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ARTICLE

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Mapping multiscale breeding bird species distributions across the United States and evaluating their conservation applications

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Abstract

Species distribution models are vital to management decisions that require understanding habitat use patterns, particularly for species of conservation concern. However, the production of distribution maps for individual species is often hampered by data scarcity, and existing species maps are rarely spatially validated due to limited occurrence data. Furthermore, community-level maps based on stacked species distribution models lack important community assemblage information (e.g., competitive exclusion) relevant to conservation. Thus, multispecies, guild, or community models are often used in conservation practice instead. To address these limitations, we aimed to generate fine-scale, spatially continuous, nationwide maps for species represented in the North American Breeding Bird Survey (BBS) between 1992 and 2019. We developed ensemble models for each species at three spatial resolutions—0.5, 2.5, and 5 km—across the conterminous United States. We also compared species richness patterns from stacked single-species models with those of 19 functional guilds developed using the same data to assess the similarity between predictions. We successfully modeled 192 bird species at 5-km resolution, 160 species at 2.5-km resolution, and 80 species at 0.5-km resolution. However, the species we could model represent only 28%–56% of species found in the conterminous US BBSs across resolutions owing to data limitations. We found that stacked maps and guild maps generally had high correlations across resolutions (median = 84%), but spatial agreement varied regionally by resolution and was most pronounced between the East and West at the 5-km resolution. The spatial differences between our stacked maps and guild maps illustrate the importance of spatial validation in conservation planning. Overall, our species maps are useful for single-species conservation and can support fine-scale decision-making across the United States and support community-level conservation when used in tandem with guild maps.

However, there remain data scarcity issues for many species of conservation concern when using the BBS for single-species models.

KEYWORDS
avian, biodiversity metrics, Biomod, conservation, ensemble model, remote sensing, richness, species distribution modeling

INTRODUCTION

One of the biggest challenges in conservation is the lack of consistent, nationwide, spatially explicit species occurrence data necessary for planning and management (Schmidt-Traub, 2021; but see eBird and the Breeding Bird Survey). Detailed spatial information is essential for managers reconciling conservation, human land use, and climate change with protecting species and the ecosystem services they provide (e.g., pollination). Despite the importance of consistent species and higher-order maps for management and the longstanding availability of the data and methods necessary to generate such maps, there is still a need to create maps that are spatially continuous (wall to wall), include spatial validation, and relevant to fine-scale management (Hughes et al., 2021; Lee-Yaw et al., 2022; Peterson et al., 2018). Species distribution models (SDMs) are typically used to generate such products (Elith & Leathwick, 2009; Franklin, 2010; Peterson et al., 2011). However, many existing distribution maps are based on guild or other aggregated occurrence data due to species-level occurrence data scarcities, efforts to better capture community patterns and ecosystem complexity, or both (Carroll et al., 2022; D'Amen et al., 2017; Ferrier & Guisan, 2006).

Single-species distribution models are vital to conservation decision-making for several purposes, including identifying patterns of rarity or endemism, determining the impacts of climate change on vulnerable species, evaluating the effects of habitat change, determining the effectiveness of management actions, measuring extinction rates, and analyzing reserve design efficacy (Camaclang et al., 2015; Porfirio et al., 2014; Schwartz, 2008; Sofaer et al., 2019). Single species-focused management is also an important component of conservation legislation (e.g., US Endangered Species Act, Sage Grouse Initiative; Fontaine, 2011; Schwartz, 2008). For example, in US Forest Action Plans (https://www.stateforesters.org/forest-action-plans/) and other similar conservation plans, managers must balance individual species conservation with human access across state-held lands. These sometimes competing objectives make single-species spatial data and fine-scale maps critical in supporting managers' ability to make conservation decisions effectively (Guisan et al., 2013).

Community-level maps based on macroecological models can also provide information for conservation planning. Some ecologists have argued in favor of mapping at higher taxonomic levels, such as communities, with the justification that modeling multiple species provides additional information about species assemblages that can be missed with single-species models (Anderson et al., 2002). However, models of biodiversity at higher taxonomic levels lack the specificity required for detailed conservation interventions and management decisions, necessitating the development of high-quality, spatially validated, single-species models.

There are several approaches to handling individual species' observation scarcity, but a common one is modeling taxonomic or functional guild-level richness, herein guild richness (Zakharova et al., 2019). Guild models aggregate data from species, often based on functional or taxonomic traits, and produce one species richness value for each sampling point. The primary benefits of generating maps based on all species data within a guild or region are that data-poor species can contribute to species richness estimates and complex data are synthesized into a simpler form (Brown et al., 2004; Ferrier & Guisan, 2006; Guisan & Rahbek, 2011). However, the resulting outputs are guild-level habitat richness estimates rather than species-specific suitability or distribution maps. While guild maps are useful in many conservation applications, they do not support species-specific planning, and thus, they only represent a portion of the information needed in spatial conservation planning.

Another alternative to individual species models is joint species distribution models (JSDMs), which can be used to generate single-species models using data across multiple species data sets (Pichler & Hartig, 2021; Schliep et al., 2018; Thorson et al., 2016). JSDMs account for the interaction of species sharing resources, can accommodate both abundance and occurrence data, and model environmental filtering at the community level. However, JSDMs are computationally expensive, and interpretation of the resulting residual correlation matrix is challenging. Using various Bayesian frameworks with

priors that provide block structure to the covariance matrix can cut computation time and improve model interpretability. However, despite suggestions that rare species benefit from JSDMs (Ovaskainen & Soininen, 2011; Pollock et al., 2014), recent evidence shows that in many instances, JSDMs do not improve predictions for rare species or communities compared to stacked species distribution models (S-SDMs) (Zurell et al., 2020). Further, JSDMs tend to overpredict species richness (Wilkinson et al., 2021; Zurell et al., 2020) and do not consistently improve single-species predictions (Zurell et al., 2020). Given these issues, JSDMs are not necessarily the best alternative to stacked aggregated or individual single-species distribution models (Norberg et al., 2019). While alternative approaches can be beneficial for capturing community dynamics, preserving ecosystem function, or serving as a surrogate for rare or undersampled species, managers, particularly those focusing on particular species of conservation concern, still rely on and seek single-species maps.

Individual species distribution maps, when available, can also be stacked to generate guild or community-level maps (often called stacked species distribution models or S-SDMs; Algar et al., 2009; Ferrier & Guisan, 2006). S-SDMs were initially created to forecast species' responses to climate change and estimate no-analog communities for conservation (Ferrier & Guisan, 2006; Williams & Jackson, 2007). While S-SDMs allow for individual species forecasting, evidence indicates that S-SDMs overpredict species richness due to missed community assembly rules (e.g., competitive exclusion; Guisan & Rahbek, 2011; Mateo et al., 2012; but see D'Amen et al., 2015; Lehmann et al., 2002). These overprediction biases can be eliminated through spatially explicit species assemblage modeling (SESAM), species-specific threshold selections, stacking continuous rather than binary maps (Calabrese et al., 2014; Guisan & Rahbek, 2011; Mateo et al., 2012; Pineda & Lobo, 2009), or using similar alternative methods (e.g., joint species distribution models; Pollock et al., 2014). However, evaluating the performance of newly generated stacked maps against their guild or community counterparts is still important to gain insights into SDM performance for conservation applications.

