

ARTICLE

Methods, Tools, and Technologies

North American Breeding Bird Survey underestimates regional bird richness compared to Breeding Bird Atlases

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Abstract

Standardized data on large-scale and long-term patterns of species richness are critical for understanding the consequences of natural and anthropogenic changes in the environment. The North American Breeding Bird Survey (BBS) is one of the largest and most widely used sources of such data, but so far, little is known about the degree to which BBS data provide accurate estimates of regional richness. Here, we test this question by comparing estimates of regional richness based on BBS data with spatially and temporally matched estimates based on state Breeding Bird Atlases (BBA). We expected that estimates based on BBA data would provide a more complete (and therefore, more accurate) representation of regional richness due to their larger number of observation units and higher sampling effort within the observation units. Our results were only partially consistent with these predictions: while estimates of regional richness based on BBA data were higher than those based on BBS data, estimates of local richness (number of species per observation unit) were higher in BBS data. The latter result is attributed to higher land-cover heterogeneity in BBS units and higher effectiveness of bird detection (more species are detected per unit time). Interestingly, estimates of regional richness based on BBA blocks were higher than those based on BBS data even when differences in the number of observation units were controlled for. Our analysis indicates that this difference was due to higher compositional turnover between BBA units, probably due to larger differences in habitat conditions between BBA units and a higher likelihood of observing geographically restricted species. Our overall results indicate that estimates of regional richness based on BBS data suffer from incomplete detection of a large number of rare species, and that corrections of these estimates based on standard extrapolation techniques are not sufficient to remove this bias. Future applications of BBS data in ecology and conservation, and in particular, applications in which the representation of rare species is important (e.g., those focusing on

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biodiversity conservation), should be aware of this bias, and should integrate BBA data whenever possible.

KEYWORDS

BBS, biodiversity, birds, Breeding Bird Atlases, habitat heterogeneity, incomplete detection, North American Breeding Bird Survey, sampling effort, species richness

INTRODUCTION

Recent interest in the effects of global change on the world's biodiversity has emphasized the need for standardized data on large-scale patterns of species diversity and their change through time (Ball-Damerow et al., 2019; Dornelas et al., 2014; Sorte & Somveille, 2020; Troia & McManamay, 2016; Verheyen et al., 2017). One of the largest and most widely used sources of such standardized data is the North American Breeding Bird Survey (hereafter, BBS; Sauer, Pardieck, et al., 2017). The BBS is unique in both its spatial extent (~5000 secondary routes spread over

most of the United States and Canada) and temporal scale (>50 years of annual surveys) and has followed the same sampling protocol since the initiation of the project in the mid-60s (Sauer, Niven, et al., 2017). Due to these advantages, BBS data have been used in numerous studies for quantifying patterns of spatial and temporal variations in biodiversity and analyzing biodiversity responses to climate, habitat conditions, land-use modification, and human disturbances (Table 1). Many of these studies were explicitly designed to aid in biodiversity conservation (Hudson et al., 2017; Rosenberg et al., 2017). For the same reason, BBS data have often been used as a yardstick for

TABLE 1 Selected examples for recent applications of BBS data in ecology and conservation

Source	Main focus of the study
Farwell et al. (2020)	Effect of habitat heterogeneity on species diversity
Elsen et al. (2020)	Effect of temperature on species diversity
Fogarty et al. (2020)	Interannual variation in climate on bird species abundance
Saracco and Rubenstein (2020)	Climatic effects on population decline
Curley et al. (2020)	Temporal changes in migratory distances
Rushing et al. (2019)	Spatiotemporal range dynamics
Valle et al. (2018)	Biogeographic shifts in response to predicted climate change
Cady et al. (2019)	Species responses to drought
Janousek et al. (2019)	Long-term population trends
Clement et al. (2019)	Effects of climate change and land-cover change on bird distribution
Shaffer et al. (2019)	Effect of crop production on habitat loss for grassland birds
Jarzyna and Jetz (2018)	Effect of scale on temporal changes in functional and taxonomic diversity
Sofaer et al. (2018)	Ability of distribution models to predict responses to climate change
Rich and Currie (2018)	Effect of climatic variables on distribution ranges
Wu et al. (2018)	Responses to climate change in US national parks
Stanton et al. (2018)	Effects of agricultural drivers on farmland bird decline
Regos et al. (2018)	Community responses to temporal changes in land use
Harris et al. (2018)	Diversity responses to climate change
Barnagaud et al. (2017)	Temporal variation in functional diversity
Huang et al. (2017)	Trends and drivers of long-term changes in bird abundance
Handel and Sauer (2017)	Roadside versus off-road long-term changes in bird populations
Koenig et al. (2017)	Drivers of long-term population decline
Martin et al. (2017)	Dispersal and biotic homogenization

Abbreviation: BBS, Breeding Bird Survey.

evaluating the performance of new modeling tools in ecology (Link et al., 2020; Saracco & Rubenstein, 2020; Valle et al., 2018) and conservation (Cam, Nichols, Sauer, et al., 2002; Polasky et al., 2001), as well as for testing general concepts and theories of community ecology such as the scaling of population variability (Keitt & Stanley, 1998), the species pool hypothesis (Cam et al., 2000), biotic homogenization (Martin et al., 2017; Sorte & McKinney, 2007), abundance–occupancy relationships (Zuckerberg, Porter, et al., 2009), area-heterogeneity trade-off (Chocron et al., 2015), the insurance hypothesis (Valone & Barber, 2008), diversity–stability relationships (Catano et al., 2020), and many more (Bertuzzo et al., 2011; Hansen et al., 2011; Maurer et al., 2013; McGill, 2003; Mikkelsen et al., 2011; Mimet et al., 2019; Osorio-Olvera et al., 2020).

In spite of these widespread and diverse applications, BBS data, as with any survey of biodiversity data, are subject to sampling limitations. Such limitations arise from both incomplete detection of individuals (Kendall et al., 1996) and species (Boulinier et al., 1998) at the scale of the observation unit; imperfect availability and perceptibility (Handel & Sauer, 2017; Leston et al., 2015; Lituma et al., 2017; Rushing et al., 2019); and a limited number of observation units at the regional scale (i.e., a too-small sample size). These sources of sampling limitations may lead to negative bias in estimates of species richness. However, while the issue of incomplete detection within observation units is well recognized and often taken into account in the analysis of BBS data (Cam, Nichols, Hines, et al., 2002; Chocron et al., 2015; Clement et al., 2016; Moral et al., 2018; Rushing et al., 2019), the issue of sample size limitation is usually ignored. Importantly, even if detection probability is perfect, regional-scale estimates of richness might be biased due to sample size limitation and absence of certain habitats or environmental combinations in the relevant set of observations (Lawler & O'Connor, 2004). Such sampling limitation is particularly problematic in studies focusing on biodiversity conservation where documenting rare species and species with narrow ecological niches is of critical importance. Nevertheless, none of the studies mentioned above has attempted to evaluate the existence or magnitude of this source of bias.

Another source of data that are increasingly used for analyzing spatial and temporal patterns of bird distribution in North America is state Breeding Bird Atlases (hereafter, BBA). Such atlases consist of concerted, intensive efforts to map the geographical distribution of breeding birds at the level of an entire state. Recently, there has been a considerable progress in the publication of “second-generation” and even “third-generation” atlases, enabling state-level comparisons of species distributions over periods of two decades and more (Beck et al., 2018, see <https://www.pwrc.usgs.gov/bba/index.cfm?fa=bba>.

BbaHome&view=list for an updated list). This progress has opened new opportunities for analyzing long-term responses of birds to natural and anthropogenic changes in the environment (Jarzyna et al., 2015, 2016; Kujala et al., 2013; Melles et al., 2011; Sadoti et al., 2013; van der Hoek et al., 2015; Zuckerberg, Woods, et al., 2009).

