




## ARTICLE

# Mapping breeding bird species richness at management-relevant resolutions across the United States

Kathleen A. Carroll  | Laura S. Farwell | Anna M. Pidgeon |  
 Elena Razenkova | David Gudex-Cross | David P. Helmers |  
 Katarzyna E. Lewińska | Paul R. Elsen  | Volker C. Radeloff 

SILVIS Lab, Department of Forest and  
 Wildlife Ecology, University of Wisconsin-  
 Madison, Madison, Wisconsin, USA

**Correspondence**

Kathleen A. Carroll  
 Email: [kcarroll7@wisc.edu](mailto:kcarroll7@wisc.edu)

**Present address**

Laura S. Farwell, Conservation Science  
 Partners, Truckee, California, USA

Paul R. Elsen, Wildlife Conservation  
 Society, Global Conservation Program,  
 Bronx, New York, USA

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**Abstract**

Human activities alter ecosystems everywhere, causing rapid biodiversity loss and biotic homogenization. These losses necessitate coordinated conservation actions guided by biodiversity and species distribution spatial data that cover large areas yet have fine-enough resolution to be management-relevant (i.e.,  $\leq 5$  km). However, most biodiversity products are too coarse for management or are only available for small areas. Furthermore, many maps generated for biodiversity assessment and conservation do not explicitly quantify the inherent tradeoff between resolution and accuracy when predicting biodiversity patterns. Our goals were to generate predictive models of overall breeding bird species richness and species richness of different guilds based on nine functional or life-history-based traits across the conterminous United States at three resolutions (0.5, 2.5, and 5 km) and quantify the tradeoff between resolution and accuracy and, hence, relevance for management of the resulting biodiversity maps. We summarized 18 years of North American Breeding Bird Survey data (1992–2019) and modeled species richness using random forests, including 66 predictor variables (describing climate, vegetation, geomorphology, and anthropogenic conditions), 20 of which we newly derived. Among the three spatial resolutions, the percentage variance explained ranged from 27% to 60% (median = 54%; mean = 57%) for overall species richness and 12% to 87% (median = 61%; mean = 58%) for our different guilds. Overall species richness and guild-specific species richness were best explained at 5-km resolution using  $\sim 24$  predictor variables based on percentage variance explained, symmetric mean absolute percentage error, and root mean square error values. However, our 2.5-km-resolution maps were almost as accurate and provided more spatially detailed information, which is why we recommend them for most management applications. Our results represent the first consistent, occurrence-based, and nationwide maps of breeding bird richness with a thorough accuracy assessment that are also spatially detailed enough to inform local management decisions. More broadly, our findings highlight the importance of explicitly considering tradeoffs between resolution and accuracy to create management-relevant biodiversity products for large areas.

**KEYWORDS**

avian, biodiversity metrics, distribution model, distributions, machine learning, macroecology, remote sensing, richness

**INTRODUCTION**

Accurate biodiversity maps that cover large areas, are consistent across various management units, and have a fine resolution are essential for mitigating biodiversity loss. In general, biodiversity maps can be derived from species range maps, potential habitat maps, or species distribution models that combine sample plot occurrence data with predictor variables. Each of these approaches has inherent benefits and disadvantages.

At global to continental scales, analyses of biodiversity patterns are typically based on expert-drawn species range maps from which species richness is derived, but resulting data sets mischaracterize spatial patterns of richness at finer resolutions (e.g.,  $<1^{\circ}$ – $2^{\circ}$  or  $\approx 100$ – $200$  km; Hurlbert & Jetz, 2007). Such coarse-resolution maps can provide broad perspectives about multitaxa diversity and macroecological relationships (Burns et al., 2003; Grenyer et al., 2006; Schipper et al., 2008). However, biodiversity maps derived from species range maps are only reliable at coarse resolutions, often diverge strongly from field surveys, can have high spatial bias, contain no abundance information, and have unknown accuracy (Cantú-Salazar & Gaston, 2013; Graham & Hijmans, 2006; Hughes et al., 2021). Furthermore, because species are not present uniformly throughout their range, resulting richness maps often misidentify biodiversity hotspots (Hurlbert & Jetz, 2007; Peterson et al., 2018), which can lead to conservation prioritization that is both biologically ineffective and economically inefficient (Brown et al., 2015).

Maps of potential habitat provide an alternative to assessing biodiversity because they can be derived at finer resolutions (Brooks et al., 2019). For the United States, the US Geological Survey (USGS) has generated fine-scale maps of potential habitat for  $\sim 1600$  terrestrial vertebrates at 30-m resolution (Gergely et al., 2019) by identifying suitable habitat within national range maps for each species. Similar maps at  $\leq 1$ -km resolution exist for forest species (Rosas, Peri, Lencinas, & Martinez Pastur, 2019), mammals (Rondinini et al., 2011), insects (Rosas, Peri, Carrara, et al., 2019), amphibians (Ficetola et al., 2015), and threatened species (Xu et al., 2017), both globally and for some countries. However, potential habitat maps are limited in their management application because of the difference between fundamental and realized niches (Kearney, 2006; Kearney & Porter, 2004; Pearman et al., 2008), which means that species typically

do not occupy all potential habitats. Furthermore, maps of potential habitat have unknown and almost impossible-to-quantify accuracy because errors in the vegetation maps used to delineate habitat are difficult to propagate into the resulting biodiversity maps. There is also no independent so-called ground truth if an area mapped as potential habitat is indeed suitable for a given species unless it occurs there.

Predictive species distribution maps can be generated over large areas at fine-enough resolutions for local management actions to advance resource planning capability (Bateman et al., 2020; Jetz et al., 2012; Johnston et al., 2021). The increase in remotely sensed environmental variables relevant for conservation (He et al., 2015; Turner et al., 2003), including indices designed explicitly for biodiversity and species distribution models (Hobi et al., 2017; Wüest et al., 2020), and increases in publicly available occurrence data sets both from agencies (e.g., breeding bird survey) and volunteer geographic information (e.g., eBIRD) make species distribution models increasingly suitable for biodiversity assessments and conservation planning (Muscatello et al., 2020; Zurell et al., 2020). The availability of fine-scale species and habitat data have resulted in many species distribution models focused on biodiversity conservation, including regional to global maps (Hoskins et al., 2020; Tulloch et al., 2015; Wang et al., 2021). These species distribution maps can provide the fine-scale data necessary to identify areas critical for species conservation, like NatureServe's Map of Biodiversity Importance. However, species-distribution-based maps are subject to the same shortcomings as potential habitat map and coarse species distribution maps without validation, namely, high error rates that can misdirect conservation and are rarely quantified (Guillera-Arroita et al., 2015; Loiselle et al., 2003; Seo et al., 2009).

There are currently no biodiversity maps available for the United States based on species distribution models that are at fine resolutions, consistent over large areas, and provide spatial accuracy assessments to support local decision-making. Spatial accuracy assessments are critical because of tradeoffs between resolution and accuracy when predicting biodiversity across large areas, so managers need to decide which data sets best meet their needs. The tools, methods, and data exist to generate management-relevant, fine-scale biodiversity maps, but there are gaps between published scientific products and management needs, which is referred to as the science–

management gap (Arlettaz et al., 2010; Cook et al., 2010; Knight et al., 2008). Maps with well-specified accuracy, that is, with accuracy assessments based on independent validation data, and depicting spatial variability in prediction accuracy, including the upper and lower bounds of those predictions, are rare. Without maps demonstrating the reliability or uncertainty of biodiversity predictions, conservation decisions will be inefficient at best (Ladle & Hortal, 2013). Thus, the science–management gap can be overcome by quantifying uncertainty because land management and conservation can be based on consistent and clearly validated maps (Rocchini et al., 2011).

In addition to consistent biodiversity maps with well-specified accuracy, it is important to consider which biodiversity metrics to map to further reduce the science–management gap. The reason is that some of the biodiversity metrics that are central for macroecology, such as overall species richness, are less important for management because common species typically dominate overall richness. Managers, instead, typically focus on functional guilds that are declining (e.g., grassland birds) or on species of management concern (e.g., threatened and endangered species). Maps of guild-level richness can provide managers with critical information lacking in species-richness-only conservation planning (Lelli et al., 2019). Guild-based approaches provide a management-relevant view of biodiversity because management often focuses on multiple rather than single species to maximize management effects. Furthermore, guild-based metrics can also account for inconspicuous, poorly known or sampled, and rare species for which there are not enough observations to model species-level distributions accurately and that may otherwise be missed in management efforts. Guilds defined based on habitat affinity, diet, foraging strategy, nest type, and migratory strategy can help manage species with similar life-history traits and adaptations (Root, 1967). Thus, focusing on guild-level species richness in predictive diversity modeling could result in products aligning more closely with management goals and having higher accuracy.

