Remote Sensing of Environment 295 (2023) 113661

Contents lists available at ScienceDirect

Remote Sensing of Environment

journal homepage: www.elsevier.com/locate/rse

Multi-grain habitat models that combine satellite sensors with different resolutions explain bird species richness patterns best

E.M.O. Silveira [a,*], A.M. Pidgeon [a], L.S. Farwell [b], M.L. Hobi [c], E. Razenkova [a], B. Zuckerberg [a], N.C. Coops [d], V.C. Radeloff [a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[b] Pacific Birds Habitat Joint Venture, 901 SE Oak Street, Suite 103, Portland, OR 97215, USA
[c] Swiss Federal Research Institute WSL, Zuercherstrasse 111, 8903 Bimensdorf, Switzerland
[d] Integrated Remote Sensing Studio, Department of Forest Resources Management, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

ARTICLE INFO

Edited by Marie Weiss

Keywords:
Biodiversity
DHIs
Image texture
NDVI
Productivity

ABSTRACT

Animals select habitat at multiple spatial scales, suggesting that biodiversity modeling, for example of species richness, should be based on environmental data gathered at multiple spatial scales, and especially multiple grain sizes. Different satellite sensors collect data at different spatial resolutions and therefore provide opportunities for multi-grain habitat measures. The dynamic habitat indices (DHIs), which are derived from satellite data, capture patterns of vegetative productivity and predict bird species richness well. However, the DHIs have only been analyzed at single resolutions (e.g., 1-km), and have not yet been derived from high-resolution satellite data (< 10 -m). Our goal was to predict bird species richness based on measures of vegetation productivity (DHIs, NDVI median and NDVI percentile 90th) across a range of spatial resolutions both from different sensors, and from resampled high-resolution imagery. We analyzed bird species richness within 215 forest, grassland and shrubland plots (56.25 ha) located at 26 terrestrial field sites of the National Ecology Observatory Network (NEON), in the continental US. To obtain our multi-resolution measures of vegetation productivity, we acquired data from Planetscope (3-m), RapidEye (5-m), Sentinel-2 (10-m), Landsat-8 (30-m) and MODIS (250-m) from 2017 to 2020, generated time series of NDVI, calculated the three DHIs (cumulative, minimum and variation), NDVI median and the 90th percentile NDVI and calculated 1st and 2nd order texture measures. We evaluated the performance of the derived measures to predict bird species richness of habitat specialist guilds based on (i) univariate models (ii) multivariate models with single-resolution measures and (iii) multivariate models with multi-resolution measures. Single-spatial resolution measures predicted bird species richness moderately well (R^2 up to 0.51) and the best performing spatial resolution and measure differed among bird species guilds. High-spatial resolution (3–5 m) measures outperformed medium-resolution measures (10–250 m). Models for all guilds performed best when incorporating multiple resolutions, including for all species richness ($R^2 = 0.63$) and for forest ($R^2 = 0.72$), grassland ($R^2 = 0.53$) and shrubland specialists ($R^2 = 0.46$). In addition, models based on multi-resolution data from different sensors performed better than models based on resampled high-resolution data for any of the guilds. Our results highlight, first, the value of the DHIs derived from high-resolution satellite data to predict bird species richness and, second, that remotely-sensed vegetation productivity measures from multiple spatial resolutions offer great promise for quantifying biodiversity.

1. Introduction

Ecological theory suggests that environmental data with multiple resolutions can capture habitat heterogeneity better than those with just a single resolution (Mayor et al., 2009). Furthermore, because birds select habitat at multiple spatial scales, inclusion of environmental data of different spatial resolutions, or ‘grains’, is necessary when predicting bird species richness (McGarigal et al., 2016). Habitat heterogeneity is related to the spectral variation captured by remote sensing images, as stated in the spectral variability hypothesis (Palmer et al., 2000), however, relationships between spectral variation, habitat heterogeneity and species diversity are affected by scale (Fassnacht et al., 2022).

* Corresponding author.
E-mail address: esilveira@wisc.edu (E.M.O. Silveira).

https://doi.org/10.1016/j.rse.2023.113661
Received 26 January 2023; Received in revised form 30 May 2023; Accepted 31 May 2023

Among the two aspects of scale, grain and extent (Guisan and Thuiller, 2005; Jackson and Fahrig, 2012, 2015), we focus here on grain. Analyzing bird-habitat relationships at a single grain, such as satellite data with a single spatial resolution, fails to fully capture the multiple spatial scales at which birds select habitat (Cushman and McGarigal, 2004). Combining data from multiple grains can better capture important local and landscape features across different habitat types and features of interest, improving models of all-bird richness and the richness of habitat specialists.

Satellite data provide exceptional opportunities for habitat measures at a wide range of grains ranging from sub-meter to kilometer (Estes et al., 2008; Woodcock and Strahler, 1987). Grain size is especially important when utilizing image textures (Haralick et al., 1973) derived from individual reflectance bands or vegetation indices to quantify biodiversity (Culbert et al., 2012; Farwell et al., 2020, 2021; Tuanmu and Jetz, 2015). For example, high-resolution image texture from 1-m aerial photos explains up to 57% of the variability in bird species richness in a semiarid landscape in US (St-Louis et al., 2006). Similarly, textures derived from RapidEye (5-m), SPOT-5(10-m), and Aster (15-m) images are strong predictors of bird species richness in Turkish pine forests ($R^2 = 0.73$) (Ozdemir et al., 2018). Across grassland, shrubland, and forest sites in the conterminous US, medium-resolution Sentinel-2 (10-m) and Landsat-8 (30-m) texture measures of vegetation heterogeneity perform well in bird species richness models (Farwell et al., 2020, 2021). Similarly, productivity measures derived from MODIS-1-km (Moderate Resolution Imaging Spectroradiometer) data are strong predictors of bird species richness both across the conterminous US (Hobi et al., 2017, 2021) and globally (Radeloff et al., 2019). However, bird biodiversity models are usually based on satellite data from one sensor and hence with a single spatial grain. The question is if it is beneficial to combine data from different satellite sensors with different grains as ecological theory predicts (McGarigal et al., 2016).

Spatial resolution affects which vegetation characteristics are captured by satellite images and that may affect how well they can predict bird species richness (Bar-Massada et al., 2012). In general, the explanatory power of higher resolution data outperforms that of coarser resolution data in models of bird species richness because finer resolution data can better capture vegetation complexity that is important for bird communities (e.g., vegetation height heterogeneity) (Farwell et al., 2021). For example, vegetation measures based on 2-5 m resolution imagery outperform those derived from 10 to 250 m in models of woodlands bird species richness in France (Sheeren et al., 2014) and pine forests in Turkey (Ozdemir et al., 2018). Similarly, medium-resolution Sentinel-2 (10-m) texture measures outperform 30-m texture measures in models of bird species richness in the US (Farwell et al., 2021).

However, measures derived from high spatial resolution data do not always have good performance in biodiversity models (e.g., models of tree species or bird species richness), particularly if pixels are much smaller than habitat features of interest or when there is high intra-class spectral variability, such as among the crown, shade, leaves, and bark of trees (Nagendra and Rocchini, 2008). Conversely, if spatial resolution is too coarse, then small or dispersed habitat features and finer resolution landscape characteristics that influence animal distributions may be lost (Gottschalk et al., 2011; Turner, 1989). The size, complexity, and spatial arrangement of landscape features will depend on habitat type (Nagendra, 2001), and the scale-dependence of many landscape metrics suggests there is no single grain that is optimal for all habitat types and landscape patterns (Wu et al., 2002). The grain at which birds select their habitat is often unknown, which is especially problematic when dealing with many species.

In addition to spatial resolution, it is important to consider which satellite image measures explain bird species richness patterns best. Remotely-sensed productivity measures are good indicators of available energy and habitat heterogeneity. More available energy can support higher species richness (Wright, 1983) and the spatial variability or spatial heterogeneity of vegetated surfaces affects species richness. The spectral variability hypothesis states that species richness will be positively related to spatial measure (e.g., standard deviation). Higher spectral variation of remote sensing images is related to higher habitat heterogeneity (Palmer et al., 2000) and hence higher bird species richness (St-Louis et al., 2006). For example, the dynamic habitat indices (DHIs) (Berry et al., 2007), which summarize satellite data in three indices relevant for biodiversity (cumulative, minimum, variation) are strong predictors of bird species richness in North America (Coops et al., 2009a, 2009b; Hobi et al., 2017, 2021), Asia (Suttidate et al., 2019; Zhang et al., 2016), and globally (Coops et al., 2018; Radeloff et al., 2019).

Image texture analysis holds promise for quantifying habitat heterogeneity in structurally complex landscapes (Wood et al., 2012), which is why texture measures are also strong predictors in models of bird species richness (Farwell et al., 2021). Image texture can be derived from individual reflectance bands (Lu and Batistella, 2005), vegetation indices such as the as the Normalized Difference Vegetation Index (NDVI) (Wood et al., 2012, 2013), or annual measures of productivity, such as the cumulative DHI (Carroll et al., 2022). For example, homogeneity texture measure derived from cumulative DHI is an effective predictor in models of tropical forest birds' richness (Suttidate, 2016). However, while DHIs and derived measures have been successfully employed in biodiversity models, they were always obtained at a single grain (medium or coarse spatial resolution). Furthermore, DHIs derived from high-resolution data have yet to be derived and tested in bird species richness models. Accordingly, the question remains if measures derived from DHIs across multiple spatial resolutions can better predict total species richness and richness of forest, grassland and shrubland specialists and if high-resolution DHI measures have higher explanatory power than medium-resolution measures in models of bird species richness.

Our goal here was to predict bird species richness based on measures of vegetation productivity derived at multiple spatial resolutions. Specifically, we aimed to:

(1) calculate DHIs (cumulative, minimum and variation), median NDVI and the 90th percentile NDVI to derive a suite of vegetation productivity measures (1st and 2nd order textures) based on PlanetScope (3-m), RapidEye (5-m), Sentinel-2 (10-m), Landsat-8 (30-m), and MODIS (250-m) NDVI data;
(2) evaluate the performance of vegetation productivity measures in univariate models of bird species richness. We expected that all productivity measures would have a positive relationship with bird species richness, but high-resolution measures would have higher explanatory power than lower resolution measures;
(3) assess if there is a best-performing resolution and measure to predict richness. We expected that best-performing resolution and measure differs by bird habitat guild because forest, grassland, and shrubland habitats are typified by landscape features and patterns of differing size and complexity, so that birds that specialize in each of these habitats may be more or less responsive to habitat measures at different resolutions;
(4) compare the performance of the multi-resolution productivity measures versus single-resolution 3-, 5-, 10-, 30-, and 250-m NDVI data in multivariate models to predict all-species richness and richness of forest, grassland and shrubland habitat specialist guilds. We predicted that multi-resolution models would outperform single resolution models;
(5) resample the high-resolution data (3-m, PlanetScope) to 5-, 10-, 30-, and 250-m to compare resampled productivity measures versus original sensor-derived measures in bird species richness models.