Maps spanning various spatial resolutions and ecological levels are necessary to support conservation goals, but down- or upscaling maps present challenges. For instance, S-SDMs could be upscaled to create maps similar to community richness maps. However, there is likely to be a data scarcity-driven tradeoff between accuracy and resolution in these products (Figure 1a). This tradeoff is likely more prominent in single-species mapping efforts than in guild mapping efforts because as spatial resolution becomes finer, the number of species included in a stacked map declines more quickly relative to a guild map (Figure 1a). Therefore, we would expect stacked maps to be more biased toward common species within any given guild, and there is likely a minimum threshold resolution at which aggregating single-species maps no longer adequately informs guild-level conservation goals.

We aimed to model and map single-species distributions and determine which species had sufficient data for individual species mapping at different management-relevant resolutions (0.5, 2.5, 5 km). We also sought to compare aggregates of our single-species maps (stacked maps, Figure 1b) with those generated using functional guild richness data (guild maps, Carroll et al., 2022) to determine where, spatially, stacked maps differed from guild maps across resolutions and by how much. We expected that we would be unable to model a small proportion of species surveyed by the North American Breeding Bird Survey (BBS) at the coarsest resolution (5 km) due to insufficient sample sizes, and many more species would lack sufficient observations for distribution models at the finest resolution (0.5 km). Therefore, we expected individual species or guilds with few observations (e.g., threatened species) would necessitate coarser resolution than common species or data-rich guilds (e.g., forest affiliates). We also expected to find spatial differences between our stacked maps and guild maps, with these differences being most pronounced in guilds with few observations (e.g., frugivores) and at the finest resolution (0.5 km).

METHODS

Breeding Bird Survey data

The North American BBS is a joint effort between the USGS Patuxent Wildlife Research Center and the Canadian Wildlife Service's National Wildlife Research Center. The BBS consists of a series of 3-min point counts encompassing a 0.4-km radius, organized along routes that are run annually during the breeding season (typically June, $n > 4100$ routes). Full BBS routes are approximately 39.4 km along secondary roads, with data for each survey stop approximately 0.8 km apart. All BBS data are publicly available at the species level, and over 400 species are represented in the data set (https://www.pwrc.usgs.gov/bbs/).

We subset single-species BBS data for the conterminous United States to only data from routes collected according to the BBS protocol (collected during set months) and in suitable weather conditions (e.g., good visibility, little to no wind or precipitation). We also removed data from the first year in which routes were

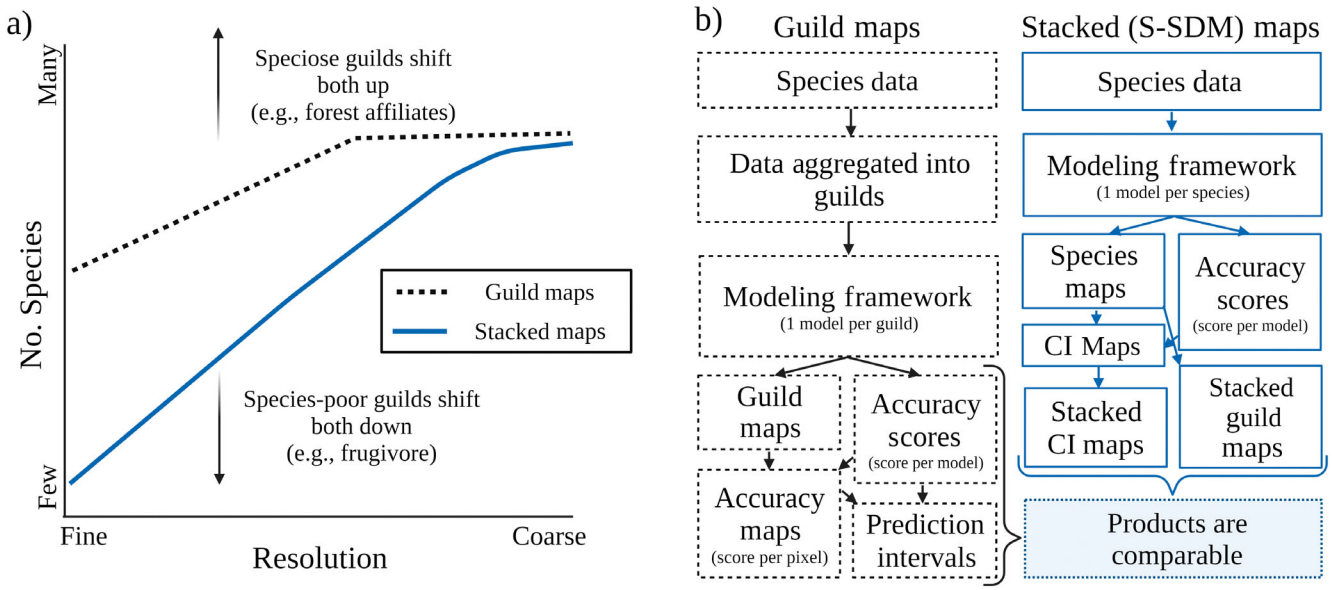

FIGURE 1 (a) Tradeoff between resolution and number of species using guild model approach (black/dashed) and stacked species distribution models (S-SDMs, solid blue) and (b) a schematic representing methodological differences between each. Figure created using Biorender.

monitored and the first time a given observer monitored the route to reduce potential observer effects. We selected BBS data because it has fixed observer effort, seasonal alignment, and data spanning several decades (Feng & Che-Castaldo, 2021; Scher & Clark, 2023). We used BBS data collected between 1992 and 2019 ($n = 2981$ route-years), as our exploratory analyses indicated species patterns were similar to patterns within the period covered by our predictor variables (2013–2019; see Appendix S1 for further details), and we wanted to boost our sample size for the modeling phase, as sample size is closely tied to SDM performance. We reformatted the BBS data to binary presence–absence data and retained only species with at least 100 detections at each of the three resolutions ($n = 199$ species at 5 km or route level, $n = 163$ at 2.5 km or first-10-stop level, $n = 81$ at 0.5 km or first-stop level; van Proosdij et al., 2016; Wisz et al., 2008). We selected these three resolutions (0.5, 2.5, and 5 km) because they sample an areal extent equivalent to our three BBS route sets. For example, a hypothetical BBS route's 50 stops sample an area of land 40 km long by 0.8 km wide, or approximately 32 km^2, similar to the 25 km^2 sampled by a 5-km resolution pixel. Similarly, the areal extent of a 2.5-km^2 pixel (6.25 km^2) is similar to the 8 km^2 sampled by the first 10 stops of a BBS route, and a 0.5-km^2 pixel is similar in area to the area sampled by one stop. While the geographic coordinates of the first stop of each BBS route are known, those of the subsequent 49 stops are not available, and surveyors may use differing and imprecise methods (e.g., car odometers) to navigate to subsequent stops along a route. In determining initial BBS route locations, BBS staff make an effort to ensure that each BBS route is located within one vegetation type (K. Pardiek, personal communications). Further, a previous assessment revealed that 5- and 2.5-km-resolution pixels centered on the first BBS stop effectively represent environmental variables associated with the route (Carroll et al., 2022). Therefore, we linked environmental data in a 0.5-km pixel with bird data in the first stop of each route, data in 2.5-km-resolution pixels centered on the first stop with bird data in the first 10 stops of each route, and in 5-km-resolution pixels centered on the first stop with route-level bird data.