Our goal was to develop nationwide predictive models of overall breeding bird species richness and guild-level richness at resolutions useful for land management and planning across the contiguous United States with clear accuracy metrics. We focused on bird richness because birds are highly sensitive to environmental change (Bateman et al., 2016; Hausner et al., 2003; Sekercioglu, 2006), occupy diverse ecological niches, implement a variety of life-history strategies (Hildén, 1965), and bird occurrence data are abundant (Hudson et al., 2017; Ralph et al., 1995; Simons et al., 2007). Our objectives were to (1) map overall bird species richness and richness for 19 guilds based on habitat affiliation, migratory strategy,

range size, nesting strategy, diet, conservation status, and population trend at scales relevant to management (i.e.,  $\leq 5$ -km resolution) and (2) compare tradeoffs in resolution and prediction accuracy among 3 resolutions (0.5, 2.5, and 5 km) of richness estimates for each guild based on 3 levels of occurrence data. We expected large-ranged and generalist species guilds to have models with higher prediction accuracy than specialist species guilds because of the higher number of observations and species in the former categories. We also expected the canopy-nesting species guild model to have higher prediction accuracy than the ground-nesting species guild model based on the satellite data-derived variables we examined, including many forest-canopy-specific metrics, because the satellites detect canopy characteristics better than understory characteristics.

The three resolutions we examined (0.5, 2.5, and 5 km) represent different scales meaningful to bird species' ecology, relevant to management decisions, and based on different summaries of occurrence data. The 0.5-km resolution represents both the radius within which birds are recorded in our data set (Breeding Bird Survey) and the area encompassing most small-bodied Passeriformes' home ranges. Notably, most species in the conterminous United States are within this taxonomic order. We expected maps created at 0.5-km resolution would be most beneficial for managers working in areas of small extent and on guilds composed of declining, rare, or small-ranged species. We expected the 2.5-km resolution to balance scale and accuracy best given our bird survey data (see section "[Methods](#)"). We also expected that this resolution would be best for managers interested in a broader species pool, broad-scale home range dynamics and relationships, and population-level trends in habitat use (McLoughlin & Ferguson, 2000). We expected the 5-km resolution to have the highest accuracy and be most relevant for managers interested in broad spatial patterns of bird diversity working over large jurisdictions on state- to national-scale questions.

## METHODS

### North American breeding bird survey data

The North American Breeding Bird Survey (BBS) is an avian monitoring program jointly coordinated by the USGS Patuxent Wildlife Research Center and the Canadian Wildlife Service's National Wildlife Research Center. The BBS program began in 1966 and currently includes over 4100 survey routes across North America. Skilled volunteers conduct the surveys each June along 39.4-km (24.5-mile) routes along secondary roads. A surveyor stops approximately every 800 m (0.5 miles) along the

route to conduct a 3-minute point count, recording all birds detected within a 400-m (0.25-mile) radius. The raw data, metadata, and trend estimates for 420 species are publicly available (<https://www.pwrc.usgs.gov/bbs/>). The raw data include the number and species identification of birds surveyed at each stop and the route's starting coordinates (Pardieck et al., 2020). Digital route maps were available until 2012 but are no longer accessible, and for routes shifted or started after 2012, only the starting point location is provided.

## North American breeding bird survey preprocessing

We focused on BBS routes surveyed between 1992 and 2019 because these years correlated with species patterns from 2013 to 2019 (the timeframe of our predictors) and greatly increased the sample size (Appendix S1: Figures S3–S7). We removed from consideration non-randomly established routes, surveys conducted in inclement weather, and surveys conducted by first-year observers ( $n = 2748$ ) (Farwell et al., 2020). We subdivided bird occurrence data into three subsets that aligned with the three resolutions we analyzed: (1) first-survey-stop data, with 0.5-km square buffers for sampling predictive variables centered on the first-stop location; (2) first-10-stops of data, with 2.5-km square buffers centered on the first-stop location; and (3) full-route data, with 5-km-resolution squares centered on route centroids (for routes for which the full route location line file was available) or the routes' first-stops.

$$B = (2d)^2 \quad (1)$$

We determined buffer size based on the detection area covered by a given number of stops using Equation (1), where  $B$  represents buffer size and  $d$  the summed distance over which birds were surveyed in consecutive BBS route point counts at the three scales of analysis (i.e., the buffer radius). We did not use true buffers for the full-route analysis owing to either route line file issues or missing route location information. Instead, we determined buffer size using Equation 1 with a 5-km diameter for the 39.4-km BBS routes (the distance of an entire BBS route) and used that area in the shape of a square around centroids (where available) or route starting points if line files for routes were unavailable. We conducted a robustness check and found no difference when we compared our alternative square buffers for the 5-km-resolution analysis to true buffers around the subset of available line files (Appendix S1: Table S1 and Figures S1 and S2).

## Predictor data

We analyzed 66 variables known or suspected to influence bird richness patterns (Table 1) (Elsen et al., 2021; Farwell et al., 2021; Gudex-Cross et al., 2021). We derived data layers from all available full-year Landsat 8 data from 2013 to 2019, with a few exceptions (Table 1; Appendix S2). We generated image texture (using cumulative dynamic habitat index data) and thermal metrics by assigning a value to the central pixel within a  $17 \times 17$ -pixel moving window. To generate continuous data layers of our predictor variables at each spatial resolution, we resampled our input data layers using nested grids of 0.5-, 2.5-, and 5-km resolution in ESRI Arc Pro and Python version 3.6, matching the three scales at which we extracted bird occurrence data for calculating richness.

## Guilds

We estimated species richness for 19 guilds based on habitat affiliation, migratory strategy, range size, nesting strategy, diet, conservation status, and population trend—the specific guilds were forest affiliates, grassland affiliates, shrubland affiliates, forest specialists, grassland specialists, shrubland specialists, residents, long-distance migrants, short-distance migrants, ground nesters, midstory/canopy nesters (grouped), threatened species (including all higher classifications such as endangered species), species with decreasing population trends, species with stable or increasing population trends (grouped), large-ranged species, small-ranged species, insectivores, granivores, and frugivores (Carroll et al., 2022). We based affiliate and specialist statuses on the International Union for Conservation of Nature (IUCN) Habitats Classification Scheme (Version 3.1). Habitat specialist species were defined as those with only one habitat of major importance, while affiliates had two or more during the breeding season (IUCN 2021). We adopted BBS designations for migration and nesting strategy (Pardieck et al., 2020) and followed the International Union for Conservation of Nature (IUCN) Red List of Threatened Species for defining threatened species and IUCN population trends from BirdLife International for stable and increasing versus decreasing species (Birdlife International, 2021). We classified short-distance migrants as migratory birds wintering primarily in the United States and Canada and long-distance birds as neotropical migrants. We determined range size by taking the median of all BBS species' ranges and designating ranges below the median as small-ranged and those above the median as large-ranged (Elsen et al., 2020;

**TABLE 1** Covariate type, name, metric, spatial and temporal resolution, and source

Covariate type	Covariate	Covariate metric	Spatial resolution	Temporal resolution
Vegetation	Dynamic habitat indices	Cumulative	30 m	2014–2019
		Minimum	30 m	2014–2019
		Variation	30 m	2013–2019
	Texture	1st-order SD	30 m	2013–2019
		Contrast	30 m	2013–2019
		Dissimilarity	30 m	2013–2019
		Homogeneity	30 m	2013–2019
		Entropy	30 m	2013–2019
		Uniformity	30 m	2013–2019
		Correlation	30 m	2013–2019
		Mean	30 m	2013–2019
		Variance	30 m	2013–2019
	Biomass		30 m	2000
	Canopy height		30 m	2000
	Land cover	Proportion forest	30 m	2016
		Proportion shrubland	30 m	2016
		Proportion grassland	30 m	2016
		Proportion wetland	30 m	2016
		Forest edge	30 m	2016
		Shrubland edge	30 m	2016
		Grassland edge	30 m	2016
		Wetland edge	30 m	2016
		Forest core	30 m	2016
		Shrubland core	30 m	2016
		Grassland core	30 m	2016
		Wetland core	30 m	2016
	Net primary productivity (NPP)		30 m	2013–2019
	Enhanced vegetation index (EVI)	Peak greenness	30 m	2013–2019
		Median greenness	30 m	2013–2019
Anthropogenic	Housing density	Block-level housing density	1 km	2010
	Land cover	proportion agriculture	30 m	2016
		Proportion urban	30 m	2016
		Agriculture edge	30 m	2016
		Urban edge	30 m	2016
		Agriculture core	30 m	2016
		Urban core	30 m	2016
Climate	Thermal heterogeneity	Summer	30 m	2013–2019
		Winter	30 m	2013–2019
	Relative temperature	Summer	30 m	2013–2019
		Winter	30 m	2013–2019
	Temperature amplitude	Annual	30 m	2013–2019
	Cloud cover index		30 m	2013–2019

