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Habitat heterogeneity captured by 30-m resolution satellite image texture predicts bird richness across the United States

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Abstract. Species loss is occurring globally at unprecedented rates, and effective conservation planning requires an understanding of landscape characteristics that determine biodiversity patterns. Habitat heterogeneity is an important determinant of species diversity, but is difficult to measure across large areas using field-based methods that are costly and logistically challenging. Satellite image texture analysis offers a cost-effective alternative for quantifying habitat heterogeneity across broad spatial scales. We tested the ability of texture measures derived from 30-m resolution Enhanced Vegetation Index (EVI) data to capture habitat heterogeneity and predict bird species richness across the conterminous United States. We used Landsat 8 satellite imagery from 2013–2017 to derive a suite of texture measures characterizing vegetation heterogeneity. Individual texture measures explained up to 21% of the variance in bird richness patterns in North American Breeding Bird Survey (BBS) data during the same time period. Texture measures were positively related to total breeding bird richness, but this relationship varied among forest, grassland, and shrubland habitat specialists. Multiple texture measures combined with mean EVI explained up to 41% of the variance in total bird richness, and models including EVI-based texture measures explained up to 10% more variance than those that included only EVI. Models that also incorporated topographic and land cover metrics further improved predictive performance, explaining up to 51% of the variance in total bird richness. A texture measure contributed predictive power and characterized landscape features that EVI and forest cover alone could not, even though the latter two were overall more important variables. Our results highlight the potential of texture measures for mapping habitat heterogeneity and species richness patterns across broad spatial extents, especially when used in conjunction with vegetation indices or land cover data. By generating 30-m resolution texture maps and modeling bird richness at a near-continental scale, we expand on previous applications of image texture measures for modeling biodiversity that were either limited in spatial extent or based on coarse-resolution imagery. Incorporating texture measures into broad-scale biodiversity models may advance our understanding of mechanisms underlying species richness patterns and improve predictions of species responses to rapid global change.

Key words: avian biodiversity; Breeding Bird Survey; conservation; Enhanced Vegetation Index; heterogeneity–diversity relationship; intermediate heterogeneity hypothesis; Landsat 8; satellite remote sensing; species-energy theory.

Introduction

Global change is causing precipitous declines in biodiversity (IPBES 2019), with current extinction rates between 100 and 1,000 times higher than the historic background rate (Pimm et al. 2014, Ceballos et al. 2017). Addressing this conservation challenge requires accurate assessments of the factors that determine broad-scale patterns of species diversity (Pereira et al. 2013, Jetz et al. 2019). Vegetation heterogeneity is an important determinant of species distributions and richness (MacArthur 1964), with similar or higher explanatory power than available energy or climatic factors for predicting biodiversity (Bohning-Gaese 1997, Kerr and Packer 1997, Stein et al. 2014). Heterogeneity can positively promote diversity by expanding niche space in structurally complex environments (Tews et al. 2004), increasing access to microhabitats that provide refugia from adverse conditions and stochastic events (Keppel et al. 2012, Robinson et al. 2016, Elsen et al. 2020), and increasing isolation leading to genetic divergence and speciation (Vuilleumier 1969, Graves 1985) through mechanisms related to niche conservatism (Pyron et al. 2015).

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Quantifying environmental heterogeneity across large areas using field-based methods is costly and logistically challenging. Satellite remote-sensing data provide an opportunity to generate heterogeneity metrics at regional to global extents (Nagendra et al. 2013, Rocchini et al. 2015). Remotely sensed data have the advantage of providing wall-to-wall mapping of continuous measures of landscape characteristics, at resolutions relevant for both species and land management (Kerr and Ostrovsky 2003, Kennedy et al. 2014). Measures of heterogeneity derived from satellite imagery, such as topographic and land cover metrics, effectively predict large-scale patterns of biodiversity (Rahbek and Graves 2001, Coops et al. 2009). However, these common measures of environmental heterogeneity have limitations. For instance, topographic indices based on digital elevation models are often used as proxies for variability in vegetation and temperature, but are static, indirect measures of habitat that cannot account for temporal dynamics (Rahbek and Graves 2001, Ruggiero and Hawkins 2008). Similarly, categorical land cover classifications provide important information regarding between-class heterogeneity (Boulinier et al. 2001, van Rensburg et al. 2002), but broadly aggregate habitat types and ignore variability within land cover classes (Herold et al. 2008).

An alternative approach is to directly quantify environmental heterogeneity using the spectral properties of satellite imagery. Image texture is the visual effect produced by the spatial distribution and variation of spectral values across the pixels of an image (Haralick et al. 1973, Hall-Beyer 2017). Image texture analysis holds particular promise for quantifying within-habitat variability in structurally complex landscapes (Kayitakire et al. 2006, Wunderle et al. 2007, Wood et al. 2012). In local and regional studies, texture measures derived from medium-resolution (30-m) satellite imagery effectively predicted bird species richness within various habitat types, including forests (Culbert et al. 2012, Suttidate 2016), desert-scrub ecosystems (St-Louis et al. 2009, 2014), and grasslands (Bellis et al. 2008, Culbert et al. 2012). Coarse-resolution (250-m) image texture measures derived from MODIS satellite imagery also helped explain spatial variation in bird richness across the conterminous United States. (Tuanmu and Jetz 2015). However, there is currently a lack of studies using medium-resolution texture measures to describe bird richness patterns at macroecological scales, which is unfortunate, because textures derived from 30-m imagery can capture finer-scale heterogeneity of breeding habitats, which strongly influence the distribution and abundance of birds (Hepinstall and Sader 1997, St-Louis et al. 2009, Culbert et al. 2012).

Texture measures derived from vegetation indices, such as the normalized difference or the enhanced vegetation index (NDVI, EVI), are effective predictors of bird species richness (St-Louis et al. 2009, Ozdemir et al. 2018). By quantifying the "greenness" of spectral imagery, vegetation indices characterize energy available through photosynthesis and are strongly and positively correlated with net primary productivity (Paruelo et al. 1997, Sims et al. 2006). Thus, such indices can be used to test the species-energy theory, which predicts that regions with higher overall productivity can support more species and higher total abundances of individuals, due to increased quantity and availability of resources (Wright 1983, Currie 1991). While vegetation indices are strong predictors of bird species richness at regional to continental scales in their own right (Bailey et al. 2004, Evans et al. 2006), deriving texture measures from these indices provides additional information about spatial patterns of energy availability and habitat heterogeneity (St-Louis et al. 2009, Tuanmu and Jetz 2015). Thus, the species-energy theory and heterogeneity–diversity hypotheses are not mutually exclusive; the challenge lies in determining their relative importance and complementarity in explaining patterns of species diversity (Hurlbert and Haskell 2003, Kreft and Jetz 2007, Coops et al. 2009).

Bird species richness is an effective indicator of complex, community-level response to environmental heterogeneity (Davies et al. 2007, Veech and Crist 2007). Birds exhibit a wide range of space-use behaviors (Leonard et al. 2008) and habitat associations across multiple spatial scales (Warren et al. 2005, Mitchell et al. 2006). Birds are also facing dramatic global declines (Gaston et al. 2003, IUCN 2019). In North America, 37% of bird species are under high risk of extinction without significant conservation action (NABCI 2016). The ready availability of bird richness and distribution data for North America provides an opportunity to explore continental-scale relationships between species richness and remotely sensed heterogeneity metrics. By doing so, we can improve our understanding of large-scale landscape characteristics that may be driving or limiting factors for birds and other species (Flather and Sauer 1996, Hudson et al. 2017).

Our primary goal was to develop a suite of 30-m resolution texture measures based on Landsat 8 EVI imagery as direct measures of vegetation heterogeneity and to evaluate whether they increase explanatory power of bird richness models at a near-continental scale. We predicted that our EVI-based heterogeneity metrics would positively correlate with bird species richness, supporting a positive heterogeneity–diversity relationship. Our second goal was to assess whether EVI-based texture measures would improve the overall explanatory power of bird richness models compared to models based on EVI alone. Because habitat heterogeneity and available energy both influence species richness, we predicted that texture measures would have significant positive effects on bird richness independent of the influence of EVI. Our third goal was to evaluate the relative influence of texture on bird richness patterns compared with productivity and other commonly used indices of environmental heterogeneity based on topography and land cover. Again, we predicted that a texture measure would increase the fit of models that also included topographic and land cover metrics, because EVI-based textures provide direct measures of environmental heterogeneity and can capture variation within land cover classes.

