Ecology, 91(6), 2010, pp. 1569–1576

Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird

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Abstract. A topic of recurring interest in ecological research is the degree to which vegetation structure influences the distribution and abundance of species. Here we test the applicability of remote sensing, particularly novel use of waveform lidar measurements, for quantifying the habitat heterogeneity of a contiguous northern hardwoods forest in the northeastern United States. We apply these results to predict the breeding habitat quality, an indicator of reproductive output of a well-studied Neotropical migrant songbird, the Black-throated Blue Warbler (*Dendroica caerulescens*). We found that using canopy vertical structure metrics provided unique information for models of habitat quality and spatial patterns of prevalence. An ensemble decision tree modeling approach (random forests) consistently identified lidar metrics describing the vertical distribution and complexity of canopy elements as important predictors of habitat use over multiple years. Although other aspects of habitat were important, including the seasonality of vegetation cover, the canopy structure variables provided unique and complementary information that systematically improved model predictions. We conclude that canopy structure metrics derived from waveform lidar, which will be available on future satellite missions, can advance multiple aspects of biodiversity research, and additional studies should be extended to other organisms and regions.

Key words: bird diversity; Black-throated Blue Warbler; canopy structure; Dendroica caerulescens; *habitat quality; Hubbard Brook Experimental Forest, New Hampshire, USA; Neotropical migratory birds; northern hardwoods forests; remote sensing; waveform lidar data.*

INTRODUCTION

Ecologists have long sought to explain patterns of biodiversity based on latitude, area, environmental heterogeneity, evolutionary rates, and other factors. Prior to the availability of satellite data, field-based studies at local spatial scales revealed the strong role of vegetation structure in driving biodiversity (e.g., Ralph et al. 1995). The classic work of MacArthur and MacArthur (1961) refined the broad concept of vegetation structure by defining foliage height diversity (FHD) as a measure of canopy layering, and suggesting its use as a predictor of bird species diversity. Variations on the FHD concept have led to the development of several indices of forest structural complexity incorporating vertical and horizontal variation in tree size, canopy cover, shrub size, shrub cover, coarse woody debris, and snags (McElhinny et al. 2005). More generally, vegetation structure refers to the horizontal and vertical distribution of vegetation canopy elements (Franklin et al. 2002). Structural complexity influences the abundance and distribution of species by creating a greater variety of microclimates and microhabitats, which in turn produce more diverse food and cover for a broader range of species and greater numbers of individuals (Hunter 1999, Whittaker et al. 2001, Hill et al. 2004). Indeed, after accounting for vegetation structure, vegetation diversity and composition did not explain any more variation in bird species richness in the forests of eastern North America (MacArthur and MacArthur 1961).

Currently, a broad suite of work aims at testing the utility of vegetation structure for studies of biodiversity, and to develop guidelines for the next generation of satellite sensors for quantifying vegetation structure, understanding biodiversity patterns, and managing habitat. Toward this end, field-based understanding of vegetation structure and biodiversity is being advanced via use of lidar observations for a range of ecological applications (Lefsky et al. 2002, Bergen et al. 2009). Heterogeneity can be calculated directly from lidar-

Manuscript received 12 September 2009; revised 4 January 2010; accepted 7 January 2010. Corresponding Editor: J. Franklin.

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derived forest structure, using canopy profile (waveform) metrics (Drake et al. 2002, Goetz et al. 2007) and integrated measures of the vertical complexity of canopies that take into account the roughness, slope, and the number and amplitude of peaks in the waveform data (Dubayah and Drake 2000, Lefsky et al. 2002). Previous work has demonstrated the utility of aircraft lidar-derived environmental variables in predicting species richness in forested systems (see Vierling et al. 2008), but the question of how well lidar data can be used to improve predictions of species habitat suitability and range distributions, particularly in areas with relatively low landscape heterogeneity, remains little known (Hinsley et al. 2009, Seavy et al. 2009). Here we investigate the utility of novel waveform lidar-derived habitat variables in explaining habitat quality, in terms of occupancy patterns through time, by the Black-throated Blue Warbler, a well-studied Neotropical migrant breeding bird in northern hardwoods forests (Holmes 1994, 2007). We test the ability to predict habitat quality using models developed from the observations.