2. Methods

2.1. Study area

Our study area encompassed 215 plots located within 26 terrestrial sites of NEON (National Ecological Observatory Network) in the continental US (Fig. 1). Each site has a variable number of plots (ranging from 1 to 13) depending on the size of the site. Plots were places based on a spatially balanced random design (Barnett et al., 2019a, 2019b) and all plots are separated by a minimum distance of 250-m. We selected sites where bird data was available and which are dominated by forests (106 plots), grasslands (49 plots), or shrublands (60 plots), totaling 215 plots. NEON sampling plots are 750 × 750 m in size (56.25 ha). We selected sites dominated by forests, grasslands, and shrublands because these represent broad-scale vegetation associations for breeding birds in the US.

2.2. NEON bird data

To calculate bird species richness, we analyzed the NEON breeding landbird dataset from 2017 to 2020 (NEON, 2020). The dataset is designed to characterize landbirds, i.e. terrestrial species exclusive of raptors and upland game birds, but not typically associated with aquatic habitats (Thibault, 2020). Birds were sampled using point counts, which were conducted by skilled, paid observers who had prior experience conducting avian field surveys and who had received a score of >90% on a NEON-administered test of knowledge of birds by sight and sound (Thibault, 2020). Each site was surveyed by 1–3 observers annually, often by the same observers across years, with a total of 49 unique observers conducting counts at the 26 terrestrial sites from 2017 to 2020 (NEON, 2020). Counts at each point consisted of a 2-min settling-in period followed by a 6-min count period during which all birds seen and heard were recorded (Thibault, 2020). Counts were conducted during the early morning, from 30 min before sunrise, given sufficient light to identify birds visually, and ended no later than 5 h after official sunrise, depending on the weather and other ambient conditions (Thibault, 2020). Counts were conducted annually, during the optimal sampling window for breeding birds at each site (specific sampling windows listed in Thibault, 2020), although we cannot know whether every bird detected was breeding or attempting to breed. Within each sampling plot, birds were surveyed at nine points distributed in a 3 × 3 array, with 250-m spacing between points (Fig. 1). We excluded species that were poorly sampled and observations >125 m from the observer. Additional information on the landbird dataset is available at NEON Breeding landbird point counts, 2020. We aggregated data on bird species presence from 2017 to 2020 to calculate total species richness as the cumulative number of species recorded within each sampling plot, across all years of the study. We also calculated richness within three habitat specialist guilds: forest (75 species), grassland (14 species), and shrubland (27 species).

2.3. Multi-resolution measures of vegetation productivity

We generated our measures of vegetation productivity in four steps: (1) image acquisition, (2) calculation of time series of NDVI, (3) calculation of DHIs, median and the 90th percentile NDVI, (4) calculation of texture measures. Then, to obtain our multi-resolution measures of vegetation productivity within NEON sites (objective 1), we acquired data from satellite sensors with different spatial resolutions from 2017 to 2020: PlanetScope (3-m), RapidEye (5-m), Sentinel-2 (10-m), Landsat-8 (30-m) and MODIS (250-m). We used all images from all seasons from 2017 to 2020 to match the available NEON bird data and to generate a monthly composite from which to calculate DHIs. We selected the NDVI as our vegetation productivity proxy because it can be calculated from all sensors, whereas actual measures of productivity, such as GPP (gross primary productivity), can not.

We acquired cloud-free images of Planet Surface Reflectance (SR) Product (4-band scene orthorectified, surface reflectance, 16 bit) and RapidEye ortho tile product Level 3A (5-band scene, orthorectified, surface reflectance, 16 bit) from planet explorer (Planet Team, 2021).

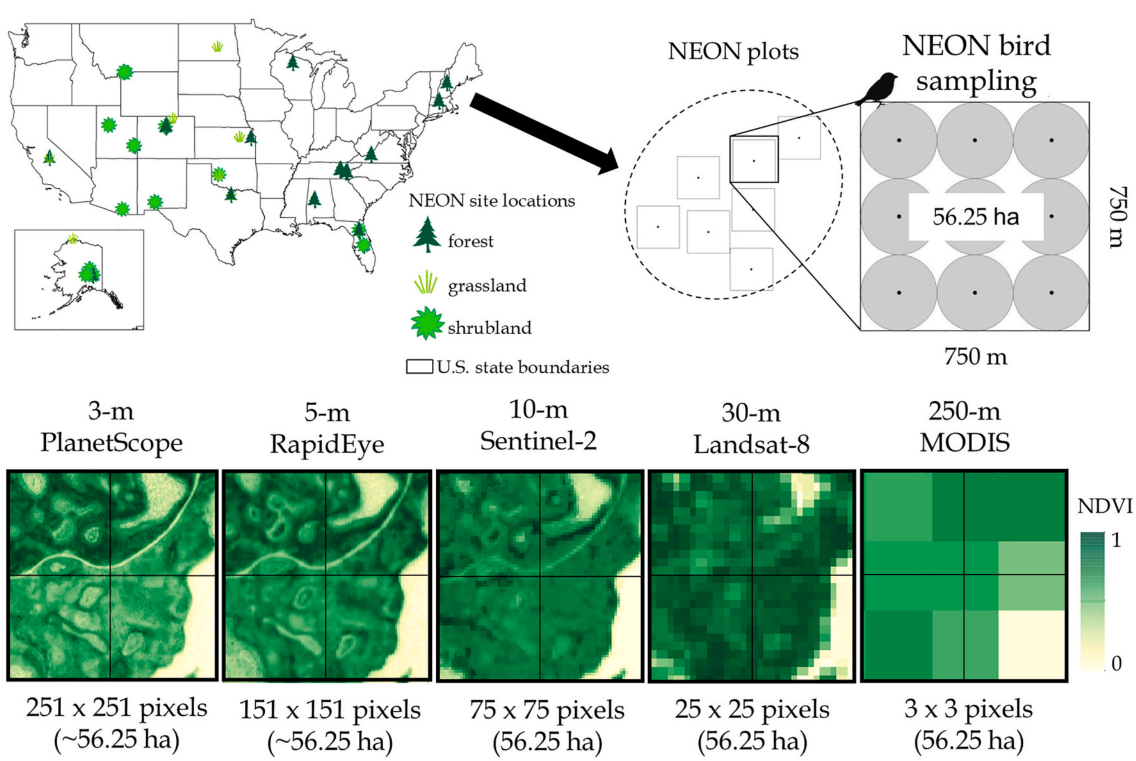

Fig. 1. The NEON terrestrial sites in the continental US and the moving window sizes that we used to calculate texture measures from PlanetScope, RapidEye, Sentinel-2 Landsat-8, and MODIS NDVI images.

For Sentinel-2 and Landsat-8, we analyzed surface reflectance data (12 bit), available in Google Earth Engine ("COPERNICUS/S2_SR" and "LANDSAT/LC08/C01/T1_SR", respectively) (Gorelick et al., 2017). We used the Sentinel-2 and Landsat-8 scene classification band to mask clouds, shadows, and snow (Foga et al., 2017). For MODIS we analyzed the NDVI from MOD13Q1, Collection 6.1, 12 bit, available in Google Earth Engine (Gorelick et al., 2017). We also masked clouds, shadows and snow based on MODIS quality assurance (QA) flags. Details on QA flags for Sentinel-2, Landsat-8 and MODIS are presented in Table S1.

For PlanetScope, RapidEye, Sentinel-2 and Landsat-8 (for MODIS we used MOD13Q1 NDVI product), we then calculated NDVI. We did not adjust the NDVIs to account for differences in bands among sensors, because we wanted to maintain the original spectral sensor characteristics when calculating NDVI (Table S2). However, the differences are relatively small when vegetation indices are calculated from surface reflectance data (Guyot and Gu, 1994; Steven et al., 2003). Thus, based on the NDVI from each sensor, first, we selected the highest NDVI value in each month of each year from 2017 to 2020. Second, we selected median monthly values to generate a monthly time series. We then summed the values to generate the cumulative DHI (Fig. 2), selected the minimum value to have the minimum DHI and calculated the coefficient of variation to generate the variation DHI. Pixels classified as snow (zero productivity) we set to zero. In addition, to ensure we did not have to fill any gaps due to cloud cover, we computed the valid observation in each pixel to ensure we had at least two valid pixel per month among the four possible years. We also calculated median NDVI, and the 90th percentile NDVI of each sensor.

Finally, we calculated 1st and 2nd order texture metrics (Haralick et al., 1973) based on the three DHIs (cumulative, minimum and variation), the median NDVI, and the 90th percentile NDVI of each sensor. For the texture analyses, we applied moving windows of 250 $\times$ 250 pixels for PlanetScope, 151 $\times$ 151 pixels for RapidEye, 75 $\times$ 75 pixels for Sentinel-2, 25 $\times$ 25 pixels for Landsat-8 and 3 $\times$ 3 pixels for MODIS. We assumed that sensors geolocation errors did not affect our analysis because our moving window sizes are large in terms of the number of pixels that were included, and thereby compensate for such errors. The only possible is MODIS (3 $\times$ 3 window size), however MODIS data have excellent geolocation accuracy with means close to zero and root-mean-square errors (RMSEs) of only 54 m (Lin et al., 2019).

We adopted different window sizes in order to capture the same spatial extent (56.25 ha equivalent to the size of a single NEON plot) with each sensor (Fig. 1). For each resolution, we calculated two 1st order texture measures (statistical summaries of mean and standard deviation), and three 2nd order texture measures (GLCM; gray- level co-occurrence matrix): homogeneity (contrast group), uniformity (orderliness group) and correlation (descriptive statistics group). We chose these textures because they are less correlated with each other than other textures and provide high predictive power in bird species richness models (Farwell et al., 2021). We extracted the value of the central pixel of the moving window to obtain our 25 measures for each spatial resolution and for each plot (total of 125 measures) (Table S3).

To calculate the 2nd order texture metrics, we reduced the quantization level of all NDVI images to 8-bit (GLCMs with dimensions of 256 rows $\times$ 256 columns) to minimize zeros in the co-occurrence matrix. Because the GLCM summarizes the likelihood that specific combinations of gray levels will occur next to each other, an image with a higher number of gray levels will tend to contain mostly zeroes because any two gray levels are unlikely to occur next to each other in a given analysis window.

