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THE INFLUENCE OF VERTICAL AND HORIZONTAL HABITAT STRUCTURE ON NATIONWIDE PATTERNS OF AVIAN BIODIVERSITY

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Abstract.—With limited resources for habitat conservation, the accurate identification of high-value avian habitat is crucial. Habitat structure affects avian biodiversity but is difficult to quantify over broad extents. Our goal was to identify which measures of vertical and horizontal habitat structure are most strongly related to patterns of avian biodiversity across the conterminous United States and to determine whether new measures of vertical structure are complementary to existing, primarily horizontal, measures. For 2,546 North American Breeding Bird Survey routes across the conterminous United States, we calculated canopy height and biomass from the National Biomass and Carbon Dataset (NBCD) as measures of vertical habitat structure and used land-cover composition and configuration metrics from the 2001 National Land Cover Database (NLCD) as measures of horizontal habitat structure. Avian species richness was calculated for each route for all birds and three habitat guilds. Avian species richness was significantly related to measures derived from both the NBCD and NLCD. The combination of horizontal and vertical habitat structure measures was most powerful, yielding high R^2 values for nationwide models of forest (0.70) and grassland (0.48) bird species richness. New measures of vertical structure proved complementary to measures of horizontal structure. These data allow the efficient quantification of habitat structure over broad scales, thus informing better land management and bird conservation. *Received 10 January 2013, accepted 30 September 2013.*

Key words: biodiversity, biomass, Breeding Bird Survey, canopy height, NBCD, NLCD, structure.

La Influencia de la Estructura Vertical y Horizontal del Hábitat en los Patrones de Diversidad de Aves a Escala Nacional

Resumen.—Con recursos limitados para la conservación, la identificación precisa de los hábitats de alto valor para la aves es crucial. La estructura del hábitat afecta la diversidad de aves pero es difícil de cuantificar en grandes extensiones de terreno. Nuestra meta fue identificar qué medidas de la estructura vertical y horizontal del hábitat están más fuertemente relacionadas con los patrones de diversidad de aves dentro de los límites de los Estados Unidos, y determinar si las nuevas medidas de la estructura vertical se complementan con las medidas existentes y principalmente de la estructura horizontal. Calculamos la altura del dosel y la biomasa para 2546 rutas del Censo Norteamericano de Aves Reproductivas a partir del Conjunto Nacional de Datos de Biomasa y Carbono (NBCD, por sus siglas en inglés) como medidas de la estructura vertical del hábitat, y usamos las medidas de composición y configuración de la cobertura del terreno de la Base de Datos Nacional de Cobertura del Terreno (NLCD) como medidas de la estructura horizontal del hábitat. La riqueza de especies de aves fue calculada para cada ruta, para todas las aves y tres tipos de hábitat. Las medidas derivadas de el NCBD y el NLCD estuvieron significativamente relacionadas con la riqueza de especies de aves. La combinación de las medidas de estructura horizontal y vertical del hábitat fue más poderosa, derivando mayores valores de R^2 para los modelos a escala nacional de riqueza de especies de aves de bosques (0.70) y praderas (0.48). Las nuevas medidas de la estructura vertical se establecieron como medidas complementarias de la estructura horizontal. Estos datos permiten la cuantificación eficiente de la estructura del hábitat en grandes escalas, de manera que informan mejores prácticas de manejo de la tierra y de conservación de las aves.

Avian biodiversity is under severe threat from human-caused habitat loss and fragmentation (Gaston et al. 2003). With limited resources for habitat conservation, the accurate identification of high-value bird habitat is crucial (Turner et al. 2003). Although some broad-extent maps of biodiversity are available (Myers et al. 2000, Buckton and Ormerod 2002), the spatial resolution of these

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maps is too coarse to be of direct relevance for resource managers. Therefore, spatially detailed maps of avian species richness are needed for land management and biogeography alike, and making such maps for broad areas requires the prediction of species richness based on environmental correlates, because comprehensive surveying is logistically not feasible. The question is which environmental correlates can predict avian species richness best.

Primary drivers of bird biodiversity include productivity, climatic stability, and habitat structure (MacArthur 1972). Productivity and climatic stability drive biodiversity patterns at broad scales, and measures of these factors are often considered when analyzing broad-extent patterns of avian biodiversity (Hawkins et al. 2003, Hurlbert and Haskell 2003, Davies et al. 2007). Habitat structure has also long been recognized as a major factor influencing biodiversity (MacArthur and MacArthur 1961, Wiens 1974, Willson 1974, Tews et al. 2004). When considering the influence of habitat structure on avian biodiversity, it is critical to consider both vertical and horizontal dimensions. Vertical habitat (or vegetation) structure is defined as the bottom-to-top configuration of aboveground vegetation at a site (Brokaw and Lent 1999). We define horizontal habitat structure as the composition and configuration of a landscape with regard to land-cover class (Turner et al. 2001).

Studies that have related biodiversity patterns to habitat structure in general, and to vertical structure in particular, have focused primarily on local scales, for two main reasons. First, habitat structure is much more heterogeneous at local scales than productivity or climatic stability. Second, many traditional measures of habitat structure, such as foliage height diversity (MacArthur and MacArthur 1961, Erdelen 1984), are labor-intensive, field-based measures, which are impractical to collect over geographically expansive study areas. As data acquisition and analysis resources continue to improve, it is important to consider new approaches to quantifying habitat structure over broad (e.g., national) geographic extents and to evaluate the ability of these measures to explain observed patterns of avian biodiversity.