Methods

Image texture measures

We calculated a suite of texture measures based on Landsat 8 EVI composite images available in Google Earth Engine (GEE; *available online*).[2] The 30-m resolution, 8-d EVI composite product (GEE Image ID LANDSAT/LC8_L1T_8DAY_EVI) was generated from Level L1T orthorectified scenes, using top-of-atmosphere (TOA) reflectance that accounts for solar angle and seasonal variation in Earth–Sun distance (Chander et al. 2009). The EVI was calculated based on three bands (near-infrared, red, and blue) of each image (Huete et al. 2002). We selected EVI over NDVI because it is less sensitive to soil background and atmospheric effects and less prone to saturation at high levels of biomass (Huete et al. 2002). To create a smooth composite image for texture analysis, we extracted 90th percentile EVI values from available images between May–September during 2013–2017, thereby characterizing peak greenness of vegetation during the summer growing season while excluding spuriously high EVI values (Culbert et al. 2009, Tuanmu and Jetz 2015). We masked pixels covered by permanent water bodies using a static water mask also derived from Landsat imagery (Hansen et al. 2013).

In image texture analysis, central pixels within a moving window are assigned a value based on the spectral variability of neighboring pixels (Hall-Beyer 2017). First-order textures are statistical summaries (e.g., mean, variance) of pixel spectral values within the moving window, while second-order textures are based on the gray-level co-occurrence matrix (GLCM) and thus take into account the spatial arrangement and relationships among neighboring pixels (Haralick et al. 1973). Using GEE, we calculated one first-order and six second-order texture measures from the 90th percentile EVI composite (see Table 1 for list of texture measures and descriptions), which we selected based on their performance in predicting local and regional bird richness patterns (St-Louis et al. 2009, Culbert et al. 2012). We used a moving window size of 5 × 5 pixels (2.25 ha), an area large enough to encompass one or more typical breeding bird territories (Leonard et al. 2008, Jones 2011) while capturing relatively fine-resolution landscape features. We selected a single moving window size for our analysis because texture measures across varying window sizes tend to be highly correlated and have similar relationships with bird richness (St-Louis et al. 2006, Culbert et al. 2012).

[2] http://earthengine.google.org

Ancillary environmental variables

To test how well texture measures predict bird richness compared to more commonly used abiotic and biotic predictors of biodiversity, we calculated two metrics based on topography and three metrics based on land cover. We analyzed elevation data from the National Elevation Dataset (NED), which provides seamless elevation coverage for the conterminous United States at 1 arc-second (~30 m) resolution (GEE Image ID USGS/NED). We also derived the terrain ruggedness index (TRI) from the NED, which quantifies topographic heterogeneity by taking the square root of the sum of squared differences between an elevation pixel and the eight pixels surrounding it (Riley et al. 1999). To characterize land cover composition, we analyzed 30-m resolution 2011 National Land Cover Data, also derived from Landsat imagery (NLCD; GEE Image ID USGS/NLCD). We focused on three dominant land cover classes that provide habitat for terrestrial birds: forest (deciduous, evergreen, and mixed classes combined), shrubland, and grassland cover.

Breeding bird data

The North American Breeding Bird Survey (BBS; Sauer et al. 2017) is a long-term, annual survey of ~3,000 routes across the United States and Canada. Volunteer observers record all birds seen and heard during 50 3-minute counts spaced evenly (0.8 km apart) along each 39.4-km route. Surveys are conducted during the height of the breeding season between May and July, with additional guidelines for time of day and weather conditions intended to increase detectability and reduce biases in the data (Robbins et al. 1986). We removed surveys of non-randomly established routes, surveys conducted in inclement weather or outside of established date and time ranges, and surveys that did not follow other BBS sampling protocols based on the BBS quality codes. We also removed surveys conducted by first-year observers on a given route to reduce potential observer effects (Kendall et al 1996).

We restricted our analyses to data collected during 2013–2017, i.e., all BBS data collected after the launch of Landsat 8 that were available at the time we conducted our analysis. For each BBS survey route within the conterminous United States, we calculated route-level species richness as the cumulative number of unique species observed during the 5-yr period. We excluded rare species with insufficient data (<30 observations), species not adequately sampled by diurnal transect surveys (i.e., raptors and crepuscular species), and species associated with habitats under-sampled by BBS route locations (i.e., marine, coastal, and freshwater species). After pre-processing, 2,749 BBS survey routes remained for analysis (Fig. 1), with a total of 535,676 observations of 332 bird species (Appendix S1: Table S1). We analyzed total bird richness and richness of habitat

TABLE 1. Image texture measures, descriptions, and formulae.

Texture type† and name	Description	Formula‡
First-order measure		
Standard deviation	dispersion of pixel values	$\sqrt{\frac{\sum \lvert x-\bar{x}\rvert^2}{n}}$
Second-order measures of "contrast"		
Contrast (also called sum of squares variance)	exponentially weighted difference in values of adjacent pixels	$\sum_{n=0}^{N-1} n^2 \left\{ \sum_{i=1}^{N} \sum_{j=1}^{N} p(i,j) \right\}$
Dissimilarity	linear difference in values of adjacent pixels	$\sum_{n=0}^{N-1} n \left\{ \sum_{i=1}^{N} \sum_{j=1}^{N} p(i,j) \right\}$
Homogeneity (also called inverse difference moment)	similarity of values between adjacent pixels; smoothness of the image.	$\sum_i \sum_j \frac{1}{1+(i-j)^2} p(i,j)$
Second-order measures of "orderliness"		
Entropy	disorderliness (or "randomness") in spatial distribution of pixel values.	$-\sum_i \sum_j p(i,j) \log(p(i,j))$
Uniformity (also called angular second moment)	orderliness in spatial distribution of pixel values	$\sum_i \sum_j \{p(i,j)\}^2$
Second-order descriptive statistic		
Correlation	linear dependency of values on those of neighboring pixels (0 = uncorrelated, |1|=perfectly correlated)	$\frac{\sum_i \sum_j (ij) p(i,j) - \mu_x \mu_y}{\sigma_x \sigma_y}$

†FromHall-Beyer (2017).
‡FromHaralick et al. (1973).

specialists within three broad habitat types for birds: forest, grassland, and shrubland (Appendix S1: Table S1). We defined habitat specialists as birds known to primarily occur in only one habitat type during the breeding season, and determined specialization based on habitat designations of major importance from BirdLife International (IUCN 2019) and detailed species accounts from Birds of North America (Rodewald 2015). Of the 332 species included, we identified 95 forest specialists (29% of species evaluated), 16 grassland specialists (5%), and 38 shrubland specialists (11%). Some species were not affiliated with any of these three habitats, or were affiliated with one or more habitats but were not identified as specialists.

Statistical analysis

To relate our remotely sensed data to bird species richness, we calculated the mean value of each environmental predictor within 19.7 km of the centroid of each BBS route (sensu Flather and Sauer 1996, Pidgeon et al. 2007). We selected a radius one-half the length of a BBS route to ensure that each sampled landscape would contain the entire BBS route, and defined route centroids as the center of the minimum bounding rectangle encompassing each route. Because BBS richness data conformed closely to a normal distribution (results not shown), we used linear regressions to relate environmental predictors to bird richness. We included both linear and quadratic terms of predictors in regression models to account for potential nonlinear relationships between bird richness and environmental variables. For all analyses, we fitted models for all species combined and for each species group (forest, grassland, and shrubland).

To test the performance of texture in predicting bird richness, we first evaluated each texture measure individually in single-texture models, including both linear and quadratic terms. We used coefficient estimates to assess the strength and direction of relationships between each texture and bird richness, and adjusted R^2 values to evaluate the explanatory power of models. We also used results of single-texture models to inform which textures to include in subsequent multivariate analyses. Because different texture measures represent different landscape characteristics and might complement each other to predict bird richness, we also tested models incorporating multiple textures. However, because many texture measures are correlated (Baraldi and Parmiggiani 1995), we checked for collinearity by calculating pairwise Spearman's correlation coefficients. We found strong correlations among some textures (Appendix S1: Fig. S1), and thus only included uncorrelated textures ($|r| < 0.7$) in multiple texture models.