An important advantage of BBA over the BBS, when such atlases are available, is a greater coverage of the state area (Gibbons et al., 2007). Historically, this advantage has often come at the cost of higher variability in sampling protocols and unknown sampling efforts, which reduced the quality and potential applications of the data. However, most second-generation atlases include information on sampling efforts and provide more detailed information on the sampling protocol (McGowan & Corwin, 2008; Renfrew, 2013; Wilson et al., 2012).

Both BBS and BBA data have been used extensively to document and analyze patterns of regional diversity. However, although some BBA publications allude to BBS temporal trends in their species descriptions (McGowan & Corwin, 2008; Renfrew, 2013; Wilson et al., 2012), we are not aware of any systematic attempt to quantify and compare estimates of *large-scale regional diversity* based on the two data sources. Such comparison is important because a strong similarity between BBA and BBS estimates of regional richness may strengthen our confidence in the credibility of both datasets. On the other hand, significant differences between estimates may help identify potential sources of bias, thereby providing important information for better interpretation of past and future studies based on the BBS data.

Here, we compare estimates of regional richness based on BBS versus BBA data in an attempt to evaluate the existence, magnitude, scales, and sources of differences in such estimates. Specifically, we ask two main questions: (1) Are estimates of regional richness (number of species at the scale of a large region such as a state) based on BBS and BBA data similar? (2) If not, what are the reasons for the observed differences? As elaborated below, we expected that estimates of regional richness based on BBA data would be higher than corresponding estimates based on BBS data; and that these differences would relate to underlying differences in the number of observation units, their geographical distribution, the environmental characteristics of the observation units, and the sampling procedures applied within the observation units.

Theoretical considerations and predictions

Our hypothesis that estimates of regional richness based on BBA data would be higher than those based on BBS

data was based on three main considerations. First, the total area covered by BBA blocks in each state is much larger than that covered by BBS routes. This difference is expected to result in higher estimates of regional richness because larger areas support larger numbers of individuals, thereby increasing the likelihood of detecting species with low abundance (Connor & McCoy, 1979). Second, larger areas may also encompass wider ranges of environmental conditions, thereby providing suitable habitat conditions to a larger number of species with different ecological requirements (Williams, 1964). Although survey effort within BBA blocks may not fully represent the range of environmental conditions within the block, BBA protocols encourage either complete coverage or representative sampling of habitats (Beck et al., 2018).

Third, there are differences in sampling efforts within observation units of the two data sources: BBS routes are sampled by 50-point counts, each lasting 3 min (a total of 2.5 h per observation unit per year). In contrast, BBA observers are explicitly directed to maximize the number of species observed per block (Beck et al., 2018) and often return repeatedly to the same block over the course of the collection period. Thus, BBA observations are often distributed over an entire season, and at different times of day, while BBS observations provide only a 1-day snapshot of the local bird community.

Differences in size, shape, and geographical distribution between BBA blocks and BBS routes may introduce further differences to estimates of regional richness, for example, due to biases in the representation of land-cover conditions (Van Wilgenburg et al., 2015; Veech et al., 2017). Moreover, while BBA observers only need to document the sightings of new species, BBS observers need to count the number of individuals of each species they observe. Under the constraint of 3 min per stop, such counting, particularly of common species, may reduce the likelihood of detecting rare species, thereby leading to a negative bias in estimating local richness. Interestingly, a simple calculation indicates that the actual area sampled along a BBS route is rather similar to the area of a BBA block: Each point count along a BBS route samples an area with a radius of 0.4 km (a total of 25.12 km² per route), while BBA blocks are approximately 5 × 5 km in size. However, due to their elongated shape, BBS routes may intersect more habitats than BBA blocks, thereby “sampling” more species with different ecological requirements and increasing richness (Bacaro et al., 2015; Kunin, 1997).

Still, the fact that BBS observations are limited to roadsides may lead to underrepresentation of regional environmental conditions, thereby offsetting the effect of the elongated shape of BBS routes on habitat heterogeneity. For example, it can be expected that high-altitude habitats, or areas with rough topography, would be underrepresented by BBS routes relative to BBA blocks.

Such underrepresentation of certain habitat conditions is expected to reduce the range of environmental conditions (i.e., the magnitude of habitat heterogeneity) within routes, while increasing the similarity in environmental conditions between routes. The first effect is expected to reduce the local richness (number of species at the scale of the observation unit) and the second is expected to reduce the magnitude of compositional turnover (the magnitude of variation in species composition among observation units). Both effects may result in lower estimates of regional richness in the case of BBS data. Direct disturbances caused by road construction and vehicle traffic may also lead to reduced richness and detectability along BBS routes (Griffith et al., 2010).

Based on the above considerations, we formulated eight predictions for expected differences in environmental conditions and species diversity between BBA and BBS data (Table 2). We tested these predictions by comparing the distribution of key environmental variables (elevation, precipitation, and temperature) and estimates of species diversity (regional richness, local richness, and compositional turnover) between BBS routes and BBA blocks in five states in the Northeastern United States: Massachusetts, Michigan, New York, Pennsylvania, and Vermont (a total area of 415,150 km²).

TABLE 2 Predictions tested in this study

No.	Prediction
1	At the regional scale, BBA blocks sample a larger range of environmental conditions than BBS routes
2	At the local scale (the scale of the observational unit), BBA blocks are more heterogeneous in their environmental conditions than BBS routes
3	Estimates of regional richness based on BBA data would be higher than those based on BBS data
4	Much of the differences in regional richness between the two data sources would be accounted for by underlying differences in sample size (number of observation units)
5	Estimates of regional richness based on BBA data would be higher than those based on BBS data also after controlling for underlying differences in the number of observations
6	Local richness in BBA blocks would be higher than that of BBS routes
7	Compositional turnover among BBS routes would be smaller than that among BBA blocks
8	Some of the variation in local richness among BBA blocks and BBS routes would be accounted for by underlying differences in sampling effort

Abbreviations: BBA, Breeding Bird Atlases; BBS, Breeding Bird Survey.

METHODS

State BBA

BBA atlases span 5–6 years of focused survey effort of species presence between April and September in $\sim 5 \times 5$ km blocks by thousands of volunteers guided by expert birders, with the intention of detecting as many species as possible in as large an area within a state (Beck et al., 2018). Our analysis was based on second-generation atlases of five states sampled during the 2000s (Table 3): Massachusetts (Kamm et al., 2013), Michigan (Chartier et al., 2013), New York (McGowan & Corwin, 2008), Pennsylvania (Wilson et al., 2012), and Vermont (Renfrew, 2013). The data obtained from the five atlases were used to create an integrated presence-absence table summarizing the occurrence of all species recorded in all blocks for which data were available in the five atlases ($278 \text{ species} \times 16,606 \text{ blocks} = 4,616,468$ presence-absence data, see Appendix S1 for technical details).

The Breeding Bird Survey

The BBS is a roadside survey in the United States and Canada sampling for species presence and abundance annually around June. Each route is 40 km long and consists of 50 stops separated by 800 m. A single observer conducts a 3-min point count at each stop (Sauer, Niven, et al., 2017; Sauer, Pardieck, et al., 2017).

In order to prevent bias caused by year-to-year fluctuations in bird distribution, we used BBS data for each state only from the years overlapping that state's BBA. For example, since New York's second atlas was conducted between 2000 and 2005, we used BBS routes sampled in New York from those years. We coded a species from the BBS as present if it appeared in at least one survey during the survey period. This procedure made the BBS data

comparable to the BBA data, where one sighting of a bird in a given block over the whole survey period was coded as presence ($213 \text{ species} \times 281 \text{ routes} = 59,853$ presence/absence data). Species that were observed only in one dataset (BBA vs. BBS) were coded as absent in the other (see Appendix S1 for further details).