(Continues)

**TABLE 1** (Continued)

Covariate type	Covariate	Covariate metric	Spatial resolution	Temporal resolution
	Winter habitat indices	Duration	30 m	2013–2019
		Variability	30 m	2013–2019
		Subnivium	30 m	2013–2019
	Bioclimatic variables (BIOCLIM; C° or mm)	Annual mean temperature	1 km	1990–2019
		Mean diurnal range of temperature	1 km	1990–2019
		Isothermality	1 km	1990–2019
		Seasonality of temperature	1 km	1990–2019
		Maximum temperature of warmest month	1 km	1990–2019
		Minimum temperature of coldest month	1 km	1990–2019
		Temperature annual range	1 km	1990–2019
		Mean temperature of wettest quarter	1 km	1990–2019
		Mean temperature of driest quarter	1 km	1990–2019
		Mean temperature of warmest quarter	1 km	1990–2019
		Mean temperature of coldest quarter	1 km	1990–2019
		Annual precipitation	1 km	1990–2019
		Precipitation of wettest month	1 km	1990–2019
		Precipitation of driest month	1 km	1990–2019
		Seasonality of precipitation	1 km	1990–2019
		Precipitation of wettest quarter	1 km	1990–2019
		Precipitation of driest quarter	1 km	1990–2019
		Precipitation of warmest quarter	1 km	1990–2019
		Precipitation of coldest quarter	1 km	1990–2019
Geomorphological	Terrain Ruggedness Index	...	30 m	...
	Elevation	...	30 m	...

*Notes:* Each raster layer is a mean value (not time series) over the temporal resolution listed, resampled at the three resolutions (0.5, 2.5, and 5.0 km). We sampled all variables to coarser resolutions except for the BIOCLIM variables for the 0.5-km resolution. Additional information for how we calculated each suite of covariates or their source is available in Appendix S2.

Farwell et al., 2020). Lastly, we assigned each species a foraging type class based on the Elton Traits database (Wilman et al., 2014).

## Building richness models

Our first objective was to develop models of overall bird species richness and richness within our 19 guilds. We chose random forest as our modeling framework because it works well for large data sets with nonlinear trends,

collinear variables, and missing data. Random forests are also helpful in making predictions when there are only a few samples in large areas, which was the case for several guilds (Liaw & Wiener, 2002; Mi et al., 2017).

To avoid overfitting and to reduce the number of variables, we ranked explanatory variables using the random forest permutation-based score of importance and employed a stepwise forward variable introduction using the VSURF package for variable selection in R Statistical Software (Version 4.0.5; Genuer et al., 2015; R Core Team, 2021). While random forests are generally



insensitive to highly correlated metrics, both variable importance and overall variation explain decrease when metrics overlap in multidimensional feature space (De'ath & Fabricius [2000], but see Fox et al. [2017]). Thus, we selected the highest performing, most parsimonious predictor variables for each guild and resolution to maximize model performance.

We used the VSURF and caret R packages to determine the top predictive model for each guild at each resolution (19 guilds + overall richness  $\times$  3 resolutions = 60 models) and used 70% of observations for training and 30% for validation (Genuer et al., 2015; Kuhn, 2021). Once we identified the input variables for each model, we parameterized 500 random forest trees (*ntree*) to ensure the errors stabilized for each guild (Lawrence et al., 2006). We then reevaluated fit metrics and hyperparameters using k-fold cross-validation and our 30% holdback data set to determine the models' reliability. We reevaluated hyperparameters, including the number of trees grown (*ntree*) and the number of predictors tested at each node (*mtry*), to select the best hyperparameters for each final guild and resolution model (Roberts et al., 2017). We used the root mean square error (RMSE) to select the best performing *mtry* for each model and evaluated error convergence on random forest plots for *ntree*.

Both sampling variability and stochastic processes contribute to prediction variance in random forest predictions (Wager et al., 2014). Thus, it is important to determine the properties of the distribution of our results and estimate the prediction intervals of our models. Prediction intervals, which are similar to confidence intervals but encompass the full range of predictions, are essential for managers because they indicate the range of richness values that can be expected, as well as how accurate our models were. We mapped prediction intervals using the k-fold cross-validation results. We then determined which pixels had wider prediction intervals and, hence, more uncertainty in the richness values. We further assessed the accuracy of the predictions by plotting model residuals. Each of these assessments can be used by managers to determine which of our predictive richness maps might be most useful.

## Comparison of model performance

Our second objective was to compare tradeoffs in resolution and richness model performance for each guild, and we did so using several metrics. We examined all 19 guilds and overall species richness at all 3 resolutions, such that each guild  $\times$  resolution combination had a unique model. Our performance metrics included

percentage variance explained (pseudo- $R^2$ ), RMSE, and symmetric mean absolute percentage error (sMAPE). The percentage variance explained was calculated based on the complete data set, whereas RMSE and sMAPE were generated separately for test and training data sets. We omitted raw RMSE from our output for model comparison because it is scale-dependent and not easily comparable across models. Instead, we used percentages of RMSE. We also chose sMAPE because it is an easily interpretable and comparable error metric and works well on data with zero values. To facilitate interpretation of the sMAPE values, we rescaled it to 0%–100%. Raw RMSE is in the same unit as the response (i.e., bird richness), and, as with sMAPE, the closer the test RMSE is to the training RMSE, the better the model performed. We divided RMSE values by the sample means for better comparability, so all RMSE values are reported as percentages.

We calculated both RMSE and sMAPE because the two indices weigh large errors differently and, thus, provide unique information. RMSE gives a higher weight to larger errors, so RMSE is always larger than or equal to sMAPE. For this reason, a larger difference between RMSE and sMAPE indicates a larger error variance. While one or both of these metrics are often reported, RMSE is more useful when signed values are needed (sMAPE relies on absolute values) and when the cost of increasing errors is increasingly bad (e.g., when estimations being off by six is more than twice as bad as being off by three). For this application, sMAPE is a better metric than RMSE because large errors do not require stronger penalties in this circumstance, but RMSE is now used more frequently, so both are provided. Interpreting how to evaluate model performance using RMSE and sMAPE can still be challenging. For this reason, focusing on the differences between test and training scores is helpful. The RMSE and sMAPE training scores indicate how well the model predicts the data used to build it, whereas the test scores indicate how well the model predicts unknown data and, hence, how generalizable it is. Thus, the test scores and differences (test minus training) provide useful information about the model's performance.

## Richness maps

To create guild-specific continuous richness maps at resolutions of 0.5, 2.5, and 5 km, we applied our models independently to raster layers resampled to each resolution, retaining those with  $\geq 50\%$  variance explained. Unlike predictions of the likelihood of occurrence for single species, we predicted breeding bird species richness with our random forest models, meaning low values were as likely

to be correct as high values and that it would not be appropriate to apply a minimum threshold to our guild maps. After generating all maps, we then exported them in tagged image file format (TIFF). We examined each map to determine whether there was disagreement in specific areas by subtracting standardized quantiles of richness values from lower-resolution maps from higher-resolution maps (i.e., 5–2.5, 2.5–0.5, and 5–0.5 km richness). We also used the prediction intervals generated during the model assessment to generate lower and upper prediction interval maps for each richness map.

## RESULTS

We successfully modeled and predicted bird species richness for 19 bird guilds plus overall richness at 3 resolutions across the conterminous United States. We found substantial differences in the richness values predicted depending on resolution, illustrating the tradeoffs we expected. The coarsest-resolution predictions had the highest accuracy, but finer resolutions may be more relevant for management. Limiting models to first-survey-stop bird data allowed us to make predictions at the 0.5-km resolution, but the number of observations decreased from 2,146,694 at the route level to 264,034. As expected, limiting the observations to either the 0.5- or 2.5-km data resulted in lower richness values per route compared to the full route 5 km data (Figure 1). Across guilds, average richness decreased from 65.4 (SD = 17.5) at 5-km resolution to 46.8 (SD = 15.5) at 2.5-km resolution and declined further to 18.5 (SD = 7.5) at 0.5-km resolution. The differences in guild-level richness among scales were most pronounced for large-ranged species, midstory/canopy nesters, and species with stable or increasing populations and less pronounced for grassland affiliates, grassland specialists, shrubland specialists, threatened species, small-ranged species, and frugivores (Figure 1). There were few observations of grassland affiliates, grassland specialists, shrubland specialists, threatened species, small-ranged species, and frugivores at all scales, and the average richness within these guilds was <1 at 0.5-km resolution, rendering predictions at this scale not meaningful.