To assess whether EVI-based textures of habitat heterogeneity complement EVI as a measure of available energy in predicting bird richness, we assessed a model including only EVI as a predictor. We then ran a series of multiple linear regression models combining EVI with one or more textures as predictors. Again, we first checked for collinearity and did not find strong correlations between EVI and our suite of textures ($|r|$ range = 0.1–0.4; Appendix S1: Fig. S1). We evaluated adjusted R^2 values to compare the predictive performance of models with and without textures. Using the best performing model based on the adjusted R^2, we produced predictive maps of total breeding bird richness and for habitat specialists within each habitat group.

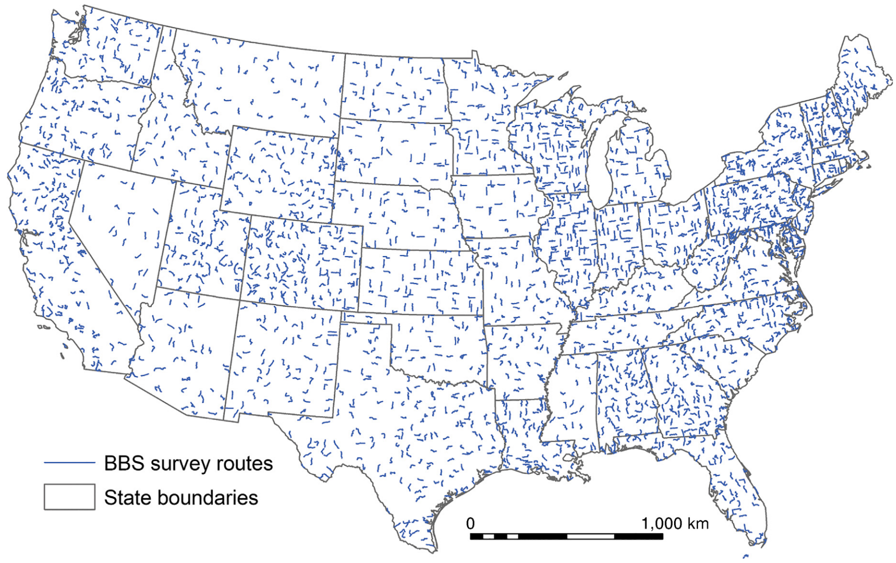

Fig. 1. Map of the conterminous United States, illustrating Breeding Bird Survey (BBS) route locations (2013–2017).

To evaluate the relative importance of texture compared to more commonly used measures of environmental heterogeneity in predicting bird richness, we fitted a global model including our two topographic metrics (elevation, TRI), three land cover metrics (proportion of forest, grassland, and shrubland cover), productivity (EVI), and a single-texture measure (dissimilarity). We opted to use dissimilarity because it was the best predictor in single-texture models for total species richness and is an intuitive metric of habitat heterogeneity. We centered and standardized all predictors to allow for unbiased comparisons of effect sizes. We then generated a set of linear regressions including all possible combinations of these seven predictor variables and their quadratic terms. Because of the large number of variables in the global model, we ranked models using the Bayesian information criterion (BIC), which penalizes over-parameterized models. Prior to fitting models, we assessed collinearity among predictors (Appendix S1: Fig. S2). The highest correlation was $r = -0.72$, between EVI and proportion of shrubland cover, with all other correlations $|r| < 0.7$. As an additional collinearity check, we calculated variance inflation factors (VIFs) for each predictor in top-ranked models and removed predictors with VIFs above a cut-off value of 10 (O'Brien 2007). We used adjusted R^2 values to assess the total explanatory power of top-ranked models, and evaluated the contribution of each variable in predicting bird richness by plotting their effect sizes (standardized regression coefficients) with 95% confidence intervals. To further evaluate the relative importance of predictors, we used hierarchical partitioning to assess the independent and joint contributions of each predictor to overall variance explained (Chevan and Sutherland 1991). In hierarchical partitioning analysis, joint contributions represent the explanatory power of each predictor that cannot be disentangled from other predictors due to multicollinearity, while independent contributions represent the variance uniquely explained by each predictor (Mac Nally 2000).

Last, we checked for potential biases arising from spatial autocorrelation of BBS route locations by calculating Moran's I and analyzing model residuals in correlograms using 500 permutations. All statistical analyses were performed in R version 3.5.1 (R Core Team 2018; see Appendix S1: Table S2 for list of R packages used).

Results

Texture characterization of habitat heterogeneity

Texture measures based on Landsat 8 EVI imagery reflected general patterns of vegetation productivity across the conterminous United States, but provided additional information on its spatial patterning (Fig. 2). Texture measures captured differences and transitions between land cover types, as well as within-habitat heterogeneity categorized as homogeneous by land cover classes (Fig. 3). For example, in a heavily forested landscape in the central Appalachian region, texture measures were highest in mixed forests and at transitions between forest types, but they also captured heterogeneity in areas classified as homogeneous deciduous forest (Fig. 3a). In the mixed-grass Moreau Prairie of South Dakota, texture measures captured heterogeneity in vegetation among rolling plains and buttes in a landscape predominantly classified as homogeneous grassland (Fig. 3b). Similarly, in a desert-scrub landscape in the Chihuahuan desert, texture measures revealed

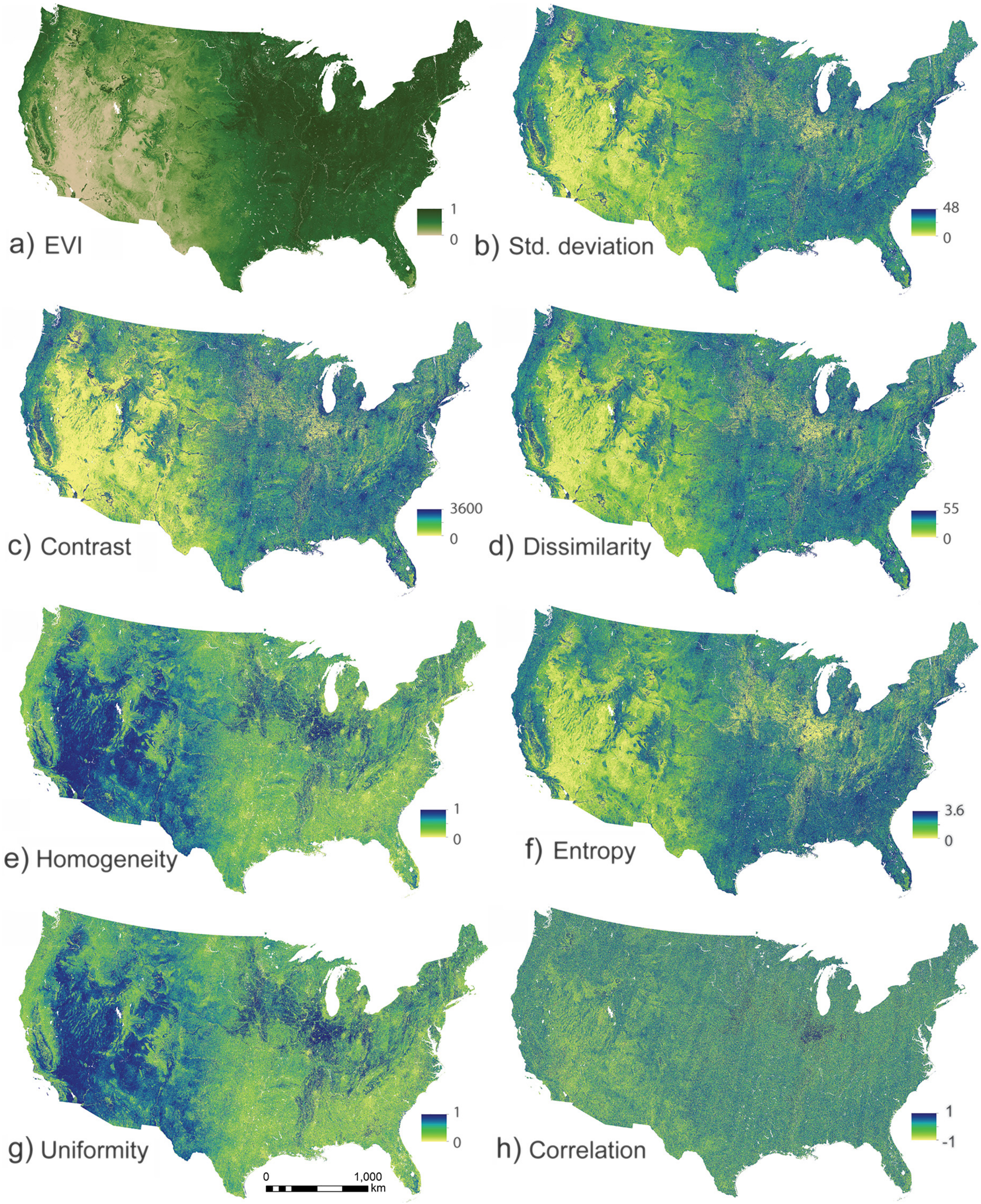

FIG. 2. Maps of the conterminous United States, showing (a) peak greenness enhanced vegetation index (EVI) based on Landsat 8 satellite imagery, and patterns of habitat heterogeneity captured by (b) first-order standard deviation texture and (c–h) six second-order textures derived from the EVI layer shown in panel a. See Table 1 for texture descriptions.