Predictor variables

We included 66 variables previously used to model bird guild distributions, encompassing vegetation productivity, human land use, climate, and geomorphology, to model individual species distributions (Elsen et al., 2020, 2021; Farwell et al., 2020; Gudex-Cross et al., 2021)—see Appendix S1. Specifically, we included the dynamic habitat indices (DHIs; Radeloff et al., 2019), image texture measures (Farwell et al., 2020), housing density (Radeloff et al., 2018), cloud cover (Carroll et al., 2022), winter habitat indices (WHIs; Gudex-Cross et al., 2021), bioclimatic variables (BIOCLIM), thermal metrics (Elsen et al., 2021), and elevation. We derived the DHIs, image texture measures, cloud cover, WHIs, and thermal

metrics from full-year Landsat 8 data from 2013 or 2014 to 2019 (Table 1; Carroll et al., 2022).

Each variable we included has been individually demonstrated to predict bird species distributions well at fine resolutions. For example, the DHIs (including cumulative, minimum, and variation DHI metrics) each capture unique aspects of vegetation productivity. Image texture metrics calculated on Landsat-based DHI maps integrate multiple facets of landscape heterogeneity, including structural and compositional heterogeneity of vegetation (Farwell et al., 2020, 2021). We included first-order (e.g., mean, variance) and second-order texture metrics (e.g., entropy, correlation); second-order measures consider the spatial arrangement of pixels. Texture metrics are particularly useful predictors in landscapes with high structural complexity. Our thermal metrics, including thermal heterogeneity, relative temperature, and temperature amplitude, capture small-scale (microclimatic) to large-scale (latitudinal and longitudinal) temperature patterns, as well as seasonal temperature ranges (Elsen et al., 2020, 2021). Our cloud cover and housing density metrics predict guild-level bird richness (Carroll et al., 2022). Finally, our WHI metrics (winter season length, snow cover variability, and subnivium conditions) have consistently equaled or outperformed other abiotic variables (e.g., climate, topography) as predictors of avian

TABLE 1 Overview of satellite-based predictor variables generated for bird species modeling.

Category	Variable	Description	Relevant references
Vegetation	Dynamic habitat indices (DHIs)	The DHIs are metrics (cumulative, minimum, variation) of vegetation productivity. Cumulative DHI values characterize high available energy annually, minimum DHI indicates lowest productivity, and interannual variation DHI values characterize variation in productivity across a calendar year.	Hobi et al. (2017), Radeloff et al. (2019)
	Texture of cumulative DHIs	Image texture metrics calculated on Landsat-based DHI maps integrate multiple facets of landscape heterogeneity.	Berry et al. (2007), Farwell et al. (2020, 2021)
Anthropogenic	Housing density	Housing density is based on block-level mapped housing and population counts from the 2010 decennial US Census data.	Carroll et al. (2022)
Climate	Thermal heterogeneity	Seasonal thermal heterogeneity metrics (summer and winter) capture fine-scaled microclimatic patterns that vary over space and time.	Elsen et al. (2020, 2021)
	Relative temperature	Relative temperature metrics (summer and winter) capture broader latitudinal and longitudinal temperature patterns.	
	Temperature amplitude	Temperature amplitude captures the difference between median summer and winter relative temperatures.	Carroll et al. (2022)
	Cloud cover index	Our cloud cover index captures standardized cumulative cloud count across Landsat 8.	Carroll et al. (2022)
	Winter habitat indices (WHIs)	We included the three WHIs: winter season length, snow cover variability, and subnivium conditions. Winter duration is measured as snow season length, that is, the number of days between the first and last snow detection; snow cover variability characterizes how often the ground switches between snow-covered and bare (e.g., precipitation and melt events, large fluctuations in temperature); and subnivium conditions represent the thermal refugia properties of snow.	Gudex-Cross et al. (2021, 2022)

Note: Each newly generated predictor variable was analyzed over the full Landsat 8 period unless otherwise noted in Appendix S1, which includes further predictor variable details.

species richness at national (Gudex-Cross et al., 2021) and global (Gudex-Cross et al., 2022) scales.

Ensemble distribution modeling

There are a multitude of ways to model species distributions (Elith & Graham, 2009), and ensemble modeling offers one approach to compare and use various models (Araújo & New, 2007). We used the BIOMOD2 package in R (version 4.1.2) to generate ensemble predictive habitat suitability maps for all bird species at 0.5-, 2.5-, and 5-km resolutions (Thuiller et al., 2009, 2016). BIOMOD can run up to 10 single models, compares well with other approaches, particularly when analyses are based on small sample sizes (Luo et al., 2017), and reduces uncertainties that arise from models built from a single modeling framework (Hao et al., 2019; Thuiller et al., 2016).

We conducted a preliminary analysis using six species to calibrate and test our BIOMOD models—see Appendix S2. In these preliminary analyses, we examined model predictive performance and computation time for species from various guilds (e.g., one frugivore, one habitat specialist), and we retained the generalized linear model, boosted regression tree, flexible discriminant analysis, multiple adaptive regression splines, and random forest (RF). We dropped the artificial neural network, surface range envelope, generalized additive model, classification tree analysis, and two maximum entropy models (MAXENT.Phillips and MAXENT.Phillips.2) due to either poor predictive performance or data structure requirements (Guillera-Arroita et al., 2014). We used the default settings for all preliminary and final models. We calibrated preliminary and final models using 80% of the data, withheld the remaining 20% for evaluating model predictions, and employed three cross-validation runs through BIOMOD (Lobo & Tognelli, 2011; because we used true absence data, we allowed BIOMOD2 to randomly select withheld data, but see Phillips et al., 2009).

We then used ensemble models to generate raster files for each species that had a true skill statistic (TSS) of 0.6 or higher (Pearce & Ferrier, 2000, $n = 192$ at 5 km, $n = 160$ at 2.5 km, $n = 80$ at 0.5 km). We chose TSS because it quantifies how well the model distinguishes presence and absence based on omission and commission errors and is unaffected by prevalence (Allouche et al., 2006). We also evaluated model performance based on receiver operating characteristic (ROC, which generates plots to produce area under the curve [AUC] measures) and Cohen's kappa (Kappa, which measures the proportion of all possible presences and absences predicted correctly after accounting for chance)—all of which BIOMOD provides. Each of these performance metrics has unique ranges that indicate good model performance. For instance, AUC values between 0.7 and 0.9 represent useful applications, and values over 0.9 indicate high accuracy (Pearce & Ferrier, 2000). Like TSS, ROC aims to determine the best balance of sensitivity and specificity (Guisan et al., 2017). Alternatively, the Kappa statistic measures the proportion of all possible presences and absences predicted correctly after accounting for chance. Kappa values between 0.6 and 0.8 are considered good, and values greater than 0.8 are excellent. Research on other organisms suggests that Kappa is a more robust metric for model performance than ROC, but the two are highly correlated (Manel et al., 2001). Next, we produced ensemble mean and upper and lower CIs for each species at each resolution. Finally, we subtracted the lower continuous CI maps from the upper continuous CI maps to produce maps of the predicted range of CI values.

