Forest Ecology and Management 595 (2025) 122974

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Passive acoustic monitoring paired with dynamic occupancy models indicates benefits of even-aged forest management for Wood Thrush

Cameron J. Fiss[a,*], Jeffery L. Larkin[b,c], Lauren Chronister[a], Justin Kitzes[a]

[a] Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA
[b] Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705, USA
[c] American Bird Conservancy, The Plains, VA 20198, USA

ARTICLE INFO

Keywords:
Dynamic occupancy
ARU
Wood Thrush
Forest management
Lidar
Passive acoustic monitoring

ABSTRACT

Forest management is critical for ensuring a sustainable source of wood fiber and maintaining the integrity of ecosystem services. Understanding relationships between management and wildlife can help identify ways to best meet both wildlife and forestry objectives. Wood Thrush is an imperiled forest songbird, but the majority of studies regarding its relationships with management are based on static occupancy or abundance, which provide an incomplete assessment of habitat quality if movement occurs throughout the breeding season. We used within-season dynamic occupancy models and passive acoustic recorders to monitor Wood Thrush occupancy dynamics in response to LiDAR-derived forest structure in Pennsylvania. Over the entire breeding season Wood Thrush used 54 % of sites but on any given day only 14 %-18 % of sites were occupied, indicating substantial movement. Settlement had a significant quadratic relationship with canopy variation and understory density, and vacancy had a significant quadratic relationship with midstory density and a positive relationship with dry oak forests. Predictive maps revealed that areas within 500 m of overstory removals 4–25 years post-harvest had mean predicted daily settlement rates 50 % - 130 % higher than mature forest and areas within 500 m of overstory removals 11–25 years post-harvest had mean predicted daily vacancy rates 25 % lower than mature forest. Our study suggests that implementing even-aged management practices can create vegetation conditions that improve habitat quality for Wood Thrush. Finally, our study demonstrates that passive acoustic sampling with human-validated machine-learning outputs provides an efficient means of obtaining robust datasets necessary for dynamic occupancy modeling.

1. Introduction

Forest management is an important tool for maintaining forest health, meeting resource needs, and providing habitat for wildlife (Loehle et al., 2024). Management can constitute a variety of practices ranging from largely hands-off approaches to silvicultural treatments that alter forest structure across understory, midstory, and canopy layers (Nyland, 2016). In the eastern US, even-aged management is one approach used to harvest timber and regenerate forest (Keyser et al., 2016). Even-aged management is primarily accomplished using methods such as clearcuts, overstory removals, seed tree, or shelterwood harvests, depending on site conditions (*e.g.*, presence of advanced regeneration) prior to management (Palik et al., 2020). For species dependent on early-successional vegetation communities, the stand-level benefits of even-aged management are evident (DeGraaf and Yamasaki, 2003, King and Schlossberg, 2014), for other species, fine and coarse-scale effects of even-aged management on habitat quality are less clear. Understanding how wildlife habitat quality is affected by even-aged management practices is valuable for developing forest management strategies that consider both forestry and wildlife goals.

One species that exhibits varying responses to forest management is the Wood Thrush (*Hylocichla mustelina*). Wood Thrush is a Nearctic-Neotropical migratory species that breeds in the United States and winters in southern Mexico through Central America. On the breeding grounds, Wood Thrush are strongly linked to eastern deciduous forests with their range bounded by eastern Texas and Minnesota in the west and extending to north Florida and southern Ontario and New Brunswick in the east (Evans et al., 2011). The core of the Wood Thrush breeding population occurs in central Appalachian forests from Tennessee to New York. The species is categorized as one of high

* Corresponding author.
E-mail address: fisscameron@gmail.com (C.J. Fiss).

https://doi.org/10.1016/j.foreco.2025.122974
Received 11 March 2025; Received in revised form 1 July 2025; Accepted 3 July 2025
Available online 12 July 2025

conservation concern by Partners in Flight, a multinational avian conservation organization, with populations estimated to have declined by roughly 50 % since 1966 and an annual rate of decline of 1.12 % during this time (Sauer et al., 2022). The species is typically associated with mature, mesophytic forest conditions in which it establishes breeding territories (Rosenberg et al., 2003, Lambert et al., 2017). Within such sites, Wood Thrushes build nests in the understory or lower midstory layers (Hoover and Brittingham 1999, Evans et al., 2011). Within this context, Wood Thrush are known to demonstrate various responses to forest management, with some studies indicating beneficial effects of even-aged management (King and DeGraaf, 2000, Dellinger et al., 2007, Goodale et al., 2009) and others suggesting negative effects of similar silviculture practices (Wang et al., 2006, Newell and Rodewald, 2012, Morris et al., 2013).

However, the majority of previous studies of Wood Thrush in managed forests were based on static occupancy or abundance estimates, which may provide an inadequate proxy for habitat quality compared to, for instance, reproductive success or survival (Johnson, 2007). Relatively few studies have assessed Wood Thrush reproduction in silviculturally managed landscapes in the central Appalachians (*e.g.*, Duguay et al., 2001, Dellinger et al., 2007) where the majority of the species breeds (Evans et al., 2011), perhaps given the added challenges and effort associated with nest searching and monitoring. More recently, it has been suggested that within-season occupancy dynamics of songbirds may provide a better proxy for habitat quality than static occupancy or abundance estimates without the added effort required to conduct nest searching and monitoring (Betts et al., 2008, McClure and Hill, 2012). For instance, Betts et al. (2008) showed that Black-throated Blue Warblers (*Setophaga caerulescens*) were more likely to settle and less likely to vacate sites with high hobblebush (*Viburnum alnifolium*) density, a shrub known to influence this warbler's habitat quality. As such, understanding Wood Thrush breeding season occupancy dynamics and their relationship to forest structure and management would allow us to better inform forest management actions for Wood Thrush that maximize season-long habitat quality.

To better evaluate the relationship between Wood Thrush, forest structure, and even-aged forest management, we used automated recording unit (ARU) arrays to passively sample landscapes for Wood Thrush throughout the entire breeding season. We combined passive acoustic data with light detection and ranging (LiDAR) data and within-season dynamic occupancy models to understand how forest structure influences Wood Thrush breeding season occupancy dynamics. We modeled Wood Thrush occupancy dynamics using LiDAR-derived forest structure covariates because Wood Thrush are likely to respond to forest structure and not directly to even-aged treatments themselves. Instead, we used our model to generate spatially explicit predictive maps, highlighting patterns of occupancy dynamics in relation to even-aged forest management. This approach allowed for a more mechanistic understanding of the link between Wood Thrush, forest structure, and even-aged management. Our study had three main objectives, including 1) determine whether Wood Thrush breeding season occupancy is dynamic (*i.e.*, within-season movement occurs) in managed forest landscapes 2) determine which aspects of forest structure and which forest plant community types are associated with Wood Thrush occupancy dynamics and 3) evaluate if even-aged forest management improves habitat quality by evaluating settlement and vacancy rates in relation to various treatment types. We predicted that Wood Thrush settlement would align with well understood aspects of the species' breeding ecology, including tall complex canopies, moist mesophytic forests, and well developed under- and midstories (Evans et al., 2011, Lambert et al., 2017) as individuals find higher quality habitat over the breeding season (*e.g.*, Betts et al., 2008). We predicted that settlement would occur near managed stands for two reasons 1) under, midstory, and canopy complexity could be high adjacent to managed areas, and 2) Wood Thrush are associated with dense early-successional vegetation during the post-breeding period and prior to migration (Stoleson, 2013) and may choose to make second (or later) breeding attempts closer to areas that better prepare them for migration.

2. Methods

2.1. Study area

We collected passive acoustic data in central Pennsylvania (PA) USA from 20 May to 8 July 2020 and 2021. All data were collected on large tracts of public forest in central PA's Allegheny Plateau physiographic province, which is characterized by relatively high elevation, steep rolling hills, and deep valleys. Specifically, we collected data in two study areas that represent actively managed forest landscapes, including State Game Lands (SGL) 25 (N = 125) in 2020, and SGL 60 (N = 79) in 2021 (Fig. 1). Management conducted within the past 40 years largely consisted of even-aged treatments that maintain some legacy structure, including shelterwood harvests (10–15 m^2 / ha residual basal area after second-entry) and overstory removal harvests with retained live trees and snags (2–10 m^2 / ha residual basal area).

Forests in both study areas are broadly characterized by four main community types, mixed oak, dry oak heath (hereafter dry oak), mixed hardwood, and northern hardwood. The mixed oak community had canopies dominated by a variety of oak (*Quercus* spp.) and hickory (*Carya* spp.) species, and often red maple (*Acer rubrum*) with understories that typically contained a mix of witch hazel (*Hamamilis virginiana*) and flowering dogwood (*Cornus florida*). Dry oak communities (primarily SGL 60) were characterized by chestnut oak (*Q. montana*), black gum (*Nyssa sylvatica*) and sassafras (*Sassafras albidum*) and understories of mountain laurel (*Kalmia latifolia*), scrub oak (*Q. ilicifolia*), and huckleberries (*Gaylussacia* spp.). Northern hardwood communities (primarily SGL 25) were represented by canopy species including American beech (*Fagus grandifolia*), sugar maple (*A. saccharum*), and pin cherry (*Prunus pensylvanica*), and understory plants included striped maple (*A. pensylvanicum*) and hornbeam (*Carpinus carolinea*), for example. Mixed hardwood communities had canopies dominated by black cherry (*P. serotina*) and red maple but were otherwise similar to northern hardwood communities. We used forest inventory data provided by the Pennsylvania Game Commission to place sampling locations using a stratified random procedure where broad forest age-class categories (0–6, 7–20, 21–39, >40 years post-harvest) acted as strata. Sampling locations were placed at least 250 m apart to avoid double-counting of Wood Thrush.