Environmental data

We characterized each observation unit by two climatic variables that are known to be important in determining patterns of breeding bird distribution in North America—mean annual precipitation and mean summer temperature (Barbet-Massin & Jetz, 2014; DesGranges & LeBlanc, 2012; Northrup et al., 2019). Both variables were determined using 800 m resolution PRISM data (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>) from the period 2000 to 2011 (the entire period for which we analyzed BBA and BBS data). In the case of BBS data, we used a buffer of 400 m around the route (the distance at which birds are assumed to be detected during the survey) to calculate the two variables. For each buffer, we calculated the mean value of each climatic variable in each year and then averaged the resulting values to obtain a single characteristic value for each variable in each buffer. A similar procedure was applied for each BBA block.

For each observation unit, we extracted the mean elevation and elevation range (maximum – minimum elevation) using 90m resolution data from the Shuttle Radar Topography Mission (Jarvis et al., 2008). We focused on elevation range as a measure of topographic heterogeneity as it is the most common index used and was the measure used in almost all previous analyses of bird responses to environmental heterogeneity (Stein & Kreft, 2015). Land-cover characteristics were determined for each observation unit using 30 m resolution National

TABLE 3 Characteristics of the BBA and BBS data used in the study

States	Survey years	BBA blocks		BBS routes	
		Sample size	Sampling effort (hours)	Sample size	Sampling effort (hours)
Massachusetts	2007–2011	1031	42.01 $\pm$ 30.94	22	7.61 $\pm$ 2.83
Michigan	2002–2008	4754	7.63 $\pm$ 14.27	58	10.34 $\pm$ 4.81
New York	2000–2005	5267	29.46 $\pm$ 35.84	90	10.47 $\pm$ 4.59
Pennsylvania	2004–2008	4937	21.78 $\pm$ 32.29	92	10.46 $\pm$ 3.23
Vermont	2003–2007	336	77.54 $\pm$ 62.45	19	9.74 $\pm$ 3.11

Note: Sampling effort indicates the number of hours (mean $\pm$ SD) spent surveying the observation unit (BBA block or BBS route). For BBA blocks, it is based on the atlas information. For BBS routes, it is calculated as the total time of point counts per route (2.5 per year) $\times$ number of years that the route was surveyed during the period that matches the corresponding state atlas.

Abbreviations: BBA, Breeding Bird Atlases; BBS, Breeding Bird Survey.

Land Cover Database 2006 data (Fry et al., 2011), since these data overlap with the time period of most state atlases (with the exception of New York that was terminated in 2005). The classification includes 15 natural and human-modified land-cover types in our study area (see Fry et al., 2011 for details). For each BBA block and BBS route, we calculated the relative area of each land-cover type, the number of land-cover types (hereafter, land-cover richness), and the Shannon–Wiener diversity index (hereafter, land-cover diversity).

Data analysis

Our analysis focused on the entire region for which we had data (the area covered by the five atlases). However, to better understand the patterns obtained at the regional scale and to evaluate the robustness of our results, we conducted most kinds of analyses also at the scale of individual states. Although we had complete information for the routes and blocks in each state, we considered our data as “samples” representing larger “populations” of routes and blocks in the United States and therefore applied statistical procedures when testing each of our predictions. All analyses were performed in R (R Core Team, 2021).

Prediction 1 (at the regional scale, BBA blocks would sample a larger range of environmental conditions than BBS routes) was tested by comparing the ranges of mean annual precipitation, mean summer temperature, and mean elevation, between BBA blocks and BBS routes in each state and over the entire area. The range of each variable (hereby, elevation, precipitation, and temperature) was quantified as the difference between the highest and lowest values of that variable in the relevant dataset. For example, the range of precipitation among BBA blocks in a given state was determined as the difference in mean annual precipitation between the blocks with the highest and lowest mean values of precipitation in that state. Since our hypothesis is directional, a one-tailed paired t test ($n = 5$ states), as well as a corresponding nonparametric Wilcoxon signed-rank test (due to the small sample size), were used to determine the significance of the observed differences in each variable (Hollander et al., 2013).

Prediction 2 (at the local scale, BBA blocks would be more heterogeneous in their environmental conditions than BBS routes) was tested using three widely used measures of environmental heterogeneity (Stein et al., 2014): elevation range, land-cover richness, and land-cover diversity. For each measure, we constructed a mixed-effect model using the `lmer` and `glmer` functions in the `lme4` package in R (Bates et al., 2015), with environmental heterogeneity as the response variable, data source as

a fixed effect and state as a random effect. For land-cover diversity, we ran a linear mixed model (hereafter, LMM) with Gaussian distribution; for elevation range, due to a strong positive skewness, we ran a generalized linear mixed model (hereafter, GLMM) with Gamma distribution; and for land-cover richness count data, we ran a GLMM with a Poisson error structure.

Prediction 3 (estimates of regional richness based on BBA data would be higher than those based on BBS data) was tested by comparing the total number of species recorded in BBS routes versus BBA blocks for each state. We used a one-tailed pairwise t test ($n = 5$ states) and a corresponding nonparametric Wilcoxon test to determine the significance of the observed difference.

Prediction 4 (much of the difference in regional richness between the two data sources would be accounted for by underlying differences in sample size) was tested using Monte Carlo simulations. Such simulations were used to estimate the number of species (S) in a random sample of n BBA blocks, where n is the number of BBS routes within the relevant area. This procedure allowed us to determine the expected number of species in samples of BBA blocks when the size of these samples (the number of observation units) is equal to the corresponding number of BBS routes, thereby controlling for differences in sample size between the two data sources.

We defined S_n^{BBA} as the number of species in a random sample of n BBA blocks (i.e., matching the number of BBS routes within the relevant area) and S_{All}^{BBA} as the total number of species in all BBA blocks within the relevant area. We interpreted the difference between S_{All}^{BBA} and the mean value of S_n^{BBA} in 1000 random samples (with replacement) of n BBA blocks as the contribution of the difference in sample size to the observed difference in regional richness between the BBA and BBS data.

Prediction 5 (estimates of regional richness based on BBA data would be higher than those based on BBS data also after controlling for underlying differences in the number of observations) was tested by comparing the mean number of species in 1000 random samples (with replacement) of n BBA blocks (S_n^{BBA}) with the number of species in all the BBS routes (n) in the relevant area (S_n^{BBS}). The statistical significance of the difference was determined as the fraction of BBA samples with $S_n^{BBA} < S_n^{BBS}$.

Prediction 6 (local richness in BBA blocks would be higher than that of BBS routes) was tested using a LMM (Gaussian distribution) with data source as a fixed effect and state as a random effect. We also performed a more complex analysis that included the three environmental variables, the three measures of habitat heterogeneity, and sampling effort as independent variables (see Prediction 8).

Prediction 7 (compositional turnover among BBA blocks would be higher than that among BBS routes) was

tested using two complementary approaches. First, we calculated the degree of species similarity (using the Jaccard index) among all observation units within each data source and compared the mean values of similarity obtained for BBA versus BBS units using a permutation test for difference between means with the `perm.t.test` function in the `GmAMisc` package in R (Alberti, 2021; Moore et al., 2016). Second, we compared the dispersion of BBA versus BBS observation units using the distance-based test for homogeneity of multivariate dispersion—also using the Jaccard index as a measure of species similarity—with the `betadisper` function in the `vegan` package in R (Anderson et al., 2006; Oksanen et al., 2020). Briefly, the `betadisper` function reduces Jaccard distances to principal coordinates, on which we tested difference in dispersion distance using ANOVA and a Tukey's honestly significant difference test (Anderson et al., 2006). We expected that BBS routes would show significantly lower values of compositional similarity and smaller dispersion in the ordination space than BBA blocks.