vegetation heterogeneity in and around drainages west of the Pecos River, within areas classified as homogeneous shrubland (Fig. 3c). In addition to the heterogeneity of natural habitats, texture measures captured heterogeneity in human-modified landscapes. For example, in the Central Valley of California, texture measures highlighted heterogeneity of green spaces within suburban areas, along road corridors, and in edge habitats

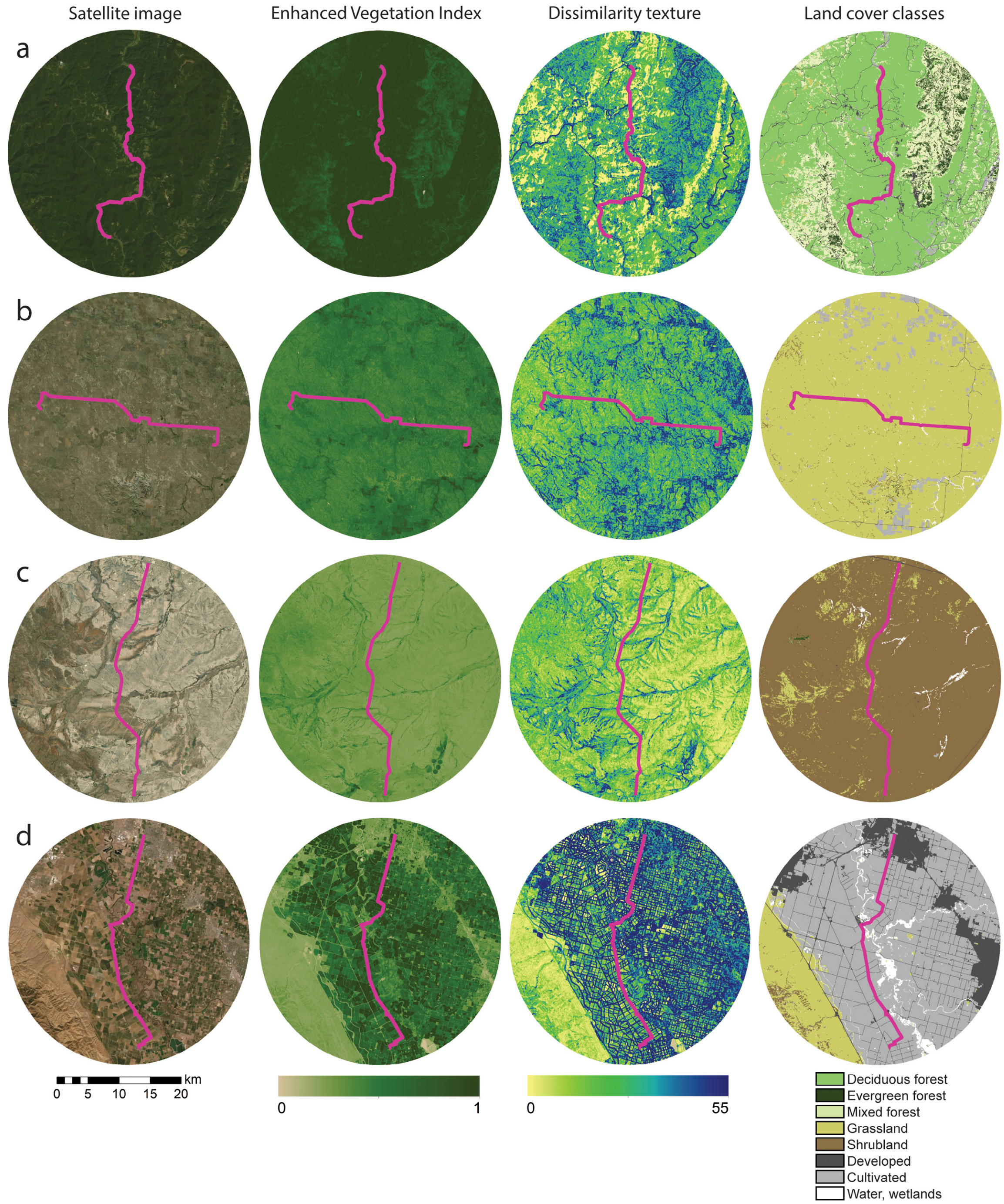

FIG. 3. Data layers corresponding to four sampled landscapes (a–d), illustrating different features of habitat heterogeneity captured by texture (presented here for “dissimilarity”). Circles represent 19.7-km radius landscapes surrounding Breeding Bird Survey (BBS) routes (shown as magenta lines). First column: true color satellite images (DigitalGlobe 0.5-m imagery, obtained from ESRI World Imagery); second column: peak greenness enhanced vegetation index (EVI); third column: dissimilarity texture (higher values indicate greater heterogeneity); fourth column: land cover classes from the 2011 National Land Cover Database (Homer et al. 2015). Four distinct habitat types are represented: (a) heavily forested landscape in the central Appalachian Mountains of West Virginia (38°28′54″ N, 80°3′1″ W); (b) mixed-grass prairie in the Great Plains of northwest South Dakota (45°10′43″ N, 102°44′5″ W); (c) arid shrubland in the Chihuahuan Desert of western Texas (30°46′44″ N, 103°23′23″ W); (d) croplands and suburbs in the Central Valley outside of Modesto, California (37°39′30″ N, 121°13′41″ W). [Correction added on July 30, 2020, after first online publication: Fig. 3 was replaced following initial release due to an author error which provided an incorrect final version. The missing entry for water/wetlands has been restored in the key and the imagery in row (c) was replaced with the correct images from the version accepted for publication]. [Color figure can be viewed at wileyonlinelibrary.com]

between croplands and development, and also captured the relative homogeneity within individual crop fields and in neighboring undeveloped hills (Fig. 3d).

Some residual patterns remained in the base EVI composite due to areas of overlap in Landsat paths with higher numbers of observations, a common issue when working with Landsat data across broad spatial extents (Young et al. 2017). These residual patterns are most visible in the correlation texture map (Fig. 2h). However, despite some residual artifacts in our texture maps we still observe clear general patterns, and it is unlikely that path discrepancies affected our results as <0.005% of pixels in any sampling unit would be affected by Landsat path edge overlap.

Texture measures as predictors of bird species richness

As predicted, we found positive relationships between texture measures of heterogeneity and total bird species richness (Table 2). Because second-order homogeneity and uniformity are measures of habitat homogeneity, negative relationships between these variables and bird richness represent positive relationships with heterogeneity. However, we observed significant non-linear relationships between most texture measures and total bird richness, indicating a positive unimodal relationship. In texture-only models, individual texture measures explained 4–21% of the variance in total bird richness across the conterminous United States, with second-order dissimilarity being the strongest single-texture predictor.