2.2. Machine-learning classifier

We used AudioMoth 1.1 recorders (Open Acoustic Devices; Hill et al., 2018) to gather passive acoustic data targeting the songbird dawn chorus. We deployed ARUs prior to the start of the sampling period (1 May to 10 May each year). ARUs were programmed to record from 0600 to 0800 EDT each day. Each ARU was placed in a sealed plastic bag with a small desiccant packet for waterproofing and then within a brown mesh bag for concealment (Figure S1). We note that protecting ARUs within plastic bags does not affect species identification (Osborne et al., 2023). Technicians placed ARUs on small woody stems (<20 cm DBH) using plastic cable ties strung through the top of the mesh bag. ARUs were attached to trees at approximately 1.5–2 m above the ground.

We used a machine-learning classifier to detect possible instances of Wood Thrush vocalizations in recordings at each sample location. Specifically, we used the OpenSoundscape software (version 0.7.1; Lapp et al., 2023b), to train a Resnet18 Convolutional Neural Network (CNN) with a class for Wood Thrush song and classes for several other songbird species. The training data were gathered from publicly available recordings downloaded from xeno-canto.org and annotations were made by technicians experienced in avian vocalizations using Raven Pro software (Bioacoustics Research Program 2019). We report performance metrics recommended by Knight et al. (2017) and further details on the

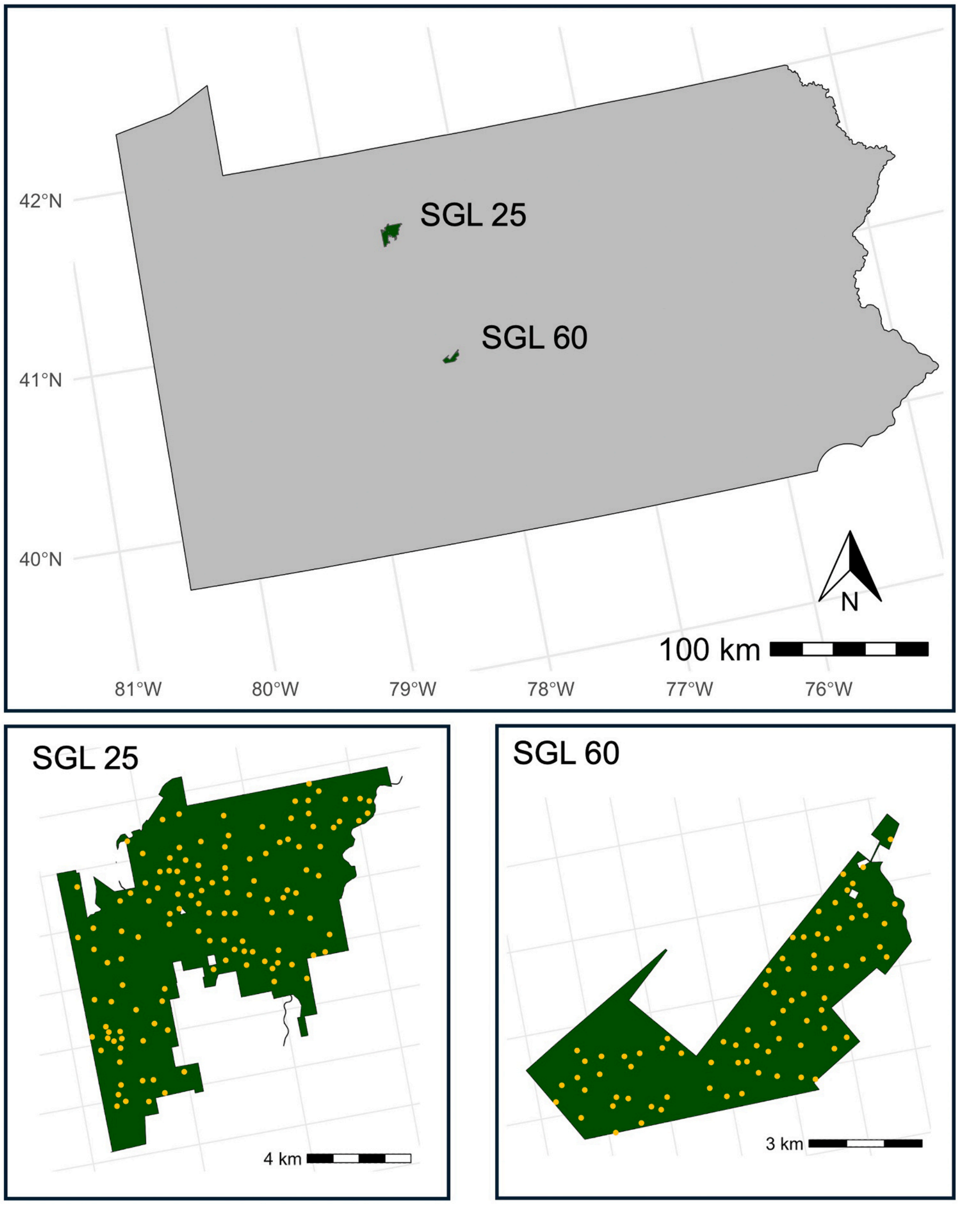

Fig. 1. Wood Thrush occupancy dynamics were estimated in two study areas (SGL 25 and SGL 60) in central PA from 20 May to 08 July in 2020 and 2021 representing a period from early- to late breeding season for the species. The top map shows the location of both study areas in PA. Bottom maps show the sampling strategy in both study areas with yellow dots representing sampling locations. All survey areas were sampled using autonomous recording units.

classifier and its training in the supplemental material (Fig. S2).

We then used our trained Wood Thrush classifier to rank each 4-s clip of audio from the ARU data across a 50-day window (20 May to 8 July) from all sample locations based on the model's confidence of Wood Thrush song presence. This window represents early- to late breeding season in the central Appalachian region for the species and likely captures multiple nesting attempts and double-brooding behavior; still this window is late enough that it is unlikely to capture vocalizations from migrating individuals (Roth and Johnson, 1993). We then used a classifier-guided listening approach, whereby technicians skilled in Wood Thrush vocal identification listened to the highest scoring clips to verify presence or absence of Wood Thrush. Specifically, technicians listened to only the single highest-scoring 4-s clip at each sample location for each of three 30-min sampling periods (0600–0630, 0645–0715, 0730–0800) for each day and repeated this process across all 50 days to build the dynamic occupancy model detection history. All other 4-s clips ranked by the classifier that were not the highest scoring of any 30-min survey window were discarded. This process resulted in a detection history whereby three secondary periods (30 min each) occurred within a single day, and each day of the 50-day survey window represented a different primary period, between which transitions in occupancy could occur.

2.3. Covariates

Raw LiDAR data with 10–18 pulses/m^2 were gathered from the USGS National Map. Specifically, we used LiDAR data sets that were collected during spring 2019, which targeted leaf-off conditions in PA. LiDAR metrics intended to describe both horizontal and vertical characteristics of forests (see below) were summarized from point cloud data using the "*lidR*" package (Roussel et al., 2020) in program R (R Core Team 2023), with all LiDAR return heights normalized based on a triangulated irregular network (TIN) algorithm to construct the digital terrain model from ground returns (Fisher et al., 2024). Our final set of LiDAR-derived forest structure metrics summarized point cloud data at a 10 m by 10 m pixel resolution. Additional details relating to the LiDAR data used herein can be found in Fisher et al. (2024).

We develop a set of covariates based on a priori expectations of their effect on Wood Thrush occupancy (Table 1). Our initial set of covariates included the proportion of returns (*i.e.*, the intersection of LiDAR with an object) within the 1–4 m stratum (hereafter understory density) and within the 4–10 m stratum (hereafter midstory density). To evaluate distribution of vegetation layers, we derived a multi-story profile measure, calculated as the difference between the second and third vegetation height quartiles divided by canopy height; here low values indicate single or two-layered stands and high values indicate multi-layered stands (Zellweger et al., 2013). We also generated LiDAR-derived metrics representative of canopy height and canopy structure, including the height at which 95 % of LiDAR returns occurred (hereafter canopy height), and canopy variation – a measure of canopy complexity calculated as the standard deviation of canopy height across a 30 m radius (Roussel et al., 2020). All LiDAR-derived covariates were extracted as means from a set of spatial scales including 50 m, 100 m, 250 m, and 500 m radii surrounding sampling locations using the "*raster*" package in R (Hijmans 2015). In addition to LiDAR-derived metrics, we gathered forest community type from each stand in our study areas using inventory data provided by the Pennsylvania Game Commission. We simplified these types into four main categories: dry oak, mixed oak, mixed hardwood, and northern hardwood. Finally, we calculated the Euclidean distance from each sampling location to the nearest stream of any order using the "*sf*" package in R (Pebesma, 2018). Stream data were gathered from the National Hydrography Dataset (https://www.usgs.gov/national-hydrography/national-hydrography-dataset).

