The Journal of Wildlife Management; DOI: 10.1002/jwmg.21295

Research Article

Assessing Conservation Lands for Forest Birds in an Exurban Landscape

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ABSTRACT Exurban development is the fastest growing type of land use in the United States and is prominent in the southern Appalachian region. A potential consequence of exurban development is the loss and fragmentation of wildlife habitat. We used a Bayesian model that accounts for false positive and false negative detections to make inferences about how the occupancy of 6 forest-dwelling, Neotropical migrant birds is related to multi-scale attributes of exurban development on land managed under 3 different conservation frameworks: national forest, land trust, or unprotected property in Macon County, North Carolina, USA during 2 breeding seasons. We performed Bayesian model selection and model averaging with a Bayesian Information Criterion weights approximation, and we evaluated models' predictive ability. We compared results from our occupancy model to those from a traditional model assuming data had no false positives. Results indicated that landscape- and local-scale covariates were more strongly related to posterior occupancy probabilities than site-scale covariates and that landscape composition and elevation were more strongly associated with occupancy probabilities than configuration. In particular, occupancy had a positive relationship with elevation and percent forest and a negative relationship with percent development. The black-throated blue warbler (*Setophaga caerulescens*) and wood thrush (*Hylocichla mustelina*) had the lowest posterior occupancy probabilities of the focal species, suggesting that these species may need particular conservation attention. National forest sites had high occupancy, but land trust sites exhibited patterns similar to unprotected sites. Our findings can provide guidance to county land use planners and land trusts as they respond to exurban development. Also, our study demonstrates the application of an improved occupancy model that can generate more accurate inference by accounting for both types of imperfect detection while describing heterogeneity across sites and survey occasions.

KEY WORDS Bayesian, conservation easement, development, exurban, false positive, land trust, National Forest, Neotropical migrant, occupancy model, southern Appalachia.

Urbanization is a principal cause of worldwide loss and fragmentation of wildlife habitat (Brown et al. 2005, Hansen et al. 2005). As a result of urban development, patches of native vegetation become smaller and more isolated, there is more edge, new vegetation types (e.g., ornamental plantings, exotic plant species) are introduced, and anthropogenic disturbances (e.g., noise, pollution, pedestrians) increase (Andrén 1994, Fahrig 2003, Husté and Boulinier 2011). Frequently, native vegetation is lost, the structure of vegetation is changed, or the quality of wildlife habitat declines because of development (Theobald et al. 1997, Chace and Walsh 2006, Bonier et al. 2007).

Received: 24 June 2017; Accepted: 1 May 2017

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Exurban development, a particular type of urbanization, is characterized by the construction of low-density residential homes (no more than 10 people per ha; Theobald 2004) in a rural landscape that had been dominated by native vegetation and agriculture. Exurbanization often occurs near natural amenities such as protected areas, outdoor recreation, pleasant weather, and attractive scenery, and it is the fastest growing type of land use in the United States (Theobald 2001, Brown et al. 2005, Hansen et al. 2005, Wade and Theobald 2010). Currently, exurban land use covers about 25% of the lower 48 states, and eastern deciduous forests in the southeastern and mid-Atlantic United States are some of the areas where exurban development has been most extensive (Brown et al. 2005, Hansen et al. 2005).

At the same time, eastern deciduous forests have a rich biodiversity, including many species of Neotropical migrant passerines. Passerines are a suitable focal taxon for investigating the effects of urbanization because their ecologies are well

known and birds appear to respond to their surroundings at multiple spatial scales (Orians and Wittenberger 1991, Pearson 1993, Hostetler and Holling 2000, McDonnell and Hahs 2008). Generally, the birds most sensitive to exurban development are Neotropical migrant, forest-dwelling, area-sensitive, ground-nesting, or habitat-specialist birds (Askins 1995, Marzluff et al. 2001, Allen and O'Connor 2000, Chace and Walsh 2006, McKinney 2006).

Whereas areas with rich biodiversity may experience high rates of exurban development, these areas may also have national forests or national parks that both attract people to live in the area and provide refugia for species that lose habitat on private land (Hansen et al. 2002). There may also be local land trusts that assist conservation-minded landowners to establish conservation easements on their property. However, few studies compare how wildlife fare on federal land, land trust-managed land, and unprotected land during regional land use change (Benson et al. 2011, Wood et al. 2014).

When assessing the effects of land use on wildlife, land use patterns typically are measured in terms of landscape composition and configuration. Previous studies reported that birds respond strongly to composition, often requiring a minimum amount of habitat to occupy an area (McGarigal and McComb 1995, Fahrig 2003). How habitat elements are arranged (i.e., landscape configuration) is especially influential for species with low vagility, high site fidelity, and high mortality in unsuitable vegetation types (Fahrig 1998, Villard et al. 1999, Lichstein et al. 2002).

The scale at which land use patterns are measured is also important (Villard et al. 1999). Different factors may influence the distribution of a species at different scales, and the influence of a factor on the distribution of a species may vary across multiple scales. For example, broad-scale features, such as biogeographical history and climatic gradients, may determine where species occur at a large scale, but fine-scale attributes, such as habitat condition and species interactions, may explain where species occur at the local scale (Bergin et al. 2000, Boulinier et al. 2001, Betts et al. 2007, Whittingham et al. 2007, Lindström et al. 2013). A single scale that is optimal for the study of various passerine species has not been identified, and the scale at which patterns affect birds varies depending on the bird's life history (Mitchell et al. 2001, Lee et al. 2002). Identifying which land use features are influential and the spatial scale at which birds respond to them will help inform avian conservation and land use planning (Hostetler 1999, Lerman and Warren 2011, Pennington and Blair 2011).

Our study occurred in the southern Appalachian region, a biologically rich area containing 12 Audubon Global Important Bird Areas (Southern Appalachian Man and the Biosphere 1996, National Audubon Society 2010). We chose to focus on forest-dwelling, Neotropical migrants because their populations have been declining in recent decades (Askins 1995). In addition, our study region has a relatively high percent forest cover but amenity-driven residential development has contributed to forest fragmentation, especially at higher elevations on previously undeveloped slopes (Gragson and Bolstad 2006). The goal of our project was to estimate occupancy probabilities for 6 forest-dwelling, Neotropical migrant birds on land managed under 3 different conservation frameworks (i.e., national forest, land trust, or unprotected property) across a geographically diverse county experiencing exurbanization. We developed a set of candidate models based on *a priori* hypotheses of covariates that might be related to detection or occupancy probabilities (Burnham and Anderson 2002). We expected that occupancy probabilities would be most affected by percent forest and percent developed because previous studies have indicated that landscape composition is a primary influence of avian distribution (Andrén 1994, McGarigal and McComb 1995, Fahrig 1997). We expected that percent forest would have a larger effect at the local scale and percent developed would have a larger effect at the landscape scale because variability was greater at those scales. In other words, because there was more variability in percent forest than percent developed at the local scale, we expected that percent forest would relate to occupancy more than percent developed at this scale.