Vertical habitat structure exhibits a strong relationship with avian species richness. Vertical structure directly affects birds through its influence on perching, nesting, and foraging sites (Brokaw and Lent 1999), and areas with greater vertical structure thus provide more niches. Avian species richness is positively correlated with foliage height diversity (MacArthur and MacArthur 1961, Erdelen 1984) as well as canopy height (Goetz et al. 2007). Unfortunately, robust measures of vertical structure for broad geographic areas have been lacking (Bergen et al. 2009).

Horizontal habitat structure strongly affects biodiversity at broad scales. Landscape metrics derived from land-cover classifications capture, for example, measures of landscape configuration such as habitat fragmentation (Donovan and Flather 2002), landscape heterogeneity (Atauri and de Lucio 2001), habitat isolation (Krauss et al. 2003), and measures of landscape composition such as proportion of vegetation class (Farina 1997). In general, there is a positive relationship between high horizontal habitat structure (generally termed "habitat heterogeneity") and biodiversity (Tews et al. 2004). Furthermore, although land-cover classifications implicitly capture some information about vertical structure (e.g., a deciduous forest would be expected to have more complex vertical structure than a grassland), they contain no information about heterogeneity of vertical structure within a single land-cover class.

Because direct measurement of vertical habitat structure is costly and time consuming, patterns of association between vertical habitat structure and species diversity have traditionally been limited to local-scale studies (Clawges et al. 2008). Although LiDAR (light detection and ranging) can be used to quantify vertical habitat structure at the landscape scale (Hyde et al. 2006, Bergen et al. 2009) and predict avian biodiversity (Goetz et al. 2007, Clawges et al. 2008, Seavy et al. 2009, Lesak et al. 2011), there are currently no national wall-to-wall LiDAR data sets (or even statewide data sets in most areas) that would support macroecological investigations. However, a recently released data set has the potential to capture high-resolution vertical vegetation structure at the national scale. The National Biomass and Carbon Dataset 2000 (NBCD; Kellndorfer et al. 2011), derived from multiple data sets, including the Shuttle Radar Topography Mission, provides high-resolution (30-m) nationwide estimates of basal area-weighted canopy height and aboveground live dry biomass (Kellndorfer et al. 2004, 2006; Walker et al. 2007). The NBCD seems promising, but the ability of this data set to characterize ecologically meaningful vertical habitat structure has not yet been tested.

Our overall goal in the present manuscript was to evaluate the relationship of avian species richness with vertical and horizontal habitat structure for different habitat guilds over broad spatial extents. We analyzed the conterminous United States as a whole, as well as three individual ecoregion provinces. A key focus was to evaluate the effectiveness of the NBCD in characterizing vertical habitat structure in a manner sufficient to explain avian species richness patterns and, subsequently, to investigate the relative importance and complementarity of measures of vertical and horizontal structure. We expected a positive relationship between overall avian species richness and (1) vegetation height, (2) vegetation height variability, (3) biomass, and (4) biomass variability because an increase in these measures would indicate an increase in the number of potential habitat niches. For birds strongly associated with forest, grassland, and shrubland habitat, we predicted that the amount of the preferred habitat type would be the strongest explanatory variable in a model of species richness for that habitat guild. In terms of other measures of horizontal structure, we expected that higher levels of landscape diversity would lead to higher species richness. We expected that measures of vertical habitat structure from the NBCD would capture new information that was not already present in the measures of horizontal structure, and that these measures would be most useful in heavily forested ecoregions, where existing land-cover classifications fail to capture the heterogeneity present in forest. Lastly, we expected that multivariate models combining measures of both horizontal and vertical structure would exhibit the highest explanatory power.

Methods

Our study area encompassed the conterminous United States. Avian species richness was calculated from the North American Breeding Bird Survey (BBS), an annual survey of ~3,000 routes across the study area (Fig. 1). Along each 39.4-km route, fifty 3-min point counts are conducted, and all birds heard or seen

