The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness

Scott J Goetz, Mindy Sun, Scott Zolkos, Andy Hansen and Ralph Dubayah

1 Woods Hole Research Center, 149 Woods Hole Road, Woods Hole, MA 02540, USA
2 Department of Ecology, Montana State University, Bozeman, MT 59717, USA
3 Department of Geographical Sciences, University of Maryland, College Park, MD 20740, USA

E-mail: sgoetz@whrc.org

Received 18 September 2013, revised 17 February 2014
Accepted for publication 4 March 2014
Published 19 March 2014

Abstract
Recent advances in remote sensing and ecological modeling warrant a timely and robust investigation of the ecological variables that underlie large-scale patterns of breeding bird species richness, particularly in the context of intensifying land use and climate change. Our objective was to address this need using an array of bioclimatic and remotely sensed data sets representing vegetation properties and structure, and other aspects of the physical environment. We first build models of bird species richness across breeding bird survey (BBS) routes, and then spatially predict richness across the coterminous US at moderately high spatial resolution (1 km). Predictor variables were derived from various sources and maps of species richness were generated for four groups (guilds) of birds with different breeding habitat affiliation (forest, grassland, open woodland, scrub/shrub), as well as all guilds combined. Predictions of forest bird distributions were strong ($R^2 = 0.85$), followed by grassland (0.76), scrub/shrub (0.63) and open woodland (0.60) species. Vegetation properties were generally the strongest determinants of species richness, whereas bioclimatic and lidar-derived vertical structure metrics were of variable importance and dependent upon the guild type. Environmental variables (climate and the physical environment) were also frequently selected predictors, but canopy structure variables were not as important as expected based on more local to regional scale studies. Relatively sparse sampling of canopy structure metrics from the satellite lidar sensor may have reduced their importance relative to other predictor variables across the study domain. We discuss these results in the context of the ecological drivers of species richness patterns, the spatial scale of bird diversity analyses, and the potential of next generation space-borne lidar systems relevant to vegetation and ecosystem studies. This study strengthens current understanding of bird species–climate–vegetation relationships, which could be further advanced with improved canopy structure information across spatial scales.

Keywords: canopy, climate, diversity, energy, habitat, lidar, remote sensing, scale, structure, breeding bird survey

1. Introduction

Ecologists have long sought to explain the distribution patterns of species diversity, which is an increasingly important
Figure 1. Distribution of BBS routes throughout North America and the number of GLAS lidar shots within 200 m of each route (upper left). The inset details the locations of the GLAS shots (right) and the histogram shows their height (m) distribution (lower left).

research goal as climate change is expected to alter these patterns considerably (e.g. Parmesan 2006, Bellard et al 2012). Animal species richness and abundance distribution patterns have often been explained in terms of environmental variables, including climate and vegetation properties (e.g. Kerr 2001, Ricklefs 2004, Ceballos and Ehrlich 2006, Mittelbach 2010). Past work hypothesized animal species richness is more strongly related to climate and energy (e.g. productivity) at large spatial scales but more closely related to habitat diversity at regional to local scales (Blackburn and Gaston 1996, Currie et al 1999, Deppe and Rotenberry 2008, Kerr 2001, Kerr and Packer 1997, Mittelbach et al 2001). The relative importance of these environmental variables for predicting bird species richness has been explored at various scales (e.g. Cueto and Casenave 1999, Saura et al 2004, Coops et al 2009, Hinsley et al 2009, Hansen et al 2011, Bar-Massada et al 2012, Fitterer et al 2012), but is still not well defined across scales. This is partly because measurements of vertical habitat heterogeneity and canopy structure (i.e. the horizontal and vertical distribution of canopy elements) have not been widely or consistently available across a range of locations, despite having long been recognized as important determinants of microclimates and microhabitats, and consequently the abundance and distribution of species (MacArthur and MacArthur 1961, Whittaker et al 2001).

Light detection and ranging (lidar) is advancing field-based understanding of these ecological interactions by providing novel information on spatial and vertical canopy structure and the impact of this structure on habitat diversity and quality (Bergen et al 2009, Lefsky et al 2002, Turner et al 2003, Vierling et al 2008). There is now a rapidly growing number of studies utilizing airborne lidar for biodiversity research, and many studies have found moderate to strong relationships between remotely sensed vegetation canopy structure, habitat quality, species richness and abundance, and habitat use (Bradbury et al 2005, Clawges et al 2008, Goetz et al 2010, 2007, Hill et al 2004, Lesak et al 2011, Seavy et al 2009, Swatantran et al 2012). However, these studies have been limited because airborne lidar data is generally not available over large areas. Consequently it has been difficult to test hypotheses relating the impact of variations in canopy structure to bird species richness patterns over large scales in a systematic fashion. A unique global vegetation canopy structure data set was acquired from space by GLAS (GeoScience Laser Altimetry System) onboard ICESat (the Ice, Cloud, and Land Elevation Satellite) from 2003 to 2009 (Schutz et al 2005). The GLAS data set provides the first opportunity to explore the importance of structure relative to other vegetation properties over large spatial extents and across broad gradients in climate and other environmental factors.

Here we investigate the patterns of breeding bird species richness across the coterminous United States and southern Canada, a domain established by the existence of well-documented bird observation data sets provided by the North American Breeding Bird Survey (BBS) (Pardieck and Sauer 2007, Ralph et al 1995) (figure 1). We predict species richness
using models that incorporate a range of environmental and vegetation variables, and assess the relative importance of different influences on bird richness patterns across the study domain. Important aspects of this work include; (i) derivation and use of a range of satellite remote sensing variables, including vegetation canopy structure metrics, (ii) application of climate data that capture extremes and variability as well as mean conditions, (iii) application of advanced machine learning methods (ensembles of regression trees) for data mining and predictive model development within buffer zones surrounding BBS routes, (iv) robust model results and cross validation, (v) production of continuous, relatively high resolution (1 km) maps of species richness for various bird habitat guilds. Whereas some of these topics have been explored in past biodiversity research (see above), few have incorporated all of these elements or considered the relative importance of factors driving species richness patterns consistently across large spatial extents and a diversity of habitat types.

