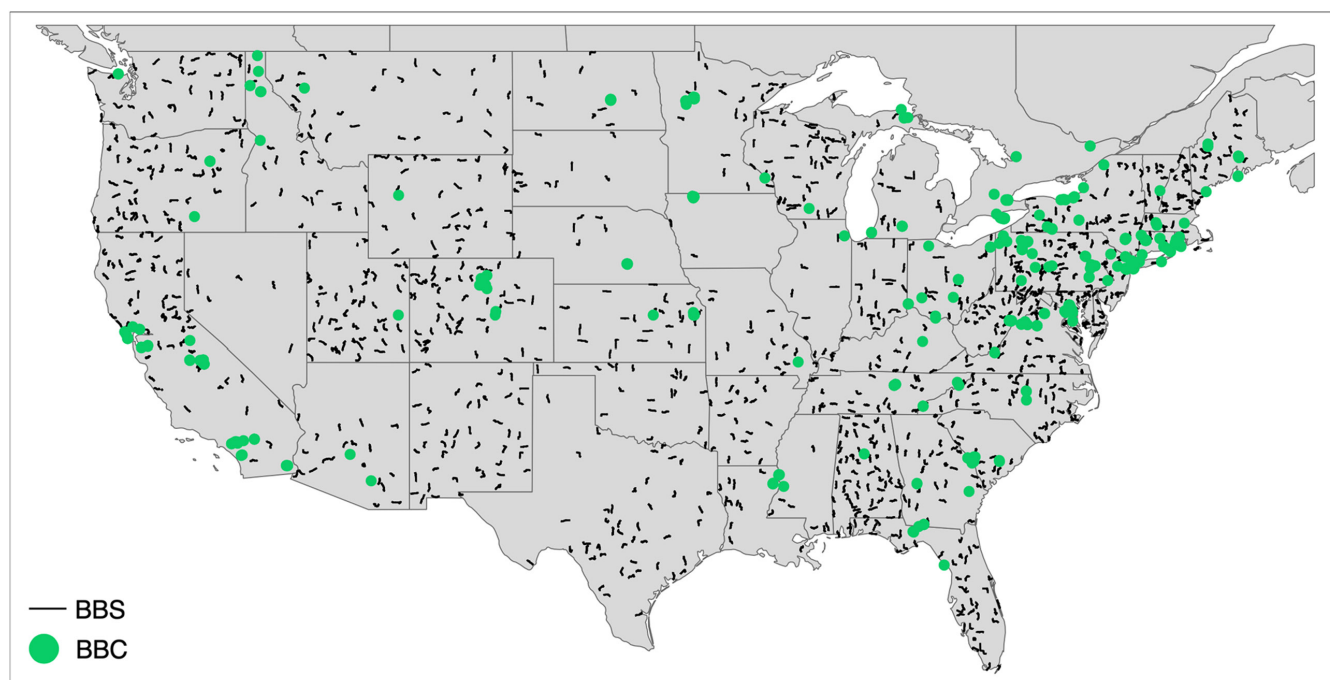


FIGURE 2 Map showing the locations of Breeding Bird Survey (BBS; lines) and Breeding Bird Census (BBC; circles) sites used in this study in North America. Map projection is WGS84.



We used the remotely sensed normalized difference vegetation index (NDVI) during the breeding season as a proxy for vegetation productivity at each bird survey location. At each BBS route within a 1-km buffer around the 40-km survey route path, and at each BBC plot using a circle with the same area as the plot centred on the latitude–longitude coordinate of the site, we obtained mean NDVI during the breeding season (averages of biweekly observations for May, June and July) for the year of sampling from GIMMS NDVI-3g (Pinzon & Tucker, 2014). We averaged breeding season NDVI across years (2000–2004) for BBS routes. GIMMS NDVI is at a relatively coarse spatial resolution ($1/12^\circ$, ~8 km) compared to other NDVI data sources such as AVHRR (1 km; Vermote & Program, 2019) and MODIS (250 m; Didan, 2015). However, 89% of the BBC dataset comes from years pre-2000, and GIMMS is the only data source covering that time period. As a check on the robustness of this decision, we confirmed that results using GIMMS, AVHRR and MODIS NDVI data at BBS routes in 2000–2004 were all highly correlated (Table S1). We also found strong correspondence between the results of our ordinary least squares regressions using NDVI from each of these three sources predicting various properties of the BBS data (Table S2).

We also calculated landscape diversity on BBS routes and at BBC sites. We characterized landscapes using the categorical land cover classes available in the National Land Cover Database 2001 (NLCD; Homer et al., 2004), and additionally separated forest classes (deciduous, mixed and coniferous forest NLCD categories) into edge and core categories as edge and core forest habitats support different avian communities. We categorized forest pixels in the NLCD into core and edge as implemented in R package SDMTTools (Vanderwal et al., 2019); however, it is important to note that the proportion of edge and core pixels in a landscape will differ depending on the raster resolution and definition of 'edge' pixels. For the same buffer area as used for NDVI at BBC and BBS sites within the coterminous US, we then calculated the Shannon diversity index (H' ; Shannon, 1948) based on the proportion cover of these different land cover classes.

2.2 | Testing the MIH

To test the predictions of the MIH (Predictions 1 and 2: Table 1), we calculated community territory density (the total number of territories across species divided by the area of the plot) for each BBC survey location. We used ordinary least squares regression to determine the relationship between community territory density and mean breeding season NDVI of the BBC plot. Additionally, we conducted individual-based rarefaction for each BBC plot using the MOBR package in R (McGlinn et al., 2019). To compare rarefied richness across sites, we obtained expected species richness for each BBC site for a sample of 175 territories, a sample size selected to maximize the number of BBC sites that could be compared. We then used ordinary least squares regression to determine the relationship between the rarefied number of species and NDVI of the BBC plot.