Table 1
Description of variables used to model detection probability, probability of initial occupancy, probability of settlement and probability of vacancy of Wood Thrush using dynamic occupancy models.

Variable		Data Source	A priori reference	Submodels
Study Area	Factor			All
Canopy Height	Continuous	LiDAR	Bertin, (1977), Hoover and Brittingham, (1998)	Occupancy, Settlement, Vacancy
Canopy Variation	Continuous	LiDAR	Lambert et al. (2017)	Occupancy, Settlement, Vacancy
Understory Density	Continuous	LiDAR	Hoover and Brittingham, (1998)	Occupancy, Settlement, Vacancy
Midstory Density	Continuous	LiDAR	Bakermans et al. 2012	Occupancy, Settlement, Vacancy
Multi-story Profile	Continuous	LiDAR	Bakermans et al. 2012	Occupancy, Settlement, Vacancy
Distance to Stream	Continuous	National Hydrologic Database	Evans et al. (2011), Jirinec et al. (2016)	Occupancy, Settlement, Vacancy
Northern Hardwood	Factor	PGC Inventory		Occupancy, Settlement, Vacancy
Mixed Hardwood	Factor	PGC Inventory		Occupancy, Settlement, Vacancy
Mixed Oak	Factor	PGC Inventory		Occupancy, Settlement, Vacancy
Dry Oak	Factor	PGC Inventory		Occupancy, Settlement, Vacancy
Day of Season	Continuous			Detection

2.4. Statistical analyses

Dynamic occupancy models (MacKenzie et al., 2003) are an extension of the traditional static occupancy model (MacKenzie et al., 2002). Compared to the traditional occupancy model, dynamic occupancy models estimate two additional parameters including colonization, the probability an unoccupied site becomes occupied, and extinction, the probability that an occupied site becomes unoccupied. In addition to initial occupancy and detection probability, colonization and extinction can be estimated as a function of covariates. Estimating these additional parameters requires both primary and secondary sampling periods, where secondary sampling periods occur within a primary period. Populations are assumed to be closed across secondary periods (allowing for estimation of detection probability) and allowed to be open across primary periods (allowing for estimation of colonization or extinction).

Dynamic occupancy models are often applied to measure metapopulation dynamics or species' responses to conservation or restoration actions over multiple years (*e.g.*, Gordon et al., 2024). However, primary periods (periods between which colonization and extinction are estimated) can also occur within a single season, for example from early to late breeding season for songbirds (*e.g.*, McClure and Hill, 2012). Within-season, colonization and extinction are more appropriately referred to as settlement and vacancy. Because they can record continuously, ARUs deployed within-season provide the opportunity to evaluate settlement and vacancy at an even finer temporal scale, which may be appropriate for highly vagile species. Here we used ARUs to estimate the probability of settlement and vacancy on a daily time-scale (*i.e.,* each day is a primary period). One advantage to this approach is that if the direction of covariate effects on settlement and vacancy remains consistent across the season, more instances of settlement and vacancy may improve precision of parameter estimates. However, when evaluating dynamics on such a fine time scale, it is important to address whether apparent movements are reflective of actual shifts in a species range, or simply a reflection of temporary emigration (TE) (Valente et al., 2017; see below).

We compared a suite of dynamic occupancy models for Wood Thrush using the "*unmarked*" package (Fiske and Chandler, 2011) in the statistical software program R (R Core Team, 2023). Prior to comparing complete models, we determined the most informative spatial scale and polynomial structure for each LiDAR variable and distance to stream. To do this, we constructed univariate models for each covariate at each scale (LiDAR covariates only) for initial occupancy, settlement, and vacancy submodels separately. We repeated this process including a quadratic term for each variable. We chose the best spatial scale and polynomial structure for each covariate and each submodel based on Akaike Information Criterion (AIC) score similar to McNeil et al. (2023). Rankings for all intermediate level models used to select best polynomial structure and scale for each covariate are presented in the supplemental material (Table S1). Next, we sequentially determined the best model structure, based on AIC, for detection probability, followed by the initial occupancy submodel, then the settlement submodel, and finally the vacancy sub model (similar to McClure and Hill, 2012). Our final, fully parameterized, model included the effects of habitat covariates on the probability of initial occupancy at a site, daily settlement probability at a site, and daily vacancy probability at a site. For detection probability, we compared a null model to univariate models that included day of season, study area, and ambient noise level calculated in dBFS across the full 30-min survey interval (Lapp et al. 2023a). We note that the coefficient for day of season includes both the effects of ordinal date as well as the effects of time since sunrise, as each subsequent day would have an earlier sunrise. These two effects are thus confounded and estimated together in our model. Because we did not have strong a priori expectations for the best combination of covariates, to determine the best model structure for initial occupancy, we fit all possible subsets of up to four covariates while holding the detection probability submodel structure constant using the best structure from the previous step. We then compared all possible subsets of up to four covariates for settlement and then vacancy submodels, maintaining the best covariate structure from the previous steps both times. We limited detection probability to univariate models to avoid overfitting the fully parameterized model. Our initial best ranked model based on AIC showed evidence of overdispersion (c-hat = 1.82) and thus we reranked all models using Quasi Akaike's Information Criterion (QAICc; Burnham et al., 1998) with the "*aicmodavg*" package (Mazerolle and Mazerolle, 2017). We considered covariate effects significant if their associated 95 % confidence intervals did not overlap 0. To evaluate whether our dynamic model was confounding Wood Thrush occupancy dynamics with TE, we compared the results from our best model to models that used alternative sampling structures (*i.e.,* constructed with fewer primary periods and where secondary periods were separated by at least 24 h, as per the recommendation of Valente et al. (2017). A comparison of results from reported and alternative model structures is included in supplemental materials (Figs. S3–S5).

Next, we tested whether Wood Thrush occupancy patterns were better explained by dynamic occupancy models with vacancy and settlement parameters compared to static models that assume no settlement or vacancy of sites. To do this, we compared our best dynamic occupancy model to a static occupancy model using QAICc (*e.g.*, Betts et al., 2008, McClure and Hill, 2012). The static occupancy model was fit using the same data and the same model structure for the initial occupancy and detection sub models as the best dynamic model, but unlike the dynamic model contained no parameters for either settlement or vacancy (*i.e.*, movement parameters).

To demonstrate how relationships between Wood Thrush occupancy dynamics and forest structure are linked to even-aged forest management, we generated spatially explicit predictive maps of initial occupancy, settlement, and vacancy across SGL 25. Predictive maps were based on the combination of all covariates selected in the top model. We summarized predicted parameter values (initial occupancy, settlement, and vacancy) in, and surrounding (based on the scale of covariates in the top model), two treatment types, including shelterwood and overstory removal harvests using the "*raster*" package in R (Hijmans 2015). We further separated overstory removal harvests into three age categories, including 0–3 years post-harvest, 4–10 years post-harvest, and 11–25 years post-harvest, the latter two age-classes roughly representing the stand-initiation and stem-exclusion stages of stand development, respectively (Graboski et al., 2020).

3. Results

We detected Wood Thrush at 101 out of a total of 187 sites for a naïve occupancy of 54 % for the entire sampling period. However, on any given day only 14 %-18 % of sites were occupied. Our final model set consisted of 374 models that we fit and compared to evaluate Wood Thrush occupancy dynamics (Table 2). Our best model had a QAICc of 4333.3 and the null model had a QAICc of 4484.5. The best model included significant effects of canopy height, canopy variation, distance to stream, mid- and understory density and forest type. There was no support for the static occupancy hypothesis as this model had QAICc of 6245.9. Initial modeling stages indicated that most covariates (>75 %) better explained Wood Thrush occupancy dynamics when considered as quadratic terms. Canopy variation and understory density (both 500 m scales) and midstory density (250 m scale) were most informative at spatial scales larger than canopy height (50 m for initial occupancy and settlement and 100 m for vacancy). Trends in parameter estimates and predicted values between our model and models built using alternative sampling schedules that may better isolate TE were nearly congruent, suggesting that our model was not modeling effects of TE (Figs. S3-S5).

Our best ranked model for Wood Thrush occupancy dynamics included significant covariates for all submodels, and the variance inflation factor for all covariates was < 3.1 indicating absence of multicollinearity (Table 3.). Detection probability was best explained by a study area effect (β = 0.70, SE = 0.1) whereby probability of detection was significantly higher in the SGL 25 study area (58.8 %) compared to the SGL 60 study area (41.4 %), however, there was no support for the effect of study area on initial occupancy, settlement, or vacancy. Initial occupancy of sites was best explained by a negative effect of distance to the nearest stream, a significant quadratic effect of canopy variation at the 500-m scale, a significant quadratic effect of a canopy height at the 50-m scale and non-significant quadratic relationship with midstory density at the 250-m scale (Fig. 2). Daily probability of settlement was best explained by significant quadratic effects of canopy variation

Table 2
A subset of the top five QAICc ranked models explaining Wood Thrush occupancy dynamics between 20 May and 08 July in central Pennsylvania study areas with active forest management. Parameter p = detection probability, Ψ=initial occupancy, γ=settlement, and ε=vacancy. In addition to the top five models a null model and a static occupancy model (no settlement or vacancy parameters) are shown for comparison.