2.4. Statistical analyses

Our statistical analysis encompassed three main steps: (i) univariate models of bird species richness, (ii) multivariate models of bird species

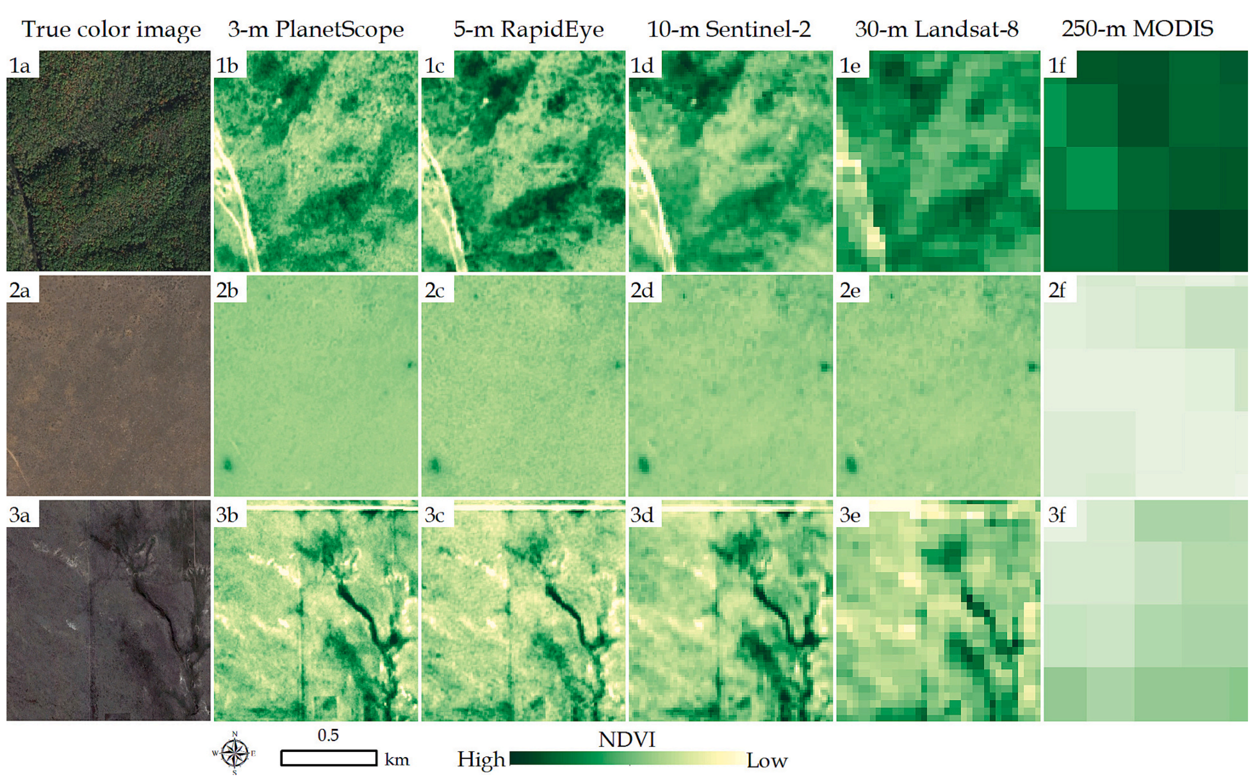

Fig. 2. Examples of the input data for forest, grassland and shrubland habitats (rows 1–3). Columns: (a) true-color satellite image from Google Earth (WorldView images acquired in 10/22/2019, 10/20/2017 and 06/11/2021 for forest, grassland and shrubland habitats, respectively); (b) NDVI Cumulative DHI from PlanetScope (3-m); (c) NDVI Cumulative DHI form RapidEye (5-m); (d) NDVI Cumulative DHI from Sentinel-2 (10-m); (e) NDVI Cumulative DHI from Landsat-8 (30-m); (f) NDVI Cumulative DHI from MODIS (250-m). We calculated the DHIs based on available images from each respective sensor from 2017 to 2020. Squares represent 750 $\times$ 750 m NEON plots.

richness, and (iii) hierarchical partitioning analysis. To evaluate the performance of our measures in univariate models of bird species richness (objective 2) and assess if there is a best performing resolution and measure (objective 3), we explored the relationships between our 125 measures versus the richness of all bird species and of habitat guild specialists in univariate linear regression models. We based the selection of best predictors on the coefficient of determination-$R^2 > 0.30$ (Moore et al., 2013).

For objective 4 we compared the performance of the multi-resolution measures (3-250 m) versus 3-, 5-, 10-, 30-, and 250-m single spatial resolution NDVI in models of bird species richness. To do so, we fitted multivariate models of bird species richness including all 125 predictors for each habitat group. We generated linear models with all possible subsets of predictors for each category (3-, 5-, 10-, 30-, and 250 and 3-250 m) to identify the top-ranked model for each category and guild based on the Bayesian information criterion (BIC) (Brewer et al., 2016). We chose BIC instead of the Akaike information criteria because BIC is more conservative in terms of how many variables are included. One of the main drawbacks of AIC is its tendency to favor high dimensional models (Chakrabarti and Ghosh, 2011).

To check for multicollinearity, we evaluated the variance inflation factors (VIFs) (Booth et al., 1994). We then compared the performance of multi-grain multivariate models versus single-grain multivariate models based on the adjusted coefficients of determination (R^2 adj). We also assessed the relative influence of predictors in each top-ranked model of bird species richness. To do so, we conducted hierarchical partitioning analyses of the top-ranked models to calculate the percentage of the independent effect of each predictor. Hierarchical partitioning estimates the contribution of each predictor to the total variance explained of a regression model. (Chevan and Sutherland, 1991). All statistical analyses were conducted in R (R Core Team, 2020).

To check for spatial autocorrelation of NEON sampling locations, we fitted non-parametric covariance functions and analyzed model residuals of all bird richness, forest, grassland and shrubland specialists. We generated spline correlograms with bootstrap confidence envelopes, using 1000 permutations and a 95% confidence level as our threshold (Bjornstad and Falck, 2001).

2.5. *Resampling analysis*

Different spatial resolutions can be analyzed either by (1) combining data from satellite sensors with different resolutions, or by (2) resampling high-resolution satellite data to coarser resolutions. The advantage of combining satellites is that coarser-resolution satellites typically have better signal-to-noise ratio (i.e., the degree to which the signal is affected by noise), and often provide more frequent observations, which makes the calculation of the DHIs more robust. The advantage of upscaling high-spatial resolution data is that comparisons are unaffected by differences in band characteristics and image dates. Thus, for objective 5, we resampled the 3-m PlanetScope imagery to 5-, 10-, 30-, and 250-m resolutions. Because there is a big gap between the 30-m Landsat and the 250-m MODIS data, we also resampled the 3-m PlanetScope to 100-m and added the 100-m derived-measures in our modeling approach. For the comparisons, first, we generated Spearman correlation matrix to evaluate differences between resampled PlanetScope and original-sensor measures. Second, we tested the resampled data in our multivariate models of bird species richness to compare the performance of the corresponding resampled predictors as selected in our multivariate multi-resolution top-ranked models versus our original-sensor data.

3. Results

3.1. *The dynamic habitat indices, median NDVI and the 90th percentile NDVI from multiple resolutions*

We successfully generated the three DHIs (cumulative, minimum and variation), median NDVI and the 90th percentile NDVI from PlanetScope, RapidEye, Sentinel-2, Landsat-8 and MODIS imageries for the 215 plots located within 26 terrestrial sites of NEON (Fig. 3). Based on these, we then obtained our texture measures (mean, standard deviation, uniformity, homogeneity, and correlation). Among the three DHIs, minimum DHI was the most strongly correlated with cumulative and variation DHI while the correlation of cumulative and variation DHI was at most −0.54 for any sensor (Table S4). We found positive relationships among cumulative and minimum DHI versus NDVI median, and NDVI percentile 90th, and negative relationship with variation DHI. In addition, when values for variation DHI were around one, minimum DHI was zero (Fig. S1 – S5).

When comparing measures derived from cumulative DHI of different sensors, mean had the highest Spearman correlation ($r = 0.9$–1), followed by uniformity ($r = 0.5$–0.9). Homogeneity from cumulative DHI had moderate correlation ($r = 0.3$–0.9), while standard deviation and correlation, presented weak correlations among sensors ($r = 0.2$–0.7 and 0.1–0.7, respectively) (Fig. S6). When comparing measures derived from minimum DHI, mean also had the highest correlation ($r = 1$), however, standard deviation, uniformity, homogeneity, and correlation) had low to moderate correlations ($r = 0$–0.7). Exceptions were between PlanetScope and RapidEye, reaching $r = 0.9$ (Fig. S7). Variation DHI also had higher correlation among mean-derived measures ($r = 0.9$–1), however, the remaining textures had lower to moderate correlations ($r = 0$–0.7) (Fig. S8).

3.2. *Performance of vegetation productivity measures in univariate models of bird species richness*

Results of our univariate linear regression models showed that individual measures were very weak ($R^2 < 0.3$), weak ($0.3 < R^2 > 0.5$) or moderately ($0.5 < R^2 > 0.7$) correlated with bird species richness patterns. Most measures were positively related with richness of all birds and of forest specialists (the exceptions being homogeneity and uniformity because these textures are measures of habitat homogeneity), but negatively related with grassland and shrubland specialist richness. The coefficient of determination (R-squared) ranged from 0.01 to 0.43 (all bird species), 0.02–0.51 (forest specialists), 0.01–0.33 (grassland specialists) and 0.01–0.38 (shrubland specialists) (Table S5 – S9).

We also evaluated the performance of productivity measures in univariate models of bird species richness to assess if there is a best performing resolution and measure. We found that best performing resolution and measures differed among bird species guilds in univariate models (Fig. 4, Table S10), thus birds that specialize in each of these habitats may be more or less responsive to habitat measures at different resolutions. Measures derived from RapidEye imagery performed best for all bird species richness, and for grassland and shrubland specialists, whereas measures derived from Landsat-8 and MODIS imagery were best of forest specialist richness. In models of all bird species richness, the 5-m homogeneity texture from cumulative DHI (RE_CumDHI_HOM) had the highest explanatory power ($R^2 = 0.43$). In models of forest specialist' richness, the 30-m cumulative DHI (L8_CumDHI_MEAN) and 250-m cumulative DHI (MOD_CumDHI_MEAN) had the highest explanatory power ($R^2 = 0.51$), followed by 10-m cumulative DHI (S2_CumDHI_MEAN; $R^2 = 0.49$) and 3-m 90th percentile NDVI (PS_NDVIp90_MEAN; $R^2 = 0.48$) (Fig. 4; Table S10).