METHODOLOGY

The distribution of the Black-throated Blue Warbler is highly variable at a landscape scale, with areas of high abundance related to the density of the understory shrub layer (Doran and Holmes 2005), which subsequently influences reproductive success (Rodenhouse et al. 2003) (see Plate 1). In the northeastern United States, Black-throated Blue Warblers tend to occupy mature deciduous forests with a well-developed and high-density understory (Steele 1992, Holmes 1994, Doran and Holmes 2005). Our working hypothesis was that deciduous tree cover and understory structure and density are both vegetative characteristics that are important to habitat quality, and can be identified using a combination of optical and lidar remote sensing. To test this, we analyzed a long-term data set of bird observations collected at the Hubbard Brook Experimental Forest (HBEF), located in the southern region of the White Mountain National Forest in central New Hampshire. The HBEF is a 3160-ha forested watershed, ranging in elevation from 222 to 1015 m, dominated by northern hardwoods. More detailed site descriptions can be found in Schwarz et al. (2001) and are *available online*.[8]

Bird data sets

Data on the distribution and abundance of Black-throated Blue Warblers were collected across a survey grid consisting of 371 points along 15 north–south transects established throughout the HBEF (Fig. 1; Schwarz et al. 2001). Transects, systematically arrayed across the Hubbard Brook watershed, were 500 m apart with survey points along the transect separated by either 100 or 200 m. Survey locations were visited three times during the peak breeding seasons (late May through June) of 1999, 2000, and 2006 and twice in 2001. During each visit the abundance of Black-throated Blue Warblers was surveyed for 10 min using fixed 50 m radius point counts (Ralph et al. 1995, Doran and Holmes 2005). Locations of individual birds were mapped in order to avoid multiple recording of the same birds at adjacent points. Additionally, each individual was assigned to only one point. Surveys were performed by multiple trained observers to limit error in observer accuracy. We did not correct for detection probability (p) as within three 10-min point counts detection probability for this species was 99.9% (Betts et al. 2008).

Using bird survey data collected over the four years, annual presence/absence was determined at each of the 371 survey sites. Black-Throated Blue Warblers were considered present at a site if an individual was observed within a 50 m radius of the survey location, (i.e., abundance was greater than zero). These data were used to classify each survey site based on the number of years that the species was present (0, 1, 2, 3, or 4) over the duration of the study (after Doran and Holmes 2005). We used this index of multiyear presence (hereafter "prevalence") as a surrogate for habitat quality for this species (hereafter "habitat quality"). Prevalence was calculated using all four years of data, as well as a separate index using only three years of observations (1999, 2000, and 2001), reserving an additional survey year (2006) for testing predictions of habitat quality.

Waveform lidar data sets

Full waveform lidar data were acquired in July of 2003 over the HBEF with the Laser Vegetation Imaging Sensor (LVIS), a scanning laser altimeter (Blair et al. 1999), mounted on a NASA aircraft. LVIS digitizes the return signal and converts the waveforms to units of distance by accounting for the time elapsed between the initial laser pulse and the return, thereby providing data sets that simulate observations expected from future satellite missions. Waveform lidar measurements are distinct from more common discrete return lidar, which record a far smaller number of returned signals.

Three products were derived directly from the LVIS waveform data at a nominal footprint size of 12 m, including ground elevation, canopy height, and the height of median return (HOME) (see Appendix A). Canopy height was calculated in reference to the ground return using an algorithm that locates the first increase above a mean noise level, designated as the initial canopy return, and the center of the last Gaussian pulse, designated as the ground return. Canopy height was calculated as the difference in height between the two. HOME was derived as the height above the ground of the median energy return of the waveform.

