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Citation	Vogeler, J. C., Hudak, A. T., Vierling, L. A., Evans, J., Green, P., & Vierling, K. I. T. (2014). Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests. Remote Sensing of Environment, 147, 13-22. doi:10.1016/j.rse.2014.02.006
DOI	10.1016/j.rse.2014.02.006
Publisher	Elsevier
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Remote Sensing of Environment 147 (2014) 13–22

Contents lists available at ScienceDirect

Remote Sensing of Environment

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

Terrain and vegetation structural influences on local avian species richness in two mixed-conifer forests

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ARTICLE INFO

Article history:
Received 2 November 2011
Received in revised form 6 February 2014
Accepted 9 February 2014
Available online 12 March 2014

Keywords:
Forest birds
LiDAR
Landsat
Species richness modeling
Avian nesting guilds
Predictive maps

ABSTRACT

Using remotely-sensed metrics to identify regions containing high animal diversity and/or specific animal species or guilds can help prioritize forest management and conservation objectives across actively managed landscapes. We predicted avian species richness in two mixed conifer forests, Moscow Mountain and Slate Creek, containing different management contexts and located in north-central Idaho. We utilized general linear models and an AIC model selection approach to examine the relative importance of a wide range of remotely-sensed ecological variables, including LiDAR-derived metrics of vertical and horizontal structural heterogeneities of both vegetation and terrain, and Landsat-derived vegetation reflectance indices. We also examined the relative importance of these remotely sensed variables in predicting nesting guild distributions of ground/understory nesters, mid-upper canopy nesters, and cavity nesters. All top models were statistically significant, with adjusted R^2s ranging from 0.05 to 0.42. Regardless of study area, the density of the understory was positively associated with total species richness and the ground/understory nesting guild. However, the relative importance of ecological predictors generally differed between the study areas and among the nesting guilds. For example, for mid-upper canopy nester richness, the best predictors at Moscow Mountain included height variability and canopy density whereas at Slate Creek they included slope, elevation, patch diversity and height variability. Topographic variables were not found to influence species richness at Moscow Mountain but were strong predictors of avian species richness at the higher elevation Slate Creek, where species richness decreased with increasing slope and elevation. A variance in responses between focal areas suggests that we expand such studies to determine the relative importance of different factors in determining species richness. It is also important to note that managers using predictive maps should realize that models from one region may not adequately represent communities in other areas.

1. Introduction

Biodiversity is central to ecosystem functioning worldwide (Hooper et al., 2005). As human influences on the environment continue to grow, understanding and quantifying the factors driving biodiversity have received increased attention to support management and conservation efforts (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Although numerous factors can affect biodiversity, vegetation structure is frequently identified as an important driver at the local scale (Farley, Ellis, Stuart, & Scott, 1994; Goetz, Steinberg, Dubayah, & Blair, 2007; MacArthur & MacArthur, 1961; Sallabanks, Haufler, & Mehl, 2006). Greater vegetation structural complexity is thought to maintain higher biodiversity across a range of taxonomic groups by providing a variety of microclimates and microhabitats (Carey, 1998; MacArthur & MacArthur, 1961; Müller & Brandl, 2009; Verschuyl, Hansen, McWethy, Sallabanks, & Hutto, 2008; Vierling et al., 2011). Different aspects of vegetation structure may be important to wildlife species for life history needs, such as reproduction, cover from predation and weather, and foraging (Bradbury et al., 2005).

Light Detection and Ranging (LiDAR) is an effective technique for acquiring fine-resolution, three-dimensional vegetation structure data relevant to the study of animal diversity, yet with wider spatial extent than field-based measures (Hyde et al., 2005; Müller, Stadler, & Brandl, 2010; Vierling, Vierling, Gould, Martinuzzi, & Clawges, 2008; Vierling et al., 2011). The well-documented relationships between bird diversity and field-sampled vegetation structure

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http://dx.doi.org/10.1016/j.rse.2014.02.006
0034-4257/

(MacArthur & MacArthur, 1961; MacArthur, Recher, & Cody, 1966) have made this taxonomic group a focus of many studies exploring the relationship between LiDAR-derived three-dimensional vegetation structure in modeling wildlife habitat associations (Clawges, Vierling, Vierling, & Rowell, 2008; Goetz et al., 2007; Müller et al., 2010). The diversity of birds is of particular interest in a wide array of studies, owing to the importance of birds as indicators of ecological function and degradation (Carignan & Villard, 2002).

While many of the studies utilizing LiDAR data to examine bird diversity relationships agree with previous findings indicating that some metric of foliage height diversity is a strong predictor of bird diversity (e.g. MacArthur & MacArthur, 1961; MacArthur et al., 1966), there is great variability in the metrics included. Some studies utilize LiDAR in addition to other sources of remotely sensed data (Clawges et al., 2008; Goetz et al., 2007; Jones, Arcese, Sharma, & Coops, 2013), while others incorporate LiDAR metrics alone (e.g. Lesak et al., 2011; Müller et al., 2010) in their analyses. Additionally, the studies have been conducted in a variety of different forest types (Mueller & Vierling, 2014), and there are a diversity of non-LiDAR metrics incorporated in the studies. For example, Flaspohler et al. (2010) incorporated the size of forest fragments in their study of Hawaiian bird diversity, and the incorporation of landscape characteristics such as patch size, patch shape, and horizontal heterogeneity of vegetation structure are limited in the existing LiDAR-based studies of bird diversity. It is important to consider additional environmental characteristics in these studies because although vertical vegetation structure is undoubtedly an important influence on avian diversity in some communities, the responses of bird communities to vegetation structure may also be influenced by a variety of ecological variables such as topographic gradients (Rompré, Robinson, Desrochers, & Angehr, 2007), landscape patterns (Saab, 1999), and management regimes (Twedt, Wilson, Henne-Kerr, & Hamilton, 1999).