2.3 | Testing the NSH

We examined the range of NDVI values a species occurred at to measure specialization and position along the productivity niche axis. Specifically, whether assemblages at high NDVI consisted of species with narrower NDVI ranges on average (Prediction 3: Table 1). We conducted this analysis for the BBS dataset only as it is more geographically extensive and encompasses more of species ranges than the BBC. We calculated the mean NDVI position for each species by averaging NDVI across all of the BBS routes at which a species was present in two or more years from 2000 to 2004 weighted by count at each site, and the NDVI range of the species by subtracting the minimum NDVI the species was observed at from the maximum NDVI value.

In the second analysis, we grouped BBS routes into 17 evenly spaced NDVI bins (bin width of 0.05 NDVI units). For each NDVI bin, we calculated the mean NDVI range of the species occurring in that bin. We used ordinary least squares regression to determine the relationship between mean NDVI range of species within a bin as a function of the bin's mean NDVI. However, because species occur in multiple NDVI bins, these data points are not independent. To estimate the likelihood of observing a value as extreme as the empirical slope between mean NDVI range and NDVI bin, we developed a null model to provide an expected distribution of slope estimates to compare to our empirical estimate (see Figure S2 for schematic). The goal for our null model was to sample a set of species in which the existing relationship between species mean NDVI position and NDVI range was disrupted, without creating combinations of NDVI position and NDVI range that are impossible (e.g. a species with a mean NDVI position of 0.9 and a NDVI range of 0.9). We drew on null models from studies of the mid-domain effect and Rapoport's Rule that describe how the latitudinal limits of a distribution constrain the midpoint of a geographical distribution (Arita et al., 2005; Colwell & Hurtt, 1994) to randomly shuffle where along the NDVI gradient species occurred while holding each species' empirically observed NDVI range constant. We used the below constraints on the minimum and maximum possible mean NDVI positions (μ_{\min} and μ_{\max}) for each species i given its NDVI range, where Min is the minimum observed NDVI value across all BBS routes, Max is the maximum observed NDVI value across all routes, \min_i and \max_i are the minimum and maximum NDVI values for a particular species, and μ_i is the mean NDVI value for that species:

$$\mu_{\min} = \text{Min} + (\mu_i - \min_i)$$

$$\mu_{\max} = \text{Max} - (\max_i - \mu_i)$$

With these constraints as the minimum and maximum possible NDVI mean values for each species, we sampled from a uniform distribution bounded by those constraints to find a null NDVI distribution for each species. We then calculated the average NDVI range for the set of species whose shuffled ranges fell within each NDVI bin, and estimated the slope of the linear relationship

between average NDVI range and NDVI (Figure S3). Note that because the sampling was done with respect to each species, the total number of species in the null dataset is the same as the empirical pattern, but the number of species in each NDVI bin in the null model is not necessarily the same as empirically observed. We repeated this process 999 times, and compared our empirical slope to this distribution of null slopes to obtain a bootstrapped p -value.

To explore the relationship between NDVI range and foraging guild, we also examined the distribution of species' NDVI ranges in each foraging guild, and described patterns in species richness in foraging guilds as productivity increases using the BBS dataset.

To test the hypothesis that communities in high productivity sites were more likely to support a greater diversity of foraging niches (Prediction 4: Table 1), we conducted a second null model analysis using both BBS and BBC datasets. This null model was designed to provide a null expectation for increases in foraging guild richness along a productivity gradient due solely to sampling effects from increases in species richness. For each dataset, we binned surveys by NDVI values (bin size of 0.05 for BBS and 0.07 for BBC; 17 bins for BBS and seven bins for BBC) and compiled the list of species observed in each bin as the available species pool for a given position along the NDVI gradient. NDVI bins with fewer than 15 sites were removed from analysis. For each BBS or BBC survey, we sampled the same number of species as empirically observed from the relevant species pool 999 times and recorded the number of unique foraging guilds observed in the sample to obtain a null prediction of number of foraging guilds. We compared

the average number of foraging guilds across the null simulations with the actual observed number of foraging guilds using a z -score, where FG_{obs} is the observed number of foraging guilds at that survey location, μ_{FGnull} is the mean number of foraging guilds observed in the null model simulations and σ_{FGnull} is the standard deviation of the number of foraging guilds observed from the null model simulations:

$$z = \frac{(FG_{obs} - \mu_{FGnull})}{\sigma_{FGnull}}$$

We examined how this z -score of foraging guild diversity varied along the NDVI gradient for both the BBS and BBC using ordinary least squares regression.

3 | RESULTS

Species richness was positively correlated with mean NDVI in the BBS (slope = 51.60, $R^2 = 0.45$, $p < 0.001$) and weakly positively correlated with mean NDVI in the BBC (slope = 8.72, $R^2 = 0.02$, $p < 0.01$; Figure 3a,b). In addition, as NDVI increased, landscape diversity strongly increased along BBS routes (slope = 1.92, $R^2 = 0.45$, $p < 0.001$) but did not at BBC sites (slope = 0.26, $R^2 = 0.01$, $p = 0.10$; Figure 3c,d). Species richness is positively correlated with landscape diversity in both datasets ($p < 0.001$), but landscape diversity explains 26% of the variation in species richness at BBS sites and only 4% at BBC sites.