Prediction 8 (some of the variation in local richness among BBA blocks and BBS routes would be accounted for by underlying differences in sampling effort) was tested in two steps. First, we regressed local richness of all BBA blocks and BBS routes against log-transformed sampling effort (number of survey hours) using a linear model (LM) with Gaussian distribution to verify that local richness in the two data sources is influenced by sampling effort. Using the `lmer` function in the `lme4` package in R, we also ran an extended LMM with local richness as the response variable (Gaussian distribution) and log-transformed sampling effort, the three environmental variables (elevation, precipitation, and temperature), the three measures of habitat heterogeneity (elevation range, land-cover richness, and land-cover diversity), data source, the interaction between sampling effort and data source, and state (as a random factor) as independent variables. All fixed effects were standardized prior to running the LMM using the `scale` function in R. We expected that the effect of sampling effort would be statistically significant also in this extended model.

In a second step, we matched each BBS route with a single BBA block (the one with the largest geographic overlap with that route based on area), thereby creating a set of matched pairs of BBA and BBS units. We then calculated the difference in richness between the BBA block and BBS route in each pair (as a response variable) and regressed the difference in richness against the corresponding difference in log-transformed sampling effort using a LMM with state as a random effect with the `lmer` function in the `lme4` package in R. We expected that much of the differences in local richness between matched BBA blocks and BBS routes would be accounted for by the corresponding differences in sampling effort.

RESULTS

Prediction 1: At the regional scale, BBA blocks would sample a larger range of environmental conditions than BBS routes

As expected, BBA blocks exhibited a larger range of elevation, precipitation, and temperature in each state as well as in the entire study region (Figure 1). These differences were statistically significant for all variables (elevation: $t = 3.57$, $p < 0.05$; precipitation: $t = 4.39$, $p < 0.05$; temperature: $t = 7.94$, $p < 0.01$; paired t tests with states as the observation units). A corresponding nonparametric Wilcoxon signed-rank test revealed similar results ($p < 0.05$ for all cases).

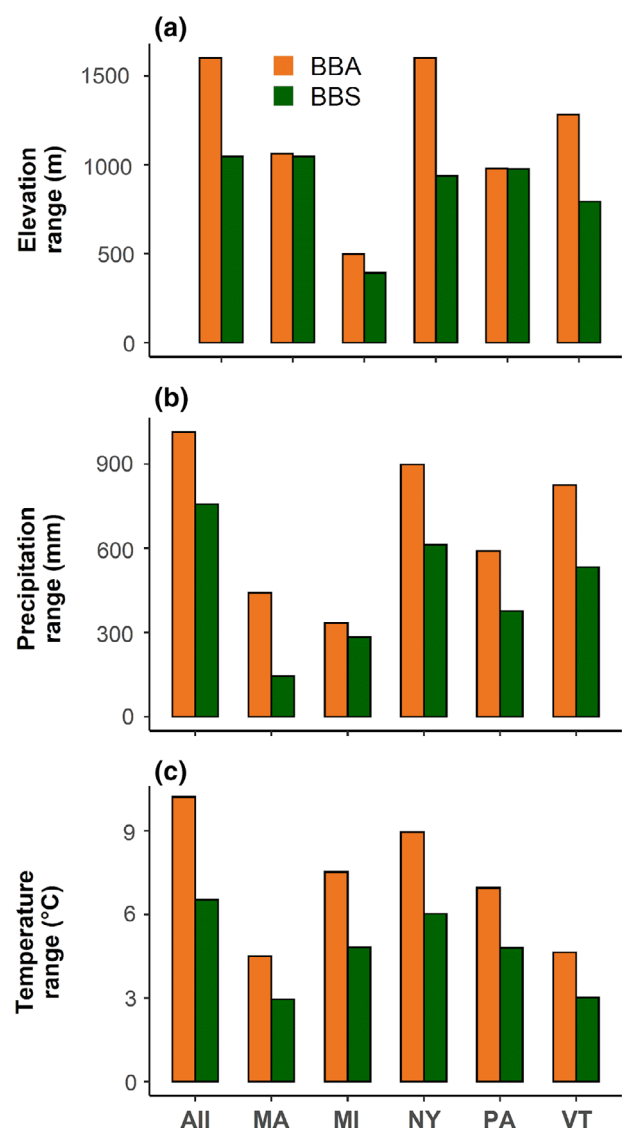


FIGURE 1 Range of elevation (a), precipitation (b), and temperature (c), across all observation units for Breeding Bird Atlas blocks (BBA, orange) and Breeding Bird Survey routes (BBS, green) in the entire study region (All) and in each state

Prediction 2: At the local scale, BBA blocks would be more heterogeneous in their environmental conditions than BBS routes

Contrary to our prediction, for all measures of heterogeneity (land-cover richness, land-cover diversity, and elevation range), BBA blocks were less heterogeneous than BBS routes (Figure 2). This difference was statistically significant in a mixed-effects model with state as a random effect as well as for each individual state ($p < 0.001$ for all cases).

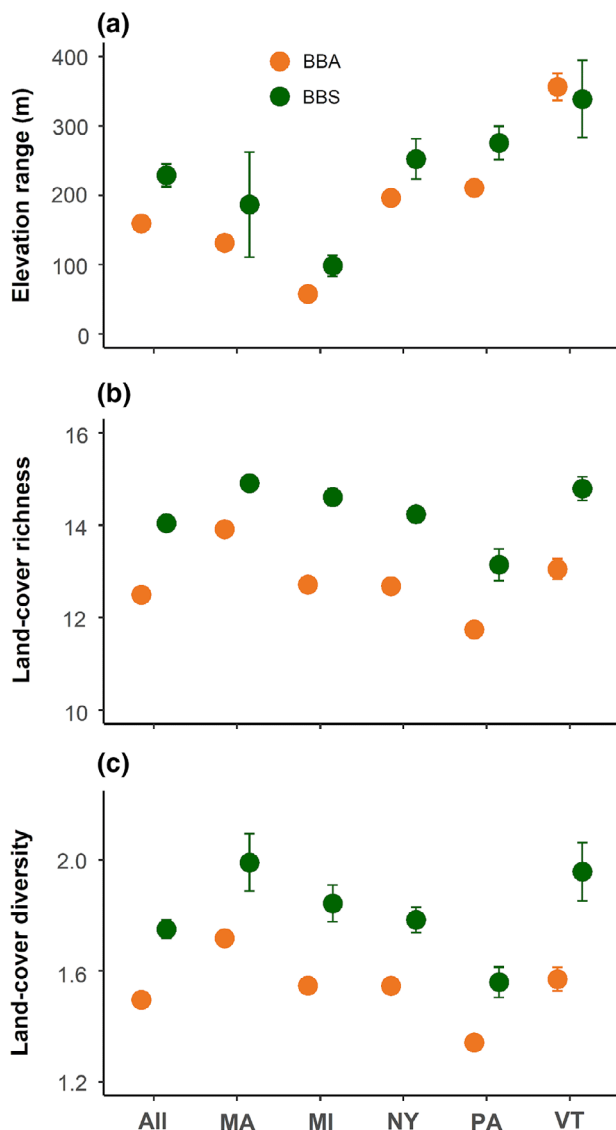


FIGURE 2 Local heterogeneity of Breeding Bird Atlas blocks (BBA, orange) and Breeding Bird Survey routes (BBS, green) quantified using three measures of heterogeneity (elevation range, land-cover richness, and land-cover diversity) within each observation unit for the entire study region (All) and for each state. Error bars indicate 95% confidence intervals (not visible when narrower than the symbol)

Prediction 3: Estimates of regional richness based on BBA data would be higher than those based on BBS data

Consistent with this prediction, estimates of regional richness based on BBA data were higher than those based on BBS data for the entire region as well as for each state ($p < 0.001$, paired t test with states as the observation units, Figure 3). As with Prediction 1, a corresponding nonparametric Wilcoxon signed-rank test confirmed this ($p < 0.05$).