Our main objective was to explore local species richness patterns in western North America, where only two studies have examined the relationships between LiDAR structure and bird diversity in conifer-dominated forests (Clawges et al., 2008; Jones et al., 2013). These studies have shown that LiDAR-derived variables are useful predictors of species richness, and our objective was to expand upon these studies in two fundamental ways. First, few studies have simultaneously included vertical and horizontal structural heterogeneities, terrain, and vegetation reflectance features within the same analysis of bird species richness. Second, although a few LiDAR-based studies have grouped avian species by broad habitat associations (Goetz et al., 2007; Jones et al., 2013), the use of forest-specific nesting guilds for examining LiDAR-derived forest structure relationships has yet to be explored. Finally, it is important to determine whether the same ecological variables that are important in one mixed-coniferous forest might differ in another mixed-coniferous forest. Our objectives therefore were to model total species richness and nesting guild richness (ground/understory nester, mid-upper canopy nester, and cavity nester) using a wide variety of environmental metrics, and to compare the relative importance of metrics in predicting species richness between two different study areas of mixed-coniferous forest.

2. Methods

2.1. Study areas

We sampled two study areas in north-central Idaho: Moscow Mountain and the Slate Creek drainage. Moscow Mountain is a ~20,000-ha peninsula of mixed conifer forest bordered on three sides by agricultural lands located ~20 km northeast of the city of Moscow, Idaho (46°49′N, 116°50′W). The majority of ownership belongs to private industrial logging companies with additional minority ownership of lands divided among the University of Idaho Experimental Forest, the City of Troy watershed, and small private landowners. Forest tree species include Western red cedar (*Thuja plicata*), Grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), Western larch (*Larix* occidentalis), Lodgepole pine (*Pinus contorta*), Western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*), Western white pine (*Pinus monticola*), and Subalpine fir (*Abies lasiocarpa*). The managed landscape is a mosaic of forest successional stages with the majority of the landscape ranging from recently logged to mature multi-story, with a small proportion of old multi-story stands (Falkowski, Evans, Martinuzzi, Gessler, & Hudak, 2009), and elevations ranging from 816 to 1242 m.

The Slate Creek study area is located on public land held by the National Forest Service within the Salmon River Ranger District of the Nez Perce National Forest of central Idaho (45°38′N, 116°2′W). In this landscape, our study focused upon a subset of the National Forest in the Slate Creek drainage ~30,000 ha in extent, with elevations ranging from 1125 to 2250 m. Higher elevation survey locations were located in the Gospel Hump Wilderness. Slate Creek includes the same tree species as Moscow Mountain, but with different relative proportions (dominant species at Moscow Mountain were Western red cedar and Grand fir while Douglas-fir and Lodgepole pine were dominant at Slate Creek). Slate Creek differs from Moscow Mountain in that it has larger topographic gradients and is less intensively managed with the full range of successional stages represented and a greater proportion within late-seral stages. While the Moscow Mountain study area is situated along the forest-agricultural land ecotone at the western extreme of the coniferous forest belt of north-central Idaho, the Slate Creek study area occurs within this coniferous forest belt.

2.2. Bird surveys and richness calculations

We randomly selected point count locations from study area maps stratified by forest structure. We used handheld Garmin Global Positioning System (GPS) units in conjunction with aerial photographs to locate the predetermined sample points in the field. Due to the 4-year gap between LiDAR acquisition and bird surveys at Slate Creek, sample sites within recently disturbed forest stands were relocated to an alternative random location within that stratum.

Avian point count surveys were conducted in the Moscow Mountain and Slate Creek study areas during the breeding seasons of 2009 and 2010, respectively following Vogeler, Hudak, Vierling, and Vierling (2013). Each of the 151 survey sites on Moscow Mountain and 164 survey sites at Slate Creek were visited twice during the season to increase the likelihood of detecting the majority of breeding bird species. Each survey point was separated by at least 250 m, and we used 8-minute variable-radius point count methods, where all bird individuals identified by sight or sound were recorded and distances were estimated (Reynolds, Scott, & Nussbaum, 1980). A single observer (Vogeler) conducted the point counts at Moscow Mountain in 2009 while two observers were used at Slate Creek for the 2010 surveys (Vogeler plus one technician). For the 2010 Slate Creek survey with two observers, there was intensive pre-season training to calibrate species identification and distance estimation between the observers. Additional details on the point count methodology used in this study can be found in Vogeler et al. (2013).

Point specific species richness was calculated using the birds that were detected within 75 m from the point count center. Recent studies have shown that low detectability at this spatial scale can be attributed to low occurrence and not the product of detectability issues (Dorazio, Royle, Soderstrom, & Glimskar, 2006, but see Alldredge, Pollock, Simons, & Shriner, 2007), including one study occurring in a geographic region with comparable forest structure (Verschuyl et al., 2008). To reduce the bias of rare species that may only be passing through the site, we adjusted our species richness values by removing any species with fewer than three independent detections during the season. Individuals recorded while flying over the site were also removed (Reynolds et al., 1980). Partial identifications were excluded, e.g. UNWA (unknown warbler), to include only confident identifications in the species richness calculation. Point counts from both visits to each survey site were pooled, and the total number of unique species observed in the 75 meter radius survey site was recorded as the total species richness for that location. Three nesting guild delineations were used in this study following the methods of Salek, Svobodova, and Zasadil (2010): ground and understory; mid-upper canopy; and cavity. We compiled nest location preferences for all species detected using Birds of North America (2013). Guild specific species richness was calculated using the same methods as total species richness for the 75 meter radius scale at each survey location.

2.3. LiDAR and Landsat data

Airborne multiple-return discrete LiDAR data were utilized to derive all vegetation structure metrics. Data acquisition occurred at Slate Creek and Moscow Mountain in the summers of 2006 and 2009, respectively. Both LiDAR surveys were conducted by Watershed Sciences, Inc. (Corvallis, OR) with a Leica ALS50 system with point densities of ≥4 points/m^2. The Moscow Mountain and Slate Creek flights had average vertical accuracies of 4.3 cm and 8.8 cm, respectively. Ground returns were classified using the Multiscale Curvature Classification (MCC) algorithm (Evans & Hudak, 2007) then subsequently interpolated into a 1-m digital terrain model (DTM). The DTM was subtracted from the all-return data to calculate canopy heights, which were then binned into 20 m × 20 m grid cells for the purpose of calculating height-based statistical metrics including height maximum, mean, and standard deviation. See Evans, Hudak, Faux, and Smith (2009) for a complete list of canopy metrics that can be generated from the LiDAR height distributions. Although there was a 4 year gap between the LiDAR acquisition and the collection of field data at Slate Creek, Vierling, Swift, Hudak, Vogeler and Vierling (2014) found that a 6 year gap between LiDAR acquisitions and the collection of bird field data changed the mapped output of total species richness in the non-harvest areas of Moscow Mountain by <1 species (out of 23), and the Slate Creek sites were similar to the non-harvest areas used in the Vierling et al. (2014) study.