For most guild models, the patterns of richness values were similar across resolutions resulting in high-correlation coefficients between richness for different resolutions, especially when comparing 2.5 km versus either 0.5 or 5 km (Figure 2). Specifically, when calculating correlations between the predictions from pairs of models of different resolutions (Figure 2), 21 of the 60 (35%) model pairs had Pearson's correlation coefficients of  $\geq 0.90$ , and only 10 (17%) had correlation coefficients  $\leq 0.70$ . Only the

0.5-km resolution frugivore richness model predictions had a correlation of <0.5 with the 2.5- and 5-km resolution predictions. The 5- versus 2.5-km predictions had correlation coefficients between 0.80 and 1 for all guilds.

## Predictor variables

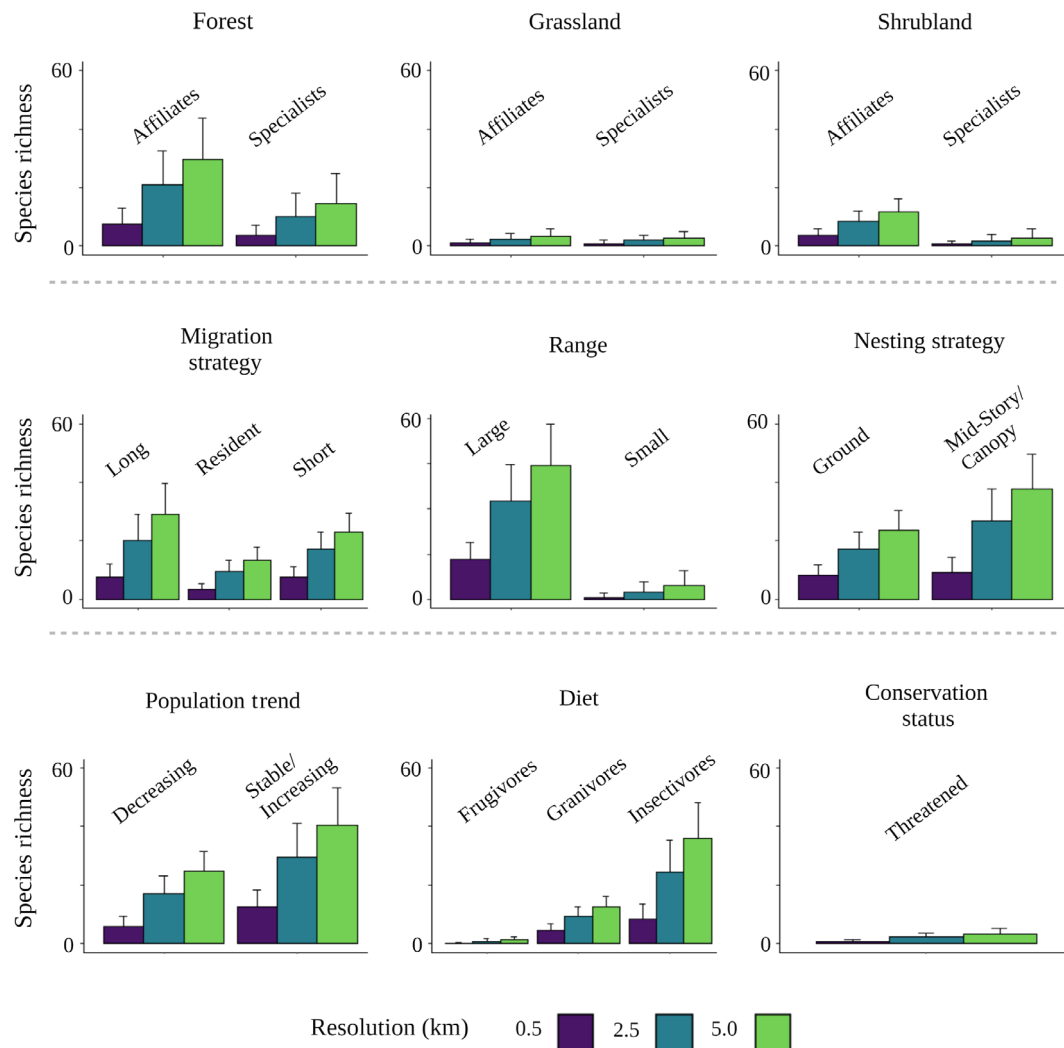
Of 66 candidate variables, 64 were included in our 60 models. All variables except the core of grassland cover and edge of wetland cover occurred in at least one model, with a mean frequency of 24 variables per model. Mean relative winter temperature, mean terrain ruggedness index, mean canopy height, mean peak net primary productivity, total precipitation in the wettest month, mean temperature in the coldest quarter, mean temperature in the warmest quarter, and annual mean diurnal temperature range variables were the most commonly selected variables, each of which was included in at least 45 of the 60 models (Appendix S3: Figure S1) (Carroll et al., 2022).

## Model performance

Matching our expectations, the 5-km-resolution models performed best across all guilds (from 50% to 87% variance explained for granivores and shrubland specialists, respectively) (Table 2). However, the 2.5-km models performed almost as well (from 50% to 79% variance explained for granivores and shrubland specialists, respectively). There was an inflection point in variation explained among the different resolutions, indicating that the relationship between resolution and model performance was not linear (Figure 3 and Table 2).

The models for forest specialists performed better than the models for forest affiliates according to RMSE, sMAPE, and the percentage variance explained (Table 2). Similarly, the models for shrubland specialists performed better than the models for shrubland affiliates for all metrics except the difference between test and training sMAPE at the 2.5-km resolution. Model performance metrics of grassland habitat specialist versus affiliate models were inconsistent, with specialist models performing better at all resolutions based on the percentage variance explained and affiliate models performing better based on the difference between test and training sMAPE and RMSE at 2.5- and 5-km resolutions. Interestingly, the ground-nesting guild models performed better across all resolutions based on the percentage variance explained, and the midstory/canopy nesting models only performed better at the 5-km resolution based on the difference in training and test sMAPE and RMSE, despite expectations





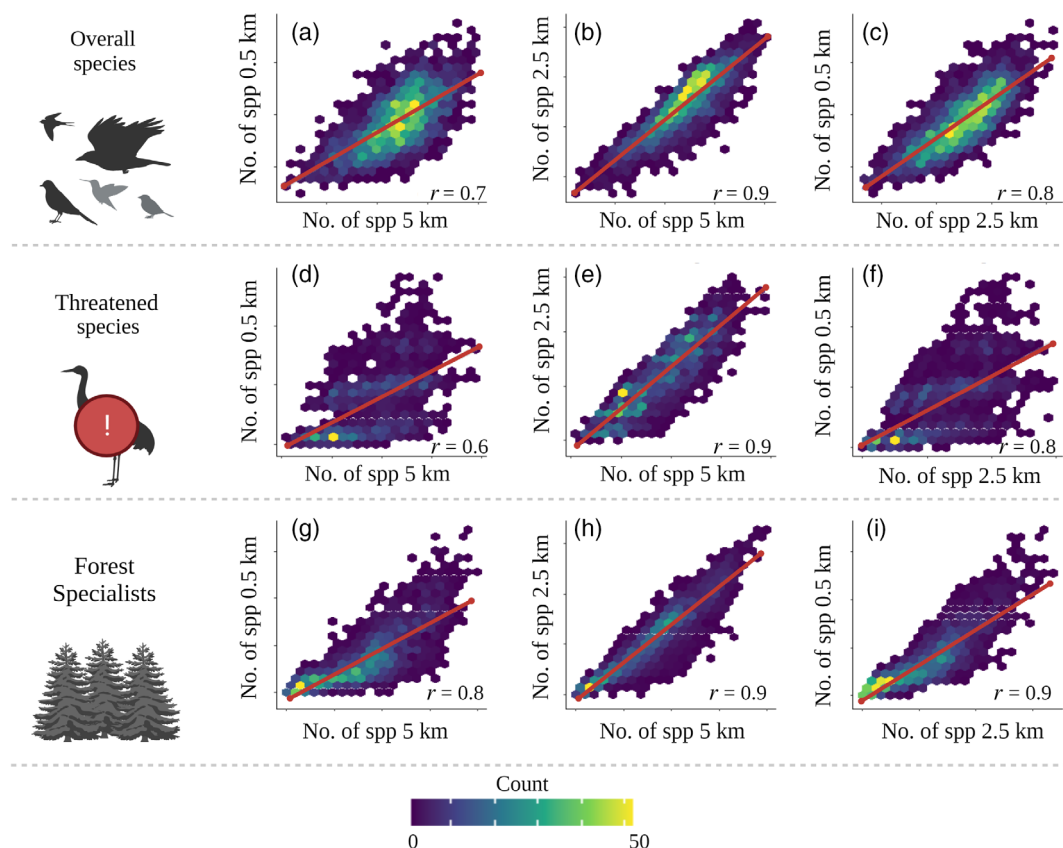
**FIGURE 1** Average species richness, from North American Breeding Bird Survey data, 2013–2019, by functional and life history guilds, modeled at three spatial resolutions, based on the 0.5-km resolution (first bird survey stop), 2.5-km resolution (first 10 survey stops), and 5-km resolution (full route data), respectively. The error bars here represent 1 SD.

that the ground-nesting models would have worse performance metrics (Table 2).