In addition to canopy height, HOME, and ground elevation, we derived two novel higher-level products

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[8] ⟨www.hubbardbrook.org/⟩

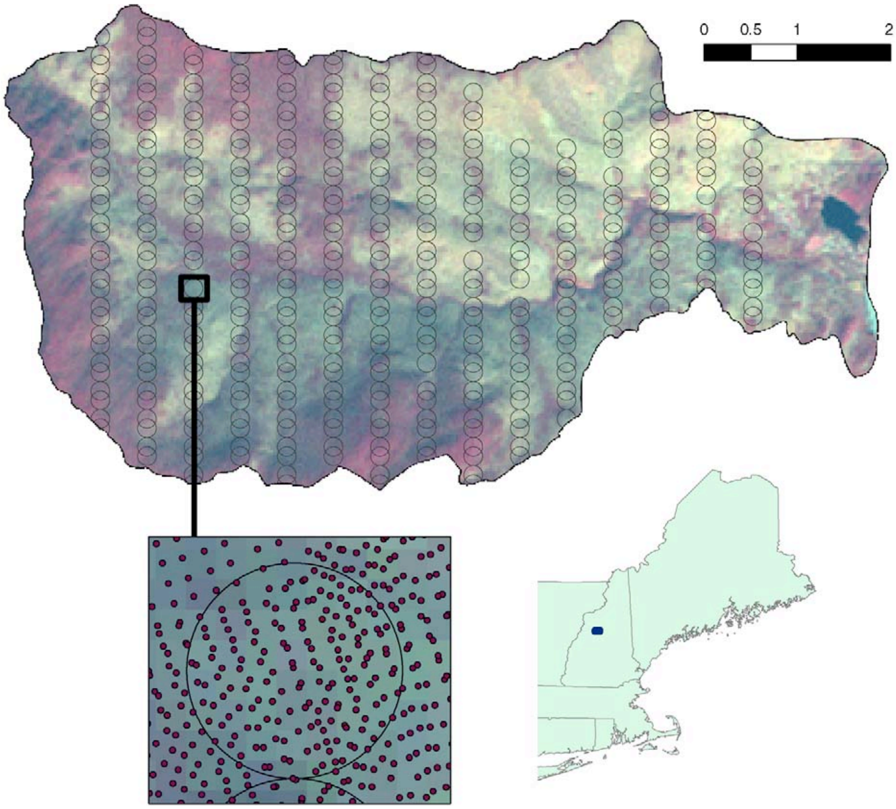

FIG. 1. Map of the 3160-ha Hubbard Brook Experimental Forest, Woodstock, New Hampshire, USA, showing a Landsat NDVI (normalized difference vegetation index) image and the 15 transects spanning the valley along which Black-throated Blue Warbler (*Dendroica caerulescens*) abundance was quantified. The lower left image shows the density of lidar shots (centroids shown) within a given bird survey location (50 m radius).

that provide information on the vertical distribution of vegetation components as well as the structural complexity of the canopy. Canopy complexity (COMP) was calculated as an integrated measure of the waveform, taking into account the number and amplitude of peaks in a waveform: COMP $= -\text{sum}\ (p \times \log(p))$ where p is the probability that a certain amplitude occurs. Although we refer to COMP as canopy complexity, it is not a biophysical measurement as such, but rather a metric that essentially characterizes how the waveform diverges from a uniform surface. In forested regions the complexity of a waveform is determined by the vertical complexity of vegetation structure. We also calculated a vertical distribution ratio (VDR; Goetz et al. 2007) as an index of the vertical distribution of intercepted canopy components, ranging between 0 and 1: VDR = [CH − HOME]/CH. In general, forested regions characterized by a relatively shorter distance between CH and HOME, such as from a greater understory canopy component, will exhibit lower VDR values.