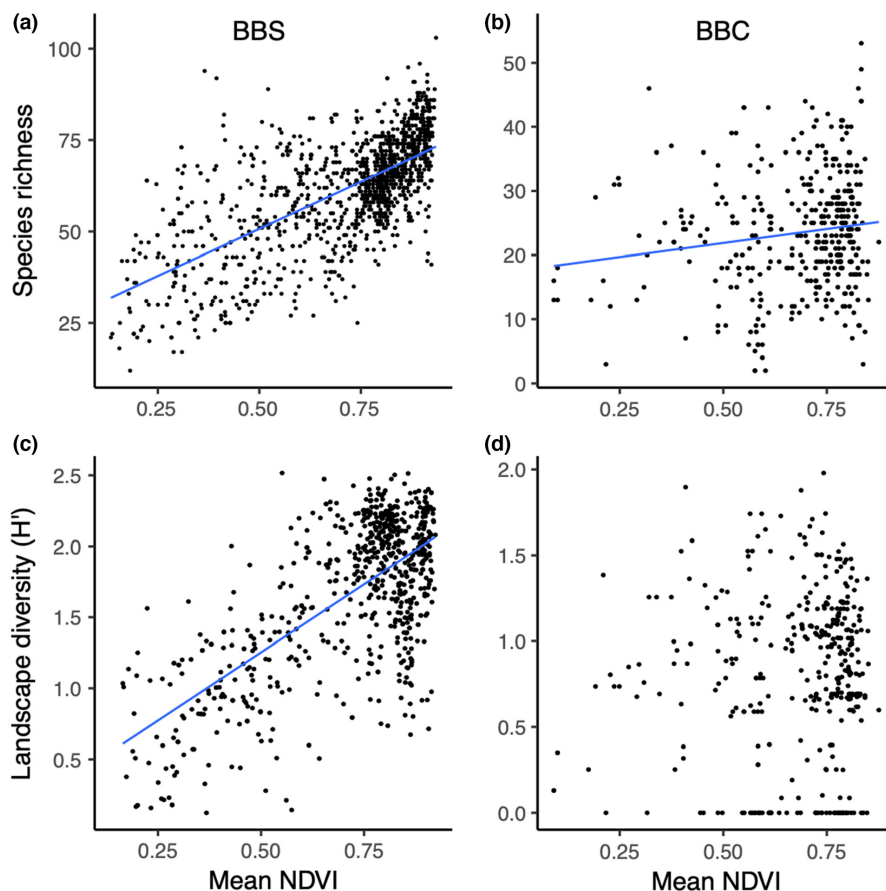


FIGURE 3 Breeding Bird Survey (BBS) and Breeding Bird Census (BBC) data in North America. (a) Species richness increases with NDVI on BBS routes ($R^2 = 0.45$, $p < 0.001$). (b) Species richness increases with NDVI at BBC sites ($R^2 = 0.02$, $p < 0.01$). (c) Landscape diversity increases with productivity on BBS routes ($R^2 = 0.45$, $p < 0.001$). (d) Landscape diversity does not increase strongly with productivity on BBC routes ($R^2 = 0.01$, $p = 0.10$). Blue lines are the regression lines. NDVI, normalized difference vegetation index.

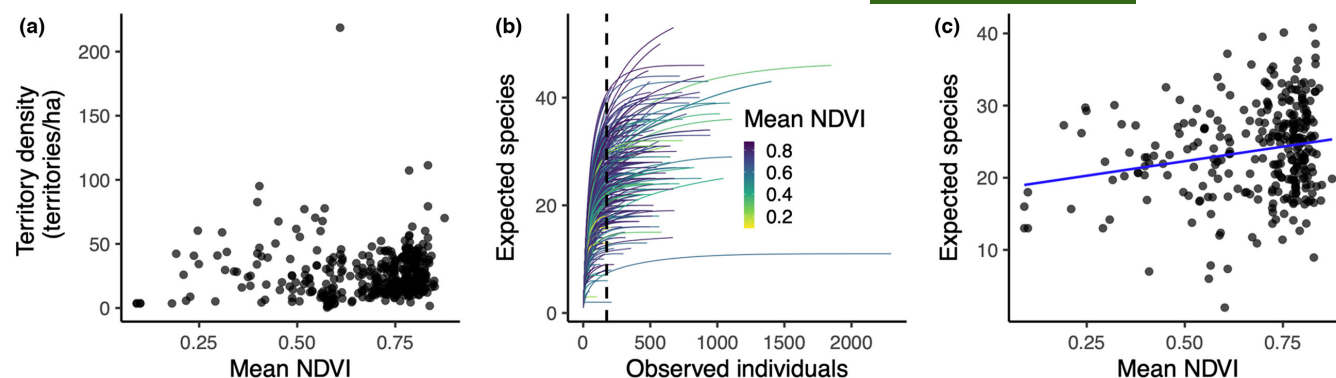


FIGURE 4 Breeding Bird Survey (BBS) and Breeding Bird Census (BBC) data in North America. (a) Community territory density (number of territories/ha) does not change with increasing NDVI across BBC sites (Prediction 1: Table 1). (b) Individual-based rarefaction curves for BBC sites (expected number of species per observed individual), colours of the curves indicate mean NDVI of the BBC site. The vertical dashed line at 175 individuals indicates the value of observed number of individuals used for each site to produce (c), which shows the expected number of species given 175 individuals observed for each BBC site (Prediction 2: Table 1). Rarefied species richness increases with NDVI across BBC sites ($R^2 = 0.04$). Blue line is the regression line. NDVI, normalized difference vegetation index.