The percentage variance explained differed considerably between the 0.5-km and coarser resolutions. Our models of overall species richness explained between 27% and 60% of the variance, depending on the resolution. Some of our guild richness models, but not all of them, performed better, with percentage variance explained ranging from 12% to 87% (median = 61%, mean = 58%). The percentage variance for overall species richness and guild-specific richness was greatest at 5-km resolution, except for granivores (Table 2). At 5-km resolution, the best performing models (percentage variance explained >80%) were forest affiliates, forest specialists, shrubland specialists, and small-ranged species (in that order). All guilds had at least one model with sufficiently high performance (>50% variance explained) to allow nationwide predictions.

Our second performance metric, RMSE percentage, validated our models using separate training and test subsets of the data. Our training RMSE percentage ranged from 6% to 49% for all models (median = 14%, mean = 16%) and our test RMSE percentage ranged from 14% to 94% (median = 33.89%, mean = 35.74%) (Table 2). The difference between test and training data RMSE ranged from 8% to 84%. Similarly, we found that for sMAPE and the percentage variance explained, the best performing models based on RMSE were at 5-km resolution. These models always had the closest training and test RMSE percentage values.

We also evaluated the sMAPE of both training and test data to compare model performances. Model performance based on sMAPE indicated that all 5-km-resolution models outperformed the other two resolutions (Table 2). The best performing models based on sMAPE (<10%) were those of forest affiliates, shrubland affiliates, forest specialists,



**FIGURE 2** Hexplots comparing number of species (no. of spp) detected at different resolutions for (a–c) overall species richness, (d–f) threatened species richness, and (g–i) forest specialist species richness at 5 versus 0.5 km (a, d, g), 5 versus 2.5 km (b, e, h), and 2.5 versus 0.5 km (c, f, i). The red lines represent the fitted line, and  $r$  is the Pearson's correlation coefficient.

residents, long-distance migrants, short-distance migrants, ground-nesting species, midstory/canopy nesting species, threatened species, decreasing populations, increasing populations, large-ranged species, insectivores, and granivores (in that order). Notably, many guilds had a sMAPE <10% for both 2.5- and 5-km-resolution models. We determined which resolution had the closest sMAPE percentage values for training and test data and found that the differences ranged from 3% to 12% across all three resolutions. Interestingly, the differences in sMAPE did not follow the same patterns as the other performance metrics, with some 0.5-km models outperforming those at 2.5- or 5-km resolutions (e.g., models of frugivore richness).

## Richness maps

We generated 42 maps of bird richness covering the 19 guilds plus 2 for overall species at our 3 resolutions and limited maps to only those where models explained >50% of the variance (Figure 4). For the overall species maps, predictions of bird species richness ranged from 14 to 79 (mean = 42, SD = 11) at the 2.5-km resolution

and 27 to 97 (mean = 60, SD = 12) at 5 km. Among guilds, predicted bird species richness ranged from 1 to 23 at the 0.5-km resolution (mean = 3, SD = 2;  $n = 6$ ), 1 to 74 at 2.5 km (mean = 14, SD = 5;  $n = 17$ ), and 1 to 91 at 5 km (mean = 19, SD = 6;  $n = 19$ ). The highest predicted average species richness at 0.5 km was achieved by the forest affiliate guild (mean = 7, SD = 5), whereas at 2.5- and 5-km resolution, the highest average predicted richness was achieved by large-ranged species (mean = 38, SD = 12 at 2.5-km resolution, and mean = 55, SD = 14 at 5-km resolution). The shrubland specialist species guild had the lowest average predicted species richness (mean = 2, SD = 2) at the 0.5-km resolution, the threatened species guild at 2.5 km (mean = 3, SD = 1), and the frugivore species guild at 5 km (mean = 2, SD = 1).

In addition to the richness maps, we also made maps of the prediction intervals for each model (Figure 5) and the spatial agreement between resolutions (Figure 6). There were clear differences in predicted richness at the different resolutions for some guilds and overall species richness, especially in the central United States (Figure 6).

**TABLE 2** The percentage variance explained, training and testing root mean square error (RMSE) percentage at each resolution by guild, the difference between test and training data RMSE values (test–train RMSE), training and testing symmetric mean absolute percentage error divided by 2 (symmetric mean absolute percentage error [sMAPE], %), and the difference between test and training data sMAPE values (test–train sMAPE)

Guild	Resolution (km)	Percentage variance explained	Train RMSE	Test RMSE	Test–train RMSE	Train sMAPE	Test sMAPE	Test–train sMAPE
Overall species richness	0.5	27	14	33	19	7	14	7
	2.5	54	8	21	12	4	9	5
	5.0	60	6	14	8	2	6	3
Forest affiliates	0.5	56	19	46	27	10	21	11
	2.5	73	11	26	15	6	13	7
	5.0	80	8	17	9	4	9	5
Grassland affiliates	0.5	61	37	86	50	59	66	7
	2.5	71	19	47	28	25	33	8
	5.0	75	15	36	21	13	19	6
Shrubland affiliates	0.5	42	19	46	27	12	22	9
	2.5	62	11	27	16	5	12	7
	5.0	71	8	20	12	3	8	4
Forest specialist	0.5	66	24	60	36	20	32	12
	2.5	79	14	35	21	12	22	10
	5.0	85	10	24	14	7	13	6
Grassland specialists	0.5	63	36	89	54	58	67	10
	2.5	74	20	47	27	30	37	7
	5.0	79	15	35	20	15	20	5
Shrubland specialists	0.5	59	48	–	–	61	72	12
	2.5	79	26	64	38	23	27	4
	5.0	87	21	52	31	12	18	6
Residents	0.5	42	21	47	26	14	22	9
	2.5	60	10	25	15	5	11	6
	5.0	65	8	18	11	3	7	4
Long-distance migrants	0.5	41	18	46	28	10	21	11
	2.5	62	10	25	15	5	11	6
	5.0	69	7	19	12	3	8	4
Short-distance migrants	0.5	29	15	38	23	7	17	9
	2.5	54	8	20	12	3	8	5
	5.0	69	6	14	8	2	5	3
Ground nesters	0.5	30	15	38	23	8	16	9
	2.5	45	9	23	14	4	9	5
	5.0	51	7	17	10	3	7	4
Midstory/canopy nesters	0.5	34	9	42	33	9	19	9
	2.5	61	9	22	13	4	10	5
	5.0	68	6	15	9	3	6	4
Threatened	0.5	31	40	94	53	53	59	6
	2.5	59	17	43	26	18	26	8
	5.0	67	12	29	17	7	14	7

(Continues)

**TABLE 2** (Continued)

<b>Guild</b>	<b>Resolution (km)</b>	<b>Percentage variance explained</b>	<b>Train RMSE</b>	<b>Test RMSE</b>	<b>Test–train RMSE</b>	<b>Train sMAPE</b>	<b>Test sMAPE</b>	<b>Test–train sMAPE</b>
Decreasing	0.5	34	19	46	27	11	21	10
	2.5	<b>51</b>	<b>10</b>	<b>24</b>	<b>14</b>	<b>4</b>	<b>10</b>	<b>5</b>
	5.0	<b>59</b>	<b>7</b>	<b>16</b>	<b>9</b>	<b>3</b>	<b>6</b>	<b>4</b>
Stable/increasing	0.5	39	14	34	20	7	15	8
	2.5	<b>61</b>	<b>9</b>	<b>21</b>	<b>13</b>	<b>4</b>	<b>10</b>	<b>5</b>
	5.0	<b>66</b>	<b>7</b>	<b>15</b>	<b>9</b>	<b>3</b>	<b>6</b>	<b>4</b>
Large-ranged	0.5	36	14	34	20	7	14	8
	2.5	<b>65</b>	<b>8</b>	<b>20</b>	<b>12</b>	<b>4</b>	<b>9</b>	<b>5</b>
	5.0	<b>73</b>	<b>6</b>	<b>14</b>	<b>8</b>	<b>2</b>	<b>6</b>	<b>3</b>
Small-ranged	0.5	<b>66</b>	<b>49</b>	–	–	<b>66</b>	<b>75</b>	<b>9</b>
	2.5	<b>82</b>	<b>25</b>	<b>56</b>	<b>31</b>	<b>27</b>	<b>36</b>	<b>9</b>
	5.0	<b>86</b>	<b>18</b>	<b>40</b>	<b>22</b>	<b>13</b>	<b>23</b>	<b>11</b>
Insectivores	0.5	38	19	44	25	11	20	9
	2.5	<b>61</b>	<b>10</b>	<b>26</b>	<b>16</b>	<b>5</b>	<b>12</b>	<b>7</b>
	5.0	<b>67</b>	<b>7</b>	<b>17</b>	<b>10</b>	<b>3</b>	<b>7</b>	<b>4</b>
Granivores	0.5	37	17	40	23	9	17	8
	2.5	<b>50</b>	<b>10</b>	<b>23</b>	<b>13</b>	<b>4</b>	<b>10</b>	<b>6</b>
	5.0	<b>50</b>	<b>7</b>	<b>17</b>	<b>11</b>	<b>3</b>	<b>7</b>	<b>4</b>
Frugivores	0.5	12	–	–	–	94	98	4
	2.5	41	30	69	39	43	50	7
	5.0	<b>55</b>	<b>18</b>	<b>42</b>	<b>24</b>	<b>18</b>	<b>24</b>	<b>6</b>
Minimum		12	6	14	8	2	5	3
Mean		58	16	36	21	15	22	7
Median		61	14	34	20	7	16	6
Maximum		87	49	94	54	94	98	12