Model	K	QAICc	Delta QAICc	QAICc Wt.
p(study area) Ψ(stream + canopy var_500 + canopy var_500^2 + midstory_250 + midstory_250^2 + canopy_50 + canopy_50^2) γ(stream + stream^2 + canopy var_500 + canopy var_500^2 + canopy_100 + canopy_100^2 + understory_500 + understory_500^2) ε(canopy_50 +canopy_50^2 + midstory_250 + midstory_250^2 + dry oak)	26	4333.28	0.00	0.23
p(study area) Ψ(stream + canopy var_500 + canopy var_500^2 + midstory_250 + midstory_250^2 + canopy_50 + canopy_50^2) γ(stream + stream^2 + canopy var_500 + canopy var_500^2 + canopy_100 + canopy_100^2 + understory_500 + understory_500^2) ε(canopy_50 +canopy_50^2 + midstory_250 + midstory_250^2 + dry oak + study area)	27	4334.01	0.73	0.16
p(study area) Ψ(stream + canopy var_500 + canopy var_500^2 + midstory_250 + midstory_250^2 + canopy_50 + canopy_50^2) γ(stream + stream^2 + canopy var_500 + canopy var_500^2 + canopy_100 + canopy_100^2 + understory_500 + understory_500^2) ε(stream + stream2 + canopy_50 + canopy_50^2 + midstory_250 + midstory_250^2 + dry oak)	28	4334.48	1.20	0.13
p(study area) Ψ(stream + canopy var_500 + canopy var_500^2 + midstory_250 + midstory_250^2 + canopy_50 + canopy_50^2) γ(stream + stream^2 + canopy var_500 + canopy var_500^2 + canopy_100 + canopy_100^2 + understory_500 + understory_500^2) ε(canopy_50 +canopy_50^2 + midstory_250 + midstory_250^2 + multi-story profile_100 + dry oak)	27	4334.93	1.65	0.10
p(study area) Ψ(stream + canopy var_500 + canopy var_500^2 + midstory_250 + midstory_250^2 + canopy_50 + canopy_50^2) γ(stream + stream^2 + canopy var_500 + canopy var_500^2 + canopy_100 + canopy_100^2 + understory_500 + understory_500^2) ε(canopy_50 +canopy_50^2 + midstory_250 + midstory_250^2 + mixed oak + dry oak)	27	4335.60	2.32	0.07
Null	4	4484.16	150.88	0.00
Static Occupancy Model p(study area) Ψ(stream + canopy_100 + understory_500 + understory_500^2 + dry oak)	9	6245.91	1912.63	0.00

Table 3
Parameter estimates (mean) and 95 % confidence intervals (lower, upper) for all covariates included in the top model of Wood Thrush dynamic occupancy. Most covariates included in initial occupancy, settlement, and vacancy submodels have both linear and associated quadratic effects.

Submodel	Covariate	Linear Effect			Quadratic Effect		
		Mean	Lower	Upper	Mean	Lower	Upper
Detection	Study Area	0.70	0.51	0.90			
Initial Occupancy	Stream	−0.79	−1.68	0.11			
	Canopy Variation 500	1.75	0.34	3.16	−1.31	−2.56	−0.05
	Canopy Height 50	0.53	−0.22	1.29	0.75	0.13	1.38
	Midstory 250	1.18	−0.03	2.40	−0.54	−1.24	0.17
Settlement	Stream	−0.65	−0.86	−0.44	0.20	0.05	0.35
	Canopy Variation 500	0.69	0.48	0.90	−0.34	−0.48	−0.19
	Canopy Height 100	0.47	0.23	0.69	0.13	−0.01	0.26
	Understory 500	0.88	0.57	1.18	−0.38	−0.62	−0.13
Vacancy	Canopy Height 50	−0.09	−0.30	0.11	−0.43	−0.62	−0.23
	Midstory 250	−0.88	−1.15	−0.61	0.36	0.19	0.52
	Dry Oak	1.29	0.71	1.87			

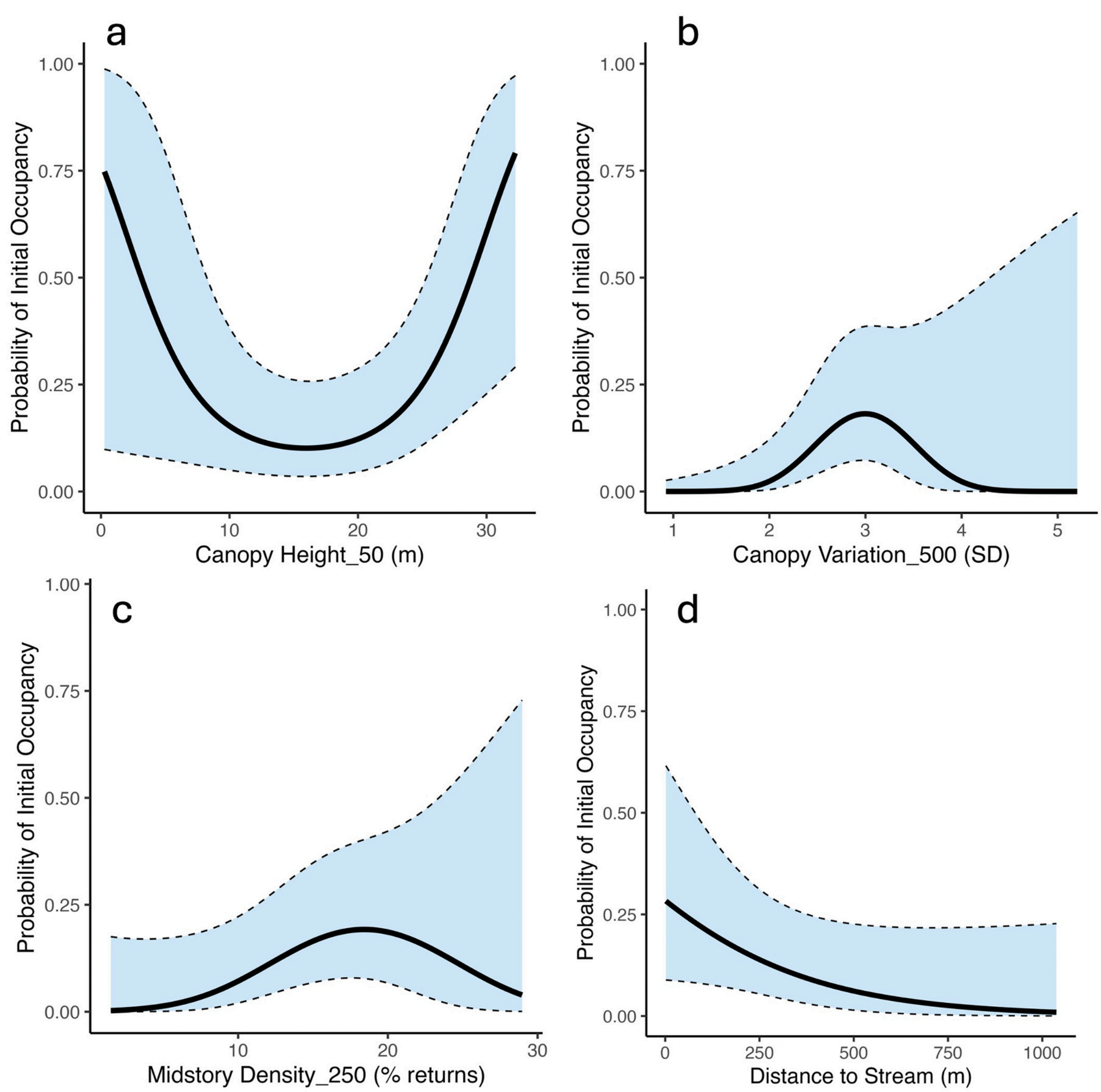

Fig. 2. The effect of (a) canopy height, (b) canopy variation, (c) midstory density, and (d) distance to the nearest stream on probability of initial occupancy of Wood Thrush at two study areas in central Pennsylvania. All sampling locations were surveyed between 20 May and 08 July 2020 and 2021 using autonomous recording units.

(500 m), understory density (500 m), and distance to stream whereby daily probability of settlement was ~14 % within 10 m of a stream and ~3 % 500 m from a stream. The quadratic effect of canopy height (100 m) was also included in the best model for settlement but overlapped 0 (Fig. 3). Daily probability of vacancy was best explained by significant quadratic effects of canopy height (50 m) and midstory density (250 m), and an effect of dry oak whereby dry oak forest communities had significantly higher (49 %) vacancy probability than all other forest community types (21 %) (Fig. 4).