3.1 | MIH predictions

Community territory density did not vary systematically with NDVI on BBC survey plots ($p = 0.546$; Figure 4a). Individual-based rarefaction curves for low and high NDVI BBC plots followed distinct trajectories, with high NDVI sites tending to increase in richness faster with number of territories sampled than low NDVI sites (Figure 4b,c). Expected species richness based on a fixed number of total territories (175) increased with NDVI (slope = 8.06, $R^2 = 0.04$, $p < 0.001$; Figure 4c).

3.2 | NSH predictions

Terrestrial bird species in the BBS showed broad variation in combinations of NDVI niche breadth and position, with more species clustered at higher values of mean NDVI although those species showed a wide breadth of NDVI ranges (Figure 5a). Aggregating spatially by NDVI bins, the mean NDVI range of species present in a given bin decreased with increasing NDVI, indicating a higher number of species with narrower NDVI niche breadth at higher NDVI sites (Figure 5b). The observed negative slope was much steeper than expected from the null model (slope = -0.142 , $p = 0.001$; see Figure S3 for null slope distribution).

To explore how species NDVI ranges (capturing the habitat niche) relate to foraging guild (capturing the diet niche), we examined how NDVI range varied across foraging guilds and how foraging guild richness varied with NDVI. Although most foraging guilds included species with high NDVI ranges indicating a broad productivity niche, guilds with lower NDVI ranges included foliage gleaning insectivores (both upper and lower canopy) and bark excavators, a group that includes most woodpeckers (Figure 5c). Guilds with higher median NDVI range included air hawkers (includes swifts, swallows, tyrant flycatchers), granivores and bark gleaners (Figure 5c). Both the number of species and number of

foraging guilds increased with NDVI, especially between NDVI values of 0 and 0.5 (Figure 5d). Omnivore and granivore foraging guilds showed richness that is fairly constant across NDVI values, while insectivore guilds showed substantial increases in species richness with NDVI (Figure 5d).

At low NDVI values, the observed number of foraging guilds was similar to or lower than the null-predicted number of foraging guilds in BBS and BBC surveys (Figure 6a,b). As NDVI increased, more foraging guilds were observed than expected from the null model in the BBS (slope = 3.02, $R^2 = 0.25$, $p < 0.001$) and to a much weaker degree in the BBC (slope = 0.822, $R^2 = 0.01$, $p = 0.083$).

4 | DISCUSSION

Although a positive relationship between productivity and avian richness has been widely documented over broad geographical extents, the mechanisms underlying this relationship have remained elusive. This study compared results from the widely used BBS dataset with a less examined dataset, the BBC, allowing for tests of two competing hypotheses. By drawing on these two complementary datasets, each with its own strengths and weaknesses, we have found some support for the assumptions and predictions of the NSH over the MIH.

We found that the strong positive productivity–richness relationship observed in the BBS and well documented in other datasets (Davies et al., 2007) is not generalizable to the BBC, which exhibited a much weaker relationship between species richness and NDVI. We suggest that this comparison to the BBC may provide an important insight into drivers of the observed pattern. While a previous examination of forested BBC sites found stronger support for a productivity–richness relationship and an increase in density of breeding pairs with productivity in 98 BBC sites (Mönkkönen et al., 2006), the results of this study indicate that this may not hold true when considering a broader range of the NDVI gradient which