Notes: The minimum, maximum, and median exclude overall species richness, and all values except resolution are percentages. Resolutions represent the area the explanatory variables were sampled over, including 0.5 km (first-stop), 2.5 km (ten-stops), and 5 km (full routes). Missing values denote models without predictive power for that data set or metric. Models with percentage variance explained  $\geq 50\%$  are bolded.

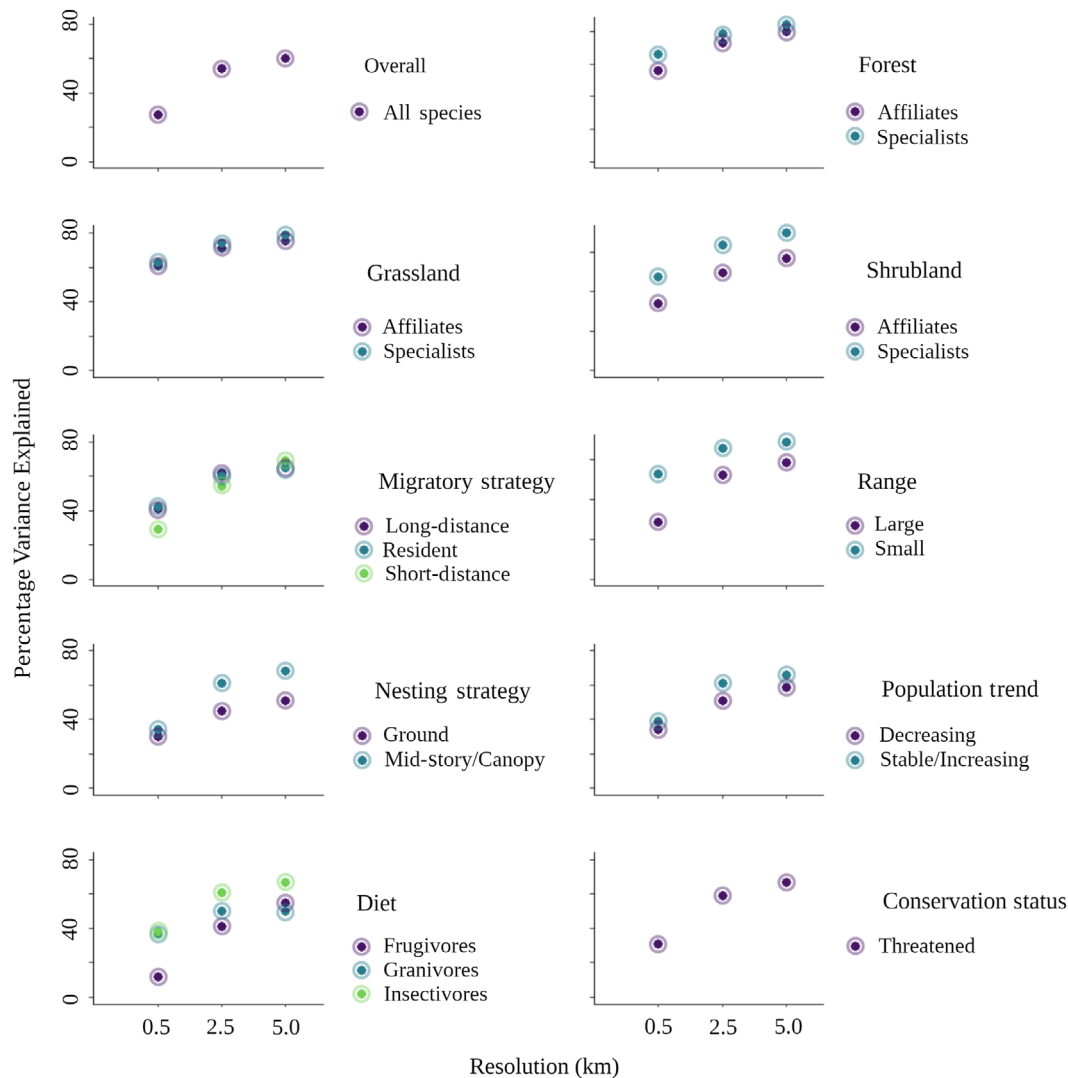
## DISCUSSION

We generated standardized richness maps for 19 breeding bird guilds plus overall species richness at 0.5-, 2.5-, and 5-km resolution, thereby addressing our first objective: to map breeding bird species richness at scales relevant to management. We also addressed our second objective by comparing tradeoffs in resolution and prediction accuracy for models of richness estimates for different guilds at three spatial resolutions based on three levels of occurrence data. We found that the 2.5-km-resolution richness maps best balanced resolution versus accuracy, so they are our recommendation for most management applications. Even though the 5-km resolution models almost always had the best performance metrics, the 2.5-km-resolution maps performed nearly as well, based on both performance metrics

and correlation coefficients, but at half the resolution and hence four times more pixels (Table 2 and Figures 3 and 4). This tradeoff is important, given that many management units and properties are quite small, which means that the finer 2.5-km-resolution pixels can provide substantially more information about the spatial pattern of species richness within these properties than the 5-km resolution. Further, management decisions are often made within a small area, such as a single watershed or forest stand, and thus, more detailed maps can support finer-scale decisions.

## Predictive variables

Our variables effectively predicted breeding bird richness for all guilds at one or more resolutions, and typically all three.



**FIGURE 3** Percentage variance explained by guild for each spatial resolution, as well as for overall species richness

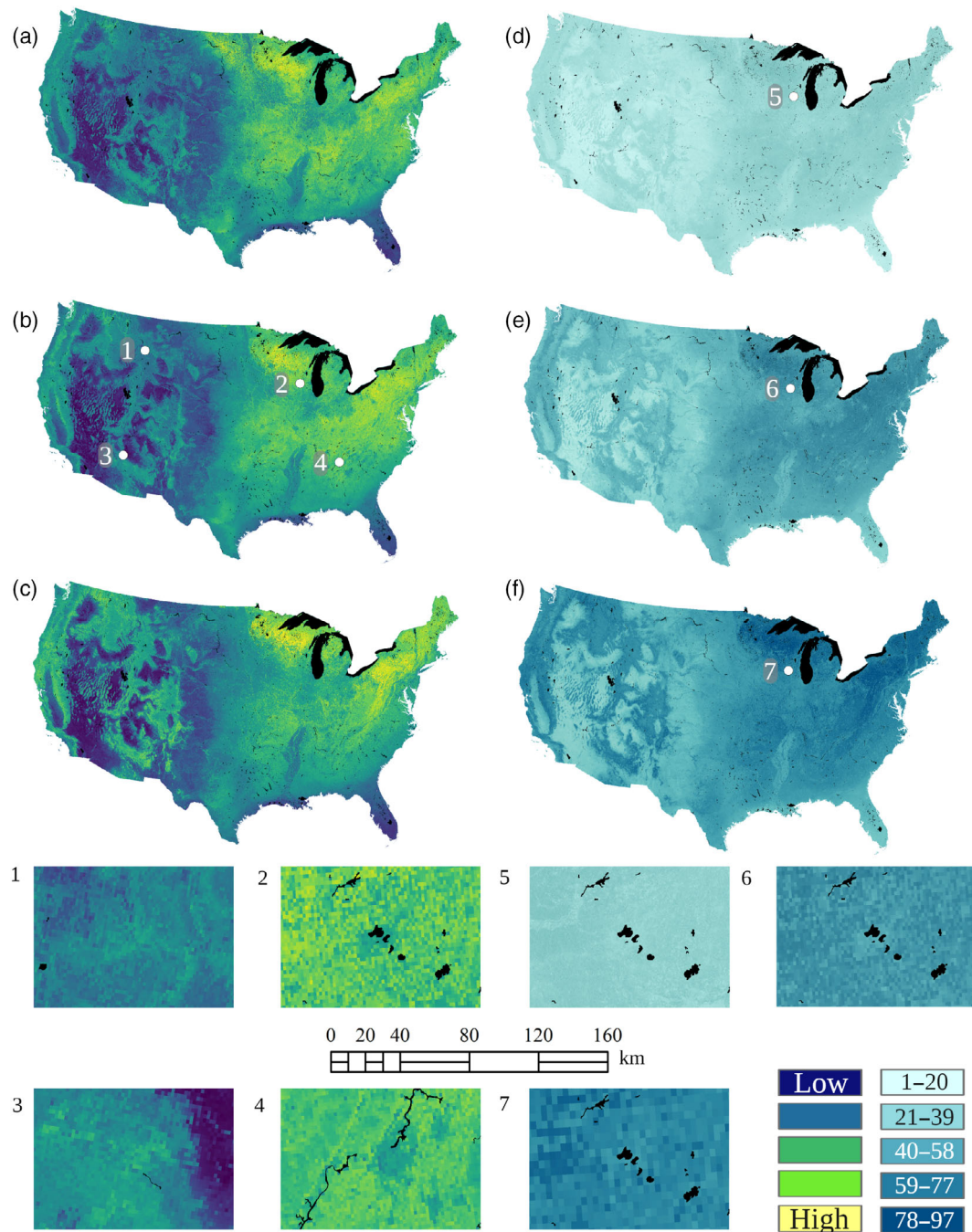
Of the 66 variables, many were generated from satellite data specifically for this analysis to predict fine-scale bird richness (Appendix S2). Our variables fit well within the framework of essential biodiversity variables (EBVs) (Pereira et al., 2013), representing a core set of complementary biological measurements intended to capture changes in biodiversity, because our variables allow us to make better predictions of species distributions and abundances. However, several EBV classes have poor alignment with remote sensing products, making it challenging to generate seamless data products (Skidmore et al., 2021). Our variables do not overcome that limitation, but given their value for distribution modeling, all of the variables included here are already or will be made publicly available at [silvis.forest.wisc.edu](https://silvis.forest.wisc.edu).