Single-date Landsat 5 TM images were used to create a normalized difference vegetation index (NDVI) map for the study areas. Seto, Fleishman, Fay, and Betrus (2004) and Bailey et al. (2004) demonstrated the use of single date Landsat-derived NDVI measures in species richness models. We selected Landsat 5 images from the 2009 and 2010 summer seasons with minimal cloud cover and post snow melt: resultant image dates were July 3, 2009 (Moscow Mountain; path/row 43/27; 0% cloud cover) and August 5, 2010 (Slate Creek; path/row 45/28; 3% cloud cover). The image dates represent late growing season reflectance from the landscapes as opposed to the early season reflectance characteristic of the habitat during the period when birds are selecting breeding habitat. Due to cloud cover and snow patches, images from earlier in the season were not suitable for reliable extraction of model metrics. The higher elevations at Slate Creek and the persistence of snow later into the season at this study area help to justify the image acquisition a month later than the lower elevation Moscow Mountain study area.

Calibration parameters for each Landsat 5 band were acquired from the metadata file accompanying the image downloaded from USGS in order to calculate at-sensor reflectance; at-surface reflectance was achieved using the band minimum dark subtraction method. We derived NDVI following Tucker (1979).

Model metrics derived from LiDAR and Landsat were calculated for the bird survey locations using zonal statistics in ArcGIS for the local 75 meter radius plot in order to match the scale of the avian response variables. At the 20 m × 20 m pixel size of the LiDAR-derived topographic, vertical, and the horizontal structure metrics, approximately 37 whole pixels and 23 partial pixels were weighted in the 75 meter buffer metric extraction, with total counts varying as a function of where in the center pixel the point count location was located. The 30 m resolution of the Landsat-derived NDVI map included approximately 13 whole and 12 partial pixels in metric calculations, which are exact counts that also depended on survey location in the center pixel.

2.4. Predictive modeling and statistical analyses

After the removal of point count locations with noise disturbance capable of affecting bird detections, inclement weather that may impact bird behavior, or errors involved in the maps derived from remotely sensed variables (such as cloud cover in the Landsat images), a total of 142 points at Moscow Mountain and 134 points at Slate Creek were used in the statistical analyses. We utilized general linear models to explore relationships between bird species richness and a variety of remotely-sensed forest metrics. We included seven variables in our modeling framework and broadly categorized them into the following four groups: vertical forest structure, horizontal forest structure, topographic characteristics, and vegetation greenness (Table 1).

LiDAR data accommodates the extraction of a variety of height and density metrics, although we only wanted to include a few to represent vertical forest structure in this analysis. As a form of preliminary variable selection we utilized the free search procedure in HyperNiche, a non-parametric habitat modeling software, to determine the single best LiDAR structure predictor for each study area-specific response variable from a suite of LiDAR height and density metrics. The local linear estimates within HyperNiche selected the proportion of returns within stratum 2 (1.0–2.5 m above ground), which represents the density of vegetation in the understory, as the best LiDAR vertical structure predictor for all Slate Creek response variables. Understory density (Ustory) was also selected as the best single predictor for Moscow Mountain total species richness (TSR) and the ground/understory nesting guild (GSR1), while canopy density (Canopy) best predicted the mid-/upper-canopy nesting guild (GSR2) and the cavity nesting guild species richness (GSR3). Many of the previous LiDAR-based studies examining avian communities have identified the importance of vertical height diversity in predicting bird diversity. Therefore, we choose to include the standard deviation of height (HSD) as a third vertical structure variable to facilitate comparisons of our findings with those of previous studies. While other variables such as canopy height may also influence avian diversity, the model selection process identified the metrics of greatest influence at our study areas.

In order to address “horizontal” forest patch diversity, we also included the diversity of forest classes in our modeling approach. We created an eight-level classification of both landscapes by combining LiDAR-derived mean height and canopy density classes mapped at 20 m spatial resolution (Fig. 1). We overlaid 75 meter radius buffers surrounding our point count locations onto the 8-level classification map in ArcGIS, and then utilized FRAGSTATS (McGarigal, Cushman, Neel, & Ene, 2002) to calculate the Shannon Diversity Index of patches among these different forest classes within the buffered area. This patch diversity metric (Patch) was included in the models to represent horizontal forest patch diversity. LiDAR also provides digital terrain models (DTMs) which we used to extract mean elevation (Elev) and mean slope (slope; Table 1).

General linear models were created in the statistical software program, R (R Development Core Team, 2012) to test for significant relationships among the response variables (bird species richness, guild-specific richness) and a variety of remotely sensed forest metrics. We used a variance inflation factor (VIF) threshold of <3 to ensure that highly correlated variables were not included in the modeling process (Montgomery, Peck, & Vining, 2006). For our model selection approach, we calculated Akaike information criterion (AIC; Akaike, 1973) values for a candidate set of 25 models including a global model containing all predictor variables, and an intercept only model. AIC values were

Table 1
Descriptions of LiDAR and Landsat-derived metrics included in predictive models for total and guild specific species richness at two mixed conifer study areas in Idaho.

Predictor variables (75 m radius scale)	Abbrev.	Metric description
Vertical structure (LiDAR)		
Canopy height standard deviation	Height_σ	Standard deviation of mean canopy heights
Understory density	Ustory	Percentage of LiDAR returns between 1 and 2.5 m
Canopy density	Canopy	Mean density of LiDAR returns above 2 m
Horizontal structure (LiDAR)		
Patch diversity	Patch	Shannon diversity of patches classified using mean canopy height and density classes
Topographic (LiDAR)		
Slope	Slope	Mean slope calculated from digital terrain model (DTM)
Elevation	Elev	Mean elevation extracted from LiDAR-derived DTM
Vegetation greenness (Landsat)		
Normalized Difference Vegetation Index	NDVI	Mean normalized difference vegetation index indicative of vegetation greenness

then ranked to determine the model with the lowest AIC value for each of the species richness response variables; any model within 2 units of the lowest AIC value was considered a competing model (Burnham & Anderson, 2002). We calculated Akaike weights to compare the relative support of each model and importance values for individual parameters for explaining the variance of the data (Johnson & Omland, 2004). The Akaike weights can be considered to represent the probability of a model given the data, with weights summing to 1 across candidate models, and can be utilized to calculate more robust parameter estimates and weighted standard errors (Johnson & Omland, 2004).