In models of bird grassland specialist richness, the 5-m minimum DHI (RE_MinDHI_MEAN) had the highest explanatory power ($R^2 = 0.33$), followed by the 3-m mean texture of minimum DHI and the 10-m mean texture of NDVI (PS_MinDHI_MEAN and S2_NDVI median_MEAN, respectively; $R^2 = 0.30$). In predictions of bird shrubland specialist richness, the 5-m uniformity texture of minimum DHI (RE_MinDHI_UNIF) had the highest explanatory power ($R^2 = 0.38$), followed by 3-, 10-, and 30-m resolution 90th percentile NDVI (PS_NDVIp90_MEAN, S2_NDVIp90_MEAN, L8_NDVIp90_MEAN; $R^2 = 0.37$) (Fig. 4; Table S10).

Which resolution and measures predicted bird species richness in

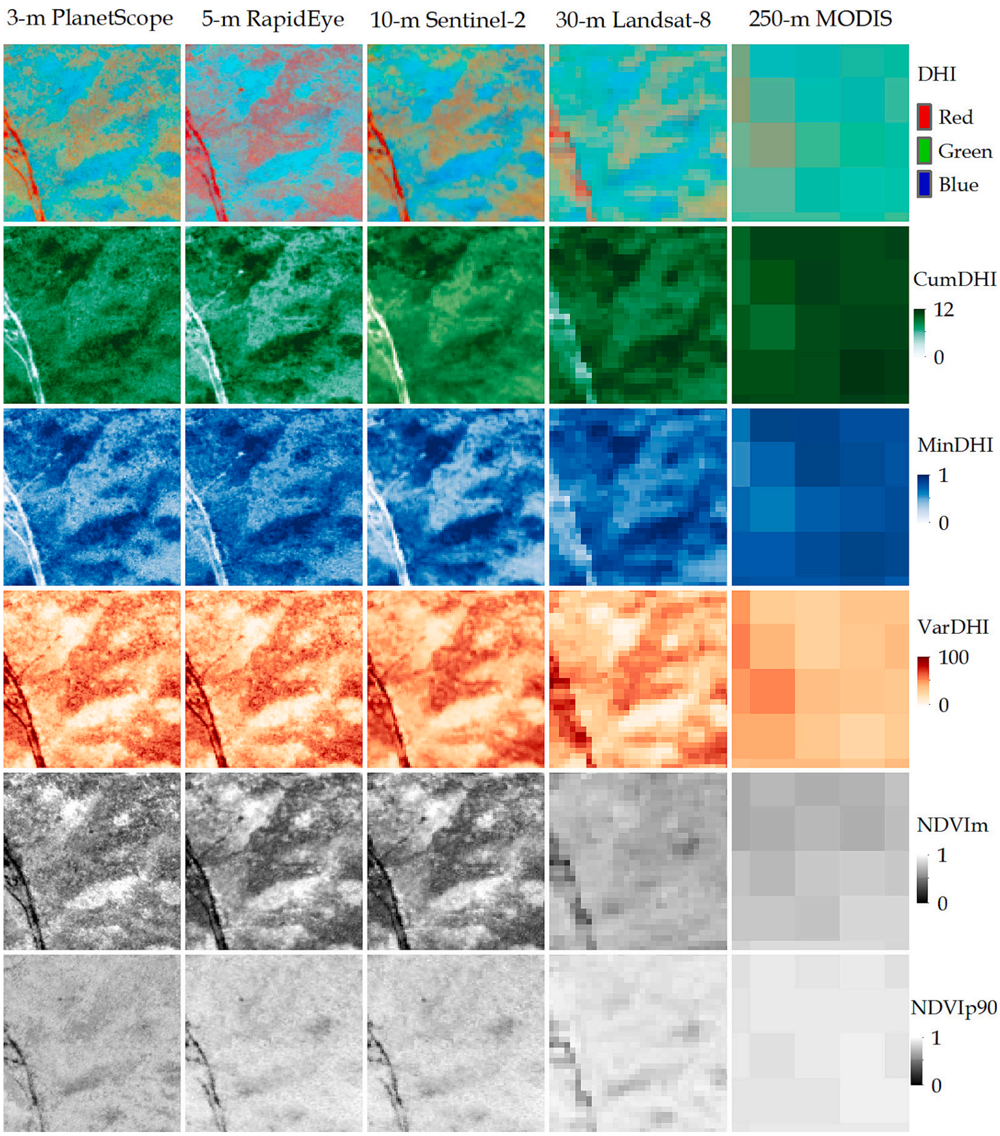

Fig. 3. Example of one NEON plot, the Great Smoky Mountains National Park (GRSM) which represents forest habitat. Shown are: the three DHIs (cumulative, minimum and variation), median NDVI, and the 90th percentile NDVI from PlanetScope, RapidEye, Sentinel-2, Landsat-8 and MODIS from 2017 to 2020. The top row shows a color composite of the three DHIs with cumulative DHI in green, minimum DHI in blue, and variation DHI in red (displayed with a percent clip stretch). Cumulative DHI is calculated as the sum of NDVI monthly median values, Minimum DHI as the minimum values and Variation DHI as the coefficient of variation of the monthly median time series. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

univariate models best differed among bird habitat guilds, but commonly included mean, homogeneity and uniformity measures derived from both cumulative and minimum DHI. In models of all bird species richness, homogeneity derived from RapidEye imagery was the strongest predictor, while in models of shrubland specialist richness, uniformity derived from RapidEye, was best. In models of forest and grassland specialist richness, the means of the DHIs performed best, however, the strongest predictor of forest specialist richness was derived from Landsat-8 and MODIS while for grasslands, measure derived from RapidEye performed best (Fig. 4).

3.3. Multivariate bird species richness models

Our multivariate analysis resulted in one top-ranked model for each grain (single resolution 3-, 5-, 10-, 30-, 250-m and multi-resolution 3-250 m) and guild (all bird species, forest, grassland and shrubland) ranked by the Bayesian information criterion (Table S11 – S14). Among multivariate models with single resolutions, the multivariate models with higher resolution measures (3–5-m) had greater explanatory power than the multivariate models with lower resolution measures (10–250-m) to predict all bird species richness and grassland specialist. However, for forest and shrublands specialists, both multivariate models with higher (3-5 m) and lower resolution measures (30–250-m) had high explanatory power (Table S15; Fig. 5).

When comparing multivariate models with single-resolution measures versus multivariate models with multi-resolution measures, our multi-resolution models of bird species richness outperformed all single-resolution models for all species, and for habitat guild specialists. The multi-resolution measures of vegetation productivity had moderate ($0.5 < R^2 < 0.7$) and high ($R^2 > 0.7$) explanatory power to predict all bird species richness and forest-specialist richness ($R^2 = 0.63$ and 0.72, respectively) and moderate and weak explanatory power to predict grassland- and shrubland-specialist richness ($R^2 = 0.53$ and 0.46, respectively) (Table S15; Fig. 5).

For all bird species, the top-ranked model ($R^2 = 0.63$) included five measures with 3- and 5-m resolution. The 5-m homogeneity texture of cumulative DHI contributed the most independent explanatory power (RE_CumDHI_HOM; 35.36%), followed by the 3-m standard deviation of the median NDVI (PS_NDVImedian_SD; (20.59%). For forest specialists, the top-ranked model included 3-, 5- and 30-m texture measures. For forest specialists, the top-ranked model included 3-, 30- and 250-m texture measures. The 3-m mean of the median NDVI contributed the most independent explanatory power (PS_NDVIp90_MEAN; 18.71%), followed by the 250-m homogeneity of the minimum DHI (MOD_MinDHI_HOM; 14.47%). For grassland specialists, the top-ranked model included 3- and 5-m texture measures and the 3-m mean of the median

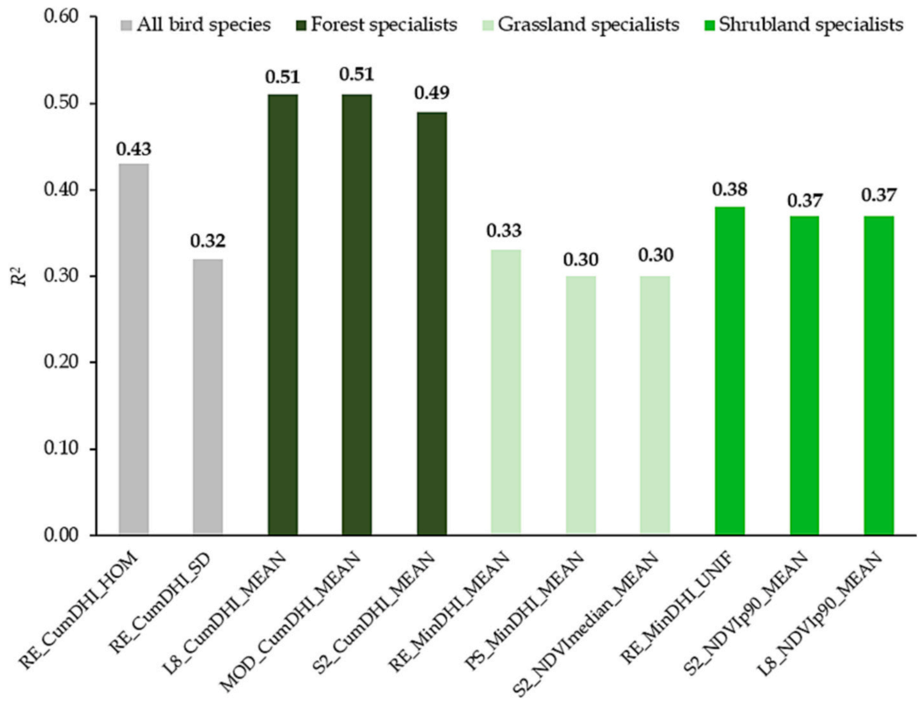

Fig. 4. Selection of top-ranking univariate linear regression models (for those with R^2 values >0.30) showing relationships between measures of vegetation productivity and the four habitat classes: all species combined and, forest, grassland and shrubland specialists. PS = PlanetScope, RE = RapidEye, S2 = Sentinel-2, L8 = Landsat-8, MOD = MODIS. SD=Standard deviation, UNIF = Uniformity, HOM = Homogeneity, and CORR = Correlation.