STUDY AREA

We focused on exurban development in Macon County, North Carolina, USA (1,347 km^2, midpoint 35.15°N, 83.42°W) in the Blue Ridge Province of the southern Appalachian Mountain region from May to July 2010 and 2011. Elevation in Macon County ranges from approximately 500 to 1,675 m (National Elevation Dataset, 10 m digital elevation model). The climate is humid and temperate, with precipitation averaging 180 cm annually at low elevations (680 m) and increasing by roughly 5% per 100-m increase in elevation (Laseter et al. 2012). Monthly mean air temperature ranges from approximately −4–24°C, with an average temperature of 3–5°C in December–February, 8–17°C in March–May, 20–22°C in June–August, and 19–8°C in September–November (Laseter et al. 2012). The dominant natural land cover is deciduous forest, but evergreen and mixed forest are also prevalent at elevations >1,350 m (Stephenson et al. 1993, Peters et al. 2013). Dominant tree species at our data collection sites were maples (*Acer* spp.), eastern black walnut (*Juglans nigra*), tulip poplar (*Liriodendron tulipifera*), pines (*Pinus* spp.), black cherry (*Prunus serotina*), oaks (*Quercus* spp.), black locust (*Robinia pseudoacacia*), and eastern hemlock (*Tsuga canadensis*). Above 1,350 m, sweet birch (*Betula lenta*) and white ash (*Fraxinus americana*) also were dominant. Land cover in the county in 2006 was approximately 83% forest, 7% grassland, 6% developed, and 2% shrub (Hepinstall-Cymerman and Allen 2011). Within 1,000 m of our data collection sites, there was 95% forest and 5% developed in the Nantahala National Forest, 68% forest and 19% developed on land trust sites, and 59% forest and 21% developed at unprotected sites on average.

METHODS

Selecting Point Count Sites

To compare covariates and occupancy probabilities at sites under a range of land conservation frameworks, we conducted point counts at sites in the Nantahala National

Forest, on fee simple (i.e., owned by the land trust) or conservation easement properties managed by land trusts, and on unprotected public and private properties across Macon County (Fig. S1, available online in Supporting Information). We focused on legal land conservation frameworks (national forest, fee simple, or conservation easement, or unprotected) but knowing this status for a property does not provide detailed information about current methods of land management. Nevertheless, unprotected sites may be expected to experience more intense land use and land cover change and a more rapid rate of change than national forest or land trust-managed land. National forest sites may be expected to have less variability among them in terms of management methods than land trust-managed or unprotected properties because national forest sites are managed with similar objectives and there are fewer decision makers compared to the number of objectives and decision makers for land trust-managed or unprotected properties.

We refer to property that is not managed by the United States Forest Service (USFS) or a land trust as unprotected because Macon County regulations minimally restrict development in these areas. We randomly selected sites throughout Macon County that represented the range of land use and land cover (LULC) classes and elevations using ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA). First, we created a layer in ArcGIS with 10,000 random points that were $\geq$200 m apart. Next, we used the selected random points to sample Macon County's parcel layer and a 2006 land cover and land use map, and we used attributes from these layers to create strata for stratified random sampling. The strata were based on elevation ($<$800 m for the low elevation stratum or $>$1,000 m for the high elevation stratum), the year structures on the property were built (no structures, before 1980, or after 1999), whether the property was part of a subdivision (yes or no), percent forest within 1,000 m ($<$50% for the low percent forest stratum or $>$80% for the high percent forest stratum), percent agriculture within 1,000 m ($<$10% for the low percent agriculture stratum or $>$25% for the high percent agriculture stratum), and percent developed within 1,000 m ($<$10% for the low percent developed stratum or $>$25% for the high percent developed stratum). The year structures were built on a property can affect avian occupancy because it relates to the structure and composition of vegetation, levels of human activity, and levels of activity of human-associated animals (e.g., domestic cats; Hansen et al. 2005, Strohbach et al. 2009). We combined all combination of elevation, year of structures, and subdivision state with the following LULC classes to create strata: high percent forest with low percent agriculture and developed, high percent agriculture with low percent forest and developed, high percent developed with low percent forest and agriculture, and high percent agriculture and developed with low percent forest. For sampling during the second breeding season, we also added a mid-elevation class (800–1,000 m).

Once we randomly selected points from each stratum, we drove to each location, assessed on-the-ground conditions, and asked permission to conduct point counts if the point was on private property. Because of difficulties in meeting with landowners and because we needed to start sampling early in the breeding season to collect enough data, we occasionally chose sites opportunistically ($<$15% of sites). If we could not contact a landowner or if a landowner declined to participate, we would ask at nearby properties if we saw signs of landowner presence, find a nearby public site, or select another random site in the stratum where we would ask permission. Sometimes points were strategically selected so that we could maximize the number of points visited per day. We occasionally ($<$5% of sites) replaced a remote point with another random point in a more accessible location. Once we had the majority of the sites ($>$90% of sites) established, we plotted the percent forest, percent agriculture, and percent developed within 1,000 m of our sites in each of the elevation classes and compared these plots to similar plots from the 10,000 random points. We targeted the final sites for our study by identifying gaps in our sample sites. At a site, we selected the specific location at which to conduct the point count so that we were as far as possible from roads while being within hearing distance of the greatest number of land cover types (e.g., forest, field, yard) as possible. If the property was large enough to fit 2 sites 200 m apart, we located 1 site in the forest and 1 site in an area near a house, lawn, or agricultural area.

We sampled properties managed by the Land Trust for the Little Tennessee and the Highlands-Cashiers Land Trust because Macon County has little county-level land use planning, but conservation easements have been used by landowners to conserve land (Best 2002, Cho et al. 2005*a*). We sampled all of the fee simple properties owned by the land trusts, and we selected the center of each site as the point count location. At properties with conservation easements where we obtained permission, we located the point count sites at the center of the properties. If a property was large enough to fit 2 sites 200 m apart and had multiple LULC classes, we situated 1 site in the forest and 1 site in an area near a house, lawn, or agricultural area.

Nearly 50% of the land in Macon County is part of the Nantahala National Forest (Norwood 2009). We randomly selected sites in the Coweeta Basin, a 2,327-ha portion of the Nantahala National Forest that is home to the USFS Coweeta Hydrologic Laboratory and the Coweeta Long Term Ecological Research (LTER) site. We split the sites in the Coweeta Basin between the high and low elevation classes, and they were close enough that they could be sampled in 1 morning. We identified the sites through the random points in ArcGIS, located them on the ground, and assessed accessibility. We selected the specific location at which to conduct the point count by walking $\geq$200 m into the forest to minimize bias from edge effects. We also sampled sites adjacent to the Bartram Trail at 2 locations near Franklin, North Carolina and 2 locations near Highlands, North Carolina. We selected the specific location at which to conduct the point count by walking $\geq$200 m along the trail from the parking area to a point surrounded by forest.

Point Count Protocol

We conducted point counts between twilight (~30 min before sunrise) and 1000 during the breeding season from early May to early July in 2010 and 2011 (Ralph et al. 1995). Each point count lasted 8 minutes, and 2 independent observers collected data during each point count. The observers were independent because there was no communication about the point count between the observers. We instructed observers to ignore each other's movements (e.g., where they looked, when they recorded a detection). The observers identified many of the birds by sound, so observers were not following each other's visual cues. Each observer recorded the species they heard or saw and indicated whether the species was within 25 m or between 25 m and 100 m. We visited each site 3 times: during the early (9 May–4 Jun), middle (26 May–20 Jun), and late (13 Jun–7 Jul) stages of the breeding season. We determined the sampling schedule strategically to reach the maximum number of sites during a morning and to vary the time of day at which we visited sites.

One observer (A) collected data in both breeding seasons, and 2 observers (B and C) collected data in 1 breeding season; observers had different levels of experience. At the beginning of the breeding season, the 2 observers for that season (A and B or A and C) conducted practice point counts and compared observations after the point counts to refine their ability to identify the focal species. We made acoustic recording of all point counts, so observers could review the recordings to check an identification they made in the field. Observer A recorded the year, date, time, and sky condition (sunny, cloudy, foggy, or rainy) for point counts during both breeding seasons. This study protocol was approved by the Institutional Animal Care and Use Committee, University of Georgia (protocol no. A2013 02-006-Y2-A0).