## Comparison of model performance by guild

We expected data-rich guilds, such as large-ranged species and generalist species guilds (e.g., species identified

as habitat affiliates rather than specialists), to be better modeled (Madon et al., 2013; Ovaskainen & Soininen, 2011), but that was not the case. Instead, our specialist species guild models performed better than generalist species guild models for all resolutions. We speculate that this was the case because specialist species guilds are often limited to a narrower range of predictive values for a given variable and a specific combination of variables, resulting in models with higher predictive power. For generalist guilds, larger sample sizes may be required to predict distributions accurately because a number of combinations of variable values can result in the same richness (Connor et al., 2018; Hernandez et al., 2006). Similarly, we expected that models of canopy nesting species would perform better than those for ground-nesting species because our remote sensing variables would characterize the canopy better than attributes of importance to ground nesters. However, we were surprised to see that that was not the case either (Table 2). Lastly, we expected that richness of our rarer or highly specialized guilds



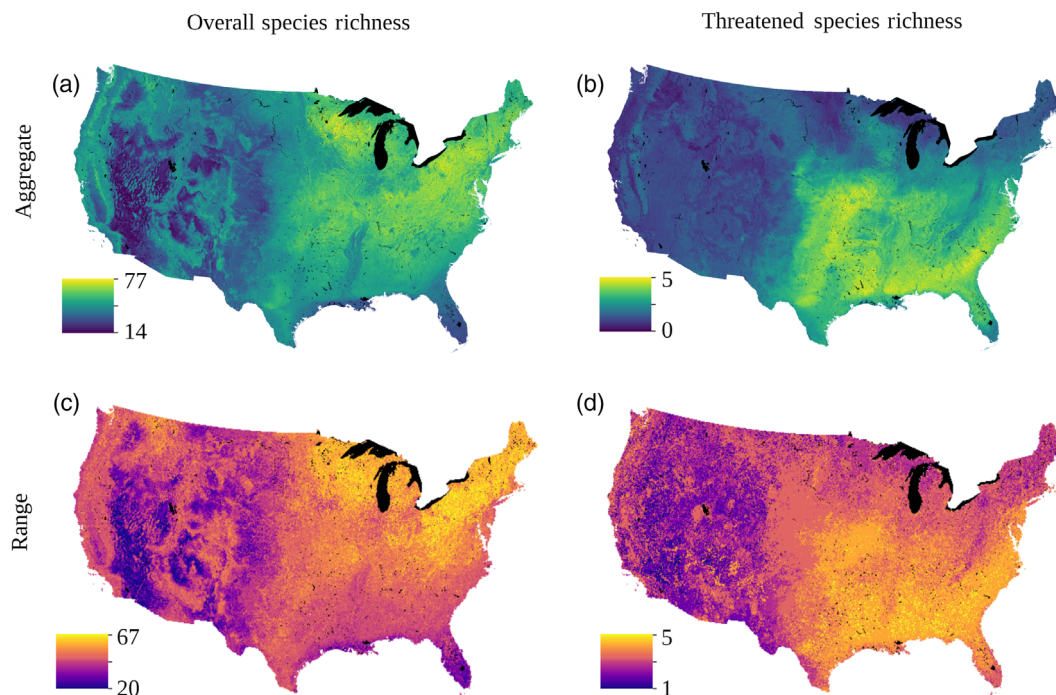


**FIGURE 4** Equal-interval standardized overall species richness at (a) 0.5-km, (b) 2.5-km, and (c) 5-km resolution that employs a relative bird richness scale to make maps at the three resolutions comparable; and absolute overall species richness at (d) 0.5-km, (e) 2.5-km, and (f) 5-km resolutions that have unique scales for each resolution across the conterminous United States. The first set of zoom-ins (1–4) illustrate standardized overall species richness at the 2.5-km resolution around (1) Bozeman, Montana, (2) Madison, Wisconsin, (3) Flagstaff, Arizona, and (4) Chattanooga, Tennessee. The second set of zoom-ins (5–7) illustrate absolute overall species richness at (5) 0.5 km, (6) 2.5 km, and (7) 5 km around Madison, Wisconsin.

(e.g., frugivores) would best be predicted at the 0.5-km resolution because finer-resolution environmental variables would better represent habitat resources within average passerine home range sizes, but there were too few bird observations at that resolution to parameterize reliable models.

### Comparison to existing products

Several previous efforts generated landscape-level biodiversity pattern maps to aid conservation efforts using species range maps (Kullberg et al., 2019; Pompa et al., 2011; Schipper et al., 2008), potential habitat maps



**FIGURE 5** Spatial pattern predictions generated by (a, b) 500 aggregate random forest models and (c, d) the range of values across 200 individual random forest trees for each pixel for (a, b) overall species richness and (c, d) threatened species richness at 2.5-km resolution

(Gergely et al., 2019; Rondinini et al., 2011; Xu et al., 2017), and species distribution maps (Bateman et al., 2020; Engler et al., 2017; Sofaer et al., 2019). With the growing availability of species occurrence data sets (e.g., BBS, Global Biodiversity Information Facility [GBIF]), predictive models of species distributions or aggregate biodiversity metrics such as species richness are an alternative way to map biodiversity (Jiguet et al., 2005; Sporbert et al., 2019; Troia & McManamay, 2016). The rich modeling environment for occurrence-based species distribution models, a growing set of remotely sensed variables designed for species distribution modeling, and growing species occurrence data sets increasingly enable the development of finer-scale biodiversity products (Jetz et al., 2012; Luque et al., 2018; Schwager & Berg, 2021).