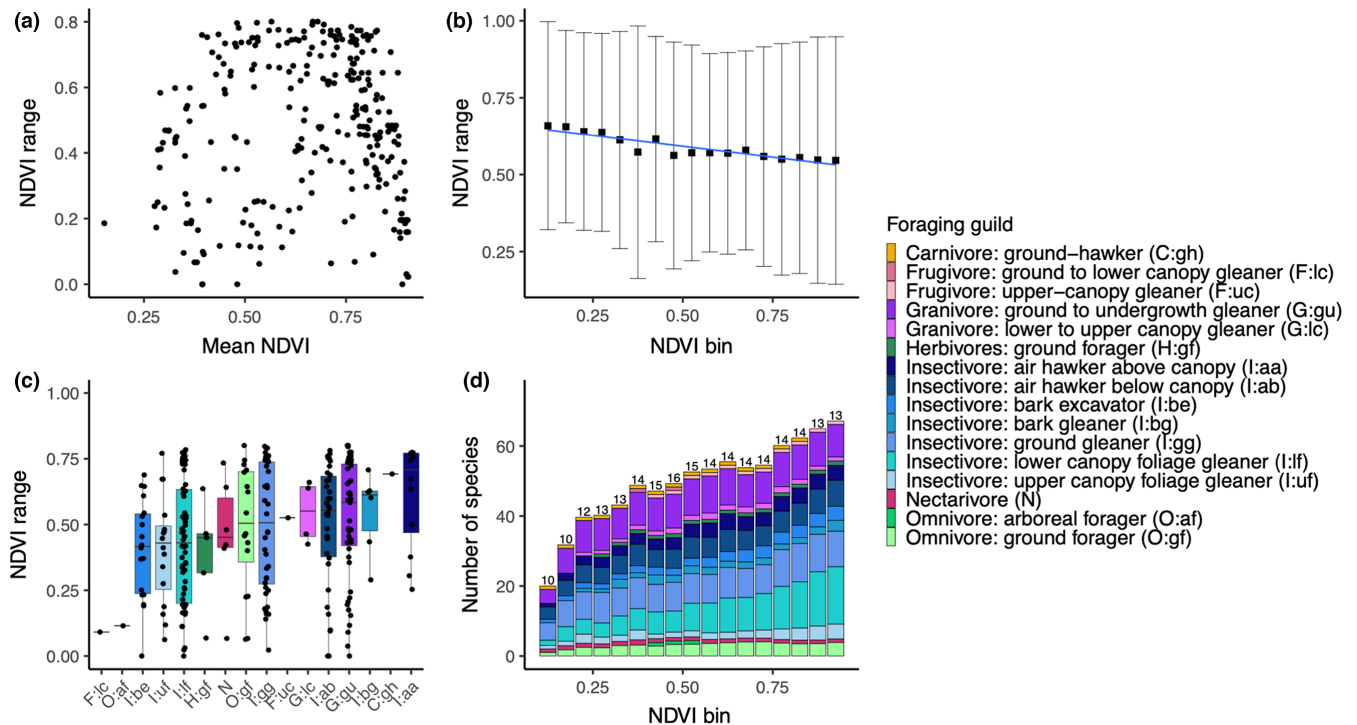


FIGURE 5 Breeding Bird Survey (BBS) and Breeding Bird Census (BBC) data in North America. (a) NDVI range (the breadth of NDVI values a species occurs over) versus mean NDVI across all sites a species occurs on in the BBS for 358 diurnal land birds. (b) For all survey routes in NDVI bins (bin size 0.05), the mean NDVI range of the species that occur in that bin (Prediction 2: Table 1). Blue line shows linear model fit. Error bars show 95% confidence intervals around the mean. As NDVI increases, mean NDVI breadth decreases (bootstrapped $p = 0.001$) while the spread of NDVI range values increases; in particular, the 0.05 percentile decreases as NDVI increases. (c) Boxplots of NDVI ranges of BBS species, grouped by foraging guild (foraging guild designations from: González-Salazar et al., 2014) and sorted by median NDVI range in each guild. Colour and x-axis abbreviation indicate foraging guild. (d) For BBS routes in a given NDVI bin, the number of species in each foraging guild indicated by colour. Total number of foraging guilds in each NDVI bin is indicated above each bar. NDVI, normalized difference vegetation index.

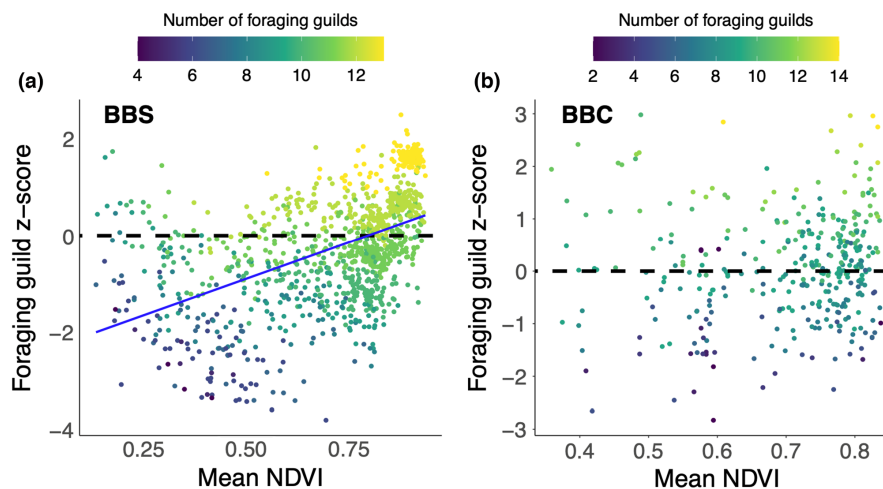


FIGURE 6 Breeding Bird Survey (BBS) and Breeding Bird Census (BBC) data in North America. Null model results testing a prediction of the Niche Specialization Hypothesis (NSH; Prediction 4: Table 1). For a given NDVI bin (0.05 for BBS, 0.07 for BBC), the null species pool consisted of the list of species occurring in that bin. Each point represents a z-score of the mean of 999 samples. Positive values indicate higher observed number of foraging guilds than the null prediction. (a) Null model results for the BBS ($R^2 = 0.25$) and (b) BBC datasets ($R^2 = 0.01$). Blue line is the regression line. NDVI, normalized difference vegetation index.



includes successional forests, grassland and shrubland habitats as well. Productivity–richness relationships are known to be scale dependent, and the fact that BBS routes are sampled at a larger spatial grain (40 km in length, ~25 km² in total surveyed area) than BBC sites (<1 km²) is consistent with the observation that such relationships may be strongest at larger scales (Storch et al., 2018). Additionally, the fact that the productivity–richness relationship varies between these geographically similar datasets helps point to a likely richness driver. Only in the roadside BBS surveys where NDVI is strongly correlated with landscape diversity does a strong productivity–richness relationship emerge, while in the BBC where survey sites are smaller in spatial scale and intentionally homogeneous in habitat the relationship is much weaker. Landscape diversity at various scales has long been known to increase avian richness (Coyle et al., 2013; Farwell et al., 2020; MacArthur & MacArthur, 1961; Tews et al., 2004), and this comparison between datasets suggests that landscape diversity may be the true driver of the BBS pattern and NDVI simply a correlate. Even at the scale of 1° grid cells, Hurlbert and Jetz (2010) found that productivity had an effect on richness above and beyond productivity's expected effect on the number of individuals that could be supported, and also attributed this to an increase in the structural complexity of terrestrial environments with productivity which presented novel foraging niches. Researchers making use of the BBS for future investigations should consider how this concurrent pattern may impact the interpretation of their results.