2. Methods

We assessed 47 bioclimatic and vegetation predictor variables of bird species richness (our response variable) for different guild types and in aggregate. We explored statistical associations and the strength of Pearson correlation coefficients for each predictor variable with species richness. We also used Random Forests, a regression tree method that calculates the average of an ensemble of individual trees using bootstrapped sampling (Cutler et al. 2007), to predict species richness. When compared against other species distribution models, Random Forests has consistently performed well (e.g. Lawler et al. 2006, Cutler et al. 2007). One advantage of the random forest method is that provides us a mechanism for interpreting how important each of the predictor variables are (i.e. their explanatory power) and how results change as predictor variables are changed (so-called partial dependence plots, described below).

2.1. Bird species richness variables

2.1.1. Breeding bird survey. We used data acquired, compiled and distributed by the BBS, which was launched in 1966 to characterize avian population trends along survey routes through time (Parideck and Sauer 2007, Ralph et al. 1995). Bird counts are conducted annually at the peak of the nesting season along ∼4100 randomly selected routes throughout the United States and Canada (www.pwrc.usgs.gov/bbs). Along each 40 km route, a trained observer conducts stops about every kilometer and records all birds heard or seen within a 3-min period. The BBS data are publically available (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles).

We note that a potential source of error in using BBS data to derive species richness is the lack of complete detectability of all species that occur along a route (Boulinier et al. 1998). Nichols et al (1998) developed a series of estimators based on capture–recapture theory to account for incomplete detection among species. The approach, however, requires assumptions that may not be met on BBS routes (e.g. closed populations, equal detection probabilities along routes) and other studies have found results of continental scale bird richness had similar results with and without the correction (Hansen et al. 2011, Phillips et al. 2010). Thus, we elected not to apply detectability corrections here.

We used the yearly summary data for each route for the years 2004–2006 (inclusive), which most closely matched the timeframe of the other data sets (predictor variables) with which we were working. Only routes and species with all three years of data were used. Bird species richness was thus derived for each of more than 3000 BBS routes in the coterminous US with a full suite of predictor variable data. We summed bird observations across all stops along each route for all three years. The number of unique species recorded totaled 668. We then used these species richness estimates as the response variable in the model development and analyses that follow.

2.1.2. Bird habitat guilds. We categorized and independently analyzed richness of bird species within breeding habitat groups (guilds) using the system developed by Peterjohn and Sauer (1993). We focus on four habitat guilds (forest, open woodland, grassland and scrub) comprising 69% of the total number of observed individuals and 61% of the total number of species (table 1). These guilds were also most broadly geographically distributed and most relevant in terms of terrestrial vegetation habitat, allowing analyses of the greatest number of bird species across a broad range of vegetated habitat types and ensuring a sufficient number of observations for statistically robust analyses.

2.1.3. Predictor variables. The predictor variables were selected to represent a spectrum of habitat characteristics that could potentially influence the richness of bird species in any particular area. We separated these into three broad categories: physical environment (20 climate and topography variables),

| Table 1. Bird breeding habitat guilds, with the number of bird species, their abundance, and the number of BBS routes with data for that specific guild. The top four guilds were selected for analysis. |
|--------|----------|----------------|------------------|
| Habitat guild | Routes | Species| Individuals |
| Forest | 1239 | 123/20 | 969,401 |
| Open woodland | 1308 | 105/20 | 2,036,529 |
| Grassland | 1285 | 60/6 | 941,448 |
| Scrub | 1286 | 45/7 | 313,590 |
| Deserts | 68 | 8 | 8,034 |
| Town | 1223 | 12 | 760,215 |
| Shore-line | 320 | 45 | 45,030 |
| River/stream | 197 | 3 | 1,457 |
| Lake/pond | 1231 | 55 | 403,344 |
| Ocean | 17 | 32 | 5,606 |
| Marsh | 1203 | 59 | 665,849 |
| Top 4 guilds | — | 333 | 4,260,968 |
| Other guilds | — | 214 | 1,889,535 |
| Top 4% of total | — | 61% | 69% |

a The number of species considered in this study.

b The number of species from Matthews et al (2011) considered in this study.
Table 2. Naming convention and brief description of the predictor variables and their source. Variables are organized according to broad categories including canopy structure, (other) vegetation properties, and physical environment. Elevation and all of the structure variables are in units of height (m) with the exception of COMP, VDR, Npeaks (unitless), and AreaBE, AreaCD (m²). Units of temperature (°C) and precipitation (mm) are used. VCF, Life Form, and Tree Leaf metrics are proportional (%). Biomass is (Mg ha⁻¹) and NPP (gC m⁻² yr⁻¹).

| Variable name | Variable description | Source |
|---------------|----------------------|--------|
| Canopy structure | CH | Canopy height | GLAS lidar |
| | HOME | Median energy of the lidar waveform | GLAS lidar |
| | COMP | Waveform complexity | GLAS lidar |
| | Npeaks | Number of peaks in the waveform | GLAS lidar |
| | AmpMax | Maximum amplitude of the waveform | GLAS lidar |
| | AreaBE | Area under the waveform | GLAS lidar |
| | CD | Height (depth) of the canopy layer | GLAS lidar |
| | AreaCD | Energy under the canopy layer | GLAS lidar |
| | VDR | Canopy vertical distribution ratio | GLAS lidar |
| Vegetation properties | NPP | Net primary productivity | MODIS-17A3 |
| | EVIarea | Integrated EVI during the growing season | MODIS-12Q2 |
| | VCF | Vegetation continuous fields (canopy cover) | MODIS-44B |
| | Biomass | Biomass density | CONUS |
| | LFcrop | Life form: crops | SYNMAP |
| | LFgrass | Life form: grass | SYNMAP |
| | LFshrub | Life form: shrub | SYNMAP |
| | LFtree | Life form: trees | SYNMAP |
| | LForban | Life form: urban | SYNMAP |
| | LLmixed | Tree leaf longevity: mixed | SYNMAP |
| | LLeverg | Tree leaf longevity: evergreen | SYNMAP |
| | LLdecid | Tree leaf longevity: deciduous | SYNMAP |
| | LTbroad | Tree leaf type: broad | SYNMAP |
| | LTmixed | Tree leaf type: mixed | SYNMAP |
| | LTneedle | Tree leaf type: needle | SYNMAP |
| Physical environment | SRTM | Elevation (meters) | SRTM |
| | bio1 | Annual mean temperature | WorldClim |
| | bio2 | Mean diurnal range (mean of monthly values) | WorldClim |
| | bio3 | Isothermality | WorldClim |
| | bio4 | Temperature seasonality | WorldClim |
| | bio5 | Max temperature of warmest month | WorldClim |
| | bio6 | Min temperature of coldest month | WorldClim |
| | bio7 | Temperature annual range | WorldClim |
| | bio8 | Mean temperature of wettest quarter | WorldClim |
| | bio9 | Mean temperature of driest quarter | WorldClim |
| | bio10 | Mean temperature of warmest quarter | WorldClim |
| | bio11 | Mean temperature of coldest quarter | WorldClim |
| | bio12 | Annual precipitation | WorldClim |
| | bio13 | Precipitation of wettest month | WorldClim |
| | bio14 | Precipitation of driest month | WorldClim |
| | bio15 | Precipitation seasonality | WorldClim |
| | bio16 | Precipitation of wettest quarter | WorldClim |
| | bio17 | Precipitation of driest quarter | WorldClim |
| | bio18 | Precipitation of warmest quarter | WorldClim |
| | bio19 | Precipitation of coldest quarter | WorldClim |

