

Landscape capability models as a tool to predict fine-scale forest bird occupancy and abundance

Zachary G. Loman  · William V. Deluca · Daniel J. Harrison ·
Cynthia S. Loftin · Brian W. Rolek · Petra B. Wood

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Abstract

Context Species-specific models of landscape capability (LC) can inform landscape conservation design. Landscape capability is “the ability of the landscape to provide the environment [...] and the local resources [...] needed for survival and reproduction [...] in sufficient quantity, quality and accessibility to meet the life history requirements of individuals and local populations.” Landscape capability incorporates species’ life histories, ecologies, and distributions to model habitat for current and future landscapes and climates as a proactive strategy for conservation planning.

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Z. G. Loman (✉) · D. J. Harrison · B. W. Rolek
Department of Wildlife Fisheries and Conservation
Biology, University of Maine, 5755 Nutting Hall, Room
210, Orono, ME 04469, USA
e-mail: zachary.loman@maine.edu

W. V. Deluca
Department of Environmental Conservation, University of
Massachusetts, 160 Holdsworth Way, Amherst,
MA 01003, USA

C. S. Loftin
Maine Cooperative Fish and Wildlife Research Unit, U.S.
Geological Survey, 5755 Nutting Hall, Room 210, Orono,
ME 04469, USA

Objectives We tested the ability of a set of LC models to explain variation in point occupancy and abundance for seven bird species representative of spruce-fir, mixed conifer-hardwood, and riparian and wooded wetland macrohabitats.

Methods We compiled point count data sets used for biological inventory, species monitoring, and field studies across the northeastern United States to create an independent validation data set. Our validation explicitly accounted for underestimation in validation data using joint distance and time removal sampling.

Results Blackpoll warbler (*Setophaga striata*), wood thrush (*Hylocichla mustelina*), and Louisiana (*Parkeisia motacilla*) and northern waterthrush (*P. noveboracensis*) models were validated as predicting variation in abundance, although this varied from not biologically meaningful (1%) to strongly meaningful

P. B. Wood
U.S. Geological Survey, West Virginia Cooperative Fish
and Wildlife Research Unit, West Virginia University,
P. O. Box 6125, 322 Percival Hall, Morgantown,
WV 26506, USA

(59%). We verified all seven species models [including ovenbird (*Seiurus aurocapilla*), blackburnian (*Setophaga fusca*) and cerulean warbler (*Setophaga cerulea*)], as all were positively related to occupancy data.

Conclusions LC models represent a useful tool for conservation planning owing to their predictive ability over a regional extent. As improved remote-sensed data become available, LC layers are updated, which will improve predictions.

Keywords Appalachians · Breeding Bird Survey · Distance sampling · Landscape Conservation Cooperatives · North Atlantic · Point counts · Removal sampling · Validation · Verification

Introduction

A long-standing criticism of wildlife habitat models is that they are developed and used without validation with independent data (Stauffer 2002). Even when models are tested, they often are examined in spatially aggregated units despite being created at finer scales (e.g., Edwards et al. 1996; Tirpak et al. 2009; Jones-Farrand et al. 2011). Aggregation integrates variation across broader scales, which weakens the confidence in validation results, and validation cannot be certain at the finer scale of model development when data are aggregated. At localized scales (< 1 km), validation of songbird habitat models is difficult, and there is a dearth in the literature of independently verified or validated models of forest bird habitat. Recent attempts to validate habitat models for forest birds have met with mixed success (Tirpak et al. 2009) or have been unsuccessful (Reilly et al. 2014).

In 2010 the U.S. Fish and Wildlife Service initiated a network of 22 Landscape Conservation Cooperatives (LCC) to integrate science and management to accomplish broad-scale natural resource conservation goals at landscape scales (U.S. Fish and Wildlife Service 2009). The North Atlantic LCC (NA-LCC) has supported the Designing Sustainable Landscapes (DSL) project with the goal of informing landscape conservation design by developing species-specific models of landscape capability (LC) applicable to 13 states in the Northeastern U.S. (NA-LCC 2011; McGarigal et al. 2016). The DSL focal area

encompasses the NA-LCC and a large portion of the Appalachian LCC (Fig. 1). Landscape capability in general is “the ability of the landscape to provide the environment [...] and the local resources [...] needed for survival and reproduction [...] in sufficient quantity, quality and accessibility to meet the life history requirements of individuals and local populations” (McGarigal et al. 2016). Landscape capability differs from other species distribution models in its inclusion of general prevalence, climate suitability, and habitat suitability, the last of which is represented at extremely fine resolution (30 m × 30 m). The habitat capability component of the landscape capability model quantifies the ability of the landscape to provide suitable and accessible habitat at relevant ecological scales (i.e., home range) of a focal organism for a given life history stage (McGarigal et al. 2016). The climate suitability component of the model is a statistical model, which predicts climate suitability across the landscape based on current occupancy. The LC approach, therefore, indicates the landscape’s ability to support local populations rather than simply identifying isolated pixels as habitat independent of local context. These models specifically developed for the northeastern United States also were designed to apply in modeled future landscapes and climate scenarios as part of proactive strategies for conservation planning (Hansen and Urban 1992; McGarigal et al. 2016). The LC models for the northeastern United States combine a suite of 24 spatial data layers representing ecological and anthropogenic variables. The LC models are parameterized with Breeding Bird Survey data (Sauer et al. 2017) and a priori knowledge of ecological requirements for individual species.