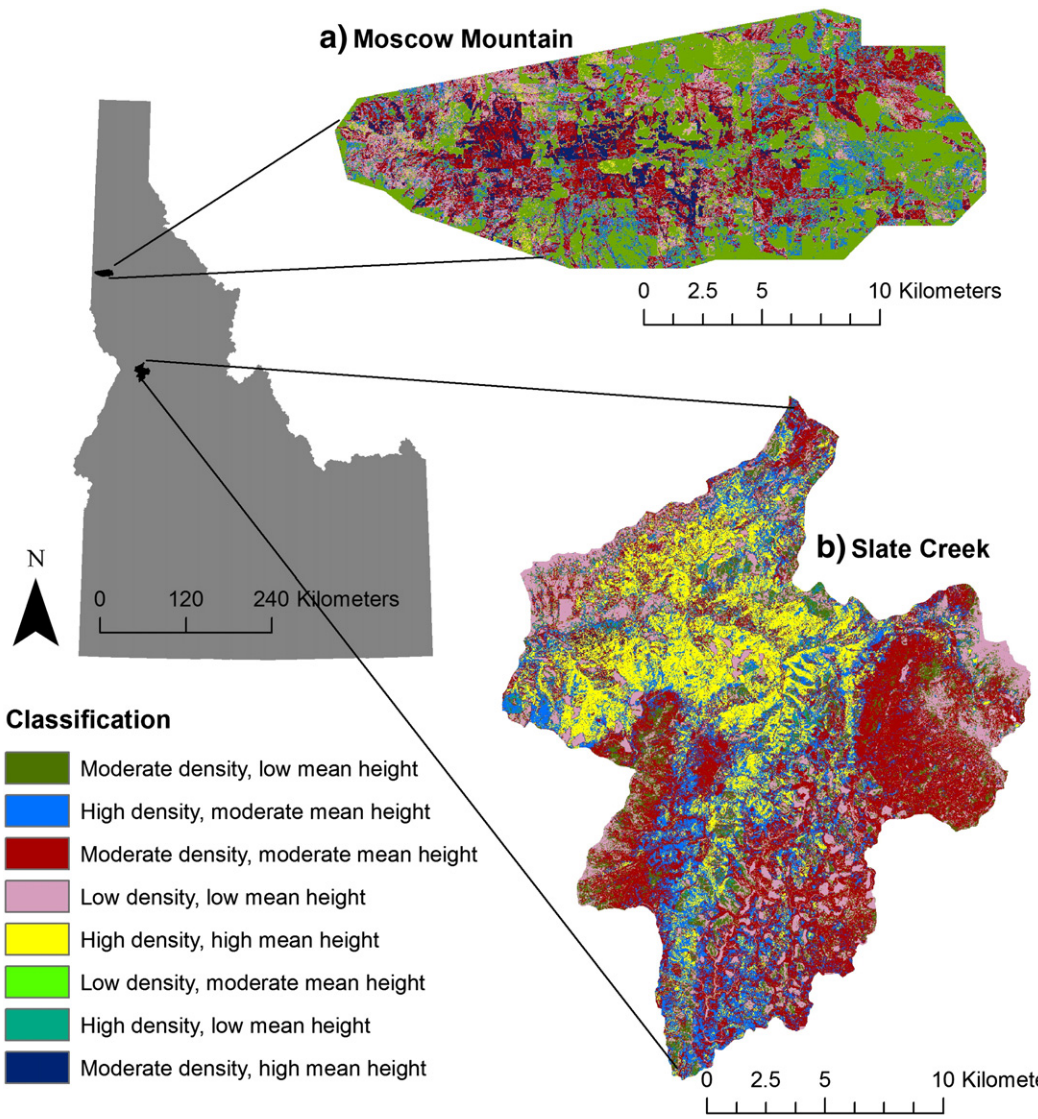

Fig. 1. LiDAR-derived forest classification utilizing mean canopy height and density metrics for a) Moscow Mountain, and b) Slate Creek. Canopy density was divided into 3 classes: low (0–40%); moderate (41–70%); and high (71–100%). The three classes of mean height include: low (0–5 m); moderate (6–15 m); and high (16 m—max height). The combination of the three density and height metrics created a 9-level classification, but the absence of the class characterized by low density and high mean height from the landscape resulted in an 8-level patch classification map. (Figure in color for print and web versions).

We mapped species richness across the two study landscapes (~50,000 ha combined) to visualize landscape patterns in species richness and to demonstrate the practical utility of our models for forest managers. The ArcGIS focal mean and standard deviation functions were applied to filter the 20 m LiDAR metrics of selected variables within the circular neighborhood of 3 cells surrounding every pixel, producing output rasters that matched the scale of the 75 meter radius point count survey plots in the field. To simulate the patch diversity metric that had been generated in FRAGSTATS, a variety function was applied to the 8-level canopy structure classification map, which was then rescaled to match the range of the patch metric calculated across the bird survey plots. Using the aforementioned prediction layers, the best model could then be applied to the study areas by applying the predict function within the yaImpute package (Crookston & Finley, 2008) in R.

Due to the strong differences between the relatively lower elevation forests of Moscow Mountain that are surrounded by agriculture and the more rugged Slate Creek landscape embedded within a larger forest matrix, we created separate models for each of the two study areas. Our site-specific model development allowed for a better understanding of whether the same forest characteristics are strong predictors of forest bird richness regardless of the surrounding landscape and elevation, although the site specific modeling approach did not provide large enough datasets for independent validation data. Therefore we utilized leave-one-out-cross-validation (LOOCV), a procedure that omits one observation at a time in the models to use as validation data, in order to calculate prediction errors for the top models for each response variable and study area. To better understand the differences in the model variables between the study areas, we conducted Welch's two-sided t-tests in R to test for significant differences between study area predictive variable means as well as the mean species richness response variables.

3. Results

3.1. Study area comparisons

A total of 78 avian species were detected in the variable-radius point counts during the two year study. Forty species occurred in both study areas in addition to 25 species unique to Moscow Mountain and 13 species unique to Slate Creek (Supplementary Table S1). The ground/understory nesting guild represented 44% and 36% of the species at Moscow Mountain and Slate Creek, respectively. At Moscow Mountain, 30% of the bird species nested in the mid-/upper canopy compared to 36% at Slate Creek. Cavity-nesters comprised 26% of Moscow Mountain species and 28% of Slate Creek species.