Prediction 4: Much of the difference in regional richness between the two data sources would be accounted for by underlying differences in sample size

Estimates of regional richness based on the overall BBA blocks were much higher than those based on the mean of 1000 random draws of subsets of blocks with sample size equal to the number of BBS routes within the relevant area (Figure 3). This difference was consistent for all states as well as for the whole region, confirming that much of the differences in regional richness between BBA blocks and BBS routes resulted from differences in sample size.

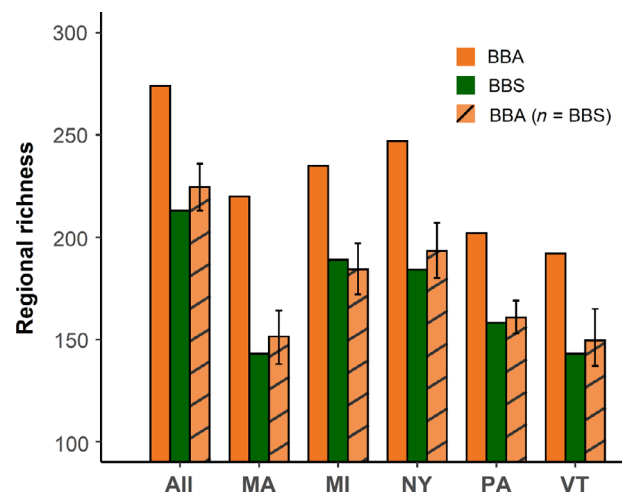


FIGURE 3 Estimates of regional bird richness based on Breeding Bird Atlas blocks (BBA, orange, see S_{All}^{BBA} in text), Breeding Bird Survey routes (BBS, green, see S_{All}^{BBS} in text) and subsets of BBA blocks with the same sample size as the corresponding BBS routes (BBA [$n = BBS$], orange striped, see S_n^{BBA} in text), for the entire study region (All) and for each state. For S_n^{BBA} , mean values are based on 1000 Monte-Carlo simulations of n BBA blocks and error bars are the corresponding 95% confidence intervals

Prediction 5: Estimates of regional richness based on BBA data would be higher than those based on BBS data also after controlling for underlying differences in the number of observations

The total number of species in all BBS routes within the study region was lower than the mean number of species in 1000 random subsets of BBA blocks with the same sample size ($n = 281, 213$ vs. 226.1 , respectively, Figure 3). This difference was highly significant: only 2 out of 1000 random subsets of 281 BBA blocks had less than the 213 species observed in 281 BBS routes. Similar patterns were obtained for all individual states except for Michigan (Figure 3).

Prediction 6: Local richness in BBA blocks would be higher than that of BBS routes

Contrary to our expectations, local richness in BBA blocks was lower than that of BBS routes (Figure 4). This difference was highly significant in a model with data source as the sole predictor and state as a random effect ($p < 0.001$), though there were also large differences among states (marginal $R^2 = 0.005$ and conditional $R^2 = 0.316$). While contrasting our prediction, this result is in accordance with our finding that BBA blocks were less heterogeneous than BBS routes in all measures of heterogeneity at the local level of the sampling unit (Figure 2).

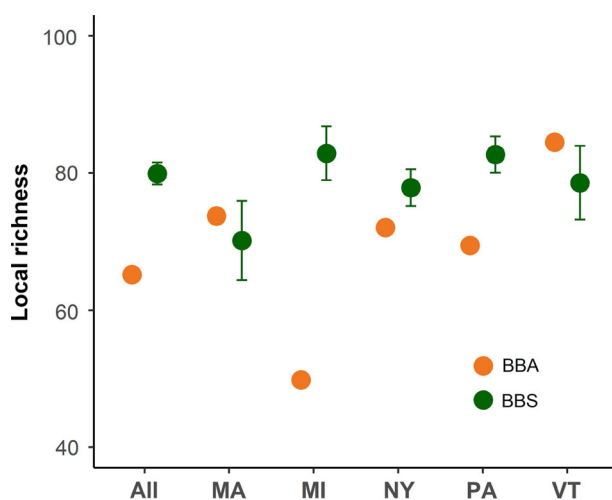


FIGURE 4 Local bird richness in Breeding Bird Atlas blocks (BBA, orange) and Breeding Bird Survey routes (BBS, green) for the entire study region (All) and for each state. Error bars indicate 95% confidence intervals (not visible when narrower than the symbol)

Prediction 7: Compositional turnover among BBA blocks would be higher than that among BBS routes

As expected, BBA blocks had significantly higher compositional turnover than BBS routes (mean values of the Jaccard index: 0.58 and 0.44, respectively, $p < 0.01$, permutation test for differences between means). This effect was statistically significant also at the level of individual

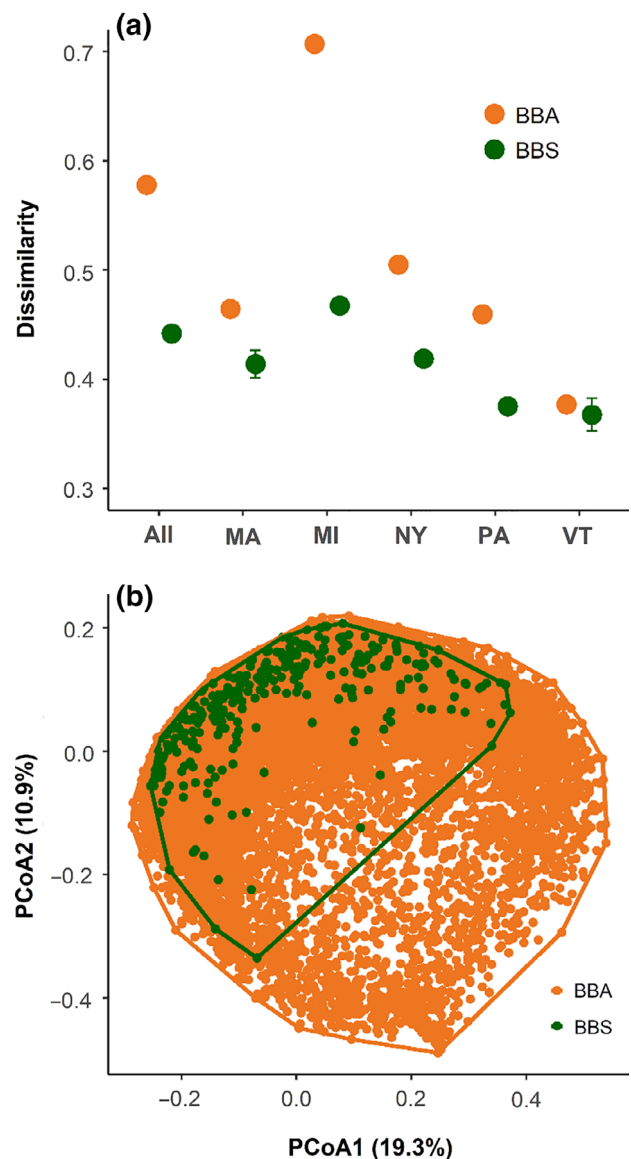


FIGURE 5 Differences between Breeding Bird Atlas blocks (BBA) and Breeding Bird Survey routes (BBS) in compositional turnover. (a) Mean Jaccard dissimilarity for BBA blocks (orange) and BBS routes (green) for the entire study region (All) and for each state. Error bars are 95% confidence intervals (unseen when narrower than the symbol). (b) Dispersion of BBA blocks and BBS routes in a two-dimensional principal coordinate analysis (PCoA) ordination space based on the Jaccard index of dissimilarity

states except for Vermont (Figure 5a). A corresponding test of homogeneity of multivariate dispersion was consistent with these results, indicating that BBA blocks had significantly higher distances to their centroid than BBS routes (0.4081 vs. 0.3117, $p < 0.001$). Figure 5b visualizes these differences by plotting all BBA and BBS units within a two-dimensional principal coordinate analysis (PCoA) ordination.