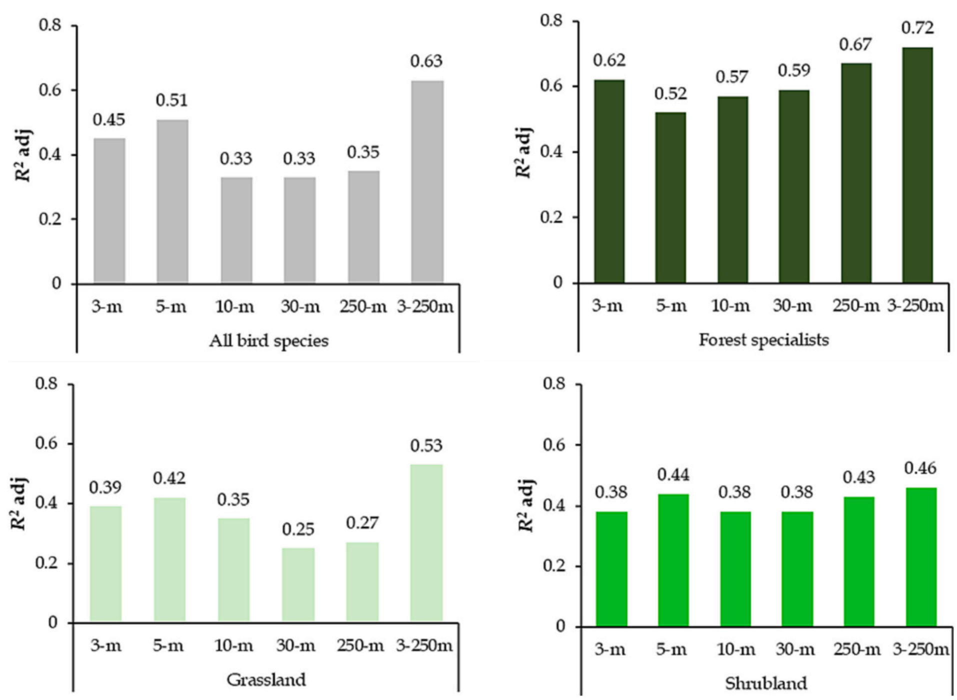

Fig. 5. Top-ranking multivariate models for all species combined and habitat guild specialists based on the original resolution of the data. Comparison between the multivariate single-resolution models for 3-, 5-, 10-, 30- and 250-m and the multivariate multi-resolution models (R^2 values of top models).

NDVI contributed the most independent explanatory power in the multi-grain model (PS_NDVImedian_MEAN; 59.10%), followed by 5-m mean of the variation DHI (RE_VarDHI_MEAN; 40.90%). For shrubland specialists, the top-ranked model included 3-, 5-, and 250-m texture measures and 5-m uniformity of the minimum DHI contributed the most independent explanatory power (RE_MinDHI_UNIF; 45.62%), followed by the 3-m mean of the 90th percentile NDVI (PS_NDVIp90_MEAN; 41.31%) (Fig. 6).

Our confidence intervals for spline correlograms of model residuals of total bird richness, forest, grassland and shrubland specialists, suggested low- to moderate-levels of spatial autocorrelation of lag distances up to approximately 500 km (Fig. S9 – S12), suggesting that significance levels may be somewhat inflated. However, spatial autocorrelation does not affect model coefficients or marginal effects, (Fletcher and Fortin,

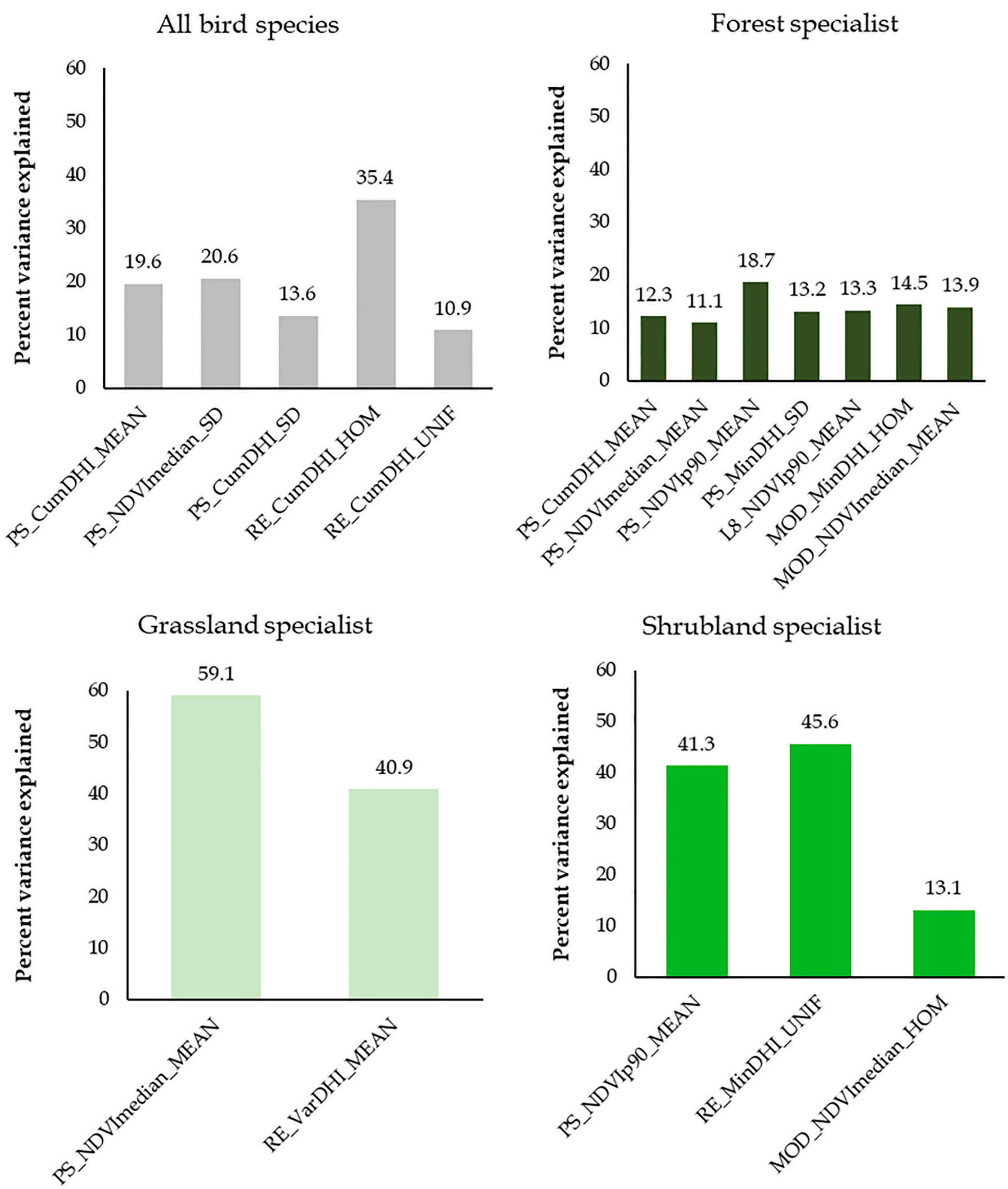

Fig. 6. Relative influence of predictors from hierarchical partitioning in each top-ranked model of bird species richness for all species combined, and habitat guild specialists. PS = PlanetScope, RE = RapidEye, S2 = Sentinel-2, L8 = Landsat-8, MOD = MODIS.

2018; Farwell et al., 2021).

3.4. *Comparison of measures based on original versus resampled resolution*

Our Spearman correlation analysis between original resolution and resampled productivity measures resulted in values ranging from 0.32 to 0.99. Correlations between measures based on RapidEye versus 5-m resampled, Sentinel-2 versus 10-m resampled, Landsat-8 versus 30-m resampled, and MODIS versus 250-m resampled PlanetScope data were on average 0.82, 0.83, and 0.83 and 0.59, respectively. In general, mean-derived measures had higher correlations than standard deviation, uniformity, homogeneity, and correlation (Table S16).

Among multivariate models with resampled single-resolution measures versus multivariate models with resampled multi-resolution measures, the multi-resolution models outperformed all single-resolution models for all species, and for forest and grassland specialists, reaching R^2 of 0.54, 0.66, and 0.41, respectively. However, for shrubland specialists, models with 5-m had greater explanatory power ($R^2 = 0.49$) (Table S17). In addition, according to our results, 100-m resolution measures did not outperform 3-m, 5-m, 10-m, 30-m and 250-m resolution measures in correlation analysis (except 100-m NDVImedian_SD for forest specialist bird richness; Table S18 – S21). The best multi-resolution models did not include any 100-m resolution measures, suggesting that 100-m spatial resolution measures did not improve our modeling approach (Table S22).

When comparing the performance of original multi-resolution models versus resampled multi-resolution models, original resolution performed best for all bird species and all habitat specialists. However, when comparing single resolution models, for all bird species, 10-, and 30-m resampled models (R^2 = 0.45 and 0.44, respectively) outperformed original models (R^2 = 0.33). For forest specialists, all multivariate models with single original resolutions outperformed resampled multi-resolution models, however, 10-m resampled measures (R^2 = 0.45) and 30-m resampled measures (R^2 = 0.44) outperformed original measures (R^2 = 0.33) for all bird species richness. In addition, 30-m resampled measures (R^2 = 0.31) and 5-m resampled measures (R^2 = 0.49) outperformed original measures in models of grasslands and shrublands specialists (Fig. 7).

4. Discussion

4.1. Measures of vegetation productivity derived from satellite sensors with different resolutions

Ours is the first study to calculate DHIs based on high resolution images (3, 5-m) resolution images. Previously, the DHIs have only been calculated based on medium-resolution Landsat (Carroll et al., 2022), or coarse resolution from MODIS (Hobi et al., 2017; Radeloff et al., 2019). We calculated multi-year composite DHIs (cumulative, minimum and variation), median NDVI and the 90th percentile NDVI from PlanetScope (3-m), RapidEye (5-m), Sentinel-2 (10-m), Landsat-8 (30-m) and MODIS (250-m). Based on these measures we calculated texture measures (mean, standard deviation, uniformity, homogeneity, and correlation).