Table 2
Comparison of means and 95% confidence intervals (in parentheses) for response and predictor variables included in models for the Moscow Mountain and Slate Creek study areas. Total species richness (TSR) and guild specific species richness values (ground/understory nesters:GSR1; mid-upper canopy nesters:GSR2; cavity nesters: GSR3) represent the number of unique species identified within a 75 meter radius at survey locations. All predictor variables were derived from LiDAR data with the exception of the Landsat-derived NDVI.

		Moscow Mountain	Slate Creek
Response variables	TSR	10.070 (9.587, 10.554)	9.209 (8.736, 9.682)
	GSR1	4.803 (4.454, 5.152)	3.448 (3.196, 3.700)
	GSR2	3.183 (2.921, 3.446)	3.948 (3.692, 4.204)
	GSR3	1.761 (1.583, 1.938)	1.791 (1.627, 1.955)
Predictor variables	Height_σ	3.260 (3.014, 3.507)	3.239 (2.998, 3.481)
	Ustory	6.847 (6.163, 7.531)	5.072 (4.500, 5.644)
	Canopy	50.248 (46.444, 54.052)	60.523 (57.687, 63.360)
	Patch	0.955 (0.888, 1.022)	0.939 (0.878, 1.001)
	Slope	7.713 (7.018, 8.408)	11.513 (10.289, 12.736)
	Elev	963.148 (947.722, 978.574)	1720.006 (1682.150, 1757.863)
	NDVI	0.744 (0.729, 0.759)	0.366 (0.355, 0.376)

Significant differences between response variable means between Moscow Mountain and Slate Creek included a higher mean GSR1 at the former, while Slate Creek exhibited a significantly higher mean GSR2 (Table 2). In our examination of differences in mean ecological variables between the study areas, significantly higher mean understory densities and NDVI values were observed at Moscow Mountain, while Slate Creek had significantly higher canopy density, slope, and elevation (Table 2). The significantly higher NDVI at Moscow Mountain may be in part due to the fact that this Landsat image was acquired closer to peak green-up, or over a month sooner (3 July 2009) than at Slate Creek (5 August 2010).

3.2. Total species richness and nesting guild richness

LiDAR-derived vertical structure variables were significant predictors of total species richness at both the Moscow Mountain and Slate Creek study areas, although their predictive strength and relative importance compared to the other ecological variables varied between Moscow Mountain and Slate Creek (Fig. 2). Although top models were significant for all response variables, model performance varied between the two study areas and species richness response variables, with adjusted R^2s ranging from 0.05 to 0.42 (Table 3).

Understory density had the highest relative importance for TSR on Moscow Mountain as determined by parameter Akaike weights (0.934), although NDVI was also a significant predictor (Table 4). At Moscow Mountain, TSR increased with increasing values of both understory density and vegetation greenness (Table 4). Understory density was also a significant predictor of TSR at Slate Creek, although other significant relationships were observed among the ecological variables (Table 4). The following variables were found to significantly influence TSR at Slate Creek: understory density, canopy density, slope, and elevation (Table 4). TSR at Slate Creek decreased at higher elevations and with steeper slopes, and increased with greater understory densities (Table 4). The standard deviation of heights was selected in top models for all species richness response variables at both Moscow Mountain and Slate Creek (Table 3), but was a relatively weak predictor compared to other variables for most of the response variables (Table 4). Top models for total species richness had an adjusted R^2 of 0.15 for Moscow Mountain and 0.32 for Slate Creek. Total species richness predictive maps were created using the best model for each study area (Fig. 3).

Model performance was found to be among the highest for the ground/understory nesting guild species richness at both study areas with adjusted R^2 values of 0.26 and 0.42 for Moscow Mountain and Slate Creek, respectively (Table 3). Understory density exhibited significant positive relationships with the ground/understory nesting guild species richness at both Moscow Mountain and Slate Creek, while canopy density was negatively associated with GSR1 at both study areas (Table 4). The Landsat-derived NDVI was also highly correlated with GSR1 at Moscow Mountain, with higher values of NDVI associated with higher GSR1 values. In addition to the understory and canopy density metrics at Slate Creek, elevation was also found to have a significant influence on GSR1, where GSR1 decreased with higher elevations (Table 4).

The relative importance of ecological variables varied for the mid-/upper-canopy nesting guild at the two study areas (Fig. 2). A strong positive relationship was observed between GSR2 and canopy density at Moscow Mountain, while slope was the only significant predictor of GSR2 at Slate Creek where GSR2 decreased with increasing slopes (Table 4). Model performance was higher at Moscow Mountain with an adjusted R^2 of 0.28 compared to 0.09 for the top Slate Creek GSR2 model (Table 3).

The model R^2_{adj} values for cavity nesting species richness were the lowest of the response variables for both Moscow Mountain and Slate Creek at 0.06 for both study areas (Table 3). GSR3 decreased with increasing canopy density at Moscow Mountain. At the Slate Creek