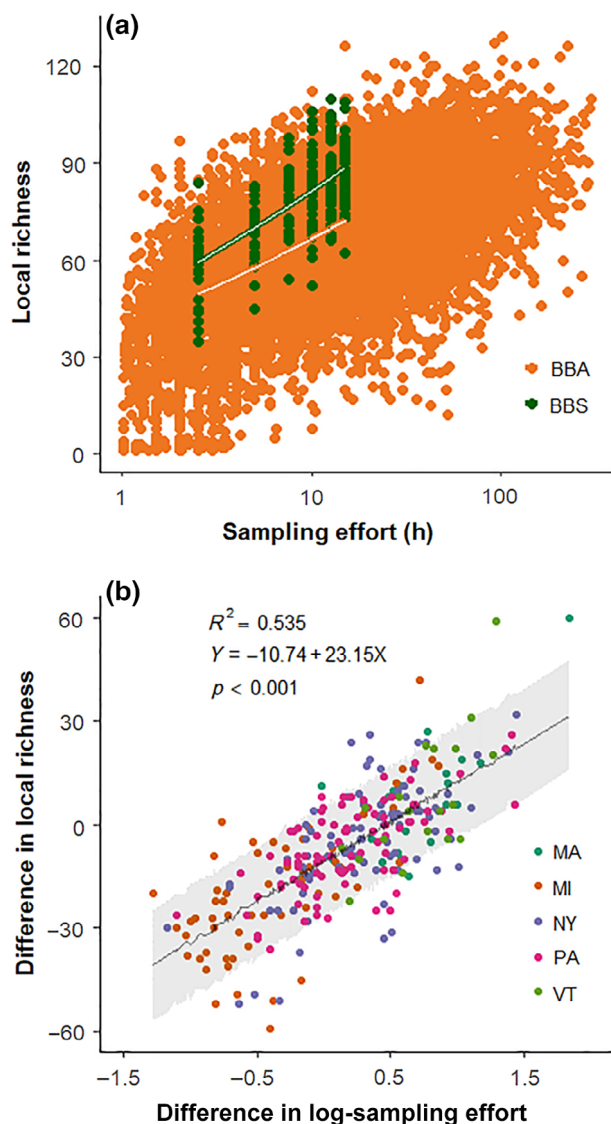


FIGURE 6 Relationships between sampling effort and local richness. (a) Effect of log sampling effort on local richness at the level of the entire study region (outliers of >300 h sampling effort were excluded). Regression lines are limited to the range of overlap between Breeding Bird Survey routes (BBS, upper regression line) and Breeding Bird Atlas blocks (BBA, lower line). Note that reported values of very low sampling effort (<0.01) are probably errors in the original data. (b) Difference in local richness between matched BBS and BBA observation units regressed against the corresponding differences in log sampling effort. Sampling effort in BBS refers to number of years with observations converted to hours

Prediction 8: Some of the variation in local richness among BBA blocks and BBS routes would be accounted for by underlying differences in sampling effort

As expected, sampling efforts in BBA blocks were both more variable and significantly higher than those of BBS routes (Table 3). Our results show that sampling effort had a positive effect on local richness for both BBS and BBA data (Figure 6a). This effect was statistically significant in a simple LM with log sampling effort as the only predictor ($p < 0.001$, adjusted $R^2 = 0.453$), as well as in an extended LMM with data source (BBA vs. BBS), the three environmental variables (elevation, precipitation, and temperature), and the three measures of heterogeneity (elevation range, land-cover richness, and land-cover diversity) as additional fixed effects and state as a random effect (Appendix S2: Table S1). The latter analysis also showed that the effect of data source on local richness was statistically significant, as well as its interaction with sampling effort (Appendix S2: Table S1). Importantly, for observation units with the same range of sampling effort, BBS routes still showed higher richness than BBA blocks (compare the two regression lines in Figure 6a). Thus, although sampling effort was higher in BBA blocks, local richness was higher in BBS routes, and this effect was statistically significant also when differences in sampling effort were controlled for (Appendix S2: Table S1).

As discussed in the Methods section, a more direct test of Prediction 8 was performed by comparing differences in local richness and sampling effort between geographically matched pairs of BBS routes and BBA blocks (Figure 6b). A LMM of these matched data with the difference in local richness as the response variable, the difference in log-transformed sampling effort as a covariate, and state as a random effect, demonstrated that much of the differences in local richness between BBA blocks and BBS routes could be accounted for by underlying differences in sampling effort (both marginal and conditional $R^2 = 0.535$, Figure 6b).

DISCUSSION

Our analysis shows that estimates of regional richness based on BBA are much higher than those obtained from BBS data representing the same geographical and temporal extents. Overall, a total of 274 species were documented in the five state atlases, while only 213 species were documented in BBS routes covering the same geographical and temporal extents. Examination of the values obtained for individual states indicates that 21%–36% of the species observed in state atlases were not

documented in the corresponding BBS routes during the matched periods (Appendix S2: Table S3). In contrast, <1% of the species that were documented in BBS routes were not documented in the matched atlases. These findings indicate that previous analyses of BBS data focusing on large-scale patterns of species diversity probably missed a large fraction of the species. While our data do not allow us to evaluate the accuracy of estimates based on either BBA or BBS data, it is clear from our results that estimates of regional richness based on BBS data suffer from a considerable bias. The actual bias is probably higher because BBA data may also suffer from incomplete detection. Clearly, any application of BBS data in ecology and conservation, and in particular, applications focusing on biodiversity conservation, should be aware of this regional bias and its underlying sources.

It has long been recognized that analyses of local richness based on BBS data should take into account the potential effects of bias caused by incomplete detection (Boulinier et al., 1998; Nichols et al., 1998). Our results demonstrate that this problem exists, and might be even more acute, in analyses focusing on larger spatial scales. One possible approach to account for this bias is to use various kinds of extrapolation techniques to estimate the “real” number of species in the relevant region (Chao et al., 2014; Colwell et al., 2004; Kunin et al., 2018). However, such extrapolations lose the link to species composition, thereby limiting the potential applications of such methods. Moreover, additional analyses of our data show that, even if such techniques are used, estimates of regional richness based on BBS data are still lower by 10%–25% than the actual number of species recorded in the corresponding BBA blocks (Appendix S2: Table S3).

Since BBA and BBS units do not differ in their sampled area (both cover ~25 km²), these differences cannot be explained by differences in the size of the sampling unit. Differences in local richness due to higher heterogeneity in habitat conditions can also be rejected as a source of the observed differences in regional richness between the two data sources, since both habitat heterogeneity (as quantified by land-cover richness, land-cover diversity, and elevation range) and local richness were higher in BBS routes (Figures 2 and 4).