Dissimilarity also had a positive unimodal relationship with forest specialist richness, and was the strongest single-texture predictor of forest specialists. By contrast, grassland specialist richness was negatively related to all texture measures except second-order correlation, while shrubland specialist richness was negatively related to all texture measures. Second-order homogeneity and first-order standard deviation explained the most variance in grassland and shrubland specialist richness, respectively. Second-order entropy and uniformity were consistently among the worst-performing textures in terms of variance explained, across all species groups. Overall, texture-only models had the highest explanatory power for shrubland specialists (42%), followed by total bird richness (24%) and forest specialists (18%), and the lowest explanatory power for grassland specialists (10%). Incorporating multiple non-collinear texture measures into models improved model performance slightly, with multivariate texture models explaining an additional 1–8% of variance in bird richness compared to the best single-texture models for each species group (Table 2).

In models comparing the predictive performance of EVI with and without texture measures, the EVI-only model explained 31% of the variance in overall

TABLE 2. Results of linear regressions relating bird species richness to single and multiple image texture measures, for all species combined and for habitat specialists within three groups (forest, grassland, shrubland).

Texture-only models	All species			Forest specialists			Grassland specialists			Shrubland specialists		
	$Est._{lin}$	$Est._{quad}$	R^2_{adj}	$Est._{lin}$	$Est._{quad}$	R^2_{adj}	$Est._{lin}$	$Est._{quad}$	R^2_{adj}	$Est._{lin}$	$Est._{quad}$	R^2_{adj}
Single textures												
Standard deviation	3.60	−3.24	0.21	1.65	−1.61	0.16	−0.41	−0.18	0.05	−1.21	0.50	**0.34**
Contrast	5.37	−2.52	0.17	2.10	−1.11	0.10	−0.30	−0.04	0.03	−1.51	0.41	0.28
Dissimilarity	3.90	−3.21	**0.21**	1.84	−1.57	**0.16**	−0.44	−0.27	0.06	−1.20	0.47	0.31
Homogeneity	−2.26	−1.71	0.12	−1.90	−0.68	0.13	0.73	−0.87	**0.09**	0.94		0.14
Entropy	2.02	−0.50	0.04	1.89	−0.18	0.07	−0.58	−0.13	0.05	−0.92	−0.15	0.07
Uniformity				−1.09		0.02	0.34		0.03	0.41	−0.12	0.01
Correlation	4.88	−1.07	0.12	2.64	−0.67	0.12	0.12		0.01	−1.50	0.26	0.30
Multiple textures												
Contrast + Homogeneity + Correlation			0.22			**0.18**			**0.10**			0.39
Dissimilarity + Entropy + Correlation			**0.24**			0.17			0.09			**0.42**

Notes: Coefficient estimates for linear ($Est._{lin}$) and quadratic ($Est._{quad}$) terms of predictors are shown for single-texture measure models. Adjusted R^2 values are shown for all models, with the highest value for each species group in bold. Empty cells indicate nonsignificant terms and models with $P > 0.05$.

Table 3. Adjusted R^2 values for linear regression models relating bird species richness with enhanced vegetation index (EVI) alone, and combined with single and multiple texture measures.

EVI + texture models	All species	Forest specialists	Grassland specialists	Shrubland specialists
EVI only	0.31	0.19	0.003	0.46
EVI + single texture				
EVI + Standard deviation	0.36	0.22	0.07	0.46
EVI + Contrast	0.33	0.21	0.04	0.46
EVI + Dissimilarity	0.37	0.23	0.09	0.46
EVI + Homogeneity	0.39	0.29	0.16	0.47
EVI + Entropy	0.37	0.28	0.13	0.47
EVI + Uniformity	0.36	0.28	0.07	0.47
EVI + Correlation	0.34	0.23	0.02	0.48
EVI + multiple textures				
EVI + Contrast + Homogeneity + Correlation	0.41	0.35	0.17	0.49
EVI + Dissimilarity + Entropy + Correlation	0.41	0.34	0.15	0.50

Notes: Results are shown for all species and for habitat specialists within three groups (forest, grassland, shrubland).

bird richness compared to 39–41% of the variance when combined with single and multiple texture measures (Table 3). However, the predictive power of EVI was highly dependent on bird habitat specializations. EVI was a strong predictor of shrub specialist richness, accounting for 46% of the variance alone and up to 50% when combined with multiple textures (Table 3). By contrast, texture measures alone (Table 2) were stronger predictors of forest and grassland specialist richness than EVI, and increased the variance explained by EVI alone from 19% to 35% for forest specialists, and from 0.03% to 17% for grassland specialists. When combined with EVI, homogeneity was the individual texture measure that added the most explanatory power to models of total bird richness and richness of forest and grassland specialists. In these models, homogeneity had a negative relationship with overall richness and forest specialist richness, and a positive relationship with grassland specialist richness. Texture measures added only 1–2% more explanatory power to EVI-only models of shrubland specialists (Table 3).

Predicted patterns of bird richness based on the best EVI-texture model generally matched observed patterns of bird richness for all species groups (Fig. 4), and geographic locations of differences between predicted and observed richness were largely random (Fig. 4). For total bird richness and forest specialists, models under-predicted richness patterns along the west coast and in the southern Rockies and northern Midwest, and over-predicted richness in the middle Rockies, the Appalachians, along the gulf coast, and in Florida. For grassland specialists, the model under-predicted richness in the northern Great Plains and Midwest, and over-predicted richness in the middle Rockies, Colorado High Plains, and parts of the arid Southwest. For shrubland specialists, predictive models tended to under-predict richness in the arid Southwest, and over-predict richness in the Intermountain West, eastern Washington, and Oregon.

Relative importance of texture

The top-ranked model also incorporating topographic and land cover metrics explained 51% of the variance in overall bird richness, and included five predictors and their squared terms: EVI, proportion of forest cover, terrain ruggedness, elevation, and the second-order texture dissimilarity (Table 4). A significant positive relationship between total bird richness and the squared term of EVI indicated that richness increased exponentially with productivity. A significant negative relationship of the squared term of proportion of forest cover indicated that richness peaked at intermediate levels of forest cover (Table 4). Bird richness also showed a positive unimodal relationship with elevation, terrain ruggedness, and dissimilarity. Although dissimilarity had the smallest effect size of the top five predictors, it had a significant positive effect and was more important for total bird richness than proportions of grassland and shrubland cover, which were not included in the top-ranked model (Fig. 5).

Hierarchical partitioning analysis, which measures the relative importance of predictors by calculating their independent and joint contributions toward variance explained, also showed that EVI and proportion of forest cover had the strongest independent effects on patterns of total bird richness (Fig. 6). However, the independent effects of dissimilarity and its squared term indicated that the texture measure uniquely explained part of the variance in total bird richness that more commonly used heterogeneity metrics could not. The combined independent contributions of dissimilarity and its squared term were greater than those of either elevation or terrain ruggedness. Joint contributions resulted from multicollinearity among our predictors (Appendix S1: Fig. S2), and reflect a degree of redundancy in variance explained among even moderately correlated predictors (Mac Nally 2000). For dissimilarity, relatively large joint contributions were a result of collinearity with elevation ($r = -0.62$), EVI ($r = 0.34$), TRI ($r = -0.24$), and