Conservation as applied by the North Atlantic LCC and used in the DSL takes a surrogate species approach (Caro 2010). The LC models were developed for focal species that are of conservation concern and were selected to be representative of species groups that share similar ecological relationships (North Atlantic LCC 2011). Among these representative species are several songbirds associated with northeastern forest habitat types used for breeding. Four species, Louisiana waterthrush (*Parkesia motacilla*), ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*) and blackburnian warbler (*Setophaga fusca*), are considered representative of various hardwood or mixed-hardwood forest habitat types. Blackpoll warbler (*Setophaga striata*) is

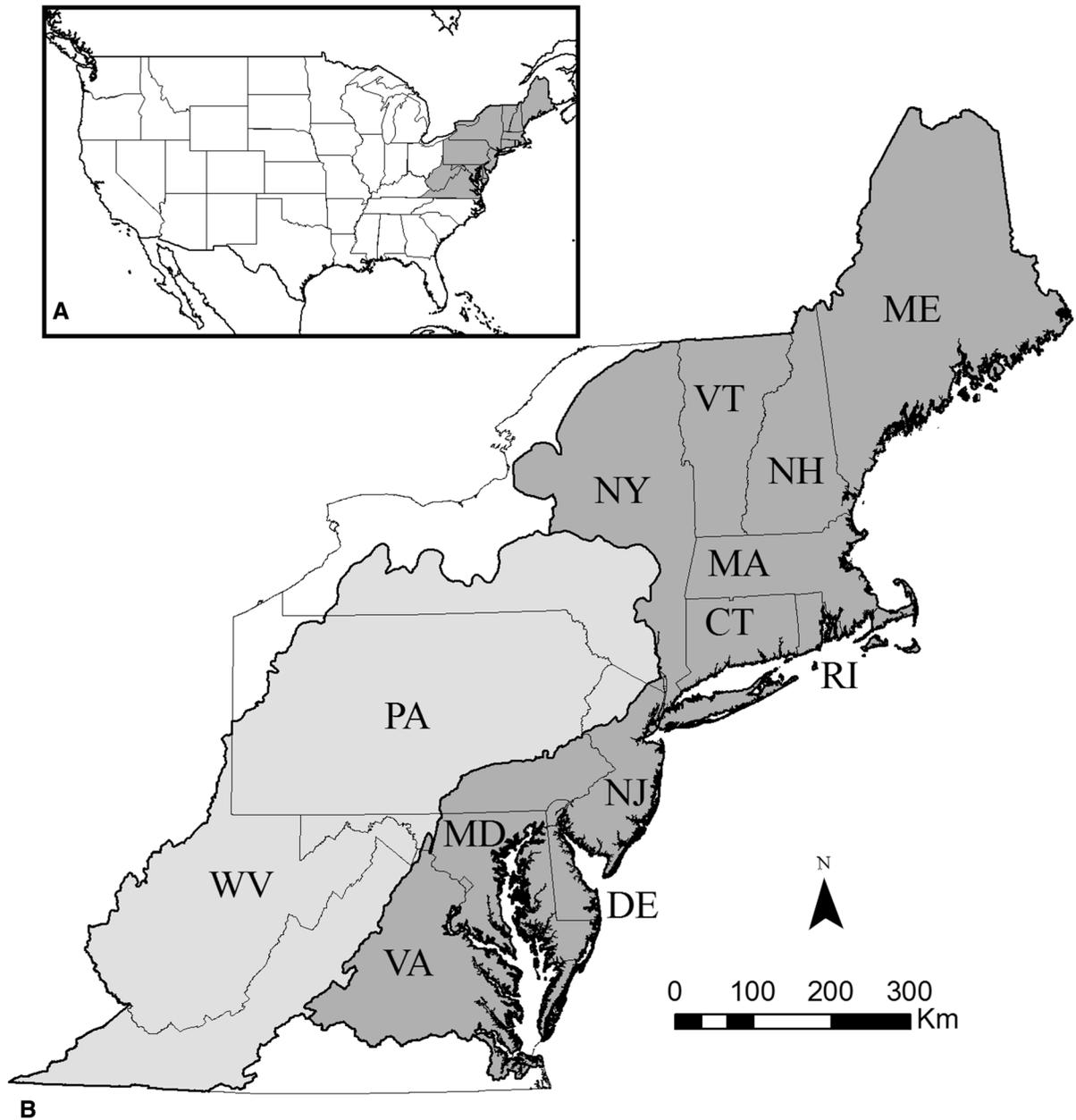


Fig. 1 **a** Extent of landscape capability models (LC; gray) within North America, and **b** portion of the appalachian landscape conservation cooperative (light gray), and the North

Atlantic landscape conservation cooperative (dark gray) within the northeastern United States

representative of spruce-fir forests. Northern water-thrush (*Parkesia noveboracensis*) is representative of a variety of swamps and forested wetland habitat types (North Atlantic LCC 2011). Cerulean warbler (*Setophaga cerulea*) is a widespread but declining high-conservation priority species that breeds in mature hardwood forest (Buehler et al. 2013). Our a priori

expectation was that models would perform best for specialists (i.e., blackpoll warbler), with performance declining as species niches become more generalized (e.g., wood thrush, blackburnian warbler; Evangelista et al. 2008). We also expected that local errors in predictor variables would decrease the efficacy of predictions for species dependent on fine-scale habitat

features (i.e., Louisiana waterthrush) such as riparian forest (Barry and Elith 2006).