vegetation properties (15 variables), and canopy structure (9 variables). We considered structure metrics separately because they have been the subject of much interest in the context of three-dimensional habitat heterogeneity, as opposed to the two (horizontal) dimensions represented by the other variables, but also because they were derived from a satellite sensor that provides samples as opposed to wall-to-wall coverages (images). These variables are listed in table 2 and are described in more detail below. Because our focus was on physical environment and vegetation, we did not consider detailed predictors of human impact such as housing density, roads or impervious cover. These factors have been well
examined by other studies and been shown to sometimes have strong local effects on bird communities (Beaudry et al. 2013, Pidgeon et al. 2007, Suarez-Rubio et al. 2013).

2.1.4. Physical environment variables. We used the WorldClim data set, which is comprised of global climate map layers representing the years 1950 to 2000 at 1 km spatial resolution (Hijmans et al. 2005). We used all variables, representing precipitation, temperature, annual bioclimatic trends (e.g., annual precipitation), seasonality (e.g., annual range in temperature) and extreme or limiting environmental factors (e.g., temperature of the coldest month) (table 2).

Topographic information was derived from the Shuttle Radar Topography Mission (SRTM) collection 4 data set (Farr et al. 2007). The spatial resolution of the SRTM data within the coterminous United States is 30 m. We note that because the SRTM data set is derived from interferometric radar imaging, it does not represent true ground surface topography for areas with vegetative cover but rather values that convolve canopy volumetric scattering with surface elevation. For our purposes these distinctions are not critical, particularly since vegetation properties (including canopy height) were independent predictors.

2.1.5. Vegetation property variables. Vegetation cover type information was derived from SYNMAP (Jung et al. 2006), a global land cover map at 1 km spatial resolution that defines vegetation functional groups by life form class, tree leaf type, and tree leaf longevity (table 2). We calculated the proportional amounts of each cover variable, categorized as a particular vegetation functional group, within a 100 m buffer surrounding each BBS route (i.e. 200 m across).

MODIS Enhanced Vegetation Index (EVI) is a spectral vegetation index responsive to canopy reflectance, light absorption and photosynthetic capacity (Huete et al. 2002). We calculated EVI from MODIS canopy reflectance products that have been corrected for variability in solar and viewing angles (Ju et al. 2010). These data sets are 1 km resolution, as are the other MODIS products we used here, spanning the years on which we focused (2004–2006). For our analyses, EVI was averaged throughout the growing season to reduce issues with cloud cover. Growing season start, end and duration were derived from the MODIS phenology products (Ganguly et al. 2010).

The amount of tree canopy cover within each 500 m cell across the study domain was derived from the MODIS vegetation continuous fields (VCF) products (Hansen et al. 2005) for the years 2003 to 2005. We used VCF collection 4 (C4), version 3, and averaged the values temporally over the 3 year period to match the BBS observations while incorporating interannual variability.

Aboveground live forest biomass of the United States and Alaska was based on a map produced by the United States Forest Service (USFS) that used a combination of FIA (Forest Inventory and Analysis) plot data and MODIS reflectance values at 250 m resolution (Blackard et al. 2008).

We also used the MODIS-based net primary productivity (NPP) product, derived from a simplified light use efficiency model using other MODIS products including canopy light absorption and incident radiation (Running et al. 2004). We used the collection 5.1 product covering the years 2004 to 2006, at a resolution of 1 km. We used MODIS NPP rather than gross primary production (GPP), as per earlier studies (e.g. Coops et al. 2009, Phillips et al. 2010), because the two variables were highly correlated ($r = 0.9$) and NPP was of more relevant to previous work on productivity—diversity relationships (e.g. Mittelbach 2010, Cusens et al. 2012).

2.1.6. Canopy structure metrics. Satellite-based lidar data from GLAS were used to derive metrics for vegetation canopy structure. We used GLAS data from shortly after launch in 2003 through 2008. The GLAS laser has an ellipsoidal footprint of approximately 65 m, spaced about 172 m apart along the orbital track. We used the L1A Global Altimetry (GLA01) and the L2 Global Land Surface Altimetry (GLA14) data sets, from which we extracted vertical waveform data, signal beginning, signal end, noise metrics, and other variables. Waveform characteristics from each GLAS shot were analyzed and quality screened (appendix A) to derive a series of metrics that characterize the vertical distribution of canopy elements (leaves, branches, boles). These metrics are summarized in table 2, but some of the more relevant ones include vegetation canopy height (CH), the height of the median amount of energy returned (HOME), and a measure of how the observed waveform diverges from a Gaussian shape after reflectance from the surface (complexity). Specifics on the derivation of these metrics, based on airborne lidar data, are provided in Goetz et al. (2010).