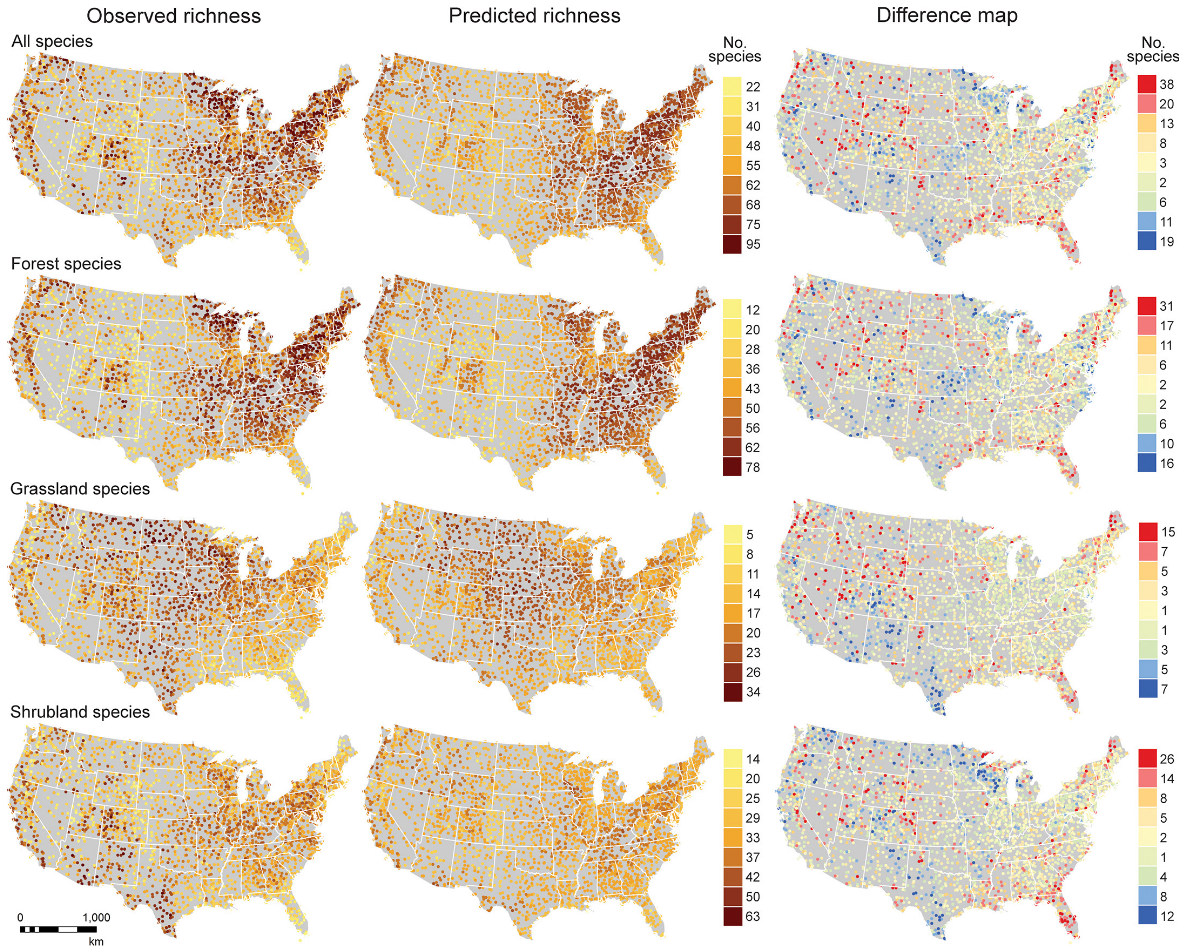

FIG. 4. Maps of observed (first column) vs. predicted (second column) bird species richness and difference from observed (third column) for all species and for habitat specialists within three groups (forest, grassland, shrubland). The rightmost column of color ramps reflects difference from observed (observed minus predicted richness), such that redder tones represent over-predictions and bluer tones represent under-predictions. Richness is mapped for 2,749 Breeding Bird Survey (BBS) routes across the conterminous United States. Predicted richness is based on the best model including EVI and image texture measure predictors for each species group.

proportion of forest cover ($r = 0.19$), and indicate that part of the variance explained by dissimilarity was redundant with these other heterogeneity metrics.

For forest specialists, the top-ranked model explained 72% of the variance in richness (Table 4), and proportion of forest cover was by far the most important predictor, followed by proportion of grassland cover and topographic measures (Figs. 5, 6). Although dissimilarity had a comparatively small positive effect on forest specialists, the combined independent contributions of dissimilarity and its squared term suggest the texture measure was an important predictor and accounted for variance that other metrics could not. EVI was not included in the top-ranked model, indicating that for forest specialists EVI had lower relative importance than the other predictors evaluated. The top-ranked model for grassland specialists explained 57% of the variance (Table 4), with elevation and EVI having the strongest effects on grassland specialist richness (Fig. 5). Dissimilarity had a relatively weak but significant negative effect on grassland specialist richness, and had a comparable independent contribution toward variance explained as EVI (Fig. 6). For shrubland specialists, two models had ΔBIC values within two of the top-ranked model and both explained 60% of variance (Table 4; Raftery 1995). Proportion of shrubland cover had the strongest positive influence on shrubland bird richness, while dissimilarity had a comparatively small but significant negative effect on shrubland specialist richness (Fig. 5). Hierarchical partitioning showed that dissimilarity independently explained more variance in shrubland specialist richness than other predictors, except proportion of shrubland cover (Fig. 6).

Variance inflation factors (VIFs) for each predictor in the top-ranked models for all species groups were <10 (mean VIF = 4.37; Appendix S1: Table S3), indicating

Table 4. Results of Bayesian information criterion (BIC) model selection, summarized for top and similarly ranked models (ΔBIC < 2; Raftery 1995) of bird species richness, for all species and for habitat specialists within three groups (forest, grassland, shrubland).

Bird group	Model rank	Int.	Elev	Elev^2	TRI	TRI^2	Forest	Forest^2	Grass	Grass^2	Shrub	Shrub^2	EVI	EVI^2	Diss.	Diss.^{2}	df	logLik	BIC	ΔBIC	Wt.	R^2_{adj}
All	1	59.92	3.00	−1.37	3.53	−1.11	4.49	−3.80	–	–	†	†	7.89	2.69	2.15	−1.69	12	−10326.8	20748.6	0.00	0.97	0.51
Forest	1	13.20	1.22	−0.64	−0.76	0.37	6.43	−1.09	−2.44	0.47	1.00	–	–	–	0.24	−0.32	13	−7940.9	15984.8	0.00	0.72	0.72
Grass	1	3.06	1.70	−0.41	−0.18	−0.08	−0.99	–	0.74	−0.11	†	†	1.23	–	−0.11	−0.16	12	−4422.3	8939.5	0.00	0.93	0.57
Shrub	1	1.78	−0.89	0.26	0.47	–	−0.17	−0.14	0.57	−0.10	1.44	0.26	†	†	−0.39	–	12	−5390.3	10875.6	0.00	0.46	0.60
	2	1.64	−0.93	0.28	0.46	–	−0.23	–	0.56	−0.10	1.53	0.23	†	†	−0.36	–	11	−5395.0	10877.2	1.57	0.21	0.60

Notes: Standardized coefficients are shown for each predictor, with model degrees of freedom (df), fit statistics (logLik, BIC, ΔBIC), weights (Wt.), and adjusted R^2 values. Predictors are intercept (Int.), elevation (Elev), terrain ruggedness index (TRI), proportion of forest cover (Forest), grassland cover (Grass), shrubland cover (Shrub), enhanced vegetation index (EVI), and dissimilarity texture (Diss.). Daggers (†) indicate predictors removed from final models due to high variance inflation factors (IVF> 10; O'brien 2007); dashes (–) indicate predictors not included in top models.

acceptable levels of collinearity among variables included in top-ranked models (O'Brien 2007). Correlograms of model residuals of overall bird richness indicated richness among BBS routes showed only a minimal degree of spatial autocorrelation (Appendix S1: Fig. S3).

Discussion

We found that texture measures derived from Landsat 8 EVI imagery were effective predictors of breeding bird richness across the conterminous United States, providing evidence that medium-resolution texture measures characterize important aspects of vegetation heterogeneity at scales relevant for biodiversity. By generating 30-m resolution texture maps of productivity and modeling bird richness at a near-continental scale (7.8 million km^2), our results expand on prior studies that were either at higher resolution but only local or regional in scope (St-Louis et al. 2006, Wood et al. 2013, Wallis et al. 2016), or near-continental in extent but at coarse resolution (Tuanmu and Jetz 2015). Medium-resolution texture measures are well-suited for characterizing features of vegetation heterogeneity such as foliage height diversity (Wood et al. 2012), successional stage (Jakubauskas 1997), and structural complexity (Guo et al. 2004), which is consistent with evidence that medium-resolution vegetation indices (e.g., NDVI, EVI) characterize biophysical features of landscapes ranging from canopy structure (Gamon et al. 1995) to plant species diversity (Gould 2000). Additionally, medium-resolution metrics characterize heterogeneity at the scale of a typical breeding bird territory (Leonard et al. 2008, Jones 2011), which coarse-resolution measures may not adequately detect (Cohen and Goward 2004, Neumann et al. 2015).