Functional guilds

We organized species according to the following functional trait or conservation status: Habitat specialization, habitat affiliation, migratory strategy, range size, nesting strategy, diet, threatened status, and population trend. Within those categories, we grouped species within 19 guild categories (herein guilds): Forest specialists, grassland specialists, shrubland specialists, forest affiliates, grassland affiliates, shrubland affiliates, residents, long-distance migrants, short-distance migrants, large-ranged, small-ranged, ground nesters, midstory/canopy nesters (grouped), insectivores, granivores, frugivores, threatened species (and higher conservation status), species with decreasing population trends, and species with stable or increasing population trends (grouped). We used the International Union for Conservation of Nature (IUCN) Habitats Classification Scheme (version 3.1) to classify habitats of affiliate and specialist species, BBS designations of migration and nesting strategy, the IUCN Red List of Threatened Species to assign conservation status, the Elton Traits database for foraging type class, and IUCN population trends from BirdLife International for population trends (BirdLife International, 2013; International Union for Conservation of Nature [IUCN], 2021; Pardieck et al., 2020; Wilman et al., 2014). We defined habitat specialist species as those with only one breeding habitat of major importance, affiliates as those with two or more habitats of importance during the breeding season, short-distance migrants as migratory birds that spend the nonbreeding period primarily in northern Mexico but not in their breeding area, long-distance migrants as those spending the

nonbreeding period primarily south of the US–Mexico border, small-ranged species as those with range sizes below the median range size of all species, and large-ranged species as those with range sizes above the median. Guild membership was not mutually exclusive (data available on Dryad).

Aggregation of single-species maps and comparisons to guild maps

We aggregated all species maps within guilds to compare with previously derived guild maps produced using the same data set and at the same resolutions (Figure 1b). We summed each of our ensemble predicted data layers (mean, upper CI, lower CI, CI difference) from the single-species models to produce four S-SDMs per guild, each with one aggregated species richness estimate per pixel. Then we compared our ensemble model-based stacked species maps to species predictions from RF-derived functional guild maps ($n = 60$). We made these comparisons using raster subtraction (for each guild × resolution pair) and density plots of species counts. We also compared stacked CI maps for each guild to guild prediction interval maps. Based on the minimum and maximum species richness values estimated at any pixel from trees within a RF (Carroll et al., 2022), we expected the guild prediction intervals to differ from the stacked intervals' estimates since the stacked interval estimates were based on 95% CIs.

RESULTS

Ensemble modeling and individual species data layers

Of the total species represented in the BBS in our study area, we successfully modeled 56% (192 of 341 species) at the 5-km resolution, 50% (160 of 317 species) at the 2.5-km resolution, and 28% (80 of 282 species) at the 0.5-km resolution due to data constraints (Carroll et al., 2023). Of the species with at least 100 observations (our modeling cutoff based on our number of predictors), we successfully modeled 96% (192 of 199 species) at the 5-km resolution, 98% (160 of 163 species) at the 2.5-km resolution, and 99% (80 of 81 species) at the 0.5-km resolution—see Appendix S3. Overall, we successfully generated 432 models and 1728 data layers (four data layers per species per resolution; Figures 2 and 3), each representing the probability of presence data for species. Due to convergence issues, we could not model several species with more than 100 observations, so 11 models were unsuccessful. Across all resolutions, all modeled species had TSS, ROC, and Kappa testing values >0.7. Testing values were between 0.80 and 0.99 (Kappa and ROC) at 2.5 and 5 km and 0.80 and 0.98 (Kappa and ROC) at 0.5 km.

Like the individual species prediction maps, our CI maps ranged from 0 to 1. Median predicted probability values for generalist or broadly distributed species were larger than those of specialists or small-ranged species (e.g., Figure 3). The spatial pattern of species CI ranges varied, following each species' predicted distributions. Areas with wider ranges between the upper and lower CI maps represent those species for which the predicted probability is less certain.

Comparisons between stacked and functional guild maps

Many ensemble-based stacked maps had high correlation coefficients with guild maps across resolutions (Figure 4). The overall species richness correlation coefficient was 0.81 at the 5-km resolution, and, across all guilds at 5 km, the median correlation coefficient between stacked maps and guild maps was 0.85 (range 0.53–0.92). All guilds had correlation coefficients >0.5, and five guilds had correlation coefficients ≥0.9 at 5 km. At 2.5 km, the median correlation coefficient for guilds versus the stacked maps was 0.87 (range 0.52–0.94), and the median overall species correlation coefficient was 0.88. At the 2.5-km resolution, the small-ranged guild had the lowest correlation coefficient, and six guilds had correlation coefficients ≥0.9. The 0.5-km-resolution correlation coefficients were lower than the 2.5- and 5-km resolutions, with a median of 0.83 (range 0.33–0.91, excluding frugivores as $n = 0$) for all guilds. The overall correlation coefficient was 0.78, and only forest specialists had correlation coefficients ≥0.9.

Despite some guilds having high correlation coefficients, the stacked maps and guild maps exhibited different species richness estimates. Our stacked maps had eight to 121 (median = 42) fewer species at 5 km, eight to 141 (median = 51) fewer at 2.5 km, and 11 to 139 (median = 85) fewer at 0.5 km compared to guild maps (Figure 5). On average, across guilds, when we modeled species individually and then stacked them, 46% of species were lost at the 5-km resolution, 56% at the 2.5-km resolution, and 78% at the 0.5-km resolution (Figure 5). Unsurprisingly, based on the number of observations that went into each model, the number of species lost at finer resolutions was more pronounced for some guilds, with small-ranged species