We found that all three DHIs (cumulative, minimum and variation), median NDVI and percentile 90th NDVI were highly correlated among sensors (Table S4). However, the derived texture measures were weakly (correlation) to moderately (standard deviation, uniformity, homogeneity) correlated among sensors (Fig. S6). Texture measures exhibited strong differences among sensors due to their differences in spatial resolution. Landscape characteristics captured by texture metrics are likely to vary among image resolutions because spatial resolution defines the level of detail of the landscapes that is measured (Warner, 2011, Hall-Beyer, 2017a, 2017b). First-order texture measures, such mean, consider all the pixel values within the neighborhood but do not account for their spatial arrangement, the way 2nd order textures such as uniformity, homogeneity, and correlation do (Haralick et al., 1973).

4.2. Measures of vegetation productivity to predict bird species richness

We derived from the DHIs, median NDVI and 90th percentile NDVI texture measures to estimate bird species richness. Our measures provide information about spectral variability which characterizes habitat heterogeneity linked to bird species richness. Our findings support the spectral variability hypothesis (Palmer et al., 2000) in that spectral variability in our results was positively related to habitat heterogeneity and hence species richness. When characterizing habitat heterogeneity,

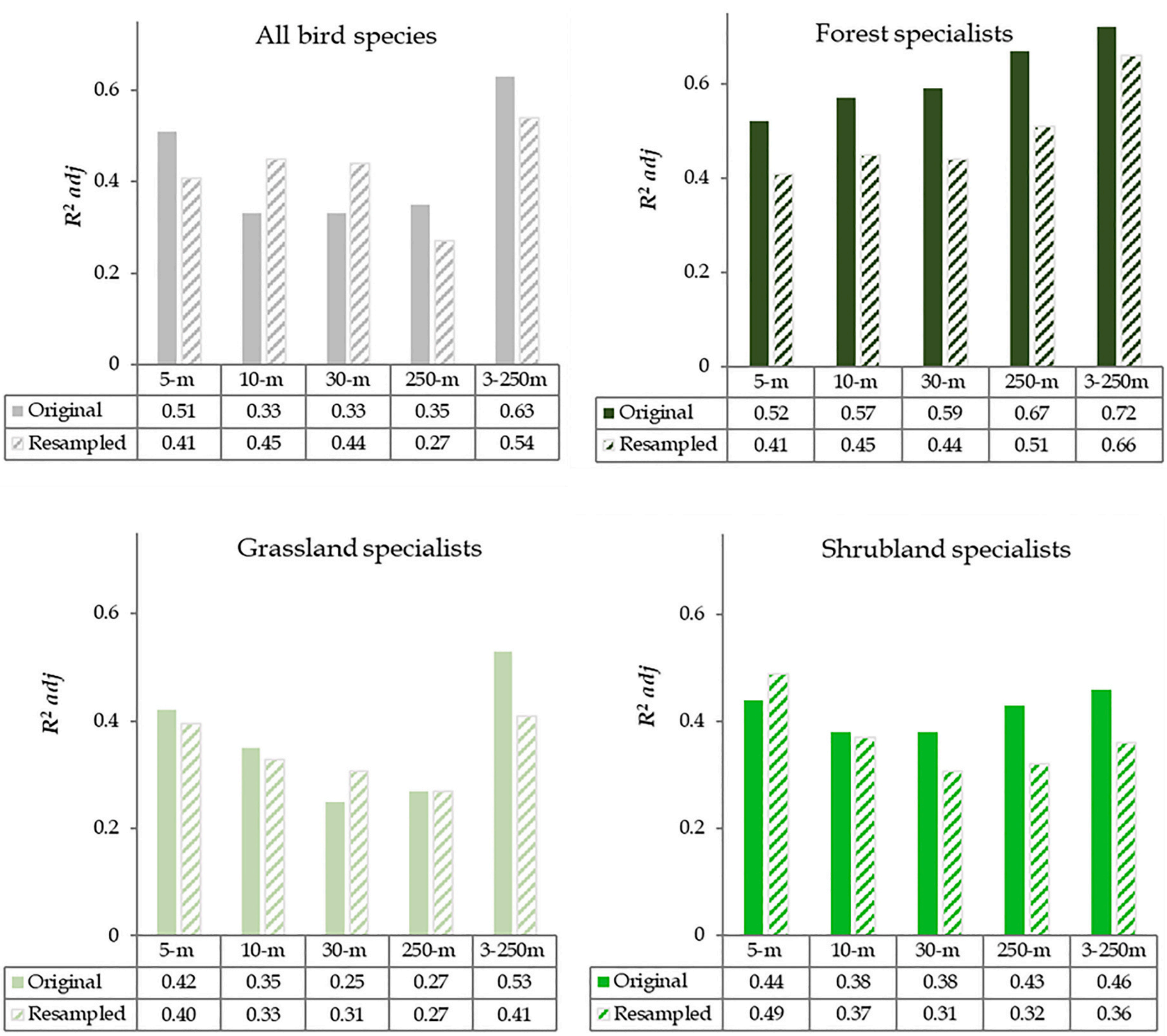

Fig. 7. R^2 values of top-ranking multivariate models for all species combined and for habitat guild specialists based on the resampled PlanetScope data. Comparison between the multivariate single-resolution models for 3-, 5-, 10-, 30-, and 250-m and the multivariate multi-resolution models.

texture measures are well-suited for capturing specific habitat features such as vegetation height and basal area (Tuominen and Pekkarinen, 2005), canopy structural properties (Estes et al., 2010), foliage-height diversity (Wood et al., 2012), and vegetation structure and composition (St-Louis et al., 2009; Campos et al., 2018; Farwell et al., 2021), which is why they improve broad-scale models of bird richness (Tuanmu and Jetz, 2015; Farwell et al., 2020).

Our single-spatial resolution measures predicted bird species richness very weak, weak and moderately well. Our positive relationship between remotely sensed productivity measures and both all-bird species richness and the richness of forest specialists were consistent with the more-individuals and habitat heterogeneity hypothesis. The more-individuals hypothesis predicts that species richness is higher where the total amount of available energy is higher because more productivity increase food availability and thus supporting more species (Leveau, 2019; Wright, 1983), although species richness sometimes declines at very high levels of energy (Mittelbach et al., 2001). The habitat heterogeneity hypothesis also explains species richness. Heterogeneity of vegetation types offers more ways to obtain resources and to provide refugia from adverse environmental conditions, resulting in an increased number of species (MacArthur, 1964; Fjeldsa et al., 2012).

However, we also found negative relationships for grassland, and shrubland specialists. This finding is consistent with some studies that found inverse relationship between heterogeneity and species diversity for these guilds in grasslands (Farwell et al., 2020; Tews et al., 2004). However, we also found negative relationships for grassland, and shrubland specialists. This finding is consistent with some studies that found inverse relationship between heterogeneity and species diversity for these guilds in grasslands (Farwell et al., 2020; Tews et al., 2004). However, in semi-arid ecosystems there is a positive relationship between texture measures and shrubland and grassland bird species richness (St-Louis et al., 2009). The negative relationship in grassland habitats may be due to grassland birds' sensitivity to patch area. For example, of 32 grassland obligate birds in North America, 16 are sensitive to the grassland patch size, and they either occur only in larger grassland patches, or their density is higher there. These species tend to avoid the edges of grasslands and have greater density away from the edges (Ribic et al., 2009). Similarly, shrubland birds avoid habitat edges (Rodewald and Vitz, 2010). Habitat edges are where image texture contrast is likely higher than in the center of patches where homogeneity is higher.

Spectral variability is influenced by both location and extent, and spectral variability characterized by a given spatial grain size is not necessarily linked to bird species richness (Schmidtlein and Fassnacht, 2017). For example, there is likely little correlation between spectral variability and bird species richness when that spectral variability stems from different agricultural crops, which provide little habitat for birds. On the other hand, apparently homogeneous spectral variability may be heterogeneous at sub-pixel levels. Habitats with little spectral variability may yet contain comparably high species richness (Schmidtlein and Fassnacht, 2017; Wilson et al., 2012).

4.3. Best performing resolution and measures to predict bird species guilds

In our univariate models of all bird species richness, grasslands and shrubland specialists, higher resolution measures performed best. For grassland and shrubland specialists, mean and uniformity from minimum DHI of 5-m RapidEye had the best R^2 (R^2 of 0.33 and 0.38, respectively). Some guilds are more likely to respond and be dependent on fine-scale habitat measures (i.e., grassland and shrubland) and are sensitive to how cumulative and minimum productivity are captured in the area (e.g., if by first or second order texture measures). We speculate that high spatial resolution (5-m) imagery captured microhabitat variations that are important for birds (vegetation density and height) (Jacobs et al., 2012). For example, individual trees could be captured at this spatial resolution.

In contrast, in univariate models of forest specialist richness, the mean cumulative DHI from Landsat-8 (30-m) and from MODIS (250-m) had the highest explanatory power ($R^2 = 0.51$).

Texture measures derived from medium resolution (10-m Sentinel-2 and 30-m Landsat) satellite imagery are strong predictors of bird species richness within forest habitats (Culbert et al., 2012; Farwell et al., 2021). However, medium spatial resolution data is too coarse to effectively capture finer features within shrubland and grassland habitats (Ali et al., 2016). In addition, globally, individual DHIs derived from MODIS (1-km) predicted bird species richness well, reaching Spearman correlations of 0.63, 0.83 and − 0.83 (Radeloff et al., 2019).

In addition to spatial resolution, the type of measure that performed best also differed among bird species guilds in univariate models. Cumulative DHI and minimum DHI had a better performance to predict bird species richness compared to variation DHI, median NDVI and 90th percentile NDVI. In forested areas, because vegetation productivity is high, cumulative and minimum DHIs are good indicators of vegetation productivity. The minimum DHI was a good predictor of bird species richness in Argentina (Nieto et al., 2015) and was the most important predictor of grassland bird species across the conterminous USA (Coops et al., 2009a). In general, in the US, the cumulative DHI has the highest predictive power in models of bird species richness, however it is highly dependent on the guild (Hobi et al., 2017).

Among the texture measures, the mean, homogeneity, and uniformity performed best. In first-order texture metrics (e.g., mean) high values indicate more productive areas. Second-order texture metrics are calculated from the gray-level co-occurrence matrix (Haralick et al., 1973). The second-order homogeneity and uniformity reflect homogeneity of the image. Homogeneity is high when adjacent pixels have similar values, and high uniformity means that certain pixel values occur frequently on adjacent pixels (Culbert et al., 2012). Similar to our findings, homogeneity is a good predictor of total bird species richness at 10-m and 30-m spatial resolution across the conterminous USA (Farwell et al., 2021).