Occupancy Model Accounting for False Positive Detections

We used occupancy models that account for both false negative (i.e., failure to detect a species that is present) and false positive (i.e., species misidenification) detection errors to avoid bias from not accounting for both kinds of imperfect detection (Royle and Link 2006, McClintock et al. 2010, Ferguson et al. 2015*b*). Our models determined the degree to which different habitat characteristics associated with exurban development related to occupancy probabilities on lands with different conservation frameworks: National Forest, land trust-managed, and unprotected sites. We used a Bayesian occupancy model that includes occupancy, true positive detection, and false positive detection probabilities. Our model distinguished the true positive and false positive processes through a subset of data with confirmed presences. Even with few confirmed presences (e.g., 3% of detections) the model generates accurate and precise posterior distributions (Miller et al. 2011, Ferguson et al. 2015*b*). We considered detections to be confirmed when both independent observers detected a species within 25 m during a point count.

We modeled occupancy probabilities as a function of site-specific covariates, true positive detection probabilities as a function of survey-specific covariates, and false positive detection probabilities varying across years. We included covariates though a logit-linear function. We modeled a constant observation confirmation probability across sites and sampling occasions.

In summary, the data were 1) whether the species was detected ($y_{it} = 1$) or not ($y_{it} = 0$), 2) whether observations were confirmed ($c_{it} = 1$) or not ($c_{it} = 0$), and 3) values of covariates in the model. The unknown values were 1) whether the site was occupied ($z_i = 1$) or not ($z_i = 0$), 2) site-specific occupancy probabilities (ψ_i), 3) site- and survey-specific true positive detection probabilities ($p11_{it}$), 4) year-specific false positive detection probabilities ($p10_s$), 5) observation confirmation probability (b), and 6) intercepts and coefficients in logit-linear functions incorporating covariates.

Simulations in Ferguson et al. (2015*b*) indicated that uninformative priors were most suitable for models with confirmed presences, linear covariate effects, and no observation confirmation errors. We used Uniform (0,1) priors for year-specific true positive detection probabilities, the observation confirmation probability, and parameters that were logit transformed before being incorporated as intercepts in the functions relating covariates to occupancy and true positive detection probabilities. We used Uniform (0,0.5) priors for the year-specific false positive detection probabilities, which suggests that if a site is unoccupied, an observer is more likely to make a true negative detection than a false positive detection. This constraint is consistent with the probability of false positive detections seen in controlled experiments (Farmer et al. 2012, Miller et al. 2012) and could aid model convergence without introducing unrealistic assumptions. We used a Normal (0,0.368) prior for all covariate coefficients because this is a vague Jeffrey's prior for a parameter on the logit scale (Lunn et al. 2012).

We analyzed 6 species of forest-dwelling, insectivorous, Neotropical migrant birds: black-and-white warbler (*Mniotilta varia*), blue-headed vireo (*Vireo solitaries*), black-throated blue warbler (*Setophaga caerulescens*), Canada warbler (*Cardellina canadensis*), veery (*Catharus fuscescens*), and wood thrush (*Hylocichla mustelina*). Of the forest-dwelling, Neotropical migrants we detected, we modeled all species that are considered endemic (blue-headed vireo, black-throated blue warbler) or on the Audubon Yellow WatchList (wood thrush, Canada warbler) for which we had relatively high rates of confirmed detections, which aids with fitting the model that accounts for false positive and false negative errors (Ehrlich et al. 1988, Audubon 2016). The percent of our point counts with confirmed presences ranged from 6.1% for the blue-headed vireo to 1.3% for the Canada warbler. The black-throated green warbler was considered endemic, but only 0.7% of our point counts had confirmed presences. We also modeled the black-and-white warbler (ground nesting, bark foraging) and veery (ground nesting, ground foraging) to represent greater life history diversity, compared to the blue-headed vireo (tree nesting, foliage foraging), black-throated blue warbler (shrub nesting, foliage foraging), wood thrush (tree nesting, ground foraging), and

Canada warbler (ground nesting, foliage foraging; Ehrlich et al. 1988).

We ran models in OpenBUGS (version 3.2.2, www.openbugs.net, accessed 20 Nov 2015) using the R2OpenBUGS package and R (version 2.15.3, www.r-project.org, accessed 6 Mar 2013). We ran 3 Markov chain Monte Carlo (MCMC) chains with $\geq$100,000 iterations, a burn in of $\geq$50,000, and thinning of 5. We assessed convergence with the Gelman-Rubin potential scale reduction factor ($\widehat{R}$), and considered chains converged if $\widehat{R} \leq 1.04$ for ψ_i, b, $p11_s$, $p10_s$, and parameters in logit-linear functions (Brooks and Gelman 1998, Gelman and Shirley 2011). If a model had not converged after 100,000 iterations, we re-ran with 200,000 iterations and a burn in of 150,000. If a model took an inordinate amount of time to run (e.g., >48 hr) or if $\widehat{R} > 1.04$ after re-running with more iterations, we judged that convergence had failed. After convergence, we obtained the mean of parameters' posterior distributions and 95% Bayesian credible intervals (BCI).

Candidate Models

We developed a set of candidate models based on *a priori* hypotheses of covariates that might be related to detection or occupancy probabilities (Burnham and Anderson 2002). Through model selection, we determined which candidate models were supported by our data (Burnham and Anderson 2002). Candidate models included site- (10×10-m plot within 100 m of point count location), local- (12.5 ha area within 200 m of point count locations), or landscape-scale (314 ha area within 1,000 m of point count locations) covariates. These scales are relevant because avian studies (Pearson 1993, Söderström and Pärt 2000, Graham and Blake 2001) have typically assessed landscapes within a 314-ha area, which Söderström and Pärt (2000) note is an area sufficient to encompass the maximum breeding home range for a variety of avian species. Previous studies reported that landscape patterns in a 5–50-ha area around point count sites had the strongest effect on passerine distributions, whereas scales under 0.79 ha were not informative (Morelli et al. 2013, Schindler et al. 2013). Also, studies have reported that some long-distance migrants are most active within a 4-ha area and are typically recaptured within a 12.5-ha area (Zach and Falls 1979, Anders et al. 1998, Morton et al. 1998, Evans et al. 2008).

For each of the 6 focal species, we ran 4 sets of *a priori* candidate models developed based on biological hypotheses about the relationship between covariates and ecological states (Burnham and Anderson 2002). We had a large set of candidate models because many of the covariates we were modeling have not been extensively explored with our focal species in our study area and our models contained more parameters than traditional occupancy models (i.e., false positive detection probability in addition to true positive detection probability and occupancy probability). Model selection with all models would have resulted in an extremely large number of candidate models. Therefore, we performed model selection focusing on 1 parameter or 1 class of covariates at a time. Posterior model weight cutoffs provided a threshold below which we did not advance a candidate model to the next set of candidate models being evaluated.

The first set of models had constant occupancy probabilities, year-specific false positive detection probabilities (to account for observer differences), and 4 candidate models describing the true positive detection probabilities that included year (all candidate models), ordinal date, sky condition, and time of day (Tables 1 and S1, available online in Supporting Information).

In all candidate models, the year affected the true positive detection probabilities. Ordinal date, sky condition, and time of day were additional covariates that occurred in some candidate models (Tables 1 and S1, available online in Supporting Information). We standardized continuous covariates to have a mean of 0 and variance of 1 because this is a common approach to aid convergence (Royle et al. 2005).