Canopy height was lowest (x¯ =8.5 m, SD=9.2) in overstory removal stands 4–10 years post-harvest and highest in mature stands >25 years since harvest (x¯=24.3 m, SD=6.2; Table 4.). Canopy variation was greatest in stands 0–3 years post-harvest (x¯=8.7 sd, SD=4.0) and lowest in mature stands (x¯=2.3, SD=2.0). The highest understory density occurred in overstory removals 4–10 years post-harvest (x¯=10.7 % of LiDAR returns, SD=7.7) and the lowest understory density occurred in recent shelterwoods 0–3 years post-harvest (x¯=2.2 % of LiDAR returns, SD=3.0). Midstory density was highest in overstory removals 11–25 years post-harvest (x¯=18.3 % of LiDAR returns, SD=10.6) and lowest in overstory removals 0–3 years post-harvest (x¯=1.7 % of LiDAR returns, SD=4.2).

Based on maps of LiDAR-derived forest structure, predicted initial occupancy was lowest in mature forest (x¯= 0.01, SD=0.03) and within 500 m of stands 0–3 years post overstory removal (x¯ =0.02; SD=0.03; Fig. 5; Table 5). Initial occupancy was highest within 500 m of overstory removals 4–10 years (x¯ =0.06, SD=0.09) and 11–25 years (x¯ =0.04, SD=0.07) post-harvest (Fig. 5). Predicted daily probability of settlement was lowest in mature stands > 25 years post-harvest (x¯ =0.01, SD=0.01) and highest in 4–10 year old overstory removal harvests (x¯ =0.02 SD=0.02). Predicted daily probability of vacancy was highest in shelterwoods 0–3 years post-harvest (x¯ =0.48, SD=0.18) and lowest in overstory removals 11–25 years post-harvest (x¯ =0.30, SD=0.14).

4. Discussion

Increasingly species-habitat relationships are understood to be dynamic, in that they shift over time (*e.g.*, over the course of a breeding season). For songbirds, dynamic occupancy patterns have been suggested to reveal movement towards areas of higher habitat quality (Betts et al., 2008, McClure and Hill, 2012). As such, studies that account for

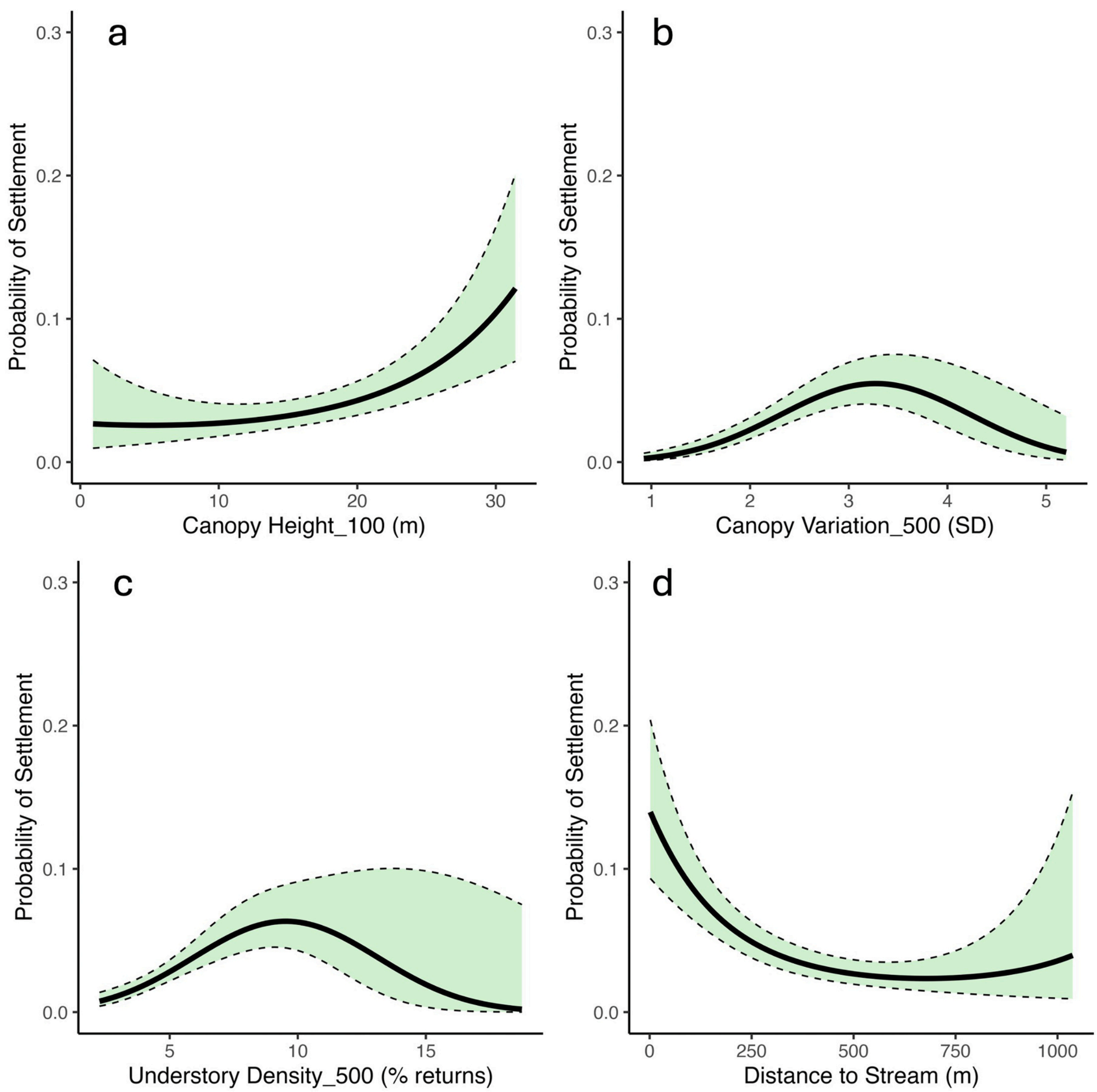

Fig. 3. The effect of canopy height (a) canopy variation (b), understory density (c) and distance to the nearest stream (d) on daily probability of settlement by Wood Thrush at two study areas in central Pennsylvania. All sampling locations were surveyed between 20 May and 08 July 2020 and 2021 using autonomous recording units.

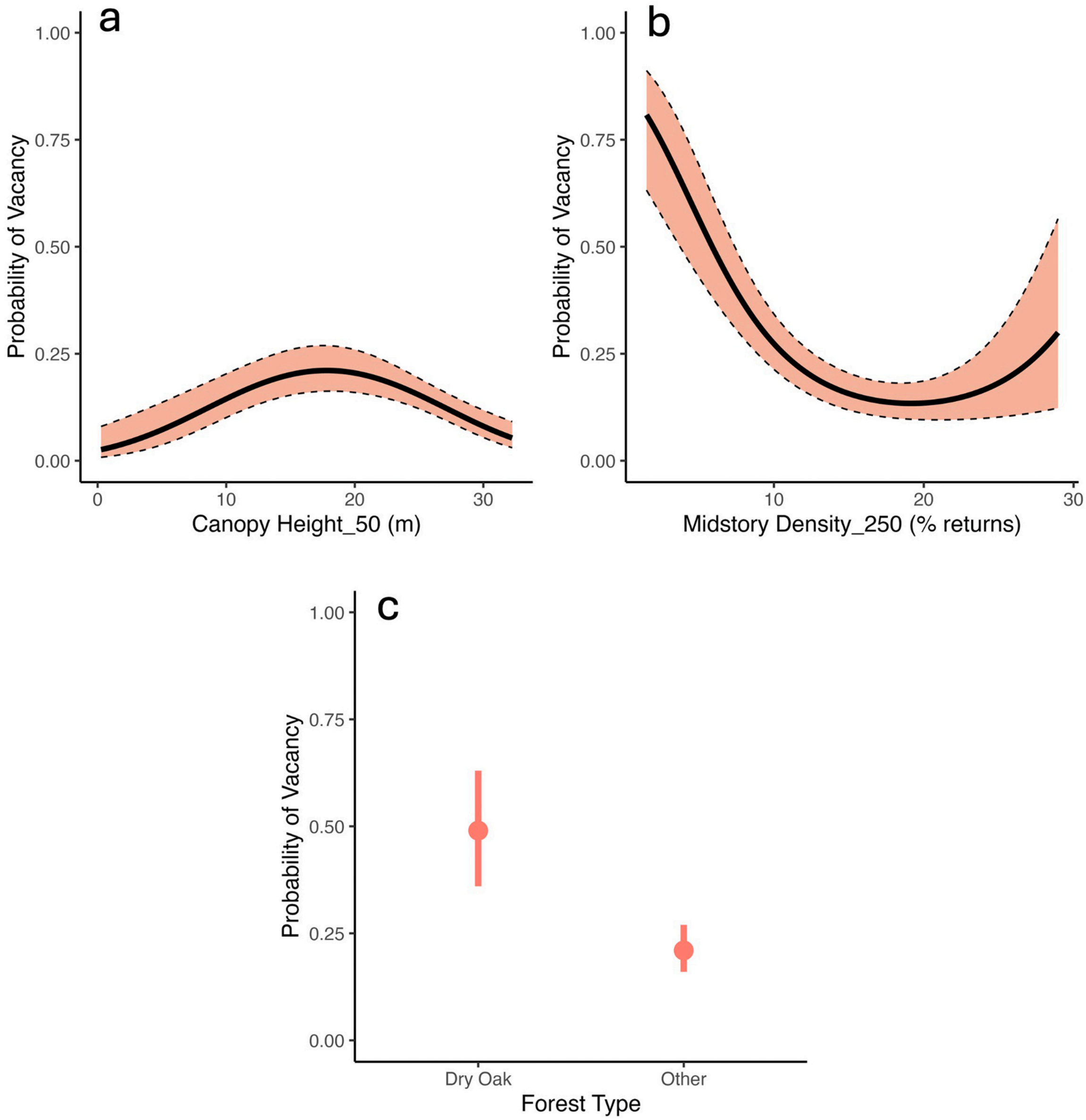

Fig. 4. The effect of canopy height (a) and midstory density (b) and forest community type (c) on the daily probability of site vacancy by Wood Thrush at two study areas in central Pennsylvania. Only dry oak was selected in the best model so there is no predicted difference between the other three forest community types, thus they are combined into "other". All sampling locations were surveyed between 20 May and 08 July 2020 and 2021 using autonomous recording units.