4.4. High resolution measures versus low resolution measures to predict bird species richness

This is the first study to test measures of vegetation productivity based on cumulative, minimum and variation DHIs, median NDVI, and 90th percentile NDVI from high-resolution data in models of bird species richness. However, our finding that high-resolution satellite data had the greatest explanatory power in models of bird species richness in the US is consistent with results of similar models of bird species richness in other countries. For example, high resolution spatial data (2-m WorldView-2) had higher predictive power than lower resolution spatial data (10-m SPOT-5, 20-m SPOT-4, 30-m Landsat 5 and 250-m MODIS) when modeling bird species richness in woodlands of southwestern France (Sheeren et al., 2014). Similarly, 1-m resolution data had better performance for predicting bird species spatial distribution in Germany than 3-, 10-, 32-, 100-, 316- -and 1000-m resolution data (Gottschalk et al., 2011). In addition, in a forested ecosystem (pine) in Turkey, texture measures from 5-m RapidEye outperformed 10-m SPOT-5 and 15-m Aster in models of bird species richness (Ozdemir et al., 2018).

For complex environments, high-resolution data is needed to capture small elements (Lausch et al., 2015) because coarse resolution images have mixed pixels, and thus are not suited to capture habitat heterogeneity (Foody and Cox, 1994; Goetz et al., 2007; Saveraid et al., 2001). Coarse resolution imagery depicts landscapes as homogenized and captures only dominant landscape patches (Saura, 2002). Smaller objects, important for birds (i.e., trees) are not captured, affecting the quality of the bird biodiversity models (Sheeren et al., 2014).

4.5. Multi-resolution versus single resolution models to predict bird species richness

We compared the performance of the multi-resolution models versus 3-, 5-, 10-, 30-, and 250-m single spatial resolution models to predict total species richness and richness of specialists. Habitat selection in birds is hierarchical (Guisan and Thuiller, 2005; Jackson and Fahrig, 2012, 2015; Johnson, 1980), suggesting that habitat measures representing a range of resolutions are best suited for predicting bird distributions, especially when modeling multiple species. Our result strongly supports that assertion. Single resolution approaches may limit the effectiveness of the models because the best performing resolution that captures the spatial pattern of species are usually unknown (Cushman and McGarigal, 2004), and also, species may interact with their environments at different spatial scales at the same time (Lawler and Edwards, 2006). Thus, as predicted, our multi-resolution models of bird species richness performed better than single-scale models for all guilds. For all species combined and grassland and specialists, a combination of measures based on PlanetScope (3-m) and RapidEye (5-m) imagery performed best while for forest and shrubland specialists, a combination of measures from PlanetScope (3-m), RapidEye (5-m), Landsat-8 (30-m) and MODIS (250-m) imagery produced the best results (Fig. 6).

Our top-ranked multi-resolution models' forest and shrubland specialists, included both high- and low-resolution measures. This may reflect the hierarchical manner in which birds select habitat across multiple spatial scales (Guisan and Thuiller, 2005; Jackson and Fahrig, 2012, 2015). Coarser resolution landscape measures capture dominant vegetation classes (e.g., forest, shrubland) that determine territory selection at broad spatial scales, while higher resolution measures capture microhabitat features of vegetation structure and composition that influence fine-scale foraging and nesting site selection (Lawler and Edwards, 2006). In contrast, for grassland specialists, only high-resolution measures (3-m PlanetScope/5-m RapidEye) were included in top-ranked models. This may reflect the importance of microhabitat features in grassland-dominated landscapes (Fletcher and Koford, 2002). The 10–250 m resolution of Sentinel-2, Landsat-8 and MODIS are likely too coarse to effectively capture such microhabitats (Ali et al., 2016, Fisher and Davis, 2010).

5. Conclusion

By analyzing remotely-sensed vegetation productivity measures from multiple spatial resolutions in bird species richness models, we found that the best performing resolutions and measures differ among bird habitat guilds, emphasizing the importance of matching the spatial resolution of predictors to the species or guilds of interest. Our finding that habitat measures derived from higher resolution imagery (3-, 5-m) are more effective predictors of bird species richness than measures derived from lower resolution imagery (10-, 30-, and 250-m) is timely, given recent advances in the availability and accessibility of high-resolution satellite imagery. In addition, our finding that multi-resolution models of bird species richness outperform single resolution models is important, because most bird diversity and distribution models use single-resolution habitat measures, but ecological theory buttresses the use of multi-resolution models. Lastly, we demonstrate that models based on multi-sensor data performed better than resampled data, emphasizing the importance of the spectral characteristics of each sensor to retrieve measures of vegetation productivity. We recommend that future studies of bird diversity incorporate habitat variables derived from high- and coarse-resolution satellites to capture a range of habitat patterns and features across the hierarchy of scales at which birds select their habitat.

Credit author statement

E.M.O·S was responsible for processing the remote sensing analysis and writing the paper. V.C.R and A.M.P were responsible for creating the research design, writing, and editing. L.S·F, M.L.H., E.R., B.Z., AND N. C·C were responsible for writing and editing. All authors discussed the results and contributed to the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by NASA's Biodiversity Program (award 80NSSSC21K1348) and the USGS Landsat Science Team (award 140G0118C0009). We also thank Planet for providing the PlanetScope and RapidEye data. We thank the two anonymous reviewers who provided valuable comments that greatly improved this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2023.113661.

References

Ali, I., Cawkwell, F., Dwyer, E., Barrett, B., Green, S., 2016. Satellite remote sensing of grasslands: from observation to management. J. Plant Ecol. 9, 649–671.
Bar-Massada, A., Wood, E.M., Pidgeon, A.M., Radeloff, V.C., 2012. Complex effects of scale on the relationships of landscape pattern versus avian species richness and community structure in a woodland savanna mosaic. Ecography 35, 393–411.
Barnett, D.T., Duffy, P.A., Schimel, D.S., Krauss, R.E., Irvine, K.M., Davis, F.W., Gross, J. E., Azuaje, E.I., Thorpe, A.S., Gudex-Cross, D., Patterson, M., McKay, J.M., McCorkel, J.T., Meier, C.L., 2019a. The terrestrial organism and biogeochemistry spatial sampling design for the National Ecological Observatory Network. Ecosphere 10 (2), 1–23.
Barnett, D.T., Adler, P.B., Chemel, B.R., Duffy, P.A., Enquist, B.J., Grace, J.B., Harrison, S., Peet, R.K., Schimel, D.S., Stohlgren, T.J., Vellend, M., 2019b. The plant diversity sampling design for the National Ecological Observatory Network. Ecosphere 10 (2), 1–18.
Berry, S., Mackey, B., Brown, T., 2007. Potential applications of remotely sensed vegetation greenness to habitat analysis and the conservation of dispersive fauna. Pacific Conserv. Biol. 13, 120–127.
Bjornstad, O.N., Falck, W., 2001. Nonparametric spatial covariance functions: estimation and testing. Environ. Ecol. Stat. 8 (1), 53–70.
Booth, G.D., Niccolucci, M.J., Schuster, E.G., 1994. Identifying proxy sets in multiple linear regression: An aid to better coefficient interpretation. In: Research Paper INT-470. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah.
Brewer, M.J., Butler, A., Cooksley, S.L., 2016. The relative performance of AIC, AICc and BIC in the presence of unobserved heterogeneity. Methods Ecol. Evol. 7 (6), 679–692.
Campos, V.E., Gatica, G.M., Cappa, F.M., Giannoni, S.M., Campos, C.M., 2018. Remote sensing data to assess compositional and structural indicators in dry woodland. Ecol. Indic. 88, 63–70.
Carroll, K.A., Farwell, L.S., Pidgeon, A.M., Razenkova, E., Gudex-Cross, D., Helmers, D. P., Lewińska, K.E., Elsen, P.R., Radeloff, V.C., 2022. Mapping breeding bird species richness at management-relevant resolutions across the United States. Ecol. Appl. 32, 1–21.
Chakrabarti, A., Ghosh, J.K., 2011. AIC, BIC and Recent Advances in Model Selection, Philosophy of Statistics. Elsevier B.V.
Chevan, A., Sutherland, M., 1991. Hierarchical partitioning. Am. Stat. 45, 90–96.
Coops, N.C., Waring, R.H., Wulder, M.A., Pidgeon, A.M., Radeloff, V.C., 2009a. Bird diversity a predictable function of satellite-derived estimates of seasonal. J. Biogeogr. 36, 905–918.
Coops, N.C., Wulder, M.A., Iwanicka, D., 2009. Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. Remote Sens. Environ. 113, 668–679.
Coops, N.C., Kearney, S.P., Bolton, D.K., Radeloff, V.C., 2018. Remotely-sensed productivity clusters capture global biodiversity patterns. Sci. Rep. 8, 1–12.
Culbert, P.D., Radeloff, V.C., St-Louis, V., Flather, C.H., Rittenhouse, C.D., Albright, T.P., Pidgeon, A.M., 2012. Modeling broad-scale patterns of avian species richness across