Current conservation planning using landscape-scale species-habitat relationship models follows a procedure of model calibration, verification, and validation (Will et al. 2005). Habitat models, including LC models, typically include spatially explicit information related to wildlife use of the landscape, however, they do not necessarily explicitly develop predictors of current animal occupancy or abundance. Instead, model outputs attempt to describe the landscape's capability to support a species, restoration potential for habitats or species, ecological integrity, ecological systems classifications, or other descriptors of landscapes correlated with organism space use or occurrence. The LC models for the northeastern United States are fine-scale (30×30 m) species-specific values ranging from 0 to 1, corresponding to the relative ability of contiguous or proximate habitat patches to support territories of focal organisms, and not occurrence, occupancy probability, or abundance per se (McGarigal et al. 2016). Validation of this metric is therefore difficult as it is impossible to test the relative capability of unoccupied patches to support breeding territories or produce offspring. Other than Breeding Bird Survey (BBS) data, few regional data sources of bird occurrence and abundance are publicly available and suitable for independent validation data set. One possibility is eBird, a citizen science-based bird occurrence data set supplied by volunteer birdwatchers (Sullivan et al. 2009) who do not follow a standardized survey protocol with consistent effort. This data set lacks systematic design, and ancillary data necessary for removal, distance, or double-observer sampling, making it difficult to account for detectability and bird availability for detection. The alternative to using a single data set with sufficient bird occurrence data is to use a compilation of existing data sets (Barker et al. 2015).

Our objective was to quantify the ability of LC models to explain variation in occupancy or abundance for the seven selected representative species with point count data collected across the modeled region. We compiled a suite of data sets each initially developed for biological inventory, species monitoring, or from systematic studies on forest birds, to generate a validation data set independent of the BBS data used in building the climate suitability and

general prevalence components of the LC models (Appendix I).

Methods

Study area

We tested LC models that span the northeastern region of the United States (Fig. 1). We used point count data collected in 34 independent research or data collection projects (Appendix 1) from across 11 states within this region to span the ranges of the model species within the region. These studies addressed various management actions influencing forest bird communities and focal species including golden-winged warbler (*Vermivora chrysoptera*) and cerulean warbler (*Setophaga cerulea*). We also included distance and removal sampling data from monitoring programs at 13 National Wildlife Refuges and eight National Park Service locations (Appendix 1) that met our criterion of being GPS point referenced.

Analytical methods

We used data collected independently from those used to create the LC models to generate an independent assessment as the best option for model assessment in comparison with simpler and more commonly used approaches (e.g., n-folds or leave-one out cross-validation; Hijmans 2012). Our study objectives were to use joint distance and removal sampling to correct for bias in count data and to test verification and validation of LC models for seven bird species representative of northeastern forest habitats. We make the distinction that verification is a less onerous task, requiring a display of some positive relationship between the model index and some metric of bird use (in this case occupancy), whereas, validation is the formal quantitative characterization of the relationship of the model index with independent abundance data (Brooks 1997). We repeated the series of steps outlined below for each of the seven species (Fig. 2).

We compiled a data set from independent sources, each with its own standardized survey protocols, and corrected for biases in point count data with joint-distance and removal sampling. We used corrected counts to test the ability of LC to explain variation in forest bird occurrence and abundance. Our primary

motivations for using both removal and distance methods were two-fold: first, using both methods together relaxes the assumptions of using either method singly, and second, we were able to test candidate models using detection covariates independently for the availability and perceptibility components of the abundance correction (Sólymos et al. 2013). We assessed local estimates of abundance and occupancy with point counts (Ralph et al. 1995) spaced > 200 m apart to generate independent counts. Observers recorded either all birds detected, all birds detected within habitat, or only males. Most detections were auditory and male skewed as expected. We removed females, juveniles, and birds denoted as flyovers from all data sets for consistency. Observers recorded time of first detection for each individual to within the nearest minute in discrete time bands between 1 and 10 min in duration depending on the study. Point counts were either 5,

10, or 15 min in duration, and most were 10 min. Observers recorded linear 2D distance in distance bands with widths ranging 10–100 m, depending on the study. Several studies also recorded detections beyond the maximum distance band. We included all distance bands in modeling perceptibility to generate abundance estimates; however, we excluded distances greater than 100 m when determining point occupancy. We used counts that commenced between 45 min before and 5 h after sunrise at each point. Some of the data sets we compiled included data collected explicitly to test effects on bird species or communities of recent disturbances that may negatively affect forest birds. We excluded any points designated as experimental treatment sites, such as those altered by clearcut harvest (Sheehan et al. 2014) or shale gas extraction (Kiviat 2013; Barton et al. 2016; Farwell et al. 2016), as these represented recent disturbances unlikely to have been