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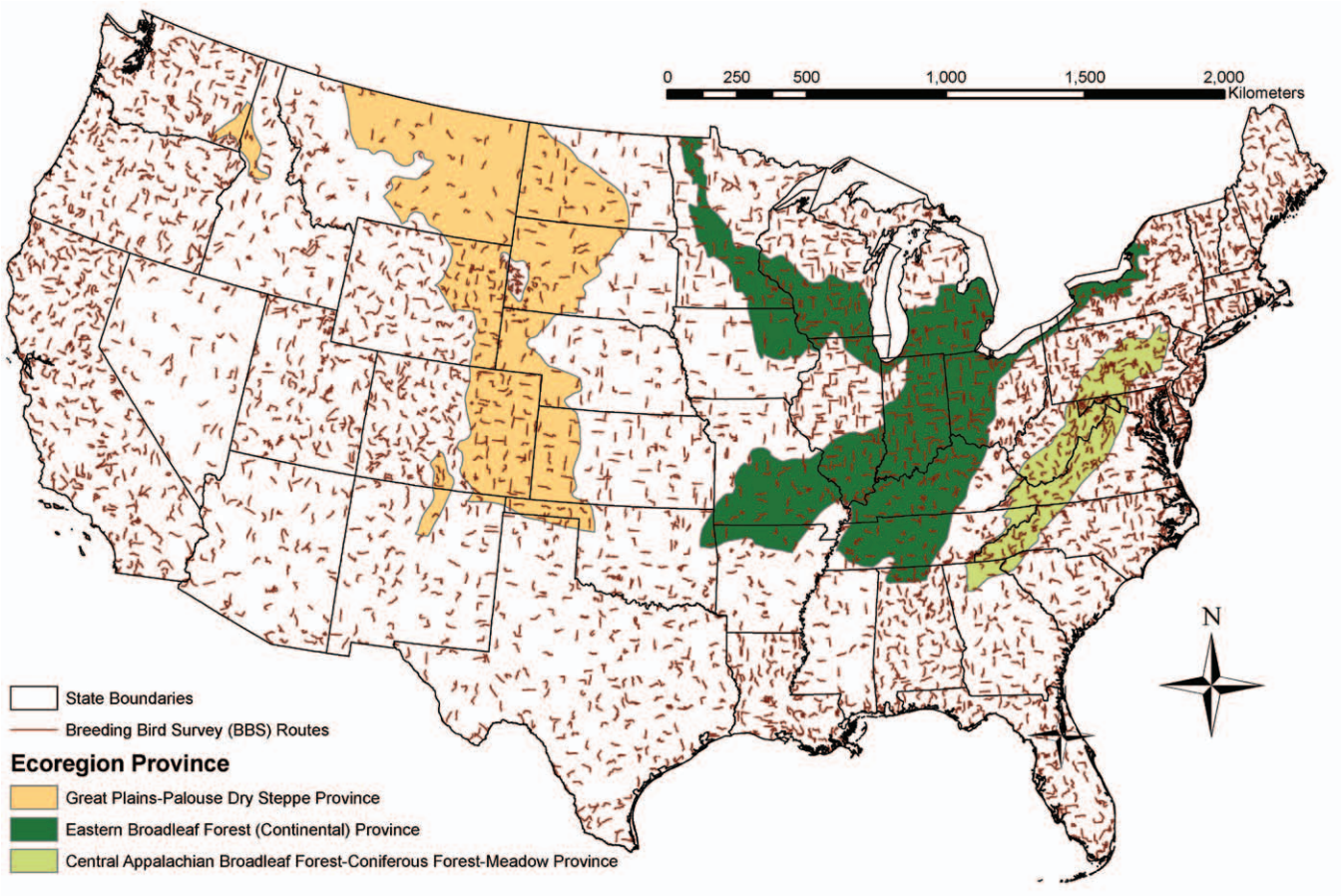


FIG. 1. Study area, including Breeding Bird Survey (BBS) routes and ecoregion provinces used in analysis.

are recorded (U.S. Geological Survey Patuxent Wildlife Research Center 2008). Because several of the data sets analyzed for habitat structure incorporated data acquired around the year 2000, we centered our analysis on that year and calculated the mean species richness of each BBS route over the years surveyed during the period 1998–2002. We removed observations collected by first-year observers (Kendall et al. 1996) or in suboptimal weather. We included landbirds only, excluding waterfowl and shorebird species, which are generally poorly characterized by BBS (Bystrack 1981). We also excluded poorly sampled landbird species, which we defined as species with <30 route-year observations ever. After the removals, we retained 2,546 routes and 373 species. We expected that relationships between species richness and habitat structure would differ among different life-history guilds. Therefore, for each route, we calculated overall species richness as well as richness within three habitat-associated guilds: forest, shrubland, and grassland. We assigned species to these guilds on the basis of habitat information provided in the Birds of North America Online database (Poole 2005) (Table S1 in online supplemental material; see Acknowledgments). Guild membership is not mutually exclusive, as some species commonly breed in more than one habitat class.

To account for the fact that some species present on a route may not be detected, it is recommended that a correction be applied to raw species-richness counts (Kéry and Schmid 2004). COMDYN is a software program that considers the raw BBS-route species-richness data from a capture–recapture model perspective and uses jackknifing to estimate species richness (Nichols et al. 1998). For each route, we used COMDYN-estimated species richness for all species and for the three guilds.

In order to relate our explanatory variables to individual BBS routes, we summarized them within a 19.7-km-radius circle (one half the length of a BBS route) around the centroid of each BBS route (as in Flather and Sauer 1996, Pidgeon et al. 2007, Rowhani et al. 2008, Rittenhouse et al. 2010). We chose this radius because it encompasses the entire BBS route, regardless of route path, and a circle because it provides a uniform area and shape around each BBS route.

To characterize vertical habitat structure, we derived measures of vegetation canopy height (Fig. 2A) and aboveground live dry biomass from the 30-m-resolution NBCD (Kellndorfer et al. 2011). The NBCD models these measures on the basis of U.S. Department of Agriculture Forest Inventory and Analysis data (FIA), the National Elevation Dataset (NED), the 2000 Shuttle Radar Topography Mission (SRTM), and the National Land Cover Database 2001 (NLCD) (Kellndorfer et al. 2004, 2006, 2011; Walker et al. 2007). From this data set we calculated mean, standard deviation, and coefficient of variation of both basal area-weighted canopy height and aboveground live dry biomass (using the NBCD's FIA-derived biomass model) within 19.7 km of each BBS route centroid, yielding six variables in all.