Landsat data sets

In addition to the lidar metrics, we examined metrics derived from optical imagery in relation to the habitat quality denoted by Black-throated Blue Warbler prevalence. Two Landsat ETM satellite images (path/row 013/029), acquired in August of 1999 and late October of 2000, were converted to top-of-atmosphere reflectance using in-band spectral irradiances and a solar geometry model to correct for Earth–Sun distances and solar zenith angle variations (Goetz 1997). The images were subsequently georeferenced. The normalized difference vegetation index (NDVI) was calculated for both the leaf-on (August) and the leaf-off (October) scenes and the two were differenced, resulting in an image of seasonal NDVI change at the nominal 30-m spatial resolution of the ETM sensor. This allowed us to evaluate and consider seasonality in vegetation cover and density. Because many users cannot process multitemporal Landsat imagery, vegetation cover type for the study region was also examined. Using a vegetation type map of the HBEF that delineated regions of deciduous, coniferous, mixed predominantly deciduous, and mixed predominantly coniferous (*available online*),[9] we produced a continuous grid of percentage deciduous hardwoods, also at 30-m resolution. These data were used along with optical and lidar data as predictors of Black-throated Blue Warbler prevalence.

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[9] ⟨www.hubbardbrook.org/gis⟩

Plate 1. (Top) Singing male Black-throated Blue Warbler (*Dendroica caerulescens*) at Hubbard Brook. (Lower left) Interior of northern hardwoods forest at Hubbard Brook, showing the dense shrub layer preferred by Black-throated Blue Warblers. (Lower right) Female Black-throated Blue Warbler and young at nest located in the shrub layer. Photo credits: upper, M. G. Betts; lower left, P. J. Doran; lower right, Nick Rodenhouse.

Spatial and statistical analyses

The lidar (LVIS) and optical (Landsat ETM) predictor variables were intersected and combined with associated bird survey points using a geographical information system (Fig. 1). The minimum, maximum, mean, and standard deviation of ground elevation, canopy height, median height, VDR, COMP, leaf-on NDVI, and NDVI difference were computed for all 30-m Landsat cells and the number of 12-m lidar shots falling within the boundaries of each 50 m radius survey cell. In the case of LVIS, the number of shots per bird survey location ranged between 15 and 96 shots (averaging 50 shots), providing robust characterization of the sites. Comparable statistics were calculated using 100 and 200 m radii, but ultimately the results based on these data sets were less robust and more prone to spatial autocorrelation (discussed later), as per other recent work (Seavy et al. 2009), so we opted to pursue here only the results based on the observation areas as sampled in the field (i.e., 50 m).

The statistical data summaries were analyzed in relation to Black-throated Blue Warbler prevalence using the ensemble decision tree method "random forests" (RF; Cutler et al. 2007), an approach that has performed consistently well relative to other models of species distribution (e.g., Lawler et al. 2006). RF models build upon the standard methods of constructing decision (classification or regression) trees as a technique for partitioning data based on a series of hierarchical binary splits of the predictor variables, resulting in a tree structure that terminates in nodes associated with discrete ranges in the response variable (Cutler et al. 2007). When using RF many trees are generated and iteratively aggregated using cross calibration, reducing error in the overall model via bootstrap aggregation techniques. In addition to constructing each tree using a different bootstrapped random sample of the data, the RF algorithm incorporates a unique approach to splitting. Typically, each node is split using the optimal split among all predictor variables; in the RF algorithm, each node is split using the best predictor among a subset of predictors chosen at random at that node. This additional layer of randomness significantly increases the accuracy of the model and makes RF more robust to variable selection and overfitting (Cutler et al. 2007).

Using the RF package in the R programming environment (R Development Core Team 2009), habitat quality was modeled based on the suite of lidar and optical predictor variables described in the *Methodology: Waveform lidar data sets* and *Landsat data sets*. The model was run using both three and four years of bird population and distribution data. Because the RF algorithm builds trees based on repeated samples of the data set, it is not essential to withhold data for testing after model creation. As a check on this, we ran the model based on the first three years of data and examined the relationship between predicted habitat quality and occupancy in the fourth year. Additionally, spatial autocorrelation is a common feature of bird distribution patterns (Betts et al. 2006), including the Black-throated Blue Warbler at Hubbard Brook, which displays spatial autocorrelation at ranges up to 500 m (Doran 2003). However, given that the RF approach repeatedly samples portions of the data (20% in this study), the likelihood of selecting points within the 500-m range is low, particularly given that the transects were located 500 m apart. Moreover, using this type of a bootstrapping approach with repeated small samples reduces the influence of spatial autocorrelation in model development (Anselin 2002).