Table 4
Mean and standard deviation values for all LiDAR covariates summarized by forest age-classes and treatment types.

Treatment/ Age-class	Canopy Height	Canopy Variation	Understory Density	Midstory Density
OR 0–3	9.8 (11.1)	8.7 (4.0)*	5.1 (6.2)	1.7 (4.2)^
OR 4–10	8.5 (9.2)^	6.5 (3.8)	10.7 (7.7)*	5.8 (7.2)
OR 11–25	15.6 (6.2)	3.5 (2.2)	6.7 (4.5)	18.3 (10.6)*
SW 0–3	23.7 (7.2)	3.7 (3.6)	2.2 (3.0)^	3.4 (5.1)
Mature >25	24.3 (6.2)*	2.3 (2.0)^	4.2 (3.6)	10.2 (7.4)

^Lowest mean value of each LiDAR-derived forest structure covariate. *Highest mean value of each LiDAR-derived forest structure covariate

possible within-season movements could provide more complete evaluations of habitat quality. Our study revealed that Wood Thrush occupancy in actively managed forest landscapes was dynamic throughout the breeding season, but overall occupancy in both landscapes remained consistent, indicating no apparent movement of Wood Thrush into or out of either landscape (Fig. S6). While per point settlement of previously unoccupied sites was relatively low, it was highest along streams adjacent to recently managed stands as a result of greater understory (1–4 m) density and canopy variation in these areas created by both the shorter complex canopy of managed sites and the tall well-developed canopy of productive streamside sites (Table 4). Settlement was also higher in sites with greater understory density aligning with the species' well-documented nest site selection (Hoover and Brittingham, 1998, Parkhill, 2021); thus, our results support the pattern, found by others, of forest birds moving towards areas of higher habitat quality during the breeding period (Betts et al., 2008, McClure and Hill, 2012). Forest management had the most notable effects on site vacancy, whereby Wood Thrush vacated forest managed within the past 11–25 years at lower rates than other areas (Table 5), indicating that they can provide stable, high-quality habitat for the species. Our results highlight the importance of vegetation structure created by even-aged forest management for creating and maintaining high-quality habitat for Wood Thrush throughout the breeding season.

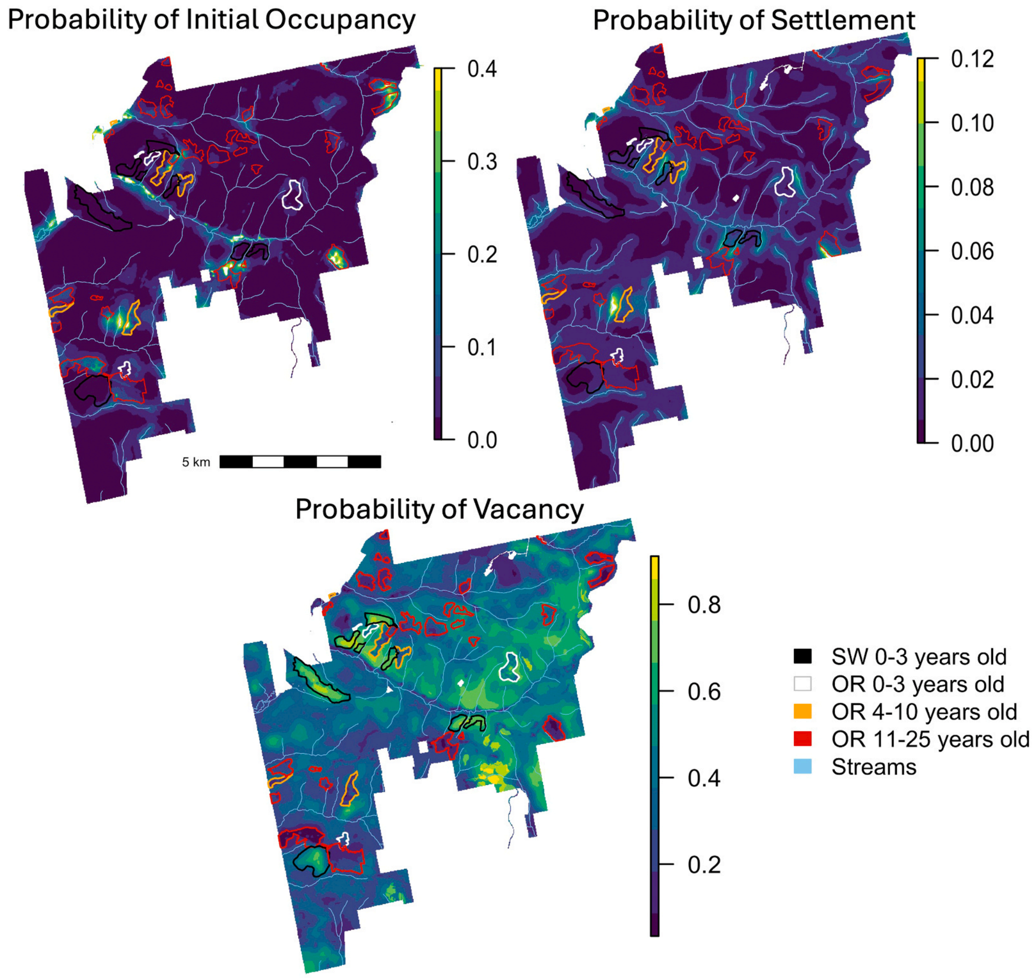

Fig. 5. Spatially explicit predictions of probability of initial occupancy (top left), daily probability of settlement (top right), and daily probability of vacancy (bottom) by Wood Thrush at SGL 25 in north central Pennsylvania. All surveys were conducted by passive acoustic monitoring from 20 May to 08 July 2020 and 2021. Sites managed using even-aged management are highlighted to show relative effects of management on Wood Thrush occupancy dynamics. Shelterwood harvests 0–3 years post-management (SW 0–3) are outlined in black, overstory removal harvests 0–3 years post-management (OR 0–3) are outlined in white, overstory removal harvests 4–10 years post-management (OR 4–10) are outlined in orange, and overstory removal harvests 11–25 years post-management (OR 11–25) are outlined in red.

Table 5
Means and standard deviations of predicted parameter values summarized by forest age-classes and treatment types within SGL 25. Values for initial occupancy and settlement were summarized within 500 m of overstory removal (OR) and shelterwood (SW) harvests because this scale was used for covariates in the occupancy and settlement submodels of the top model. Values for vacancy were summarized within 250 m of overstory removal (OR) and shelterwood (SW) harvests because this scale was used for covariates in the vacancy submodel of the top model.

Treatment Age	Initial Occupancy	Settlement	Vacancy
OR 0–3	0.02 (0.03)	0.01 (0.01)	0.48 (0.18)
OR 4–10	0.06 (0.09)	0.02 (0.02)*	0.41 (0.18)
OR 11–25	0.04 (0.07)	0.02 (0.01)	0.30 (0.14)^
SW 0–3	0.04 (0.07)	0.02 (0.01)	0.48 (0.18)
Mature >25	0.01 (0.03)^	0.01 (0.01)^	0.40 (0.14)

^Lowest mean predicted value of each parameter. *Highest mean predicted value of each parameter

Our results indicate that local landscapes (*i.e.,* 500-m radius) with recent (within 25 years) even-aged forest management provide high quality habitat for Wood Thrush as evidenced by relatively high initial occupancy and settlement rates. In line with our prediction, throughout the breeding season Wood Thrush predominantly settled in riparian sites in landscapes that had slightly older forest management history, such that managed stands in the surrounding landscape were often >3 years post even-aged management and, as a result, contained more advanced regeneration. This pattern was driven by the importance of understory density at the 500-m scale in predicting rates of settlement and the ability of even-aged management 4–25 years old to create this understory density. Wood Thrush are well known to occupy streamside sites Jirinec et al., 2016, Larkin et al., 2024) and occur at higher abundance along streams in Pennsylvania (Fiss, 2023). However, higher occupancy in local landscapes with recent management history is less reported (*e.g.*, Schlossberg et al., 2018). In fact, traditionally the species is described to occupy mature forest with well-developed canopies (Evans et al., 2011). Still, it has long been speculated that Wood Thrush may prefer landscapes characterized by management that results in a variety of forest age-classes (Ahlering and Faaborg, 2006). Our results lend support for this hypothesis. There are several reasons why Wood Thrush move towards areas with recent active forest management in the landscape. First, Wood Thrush typically nest within 1–4 m of the ground so density in this layer likely provides abundant nesting opportunities and nest concealment from predators. Further, Wood Thrush adults are known to use stands of early-successional forest during the post-breeding period, where they undergo molt prior to migration; and the use of these forest types appears to improve their condition compared to unharvested areas

(Vega Rivera et al., 1999, Vitz and Rodewald, 2006, Stoleson, 2013). Finally, immature Wood Thrush select for early-successional vegetation cover after independence from adult care (Anders et al., 1998, Vega Rivera et al., 1998). Therefore, adults may prefer areas closer to recent even-aged management because it improves nesting and survival outcomes.