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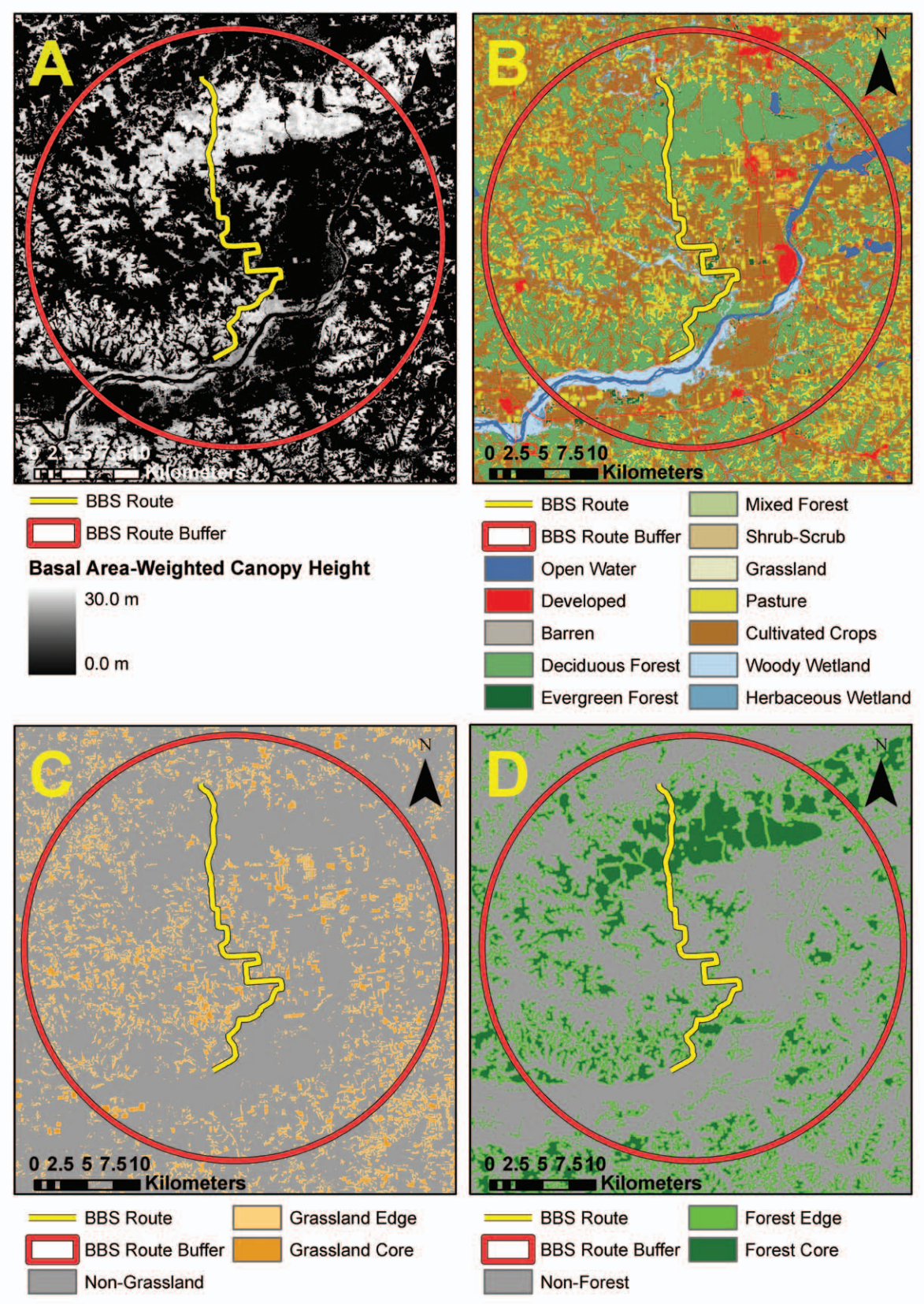


FIG 2. Data layers corresponding to a single Breeding Bird Survey (BBS) route in the study area. Data layers were summarized within circular buffers around each BBS route. (A) Basal area-weighted canopy height from the National Biomass and Carbon Dataset (NBCD). (B) Land cover from 2001 National Land Cover Database (NLCD). (C) Grassland edge and grassland core, calculated from 2001 NLCD. (D) Forest edge and forest core, calculated from 2001 NLCD.

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Analysis of horizontal habitat structure included landscape composition and configuration metrics calculated from the 2001 NLCD (Homer et al. 2004). Within 19.7 km of each BBS route centroid, we calculated the proportion of landscape for 12 land-cover classes: water, developed, barren, deciduous forest, evergreen forest, mixed forest, shrub-scrub, grassland, pasture, cultivated crops, woody wetland, and herbaceous wetland (Table S2 in online supplemental material; see Acknowledgments), the total number of land-cover classes present, and the Shannon diversity index (Shannon 1948) of land-cover class distributions (Fig. 2B).

To quantify landscape configuration, we applied morphological spatial pattern analysis (MSPA) (Vogt et al. 2007, 2009) as implemented in GUIDOS (Graphical User Interface for the Description of image Objects and their Shapes; Vogt 2010) to the 2001 NLCD. The resulting classes were core, islet, loop, bridge, perforation, edge, and branch (Soille and Vogt 2009). We calculated landscape configuration for forest, shrubland, and grassland (Table S3 in online supplemental material; see Acknowledgments). We ran GUIDOS with an eight-neighbor window and set edge distance parameters to 60, 60, and 120 m for grassland, shrubland, and forest, respectively, in order to estimate core and edge area. GUIDOS results were grouped into core (consisting of the core habitat class) and edge (consisting of islet, loop, bridge, perforation, edge, and branch). Within 19.7 km of each BBS route centroid, we calculated the total area of forest core, forest edge, grassland core, grassland edge, shrubland core, and shrubland edge (Fig. 2C, D).