2.2. Geospatial data processing

To construct predictor variable data sets that describe the average conditions for each BBS route, we established a 200 m buffer around the routes (roughly equivalent to BBS observer detection limits) and spatially intersected them with each predictor variable (figure 2). The mean value of the predictor variables was then extracted and uniquely associated with each route. In the case of discrete predictor variables (e.g. the SYNMAP variables), each BBS route was ascribed the value of the percent of area within the surrounding buffer that was categorized as some particular vegetation functional group. As part of the derivation of the various lidar metrics, we performed extensive screening to remove shots that did not produce adequate waveforms for characterizing canopy structure (appendix A). We then extracted all shots located within the 200 m buffer and calculated the mean value of the various structure metrics for each route. Routes in which there were fewer than ten GLAS shots were excluded from further analysis to avoid inadequately capturing spatial variability.

2.2.1. Random Forests. In Random Forests, we used 500 trees, each built using bootstrapped samples of the data and a randomly selected set of input variables, with an internal unbiased estimate of the generalization error produced (see appendix A). We performed each of these analyses in the R language for statistical computing (R Development Core Team 2009). Only routes where data from each predictor variable was available were used for further analysis. The
Figure 2. Maps showing BBS routes and GLAS shots overlaid on a sample of some of the predictor variables.

performance of the resulting ensemble of trees was cross-validated using 20% of the data set randomly selected and reserved for this purpose. The reserved data were used to calculate standard coefficient of determination \( R^2 \) values denoting variance explained by the predictions. Variable importance, as measured by the percent increase in mean square error, was calculated and displayed as partial dependency plots for each predictor variable. Each plot graphically depicts how bird richness (on the y-axis) would be expected to respond to changes from each predictor variable (on the x-axis), independent of all other variables. The Random Forests models for each guild, and in aggregate, were then used to generate maps across the US at 1 km spatial resolution.

2.2.2. Comparisons with USDA Forest Service bird distribution maps. To independently assess the validity of our predictions of species richness spatial distribution patterns, we compared our 1 km resolution maps with those from Matthews et al. (2011) 20 km resolution maps (henceforth referred to as the USFS data set). They evaluated 147 breeding bird species across the eastern United States (Matthews et al. 2007, 2011). We selected bird species they modeled with 'high reliability', including 53 species with habitat types that matched the breeding habitat guilds considered in our analysis. We note that Matthews et al. (2011) only considered BBS data east of the 100th meridian from 1981 to 1990, whereas the BBS data we used span the entire contiguous US from 2004 to 2006 (inclusive).

The spatial data for each bird species in our maps were reclassified from predicted incidence values (the proportion of routes with species present on a scale from 0 to 1) to presence/absence cells. Species richness values (i.e. the number of bird species per cell) were generated for each guild and results were resampled to 20 km resolution to match the cell size and spatial extent of the USFS data set. Relative species richness was calculated for both data sets, multiplying each by 100 and dividing by the maximum species richness value present. We also compared the predicted habitat center for each guild, i.e. the latitude and longitude of the geographic center of each distribution, weighted by species richness. Lastly, we explored spatial correlations between the mapped data sets, showing where they agreed best and least. More specifics on the methodological approach are described in appendix A.

3. Results

3.1. Predictor variable correlations

The predictor variables most strongly correlated with bird species richness varied by guild type (figure 3). For total species richness vegetation property variables generally had the greatest predictive capability, followed by physical environment (e.g. temperature, precipitation) and canopy structure (see also appendix figure C.1). By guild, vegetation property variables typically had the highest correlations with species
Figure 3. Correlation bar plots between predictor variables and species richness, for all birds and by guild. White bars indicate a negative and gray a positive correlation. Only significant correlations are shown ($p < 0.05$).

richness, with the exception of scrub birds (figure D.1). Considering environmental variables alone (see table 2), those most highly correlated with bird richness were also distinct for each guild. Temperature variables were most strongly correlated with forest bird richness, while precipitation variables were the strongest environmental correlates of open woodland bird richness (figure 3).

The correlation between vegetation properties, structure and bird richness were generally positive for the forest bird guild and negative for non-forest guilds (e.g. grassland). Conversely, the percent of grassland surrounding the route (lfgrass) showed a strong positive correlation for grassland bird richness whereas there was a negative correlation for forest birds (figure 3). Forest bird richness has the strongest correlations with the percent tree cover and also with EVI, percent area covered by deciduous trees, and percent area covered by broadleaf trees (figure 3). Open woodland bird richness was most dependent on climatic variables, but also on biomass and VCF. Scrub bird models were the least robust, and only climate (primarily temperature) variables were important predictors.

Further partitioning the data set for forest birds and re-running random forest models for only those routes with high productivity (NPP $> 550$ gC m$^{-2}$ yr$^{-1}$) and high vegetation canopy cover (VCF $> 50\%$) (figure E.1) allowed us to assess which predictor variables were most important for conditions that are more characteristic of densely vegetated, high productivity environments (figure 5). While climate variables were the most important predictors of forest bird richness in these environments, canopy structure metrics were also correlated (figure F.1). Compared to the entire set of forest birds, the species richness values were higher and restricted to a somewhat smaller range, but the cross-validated predictive models were still robust ($R^2 = 0.75$ for both) (figures 5(a), (e)).

The partial dependency plots in figure 5 show how predictor variables co-vary with the response variable (species richness) across their respective ranges. Notably, forest bird
Figure 4. Cross validation results (upper panels: a, c, e, g, i) for the RandomForest models comparing reserved data values (X-axis) with the predicted model values (Y-axis). Variable importance plots (lower panels: b, d, f, h, j) show the percent increase in mean square error (%IncMSE), where higher values indicate model predicted values more similar to those observed.

Species richness in high productivity areas increased with biomass and canopy vertical complexity, particularly above the 20th percentile of both variables, but declined above the ~20th percentile for all the selected climate variables. Similar results were observed for species richness in areas with high canopy cover (figure 5 lower panels), with declining richness above the ~20th percentile for all climate variables and particularly rapid increases in richness up to the 40th percentile of biomass and the 50th percentile of vertical complexity values.