There are manifold benefits to using occurrence-based products. However, our models of guild-level richness represent an approach that avoids the coarseness of range-based maps, the overpredictions of potential habitat maps, and the lack of samples for many species that precludes making occurrence maps for them. Further, the ability to validate maps and provide information about the confidence of predictions is critical for strategic planning and decision-making (Ladle & Hortal, 2013; Rocchini et al., 2011; Thuiller et al., 2019). Importantly, the patterns we found do not deviate substantially from those based on range maps and potential habitat (Gergely

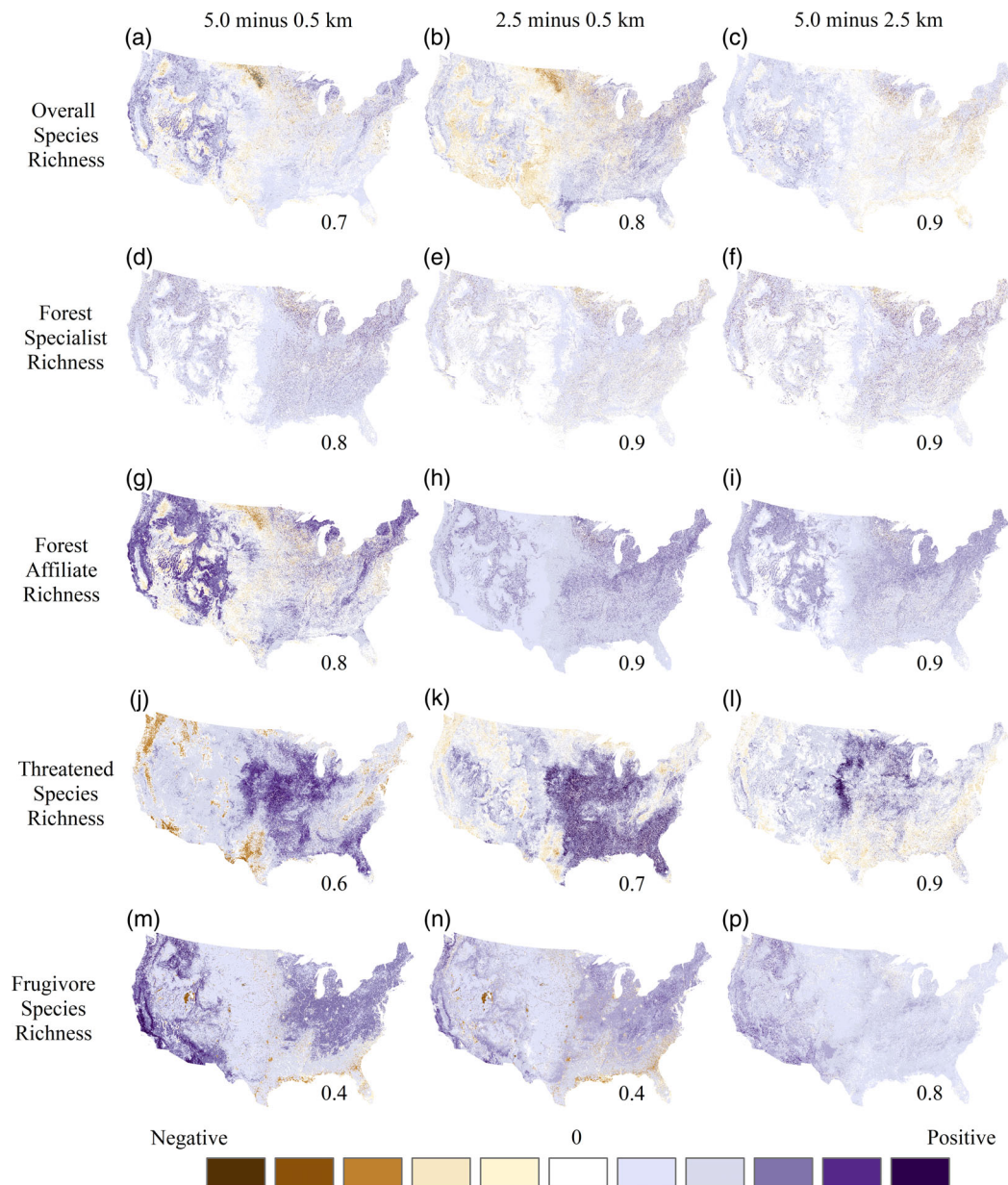
et al., 2019; Jenkins et al., 2013). However, our approach has the advantages of having a management-relevant resolution based on species observations and well-specified accuracy, including upper and lower bounds for our predictions.

### Implications and guidance for conservation

Overall, our maps address a major impediment to land management for multiple land planning units and jurisdictions, namely, the lack of accurate maps at fine enough spatial resolutions to be suitable for management and decision-making consistent across large areas and that have well-specified accuracy information, to allow for conservation planning (Kuenzer et al., 2014). Our maps thus bridge the gap between the needs of local managers for evidence-based information to support decision-making with the large number of biodiversity maps in the scientific literature (Cook et al., 2010; Fazey et al., 2005).

The high correlation between our maps at the different resolutions further supports their conservation utility (Figure 3). Which resolution is best depends on the management or conservation goal. Despite the lower accuracy of our 0.5-km maps, their high correlation with 2.5- and 5-km maps supports the credibility of the derived





**FIGURE 6** Patterns of disagreement for (a–c) overall species richness, (d–f) forest specialist species richness, (h–j) forest affiliate species richness, (k–m) threatened species richness, and (n–p) frugivore species richness when subtracting (a, d, h, k, n) 5- to 0.5-km richness, (b, e, i, l, o) 2.5- to 0.5-km richness, and (c, f, j, m, p) 5- to 2.5-km richness. All legends represent standardized quantiles for a given map rather than absolute values for better visualization. A negative value means that the higher-resolution map had higher species richness values, and a positive value means that the coarser-resolution map had higher richness values. The number in the lower right of each map represents the Pearson's correlation coefficient of the two maps. Areas in agreement (i.e., zero values) are colored white. For each guild the largest and smallest values shown are (a–c) 4 and –4, (d–f) 7 and –7, (g–i) 5 and –3, (j–l) 8 and –5, and (m–p) 8 and –5, respectively.

richness patterns. Maps for those guilds with high correlations among scales are particularly useful for managers working in small areas or at fine scales. By generating richness maps at three resolutions and making them freely available, managers can decide which resolution best meets their needs (Costello & Wicczorek, 2014). For managers seeking relatively high accuracy in predicted

values, the 5-km resolution maps are best. Alternatively, managers working to determine where conservation may be most effective for all birds or a specific guild in a small geographical area can use the 0.5-km-resolution maps. We suggest that the 2.5-km richness maps represent the best tradeoff between accuracy and resolution for most purposes.

One of the ways these products can be applied to conservation and management is through their inclusion in planning efforts, such as, for example, the development of land management plans for each national forest, as required by the National Forest Management Act (NFMA). Current regulations on National Forest Land Management Plans require place-based wildlife conservation for threatened or endangered species, species of conservation concern, and species commonly enjoyed and used by the public. Our maps of threatened and endangered species, as well as other guilds of management concern, can assist forest planners in determining where to focus wildlife conservation and where to allow more extensive human land use. However, we recognize that our products may be too coarse for organizations making land management decisions about small individual parcels. Ultimately, though, we expect that many state- and federal-level managers could integrate these richness products into ongoing or new conservation efforts, particularly when seeking to balance wildlife conservation and human use.

For those using our products for conservation planning, we suggest the following steps and considerations for selecting the best data set for a given management question. First, managers should decide what level of uncertainty in predicted species richness is acceptable for their management question. Second, the overall model performance metrics (Table 2), including percentage variance explained, RMSE, and sMAPE, provide the first indication of whether the corresponding predictive maps are suitable for their question. Third, an important consideration is how large the area being managed is and, hence, how many pixels that area would encompass, with the goal of balancing resolution and model accuracy. For example, a manager working in a relatively small planning unit (e.g., a county) and seeking to protect areas with high forest affiliate species richness may find the finer details of the 2.5-km resolution more useful, despite having slightly lower accuracy than the 5-km resolution. Fourth, we suggest downloading both the prediction interval maps (e.g., Figure 5) and the species richness maps (e.g., Figure 4). The prediction interval maps indicate the precision of estimates for a given area. Fifth, we suggest downloading the raster files that compare how much richness differs based on resolution (e.g., Figure 6). If richness patterns are very similar, that supports using the finest-resolution 500-m richness maps. The tradeoff between resolution and accuracy is partially spatially dependent (Figure 6). Maps for guilds with lower correlations among scales, such as threatened species at the 0.5-km resolution, should be used with caution (Figure 6). In such instances, the prediction interval files should be used to determine whether regional patterns are

informative before using finer-resolution maps (Figure 5). Following these steps will help managers determine which species richness map can best support their conservation efforts.

## CONCLUSION

Despite advances in species distribution modeling, few biodiversity products meet management and conservation needs directly. We developed breeding bird species richness maps at high enough resolution to be management-relevant yet consistent across the conterminous United States. These maps have well-specified accuracy based on both independent validation data and maps of prediction accuracy and upper and lower bounds of prediction richness. Furthermore, we quantified the inherent tradeoff between higher resolution and map accuracy and found that a 2.5-km resolution provided the best compromise between the two. As such, our maps can help bridge the gap between the rich literature on species distribution modeling and the need for management-relevant biodiversity products.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The rasters generated in the current study and supplemental tables (Carroll et al., 2022) are available on Dryad at <https://doi.org/10.5061/dryad.vq83bk3v0>. Bird data and ancillary remotely sensed products are publicly available and described in Appendix S2.

## ORCID

Kathleen A. Carroll  <https://orcid.org/0000-0003-3853-0501>

Paul R. Elsen  <https://orcid.org/0000-0002-9953-7961>

Volker C. Radeloff  <https://orcid.org/0000-0001-9004-221X>

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