Effects of even-aged forest management at the forest stand scale were most apparent on the likelihood of Wood Thrush vacancy, where two important trends emerged. First, Wood Thrush readily vacated sites that were managed just within the past 3 years, including both shelterwood harvest and overstory removals, although occupancy was relatively low in these treatment types to begin. Second, stands in the early stem-exclusion stage of development (11–25 years old) had the lowest rates of vacancy. Both relationships are apparently mediated by the density, or lack thereof of vegetation density within 4–10-m strata. Specifically, stands managed within the past 3 years likely have very little vegetation structure in the 4–10-m strata whereas stands in 11–25 years post overstory removal likely have a dense canopy of saplings that occupies the 4–10-m layer (*i.e.*, early stem-exclusion stage; Duguid et al., 2016; Table 4). As Wood Thrush are known to vacate sites after failed nesting attempts (Vega Rivera et al., 1999, CJF personal obs.), we suspect that high rates of nest failure in areas lacking vegetation density within the 4–10 m strata was the primary driver of vacancy rates. Indeed, previous research has found that dense midstory or overhead concealment is associated with Wood Thrush nest success (Hoover and Brittingham, 1998, Fiss, 2023), both of which are lacking in recently harvested sites, but abundant in sites 11–25 years post-harvest (whether shelterwood or overstory removal). This result could explain why some studies have found relative high Wood Thrush nest survival in even-aged harvests (Dellinger et al., 2007) and higher nest success in landscapes with even-aged forest management (Fiss, 2023).

Another explanation for apparent movement is due to tracking of prey availability. For instance, Klemp (2003) suggested that Grey Wagtails (*Motacilla cinerea*) shifted territories as a result of limited food supply in initial breeding territories. We suspect that high rates of settlement near streams could be due to increased availability of foraging sites and prey. In fact, Wood Thrush preferred prey items (Oligochaeta and Coleoptera larvae) were found to be more abundant in streamside sites in Virginia (Jirinec et al., 2016), and Wood Thrush were less likely to abandon floodplain forests in Georgia compared to upland forest (McClure and Hill, 2012). Alternatively, limited prey availability may have driven high rates of vacancy in the dry oak community type. Wood Thrush are known to forage almost exclusively on the ground and in areas with dense leaf litter layers that maintain high moisture levels (Evans et al., 2011). The dry oak community tends to occur on ridgetop sites which may be prone to soil moisture loss as the breeding season progresses. Further, the dry oak community often has dense shrubby ground cover layers and limited leaf litter. Thus, site conditions of dry oak communities may have limited prey and foraging opportunities for Wood Thrush.

Our findings support the idea that static species-habitat relationships can be a questionable assumption, even during relatively short portions of the life-cycle, such as a breeding season (McClure and Hill, 2012, Frey et al., 2016). Apparent within-season movement was also identified in Black-throated Blue Warblers in New Hampshire (Betts et al., 2008), and occurrence of 27 of 30 forest bird species was better explained by dynamic occupancy models than static occupancy models in Georgia (McClure and Hill, 2012). Still, static occupancy models appear to be the norm when evaluating species-habitat relationships (Rota et al., 2009, Valente et al., 2024). One reason this may be the case is that dynamic models require greater sampling intensity, with both primary and secondary periods required to estimate all detectability and movement parameters, which can be logistically difficult to obtain (Betts et al., 2008, Dail and Madsen, 2013). We demonstrate that ARUs with human-validated machine-learning outputs provide an efficient means of obtaining robust data sets necessary for dynamic occupancy modeling, while requiring a fraction of the field effort. We suggest that other researchers adopt similar methods to improve habitat quality assessments of songbirds.

While settlement and vacancy patterns derived from dynamic occupancy models may provide a better proxy for habitat quality compared to traditional occupancy, it is important to consider the drawbacks associated with the inability to distinguish individual identities of birds. For instance, we cannot be certain that low vacancy probability at a site is due to the same individual(s) remaining at the site or whether different individuals are moving in and forcing out others. Likewise, it is not possible to distinguish whether individuals that settle in new locations were previously forced out of higher quality habitat by dominant, more fit, individuals. In the latter case, settlement patterns could be associated with lower quality habitat. Data derived from individually marked and tracked individuals would help determine the relative occurrence and extent of these potential patterns. Ultimately, beyond estimating patterns of settlement and vacancy, understanding reproductive success and survival of individuals in relation to forest management would provide a more complete understanding of management's effect on Wood Thrush habitat quality.

5. Conclusion

In regions with moderate to high levels of mesic forest communities, even-aged forest management can promote landscapes with high quality habitat for Wood Thrush. We recommend that land managers consider landscape context when implementing even-aged forest management for the benefit of Wood Thrush. For instance, implementing even-aged regeneration methods would be most beneficial to Wood Thrush in landscapes that have riparian forest characterized by tall canopies and substantial under- and midstory complexity, while maintaining appropriate riparian buffers. In landscapes with limited or no riparian forest, even-aged management would be most beneficial when the mature forest matrix has well-developed under and midstory layers. In these scenarios, treatments aimed at improving mature forest resilience and complexity within the surrounding landscape would likely complement even-aged management. For instance, managers may need to control invasives and other undesirable species (*e.g.*, barberry [*Berberis* spp.], hay scented fern [*Dennstaedtia punctilobula*], mountain laurel, etc.) that suppress desired plant regeneration using chemical or mechanical treatments. When applying even-aged management to benefit Wood Thrush, managers should be especially cognizant of maintaining legacy structures that could benefit the species. Specifically, all overstory removal harvests in our study contained scattered residual trees resulting in a residual basal area of ~10–20 m^2 / ha and Dellinger et al. (2007) found that Wood Thrush nesting in even-aged harvest often placed nests near residual trees. Additionally, maintaining patches of understory (1–4 m) and midstory (4–10 m) structure, especially those with preferred nesting substrates (*e.g.*, witch hazel, American beech, eastern hemlock [*Tsuga canadensis*]), will likely improve the chance of Wood Thrush using stands and surrounding areas after management. Finally, in areas prone to excessive deer browsing, exclosure fencing will almost certainly create the site- and landscape-level vegetation conditions preferred by Wood Thrush more rapidly than stands that are unfenced (Parker et al., 2020). Overall, our finding that Wood Thrush habitat quality can be improved by even-aged management, especially in landscapes containing both recent and older management, supports the idea that managing forests to promote a mosaic of even-aged stands in varying age-classes is beneficial for the species (Anders et al., 1998, Ahlering and Faaborg, 2006, Fiss, 2023).

CRediT authorship contribution statement

Cameron J. Fiss: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Jeffery L. Larkin: Writing – review & editing, Funding acquisition, Supervision. **Lauren Chronister:** Writing – review & editing, Methodology, Data curation. **Justin Kitzes:** Writing – review & editing, Supervision, Investigation, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122974.

Data Availability

Data will be made available on request.