Additional partial dependency plots for all the guilds are presented in figure G.1. Notable trends include the systematic increase in forest bird richness with each of the most important predictor variables, the converse relationship for grassland birds (richness declines with increases in about half of the key predictors), and distinctly hump-shaped relationships for both open woodland and scrub birds (with highest species richness at mid-range values of the predictors). These observations were particularly evident for the canopy structure variables (right set of panels in figure G.1).

3.3. Bird species distributions and comparisons with USDA Forest Service maps

Maps of species richness derived from the BBS-route-based models (figure 6 right), and the continuous maps derived from the models being applied to the stack of spatial data layers
Figure 5. Cross validation results for forest birds in environments of high productivity (panel a) and high vegetation cover (panel e). Variable importance plots (panels b, f) are as in figure 4. Partial dependency plots (panels c, d, g, h) show the dependency of species richness (y-axis) on varying levels of the predictor variables independent of all other predictors.

(figure 6 left), both show coherent spatial patterns and strong regional gradients that vary by guild type. The route-based models and the continuous predictions show similar spatial patterns of richness, although the continuous maps reveal considerable spatial variability across the domain, with the highest total richness levels in the eastern US, particularly at higher latitudes. This pattern is even more pronounced for forest birds. High richness of open woodland birds spanned much of the eastern US as well, but was more widely distributed across the region. Grassland species richness, as expected, was particularly high in the west-central US. We did not create maps of scrub birds owing to the less robust models for that guild.

Our predicted patterns of relative species richness correlate reasonably well with those of Matthews et al. (2011). Overall, the weighted mean center of the species richness
spatial distributions (see section 2.2.2) for our study and Matthews et al (2011) was geographically close for each guild type (figure H.1). They were closest for the open woodland guild (9.3 km) and farthest for the grassland guild (179.3 km). There was, however, considerable variability in the spatial correlation patterns. In both, forest bird richness was greatest around the Great Lakes, New England and the Appalachian Mountains. The spatial pattern comparison was least similar for grassland birds, with predictions from the USFS data set being high in the mid-western states and those from ours being concentrated further west. Both maps predicted the highest relative richness of open woodland species in the central eastern US, but the USFS data set predicted a larger expanse of high values.
4. Discussion

Our results show the various data sets (table 2) used in our analyses can inform models that robustly predict the spatial patterns of bird species richness across large areas, in this case the conterminous USA. While previous studies report similar findings at national (Coops et al. 2009, Culbert et al. 2013, Pidgeon et al. 2007, Rittenhouse et al. 2012) and regional scales (Allen and O’Connor 2000, Donovan and Flather 2002), we anticipated the influence of canopy structure captured in the lidar data sets would have greater predictive capability than we observed. This expectation was based on increasing evidence, using lidar-derived canopy structure measurements, that structure is an important predictor of species richness at local to regional scales (Bradbury et al. 2005, Clawges et al. 2008, Goetz et al. 2010, 2007, Hill et al. 2004, Lesak et al. 2011, Seavy et al. 2009, Swatantran et al. 2012). Instead, our national scale estimates of forest bird guild species richness were most strongly influenced by tree canopy cover (i.e. VCF) and tree life form distribution (LFtree). Interestingly, we show robust predictions of forest bird richness even in areas of high productivity and high canopy cover, where we might expect some predictor variables to saturate in their sensitivity to increasing species richness, and canopy structure to become an important determinant of niche diversity. In these areas of high productivity and canopy cover, however, climate variables became important predictors (figure 5), indicating they capture additional information beyond even integrative variables like net primary production. In the case of woodland birds, a unimodal shape of the partial dependency plots reflects greatest species richness at intermediate vegetation cover, biomass and canopy structure values. This finding is consistent with greater landscape habitat diversity in more open woodland areas relative to, e.g. densely forested or open grasslands areas, and expectations of different woodland bird species utilizing differing vegetation types and densities.

The predicted patterns of relative species richness from our models were generally similar to those Matthews et al. (2011) mapped for the eastern US, even though different approaches were used to generate the maps produced by both studies. There are several differences worth noting. First, although both studies considered climate, elevation, and tree species properties as predictor variables, the other predictors differed substantially between the two studies. In particular, our predictions considered unique vegetation properties (e.g. biomass, productivity) and canopy structure metrics (e.g. canopy height, vertical complexity). We note these were aggregated to coarser resolution (20 km) for comparison with the Matthews et al. (2011) maps. In addition, the BBS data sets used in this study and the USDA Forest Service maps were collected more than a decade apart. We expected this to adversely impact the comparison insofar as the time lag might contribute to changes in bird species richness and/or the predictor variables, but the overall similarities between the relative richness maps was an encouraging confirmation of the utility of our higher resolution predicted richness distribution maps (figure 6). This was particularly true given we used only what Matthews et al. (2011) deemed their highest quality species predictions (appendix B), and in the context of the strength of our BBS route-based Random Forests models (figure 4).

These points noted, the strength of any predictor variable is fundamentally related to the scale at which the metric is most ecologically relevant. Our models tended to characterize forest vegetation type, cover and climate as the most important large area predictors of bird species richness, despite the considerable influence of canopy structure at more local scales. However, the inability of sample sets of 70 m GLAS lidar shots to fully characterize entire 40 km BBS routes complicates these interpretations. Canopy structure can undergo significant changes over the length of the route, and averaging all shots intersecting a route probably does not represent conditions of the entire route. A more direct analysis of bird observations within the footprint of the GLAS shots would better capture the attributes of bird species richness that are dependent on canopy structure and related habitat heterogeneity, but the BBS data were not collected with that intent (i.e. data are aggregated for all stops along the length of the routes). This does not mean that very large-scale studies of habitat structure with lidar are impractical, but it is important to note that GLAS lidar are samples (not wall-to-wall images). Despite that, we found meaningful correlations between GLAS structure metrics and bird species richness when compared in a pairwise manner (figures E.1, F.1). Moreover, the partial dependency plots (figure G.1) show reasonable and expected associations of structure metrics with forest birds (positively co-varying), woodland birds (richness peaking at intermediate values of structure metrics) and even grassland birds (negatively co-varying). Previous work with airborne lidar shows more densely sampled lidar structure metrics are useful for predicting not only richness but habitat use, thus future studies of the relative importance of species richness predictors might explore the effect of spatial averaging of structural variability that accompanies increasing lidar footprint size, as well as sampling density and terrain-influenced height estimation errors in medium to large footprint lidar systems. Such studies would be best designed in the context of potential next generation space-borne lidar systems relevant to vegetation and ecosystem studies.