According to the MIH, community abundance is expected to increase with productivity (as a proxy for resource availability), but we did not find support for this key prediction using the more robust community territory density estimates from the BBC (although the productivity–richness relationship itself is weak in the BBC). Additionally, we found through a rarefaction analysis that the number of species expected while holding the number of individuals constant increases with NDVI. While the MIH has received some support as a mechanism explaining avian richness–productivity relationships (Chiari et al., 2010; Jonsson et al., 2011; Koleff et al., 2003), our results are in agreement with other studies that indicate that the MIH alone cannot fully explain observed richness patterns (Bonn et al., 2004; Currie et al., 2004; Dobson et al., 2015; Hurlbert, 2004; Hurlbert & Jetz, 2007; Seoane et al., 2017). While natural population variability can hinder detection of support for the MIH in datasets with fewer than 5 years of observation per site (Vagle & McCain, 2020), intensive sampling at nearly 400 BBC sites provides high power for detection of MIH relationships. It is possible that the reason for the lack of a relationship between community abundance and NDVI is that NDVI is a poor proxy for the resources available to birds. Estimating resource availability over broad biogeographical scales is challenging, but the development of new citizen science efforts to do so (e.g. Hurlbert et al., 2019) will allow for more direct tests of these resource-related links in the future.

We assessed support for the NSH along two niche axes: productivity niche (measured by productivity range following Bonn et al., 2004) and foraging niche. In the BBS dataset, high productivity

environments had a greater proportion of species with narrow productivity niches. Additionally, foraging niche diversity increased above null expectations with productivity—strongly in the BBS and weakly in the BBC. The fact that this effect was more pronounced in the BBS is consistent with the finding that the NDVI gradient was strongly correlated with landscape diversity across the roadside BBS routes, while only weakly so in the BBC. The observed increase in foraging guild richness with NDVI is in accordance with previous work in birds indicating that for avian communities in particular, gradients in niche availability may be an important mechanism in mediating productivity–richness gradients (Culbert et al., 2013; Feng et al., 2020; Hurlbert & Jetz, 2007; MacArthur & MacArthur, 1961; but see Roll et al., 2015).

Nevertheless, both niche measures we used had deficiencies that could have obscured even stronger underlying relationships. While our measure of productivity range provides some coarse information about habitat utilization, it cannot easily distinguish the degree to which species specialize on finer-scale microhabitats, such as forest edges and interiors. The categorical nature of the foraging niche classification we used precluded examining differences in foraging niche breadth between species. This is because each species was assigned to only a single foraging category, even though some categories may reflect a greater range of foraging behaviour than others. Future work examining how birds partition habitat and resources both horizontally and vertically along the productivity gradient may provide increased clarity into the mechanisms by which increased productivity yields greater species richness through the NSH.

The NSH and MIH are not mutually exclusive; however, we found that if both are operating, there is relatively stronger support for the NSH—especially specialization in foraging niche—than the MIH. While there may be certain contexts in which energy availability is important in driving richness, such as seasonal variation between breeding and non-breeding periods (Hurlbert & Haskell, 2003; Somveille et al., 2018), the relative contribution of the MIH and NSH may differ when describing seasonal variation in richness as opposed to geographical variation. Our results highlight the importance of carefully considering how inferences about mechanisms can be drawn from data at macroecological scales such as the BBS, especially in the presence of confounding variables such as the concurrent gradient in landscape diversity with productivity. Future work to directly measure the true explanatory variables of interest, such as resource availability and niche breadth, at macroecological scales will be essential for definitively unravelling the mechanisms underlying productivity–richness relationships.

ACKNOWLEDGEMENTS

We would like to thank the thousands of skilled volunteers in the United States and Canada who have participated in the BBS and BBC over the years and those who have served as provincial, territorial or state coordinators for the BBS. Without their contributions, this project would not have been possible. No permits were needed to carry out this work.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This study relies on publicly accessible datasets. All code and data to reproduce analyses in this manuscript are archived at Zenodo: DOI: [10.5281/zenodo.6622132](https://doi.org/10.5281/zenodo.6622132).