Our Monte-Carlo simulations show that most of the differences in regional richness between BBS and BBA data were due to differences in sample size (number of observation units, Figure 3). At the level of the entire area, 79% of the difference in regional richness between BBS routes and BBA blocks was explained by differences in sample size (Figure 3). However, even after correcting for sample size differences, BBA blocks still showed significantly higher estimates of regional richness than BBS

routes (Figure 3), indicating that additional factors were important in determining the observed differences.

We originally expected that differences in sample size would lead to differences in estimates of regional richness by two distinct mechanisms. First, a larger sample size increases the overall area represented by the observation units, thereby increasing the likelihood of “sampling” rare species (Lawler & O’Connor, 2004). Second, a larger number of observation units may increase the range of environmental conditions represented by these observations, thereby providing suitable conditions to a larger number of species. While the first effect is obvious (Table 3), our data also show that BBA blocks cover larger ranges of elevation, precipitation, and temperature than BBS routes in all states, as well as in the overall area (Figure 1).

To evaluate the relative contribution of these two mechanisms (increasing the likelihood of sampling rare species and increasing the likelihood of sampling species with climatic requirements not represented by BBS routes) to the observed differences in regional richness, we determined for each species that was documented in BBA blocks the following four variables: (1) the number of blocks in which it was documented in the relevant area (as an inverse measure for rarity); (2) of these blocks, the portion of blocks whose precipitation conditions were outside the precipitation range captured by BBS routes; (3) the corresponding portion of blocks whose temperature conditions were outside the temperature range captured by BBS routes; and (4) whether or not it was present in BBS routes. We then tested the ability of the first three variables (frequency of occurrence in BBA blocks and tendency to occur in blocks representing precipitation and temperature conditions not represented by BBS routes) to explain the fourth variable (absence in BBS routes) using a GLM with a logit link function with the lme4 package in R. Two types of analyses were conducted. In the first (“entire region range”), the range of the climatic variables referred to the entire study region. In the second (“state-level ranges”), the range of climatic variables referred to individual states and state was included in the model as a random effect.

For all analyses, the frequency of occurrence in BBA blocks was the best and only significant predictor of species’ absences in BBS routes (entire region range: $B(\text{logit}) = -3.038$, $p < 0.0001$, Tjur’s $R^2 = 0.603$; state-level ranges: $B(\text{logit}) = -3.153$, $p < 0.0001$, marginal and conditional $R^2 = 0.996$). In general, as species became more common in BBA blocks, the likelihood that they will be absent from BBS routes strongly decreased (Figure 7). We therefore conclude that, although BBS routes fail to capture the range of precipitation and temperature conditions represented by BBA blocks, the main mechanism by which the larger sample size of BBA units

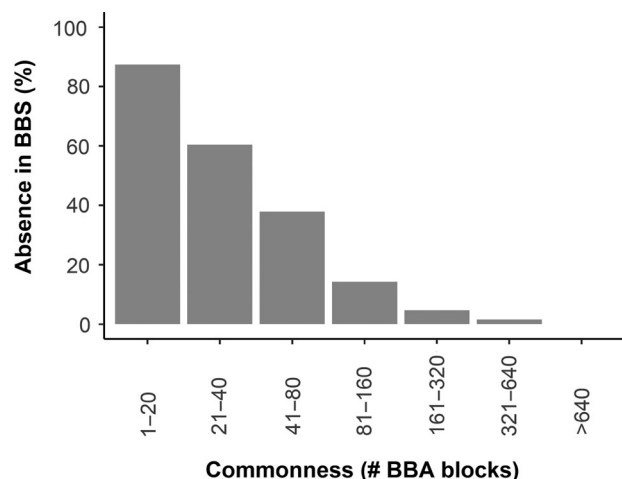


FIGURE 7 Effect of species commonness in Breeding Bird Atlas blocks (BBA) on the likelihood to be absent in Breeding Bird Survey routes (BBS). For each species in each state, we determined: (1) the number of blocks in which it occurred, and (2) whether or not it was recorded in BBS routes of that state. All species-state observations were pooled and then categorized into eight commonness categories. The figure presents the frequency of species that were absent in BBS routes within each commonness category

increased regional richness was the higher likelihood of sampling rare species.

Additional analyses revealed lack of significant differences in the distribution of the climatic variables (Appendix S2: Figure S1) and land-cover types (Appendix S2: Figure S2) between BBA blocks and BBS routes. These results are consistent with previous studies showing small bias in the representation of climatic and land-cover variables across BBS routes (Lawler & O'Connor, 2004; Veech et al., 2012, 2017) and strengthen our conclusion that differences in the representation of climatic and habitat conditions were not important in determining the observed differences in regional richness.

While much of the differences between BBA and BBS estimates of regional richness could be related to differences in sample size, BBA estimates were significantly higher than BBS estimates also when sample size differences were corrected for (Figure 3). Originally, we expected that both local richness and compositional turnover would be higher in BBA data: the first due to expected higher heterogeneity in local habitat conditions, and the second due to expected higher dissimilarity in habitat conditions among BBA blocks. The first expectation (higher local richness in BBA blocks) was not supported by our data: local richness was lower, rather than higher in BBA blocks (Figure 4). We can therefore reject the hypothesis that differences in local richness contributed to the observed differences in regional richness between BBS and BBA data.

Interestingly, and consistent with this result, BBS routes showed higher values of habitat heterogeneity than BBA blocks in all measures of heterogeneity (Figure 2). Related LMM analyses with the lme4 package in R testing the effect of habitat heterogeneity on local richness demonstrated that both land-cover richness and land-cover diversity facilitated local richness (Appendix S2: Figure S3). These positive heterogeneity–diversity relationships were consistent for both datasets (Appendix S2: Figure S3), suggesting that at least part of the observed differences in local richness between BBS routes and BBA blocks (Figure 4) were related to underlying differences in land-cover heterogeneity. However, regression lines fitted to BBA and BBS data had similar slopes (Appendix S2: Figure S3) and the difference between the intercepts of these regression lines (8.5 species) was much smaller than the observed difference in mean local richness between BBS and BBA units (14.8 species, Figure 4). Thus, even when habitat heterogeneity was accounted for, BBS routes had higher richness than BBA blocks. We conclude that additional factors were involved in determining the observed differences in local richness between the two datasets.

Our second expectation (that higher compositional turnover in BBA blocks would contribute to the differences in regional richness) was supported by the data: for all states, as well as for the entire region, BBA blocks were more dissimilar to each other in their species composition than BBS routes (Figure 5a). Consistent with this result, BBA blocks showed higher dispersion in the ordination space than BBS routes (Figure 5b). Thus, BBA and BBS data differed significantly in both local richness and compositional turnover, but these differences were in opposite directions, with differences in local richness reducing and differences in compositional turnover increasing the magnitude of differences in regional richness.

In principle, the higher compositional turnover among BBA blocks could be a sampling artifact of the larger number of observational units. To evaluate this possibility, we recalculated the magnitude of compositional turnover among BBA blocks using only those BBA blocks that best-matched BBS routes (thereby controlling for both sample size and the geographical distribution of the observation units). The results indicated that compositional turnover was higher in BBA blocks also after controlling for sample size and geographical differences (Appendix S2: Figure S4).

One potential explanation for the higher similarity in species composition among BBS routes is higher similarity in habitat conditions (Melo et al., 2009; Steinitz et al., 2006). To test this hypothesis, we compared the mean similarity in habitat conditions among BBS routes with the mean similarity in habitat conditions among the

matched BBA blocks. Two types of similarity analyses were performed using the `vegdist` function from the `vegan` package in R. The first focused on land-cover composition and was conducted using the Bray–Curtis measure of similarity (Bray & Curtis, 1957). The second involved both land-cover composition and the three environmental variables (elevation, precipitation, and temperature) and was conducted using the Gower measure of similarity (Gower, 1971).