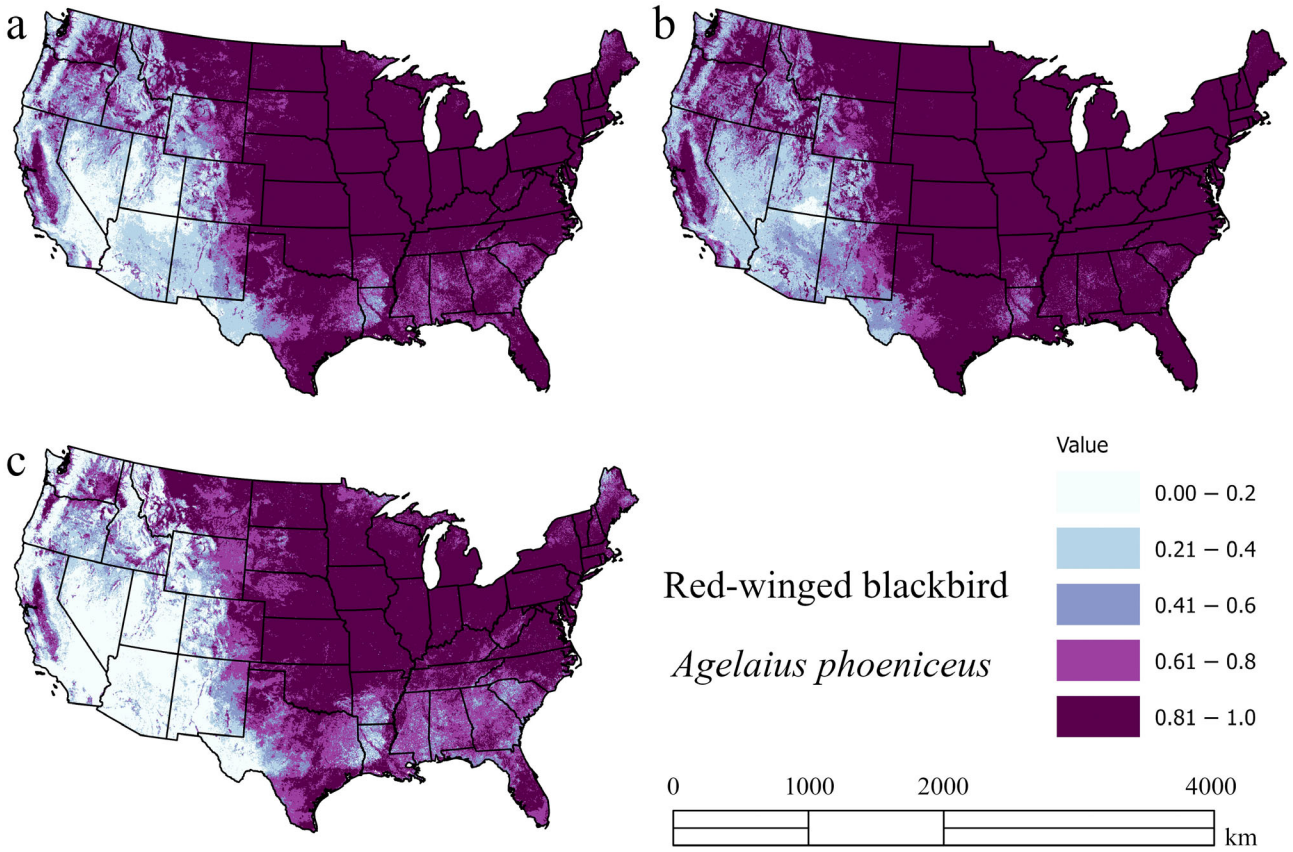

FIGURE 2 Example of the three data layers produced for each species at each resolution. This example illustrates (a) mean, (b) upper CI, and (c) lower CI at 2.5-km resolution for the probability of presence for red-winged blackbirds (*Agelaius phoeniceus*).

(79% lost at 5 km, 92% at 2.5 km) or frugivores (100% at 0.5 km) losing the greatest number of species in stacked maps and large-ranged species losing the lowest number of species (5% at 5 km, 53% at 0.5 km).

Stacked and guild maps also differed in their spatial patterns of predictions across guilds and resolutions. Guild maps had higher estimates of species richness than stacked maps, and these differences were more pronounced between East and West at the 5-km resolution (Figure 6). For example, when subtracting overall species richness based on stacked continuous values from overall guild richness (guild–stacked), values ranged from −10 to 57 species, with a median of 21 species at 5 km. At the 5-km resolution, the West had the largest predictions and the East had the lowest. Prediction differences between overall and stacked richness were more evenly spatially distributed for overall species richness at the 2.5- and 0.5-km resolutions (Figure 6). Even with differences across overall species richness at the guild level minus the stacked, our stacked still had positively skewed differences for all resolutions and methods.

We generated stacked CI range data layers and compared guild minus stacked interval data layers for each guild. For overall species richness, the stacked CIs ranged from 0 to 84 species (median = 22 species), 0 to 52 species (median = 18 species), and 0 to 21 species (median = 9 species) for the 5-, 2.5-, and 0.5-km resolutions, respectively. When we subtracted overall species richness stacked CIs from the predictive guild intervals, these values ranged from −25 to 72 species (median = 39 species), −8 to 54 species (median = 26 species), and −1 to 25 species (median = 13 species) for the 5-, 2.5-, and 0.5-km resolutions, respectively. There were some spatial differences between guild prediction intervals and stacked CIs as well, with larger intervals in northern forests. However, unlike the richness comparisons (guild minus stacked), the spatial differences between CIs and prediction intervals did not differ appreciably across resolutions.

DISCUSSION

Our ability to model and map almost 200 bird species across the conterminous United States demonstrates that mapping some individual species with high accuracy and spatial confidence intervals at conservation management-relevant resolutions (≤5 km) is possible. However, data