Contrary to our predictions, we observed nonlinear relationships between most texture measures and overall species richness, suggesting a unimodal or "hump-shaped" relationship between heterogeneity and bird richness. Yet our results are in line with previous research documenting a unimodal relationship between MODIS-derived textures and bird species richness, particularly among texture measures that effectively captured heterogeneity in human-modified landscapes such as contrast and dissimilarity (Tuanmu and Jetz 2015). These findings lend support to the "intermediate heterogeneity hypothesis," which predicts that species richness will peak at intermediate levels of environmental heterogeneity, as greater habitat diversity leads to a decrease in overall amount of each habitat type and increased fragmentation and edge effects (Fahrig et al. 2011). The "area–heterogeneity trade-off" is a related concept, which posits that as heterogeneity increases, the amount of suitable area for individual species decreases, leading to decreased overall population sizes and increased risk of local extinctions (Allouche et al. 2012).

We also found that the strength and direction of the relationship between texture measures and bird richness

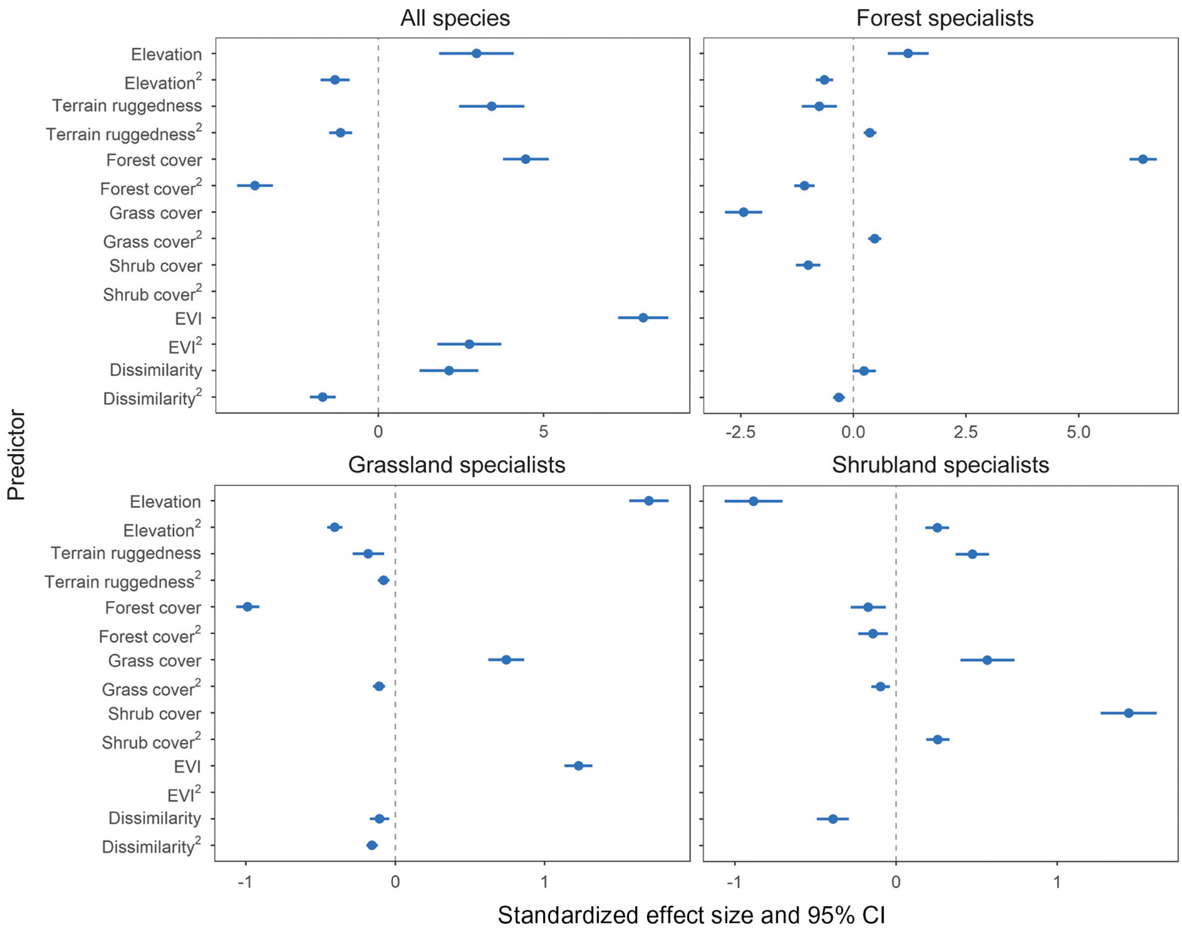

FIG. 5. Standardized effect sizes (regression coefficients) with 95% confidence intervals for predictor variables in top-ranked models for all species combined and for habitat specialists within three groups (forest, grassland, shrubland). Note that not all predictor variables are included in top-ranked models for each group.

were highly dependent on the habitat specializations of species. Texture measures were positively related with richness of all breeding birds and forest specialists, but were negatively related with richness of grassland and shrubland specialists. This finding is consistent with empirical studies (Tews et al. 2004, Cramer and Willig 2005, Veech and Crist 2007) and ecological models (Kadmon and Allouche 2007, Yang et al. 2015), which found in some cases an inverse relationship between heterogeneity and species diversity. Effects of habitat heterogeneity may vary among species groups depending on whether habitat features are perceived as heterogeneity or fragmentation (Tews et al. 2004), and the spatial and temporal scales at which animals perceive heterogeneity (Cramer and Willig 2005, Veech and Crist 2007).

Similarly, differences in the spatial resolution of vegetation patterns across habitat types may have influenced the discrepancies we observed among species groups (Bar-Massada et al. 2012). Medium-resolution imagery may be too coarse to capture fine-grain aspects of heterogeneity, particularly in comparatively homogenous grassland and shrubland habitats (Hudak and Wessman 1998, Wachendorf et al. 2018). Still, 20-m resolution image textures have been used to effectively detect heterogeneity among various management treatments in tallgrass prairies (Briggs and Nellis 1991), and 15-m resolution textures captured spatial variation in vertical structure of mixed grasslands under different grazing regimes (Guo et al. 2004). These studies suggest that medium-resolution image textures can effectively detect vegetation heterogeneity that is important for birds in seemingly homogeneous habitats. Moreover, 30-m resolution textures combined with NDVI explained up to 78% of the variance in group size of Greater Rheas (*Rhea Americana*) in pampas grasslands of Argentina (Bellis et al. 2008). Similarly, 30-m resolution textures alone explained up to 82% of the variance in shrubland/grassland bird richness in semi-arid landscapes in the Chihuahuan desert (St-Louis et al. 2009), outperforming 1-m resolution texture measures from the same study area (St-Louis et al. 2006). This suggests that a 30-m pixel size, though it cannot detect fine-resolution features (e.g., individual plants), may be a more appropriate resolution for measuring the spatial variability and