Acknowledgments

We thank Steve Matthews (USDA Forest Service) for providing his maps of bird species distribution for the eastern United States, Kevin Guay for assistance with statistical comparisons, and the BBS staff and volunteers for making their data widely available. This work was supported by the NASA Applied Sciences (Biodiversity) program managed by Woody Turner (grant NNX09AK20G).

Appendix A. Additional information on methodological approach

Lidar metric derivation. In deriving lidar metrics, we eliminated shots that did not produce adequate waveforms (e.g. shots with excessive atmospheric attenuation including clouds),
| Common name                  | Scientific name                      | Guild       |
|-----------------------------|--------------------------------------|-------------|
| Tufted Titmouse             | Baeolophus bicolor                   | Forest      |
| Purple Finch                | Carpodacus purpureus                 | Forest      |
| Veery                       | Catharus fuscescens                  | Forest      |
| Black-billed Cuckoo         | Coccyzus erythropthalmus             | Forest      |
| Black-throated Blue Warbler | Dendroica caerulescens               | Forest      |
| Yellow-rumped Warbler       | Dendroica coronata                   | Forest      |
| Magnolia Warbler            | Dendroica magnolia                   | Forest      |
| Pine Warbler                | Dendroica pinus                      | Forest      |
| Wood Thrush                 | Hylocichla mustelina                 | Forest      |
| Red-bellied Woodpecker      | Melanerpes carolinus                 | Forest      |
| Rose-breasted Grosbeak      | Pheucticus ludovicianus              | Forest      |
| Black-capped Chickadee      | Poecile atricapillus                 | Forest      |
| Ovenbird                    | Seiurus aurocapillus                 | Forest      |
| Red-breasted Nuthatch       | Sitta canadensis                     | Forest      |
| Brown-headed Nuthatch       | Sitta pusilla                        | Forest      |
| Yellow-bellied Sapsucker    | Sphyrapicus varius                   | Forest      |
| Winter Wren                 | Troglodytes troglodytes              | Forest      |
| Nashville Warbler           | Vemnivora ruficapilla                | Forest      |
| Red-eyed Vireo              | Vireo olivaceus                      | Forest      |
| White-throated Sparrow      | Zonotrichia albigollis               | Forest      |
| Northern Bobwhite           | Colinus virginianus                  | Grassland   |
| Bobolink                    | Dolichonyx oryzivorus                | Grassland   |
| Horned Lark                 | Eremophila alpestris                 | Grassland   |
| Savannah Sparrow            | Passerculus sandwichensis            | Grassland   |
| Ring-necked Pheasant        | Phasianus colchicas                  | Grassland   |
| Dickcissel                  | Spiza americana                      | Grassland   |
| Common Ground-Dove          | Columbina passerina                  | Scrub       |
| Common Yellowthroat         | Geothlypis trichas                   | Scrub       |
| Yellow-breasted Chat        | Icteria virens                       | Scrub       |
| Painted Bunting             | Passerina ciris                      | Scrub       |
| Clay-colored Sparrow        | Spizella pallida                     | Scrub       |
| Field Sparrow               | Spizella pusilla                     | Scrub       |
| White-eyed Vireo            | Vireo griseus                        | Scrub       |
| Cedar Waxwing               | Bombycilla cedrorum                  | Open woodland|
| Chuck-Will’s Widow          | Caprimulgus carolinensis             | Open woodland|
| Northern Cardinal           | Cardinalis cardinalis                | Open woodland|
| American Goldfinch          | Carduelis trisist                    | Open woodland|
| Hermit Thrush               | Catharus guttatus                    | Open woodland|
| Yellow-billed Cuckoo        | Coccyzus americanus                  | Open woodland|
| Yellow Warbler              | Dendroica petechia                   | Open woodland|
| Gray Catbird                | Dumetella carolinensis               | Open woodland|
| Blue Grosbeak               | Guiraca caerulea                     | Open woodland|
| Baltimore Oriole            | Icterus galbula                      | Open woodland|
| Orchard Oriole              | Icterus spurius                      | Open woodland|
| Loggerhead Shrike           | Laniaus ludovicianus                 | Open woodland|
| Red-headed Woodpecker       | Melanerpes erythrocephalus            | Open woodland|
| Song Sparrow                | Melospiza melodia                    | Open woodland|
| Indigo Bunting              | Passerina cyanea                     | Open woodland|
| Summer Tanager              | Piranga rubra                        | Open woodland|
| Chipping Sparrow            | Spizella passerina                   | Open woodland|
| Carolina Wren               | Thryothorus ludovicianus             | Open woodland|
| House Wren                  | Troglydys aedon                      | Open woodland|
| American Robin              | Turdus migratorius                   | Open woodland|
Figure C.1. Boxplot of the correlation (absolute value) between predictor variables and species richness, by variable class, for the model predicting richness of all birds (i.e. aggregated guilds).

specifically shots where the amplitude of the raw waveform does not exceed twice the noise threshold. We also excluded shots in which the waveform contained less than two distinct peaks (an indication that the top of the vegetation canopy was not detected), as well as shots in areas with substantial topographic relief, where canopy height estimation was problematic (Lefsky et al 2007). A total of 48,133 GLAS shots remained post screening, which was less than half of the total number of shots acquired and processed.

Random Forests models. We subsequently applied the lidar (i.e. structural information), physical environment, and vegetation properties metrics in Random Forests to assess predictor variable importance. In Random Forests, data are partitioned using a series of hierarchical binary splits on the predictor variables, with the goal of maximizing explained variance in the response variable (in our case bird species richness). A different bootstrapped random sample of the data for each tree is used to optimally split among the various predictors, improving performance by iteratively aggregating the results. Predictors are selected randomly, which acts to increase the accuracy of the model while reducing the influence of variable selection order and, in the process, minimize overfitting (Cutler et al 2007). The combined effects of the predictor variables were assessed using the mean prediction of many individual regression trees.