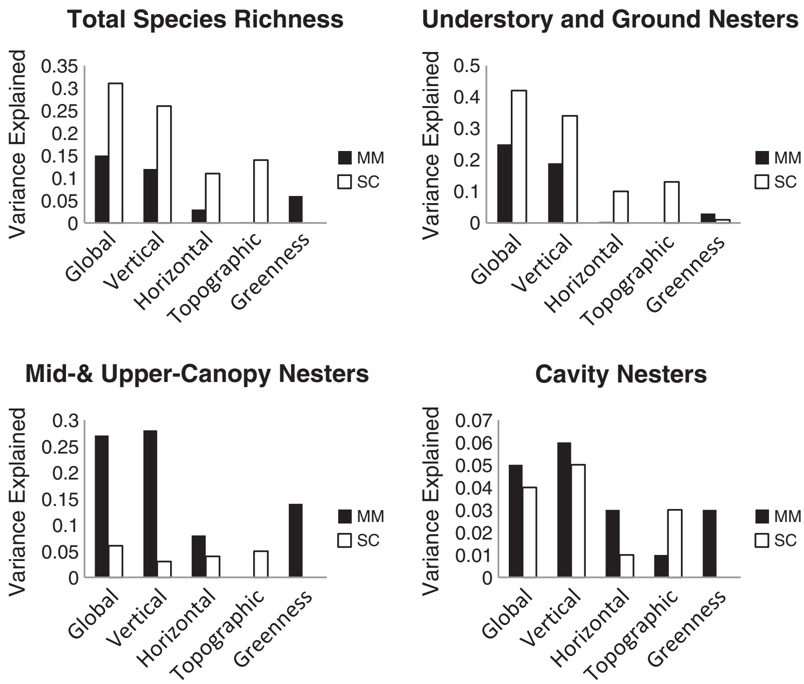

Fig. 2. Relative importance of LiDAR and Landsat forest characteristics in the prediction of response variables as defined in Table 1. Variance explained equates to the adjusted R^2 values for the associated candidate models. The LiDAR- and Landsat-derived ecological predictor variable groups and their associated variables included in the candidate models are: vertical (understory density, canopy density, and standard deviation of height); horizontal (patch diversity); topographic (slope and elevation); and greenness (NDVI). Global models include all model metrics.

study area, GSR3 increased with understory density, although not quite significant at the 0.05 confidence threshold (Table 4).

4. Discussion

4.1. Vertical structure

Vertical forest structure metrics were significant predictors for species richness patterns at both study areas, appearing in top models for all of the total and nesting guild-specific response variables. The density of the understory exhibited a strong positive influence on multiple species richness patterns including total species richness and the ground/understory nesting guild at Moscow Mountain and all of the Slate Creek richness variables with the exception of the mid-upper-canopy nesting guild. Previous studies have also noted the importance of this understory layer for bird diversity (Clawges et al., 2008; Hagar, Dugger, & Starkey, 2007). Jones et al. (2013) also found promise in utilizing the LiDAR-derived strata specific density with density in the understory significantly predicting the forest guild species richness. Through field-based efforts, Clawges et al. (2008) observed that the understory vegetation in the 0.5–2.0 meter foliage layer, comparable to our understory strata, was predominately

Table 3
Adjusted R^2 values and model selection results for top models for total bird species richness (TSR) and guild-specific response variables condensed from the original set of 25 candidate models for the Moscow Mountain (MM) and Slate Creek (SC) study areas. Models represent those with the lowest AIC value and those with a delta AIC score <2. The Akaike weights can be considered to represent the probability of a model given the data, with weights summing to 1 across candidate models. Mean square prediction errors (MSE) were calculated using a leave-one-out-cross-validation approach for all competing models.

Response variable	Study area	Competing models	R^2	p-Value	AIC	ΔAIC	Akaike weights	Prediction error
TSR	MM	Ustory, NDVI	0.152	<0.001	690.797	0	0.403	7.642
		Height_σ, Ustory, NDVI	0.152	<0.001	691.921	1.125	0.230	7.680
		Ustory, Patch, NDVI,	0.147	<0.001	692.659	1.862	0.159	7.735
	SC	Height_σ, Ustory, Canopy, Slope, Elev, Patch	0.318	<0.001	612.833	0	0.674	5.593
		Height_σ, Ustory, Canopy, Slope, Elev, patch, NDVI	0.314	<0.001	614.588	1.754	0.281	5.667
GSR1	MM	Height_σ, Ustory, Canopy, NDVI	0.263	<0.001	580.118	0	0.866	3.501
	SC	Height_σ, Ustory, Canopy, Slope, Elev, Patch	0.418	<0.001	423.423	0	0.527	1.364
		Height_σ, Ustory, Canopy, Slope, Elev, Patch, NDVI	0.421	<0.001	423.640	0.217	0.472	1.36
GSR2	MM	Height_σ, Canopy	0.281	<0.001	492.843	0	0.452	1.882
		Canopy	0.276	<0.001	494.821	1.978	0.168	1.854
	SC	Slope, Elev, Patch	0.086	0.002	485.211	0	0.315	2.171
		Height_σ, Slope, Patch	0.078	0.003	486.335	1.124	0.180	2.188
		Height_σ, Slope, Elev, Patch	0.085	0.004	486.376	1.165	0.176	2.195
GSR3	MM	Canopy	0.064	0.001	418.952	0	0.376	1.106
		Height_σ, Canopy	0.060	0.005	420.484	1.53	0.175	1.113
	SC	Ustory	0.049	0.006	368.253	0	0.185	0.906
		Height_σ, Ustory	0.054	0.010	368.631	0.378	0.153	0.908
		Height_σ, Ustory, Canopy, Slope	0.061	0.017	369.574	1.322	0.096	0.908
		Ustory, NDVI	0.042	0.022	370.228	1.975	0.069	0.919

Table 4
Global generalized linear model results (all predictor variables included) modeling avian species richness using remote sensing-derived ecological variables. Weighted parameter estimates and standard errors calculated using parameter Akaike weights (Burnham & Anderson, 2002); confidence intervals calculated at the 95% level. Starred parameters are significant in the global model at the p-value level of: *** ≤ 0.001; **0.01; *0.05.