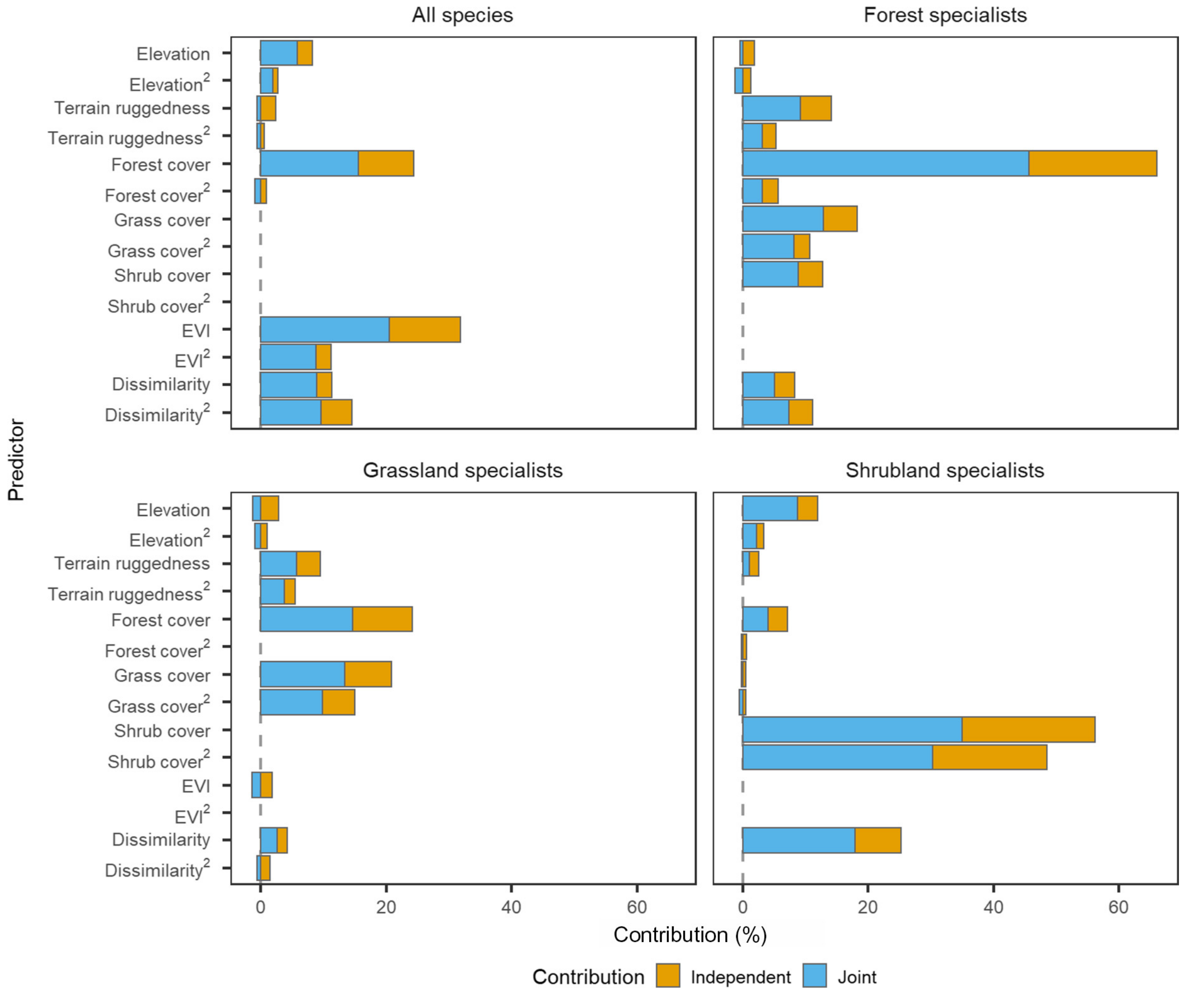

Fig. 6. Results of hierarchical partitioning analysis showing the independent and joint contributions of predictor variables included in the top-ranked models for all species combined and for habitat specialists within three groups (forest, grassland, shrubland) toward total variance explained by each model. Note that not all predictor variables are included in top-ranked models for each group.

arrangement of bird habitats across broad spatial extents.

It is important to note, however, that St-Louis et al. (2009) found strong positive relationships between medium-resolution textures and shrubland and grassland bird richness, whereas we found a negative relationship. However, we focused only on habitat specialists that may prefer more homogenous, uninterrupted areas of habitat, while St-Louis et al. (2009) also included habitat generalists that may be more tolerant of, or even attracted to, heterogeneous habitats. Additionally, both the Chihuahuan desert and Greater Rhea studies were conducted exclusively within shrubland and grassland habitats, and the heterogeneity–diversity relationship may vary depending on whether analyses are conducted *within* or *across* habitat types (Bar-Massada and Wood 2014). Analyses limited to a single habitat type may be more sensitive to subtle variations within that limited heterogeneity gradient, and these subtleties may have been lost in the wide gradient of heterogeneity values we evaluated across habitats and at a near-continental scale. Thus, the negative relationship we observed between texture measures and grassland and shrubland specialist richness was likely influenced by the relative homogeneity of these habitats compared with the structurally complex forests and human-modified landscapes also evaluated.

When combined with EVI, texture measures improved the overall performance of bird richness models compared to those based on EVI alone, emphasizing the importance of both habitat heterogeneity and available energy as complementary but distinct drivers of biodiversity (Hurlbert and Haskell 2003, Davies et al. 2007). By itself, EVI explained more variance in total bird richness and shrubland specialist richness than texture-only models, while the opposite was true for grassland specialists. This suggests that contrasting mechanisms might drive richness patterns in different habitat types.

The addition of multiple texture measures to EVI models explained only slightly more variance than EVI models including only one texture, suggesting that inclusion of multiple texture measures may not help to improve the predictive power of biodiversity models.

When we evaluated our strongest individual texture measure in our global model including productivity, topographic, and land cover metrics, we found that the dissimilarity texture had relatively low influence on total bird richness compared to EVI and proportion of forest cover. However, dissimilarity texture still had a significant positive relationship with total bird richness, and contributed more independent explanatory power than topographic metrics. For forest specialists, dissimilarity had a significant positive effect and contributed predictive power, while EVI was not even included in the top-ranked model. This suggests that within forest habitats, vegetation heterogeneity was more important for forest specialists than available energy. It has been suggested that environmental heterogeneity generally has a stronger effect in regions with higher available energy, where energy may be less limiting for biodiversity (Kerr and Packer 1997, Kreft and Jetz 2007), and that structurally complex habitats support higher species richness compared to structurally simple habitats (Hurlbert 2004, Tews et al. 2004). Our findings for forest specialists are consistent with both of these hypotheses. Our results also indicate that texture measures capture aspects of heterogeneity undetected by other measures, and that they enhance or complement more commonly used measures of environmental heterogeneity. Thus, we suggest that texture measures are best considered in biodiversity studies in conjunction with productivity or land cover metrics.

Conservation and management implications

As humans rapidly transform the Earth's terrestrial ecosystems, there is an urgent need for innovative, adaptive approaches to identify areas with high potential for supporting biodiversity (Heller and Zavaleta 2009, Jetz et al. 2019). Texture measures derived from freely available satellite data, and processed on cloud-computing platforms, have the potential to provide broad-scale, cost-effective, and readily updatable measures of habitat heterogeneity. We show here that medium-resolution texture measures capture key landscape patterns that influence species richness across broad spatial extents.

Furthermore, while improving our understanding of landscape features that currently support large numbers of species is a conservation priority, there is also a need to identify landscapes that may be resilient to future global change (Bengtsson et al. 2003, Lawler et al. 2015). A number of studies have suggested that spatially diverse and heterogeneous environments are more resilient to environmental stress, because structurally complex systems are able to absorb disturbance without loss of ecological functions and processes (Holling 1973), and provide a variety of microsite conditions that may function as refugia (Virah-Sawmy et al. 2009, Keppel et al. 2012, Elsen et al. 2020). Thus, spatially heterogeneous environments may play an important role in conserving species diversity over time by mediating the effects of environmental stress and perturbations on individuals and communities (Keppel et al. 2012, Oliver et al. 2015). Additionally, structurally complex habitats generally increase niche space by providing a greater diversity of resources and ways for organisms to exploit those resources (Tews et al. 2004, Stein et al. 2014). Our results demonstrate that landscapes with higher spatial heterogeneity in productivity can support a greater number of total species, and that this is a factor to consider when prioritizing areas for protection. However, such coarse-filter strategies to conserve heterogeneous landscapes should be complementary to, and not a replacement for, fine-filter efforts to mitigate specific threats to declining, area-sensitive habitat specialists (Schwartz 1999, Rodrigues et al. 2004, Tingley et al. 2014).

Conclusion

We demonstrate that texture measures derived from 30-m resolution satellite imagery effectively predict broad-scale patterns of bird species richness, and highlight their potential for capturing environmental heterogeneity not detected by more conventional heterogeneity metrics. Although we found positive correlations between texture measures and total bird richness and forest specialists, this relationship was frequently unimodal, and for shrubland and grassland specialists the relationship was consistently negative. Our results reflect the complexity of the heterogeneity-diversity relationship, and highlight the need for further investigation of these relationships at different spatial scales, and within- vs. across-habitat contexts. We suggest that texture measures show promise as a tool for biodiversity modeling, particularly when used in combination with other predictor variables such as productivity and land cover. Ultimately, Landsat-derived texture measures present exciting opportunities and challenges for mapping species diversity at macroecological scales, and provide direct, continuous, and cost-effective metrics for broad-scale ecological and conservation applications. The 30-m resolution texture measures we developed for the conterminous United States are *available online.*[3]

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[3] http://silvis.forest.wisc.edu/webmaps/landsat8-evi-textures

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2157/full

Data Availability Statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1c59zw3s7