Generation and comparison of relative richness maps. Species presence/absence thresholds were optimized by Matthews et al (2011), who found an optimal incidence value (IV) cutoff at 0.05 (i.e. grid cells with IV < 0.05 were reclassified as zero, indicating species absence). We subsequently explored the regional correlations between our model predictions (figure 5) and those of Matthews et al (2011) through maps of spatial

Figure D.1. Dotplots showing the correlation range of the ten strongest predictor variables by bird guild and organized by predictor variable class. Open dots indicate negative correlation and solid dots positive correlation. An empty line indicates no predictor variables in that class were among the ten most important for predicting species richness.
correlation, which we created by writing a moving window script that derived a regression model for the cell values (from both data sets) within the same $5 \times 5$-cell window and created a new map with the correlation coefficient in the window centroid. The window iterated across both data sets, producing maps of the spatial correlation between the data sets. The moving window assigned null values in regions where identical richness values (in either or both data sets) populated a $5 \times 5$ window because the standard deviation in these cases was zero. Relative species richness was calculated for both data sets, multiplying each by 100 and dividing by the maximum species richness value present. We also compared the predicted
Figure G.1. Partial dependency plots for each bird guild type, with the most important predictors shown at left and canopy structure metrics at right.

Appendix B
See table B.1.

Appendix C
See figure C.1.

Appendix D
See figure D.1.
Figure H.1. Relative richness maps from bird species model outputs of this study (left images) and Matthews et al. (2011) (middle images), and the correlation between the two data sets (right images). Green dots in the relative richness maps indicate the mean geographic center of distribution (MCD) for all birds and each guild type. White areas within the eastern US in the correlation maps indicate null value regions (see appendix A).

Appendix E
See figure E.1.

Appendix F
See figure F.1.

Appendix G
See figure G.1.

Appendix H
See figure H.1.

References
Allen A P and O’Connor R J 2000 Interactive effects of land use and other factors on regional bird distributions J. Biogeogr. 27 889–900
Bar-Massada A, Wood E M, Pidgeon A M and 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 Ecol. Lett. 15 365–77
Beaudry F, Radeloff V C, Pidgeon A M, Plantinga A J, Lewis D J, Helmers D and Butsic V 2013 The loss of forest birds habitats under different land use policies as projected by a coupled ecological-econometric model Biol. Cons. 165 1–9
Bellard C, Bertelsmeier C, Leadley P, Thuiller W and Courchamp F 2012 Impacts of climate change on the future of biodiversity Ecol. Lett. 15 365–77
Bergen K, Goetz S, Dubayah R, Henesby G, Imhoff M, Nelson R, Parker G and Radeloff V 2009 Measurements of vegetation 3D
structure for biodiversity and habitat: review and implications for spaceborne remote sensing missions. *J. Geophys. Res.* 114 G00E06

Blackard J A, Ruefenacht B, Weyermann D L, Winterberger K C, Brandeis T J, McRoberts R E and Tymcio R P 2008 Mapping US forest biomass using nationwide forest inventory data and moderate resolution information. *Remote Sens. Environ.* 112 1658–77

Blackburn T M and Gaston K J 1996 Spatial patterns in the species richness of birds in the New World. *Ecography* 19 369

Boulouinier T, Nicolas J D, Sauer J R, Hines J E and Pollock K H 1998 Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79 1018–28

Bradbury R B, Hill R A, Mason D C, Hinsley S A, Wilson J D, Balzter H, Anderson G Q A, Whittingham M J, Davenport I J and Bellamy P E 2005 Modelling relationships between birds and vegetation structure using airborne LiDAR data: a review with case studies from agricultural and woodland environments. *Ibis* 147 443–52

Ceballos G and Ehrlich P R 2006 Global mammal distributions, biodiversity hotspots, and conservation. *Proc. Natl Acad. Sci. USA* 103 19374–9

Clawges R, Vierling K, Vierling L and Rowell E 2008 The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. *Remote Sens. Environ.* 112 2064–73

Coops N C, Waring R H, Mulder M A, Pidgeon A M and Radeloff V C 2009 Bird diversity: a predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. *J. Biogeogr.* 36 905–18

Cueto V R and Casenave J L 1999 Determinants of bird species richness: role of climate and vegetation structure at a regional scale. *J. Biogeogr.* 26 487–92

Culbert P D, Radeloff V C, Flather C H, Kellndorfer J M, Rittenhouse C D and Pidgeon A M 2013 The influence of vertical and horizontal habitat structure on nationwide patterns of avian biodiversity. *Auk* 130 656–65

Currie D J, Francis A P and Kerr J T 1999 Some general propositions about the study of spatial patterns of species richness. *Ecocience* 6 392–9

Cusens J, Wright S D, McBride P D and Gillman N L 2012 What is the form of the productivity—animal-species-richness relationship? A critical review and meta-analysis. *Ecology* 93 2241–52

Cutler D R, Edwards T C, Beard K H, Cutler A, Hess K T, Gibson J and Lawler J J 2007 Random forests for classification in ecology. *Ecology* 88 2783–92

Deppe J L and Rotenberry J T 2008 Scale-dependent habitat use by fall migratory birds: vegetation structure, floristics and geography. *Ecol. Monogr.* 78 461–87

Donovan T M and Flather C H 2002 Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecol. Appl.* 12 364–74

Farr T G et al 2007 The shuttle radar topography mission. *Rev. Geophys.* 45 RG2004

Fitterer J L, Nelson T A, Coops N C, Mulder M A and Mahony N A 2012 Exploring the ecological processes driving geographical patterns of breeding bird richness in British Columbia, Canada. *Ecol. Appl.* 23 888–903

Ganguly S, Friedl M A, Tan B, Zhang X and Verma M 2010 Land surface phenology from MODIS: characterization of the collection 5 global land cover dynamics product. *Remote Sens. Environ.* 114 1805–16

Goetz S J, Steinberg D, Betts M, Holmes R, Doran P, Dubayah R and Hofton M 2010 Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* 91 1569–76

Goetz S J, Steinberg D, Dubayah R and 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.* 108 254–63

Hansen A J, Phillips L B, Flather C H and Robison-Cox J 2011 Carrying capacity for species richness as a context for conservation: a case study of North American breeding birds. *Glob. Ecol. Biogeogr.* 20 817–31