Consistent with our expectations, for both measures, BBS routes were more similar to each other than BBA blocks (Appendix S2: Figure S4). These differences were consistent for all states (Appendix S2: Figure S4). We conclude that the higher compositional turnover among BBA blocks was not a simple artifact of the larger sample size and that at least part of the differences between BBS and BBA units in compositional turnover was related to larger differences in habitat conditions among BBA units. The fact that species present in BBA blocks but absent from BBS routes were restricted to a small number of blocks, probably contributed further to the differences in compositional turnover between the two datasets (since different rare species may occur in different blocks).

Another factor that was predicted to increase estimates of regional richness based on BBA data is higher sampling effort within the observation units. Indeed, sampling effort of BBA routes was more variable and significantly higher than that of BBS routes in all states except for Michigan (Table 3). Our results also indicate that sampling effort had a positive effect on local richness (Figure 6a), and that differences in local richness between BBS routes and matched BBA blocks were positively related to the underlying differences in sampling effort (Figure 6b). These results confirm that sampling effort was important in determining the observed differences in local richness between BBS and BBA units. However, as noted earlier, despite these differences, BBA blocks had lower, rather than higher local richness than BBS routes (Figure 4). Two factors could potentially explain these results. The first is that the higher habitat heterogeneity of BBS routes offset their lower sampling effort. The fact that local richness of BBS routes was higher than that of BBA blocks when sampling efforts were similar is consistent with this hypothesis (compare the regression lines in Figure 6a).

However, it is also possible that the *effectiveness* of bird sampling within BBS routes is higher than that of BBA blocks. In other words, a unit (hour) sampling effort in BBS routes is more effective than a unit sampling effort in BBA blocks. If this explanation is correct, we would expect that increasing the sampling effort within BBA blocks would elevate their local richness to values similar (or even higher) than those of BBS routes.

To test this question, we calculated local richness in BBA blocks that overlapped with BBS routes (to control for differences in geographical distribution) but had a sampling effort of >30 h. This threshold was based on a series of linear regressions run with the `lm` function in R testing how the sampling threshold used to select the observation units affects the slope of linear regressions testing the effect of sampling effort on local richness (Appendix S2: Figure S5). Such regressions indicated that a threshold of 30 h gives a slope of 10% (i.e., any additional 10 h of sampling are expected to increase local richness by a single species, Appendix S2: Figure S5).

The results indicated that this selection of BBA blocks flipped the differences in local richness between BBS and BBA units and elevated the richness of BBA blocks to levels that were slightly though significantly higher than those of the matched BBS routes (Appendix S2: Figure S6; $p < 0.001$; marginal $R^2 = 0.01$; conditional $R^2 = 0.05$; LMM with local richness as the response variable, dataset as a fixed effect and state as a random effect, see also Appendix S2: Figure S7). We conclude that differences in the effectiveness of sampling *within* the observation units were an important source of the observed differences in local richness between BBS routes and BBA blocks.

The BBS has been used extensively to test patterns in the regional diversity of breeding birds in North America (Table 1). While the main goal of the BBS is to elucidate temporal trends in species abundances (Rosenberg et al., 2019; Sauer, Pardieck, et al., 2017), BBS data are also often used for large-scale analyses of patterns in species' distributions (Rich & Currie, 2018), static species richness (Elsen et al., 2020; Farwell et al., 2020), and conservation purposes such as identifying endangered and rare species (Hudson et al., 2017; Rosenberg et al., 2017). Our results suggest that on the regional scale, BBS data miss a large number of species, both because of the survey's inability to detect rare species (Figure 7) and the similarity in habitat conditions across BBS routes (Figure 5, Appendix S2: Figure S4). Our findings support previous studies finding that BBS data miss rare species (Robbins et al., 1989) and the potential limitations of the BBS' roadside sampling (Handel & Sauer, 2017; Van Wilgenburg et al., 2015). Our study highlights that integration of BBA data can help fill in gaps where BBS data miss rare species and different habitats across sites. The integration of BBA and BBS data in analyses of regional richness is not common, but it has been suggested before as an improvement to studies of bird richness and conservation in North America (Hudson et al., 2017; Robbins et al., 1989; Zuckerberg, Porter, & Corwin, 2009). Indeed, atlas organizers often utilize BBS data to complement the collection of BBA data (Kamm et al., 2013;

Renfrew, 2013; Wilson et al., 2012); yet analyses in the ecological literature often rely mostly or solely on BBS data (Table 1), and where integration with other data sources is used, it is rarely done with BBA data (Hudson et al., 2017; Rosenberg et al., 2019). Our results suggest that the greater coverage provided by BBA could improve studies of regional richness.

BBA data are also used to analyze the potential consequences of land-use modification (Shoffner et al., 2018; van der Hoek et al., 2015) and climate change (Jarzyna et al., 2015, 2016; Zuckerberg, Woods, & Porter, 2009). While our results support earlier studies showing limitations of BBA data, especially regarding variable survey effort (Beck et al., 2018; Kujala et al., 2013; Robertson et al., 2010; Wilson et al., 2017), modeling approaches and corrections to such limitations are possible (Isaac et al., 2014; Robertson et al., 2010; Sadoti et al., 2013; Wilson et al., 2017). For example, while we find that local richness is higher in BBS data (Figure 4), we also show that a simple correction for the effectiveness of survey effort in the BBA (Appendix S2: Figure S5) leads to an opposite pattern with a higher richness in the BBA (Appendix S2: Figures S6 and S7).

BBA data can also be used to supplement or complement BBS analyses of trend data (Peach et al., 2019; van der Hoek et al., 2015) and to provide quantitative grounding for conservation planning and management (Beck et al., 2018; Brown et al., 1995; Peach et al., 2019; Robbins et al., 1989). Given our findings that BBA data improve on BBS data in capturing rare species (Figure 7) and regional richness in general (Figure 3), our results underline the potential benefits of integrating the two datasets (Hudson et al., 2017). Finally, increasing the use of BBA data in scientific publications can serve to encourage participation in citizen-science initiatives, to provide volunteers and atlas organizers with tangible results for their work, and to increase public awareness of conservation needs and efforts (Beck et al., 2018; Theobald et al., 2015).

CONCLUSIONS

Our results show that estimates of regional richness based on BBS data are consistently lower than those based on BBA data. This difference occurs also when BBS estimates are “corrected” using various extrapolation techniques. We conclude that BBS estimates of regional richness suffer from a considerable bias and miss a large portion of the species that exist at such geographical scales. This finding is important because a major goal of the North American BBS is “to provide scientifically credible measures of the status and trends of North American

bird populations at continental and regional scales” (U.S. Geological Survey, 2007).

In fact, our results point to a fundamental trade-off between BBS and BBA data. BBS estimates of route-level richness are obtained using a fixed protocol and are therefore highly recommended for studies focusing on variation in local richness, particularly if the data are corrected for incomplete detection. However, for the reasons described earlier, these data also suffer from significant underrepresentation of regional richness. BBA data suffer from sampling issues both among blocks within states (due to variable sampling efforts) and between states (due to among-states differences in sample size), but provide a more complete (and probably, more accurate) representation of regional richness. Future studies attempting to explain patterns of variation in North American breeding bird diversity should take into account the existence of this trade-off and should use both sources of data whenever such data are available.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Ankori-Karlinsky et al., 2021) are available from Dryad (10.5061/dryad.m905qfv0h); code for data organizing and analyses (not novel) is available from Zenodo (10.5281/zenodo.5639834).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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