In addition to our nationwide analysis, we modeled avian species richness using the same variables and procedures for three ecoregion provinces that captured a gradient from mostly forested (Central Appalachian Broadleaf Forest–Coniferous Forest–Meadow [province M221, 130 routes]), to agriculture with forest (Eastern Broadleaf Forest [Continental] [province 222, 326 BBS routes]), to grassland with agriculture (Great Plains–Palouse Dry Steppe [province 331, 156 routes]) (Bailey 1995). We selected these ecoregion provinces to compare the relative influence of vertical versus horizontal habitat structure across a gradient of vertical structure, from an area with low vertical structure (Great Plains–Palouse Dry Steppe) to areas with high vertical structure (Eastern Broadleaf Forest and Central Appalachian Broadleaf Forest). The Central Appalachian Broadleaf forest is composed of open, low mountains and valleys with mixed pine–oak forest, Appalachian oak forest, northeastern hardwood forest, and spruce–fir forest and meadows, following a gradient of low elevation to high elevation. The Eastern Broadleaf Forest Province is dominated by relatively flat, rolling hills covered with broadleaf deciduous forest. The Great Plains–Palouse Dry Steppe is defined by rolling plains in the rain-shadow of the Cascade and Rocky Mountains with predominantly steppe vegetation. Averaged across the BBS route buffers, the Central Appalachian Broadleaf forest was 66% forest and 22% agriculture, the Eastern Broadleaf Forest was 29% forest and 52% agriculture, and the Great Plains–Palouse Dry Steppe was 7% forest, 26% agriculture, 52% grassland, and 10% shrubland (Bailey 1995).

Statistical analysis.—We conducted our statistical analysis four times, once for the entire data set and once for each ecoregion province. Our input data consisted of six vertical-habitat-structure variables, 14 land-cover-composition variables, and six land-cover-configuration variables, for a total of 26 explanatory variables (Table S4 in online supplemental material; see Acknowledgments). Initially, we created univariate models relating species richness of each guild to each explanatory variable. Only variables that yielded an R^2 value > 0.05 for at least one avian guild were retained for further analysis. A scatter plot of each model was inspected for evidence of nonlinear relationships.

We calculated the correlation coefficient (r) for each pair of explanatory variables; for correlations with $|r| > 0.8$, we dropped the variable with lower predictive power in the univariate models. We used hierarchical partitioning (Chevan and Sutherland 1991) and best-subsets regression (Miller 1990) to evaluate the explanatory power of the remaining variables. Hierarchical partitioning measures the relative explanatory contribution of each variable in the context of others (Chevan and Sutherland 1991). For each explanatory variable, two linear models are created for every combination of the remaining variables, one model including the variable of interest and one excluding it. The difference in a fitness parameter (adjusted R^2 in our case) is calculated for the models with and without the variable of interest, and reported as that variable's independent contribution to the model, with the independent contributions of each variable summing to 100 for each model. We performed hierarchical partitioning with the "hier.part" function (Walsh and Mac Nally 2008) in R (R Development Core Team 2012).

There is a known rounding error in the hier.part routine when more than nine explanatory variables are included (Olea et al. 2010). The error is affected by the ordering of the explanatory variables, so to account for this behavior when we used more than nine explanatory variables, we ran the routine 1,000 times, randomly permuting the order of our explanatory variables. Because of computational constraints, this function limits the maximum number of explanatory variables to 12.

In models with more than 12 explanatory variables, we used best-subsets regression to identify the top 12 variables. Best-subsets regression finds the best models (based on adjusted R^2) with a specified number of explanatory variables. For each guild, we used the LEAPS package (Lumley and Miller 2009) in R to calculate the top 10 models, limited to one, two, three, four, and five explanatory variables (50 models total). Explanatory variables were ranked by the number of times they appeared in the 50 models.

Although best-subsets regression gives an indication of variable importance, especially when there is a large pool of explanatory variables, the analysis parameters that are used, such as the number of top models considered and the number of variables per model, can affect the outcome, and within a given model there is no ranking of variable importance. For these reasons, we used best-subsets regression only to select the top 12 variables for use in hierarchical partitioning, and we drew our inferences on the more objective measure of the independent contribution from hierarchical partitioning.

RESULTS

Nationwide analysis.—We fit univariate models for each combination of species richness (overall and by the three habitat guilds) and the 26 explanatory variables, yielding 104 models (Table S4). Mean biomass and standard deviation of biomass showed some evidence of nonlinearity in their relationship to avian species richness, so these two variables were log-transformed. Variables with the strongest univariate relationships to avian species richness were mean canopy height, standard deviation of canopy height, mean biomass, and forest edge area (all with R^2 values > 0.50 for at least one guild); proportion deciduous forest, standard deviation of biomass, and forest core area (R^2

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values > 0.25 for at least one guild); and proportion evergreen forest, proportion scrub-shrub, proportion grassland, proportion cultivated crops, number of land-cover classes, Shannon diversity of land-cover classes, shrubland core area, and grassland core area (R^2 values > 0.15 for at least one guild). Among these variables, the directions of the relationships were as expected (e.g., forest birds were positively associated with canopy height and variability, whereas grassland birds were negatively associated with both). Of the 26 explanatory variables, 9 were dropped for failing to meet the minimum R^2 threshold or because of correlations with other explanatory variables (results not shown). Best-subsets regression identified the top 12 explanatory variables of the remaining 17 (results not shown), and these 12 were included in the hierarchical partitioning analysis.