RESULTS

Lidar and optical data products varied throughout the study region, with some covariation in the spatial pattern of the NDVI and canopy height reflected in the surface elevation (Appendix B). The variations largely reflect the reduced canopy height along ridgelines, and the tendency for vegetation in those locations to be coniferous species. Variation in the predictor variables across the remainder of the study area was more heterogeneous and did not obviously covary with topography or vegetation type.

General trends between lidar and optical predictor variables and bird habitat quality are shown in Appendix C. Black-throated Blue Warbler prevalence was associated with the dominance of deciduous vegetation, relatively large canopy heights, increased vertical complexity, lower VDR, high seasonal change in NDVI (the ΔNDVI), and low- to mid-elevations. Although clear trends exist between habitat quality and the selection of variables displayed, there was a substantial range of variability (both lidar and optical) within a single habitat quality class.

The RF model based on four years of distribution data explained 47% of the variation in multiyear prevalence (Fig. 2). Seasonal differences in NDVI, canopy height, elevation, and canopy complexity were consistently selected by RF as the most important predictors, based on their ability to explain variation in the dependent variable (Black-throated Blue Warbler prevalence). Variables describing spatial variability in the predictors were of lesser importance relative to the predictors themselves (see Fig. 2, variable importance).

The RF model of Black-throated Blue Warbler prevalence based on the lidar and optical data also showed good agreement between the predicted and observed habitat quality (Appendix D), although the strength of the predictions was influenced by smaller sample sizes in the poor quality class. The model produced habitat quality values in the range of 0 to 4, from which we generated a map of habitat quality for the area within and immediately surrounding the HBEF (Fig. 3). We grouped the range of predicted values into three habitat quality groups: best (quality of 3 or 4), average (1 or 2), and poor (0). Of the 242 sites predicted to have the best quality habitat, 82% were occupied for three or four years over the study period, while 17% were occupied for one or two years, and none were unoccupied. About 62% of the sites identified as average quality habitat were occupied for one or two years, while 22% of these sites were occupied for three or four years, and the remaining 16% were unoccupied. Of the 30 sites predicted as poor habitat, 33% were not occupied over the four years of study.

As with the model based on four years of data, the RF model of habitat quality derived from three years of bird observation data selected seasonal NDVI difference, elevation, canopy height, and vertical complexity as the strongest predictors of habitat quality. The three-year model displayed an ability to predict presence/absence in the fourth year of the study period, with 73 sites identified as best quality (quality of 3), 198 as average quality (2), and 100 as poor quality (1 or 0). Thus ~90% of sites identified as best-quality data were occupied in the fourth year of the study, while 81% of the average-quality sites, and only 46% of the poor-quality sites were occupied (Appendix E).