Hansen M C, Townshend J R G, Defries R S and Carroll M 2005 Estimation of tree cover using MODIS data at global, continental and regional/local scales. *Int. J. Remote Sens.* 26 4359–80

Hijmans R J, Cameron S E, Parra J L, Jones P G and Jarvis A 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25 1965–78

Hill R A, Hinsley S A, Gaveau D L and Bellamy P E 2004 Cover: predicting habitat quality for Great Tits (Parus major) with airborne laser scanning data. *Int. J. Remote Sens.* 22 4851–5

Hinsley S A, Hill R A, Fuller R J, Bellamy P E and Rothery P 2009 Bird species distributions across woodland canopy structure gradients. *Community Ecol.* 10 99–110

Huete A, Didan K, Miura T, Rodriguez E P, Gao X and Ferreira L G 2002 Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 83 195–213

Ju J, Roy D P, Shuai Y and Schaaf C 2010 Development of an approach for generation of temporally complete daily nadir MODIS reflectance time series. *Remote Sens. Environ.* 114 1–20

Jung M, Henkel K, Herold M and Churkina G 2006 Exploiting synergies of global land cover products for carbon cycle modeling. *Remote Sens. Environ.* 101 534–53

Kerr J 2001 Global biodiversity patterns: from description to understanding. *Trends Ecol. Evol.* 16 424–25

Kerr J T and Packer L 1997 Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385 252

Lawler J J, White D, Neilson R P and Blaustein A R 2006 Predicting climate-induced range shifts: model differences and model reliability. *Glob. Change Biol.* 12 1568–84

Lesky M A, Cohen W B, Parker G G and Harding D J 2002 Lidar remote sensing for ecosystem studies. *Bioscience* 52 19–30

Lesky M A, Keller M, Pang Y, de Camargo P B and Hunter M O 2007 Revised method for forest canopy height estimation from Geoscience Laser Altimeter System waveforms. *J. Appl. Remote Sens.* 1 013537

Lesak A A, Radeloff V C, Hawbaker T J, Pidgeon A M, Godbaken T and Contrucci K 2011 Modeling forest songbird species richness using LiDAR-derived measures of forest structure. *Remote Sens. Environ.* 115 2823–35

MacArthur R H and MacArthur J W 1961 On bird species diversity. *Ecology* 42 594–8

Matthews S N, Iverson L R, Prasad A M and Peters M P 2007 A Climate Change Atlas for 147 Bird Species of the Eastern United States [database] (Delaware, OH: Northern Research Station USDA Forest Service)

Matthews S N, Iverson L R, Prasad A M and Peters M P 2011 Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. *Ecography* 34 933–45
Mittelbach G G 2010 Understanding species richness—productivity relationships: the importance of meta-analyses Ecology 91 2540–4

Mittelbach G G, Steiner C F, Scheiner S M, Gross K L, Reynolds H L, Waide R B, Willig M R, Dodson S I and Gough L 2001 What is the observed relationship between species richness and productivity? Ecology 82 2381–96

Nichols J D, Boulainier T and Sauer J R 1998 Estimating rates of local species extinction, colonization, and turnover in animal communities Ecol. Appl. 8 1213

Pardieck K L and Sauer J R 2007 The 1999–2003 summary of the North American Breeding Bird Survey Bird Popul. 8 28–45

Parmesan C 2006 Ecological and evolutionary responses to recent climate change Annu. Rev. Ecol. Evol. Syst. 37 637–69

Peterjohn B G and Sauer J R 1993 North American Breeding Bird Survey annual summary 1990–1991 Bird Popul. 1 1–24

Phillips L B, Hansen A J, Flather C H and Robison-Cox J 2010 Applying species-energy theory to conservation: a case study for North American birds Ecol. Appl. 20 2007–23

Pidgeon A M, Radoloff V C, Flather C H, Lepczyk C A, Clayton M K, Hawbaker T J and Hammer R B 2007 Ecol. Appl. 17 1989–2010

Ralph C J, Sauer J R and Droge S 1995 Monitoring bird populations by point counts. General Technical Report PSW-GTR-149 USDA Forest Service, Albany, CA

R Development Core Team 2009 R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing) ISBN 3-900051-07-0. www.R-project.org

Ricklefs R E 2004 A comprehensive framework for global patterns in biodiversity Ecol. Lett. 7 1–15

Rittenhouse C D, Pidgeon A M, Albright T P, Culbert P D, Clayton M K, Flather C H, Masek J G and Radoloff V C 2012 Land-cover change and avian diversity in the conterminous United States Conserv. Biol. 26 821–9

Running S W, Nemani R R, Heinsch F A, Zhao M, Reeves M and Hashimoto H 2004 A continuous satellite-derived measure of global terrestrial primary production Bioscience 54 547–60

Schutz B E, Zwally H J, Shuman C A, Hancock D and DiMarzio J P 2005 Overview of the ICES at mission Geophys. Res. Lett. 32 L21S01

Seavy N E, Viers J H and Wood J K 2009 Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height Ecol. Appl. 19 1848–57

Seoane J, Bustamante J and Díaz-Delgado R 2004 Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution Ecol. Modell. 171 209–22

Suarez-Rubio M, Wilson S, Leimgruber P and Lookingbill T 2013 Threshold responses of forest birds to landscape changes around exurban development PLoS ONE 8 e67593

Swatantran A, Dubayah R, Goetz S, Holton M, Betts M G, Sun M, Simard M and Holmes R 2012 Mapping migratory bird prevalence using remote sensing data fusion PLoS ONE 7 e28922

Turner W, Spector S, Gardiner N, Fladeland M, Sterling E and Steininger M 2003 Remote sensing for biodiversity science and conservation Trends Ecol. Evol. 18 306–14

Vierling K T, Vierling L A, Gould W A, Martinuzzi S and Clawges R M 2008 LiDAR: shedding new light on habitat characterization and modeling Front. Ecol. Environ. 6 90–8

Whittaker R J, Willis K J and Field R 2001 Scale and species richness: towards a general, hierarchical theory of species diversity J. Biogeogr. 28 453–70