ORCID

Grace J. Di Cecco  <https://orcid.org/0000-0003-1872-5117>

Sara J. Snell Taylor  <https://orcid.org/0000-0002-0353-9613>

Ethan P. White  <https://orcid.org/0000-0001-6728-7745>

Allen H. Hurlbert  <https://orcid.org/0000-0002-5678-9907>

REFERENCES

- Abrams, P. A. (1995). Monotonic or unimodal diversity-productivity gradients: What does competition theory predict? *Ecology*, 76(7), 2019–2027. <https://doi.org/10.2307/1941677>
- Arita, H. T., Rodríguez, P., & Vázquez-Domínguez, E. (2005). Continental and regional ranges of North American mammals: Rapoport's rule in real and null worlds. *Journal of Biogeography*, 32(6), 961–971. <https://doi.org/10.1111/j.1365-2699.2005.01276.x>
- Bonn, A., Storch, D., & Gaston, K. J. (2004). Structure of the species-energy relationship. *Proceedings of the Royal Society B: Biological Sciences*, 271(1549), 1685–1691. <https://doi.org/10.1098/rspb.2004.2745>
- Boulinier, T., Nichols, J. D., Hines, J. E., Sauer, J. R., Flather, C. H., & Pollock, K. H. (1998). Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 95(13), 7497–7501. <https://doi.org/10.1073/pnas.95.13.7497>
- Butcher, G. S., Robbins, C. S., Bystrak, D., & Geissler, P. H. (1987). The breeding bird survey: Its first fifteen years, 1965–1979. *The Condor*, 89(3), 681. <https://doi.org/10.2307/1368666>
- Chiari, C., Dinetti, M., Licciardello, C., Licitra, G., & Pautasso, M. (2010). Urbanization and the more-individuals hypothesis. *Journal of Animal Ecology*, 79(2), 366–371. <https://doi.org/10.1111/j.1365-2656.2009.01631.x>
- Colwell, R. K., & Hurlbert, G. C. (1994). Nonbiological gradients in species richness and a spurious rapoport effect. *The American Naturalist*, 144(4), 570–595.
- Coyle, J. R., Hurlbert, A. H., & White, E. P. (2013). Opposing mechanisms drive richness patterns of core and transient bird species. *American Naturalist*, 181(4), E83–E90. <https://doi.org/10.1086/669903>
- Culbert, P. D., Radeloff, V. C., Flather, C. H., Kellendorfer, J. M., Rittenhouse, C. D., & Pidgeon, A. M. (2013). The influence of vertical and horizontal habitat at structure on nationwide patterns of avian biodiversity. *Auk*, 130(4), 656–665. <https://doi.org/10.1525/auk.2013.13007>
- Currie, D. J. (1991). Energy and large-scale patterns of animal and plant species richness. *American Naturalist*, 137(1), 27–49. <https://doi.org/10.1086/285144>
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7(12), 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., Ding, T.-S., Rasmussen, P. C., Bennett, P. M., Owens, I. P. F., Blackburn, T. M., & Gaston, K. J. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, 274(1614), 1189–1197. <https://doi.org/10.1098/rspb.2006.0061>
- Didan, K. (2015). MOD13Q1 MODIS/Terra vegetation indices 16-day 13 global 250m SIN grid V006. NASA EOSDIS Land Processes DAAC. <https://doi.org/10.5067/MODIS/MOD13Q1.006>
- Dobson, L. L., La Sorte, F. A., Manne, L. L., & Hawkins, B. A. (2015). The diversity and abundance of North American bird assemblages fail to track changing productivity. *Ecology*, 96(4), 1105–1114. <https://doi.org/10.1890/14-0057.1>
- Engstrom, R. T. (1989). The 1988 counts. *Journal of Field Ornithology*, 60, 5. <https://about.jstor.org/terms>
- Engstrom, R. T. (1990). 1989 counts. *Journal of Field Ornithology*, 61(Suppl), 3–4.
- Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 80, 1–25. <https://doi.org/10.1017/S1464793104006517>
- Farwell, L. S., Elsen, P. R., Razenkova, E., Pidgeon, A. M., & Radeloff, V. C. (2020). Habitat heterogeneity captured by 30-m resolution satellite image texture predicts bird richness across the United States. *Ecological Applications*, 30(8), e02157. <https://doi.org/10.1002/eap.2157>
- Feng, G., Zhang, J., Girardello, M., Pellissier, V., & Svenning, J. C. (2020). Forest canopy height co-determines taxonomic and functional richness, but not functional dispersion of mammals and birds globally. *Global Ecology and Biogeography*, 29, 1350–1359. <https://doi.org/10.1111/geb.13110>
- Gardali, T., & Lowe, J. D. (2007). The 2003 and 2004 North American breeding bird census with additions for 2001 and 2002. *Bird Populations*, 8, 116–120.
- Gardali, T., & Lowe, J. D. (2009). The 2005 and 2006 North American breeding bird census with additions for 2003 and 2004. *Bird Populations*, 6, 170–173.
- González-Salazar, C., Martínez-Meyer, E., & López-Santiago, G. (2014). A hierarchical classification of trophic guilds for North American birds and mammals. *Revista Mexicana de Biodiversidad*, 85(3), 931–941. <https://doi.org/10.7550/rmb.38023>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105–3117. <http://www.mendeley.com/research/relationships-among-species-traits-separating-levels-response-identifying-linkages-abundances/>
- Heath, S. K., Palladini, M. A., & Prentice, S. (2006). Breeding bird census: 2001. *Bird Populations*, 7, 96–113.
- Homer, C., Huang, C., Yang, L., Wylie, B., & Falls, S. (2004). Development of a circa 2000 landcover database for the United States. *Photogrammetric Engineering & Remote Sensing*, 70(7), 829–840.
- Hurlbert, A. H. (2004). Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, 7(8), 714–720. <https://doi.org/10.1111/j.1461-0248.2004.00630.x>
- Hurlbert, A. H., & Haskell, J. P. (2003a). The effect of energy and seasonality on avian species richness and community composition. *American Naturalist*, 161(1), 83–97. <https://doi.org/10.1086/345459>
- Hurlbert, A. H., Hayes, T., McKinnon, T., & Goforth, C. (2019). Caterpillars count! A citizen science project for monitoring foliage arthropod abundance and phenology. *Citizen Science: Theory and Practice*, 4(1), 1–12. <https://doi.org/10.5334/cstp.148>
- Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, 104(33), 13384–13389. <https://doi.org/10.1073/pnas.0704469104>
- Hurlbert, A. H., & Jetz, W. (2010). More than “more individuals”: The nonequivalence of area and energy in the scaling of