The second set of models had the top model(s) describing the true positive detection probabilities (i.e., models with a posterior model weight of $\geq$0.05) and 13 candidate models with site-scale covariates affecting the occupancy probabilities (Tables 1 and S2). The indicator variables described whether or not a site had >50% deciduous canopy cover, >50% evergreen canopy cover, high structural complexity, high invasive species cover, presence of coarse woody debris, presence of insect infestation, or $\geq$1 snag. We chose these variables because we thought they would relate to the quality of sites for nesting, shelter, and food availability.

An observer who specialized in southern Appalachian vegetation and did not participate in the point counts collected data for the site-scale covariates using standard releve protocols (Sawyer and Keeler-Wolf 1995). He visited the sites at the end of the breeding season after we had finished conducting point counts. Limited resources prevented the collection of site-scale covariates at all of the point count sites, so we strategically selected sites that represented the range of LULC classes and elevations and were easily located. The observer had not visited the sites during the point counts so selecting easily located sites avoided bias from the observer mistakenly sampling a different site than where we conducted point counts. The point count observers marked sites with plastic flagging and recorded a global positioning system (GPS) waypoint, but sites could still be difficult to relocate. At some sites, canopy vegetation was very dense (affecting GPS accuracy), understory was very dense (affecting flagging visibility), or animals chewed on plastic flagging.

Because some sites had missing values for site-scale covariates, we imputed these values via their respective prior distributions and the specified model structure. For example, we imputed the missing deciduous canopy cover values by modeling them as the realizations of Bernoulli trials with probability D and a Uniform (0,1) prior for D. Then we could obtain the posterior distribution of D and each of the missing deciduous canopy cover variable values. This procedure would bias inference if which records were missing was related to unmodeled predictors, but we did not expect this to be a problem because we did not select sites based on specific

Table 1. Covariates included in candidate models of the relationship between exurban development or habitat attributes and avian occupancy from May to July 2010 and 2011 in Macon County, North Carolina, USA. For a given covariate, we indicate the parameter it affected in the model, the scale of the covariate (survey occasion, site = 10×10-m plot within 100 m of point count location, local = 12.5-ha area within 200 m of point count locations, landscape = 314-ha area within 1,000 m of point count locations), and a description of how we measured the covariate.

Covariate	Parameter	Scale	Description
Yr	False positive detection, True positive detection	Survey	2010 or 2011 breeding season
Ordinal date	True positive detection	Survey	Index of days starting with 1 Jan
Sky condition	True positive detection	Survey	Sunny or cloudy, Foggy or rainy
Time of day	True positive detection	Survey	No. min after 0559
Deciduous canopy	Occupancy	Site	Whether or not a site had >50% deciduous canopy cover
Evergreen canopy	Occupancy	Site	Whether or not a site had >50% evergreen canopy cover
High complexity	Occupancy	Site	≥5% broadleaf deciduous cover in each of the understory, shrub, and ground layers or ≥1% broadleaf evergreen cover in each of the understory, shrub, and ground layers
Invasive species	Occupancy	Site	≥5% cover of 1 invasive species
Coarse woody debris	Occupancy	Site	Present or not
Snag	Occupancy	Site	Present or not
Insect infestation	Occupancy	Site	Present or not
Forest patch area ($\bar{x}$)	Occupancy	Landscape	Land use land cover (LULC) map using FRAGSTATS
Shape index forest patches ($\bar{x}$)	Occupancy	Landscape	LULC map using FRAGSTATS
Forest clumpiness index	Occupancy	Landscape	LULC map using FRAGSTATS
% house with forest	Occupancy	Local	Digitizing aerial photographs
% house with lawn	Occupancy	Local	Digitizing aerial photographs
Elevation	Occupancy	Local	$\bar{x}$ elevation from National Elevation Dataset
% forest	Occupancy	Local, Landscape	Local scale from digitizing aerial photographs; Landscape scale from a LULC map using FRAGSTATS
% developed	Occupancy	Local, Landscape	Local scale from digitizing aerial photographs; Landscape scale from a LULC map using FRAGSTATS

habitat or avian occupancy characteristics (Gelman and Hill 2007).

The third set of models had the top models(s) describing the true positive detection probabilities (i.e., models with a posterior model weight of ≥0.05) and 31 candidate models with local- or landscape-scale covariates affecting the occupancy probabilities (Table 1 and S3). We derived the landscape-scale variables from a 2006 land cover and land use map that was developed for Coweeta LTER and used the same classification scheme as National Land Cover Dataset (NLCD) maps (Hepinstall-Cymerman and Allen 2011). The overall agreement of the land cover map for the entire southern Appalachians with interpreted aerial photo points was 67% for 4 urban classes, with most of the confusion between the developed open space and low intensity urban classes with the pasture or hay class, and accuracy for all forest (i.e., deciduous, evergreen, mixed) combined was 97%. We used the 8-cell neighbor rule in FRAGSTATS (version 4, www.umass.edu/landeco/research/fragstats/fragstats.html, accessed 26 May 2013) to compute percent forest, percent developed, mean forest patch area, mean shape index for forest patches, and forest clumpiness index. We defined developed as open space, including single-family residential homes, lawns, and golf courses (NLCD class 21); low intensity (NLCD class 22); medium intensity, including developments and neighborhoods (NLCD class 23); or high intensity, including roads (NLCD class 24). The shape index measures the complexity of a patch's shape, which is related to the amount of edge (McGarigal 2015). If a patch is a square, its shape index is 1, and as a patch becomes more irregular, the shape index increases. The clumpiness index measures the aggregation of a patch type in a landscape and thus assesses fragmentation (McGarigal 2015). The index ranges from −1 (max. patch disaggregation) to 1 (max. patch aggregation), with 0 corresponding to random patch distribution.

We measured the following local-scale variables: mean elevation, percent forest, percent developed, percent house with forest, and percent house with lawn. We computed the local-scale percent cover covariates by digitizing a 200-m buffer around each point count site based on aerial photographs of Macon County (Oct 2006 and 2009 National Agriculture Imagery Program, 1-m resolution, 3 band true color). We conducted aerial photointerpretation for Macon County after the interpreter visited the field and surveyed 100 points to match ground conditions to available imagery. We assigned LULC to NLCD 2001 classes, and we calculated the mean elevation within 200 m of point count sites in FRAGSTATS. We did not include covariates that were highly correlated (Pearson's r >0.3) in the same candidate model.

The fourth set of models had the top models from model sets 2 and 3 (i.e., models with posterior model weight of ≥0.01) plus models with interactions among the site-scale covariates and the local- or landscape-scale covariates. Because the site-scale covariates were indicator variables, we modeled 2 kinds of interactions: different intercepts or different intercepts and slopes at the 2 values of the indicator variable.

Model Selection

We conducted model selection using the Bayesian Information Criterion (BIC) as an approximation to Bayes factors (Schwarz 1978; Kass and Raftery 1995; Link and Barker 2006, 2010; St-Louis et al. 2012). We used uniform prior

model weights because they favor parsimony and thus may contribute to higher predictive ability (Link and Barker 2006, Thomson et al. 2007, St-Louis et al. 2012). Also, posterior model weights appear robust to the choice of priors for parameters when uniform prior model weights are used with logistic regression (Link and Barker 2006). We calculated BIC and posterior model weights as in St-Louis et al. (2012).

For each species, we included models from the first candidate set (ψ constant and $p11$ variable) in the second (ψ with site covariates) and third (ψ with local and landscape covariates) sets of candidate models if they had a posterior model weight of $\geq$0.05. We included models from the second and third candidate set in the fourth (ψ with interactions) set of candidate models if they had a posterior model weight of $\geq$0.01. We defined the top model(s) from the fourth candidate set as the fewest models that together had $\geq$0.5 of the posterior model weight. We used model-averaged parameter means, calculated only with posterior distributions whose 95% BCIs did not span 0, in a function to predict occupancy probabilities.