References

Ahlering, M.A., Faaborg, J., 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk 123 (2), 301–312.
Anders, A.D., Faaborg, J., Thompson III, F.R., 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115 (2), 349–358.
Bakermans, M.H., Rodewald, A.D., Vitz, A.C., 2012. Influence of forest structure on density and nest success of mature forest birds in managed landscapes. The Journal of Wildlife Management 76 (6), 1225–1234.
Bertin, R.I., 1977. Breeding habitats of the Wood Thrush and veery. Condor 79, 303–311.
Betts, M.G., Rodenhouse, N.L., Scott Sillett, T., Doran, P.J., Holmes, R.T., 2008. Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. Ecography 31 (5), 592–600.
Burnham, K.P., Anderson, D.R., Burnham, K.P., Anderson, D.R., 1998. Practical Use of the Information-theoretic Approach. Springer New York, pp. 75–117.
Dail, D., Madsen, L., 2013. Estimating open population site occupancy from presence–absence data lacking the robust design. Biometrics 69 (1), 146–156.
DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. For. Ecol. Manag. 185 (1-2), 179–191.
Dellinger, R.L., Wood, P.B., Keyser, P.D., 2007. Occurrence and nest survival of four thrush species on a managed central Appalachian forest. For. Ecol. Manag. 243 (2-3), 248–258.
Duguay, J.P., Wood, P.B., Nichols, J.V., 2001. Songbird abundance and avian nest survival rates in forests fragmented by different silvicultural treatments. Conserv. Biol. 15 (5), 1405–1415.
Duguid, M.C., Morrell, E.H., Goodale, E., Ashton, M.S., 2016. Changes in breeding bird abundance and species composition over a 20 year chronosequence following shelterwood harvests in oak-hardwood forests. For. Ecol. Manag. 376, 221–230.
Evans, M., Gow, E., Roth, R.R., Johnson, M.S., Underwood, T.J., 2011. Wood Thrush (Hylocichla mustelina). birds North Am. Online (246).
Fisher, G.B., Elmore, A.J., Fitzpatrick, M.C., McNeil, D.J., Atkins, J.W., Larkin, J.L., 2024. Mapping recent timber harvest activity in a temperate forest using single date airborne LiDAR surveys and machine learning: lessons for conservation planning. GIScience Remote Sens. 61 (1), 2379198.
Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.
Fiss, C., 2023. Avian Community and Species-Specific Response to Management Targeting Improvement of Forest Age-Class Diversity (Doctoral dissertation, State University of New York College of Environmental Science and Forestry).
Frey, S.J., Hadley, A.S., Betts, M.G., 2016. Microclimate predicts within-season distribution dynamics of montane forest birds. Divers. Distrib. 22 (9), 944–959.
Goodale, E., Lalbhai, P., Goodale, U.M., Ashton, P.M.S., 2009. The relationship between shelterwood cuts and crown thinnings and the abundance and distribution of birds in a southern New England forest. For. Ecol. Manag. 258 (3), 314–322.
Gordon Jr, A.B., Drummey, D., Tur, A., Curtis, A.E., McCumber, J.C., Akresh, M.E., DiRenzo, G.V., 2024. Long-term monitoring reveals management effects on prairie warbler colonization, local extinction, and detection in a Massachusetts pine barren. Northeast. Nat. 31 (3), 418–434.
Graboski, L.E., Steiner, K.C., McDill, M.E., Finley, J.C., 2020. Predicting oak regeneration success at the stem exclusion stage of stand development in upland hardwood forests. For. Ecol. Manag. 465, 118093.
Hijmans, R.J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Hijmans, M.R.J., 2015. Package 'raster'. R. Package 734, 473.
Hill, A.P., Prince, P., Piña Covarrubias, E., Doncaster, C.P., Snaddon, J.L., Rogers, A., 2018. AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. Methods Ecol. Evol. 9 (5), 1199–1211.
Hoover, J.P., Brittingham, M.C., 1998. Nest-site selection and nesting success of Wood Thrushes. Wilson Bull. 375–383.
Jirinec, V., Isdell, R.E., Leu, M., 2016. Prey availability and habitat structure explain breeding space use of a migratory songbird. Condor Ornithol. Appl. 118 (2), 309–328.
Johnson, M.D., 2007. Measuring habitat quality: a review. Condor 109 (3), 489–504.
Keyser, P.D., Fearer, T., Harper, C.A. (Eds.), 2016. Managing oak forests in the eastern United States. CRC Press.
King, D.I., DeGraaf, R.M., 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. For. Ecol. Manag. 129 (1-3), 227–235.
King, D.I., Schlossberg, S., 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. For. Ecol. Manag. 324, 186–195.
Klemp, S., 2003. Altitudinal dispersal within the breeding season in the Grey Wagtail Motacilla cinerea. Ibis 145 (3), 509–511.
Knight, E.C., Hannah, K.C., Foley, G.J., Scott, C.D., Brigham, R.M., Bayne, E., 2017. Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. ACE 12 (2), 14.
Lambert, J.D., Leonardi, B., Winant, G., Harding, C., Reitsma, L., 2017. Guidelines for managing Wood Thrush and scarlet tanager habitat in the Northeast and Mid-Atlantic regions. High Branch Conservation Services, Hartland, VT.
Lapp, S., Stahlman, N., Kitzes, J., 2023a. A quantitative evaluation of the performance of the low-cost AudioMoth acoustic recording unit. Sensors 23 (11), 5254.
Lapp, S., Rhinehart, T., Freeland-Haynes, L., Khilnani, J., Syunkova, A., Kitzes, J., 2023b. OpenSoundscape: an open-source bioacoustics analysis package for Python. Methods Ecol. Evol. 14 (9), 2321–2328.
Larkin, J.T., Fiss, C.J., Parker, H.A., Tyree, M.C., Duchamp, J., Larkin, J.L., McNeil, D.J., 2024. Over the river and through the woods: multi-scale habitat associations of two at-risk bird species in riparian forests of the Central Appalachians. For. Ecol. Manag. 564, 121997.
Loehle, C., Miller, D.A., Kovach, A.I., Larsen-Gray, A.L., Akresh, M.E., McDonald, J.E., Kanter, J., 2024. Forest management is key for conserving biodiversity and providing ecosystem services in the United States. Forests 15 (12), 2087.
MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255.
MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84 (8), 2200–2207.
Mazerolle, M.J., Mazerolle, M.M.J., 2017. Package 'AICcmodavg'. R. Package 281, 1–220.
McClure, C.J., Hill, G.E., 2012. Dynamic versus static occupancy: how stable are habitat associations through a breeding season? Ecosphere 3 (7), 1–13.
McNeil, D.J., Fisher, G., Fiss, C.J., Elmore, A.J., Fitzpatrick, M.C., Atkins, J.W., Cohen, J., Larkin, J.L., 2023. Using aerial LiDAR to assess regional availability of potential habitat for a conservation dependent forest bird. For. Ecol. Manag. 540, 121002.
Morris, D.L., Porneluzi, P.A., Haslerig, J., Clawson, R.L., Faaborg, J., 2013. Results of 20 years of experimental forest management on breeding birds in Ozark forests of Missouri, USA. For. Ecol. Manag. 310, 747–760.
Newell, F.L., Rodewald, A.D., 2012. Management for oak regeneration: short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. J. Wildl. Manag. 76 (4), 683–693.
Nyland, R.D., 2016. Silviculture: Concepts and Applications. Waveland Press.
Osborne, P.E., Alvares-Sanches, T., White, P.R., 2023. To bag or not to bag? How AudioMoth-based passive acoustic monitoring is impacted by protective coverings. Sensors 23 (16), 7287.
Palik, B.J., D'Amato, A.W., Franklin, J.F., Johnson, K.N., 2020. Ecological Silviculture: Foundations and Applications. Waveland Press.
Parker, H.A., Larkin, J.T., Heggenstaller, D., Duchamp, J., Tyree, M.C., Rushing, C.S., Larkin, J.L., 2020. Evaluating the impacts of white-tailed deer (Odocoileus virginianus) browsing on vegetation in fenced and unfenced timber harvests. For. Ecol. Manag. 473, 118326.
Parkhill, N., 2021. Using multi-scalar habitat modelling of Wood Thrush in central Pennsylvania to inform novel forest management.
Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data.
R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL ⟨https://www.R-project.org/⟩.
Rosenberg, K.V., Hames, R.S., Rohrbaugh, R.W., Barker Swarthout, S., Lowe, J.D., Dhondt, A.A., Jr. 2003. A land manager's guide to improving habitat for forest thrushes. The Cornell Lab of Ornithology..
Rota, C.T., Fletcher Jr,, R.J., Dorazio, R.M., Betts, M.G., 2009. Occupancy estimation and the closure assumption. J. Appl. Ecol. 46 (6), 1173–1181.
Roth, R.R., Johnson, R.K., 1993. Long-term dynamics of a Wood Thrush population breeding in a forest fragment. Auk 110, 37–48.
Roussel, J.R., Auty, D., Coops, N.C., Tompalski, P., Goodbody, T.R., Meador, A.S., Achim, A., 2020. lidR: an R package for analysis of airborne laser scanning (ALS) data. Remote Sens. Environ. 251, 112061.
Sauer, J.R., Link, W.A., Hines, J.E., 2022, The North American breeding bird survey, analysis results 1966–2021: U.S. Geological Survey data release, https://doi.org/10.5066/P9SC7T11.
Schlossberg, S., King, D.I., Destefano, S., Hartley, M., 2018. Effects of early-successional shrubland management on breeding Wood Thrush populations. J. Wildl. Manag. 82 (8), 1572–1581.
Stoleson, S.H., 2013. Condition varies with habitat choice in postbreeding forest birds. Auk 130 (3), 417–428.

Valente, J.J., Hutchinson, R.A., Betts, M.G., 2017. Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models. Methods Ecol. Evol. 8 (12), 1707–1716.
Valente, J.J., Jirinec, V., Leu, M., 2024. Thinking beyond the closure assumption: designing surveys for estimating biological truth with occupancy models. Methods Ecol. Evol. 15 (12), 2289–2300.
Vega Rivera, J.H., Rappole, J.H., McShea, W.J., Haas, C.A., 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100, 69–78.
Vega Rivera, J.V., McShea, W.J., Rappole, J.H., Haas, C.A., 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. Auk 116 (2), 458–466.
Vitz, A.C., Rodewald, A.D., 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. Biol. Conserv. 127 (4), 477–486.
Wang, Y., Lesak, A.A., Felix, Z., Schweitzer, C.J., 2006. A preliminary analysis of the response of an avian community to silvicultural treatments in the southern Cumberland Plateau, Alabama, USA. Integr. Zool. 1 (3), 126–129.
Zellweger, F., Braunisch, V., Baltensweiler, A., Bollmann, K., 2013. Remotely sensed forest structural complexity predicts multi species occurrence at the landscape scale. For. Ecol. Manag. 307, 303–312.