the midwestern United States with measures of satellite image texture. Remote Sens. Environ. 118, 140–150.
Cushman, S.A., McGarigal, K., 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. Oikos 105, 117–124.
Estes, L.D., Okin, G.S., Mwangi, A.G., Shugart, H.H., 2008. Habitat selection by a rare forest antelope: a multi-scale approach combining field data and imagery from three sensors. Remote Sens. Environ. 112, 2033–2050.
Estes, L.D., Reillo, P.R., Mwangi, A.G., Okin, G.S., Shugart, H.H., 2010. Remote sensing of structural complexity indices for habitat and species distribution modeling. Remote Sens. Environ. 114, 792–804.
Farwell, L.S., Elsen, P.R., Razenkova, E., Pidgeon, A.M., Radeloff, V.C., 2020. Habitat heterogeneity captured by 30-m resolution satellite image texture predicts bird richness across the United States. Ecol Appl. 30 (8), e02157.
Farwell, L.S., Gudex-Cross, D., Anise, I.E., Bosch, M.J., Olah, A.M., Radeloff, V.C., Razenkova, E., Rogova, N., Silveira, E.M.O., Smith, M.M., Pidgeon, A.M., 2021. Satellite image texture captures vegetation heterogeneity and explains patterns of bird richness. Remote Sens. Environ. 253, 112175.
Fassnacht, F.E., Müllerová, J., Conti, L., Malavasi, M., Schmidtlein, S., 2022. About the link between biodiversity and spectral variation. Appl. Veg. Sci. 25, 1–13.
Fisher, R.J., Davis, S.K., 2010. From wiens to robel: a review of grassland-bird habitat selection. J. Wildl. Mgmt. 74, 265–273.
Fjeldsa, J., Bowie, R.C.K., Rahbek, C., 2012. The role of mountain ranges in the diversification of birds. Annu. Rev. Ecol. Evol. Syst. 43, 249–265.
Fletcher, R.J., Koford, R.R., 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. J. Wildl. Mgmt. 66, 1011–1022.
Fletcher, R., Fortin, M.-J., 2018. Spatial dependence and autocorrelation. In: Spatial Ecology and Conservation Modeling. Springer, Cham.
Foga, S., Scaramuzza, P.L., Guo, S., Zhu, Z., Dilley, R.D., Beckmann, T., Schmidt, G.L., Dwyer, J.L., Joseph Hughes, M., Laue, B., 2017. Cloud detection algorithm comparison and validation for operational landsat data products. Remote Sens. Environ. 194, 379–390.
Foody, G.M., Cox, D.P., 1994. Sub-pixel land-cover composition estimation using a linear mixture model and fuzzy membership functions. Int. J. Remote Sens. 15 (3), 619–631.
Goetz, S., Steinberg, D., Dubayah, R., Blair, B., 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. Remote Sens. Environ. 108, 254–263.
Gorelick, Noel, Hancher, Matt, Dixon, Mike, Simon, Ilyushchenko, Thau, David, Rebecca, Moore., 2017. Planetary-scale geospatial analysis for everyone. Remote Sens. Environ. 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031.
Gottschalk, T.K., Aue, B., Hotes, S., Ekschmitt, K., 2011. Influence of grain size on species-habitat models. Ecol. Model. 222, 3403–3412.
Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.
Guyot, G., Gu, X.F., 1994. Effect of radiometric corrections on NDVI determined from SPOT HRV and landsat TM data. Remote Sens. Environ. 49, 169–180.
Hall-Beyer, M., 2017. Practical guidelines for choosing GLCM textures to use in landscape classification tasks over a range of moderate spatial scales. Int. J. Remote Sens. 38, 1312–1338.
Haralick, R.M., Shanmugam, K., Dinstein, I., 1973. Textural features for image classification. IEEE Trans. Syst. Man. Cybern. SMC-3, 610–621.
Hall-Beyer, M., 2017. GLCM texture: a tutorial v. 3.0 March 2017. University of Calgary, Calgary, Alberta, Canada.
Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M., Radeloff, V.C., 2017. A comparison of dynamic habitat indices derived from different MODIS products as predictors of avian species richness. Remote Sens. Environ. 195, 142–152.
Hobi, M.L., Farwell, L.S., Dubinin, M., Kolesov, D., Pidgeon, A.M., Coops, N.C., Radeloff, V.C., 2021. Patterns of bird species richness explained by annual variation in remotely sensed dynamic habitat indices. Ecol. Indic. 127, 107774.
Jackson, H.B., Fahrig, L., 2012. What size is a biologically relevant landscape? Landsc. Ecol. 27, 929–941.
Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63.
Jacobs, R.B., Thompson, F.R., Koford, R.R., La Sorte, F.A., Woodward, H.D., Fitzgerald, J. A., 2012. Habitat and landscape effects on abundance of Missouri's grassland birds. J. Wildl. Manag. 76 (2), 372–381.
Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.
Lausch, A., Blaschke, T., Haase, D., Herzog, F., Syrbe, R.U., Tischendorf, L., Walz, U., 2015. Understanding and quantifying landscape structure–a review on relevant process characteristics, data models and landscape metrics. Ecol. Model. 295, 31–41.
Lawler, J.J., Edwards, T.C., 2006. A variance-decomposition approach to investigating multiscale habitat associations. Condor 108, 47–58.
Leveau, L.M., 2019. Primary productivity and habitat diversity predict bird species richness and composition along urban-rural gradients of Central Argentina. Urban For. Urban Green. 43, 126349.
Lin, G., Wolfe, R.E., Zhang, P., Tilton, J.C., Dellomo, J.J., Tan, B., 2019. Thirty-six combined years of MODIS geolocation trending. Proc. SPIE 1112715, 41.
Lu, D., Batistella, M., 2005. Exploring TM image texture and its relationships with biomass estimation in Rondônia, Brazilian Amazon. Acta Amaz. 35, 249–257.
MacArthur, R.H., 1964. Environmental factors affecting bird species diversity. Am. Nat. 98, 387–396.
Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Ecoscience 16, 238–247.
McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. Landsc. Ecol. 31, 1161–1175.
Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? Ecology 82, 2381–2396.
Moore, D.S., Notz, W.I., Flinger, M.A., 2013. The basic practice of statistics. In: 6th ed. W. H. Freeman and Company, New York, NY, p. 138.
Nagendra, H., 2001. Using remote sensing to assess biodiversity. Int. J. Remote Sens. 22, 2377–2400.
Nagendra, H., Rocchini, D., 2008. High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. Biodivers. Conserv. 17, 3431–3442.
NEON, 2020. Breeding landbird point counts. DP1.10003.001. In: Data Product. NEON, Batelle, Boulder, CO, USA (Accessed date: 23 January 2020). http://data.neonscience.org.
Nieto, S., Flombaum, P., Garbulsky, M.F., 2015. Can temporal and spatial NDVI predict regional bird-species richness? Glob. Ecol. Conserv. 3, 729–735.
Ozdemir, I., Mert, A., Ozkan, U.Y., Aksan, S., Unal, Y., 2018. Predicting bird species richness and micro-habitat diversity using satellite data. For. Ecol. Manag. 424, 483–493.
Palmer, M.W., Wohlgemuth, T., Earls, P., Arévalo, J.R., Thompson, S., 2000. Opportunities for long-term ecological research at the Tallgrass Prairie Preserve, Oklahoma. In: Lajtha, Kate, Vanderbilt, Kristin (Eds.), Cooperation in Long Term Ecological Research in Central and Eastern Europe. ILTER Regional Workshop, 22-25 June, 1999, Budapest, Hungary. Oregon State University, Corvallis, OR, pp. 123–128. Retrieved 17 May 2021.
Planet Team, 2021. Planet Application Program Interface: In Space for Life on Earth. https://api.planet.com.
Radeloff, V.C., Dubinin, M., Coops, N.C., Allen, A.M., Brooks, T.M., Clayton, M.K., Costa, G.C., Graham, C.H., Helmers, D.P., Ives, A.R., Kolesov, D., Pidgeon, A.M., Rapacciuolo, G., Razenkova, E., Suttidate, N., Young, B.E., Zhu, L., Hobi, M.L., 2019. The dynamic habitat indices (DHIs) from MODIS and global biodiversity. Remote Sens. Environ. 222, 204–214.
R Core Team, 2020. R: a Language and Environment for Statistical Computing. R Foundation Project, GNU project, Boston, Massachussetts, USA.
Ribic, C.A., Koford, R.R., Herkert, J.R., Hl, D., Johnson, N.D., Niemuth, D.E., Naugle, K. K., Bakker, D.W., Sample, R.B., Renfrew., 2009. Area sensitivity in north american grassland birds: patterns and processes. The Auk. 126, 233–244.
Rodewald, A.D., Vitz, A.C., 2010. Edge and area sensitivity of shrubland birds. J. Wildl. Manag. 69 (2), 681–688.
Saura, S., 2002. Effects of minimum mapping unit on land cover data spatial configuration and composition. Int. J. Remote Sens. 23, 4853–4880. https://doi.org/10.1080/01431160110114493.
Saveraid, E.H., Debinski, D.M., Kindscher, K., Jakubauskas, M.E., 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the greater yellowstone ecosystem, USA. Landsc. Ecol. 16, 71–83.
Schmidtlein, S., Fassnacht, F.E., 2017. The spectral variability hypothesis does not hold across landscapes. Remote Sens. Environ. 192, 114–125. https://doi.org/10.1016/j.rse.2017.01.036.
Sheeren, D., Bonthoux, S., Balent, G., 2014. Modeling bird communities using unclassified remote sensing imagery: effects of the spatial resolution and data period. Ecol. Indic. 43, 69–82.
Steven, M.D., Malthus, T.J., Baret, F., Xu, H., Chopping, M.J., 2003. Intercalibration of vegetation indices from different sensor systems. Remote Sens. Environ. 88, 412–422.
St-Louis, V., Pidgeon, A.M., Clayton, M.K., Locke, B.A., Bash, D., Radeloff, V.C., 2009. Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico. Ecography 32, 468–480.
St-Louis, V., Pidgeon, A.M., Radeloff, V.C., Hawbaker, T.J., Clayton, M.K., 2006. High-resolution image texture as a predictor of bird species richness. Remote Sens. Environ. 105, 299–312.
Suttidate, N., Hobi, M.L., Pidgeon, A.M., Round, P.D., Coops, N.C., Helmers, D.P., Keuler, N.S., Dubinin, M., Bateman, B.L., Radeloff, V.C., 2019. Tropical bird species richness is strongly associated with patterns of primary productivity captured by the dynamic habitat indices. Remote Sens. Environ. 232, 111306.
Suttidate, N., 2016. Spatial patterns of primary productivity derived from the dynamic habitat indices predict patterns of species richness and distributions in the tropics. University of Wisconsin-Madison. Dissertation.
Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of key-stone structures. J. Biogeogr. 31, 79–92.
Thibault, K., 2020. TOS Protocol ad Procedure: BRD-Breeding landbird abundance and diversity. NEON (National Ecological Observatory Network). NEON Document # 014041 K.
Tuanmu, M.N., Jetz, W., 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. Glob. Ecol. Biogeogr. 24, 1329–1339.
Tuominen, S., Pekkarinen, A., 2005. Performance of different spectral and textural aerial photograph features in multi-source forest inventory. Remote Sens. Environ. 94, 256–268.
Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. 20, 171–197.
Warner, T., 2011. Kernel-based texture in remote sensing image classification. Geogr. Compass 5, 781–798.
Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2013. Image texture predicts avian density and species richness. PLoS One 8.

Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sens. Environ. 121, 516–526.

Woodcock, C.E., Strahler, A.H., 1987. The factor of scale in remote sensing. Remote Sens. Environ. 21, 311–332.

Zhang, C., Cai, D., Guo, S., Guan, Y., Fraedrich, K., Nie, Y., Liu, X., Bian, X., 2016. Spatial-temporal dynamics of China's terrestrial biodiversity: a dynamic habitat index diagnostic. Remote Sens. 8, 7–9.

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23, 796–802.

Wright, D.H., 1983. Species-energy theory : an extension of species-area theory. Oikos 41, 496–506.

Wu, J., Shen, W., Sun, W., Tueller, P.T., 2002. Empirical patterns of the effects of changing scale on landscape metrics. Landsc. Ecol. 17, 761–782.