Predictive Ability of Models and Comparison to Traditional Models

The area under the receiver operating characteristic curve measures a model's ability to correctly determine which sites are occupied (Hosmer and Lemeshow 2000). To create the receiver operating characteristic (ROC) curve, the ratio of true positives (i.e., the species occupied the site and the model predicted it) to false positives (i.e., the species did not occupy the site but the model predicted the site was occupied) is plotted using various cutoff values (i.e., thresholds in occupancy probabilities that separate occupied and unoccupied sites). The area under the ROC curve (AUC) can range from 0 to 1, where 0.5 suggests the model performs no better than random and larger values indicate more discriminatory ability.

We generated ROC curves and calculated AUC values for each species' top model(s) using the R package ROCR. We obtained means of the posterior distributions for ψ_i, which represented predicted states, and z_i, which represented true states, from a top model. Currently, ROCR can only accommodate one variable with an undefined cutoff value, so we reclassified the z_i to 1 if $z_i \geq 0.5$ and 0 otherwise.

Because modeling false positive detections is not yet widespread, we compared results from a tradition occupancy model (MacKenzie et al. 2002) to results from our model. We used the covariates in the top model for each species in a traditional occupancy model that assumed no false positive detections occurred (no-FP model).

RESULTS

Occupancy Modeling

We conducted point counts and collected local- and landscape-scale covariate data at 272 sites (Fig. S1) and site-scale covariate data at 138 sites during 2 breeding seasons. Our point count data contained 157 detections and 23 confirmed presences for the black-and-white warbler, 407 detections and 50 confirmed presences for the blue-headed vireo, 134 detections and 20 confirmed presences for the black-throated blue warbler, 41 detections and 11 confirmed presences for the Canada warbler, 125 detections and 16 confirmed presences for the veery, and 185 detections and 11 confirmed presences for the wood thrush.

We computed posterior occupancy probabilities at each site for each of the 6 focal species. Occupancy ranged from extremely low to very high for the black-and-white warbler (0.01–0.90; Fig. 1), blue-headed vireo (0.01–1.00; Fig. 2), Canada warbler (0.00–0.92; Fig. 3), and veery (0.00–0.95; Fig. 4). However, posterior occupancy probabilities were very low to moderate for the black-throated blue warbler (0.00–0.57; Fig. 5) and wood thrush (0.07–0.44; Fig. 6).

The covariates that appeared most frequently in top models were percent forest within 200 m (black-and-white warbler, black-throated blue warbler, wood thrush), percent forest within 1,000 m (Canada warbler, veery), percent developed

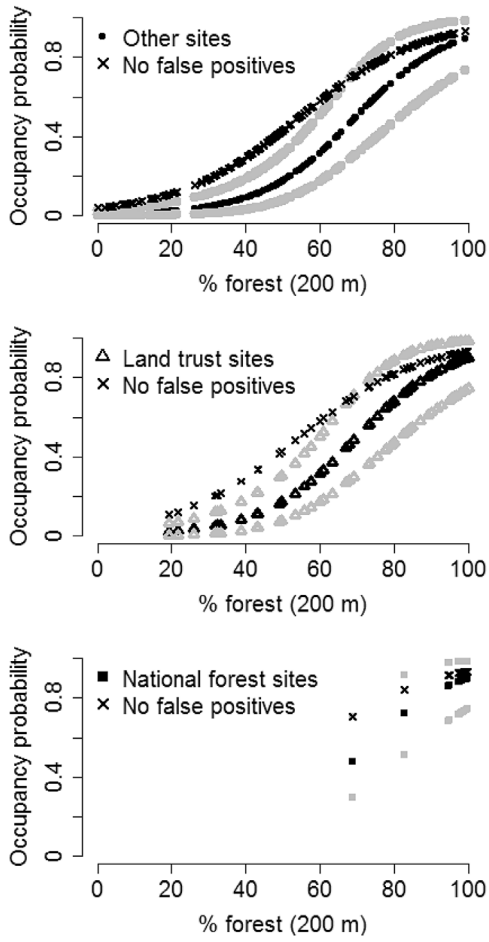

Figure 1. Posterior occupancy probabilities for the black-and-white warbler from the top-ranked model (posterior model weight = 0.76) ordered by the percent forest within 200 m of point count sites in the Nantahala National Forest (black squares), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is presented with the 95% Bayesian credible interval in gray. The mean of the posterior distribution from the model assuming no false positive detections is included (×).

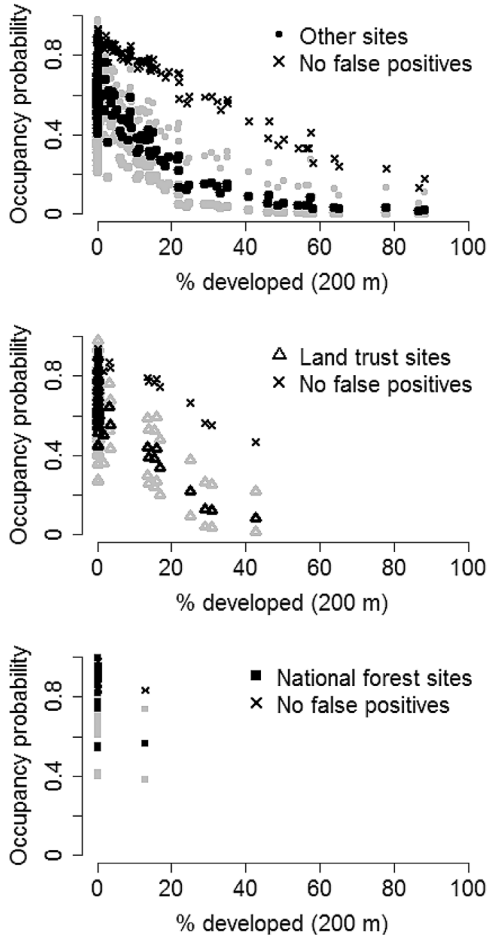

Figure 2. Posterior occupancy probabilities for the blue-headed vireo from the top-ranked model (posterior model weight = 0.48) ordered by the percent developed land within 200 m of point count sites in the Nantahala National Forest (black squares), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is presented with the 95% Bayesian credible interval in gray. The mean of the posterior distribution from the model assuming no false positive detections is included (×).