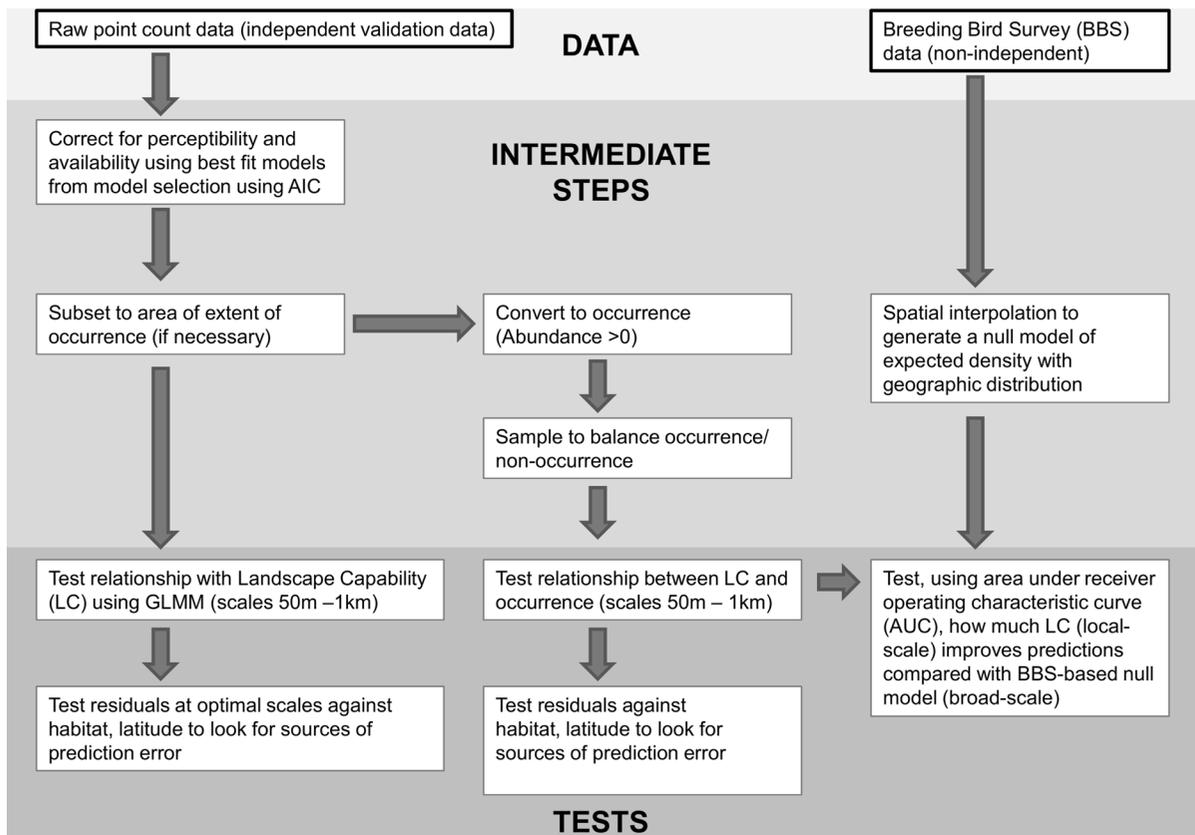


Fig. 2 Outline of the steps we undertook for each of seven species used to test landscape capability (LC) model predictive ability in the northeastern United States. Note that the process

was repeated twice for each species, once excluding and once including sites that were subjected to the experimental disturbances of timber harvest and shale gas extraction

captured in the data used to build LC models. Our goal was not to test implications of these resource extraction activities on bird communities. We tested LC model predictions also including the above described disturbed sites after other analyses to determine if removing these sites was justified. We used 30,065 point counts at 10,122 discrete spatially referenced locations that met our criteria.

Abundance estimation

We estimated abundance for seven forest-associated bird species: ovenbird, northern waterthrush, Louisiana waterthrush, wood thrush, blackburnian warbler, blackpoll warbler and cerulean warbler. We used the QPAD approach of Sólymos et al. (2013), and we corrected our observed raw count data at each point with a Horvitz-Thompson style estimator (Horvitz and Thompson 1952; Sólymos et al. 2012). Our primary purpose differed from the typical use of point counts in wildlife studies, where the objective is to understand abundance as a function of predictive covariates. Instead, we sought a point-by-point estimate of the local abundance that could be used as an independent data set to validate or invalidate the DSL LC models as a predictor of avian occurrence and abundance. We corrected naïve counts of males of each species at each point by fitting a correction from availability for detection function $p(\phi)$ (hereafter “availability”), where ϕ is the singing rate parameter, and detection probability as a function of distance $q(r_k)$ (hereafter “perceptibility”), where r_k is the distance for each respective distance band. The singing rate parameter is a homogeneous rate Poisson process, where the probability of first detection of males at time t is expressed using the exponential expression $f(t) = \phi e^{-t\phi}$, and the cumulative distribution function (CDF) is $p(t_J) = 1 - e^{-t\phi}$ for time bands t_J (Allredge et al. 2007), where $p(t_J)$ “is the probability of an individual bird singing at least once during the total cumulative time interval” (Sólymos et al. 2013). We used the half-normal detection function for the perceptibility correction component, which fits a monotonically decreasing probability of detection with increasing radial distance from the counting observer. We fit both distance and availability models in R (R Core Team 2015) with conditional maximum likelihood in package *detect* (Sólymos et al. 2014).

We used model selection to fit best covariate models for each species for both availability and perceptibility, which we ranked using Akaike’s Information Criterion (AIC; Burnham and Anderson 2012). We used eight candidate models for availability that included a time of day relative to sunrise model (TIME), with an expected decrease in the singing rate parameter (ϕ) later in the day that is typical for many passerines; time of year model (ORDINAL) with an expected decrease in singing rate with later ordinal date, with the decrease resultant from changing nesting phenological stage; and, five combinations of these parameters including their interactions as well as interactions with latitude. We used seven candidate models for the perceptibility model selection, where the perceptibility decreases with distance. This function is described with a half-normal curve, and with the width of the curve a function of covariates. We again tested models for time of day, ordinal date, and latitude, however, we also included a binary covariate for whether habitat type was forest or open as the covariates for this shape parameter. We also tested interaction models with interactions between these covariates and latitude. Latitude was included because it is correlated with several physical, climatic, and anthropogenic variables that could affect singing efficacy, ecotypic variation, and body size (Ashton 2002; Cardoso 2010), all of which could influence singing rates and perceptibility (e.g., Henwood and Fabrick 1979; Wiley 1991; Brumm 2004; Kroodsmas 2005; Weir and Wheatcroft 2011; Nemeth et al. 2013). We determined the majority habitat type within 100 m of each survey point in ArcGIS 10.4 (ESRI, Redlands, CA) based on habitat types from the Northeastern Terrestrial Habitat Classification (NETHC; Ferree and Anderson 2013). We selected the top model for perceptibility and availability independently, using models with minimum AIC, and we used these models to calculate abundance estimates at each point for each of the seven species.