For each model, we used hierarchical partitioning to derive the independent contribution of each variable (Table S5, Conterminous United States, in online supplemental material; see Acknowledgments). Standard deviation of canopy height, mean canopy height, and forest edge area had substantially higher independent contributions than the remaining variables. Proportion deciduous forest had the highest independent contribution among the horizontal composition variables, with high contributions to species richness models of all species, forest birds, and shrubland birds. The remaining variables had lower overall independent contributions but sometimes had high contributions in specific guilds. For example, grassland core area had a high contribution for grassland and shrubland bird models, and proportion cultivated crops had a high contribution in models of grassland birds. Linear models of species richness were fit as a function of the top 12 variables (Fig. 3, Conterminous United States) for all birds (adjusted $R^2 = 0.46$), forest birds ($R^2 = 0.70$), grassland birds ($R^2 = 0.48$), and shrubland birds ($R^2 = 0.27$).

Individual ecoregion province analysis.—Statistical analysis was conducted individually for the Eastern Broadleaf Forest, Central Appalachian Broadleaf Forest, and Great Plains–Palouse Dry Steppe. Based on univariate linear models of avian species richness (results not shown), variables with high maximum univariate R^2 values among guilds included proportion deciduous forest (0.40), forest edge area (0.39), and mean canopy height (0.39) in the eastern forest; mean canopy height (0.24), mean biomass (0.23), and standard deviation of biomass (0.22) in the Appalachian forest; and standard deviation of canopy height (0.53), standard deviation of biomass (0.48), and forest edge area (0.48) in the Great Plains. Some variables failed to meet our criterion of $R^2 > 0.05$ for at least one guild or were correlated with other variables and thus were dropped from further analysis, leaving 9, 8, and 16 variables from the eastern forest, Appalachian forest, and Great Plains, respectively (Table S5).

For the eastern forest and Appalachian forest, <12 variables remained in our explanatory variable pool, so we did not need to drop any remaining variables before performing hierarchical partitioning. For the Great Plains, 16 variables remained. We selected the top 12 variables as ranked from the best-subsets regression.

In the eastern forest (Table S5, Eastern Broadleaf), mean canopy height, proportion developed, and standard deviation of canopy height had the highest independent contributions. Adjusted R^2 values for guild species richness as a function of the nine explanatory variables were calculated for all birds ($R^2 = 0.27$), forest birds ($R^2 = 0.47$), grassland birds ($R^2 = 0.42$), and shrubland birds ($R^2 = 0.37$) (Fig. 3).

For the Appalachian forest (Table S5, Appalachian Broadleaf), proportion developed had the highest total independent contribution across guilds, followed by standard deviation of canopy height, standard deviation of biomass, and mean canopy height. Adjusted R^2 values for guild species richness as a function of the nine explanatory variables were calculated for all birds ($R^2 = 0.14$), forest birds ($R^2 = 0.16$), grassland birds ($R^2 = 0.29$), and shrubland birds ($R^2 = 0.08$) (Fig. 3).

In the Great Plains–Palouse Dry Steppe (Table S5, Great Plains), standard deviation of canopy height, Shannon diversity of land-cover classes, and mean biomass had the strongest independent contribution. Adjusted R^2 values for guild species richness as a function of the nine explanatory variables were calculated for all birds ($R^2 = 0.48$), forest birds ($R^2 = 0.57$), grassland birds ($R^2 = 0.63$), and shrubland birds ($R^2 = 0.40$) (Fig. 3).

Discussion

Understanding the factors that shape species diversity patterns over broad scales has long been a focus of community ecology, and there is a rich literature of macroecological investigations that test