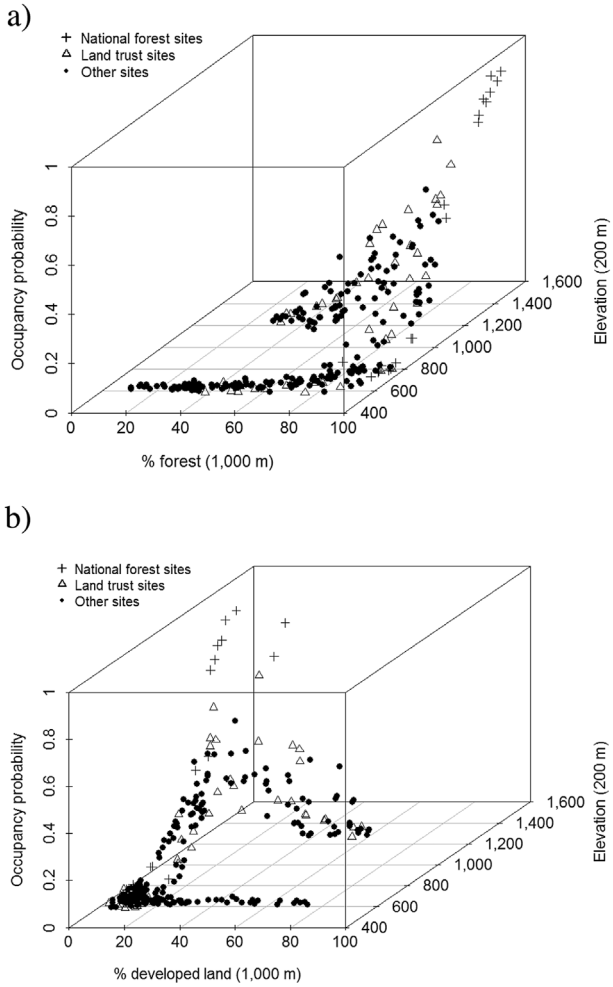

Figure 3. Posterior occupancy probabilities for the Canada warbler from top-ranked models ordered by a) the percent forest within 1,000 m of point count sites and the mean elevation within 200 m of point count sites (posterior model weight = 0.45) and b) the percent developed land within 1,000 m of point count sites and the mean elevation within 200 m of point count sites (posterior model weight = 0.35) in the Nantahala National Forest (black crosses), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is shown. The posterior distribution was also estimated from the model assuming no false positive detections, but the results are not graphed because this model overestimated the occupancy probably by at most 0.068 ($\bar{x} = 0.015$).

within 200 m (blue-headed vireo, veery), percent developed within 1,000 m (Canada warbler), and elevation (Canada warbler, veery; Tables S4–S9). As percent forest or elevation increased, posterior occupancy probabilities tended to increase (Figs., 3 1–6, S2, S3). As percent developed or forest clumpiness index increased, occupancy probabilities tended to decrease (Figs., 3 2, S2).

The relationships between covariates and occupancy probabilities were consistent across land conservation frameworks. In other words, birds at sites with similar covariate values in all 3 conservation frameworks had similar occupancy probabilities. However, there were differences in the range of covariate values present in each of the 3 land conservation frameworks. Namely, sites with the highest percent forest cover and elevation were in the national forest, sites with the lowest percent forest cover and highest percent developed land were unprotected, and land trust sites were diverse but did not have low percent forest cover or high percent developed lands. Not all national forest sites were at high elevation; there were also moderate and low elevation sites in the national forest (Figs., 4 3, S2, S3, S7, S8). Most national forest sites had >90% forest, whereas all land trust sites had ≥20% forest (Figs., 3, 5, 6, 1 S7, S9–S11). There was a large range in percent forest at unprotected sites (0–100%), but more sites had low percent forest than high (Figs., 3, 5, 6 1, S7, S9–S11). National forest sites had ≤20% developed, and land trust sites had ≤60% developed. Unprotected sites had up to 90% developed (Figs., 3 2, S7, S12). The sites with the smallest forest clumpiness index values (<0.3) were in the national forest; otherwise, values were similar at land trust and unprotected sites.

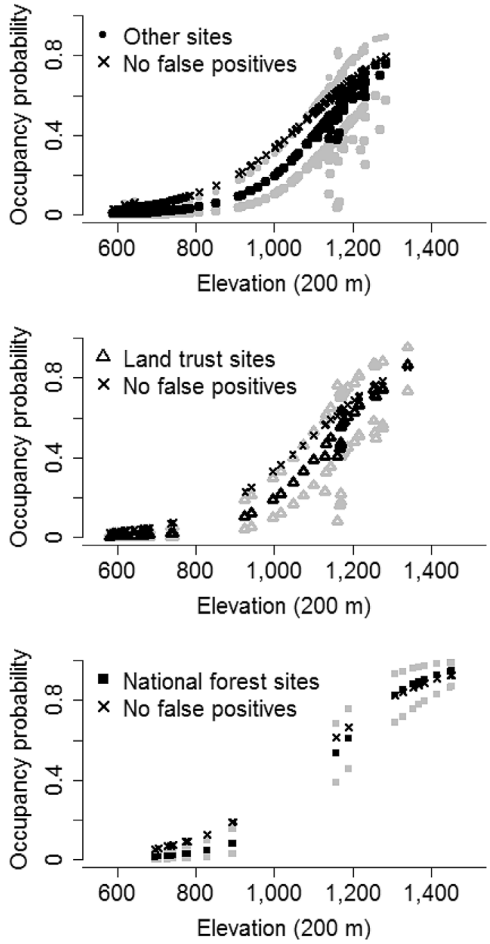

Figure 4. Posterior occupancy probabilities for the veery from the top-ranked model (posterior model weight = 0.49) ordered by the mean elevation within 200 m of point count sites in the Nantahala National Forest (black squares), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is presented with the 95% Bayesian credible interval in gray. The mean of the posterior distribution from the model assuming no false positive detections is included (×).

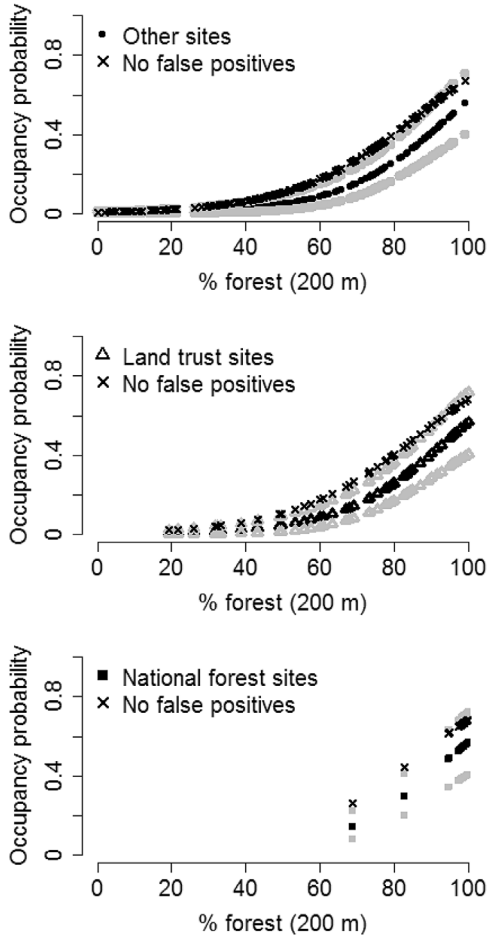

Figure 5. Posterior occupancy probabilities for the black-throated blue warbler from the top-ranked model (model posterior weight = 0.87) ordered by the percent forest within 200 m of point count sites in the Nantahala National Forest (black squares), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is presented with the 95% Bayesian credible interval in gray. The mean of the posterior distribution from the model assuming no false positive detections is included (×).

Model-averaged false positive detection probabilities ranged from 0.01 to 0.24 and were less than model-averaged true positive detection probabilities for all species and years (Table 2). For all 6 species, the top models had year-specific true positive detection probabilities that ranged from 0.30 to 0.82 (Table 2). For all species, model-averaged true positive detection probabilities were greater in year 2 than in year 1 (Table 2).

If False Positive Detection Had Not Been Modeled

The 95% BCI for occupancy probabilities from the no-FP model did not overlap with the 95% BCI resulting from our model for 3 species, indicating results would have been severely biased for these species if false positive detections had not been modeled. The black-throated blue warbler and wood thrush were species with low occupancy (0.57 and 0.44 max. occupancy probability across sites, respectively). With the no-FP model, mean occupancy probabilities for the wood thrush were overestimated across all values of percent forest with a mean bias of 0.34 (Fig. 6). Mean occupancy probabilities for the black-throated blue warbler also were overestimated by the no-FP model across all values of percent forest, but the bias was greater with large percent forest cover (Fig. 5). Biases from the no-FP model were even more severe for other species. For the black-and-white warbler, mean occupancy probabilities were most overestimated at moderate levels of percent forest (Fig. 1). At 56% forest, our model estimated 0.26 occupancy probability, but the no-FP model estimated 0.53 occupancy probability, double the occupancy probability from our model. At 22% developed, our model estimated 0.22 occupancy probability for the blue-headed vireo, when the no-FP model estimated 0.67, 3 times the occupancy probability from our model (Fig. 2). For the Canada warbler and veery, results from the no-FP model were less biased. The mean bias for the Canada warbler was 0.015, and the mean bias for the veery was 0.067 (Fig. 4). However, veery mean occupancy probabilities were underestimated by the no-FP model at high elevations.