- species richness. *American Naturalist*, 176(2), E50–E65. <https://doi.org/10.1086/650723>
- Hurlbert, A. H., & Stegen, J. C. (2014). When should species richness be energy limited, and how would we know? *Ecology Letters*, 17, 401–413.
- Jonsson, M., Englund, G., & Wardle, D. A. (2011). Direct and indirect effects of area, energy and habitat heterogeneity on breeding bird communities. *Journal of Biogeography*, 38(6), 1186–1196. <https://doi.org/10.1111/j.1365-2699.2010.02470.x>
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, 72(72), 367–382.
- Lowe, J. D. (1993). Resident bird counts 1992. *Journal of Field Ornithology*, 64(Suppl), 3–4.
- Lowe, J. D. (1994). Resident bird counts 1993. *Journal of Field Ornithology*, 65(Suppl), 3–4.
- Lowe, J. D. (1995). Resident bird counts 1994. *Journal of Field Ornithology*, 66(Suppl), 3–4.
- Lowe, J. D. (1996). Resident bird counts 1995. *Journal of Field Ornithology*, 67(Suppl), 3–4.
- Lowe, J. D., & Desante, D. F. (2012). The 2009 North American breeding bird census. *Bird Populations*, 11, 52–53.
- MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42(3), 594–598.
- Marshall, R. M. (1991). Resident bird counts 1990. *Journal of Field Ornithology*, 62, 3–5.
- Marshall, R. M. (1992). Resident bird counts 1991. *Journal of Field Ornithology*, 63(Suppl), 3–5.
- McGill, B. J. (2003). A test of the unified neutral theory of biodiversity. *Nature*, 422(6934), 881–885.
- McGlinn, D. J., Xiao, X., May, F., Gotelli, N. J., Engel, T., Blowes, S. A., Knight, T. M., Purschke, O., Chase, J. M., & McGill, B. J. (2019). Measurement of biodiversity (MoB): A method to separate the scale-dependent effects of species abundance distribution, density, and aggregation on diversity change. *Methods in Ecology and Evolution*, 10(2), 258–269. <https://doi.org/10.1111/2041-210X.13102>
- Mönkkönen, M., Forsman, J. T., & Bokma, F. (2006). Energy availability, abundance, energy-use and species richness in forest bird communities: A test of the species-energy theory. *Global Ecology and Biogeography*, 15(3), 290–302. <https://doi.org/10.1111/j.1466-822X.2006.00224.x>
- Pinzon, J. E., & Tucker, C. J. (2014). A non-stationary 1981–2012 AVHRR NDVI3g time series. *Remote Sensing*, 6(8), 6929–6960. <https://doi.org/10.3390/rs6086929>
- Robbins, C. S. (1970). Recommendations for an international standard for a mapping method in bird census work. *Audubon Field Notes*, 24, 723–726.
- Roll, U., Geffen, E., & Yom-Tov, Y. (2015). Linking vertebrate species richness to tree canopy height on a global scale. *Global Ecology and Biogeography*, 24(7), 814–825. <https://doi.org/10.1111/geb.12325>
- Sauer, J. R., Pardieck, K. L., Ziolkowski, D. J., Smith, A. C., Hudson, M. R., Rodriguez, V., Berlanga, H., Niven, D. K., & Link, W. A. (2017). The first 50 years of the North American Breeding Bird Survey. *The Condor*, 119(3), 576–593.
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185(4145), 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Seoane, J., Laiolo, P., & Obeso, J. R. (2017). Abundance leads to more species, particularly in complex habitats: A test of the increased population size hypotheses in bird communities. *Journal of Biogeography*, 44(3), 556–566. <https://doi.org/10.1111/jbi.12877>
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27(4), 623–656. <https://doi.org/10.1002/j.1538-7305.1948.tb00917.x>
- Snell Taylor, S. J., Evans, B. S., White, E. P., & Hurlbert, A. H. (2018). The prevalence and impact of transient species in ecological communities. *Ecology*, 99(8), 1825–1835. <https://doi.org/10.1002/ecy.2398>
- Somveille, M., Rodrigues, A. S. L., & Manica, A. (2018). Energy efficiency drives the global seasonal distribution of birds. *Nature Ecology & Evolution*, 2, 962–969.
- Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist*, 152(4), 510–529. <https://doi.org/10.1086/286187>
- Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity-diversity relationship. *Ecology Letters*, 21(6), 920–937. <https://doi.org/10.1111/ele.12941>
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, 31(1), 79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Vagle, G. L., & McCain, C. M. (2020). Natural population variability may be masking the more-individuals hypothesis. *Ecology*, 101(5), e03035. <https://doi.org/10.1002/ecy.3035>
- Vanderwal, A. J., Falconi, L., Januchowski, S., & Shoo, L. (2019). Package ‘SDMTools’.
- Vermote, E., & Program, N. C. (2019). NOAA climate data record (CDR) of AVHRR normalized difference vegetation index (NDVI), version 5. NOAA National Centers for Environmental Information. <https://doi.org/10.7289/V5ZG6QH9>
- White, E. P., Hurlbert, A. H., Evans, B. S., & Di Cecco, G. (2021). *weecology/bbc-data-rescue*: v1.0 (version 1.0). <https://doi.org/10.5281/zenodo.4776710>
- Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, 41(3), 496–506.

BIOSKETCH

Grace J. Di Cecco earned her PhD at the University of North Carolina in the Hurlbert Lab (<http://labs.bio.unc.edu/hurlbert/index.html>). Her research focuses on understanding how populations, communities and species distributions are shaped by environmental change.

Author contributions: Grace J. Di Cecco, Sara J. Snell Taylor and Allen H. Hurlbert conceived of the research ideas, Ethan P. White processed the BBC data, and Grace J. Di Cecco and Sara J. Snell Taylor conducted the analyses. Grace J. Di Cecco wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Di Cecco, G. J., Snell Taylor, S. J., White, E. P., & Hurlbert, A. H. (2022). More individuals or specialized niches? Distinguishing support for hypotheses explaining positive species–energy relationships. *Journal of Biogeography*, 49, 1629–1639. <https://doi.org/10.1111/jbi.14459>