	Moscow Mountain			Slate Creek		
	Parameter estimate	Standard error	Confidence interval	Parameter estimate	Standard error	Confidence interval
Total bird species richness (TSR)						
Intercept	5.246	4.002	(−2.318, 12.810)	16.252	3.415	(9.798, 22.706)***
Height_σ	−0.152	0.173	(−0.479, 0.175)	0.339	0.232	(−0.099, 0.777)
Ustory	0.211	0.058	(0.101, 0.321)**	0.161	0.077	(0.015, 0.307)*
Canopy	−0.003	0.019	(−0.039, 0.033)	−0.036	0.016	(−0.066, −0.006)*
Patch	0.434	0.741	(−0.966, 1.834)	1.257	0.900	(−0.444, 2.958)
Slope	0.064	0.064	(−0.057, 0.185)	−0.101	0.034	(−0.165, −0.037)**
Elevation	−0.004	0.003	(−0.010, 0.002)	−0.004	0.001	(−0.006, −0.002)**
NDVI	7.600	2.879	(2.159, 13.041)*	1.622	3.357	(−4.723, 7.967)
Understory and ground nesting guild species richness						
Intercept	−2.079	1.759	(−5.404, 1.246)	8.893	1.625	(5.822, 11.964)***
Height_σ	−0.090	0.115	(−0.307, 0.127)	0.114	0.112	(−0.098, 0.326)
Ustory	0.177	0.352	(−0.488, 0.842)***	0.090	0.037	(0.020, 0.160)**
Canopy	−0.035	0.010	(−0.054, −0.016)**	−0.037	0.008	(−0.052, −0.022)***
Patch	0.254	0.510	(−0.710, 1.218)	0.082	0.442	(−0.753, 0.918)
Slope	0.034	0.041	(−0.043, 0.111)	−0.019	0.017	(−0.051, 0.013)
Elevation	3.915	0.002	(3.911, 3.919)	−0.003	0.001	(−0.004, −0.002)***
NDVI	9.442	3.601	(2.636, 16.248)***	2.138	1.645	(−0.971, 5.247)
Mid- and upper-canopy nesting guild species richness (GSR2)						
Intercept	1.413	0.556	(0.362, 2.464)*	4.731	1.655	(1.603, 7.859)**
Height_σ	0.212	0.089	(0.044, 0.380)	0.180	0.134	(−0.073, 0.433)
Ustory	0.017	0.033	(−0.045, 0.079)	0.024	0.045	(−0.061, 0.109)
Canopy	0.037	0.005	(0.028, 0.046)***	0.001	0.010	(−0.018, 0.020)
Patch	1.157	0.317	(0.558, 1.756)	0.685	0.489	(−0.239, 1.609)
Slope	0.024	0.035	(−0.050, 0.090)	−0.054	0.020	(−0.092, −0.016)**
Elevation	−0.001	0.002	(−0.005, 0.003)	−0.001	0.001	(−0.002, 0.000)
NDVI	6.568	1.335	(4.045, 9.091)	0.023	2.136	(−4.014, 4.060)
Cavity nesting guild species richness (GSR3)						
Intercept	2.680	0.575	(1.593, 3.767)**	1.579	0.524	(0.589, 2.569)
Height_σ	−0.054	0.067	(−0.181, 0.073)	0.092	0.069	(−0.038, 0.222)
Ustory	−0.019	0.023	(0.062, 0.024)	0.061	0.026	(0.012, 0.110)
Canopy	−0.012	0.004	(−0.020, -0.004)*	−0.002	0.006	(−0.013, 0.009)
Patch	−0.140	0.316	(−0.737, 0.457)	0.063	0.352	(−0.051, 0.001)
Slope	<0.001	0.023	(−0.004, −0.043)	−0.025	0.014	(−0.051, 0.001)
Elevation	−0.002	0.001	(−0.004, −0.000)	−0.001	0.001	(−0.002, 0.000)
NDVI	−1.359	1.627	(−4.434, 1.716)	−0.225	1.356	(−2.788, 2.338)

comprised of woody shrubs, seedlings, and saplings. In addition to providing nesting substrates for the understory nesting guild, previous studies note the importance of a shrub layer for promoting invertebrate production, an important breeding season food source for many bird species (Diaz, 2006; Hagar et al., 2007).

The role of foliage height diversity has been noted elsewhere to be an important influence on local species richness, but canopy height variability in our study was not a consistently strong predictor of bird species richness. Goetz et al. (2007) observed a negative effect on bird species richness in areas with lower height variability. Flaspohler et al. (2010) also found positive relationships between the standard deviation of canopy height and bird species richness. While forest height diversity may undoubtedly be important for avian diversity in some study areas, our results suggest that other LiDAR-derived structure variables may be driving species richness in our study. For instance, canopy complexity may also be correlated with other forest characteristics that may influence avian communities, such as snag abundance, forest succession stage, and disturbance history (Falkowski et al., 2009; Martinuzzi et al., 2009).

The responses to canopy density were not the same for all guilds or within the same guild across the study areas. For instance, on Moscow Mountain, there was a positive relationship between canopy density and the mid-/upper-canopy nesting guild. Increased canopy density may represent greater availability of foraging and nesting substrates and/or greater amounts of cover to protect from predators (Franzreb, 1983). However, canopy density did not appear in the top models for the mid-/upper canopy nesting guild on Slate Creek and the R^2 values were all <0.09 compared to R^2 values of 0.28 for Moscow Mountain, which indicates that other variables were likely more important in influencing the species richness of this nesting guild. Approximately 70% of the species in this guild were found at both study areas, and therefore, differences between the two areas are not likely due to fundamentally different communities that respond to different forest structures. However, there are multiple variables at multiple spatial scales that we did not include in our analysis, and our results suggest that birds at the Slate Creek study area were sensitive to those of other variables.

4.2. Horizontal structure

Horizontal vegetation structure has been found to affect bird communities by increasing the spatial complexity of the habitat (Hansen, McComb, Vega, Raphael, & Hunter, 1995; Sallabanks et al., 2006). Patch diversity was included in top models within our study, but was not a strong predictor compared to other model metrics. While mostly positive relationships were exhibited by the richness response variables and patch diversity, the confidence intervals included zero. The positive relationship with patch diversity, while weak, may be a positive response to the “patchiness” of the forest. Even localized heterogeneity, caused by phenomena such as tree fall, can create gaps in the forest canopy, potentially providing diversity in the local habitat (Bergen, Gilboy, & Brown, 2007). The diversity of patch types in an area can provide a greater availability of nesting and foraging opportunities than in one patch type alone, as well as introduce additional foraging