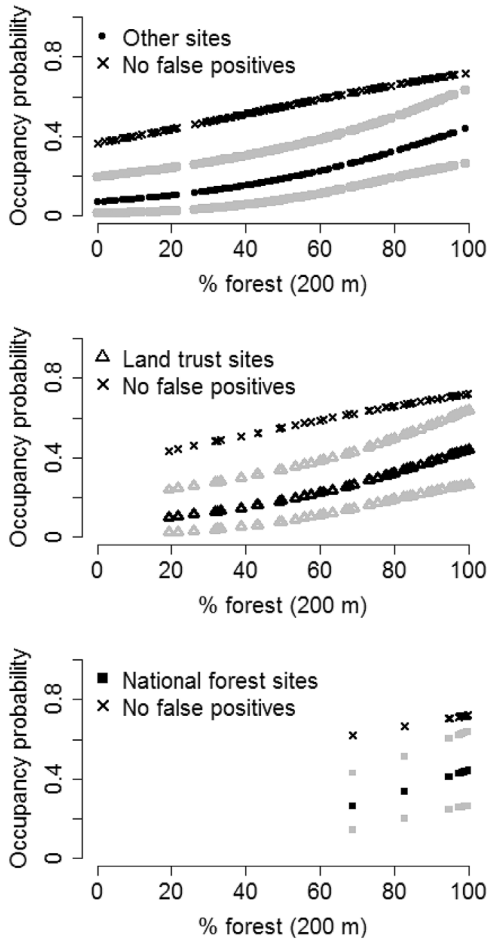

Figure 6. Posterior occupancy probabilities for the wood thrush from the top-ranked model (model posterior weight = 0.57) ordered by the percent forest within 200 m of point count sites in the Nantahala National Forest (black squares), on land trust properties (black triangles), or on unprotected properties (black circles) in Macon County, North Carolina, USA. For each point count site, the mean of the posterior distribution is presented with the 95% Bayesian credible interval in gray. The mean of the posterior distribution from the model assuming no false positive detections is included (×).

The 95% BCI from the no-FP model was >95% BCI from our top model for the blue-headed vireo across the range of percent developed (i.e., no overlap; Fig. S13). For the wood thrush, a species on the Audubon Yellow WatchList and with low occupancy from our model (0.44 max. occupancy probability across sampled sites), the BCI from the no-FP model was greater than our BCI for all values of percent forest <90% (Fig. S14). The BCI from the no-FP model was greater than our BCI for the black-and-white warbler when there was 38–51% forest (Fig. S15). However, the BCIs overlapped across the range of covariate values for the black-throated blue warbler, Canada warbler, and veery (Figs. S16–S18). The predictive ability of a top model was greatest for the black-and-white warbler (0.93) and least for the wood thrush (0.66; Table 3). However, all top models had an AUC >0.5.

DISCUSSION

Bird Occupancy

Our results suggest that avian occupancy is more strongly related to LULC attributes than conservation frameworks. Also, sites under all 3 land conservation frameworks had diverse LULC attributes. So for example, a certain occupancy probability was associated with a given level of percent forest within 200 m regardless of the land conservation framework of the site (Figs., 5, 6 1, S9–S11). When there was diversity in occupancy probabilities among different land conservation frameworks at a given covariate value, there was also diversity in occupancy probabilities within land conservation frameworks at a given covariate value (Figs. 2–4, S7, S8, S12).

We observed a greater diversity in LULC attributes in land trust sites than national forest sites. We expect that this relates to the diverse reasons a property may have been donated or bought by a land trust, in the case of fee simple properties, or the diverse reasons a land trust and landowner created a conservation easement. These reasons may not have been related to avian conservation, and our results demonstrate that land trust properties in Macon County are not conserving the habitat associated with the highest occupancy probabilities for several species of forest-dwelling Neotropical migrant birds. Currently, conservation easements or fee simple properties owned by land trusts may not provide substantially different habitat characteristics than those found on unprotected properties, with the exception that land trust sites did not have low percent forest or high percent developed. If conservation of these species is a priority for land trusts and landowners, new methods to

Table 2. Model-averaged true positive ($p11$) and false positive ($p10$) detection probabilities and posterior variances in parentheses for 2 breeding seasons ($yr1$ or $yr2$) and 6 species of forest-dwelling, insectivorous, Neotropical migrant birds: black-and-white warbler (BAWW), blue-headed vireo (BHVI), black-throated blue warbler (BTBW), Canada warbler (CAWA), veery (VEER), and wood thrush (WOTH) studied from May to July 2010 and 2011 in Macon County, North Carolina, USA.

	BAWW	BHVI	BTBW	CAWA	VEER	WOTH
p11_yr1	0.30	0.64	0.61	0.36	0.44	0.49
	(−0.0047)	(−0.0029)	(−0.0076)	(−0.013)	(−0.0054)	(−0.0087)
p11_yr2	0.40	0.78	0.82	0.39	0.63	0.59
	(−0.0022)	(−0.0014)	(−0.0047)	(−0.0068)	(−0.0043)	(−0.0065)
p10_yr1	0.01	0.24	0.03	0.01	0.01	0.09
	(−0.00012)	(−0.0019)	(−0.00033)	(−0.000024)	(−0.000077)	(−0.0011)
p10_yr2	0.09	0.14	0.03	0.00	0.03	0.12
	(−0.00064)	(−0.0015)	(−0.00013)	(−0.000021)	(−0.00013)	(−0.00081)

Table 3. Predictive ability of top models for the black-and-white warbler (BAWW), blue-headed vireo (BHVI), black-throated blue warbler (BTBW), Canada warbler (CAWA), veery (VEER), and wood thrush (WOTH) studied from May to July 2010 and 2011 in Macon County, North Carolina, USA. The occupancy (ψ) and true positive detection ($p11$) models for each species are indicated along with the posterior model weights. We measured the predictive ability of each model with the area under the receiver operating characteristic curve (AUC).

Species	ψ (landscape, local)	p_{11}	Posterior	AUC
BAWW	% forest within 200 m	Yr	0.76	0.93
BHVI	% developed within 200 m, forest clumpiness index within 1,000 m	Yr	0.48	0.76
	% developed within 200 m, forest clumpiness index within 1,000 m	Yr, ordinal date, (ordinal date)^2	0.47	0.74
BTBW	% forest within 200 m	Yr	0.87	0.85
CAWA	% forest within 1,000 m, $\bar{x}$ elevation within 200 m	Yr	0.45	0.92
	% developed within 1,000 m, $\bar{x}$ elevation within 200 m	Yr	0.35	0.91
VEER	% forest within 1,000 m, $\bar{x}$ elevation within 200 m	Yr	0.32	0.90
	% developed within 200 m, $\bar{x}$ elevation within 200 m	Yr	0.49	0.90
WOTH	% forest within 200 m	Yr	0.57	0.66

identify and conserve properties are warranted. For example, structured decision making could help land trusts prioritize land for conservation in a way that balances multiple objectives related to regional land use (Conroy and Peterson 2013, Ferguson et al. 2015*a*). Similarly, structured decision making could help landowners and land trusts to work together to identify optimal terms for a conservation easement to achieve particular conservation objectives.