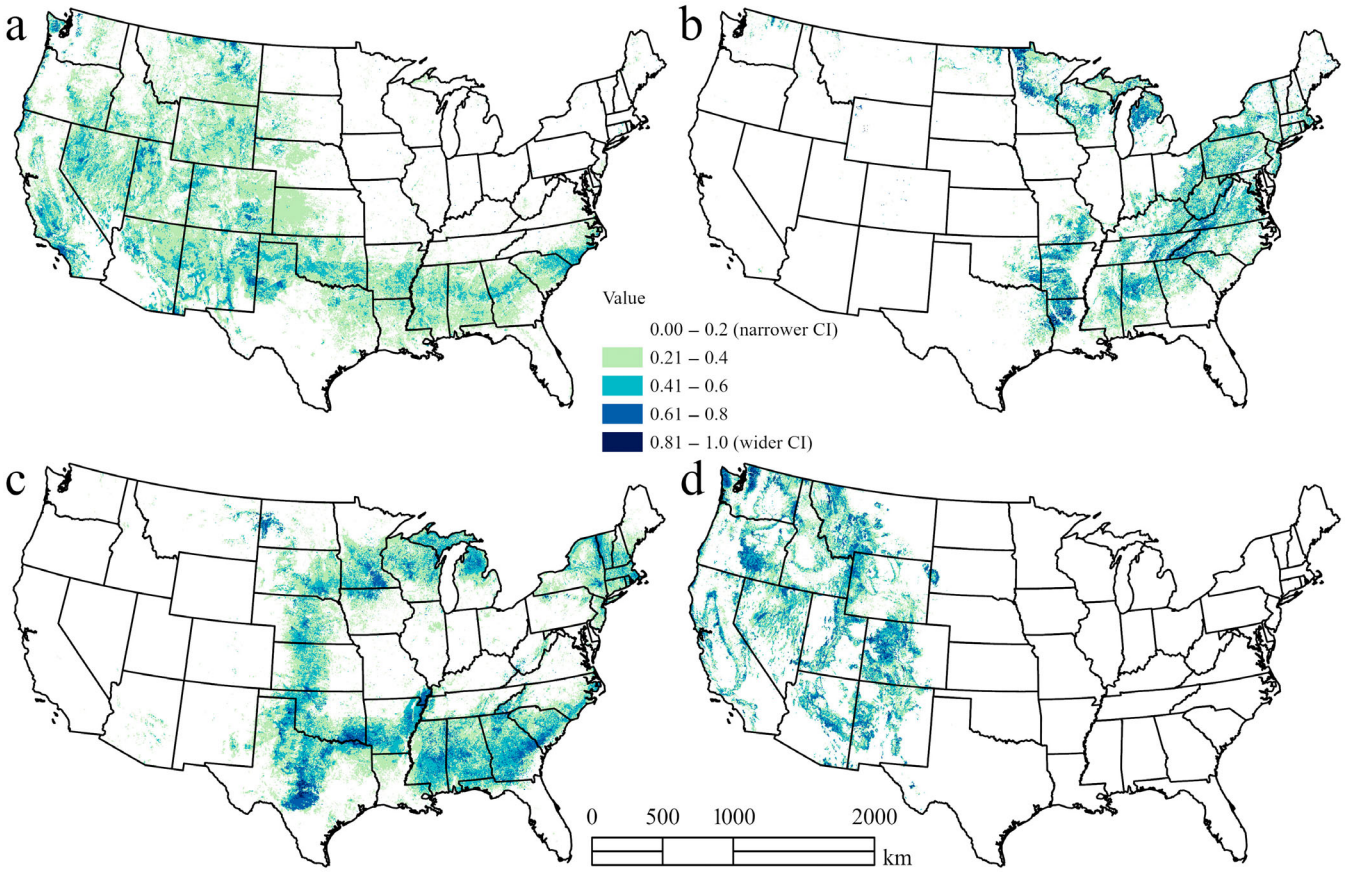

FIGURE 3 Example of CI range (upper minus lower) for (a) American robin (*Turdus migratorius*), (b) black-and-white warbler (*Mniotilta varia*), (c) field sparrow (*Spizella pusilla*), and (d) western tanager (*Piranga ludoviciana*) at 2.5-km resolution. Here, low values/lighter colors indicate narrow CIs.

scarcity issues remain for some species of conservation concern given that we could only model between 28% and 56% of species in the BBS at management-relevant resolutions (0.5–5 km, respectively). For the species we could model, our species maps can support fine-scale decision-making across the United States, either alone for single-species conservation or paired with guild maps. Furthermore, having CI maps is critical for both management application and model performance evaluation, as understanding the uncertainty of ecological models is a requirement of informed conservation (Gould et al., 2014). Importantly, model performance is not uniform across our study region, so even for models with high-accuracy scores, there may be regions of poor performance. Our CI maps provide managers the opportunity to examine how well these models perform in a specific region before using them in conservation applications. Having such maps is an advantage because it gives managers full knowledge of the accuracy of predictions within different species distribution areas, which is a critical but often overlooked component of conservation decision-making.

Ensemble modeling of individual species

Ensemble modeling enabled us to predict individual species distributions better than we could have with other methods (Hao et al., 2019, but see Hao et al., 2020) and was especially important for modeling species distribution with data limitations at fine resolutions—which is often necessary for management planning that occurs at the level of counties or state-owned land. After our initial cutoff of ≥100 observations, and despite our strong overall model performance metrics, a few species were excluded from analysis at each resolution due to data limitations or poor model performance. Unexpectedly, some species with poor model performance were not rare, endangered, small-ranged, or from a species-poor guild. Instead, several species classified as least concern showed poor model performance and were thus excluded at one or more resolutions. A likely explanation for this is that our predictor variables lacked sufficient variability to capture important habitat features at this resolution. This idea is supported by the fact that we successfully modeled some species that were excluded at 5 km at finer resolutions (e.g., *Toxostoma rufum*, brown thrasher; *Peucaea*

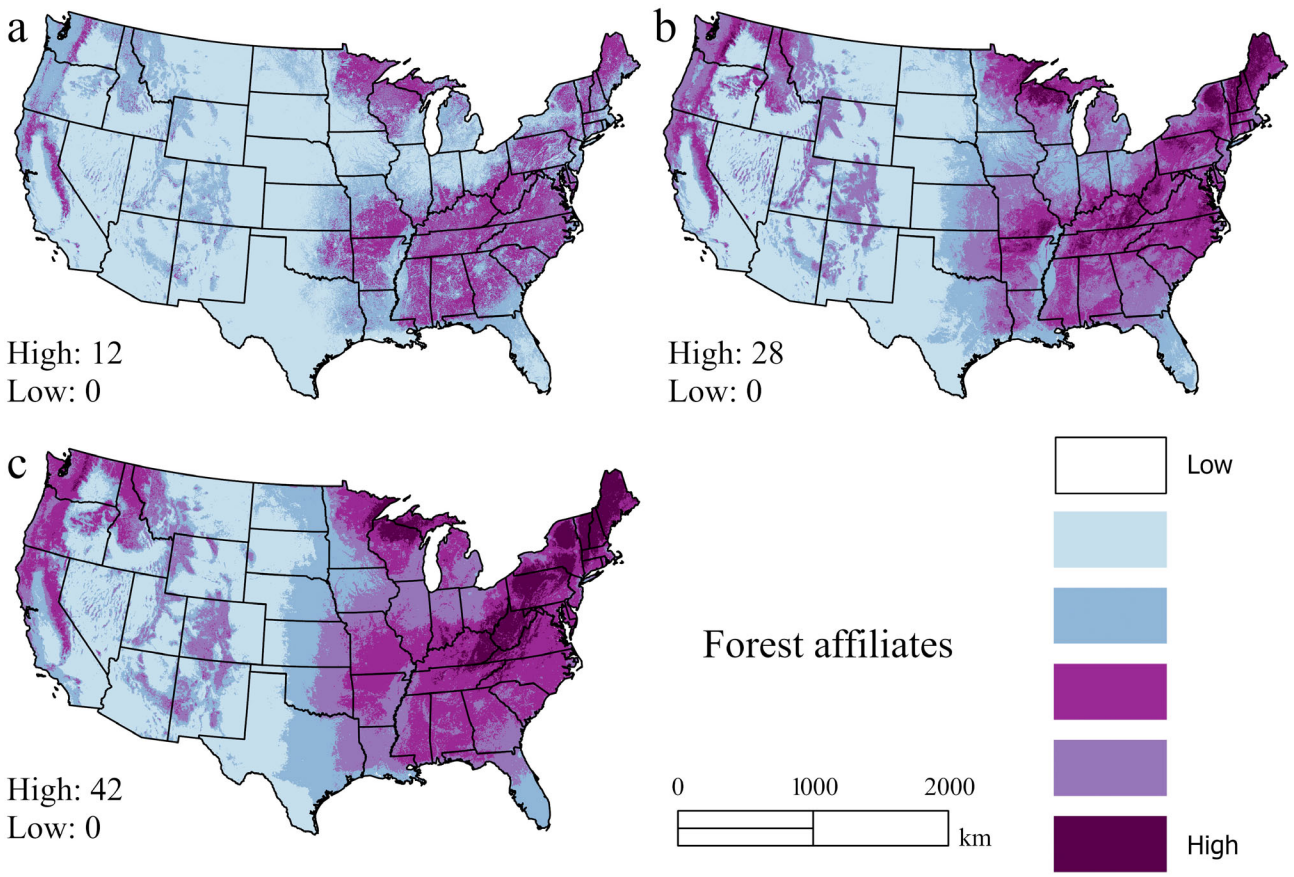

FIGURE 4 Examples of stacked maps for forest affiliates at resolutions of (a) 0.5, (b) 2.5, and (c) 5.0 km.