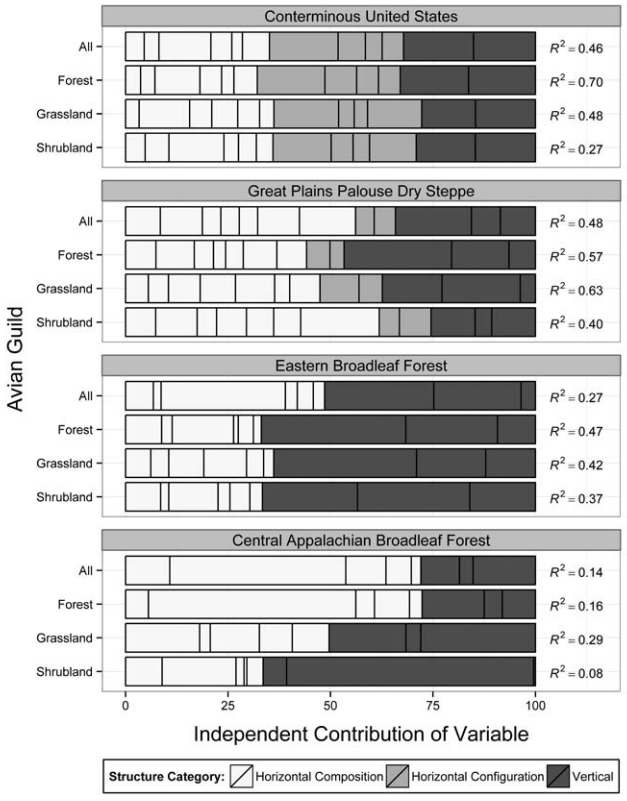


Fig 3. Independent contributions of explanatory habitat variables to models of avian species richness for all bird species and three avian habitat guilds across the conterminous United States and within three ecoregion provinces, as determined by hierarchical partitioning. The bar graphs show the contribution of individual variables, color-coded by habitat structure category. (For names and independent contributions of specific variables, see Table S5 in the online supplemental material.) The pools of variables are different among the panels (ecoregions) as a result of preliminary variable reduction (see text; e.g., no horizontal configuration variables were retained in the Eastern Broadleaf Forest or Central Appalachian Broadleaf Forest), but within each panel, the same explanatory variables were used in the four guild models and are displayed in the same order. The adjusted R^2 value for each model is displayed to the right of the bar graph.

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for patterns of association among abiotic and biotic covariates hypothesized to explain why more or fewer species are observed from place to place (e.g., Rosenzweig 1995, Nagendra 2001, Coops et al. 2009). However, there is something of a dichotomy of studies, whereby different factors are examined at different scales. Broad-scale studies typically rely on remotely sensed imagery and focus on two-dimensional (i.e., horizontal) measures of landscape structure (e.g., Griffiths et al. 2000, Donovan and Flather 2002, Pidgeon et al. 2007). By contrast, drivers of species richness in the vertical plane (MacArthur and MacArthur 1961, Erdelen 1984) are typically studied at local scales, because they are more difficult to measure directly for large areas. Our study was able to overcome this dichotomy. On the basis of a set of surrogate measures of vertical habitat structure (canopy height and biomass) derived from the NBCD, we showed that vertical habitat structure was strongly associated with nationwide and ecoregion province-level patterns of bird species richness. As expected, horizontal habitat structure measures, such as proportion of land-cover class, also contributed to explanation of species richness patterns. Measures of vertical and horizontal structure were individually useful in explaining avian species richness patterns, and both categories retained their strong and independent explanatory power when combined. Hence, vertical measures of habitat structure were complementary to existing horizontal measures, with each characterizing different components of habitat structure to explain patterns of avian species richness.

Nationwide analysis.—We expected that the measures of vertical habitat structure would provide additional information not present in the measures of horizontal structure. This was conclusively shown to be true and is perhaps the most significant finding of our study. Many of the variables most strongly related to avian species richness were measures of vertical structure. We specifically expected positive relationships between overall avian species richness and vegetation height, vegetation height variability, biomass, and biomass variability because increases in these measures usually correspond to an increase in potential habitat niches. Our univariate models were consistent with expectations in all of these cases. The positive relationship between mean canopy height and forest bird species richness specifically corroborated previous local-scale LiDAR-based findings modeling forest bird species richness as a function of canopy height (Goetz et al. 2007, Lesak et al. 2011) or foliage height diversity (Clawges et al. 2008). Though we modeled avian species richness, other studies have found LiDAR-derived canopy height to be strongly associated with other avian ecological measures, such as habitat selection (Seavy et al. 2009) or chick body mass as an indicator of habitat quality (Hinsley et al. 2006). Although measures of biomass were excluded from the national analysis because of correlation with other variables, they were strongly related to avian species richness in the univariate models. This concurs with previous findings that measures of biomass are related to bird habitat selection, abundance, or species richness, whether measured directly in the field (Saveraid et al. 2001) or remotely sensed (Imhoff et al. 1997, Bergen et al. 2007).

In addition to increasing the number of habitat niches, high canopy height and biomass may influence species richness through increased food availability. For example, lepidopteran species are an important food item fed to young in the nest, especially by passerines. In the mid-Atlantic, deciduous trees such as oaks (*Quercus* spp.), cherries (*Prunus* spp.), willows (*Salix* spp.), birches (*Betula* spp.), and cottonwood and aspen (*Populus* spp.) support the greatest species diversity of Lepidoptera (Tallamy and Shropshire 2009), and these tree species are common throughout the eastern United States. Food (arthropod) availability has been shown to influence bird distribution (Johnson and Sherry 2001). Because higher canopy height and biomass should equate to higher food availability for Lepidoptera, and availability of Lepidoptera drives higher avian reproductive success (Holmes et al. 1986), high canopy height and biomass should positively influence avian abundance and, therefore, species richness. This applies in particular to the two forested ecoregion provinces we considered, which are primarily composed of deciduous tree species.

Within habitat-based guilds, we predicted that the area of guild-relevant habitat (e.g., proportion deciduous forest in the forest bird model) would be the strongest explanatory variable in species richness models. Contrary to our prediction, the hierarchical partitioning analysis revealed that measures of habitat area were less effective in explaining variation in species richness than other habitat structure variables. For all three habitat-based guilds, measures such as standard deviation of canopy height ranked higher than guild-relevant habitat area measures. This indicates that although measures based on land-cover classifications (e.g., proportion deciduous forest) have explanatory value, more detailed measures of habitat structure, such as mean canopy height, may possess more explanatory value. This is not unexpected, in that a significant shortcoming of measures derived from land-cover classifications is that the classifications do not retain any information on within-class heterogeneity (Turner et al. 2001).