Evaluation procedures

We evaluated corrected abundance per point as a response metric to test the ability of the LC models to explain variation in point level abundance for each representative species. We used general linear mixed models (GLMM) in R with a log normal distribution (Zuur et al. 2009). We calculated mean LC within five

(50, 100, 250, 500, 1000 m) fixed radii around each point to test against point abundance, and we selected the best model for each species with minimum AIC.

We examined patterns in standardized fitted-residuals to develop a better understanding of variation in the explanatory power of the model throughout the study area (Boone and Krohn 1999). We tested for patterns in standardized residuals resultant from fitting the log transformed corrected-abundance measures with normalized LC for each respective species. We tested for over- or under-prediction (two-sided tests) in abundance by comparing residuals with latitude (O’Neil et al. 1988) and habitat type within 100 m of point locations with GLM. We used NETHC habitat types (Gawler 2008; Ferree and Anderson 2013), however, we combined some of the habitat groups owing to similarity of habitat and small sample size. We combined emergent marsh, northern swamp, central hardwood swamp, northern peatland and fens, and wet meadow/shrub marsh into a single category “wetland,” and glade/barren/savannah and ruderal shrubland/grassland into a single category “open.”

Occupancy estimation

We also tested each LC model’s ability to predict forest bird occupancy and generated threshold dependent and threshold independent statistics of the models’ predictive performances. We defined occupancy as a male territorial bird occurring within 100 m of the point count location. We derived point occupancy from abundance estimates. We used top removal models for each species to estimate the net availability for detection at each point to conclude that we sampled points adequately. Threshold dependent metrics were derived by maximizing the sum of sensitivity and specificity.

We calculated proportional improvement in the ability of LC models to predict occupancy with fine scale information compared to spatial information-only by using a calibrated area under the receiver operating curve (AUC) measure (Hijmans 2012). Although AUC is the most commonly used threshold independent measure, it can overstate the utility of the model by predicting broad regional occurrence patterns when habitat is geographically partitioned from non-habitat (Hijmans 2012). For example, a model capable of identifying the extent of occurrence of blackpoll warblers could potentially predict our fine

scale positive occurrence data without any fine scale information, because the species range is geographically restricted within the region of interest. We developed a null model using the BBS training data used by DSL to calibrate the LC models to ensure we did not overstate the LC models’ utility. We interpolated BBS counts for each species across the study region using inverse distance weighting in ArcGIS, and we normalized the results. We compared this normalized result against observed species occupancy to generate a null (spatial data only) AUC measure. We then calculated the proportional improvement in predictive ability by comparing the AUC of the LC models with the null AUC.

We independently selected all occupied sites for each species (excluding ovenbirds) and randomly sampled unoccupied sites within the appropriate LCC region or regions, until the numbers of unoccupied and occupied sites matched, to generate balanced occurrence/non-occurrence data and to ensure validity of predictive measures that are sensitive to skew (Powers 2007). Ovenbirds had more detections than non-detections, so we performed a similar procedure with only presence data. Because blackpoll warbler detections and northern waterthrush detections were primarily in the North Atlantic LCC region and cerulean warbler and Louisiana waterthrush detections were primarily in the Appalachian LCC, we used occurrence and non-occurrence data from the appropriate region for each species. We used data from the entire region for blackburnian warbler, wood thrush and ovenbird, because they occurred widely.

Results

Covariates that affected singing rate (ϕ) and effective sampling radius (τ) and that were used in best time removal sampling (Table 1) and distance sampling models (Table 2) for each species (Fig. 3) typically included a relationship with either ordinal date, latitude or both. Top models typically had a large model weight (mean weight among species for distance models = 0.82, and 0.85 for removal models). We qualitatively compared corrected counts to published density estimates to evaluate their plausibility, and we found they were similar. For example, the maximum blackpoll warbler density at occupied points was 4.8 ha^{-1} compared to $> 4.0 \text{ ha}^{-1}$ reported

Table 1 Singing rate parameter (ϕ) at mean covariate values, and with standardized covariate coefficients on log scale for top conditional likelihood-fitted removal models for each representative species used in landscape capability model validation from point counts in the northeastern United States 2005–2015

Representative Species	ϕ	Time ^a	Date ^b	Latitude	Latitude \times time	Latitude \times date	df	Weight
Northern waterthrush	0.19	0.09	–	–	–	–	2	0.63
Louisiana Waterthrush	0.14	–	– 0.28	–	–	–	2	0.84
Blackpoll warbler	0.21	–	0.27	–	–	–	2	0.97
Blackburnian warbler	0.15	–	– 0.47	– 0.01	–	0.31	4	0.61
Cerulean warbler	0.25	–	– 0.21	–	–	–	2	0.99
Ovenbird	0.22	0.10	– 0.11	– 0.40	0.04	–	5	0.90
Wood thrush	0.17	–	– 0.04	– 0.77	–	– 0.53	4	0.99

En dashes (–) indicate variables that were not included in the top model for that species

^aTime since sunrise

^bWithin-year ordinal date

Table 2 Mean effective distance radius in meters (τ) at mean covariate values, and with standardized covariate coefficients (natural log scale) for top conditional likelihood-fitted distance models for each representative species used in landscape capability model validation from point counts in the northeastern United States 2005–2015

Representative Species	τ	Time ^a	For. ^b	Lat. ^c	Lat. \times forest	Lat. \times time	Date ^d	Lat. \times date	df	weight
Northern waterthrush	82	–	–	– 0.26	–	–	–	–	2	0.53
Louisiana waterthrush	52	–	–	0.03	–	–	–	–	2	0.38
Blackpoll warbler	65	–	–	– 0.49	–	–	0.39	– 0.33	4	0.98
Blackburnian warbler	49	–	–	– 0.07	–	–	–	–	2	0.95
Cerulean warbler	87	–	–	0.40	–	–	–	–	2	0.94
Ovenbird	66	–	–	0.01	–	–	– 0.01	– 0.07	4	1.00
Wood thrush	92	–	–	0.08	–	–	–	–	2	0.93

En dashes (–) indicate variables that were not included in the top model for that species

^aTime since sunrise

^bFor. Forest habitat, as compared to nonforested habitat

^cLatitude

^dWithin-year ordinal date

by Sabo (1980), and the mean of 1.6 ha⁻¹ was within range 1.3–4.7 ha⁻¹ reported by Deluca et al. (2013).