cassinii, Cassin's sparrow). Other species were excluded across all resolutions, indicating that the suite of variables used as predictors did not capture one or more important factors determining these species' distributions. Many of our predictor variables were remotely sensed and, thus, biased toward forest canopy features. Using the remotely sensed products we included, it may be challenging to model distribution for species that (1) use a wide variety of hard-to-capture habitat features (e.g., snags), (2) occupy areas with lower density of BBS routes (e.g., Southwest United States), or (3) are prone to large population swings in unpredictable conditions. In these instances, alternative mapping approaches or additional data (e.g., eBird) are likely necessary to support fine-scale distribution maps. There may be future opportunities to produce maps for excluded species, poorly represented species (e.g., waterfowl), or year-round distributions by combining BBS and eBird.

Comparisons between stacked maps and guild maps

Correlation coefficients were generally high across all comparisons and resolutions, suggesting that most species richness patterns were preserved during stacking. The high correlation coefficients also support the assertion that the patterns of species predictions were consistent among the different modeling approaches we used. Thus, for some regions, stacking species maps to model guild richness may be effective, but identifying where stacked and guild maps diverge is critical for any conservation applications. Depending on the research question and data availability, there are instances where stacking individual species provides the best products available for conservation, given data quality, methods used, and spatial resolution. For instance, in most global assessments, stacked map approaches are commonly used in conservation mapping applications, for example, Map of Life (https://mol.org/) and IUCN global richness maps (https://www.iucnredlist.org), and are often the only available conservation products. However, we found enough differences between stacked maps and guild maps to warrant concerns over using the stacked maps to represent guilds in conservation applications where guild map data are available, despite high correlation coefficients, but see Distler et al. (2015).

We found that species richness values differed strongly and regionally between stacked and guild richness maps. As a whole, findings regarding the over- and

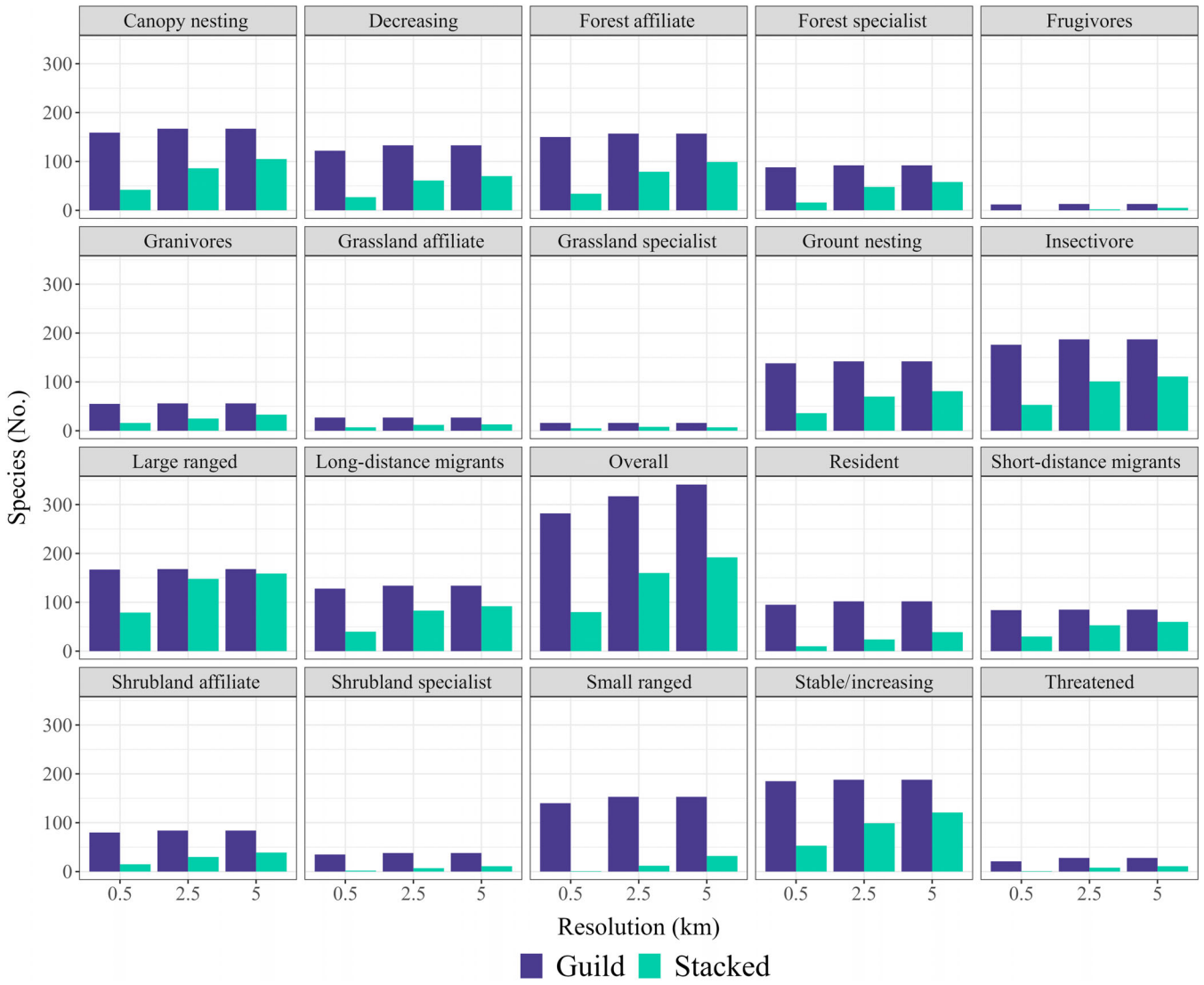

FIGURE 5 Number of species in each guild in stacked maps and guild maps.

underpredictions produced by stacking individual maps versus modeling guilds are mixed (Guisan & Rahbek, 2011; Mateo et al., 2012, but see D'Amen et al., 2015; Lehmann et al., 2002), but we generally expected that stacked maps would underpredict species richness (Figure 1a). We found both under- and overpredictions in our stacked maps in different regions, but overall, underpredictions of species richness were more prevalent and of a larger magnitude than overpredictions. In many of our maps, we found regions where the stacked guild map predicted higher species richness than the continuous guild map and regions where it predicted lower richness (Figure 6). The observed pattern of an overall positive skew in the difference maps was consistent across guilds, including guilds with very few species (e.g., frugivores). The trend toward overestimating species richness suggests that important community assemblage information (e.g., competitive exclusion) is missed during stacking.