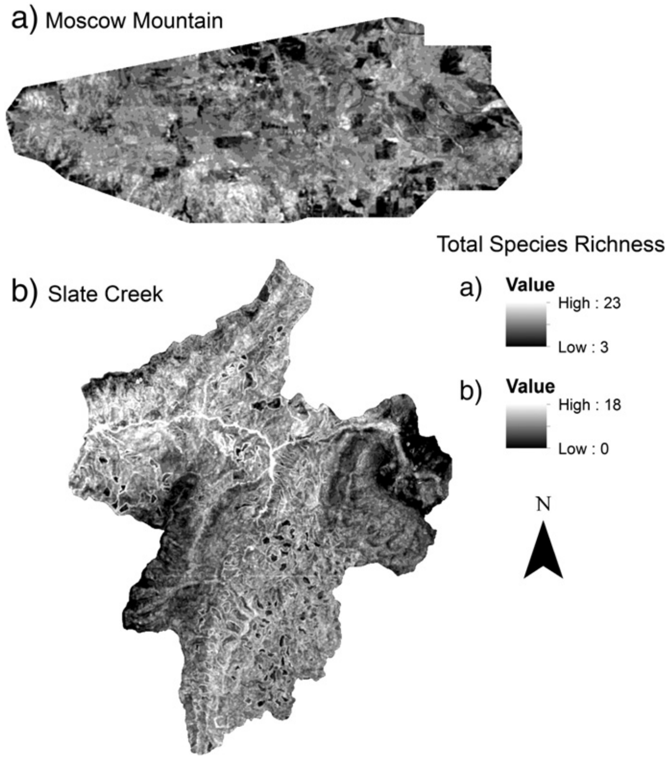

Fig. 3. Total species richness predictive maps for a) Moscow Mountain and b) Slate Creek created using top competing models for both study areas selected using AIC model selection. The Moscow Mountain predictive map utilizes the LiDAR-derived understory density and Landsat-derived NDVI. The variables included in the top model for Slate Creek are all LiDAR-derived and include: standard deviation of forest height; understory density; canopy density; slope; elevation; and horizontal patch diversity.

opportunities created by the meeting of two different patch types (Flaspohler, Temple, & Rosenfield, 2001; Salek et al., 2010). Studies agree that wildlife often select habitat at multiple spatial scales.

4.3. Topographic

Topographic variables not found to influence species richness at Moscow Mountain were strong predictors of avian species richness in the higher elevation Slate Creek. Slope was found to have a significant negative relationship with total species richness and mid-/upper-canopy nesting guild species richness at Slate Creek. In addition to a significantly higher mean slope, there was also a much larger range of slope values observed at Slate Creek, with extremely steep slopes observed at a few of the survey locations. Slope has previously been found to have negative relationships with bird diversity and species distribution (Diaz, 2006), which may be related to the influences of slope on vegetation composition and structure (Martinuzzi et al., 2009).

Elevation was also a significant predictor for both total species richness and the ground/understory nesting guild. We noted a pattern of lower total species richness at higher elevations, which has also been reported by previous studies (Terborgh, 1977), although the exact shape of the curve of that relationship has been debated (Rahbek, 1997). Many of the previous examinations of species diversity along elevation gradients have covered a broad range of elevations and vegetation zones (Rahbek, 1997; Terborgh, 1977), as opposed to the localized landscape level analyses of the Slate Creek area included in this study. It is likely that elevation had a negative influence on total species richness through reduced productivity and changes in forest complexity and composition along the elevation gradient (Terborgh, 1977).

4.4. Vegetation greenness

The Landsat-derived NDVI representing vegetation greenness was found to be an important predictor of total species richness and the ground/understory nesting guild at Moscow Mountain. NDVI is a metric often used in studies evaluating the relationship between species distributions or richness and vegetation productivity across broad spatiotemporal scales (e.g. Evans, James, & Gaston, 2006; Hurlbert & Haskell, 2003; Pettorelli et al., 2005; Seto et al., 2004). We found significantly higher NDVI at Moscow Mountain compared to Slate Creek, and NDVI was a more important predictor of total species richness at Moscow Mountain compared to Slate Creek (Verschuyl et al., 2008). Our findings are not entirely consistent with Verschuyl et al. (2008), who found that in energy-limited sites, forest productivity showed a significant positive relationship with bird species richness. However, differences in the range of NDVI values between the two studies might partially explain the different results. One of the study sites in Verschuyl et al. (2008) had a narrow range of NDVI values, and did not show a significant relationship between NDVI and bird species richness, similar to our Slate Creek results. Goetz et al. (2007) also used Landsat-derived NDVI metrics in modeling bird species richness in the eastern deciduous forests of Maryland, and found that NDVI did not significantly increase the predictive strength of the models over the use of structure variables alone. Because of an abundance of cloud cover and/or snow patches in the Landsat images that coincided with the onset of the avian breeding season, our analysis was restricted to utilizing images from the end of the breeding seasons. Thus, the site phenology represented by our NDVI maps may be somewhat disconnected from the landscape to which bird species first responded when selecting breeding sites, although still reflecting relative differences among survey sites within the same landscape. The significantly higher NDVI at the Moscow Mountain landscape may in part be due to an image acquisition date a month earlier than Slate Creek.

4.5. Comparisons between study areas and among nesting guilds

The differences in patterns of biodiversity between the study areas may reflect changes in responses of bird communities to their landscape with gradients of productivity, elevation, patch metrics, and management history. Differences between the relative importance of variables for predicting total bird species richness and guild specific species richness between landscapes may also be indicative of the complex relationships between forest birds and their habitats that go beyond the explanatory variables directly measured by LiDAR. Previous LiDAR-based studies examining bird diversity have limited their examinations to one study area, which limits the comparison of results along gradients of landscape patterns and management intensities. While our results suggest that larger landscape structure and context may impact diversity patterns and the importance of LiDAR-derived local vegetation structure, future studies should explore these relationships across larger geographic gradients where LiDAR and bird diversity datasets are available.

While the variance explained by our models was in the low to moderate range, our model R^2 values were comparable to previous studies examining avian richness in structurally diverse forests in the same geographic region using field-based vegetation sampling methods (R^2 ~ 0.19; Sallabanks et al., 2006), as well as other studies examining forest avian diversity utilizing LiDAR data (e.g. Goetz et al., 2007: R^2 ~ 0.29; Clawges et al., 2008: R^2 ~ 0.14; Lesak et al., 2011: R^2 ~ 0.20). We have no such data with which to compare our nesting guild specific results, in which the R^2 values ranged from <0.06 for the cavity nesting guild to 0.42 for the ground/understory nesters in Slate Creek. Our results, in addition to the above studies, suggest that there is a need to explore further the relative importance of other factors (e.g. snag availability for cavity nesters) that influence local species diversity in combination with additional variables.

Predictive maps for species distributions and diversity patterns have great value for multiple management and conservation efforts. Applications include but are not limited to: regional and local forest management planning; tradeoff analyses between potential management scenarios; prioritizing conservation efforts to critical habitat patches or diversity hotspots; and ecosystem service analyses. As with any modeling/mapping effort, it is important to use such products with caution ensuring that limitations of the data are well understood and considered before application.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rse.2014.02.006.

Acknowledgments

We would like to thank the National Gap Analysis Program (grant number: 08HQAG0123), the US Forest Service, and the Palouse Audubon Society for funding. This is contribution 1080 of the University of Idaho Forest, Wildlife and Range Experiment Station.

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