Occupancy

LC models ranged from excellent to fair based on Cohen's κ (Landis and Koch 1977) when ranked based on predictive assessments using proportional improvement over random assignment and accuracy (Table 3). Blackpoll warbler performed best, followed in descending order by Louisiana waterthrush, northern waterthrush, blackburnian warbler, cerulean warbler,

wood thrush, and ovenbird (Table 3). Only ovenbird had poor agreement between actual occurrence and LC modes ($\kappa < 0.4$; Landis and Koch 1977). All models were moderately sensitive to very sensitive when assessed based on their ability to correctly make positive predictions as a proportion of all actually occupied sites (sensitivity) and on their ability to make negative predictions as a proportion of all actually unoccupied sites (specificity).

The relative dependence of LC models on fine-scale spatial information is illustrated by comparing the proportional increase in threshold-independent

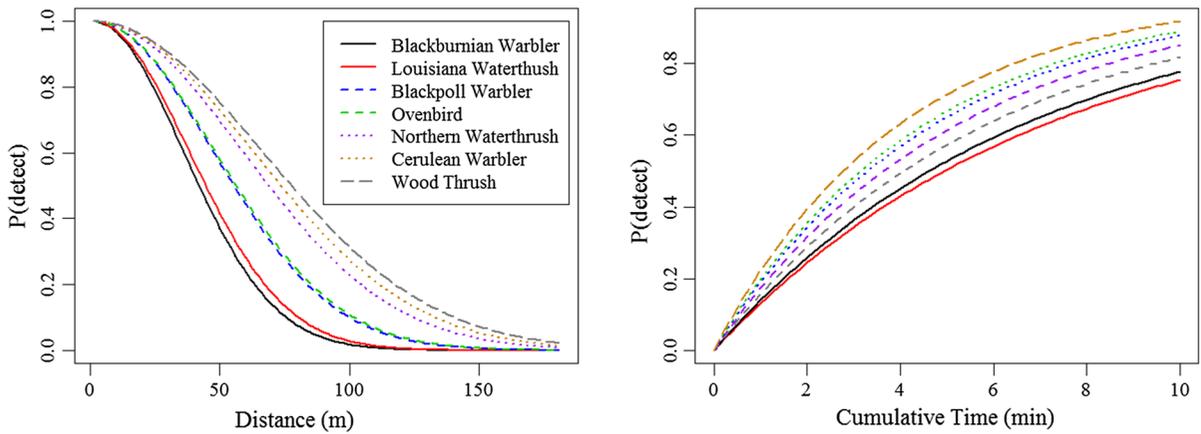


Fig. 3 Probability of detecting an individual male of each representative species as a function of radial 2D distance from an observer (left) and cumulative survey duration (right). Generated from top ranked distance sampling and removal

models respectively, fitted at mean values for survey ordinal date, latitude, and time of day since sunrise, for point counts in the northeastern United States 2005–2015

Table 3 Metrics from landscape capability (LC) model predictions for occurrence of forest bird species used in model validation from point counts in the northeastern United States 2005–2015

	Blackpoll warbler	Louisiana waterthrush	Northern waterthrush	blackburnian warbler	Cerulean warbler	Wood thrush	Ovenbird
Accuracy	0.90	0.82	0.80	0.79	0.74	0.72	0.62
Precision	0.96	0.85	0.76	0.76	0.72	0.68	0.60
Cohen’s κ^a	0.85	0.68	0.62	0.61	0.52	0.48	0.32
Sensitivity	0.79	0.78	0.86	0.85	0.79	0.85	0.67
Specificity	0.98	0.86	0.74	0.73	0.69	0.60	0.56
Type I error rate	0.02	0.14	0.26	0.27	0.31	0.40	0.45
Type II error rate	0.21	0.22	0.14	0.15	0.21	0.15	0.31
T/F positives ^b	81/3	162/29	162/50	659/206	287/114	1155/549	1098/725
T/F negatives ^c	141/21	178/45	139/27	567/114	249/76	809/203	874/501
LC buffer width	1000 m	100 m	500 m	500 m	500 m	100 m	1000 m

^aValues of Cohen’s κ (also “ κ ”; Cohen 1960) below < 0.20 typically are considered unacceptable; 0.20–0.40 is considered fair; 0.40–0.60 indicates moderate agreement; 0.6–0.8 is substantial agreement, and > 0.8 is considered excellent or “near perfect” (Landis and Koch 1977)

^bNumber of points correctly predicted as positive occurrences and the number of points falsely predicted as positive occurrences

^cNumber of points correctly predicted as negative occurrences (non-occurrences) and the number of points falsely predicted as negative occurrences (non-occurrences)

predictive ability measured by AUC from LC models over interpolated BBS data. Three species had a large ($\geq 10\%$), positive increase in AUC (correct positive prediction rate relative to incorrect positive

predictions of occurrence) when compared with the BBS broad-scale species abundance patterns. These were Louisiana waterthrush (+ 35%), cerulean warbler (+ 11%), and northern waterthrush (+ 10%). All

other species had < 5% increase in AUC. When we removed survey points with recent disturbance (e.g., owing to Marcellus shale gas development and logging), we found significantly improved prediction accuracy for only blackpoll warbler (12.5% improvement in classification accuracy, $\chi^2 = 9.6$, $P = 0.002$). For this reason, all reported statistics (including abundance results, below) omit disturbed sites for blackpoll warbler.