Stacked and guild accuracy comparison

Our S-SDM and guild model performance values were not directly comparable, but we found differences in spatial patterns for all guilds and overall species richness when comparing stacking versus guild methods. Similarly, a direct comparison of BIOMOD confidence intervals to RF prediction intervals (based on the range of values each tree in a forest produced for each pixel) is challenging. Comparisons of the spatial patterns indicated that methods performed similarly regionally, with the Western United States having lower prediction accuracy and wider CIs. Despite these

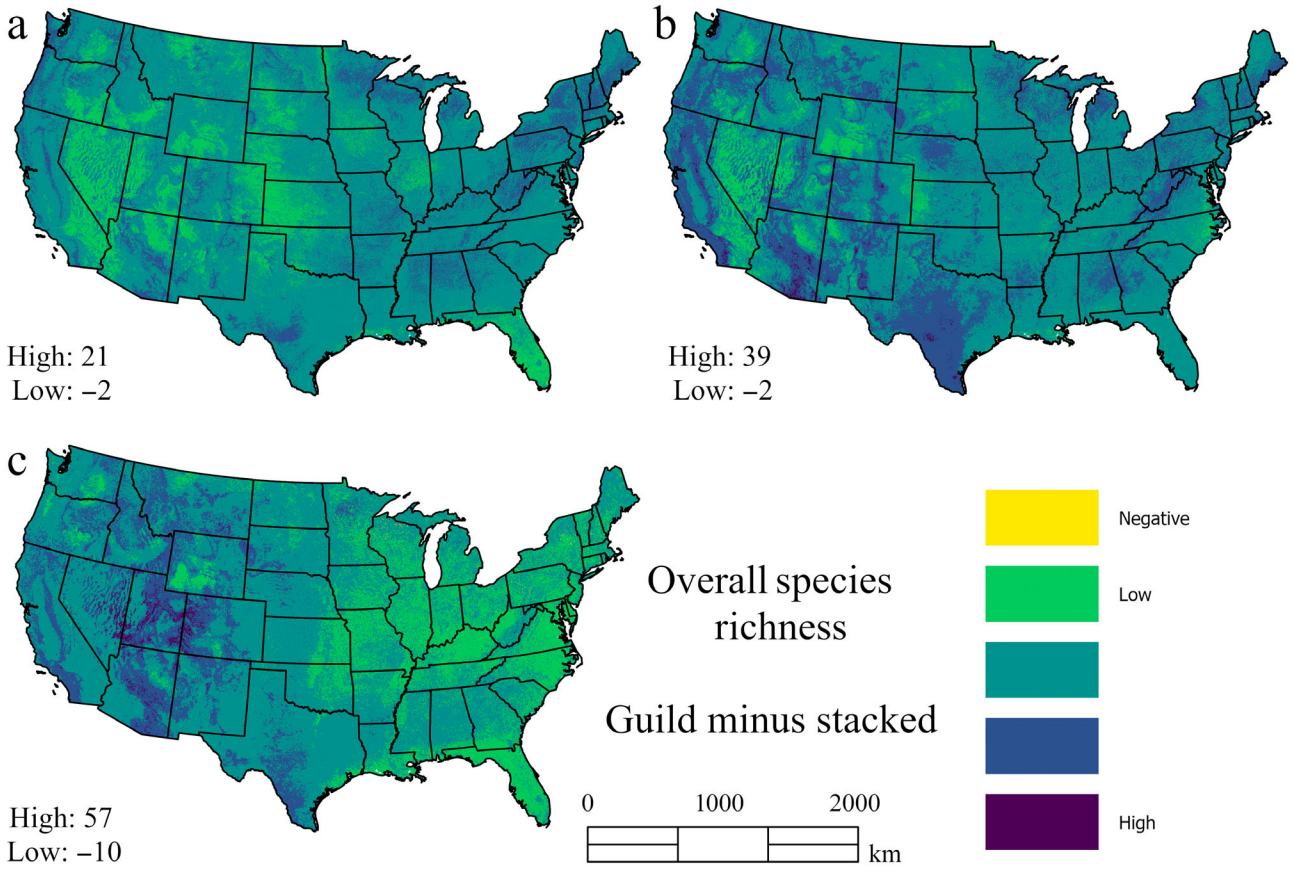

FIGURE 6 Overall guild richness minus stacked overall richness at (a) 0.5 km, (b) 2.5 km, and (c) 5 km.

differences, it is likely that the guild models more accurately represent species richness because they capture actual community assemblages better than stacked maps, which are based on the probability of presence.

Conservation implications and recommendations

In evaluating the performance of stacked maps against guilds, the differences we found were consistent with some critiques of stacked maps for other taxa (Pineda & Lobo, 2009) and reiterate the distinct contribution of guild models that capture community structure and broader species pools for species richness estimates. Guild maps incorporate more species' distributions—such as rare species dropped in individual species models—and have well-defined spatial accuracies. Thus, based on the differences between stacked and guild maps, we recommend relying on guild maps (e.g., Carroll et al., 2022) over stacked maps for community-level conservation while using individual species maps (e.g., those produced

TABLE 2 Conservation application examples for different mapping approaches.

	Individual species maps			Stacked maps			Guild maps		
Conservation application	**0.5 km**	**2.5 km**	**5 km**	**0.5 km**	**2.5 km**	**5 km**	**0.5 km**	**2.5 km**	**5 km**
Single-species conservation—rare or local species		X	X					X	X
Single-species conservation—common or widespread species	X	X							
Single-species conservation—most applications		X							
Overall community-level conservation								X	X
Most guild-specific conservation								X	

Note: All maps should be used with their prediction or CI maps at the same resolution.

here) for species-targeted conservation. The differences between stacked and guild maps illustrate the importance of the inherent tradeoffs of spatial resolution versus accuracy, determining the ecological level of study (e.g., species or community), and tailoring the type of map and production method(s) used to specific conservation goals.

Our results inform recommendations for practitioners using the stacked maps for conservation applications (Table 2). First, we recommend examining model performance to select the finest-resolution maps with high model performance, thereby balancing accuracy and resolution. Second, we recommend that practitioners using the individual species maps reference the CI maps (Figures 2 and 3) before implementing regional conservation. It is essential to understand that there is inherent uncertainty in model predictions, which we captured in the CI maps. Together, our species maps and guild maps provide distribution and uncertainty data across biological scales (individuals to communities) for the conterminous United States to support management and conservation. We recommend using them together in complementary ways rather than separately.

AUTHOR CONTRIBUTIONS

Anna M. Pidgeon and Volker C. Radeloff conceived the ideas. Kathleen A. Carroll designed the methodology, analyzed the data, and wrote the initial draft. All authors contributed data, contributed critically to the drafts, and gave final approval.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Carroll et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.gb5mkkwsk. Input data are publicly available, and sources are described in Appendix S1.

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SUPPORTING INFORMATION

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

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