Without changes in how land trusts prioritize land for conservation, national forests may become important refugia for forest-dwelling, Neotropical migrant birds in Macon County. Currently, there is habitat for forest-dwelling, Neotropical migrant birds that is not in the national forest, but as habitat is lost because of development, habitat may become concentrated in national forests because they are not developed and have forest at high elevation.

As expected, posterior occupancy probabilities increased as percent forest increased or as percent developed decreased, but quantifying that relationship provides useful information for conservation and development planning. For example, to have $\geq$0.5 probability of occupancy, generally sites were >1,200 m elevation, had $\geq$70% forest within 200 m, and had $\leq$10% developed within 200 m (Figs. 1–4). However, the black-throated blue warbler and wood thrush required approximately 95% forest within 200 m to have $\geq$0.5 probability of occupancy (Figs., 6 5). The blue-headed vireo was the only species that did not have percent forest in a top model, perhaps because the blue-headed vireo was the only focal species closely associated with coniferous forest (Morton and James 2014). Because coniferous forests were less abundant in Macon County compared to deciduous or mixed forest, the measure of percent forest may not have adequately described the availability of coniferous forest for use by the blue-headed vireo.

Whether focal species occupancy was most strongly associated with LULC attributes within 200 m or 1,000 m was variable. However, Canada warbler occupancy was consistently related to LULC attributes within 1,000 m, whereas wood thrush occupancy was consistently related to LULC attributes within 200 m. There is some evidence that Canada warbler territories (min. reported territory of 0.15 ha; Hallworth et al. 2008) are larger than wood thrush territories (min. reported territory of 0.08 ha; Roth et al. 1996), which could contribute to the Canada warbler responding to LULC attributes on a larger scale.

Notably, none of the models with posterior weights of $\geq$0.01 included site-scale covariates. Although these results could suggest that local- and landscape-scale attributes have a stronger relationship with avian occupancy, they do not mean that site-scale factors are inconsequential. Collecting site-scale covariate data at only 51% of sites and using a modeling-based approach to impute missing values could have affected inference about the relationship of occupancy to these covariates.

Managing LULC at the local- and landscape-scale can involve many stakeholders, and it may be difficult to identify optimal management decisions. For example, there has been little land use planning in Macon County during the last 30 years (Cumming and Norwood 2012). Although many Macon County landowners think the rapid growth occurring in the county is detrimental, there has not been agreement about an appropriate response (Cho et al. 2005*b*, 2009; Gragson and Bolstad 2006; Cumming and Norwood 2012). Structured decision making may also be a promising method to evaluate land management decisions because it can incorporate multiple, conflicting objectives and system uncertainty (Clemen 1996, Conroy and Peterson 2013, Ferguson et al. 2015*a*).

Posterior occupancy probabilities were highly variable across sites for all 6 species. Unsurprisingly, some sites had extremely low posterior occupancy probabilities (e.g., sites with low percent forest and high percent developed). However, for the black-throated blue warbler and wood thrush, the most suitable sites only had 0.57 and 0.44 posterior occupancy probabilities, respectively. This pattern could be because populations of the black-throated blue warbler, wood thrush, and Canada warbler, may be declining in the southern Appalachian region (Sauer et al. 2003, 2008). The sites with high Canada warbler occupancy probabilities were at sites with the highest elevation and percent forest, which were in the national forest.

Modeling Approach

Because the AUC for each species' top model was >0.5, we conclude that our models performed better than random at determining which sites were occupied. The AUC values were largest for the black-and-white warbler, Canada warbler, veery, and black-throated blue warbler, indicating

high discriminatory ability, and the species with the lowest AUC values also had the largest false positive detection probabilities (Tables, 3 2).

Model-averaged false positive detection probabilities for the blue-headed vireo were 0.24 in the first breeding season and 0.14 in the second breeding season. These were the largest false positive detection probabilities among the focal species, possibly because the blue-headed vireo's song closely resembles the song of the red-eyed vireo (*Vireo olivaceus*). The large false positive detection probability for the blue-headed vireo contributed to the large bias we observed from the no-FP model.

Although detection is a nuisance parameter and scientists and managers are fundamentally interested in occupancy, imperfect detection must be accounted for appropriately to generate accurate estimates of occupancy that can benefit management. Biases can occur in results and erroneous conclusions about wildlife conservation that can be drawn if false positives are not modeled, as we illustrated with our model application. Bias in results from the no-FP model could be quite severe, erroneously suggesting that moderate percent forest was associated with a moderate (rather than low) probability of black-and-white warbler occupancy and that low percent developed was associated with a high (rather than low) probability of blue-headed vireo occupancy. The small degree of bias in no-FP model results for the Canada warbler and veery can be explained by the low false positive detection probability for these species (Table 2).

For some species (e.g., Canada warbler and wood thrush), the bias in results from the no-FP model was consistent across the range of the covariate, but for others (e.g., black-and-white warbler, blue-headed vireo, black-throated blue warbler, and veery), the bias was not consistent. When the bias from assuming data have no false positives is not consistent across the range of the covariate, modeling false positives is even more important because results cannot be adjusted by a scalar multiple to correct for the bias.

MANAGEMENT IMPLICATIONS

Our findings suggest conservation priorities for regional planners, land trusts, and the national forest. To increase their conservation impact for forest-dwelling, Neotropical migrant birds, land trusts may want to target conservation on properties that adjoin national forest land, are at high elevation, have a high percent forest, or have a low percent development. Land trusts also may want to focus on the landscape scale rather than smaller scales. United States Forest Service decision makers could consider the importance of high elevation national forest areas to sensitive species that may lose habitat through development or climate change. Structured decision making may benefit conservation through helping stakeholders feel represented and involved in decision making because land use regulation is often a contentious topic (Conroy and Peterson 2013, Ferguson et al. 2015*a*). Conservation and development decision making can be supported by this study's detailed estimates of occupancy probabilities given different levels of key LULC features.

Our model generates useful estimates of occupancy probabilities and their relationship to LULC features that can differ dramatically from traditional occupancy model estimates. If false positive detections are not modeled, estimates of species' relationships with habitat features can be severely biased and could lead to suboptimal management decisions. Our results also indicate that local- and landscape-scale LULC attributes are correlated with the occupancy of forest-dwelling, Neotropical migrant birds. A benefit of focusing on the landscape scale for conservation decision making is that obtaining remote-sensing data at the landscape- and local-scale can be more efficient than the intensive field work that is often required to obtain site-scale data (Mitchell et al. 2001). Further, landscape models are expected to be more generalizable than local- or site-specific models (Mitchell et al. 2001).

ACKNOWLEDGMENTS

We thank J. F. Chamblee, R. J. Cooper, and J. C. Maerz for their suggestions on this project. We thank all of the Macon County landowners who participated in this project. We also thank D. Desmond, G. Wein, B. McRae, B. McLarney, C. Smalling, D. Shure, J. Love, J. Meador, J. Hunnicutt, K. McLean, P. Moore, R. Regnery, S. Guffey, and W. Swank for assistance with accessing point count sites. We thank technicians C. Beasley, N. Gatto, M. Ivey, K. Love, and C. Jordan. Funding was provided by the Coweeta Long Term Ecological Research project (NSF grant DEB-0823293); United States Department of Agriculture Cooperative State Research, Education, and Extension Service McIntire-Stennis Project (GEOZ-0159-MS); Georgia Ornithological Society; Warnell School of Forestry and Natural Resources at the University of Georgia; University of Georgia Graduate School; and Georgia Museum of Natural History.

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Associate Editor: Bill Block.

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