Abundance

The LC models we tested positively predicted some proportion of variation within point-level abundance corrected for incomplete detection probability for four of the seven species: blackpoll warbler ($R^2 = 0.59$, $F_{1100} = 146.4$, $P < 0.01$), northern waterthrush ($R^2 = 0.09$, $F_{1187} = 17.82$, $P < 0.01$), Louisiana waterthrush ($R^2 = 0.03$, $F_{11274} = 37.96$, $P < 0.01$), and wood thrush ($R^2 = 0.01$, $F_{11357} = 3.20$, $P < 0.01$). LC models did not explain variation in abundance for blackburnian warbler ($R^2 < 0.01$, $F_{1771} = 0.59$, $P = 0.44$), cerulean warbler ($R^2 = 0.01$, $F_{1771} = 2.02$, $P = 0.16$), and ovenbird ($R^2 < 0.01$, $F_{11473} = 1.06$, $P = 0.30$). There was no significant relationship between latitude and fitted model residuals (equivalent to model with “type I,” or sequential sum of squares) resulting from using LC and log abundance for any species (Table 4). Comparisons between residuals from abundance models and terrestrial habitat classification showed LC under predicted abundance of wood thrush in central oak-pine forest by 0.08 ± 0.03 males/ha ($t = 2.23$, $P < 0.03$; Table 3). This habitat prediction difference amounted to a small change in explained variance ($R^2 = 0.02$).

Discussion

LC models qualitatively performed very well to fair as predictors of species occupancy and very well to not at all as predictors of abundance for seven forest bird species within primarily forested habitats in the northeastern United States. We considered models for all seven species to be verified, because all were significantly related to rank data (occupancy). Blackburnian warbler and Louisiana and northern waterthrush LC models also were considered validated,

because models for these species additionally predicted 1–59% variation in abundance, although predicting 1% variation in abundance has little to no practical value. LC was designed to predict the capability of a landscape to provide suitable and accessible habitat at home range scales for successful reproduction, not occupancy or abundance explicitly. However, predicting the capability of the landscape to provide habitat that enables successful reproduction is not easily quantified with a single environmental variable for direct hypothesis testing, and instead would likely require long-term demographic study. Assessing suitable habitat is not the same process as assessing species abundance, because animal abundance is not necessarily a predictor of quality (Van Horne 1983). Therefore, this predictive ability with regard to occurrence, and for some species abundance, is a positive externality of the development of these models, illustrating a translation of their intended information content for practitioners, that of predicting occupancy.

A byproduct of this original design is indicated in our occupancy assessment: all models were very sensitive (viz., ability to predict true positive occurrences as a ratio of total positive occurrences). The worst performing models were not specific (viz., ability to predict true non-occurrences as a ratio of total non-occurrences). This is a typical result given that the modeling approach assesses the landscape and not species occurrence data explicitly. Locations may be unoccupied for many reasons other than landscape characteristics alone, and these reasons may be difficult to predict or are not captured in the model development process. These factors could include metapopulation dynamics (Hanski and Gilpin 1991), population influences such as presence of feral cat populations (Balogh et al. 2011), noise disturbance, and diseases that are omitted or only partially accounted for by data such as urban development layers. Similarly, poor predictive ability may reflect population decline caused by changes in habitat on the wintering grounds (Colorado et al. 2012; Stanley et al. 2015) and therefore prevent occupancy of all suitable available breeding habitat (Rappole and McDonald 1994).

Another source of discrepancy, over prediction, has been reported in other independently validated models for rare songbirds, including cerulean warbler (Thogmartin et al. 2004). Systematic over prediction based

Table 4 Number of detections of species by habitat type used in landscape capability model validation from point counts in the northeastern United States 2005–2015, and test statistics from comparisons of best fit model standardized residuals for

abundance of the species indicated in each column with habitat and latitude using a general linear model with sequential sum of squares

Habitat type ^a	BLBW	CERW	WOTH	OVEN	BLPW	NOWA	LOWA
Agricultural	28	15	49	51	5	9	13
Boreal upland forest	36	15	35	60	3	17	11
Central Oak-Pine	335	147	594	686	45	67	80
Cliff and Talus	0	0	1	2	0	0	0
Northern hardwood and conifer	331	167	501	549	40	82	84
Open ^b	3	2	11	14	1	1	0
Southern Oak-Pine	1	0	1	1	0	1	0
Urban/suburban built	8	4	34	38	1	1	3
Wetland ^c	31	13	50	74	7	11	12
All habitats combined	773	363	1276	1475	102	189	203
Habitat model							
<i>F</i>	1.18	1.02	2.75	0.37	0.9	0.72	1.92
Test-wise <i>P</i>	0.31	0.42	0.01	0.95	0.99	0.67	0.08
<i>R</i> ²	0.01	0.02	0.02	0.00	0.01	0.03	0.05
Latitude model							
<i>F</i>	0.36	0.03	0.00	0.25	0.02	0.00	0.08
Test-wise <i>P</i>	0.55	0.87	0.96	0.62	0.89	0.95	0.78
<i>R</i> ²	0.00	0.00	0.00	0.00	0.02	0.00	0.00