We predicted that higher levels of landscape diversity should lead to increased species richness (Atauri and de Lucio 2001). Although the number of land-cover classes and the Shannon diversity of land-cover classes indeed exhibited positive univariate relationships with species richness of all guilds except grassland birds (which exhibited a negative relationship), these relationships were relatively weak for both grassland and shrubland birds. Ultimately, these measures were too general, and we found that measures specific to individual land cover classes were more important than the synthetic variables.

Individual ecoregion analyses.—Our most important prediction, that measures of vertical habitat structure would add new information not already present in horizontal measures, was strongly supported by the single-province analyses as well. The hierarchical partitioning analysis ranked variables representing both vertical and horizontal habitat structure in the top five for all three ecoregions (Table S5). This is an exciting finding, because it shows that measures of vertical and horizontal vegetation structure remain complementary at the ecoregion scale. It is also notable that our measures of vertical structure from the NBCD showed strong performance even in the Great Plains, which has comparatively low vertical vegetation structure.

Our other predictions received mixed support from the single-ecoregion analyses. The relationships between overall species richness and mean canopy height, canopy height variability, biomass, and biomass variability were positive and highly significant, as expected (Goetz et al. 2007, Bergen et al. 2009), in the Great Plains–Palouse Dry Steppe and eastern forest (except biomass, which was nonsignificant), but none of these univariate relationships showed statistical significance in the Appalachian forest. As in the nationwide analysis, our prediction that proportion of the preferred habitat type would be the strongest predictor

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of species richness in habitat-based guilds was refuted by the univariate relationships. Our prediction that higher landscape diversity would lead to increased avian species richness (Atauri and de Lucio 2001) was strongly supported by the univariate relationships.

While it is challenging to quantify the relative difference in influence of measures of horizontal and vertical habitat structure in driving patterns of avian biodiversity, our results showed that both categories are important and that measures of vertical structure, as characterized by the NBCD, had strong explanatory power. In the nationwide analysis, the independent contributions of vertical structure, horizontal composition, and horizontal configuration were about evenly split. In the Great Plains–Palouse Dry Steppe, the contribution of vertical variables was slightly higher (except for shrubland birds), but still roughly one third of the independent contribution. It is notable, though, that vertical measures still had a strong contribution, given that the Great Plains–Palouse Dry Steppe is quite vertically homogeneous. In a more vertically complex ecoregion, the Eastern Broadleaf Forest, measures of vertical structure represented more than half of the independent contribution for each avian guild. This shows the value of measures of vertical structure in forested areas. In the other forested ecoregion that we considered, the Central Appalachian Broadleaf Forest, vertical measures were still important, though not as dominant. However, the models in this ecoregion yielded adjusted R^2 values that were substantially lower than those for the other study areas. This may indicate that in this ecoregion, measures of habitat structure, whether vertical or horizontal, do not adequately capture the drivers of species richness patterns.

It is notable that horizontal configuration variables (area of core and edge habitat for forest, grassland, and shrubland) had a high independent contribution in models of avian species richness for the conterminous United States but had much smaller contributions in the single-ecoregion models. Aside from grassland core and grassland edge area in the Great Plains–Palouse Dry Steppe model, all configuration variables were excluded early in our analysis because of low univariate R^2 values or correlation with other, better-performing variables (primarily landscape composition measures). This appears to be the result of two factors. First, variability in landscape configuration is much lower within a given ecoregion than across the conterminous United States, because ecoregions are defined to group areas with similar climate and physiographic characteristics (Bailey 1995). For example, forest configuration varies widely across the United States, but within the Great Plains–Palouse Dry Steppe, forests are consistently uncommon, small, and patchy, whereas in the Eastern Broadleaf Forest, forests are consistently common, large, and contiguous. The dramatic reduction in variability of these measures within a single ecoregion strips much of their explanatory power. Second, in our study, the little explanatory power these measures have within an ecoregion is highly correlated to landscape composition measures (e.g., proportion deciduous forest), which have stronger explanatory power.

Although canopy height and biomass yield important quantitative information about vegetation structure, they do not characterize the vertical arrangement of vegetation (e.g., two forests could have the same canopy height or biomass but have completely different vertical arrangements of branches and foliage). On the other hand, it seems logical that areas with higher canopy height and biomass (or high variability in those measures) likely contain a more complex arrangement of vegetation. Our results indicate that even though these measures give less insight into structural arrangement than field measurements, they nonetheless explain a significant proportion of spatial variability in avian species richness. LiDAR is one approach that is very capable of quantifying the vertical arrangement of vegetation (Dubayah and Drake 2000, Bergen et al. 2009, Hawbaker et al. 2010). At the extents for which LiDAR data are available, it can quantify vegetation structure in a manner relevant to the distribution and diversity of many species (Martinuzzi et al. 2009, Goetz et al. 2010, Palminteri et al. 2012). Unfortunately, LiDAR data sets are not publicly available for most areas, and available data sets were acquired from different sensors with different parameters, complicating their compilation. Eventually, the availability of these data sets will increase, but in the meantime, we have shown the NBCD to be a very useful data set for characterizing vertical habitat structure across the conterminous United States. We recommend that future studies of avian biodiversity, especially at broad scales, include measures of both vertical and horizontal structure.

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