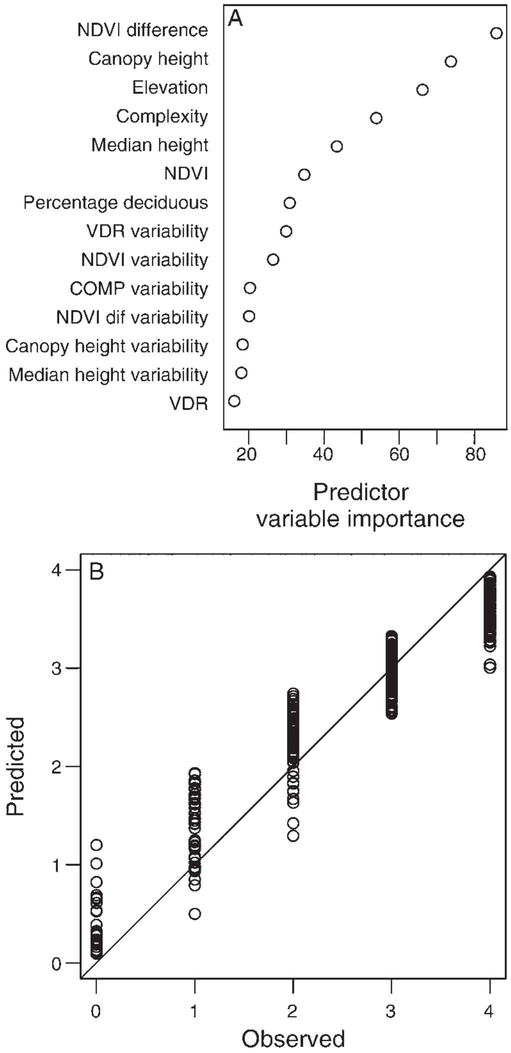

FIG. 2. (A) The relative importance of each optical and lidar predictor variable in the random forests model based on four years of Black-throated Blue Warbler observations. Predictors characterizing spatial variation include the descriptor "variability." (B) Comparison of predicted and observed Black-throated Blue Warbler prevalence, based on multiyear prevalence, with a one-to-one line showing perfect agreement.

DISCUSSION

The remotely sensed metrics of habitat quality (Appendix B) corresponded well with the intensive multiyear field observations of Black-throated Blue Warbler prevalence (Fig. 2). Black-throated Blue Warblers are known to prefer mature forests with a dominance of deciduous vegetation (Doran and Holmes 2005), and we observed a strong positive association between both habitat quality and percentage deciduousness, as well as between habitat quality and canopy height. Clear trends also existed with canopy complexity and the canopy vertical distribution ratio. Black-throated Blue Warbler prevalence increased with vertical complexity, indicating that a more complex vegetation structure represents higher quality habitat. Similarly, lower VDR values were associated with higher quality habitat. Both of these findings may be related to the preference of Black-throated Blue Warblers for locations with a well-developed understory (Steele 1992, Holmes et al. 1996, Doran and Holmes 2005), particularly the density of hobblebush (*Viburnum alnifolium*) shrubs (see Plate 1).

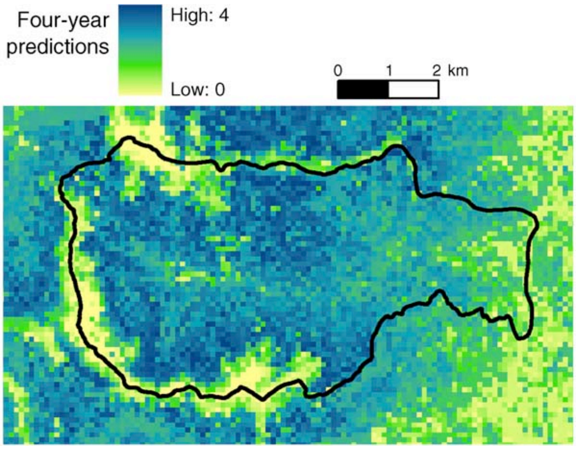

FIG. 3. Map of predicted Black-throated Blue Warbler habitat quality generated from a random forests model based on four years of observational data. The resolution of the grid cells is 50 m radius, which coincides with the audiovisual field observations of bird presence or absence.

Seasonal change in NDVI was also positively correlated with habitat quality. This trend is also most likely associated with the relationship between deciduous cover and seasonal NDVI difference, although the latter was a more consistently strong predictor (Fig. 2), owing to the smaller range of variability within each occupancy class (Appendix C). Both variables may reflect a relationship between primary productivity and habitat quality, however, because deciduous forest has greater rates of photosynthesis and primary productivity, which could sustain larger populations of foliage-dependent caterpillars, a primary food source of Black-throated Blue Warblers during the breeding season (Holmes 1994).

The map of predicted habitat quality, indicated by predicted Black-throated Blue Warbler prevalence (Fig. 3), also reveals the preference for low- to mid-elevation (400–700 m) regions. Areas of higher elevation at HBEF are dominated by coniferous species or younger vegetation along the ridgelines, reflecting both a climatic gradient and greater disturbance at elevation (Thomas et al. 2008). Again, the trend between habitat quality and elevation may not be directly causal, but rather a result of vegetation cover as influenced by elevation and disturbance regimes.