P values in bold are considered significant at $\alpha = 0.05$

BLBW blackburnian warbler; CERW cerulean warbler; WOTH wood thrush; OVEN ovenbird; BLPW blackpoll warbler; NOWA northern waterthrush; LOWA Louisiana waterthrush

^aHabitat cover types are from the Northeastern Terrestrial Habitat Classification (Gawler 2008; Ferree and Anderson 2013)

^bIncludes habitat types glade/barren/savannah and ruderal shrubland/grassland combined

^cIncludes several habitat types combined: emergent marsh, northern swamp, central hardwood swamp, northern peatland and fens, water and wet meadow/shrub marsh

on habitat types in our study may be, at least in part, the result of small-scale misattribution of habitat type (Ferree and Anderson 2013). Small patches of habitat surrounded by a matrix of unsuitable habitat, such as small streams potentially used by the Louisiana waterthrush, may be misclassified as the matrix habitat type, given that the habitat classifications are an area majority within 100 m.

Habitat selection is hierarchical in nature, and the granularity of the LC model grid (30 m x 30 m) does not inherently match the scales relevant in avian habitat selection (Orians and Wittenberger 1991). In general, integration of habitat-based models over a larger area provides the best predictive measures, as is the case with other species' LC models (Loman et al. 2017). Our evaluation of the best buffer widths to use

with LC models found that Louisiana waterthrush, a species sensitive to fine-scale landscape features (primarily streams), was better predicted by a smaller buffer width (100 m) than buffer widths for other species (1 km for blackpoll warbler and 500 m for all other species; Table 3). For other species, integrating LC over a larger area likely improves estimates through incorporation of the landscape context and total forest cover that may play an important role in habitat selection beyond the scale of an individual's territory (and which is incorporated into LC models by design) (Saab 1999; Radford et al. 2005).

Quality of predictions varied as a function of each species geographic extent of occurrence and relative habitat specialization. Models performed best for blackpoll warbler, a specialized species occurring in

subalpine elevation conifer forests (Deluca et al. 2013), and both waterthrush species, which are associated with riparian and other forested wetlands and occur in only a portion of the region and at low abundances. The likely reason for these better predictions is that specialists' occurrences are essentially simpler relationships (and therefore easier to model), whereas, generalists occur under more diverse circumstances, and therefore have more complicated relationships with more predictors influencing distributions (Barry and Elith 2006). Model performance was poorest for broadly occurring and more generalized species, particularly ovenbirds. Ovenbirds prefer forests with leaf litter for nesting and an open understory, and their occurrence is heavily reliant on the structure of understory and subcanopy layers (Porneluzi et al. 2011). Assessing understory composition structure with remote sensing is not implemented within LC models; however, technological advances such as LiDAR could be incorporated in future LC models to increase their utility for species dependent on understory features. An ovenbird habitat model implemented at a local scale in Missouri and that incorporated locally collected habitat information, including ground cover, achieved much greater occupancy prediction accuracy (94%) when tested with an independent validation data set (Sweeney and Dijak 1985), albeit over a local scale (a single national forest). Subsequent ovenbird habitat models in the same region used remotely-sensed data (Larson et al. 2003), however, the predictive ability of these models has not been assessed with independent data.

Some authors have been critical of the use of habitat models, because these models may be applied without prior evaluation with independent data (Stauffer 2002). Our verification and validation procedures provide a more robust assessment of a habitat model than other published validation approaches by explicitly accounting for underestimation in point counts. Gu and Swihart (2003) found bird habitat models can be both positively and negatively biased when detection processes are ignored, and they recommended accounting for detection errors in habitat models, as have others (e.g., Thogmartin et al. 2004). We suggest it is reasonable to extend this accounting of detection error to model validation as well. The approach we have outlined provides a guide for assessing the performance of habitat models for other species by incorporating multiple scales, using regional data,

addressing occupancy and abundance, and accounting for imperfect detection.

The inability to predict a biologically relevant proportion of the variation in abundance within species highlights the shortcomings of a traditional validation approach (Van Horne 2002). Species-habitat model verification in the traditional mode provides only a partial understanding of model performance. A supplementary “know thy model” approach, whereby explicit model performance is tested and reported, adds to the understanding of how models are useful at specified temporal and spatial scales (Will et al. 2005; Jones-Farrand et al. 2011). Under this paradigm, the pragmatic uses of models are explicitly treated as hypotheses to be tested (Jarnevich et al. 2015), as we have attempted with these and other LC models (Loman et al. 2017). We are prevented from a universal validation, at least in part, because of untestable assumptions such as system equilibrium and adequacy of sampling across all ecological gradients, and the unavoidable spatial bias in validation data (Jarnevich et al. 2015). Interpreting the results of this study through this lens of limits on validation, instead of making declarations of validation or verification, we might choose to interpret the results as follows: LC models are useful predictors of occupancy at fine scales, tending to be more consistently sensitive than specific; they can be useful as predictors of abundance to varying degrees on a species-by-species basis, especially when species habitat requirements are geographically partitioned and specialized; and, they can provide dramatically improved fine-scale prediction through the LC model's novel approach to dealing with resource requirements and accessibility. LC models scale resistance kernels to breeding territory size, growing a potential territory for every cell on the landscape. Through this outward expansion from each cell, LC models aggregate information from the local surrounding landscape to scale the relative suitability of the cell to support a breeding territory (McGarigal et al. 2016). This use of fine scale information significantly improved prediction accuracy for several species, primarily those that occur in smaller and more isolated patches of suitable habitat. The successful development of these models at such a fine scale and over a large regional extent represents a significant achievement in the development of regional models for conservation planning.

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