The RF model of bird habitat quality based on lidar and optical predictors and four years of occupancy data performed well in terms of variance explained (Fig. 2). When observed and predicted values of prevalence were grouped into best, average, and poor quality categories, comparison of the observed and predicted values demonstrated good overall agreement (Appendix D). The RF model based on three years of occupancy data performed comparably well. Although the percentage of variance explained based on the three-year model was relatively low (39%), when examined in relation to occupancy data from 2006 (year 4), the model predicted >90% of the sites occupied in 2006 (Appendix E). This is particularly interesting in that it discounts the effect of individuals showing site fidelity because the four-year gap between 2002 and 2006 makes it unlikely that the same individuals were returning to the same locations (see also Holmes 1994). Over 80% of sites identified as average and just 46% of the sites identified as poor habitat were occupied in 2006. These results were likely influenced by the relatively high abundance of Black-throated Blue Warblers in that particular year. The species occupied a greater proportion of all sites in 2006 (75.5%) than in previous years (1999, 70.5%; 2000, 60.5%; 2001, 60.2%), probably resulting in birds occupying most of the best sites and then spilling over into less suitable areas (McPeek et al. 2001, Rodenhouse et al. 2003). Thus, good quality habitat in 2006 was relatively more limited and greater abundance and occupancy at average and poor habitat sites would be expected (Holmes et al. 1996).

We believe our findings indicate more than novel species–habitat use relationships, and associated predictions of habitat quality via multiyear prevalence. Because we used species prevalence across a number of years, these results may also be indicative of the factors that influence Black-throated Blue Warbler reproductive success, namely the propensity for repeated use of high quality habitat shown to be related to the variables that influence reproductive output (Rodenhouse et al. 2003, Doran and Holmes 2005, Betts et al. 2008). That is, sites with low nest success were only occupied during periods of high abundance, whereas sites with the highest nest success were consistently occupied year after year, regardless of variability in abundance.

We conclude that novel remotely sensed data can be used successfully to characterize habitat quality and to spatially predict species prevalence and correlates of reproductive success, even over relatively large areas of high canopy cover. In addition to other predictor variables, full waveform lidar data provided an ability to characterize (three-dimensional) variability in vegetation structure, as well as surface topography, which better characterized habitat quality and thus multiyear prevalence of Black-throated Blue Warblers during the breeding season. The ability of lidar to characterize canopy vertical structure is thus likely to be particularly important in species distribution and habitat suitability models in regions like the HBEF, which are densely forested and highly productive but relatively less variable than a broader geographic region in terms of other potential predictors of habitat (such as climate or canopy cover). Additional studies that incorporate lidar canopy structure information, particularly the waveform canopy lidar that will be available on future satellite missions (Bergen et al. 2009), may help to refine models of species distribution, abundance, and other aspects of habitat quality that are relevant to biodiversity conservation and management.

ACKNOWLEDGMENTS

We acknowledge support from the NASA Applied Sciences (Ecological Forecasting), Terrestrial Ecology, and Interdisciplinary Science programs. Financial support for field data collection was provided by the U.S. National Science Foundation LTER program. The research was conducted under the auspices of the Northern Research Station, Forest Service, U.S. Department of Agriculture, Newtown Square, Pennsylvania, and is a contribution of the Hubbard Brook Ecosystem Study.

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APPENDIX A

Predictor variables used to estimate response variable (*Ecological Archives* E091-109-A1).

APPENDIX B

Lidar and optical image products of HBEF, depicting vegetation canopy height, ground elevation, the vertical distribution ratio, canopy complexity, leaf-on NDVI from August, and seasonal change in NDVI between August (leaf-on) and October (leaf-off) (*Ecological Archives* E091-109-A2).

APPENDIX C

Boxplots displaying the range in lidar and optical predictor values relative to bird habitat quality indices (*Ecological Archives* E091-109-A3).

APPENDIX D

Comparison of predicted vs. observed occupancy among habitat quality groups, as categorized by number of years of Black-throated Blue Warbler presence (*Ecological Archives* E091-109-A4).

APPENDIX E

Same as Appendix D but based on predicting the presence or absence among habitat quality groups in year 4 (2006) based on a model developed using data from three years of observations (1999–2001) (*Ecological Archives* E091-109-A5).