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Understanding Changes in Wood Thrush and Ovenbird Populations in Virginia—The Role of Forest Fragmentation and Connectivity

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Abstract

Aim: Yearly summaries of the North American Breeding Bird Survey (BBS) indicate that populations of many North American bird species are in decline. Determining the causes of these declines is the focus of much current research in avian conservation. Forest fragmentation has been linked to declines in populations of many species. In this study, the effects of forest fragmentation and connectivity as well as slope and physiographic features on two migratory bird species are explored. **Location:** This study area is Virginia, USA. **Taxon:** The species focused on are Wood Thrush (Hylocichla mustelina) and the Ovenbird (Seiurus aurocapilla). **Methods:** We used the Markov Chain Monte Carlo Generalized Linear Mixed Models (MCMCglmm) package with a Poisson distribution and a Bayesian data analysis model with a 95% probability interval. Using the Repeated Measures ANOVA, the independent and treatment variables included time at 3 different levels in 2001, 2006 and 2011; three different forest types—Core, Connected and Fragmented; 8 slope categories and 5 physiographic regions. **Results:** Results indicate that forest fragmentation has a significant impact on population sizes of Wood Thrush and Ovenbirds in Virginia and that recent changes in Virginia's landscape have had negative impacts on the populations of these bird species. Specifically, slope characteristics that influence rates of urbanization are correlated with changes in bird populations. The Coastal Plain region in Virginia contributes significantly to the populations of both the Wood Thrush and Ovenbird currently. **Main Conclusions:** Core forests areas in Virginia are in decline and this process affects the populations and distributions of Ovenbird and Wood thrush in the state.

Keywords

Fragmentation, Connectivity, Forests, Wood Thrush, Ovenbird,

Bird, Population

1. Introduction

Concerning biological diversity and conservation, [1] highlights two non-overlapping scientific paradigms: small population paradigm and declining population paradigm. Of these two, this study focuses on the latter which seeks to identify the processes by which populations are driven to extinction by agents external to them. The declining population paradigm is rooted in empiricism and therefore focuses on detecting, diagnosing and halting population decline [1]. The tenet of this study is that there is a tangible cause for the decline in populations of biological species and that probing reveals this cause. Forest fragmentation is identified as a probable agent of species decline [2] and therefore forms a key part of this study.

Forest fragmentation not only affects population densities of forest bird species, but also affects their reproduction and dispersal [3]. Forest fragmentation can impact bird species negatively by reducing food resources available to birds as a result of a reduction in core forest patch sizes. Reduction in food resources for birds also has a consequent negative impact on their fecundity, causing a decline in their numbers within a particular area [4] [5]. Forest breeding birds such as Wood Thrush and Ovenbird species, with particular preference for core forest areas, are most negatively affected by forest fragmentation.

The Wood Thrush (*Hylocichla mustelina*) breeds in North America, migrating to Central America during the winter [6]. Recently, Wood Thrushes have become a species of conservation concern because of their narrow tolerance of certain microclimatic conditions and their preference for the interior of moist deciduous forests, a forest condition that is fast declining due to timber harvesting activities. Wood Thrushes are highly sensitive to forest fragmentation due to increased nest predation and brood parasitism by the Brown-headed Cowbird [7] in forest fragments.

The Ovenbird (*Seiurus aurocapilla*) is also a fragmentation-sensitive Neotropical migrant [8] with a preference for mature deciduous or mixed forests with closed canopies and sparse understory. Pairing success of male Ovenbirds is lower in forest edges and small forest patches, compared to areas with large core forest patches [9]. Numbers of Ovenbirds are also dependent on the surrounding vegetation patterns as small forest patches with surrounding agricultural lands have fewer Ovenbirds compared with large contiguous forest patches [9] [10]. Mechanisms of forest fragmentation effects on Ovenbirds are not completely understood as nest predation rates of Ovenbirds in large contiguous forests and in fragmented forests have been shown to be similar in certain studies [9] [11] [12].

There are specific threshold sizes for the patches formed by habitat fragmen-

tation, beyond which particular species within the habitats cannot survive [13]. The relationship between habitat fragmentation and population density of the Wood Thrush and Ovenbird within Virginia can be used to identify impacts of forest fragmentation on the species in the state. These two migratory bird species were specifically chosen for this study because while they are both known to possess the ability to cross forest gaps [14], there have also been contrasting reports on how forest fragmentation driven by inter-patch distances, negatively affects their abundance [15] [16]. This presents a confusing theory on how both birds are influenced by forest fragmentation, driving a curiosity about the impact of forest patch sizes and patch connectivity on their population.

Given that human development is continuing, effective planning and management are needed to conserve biodiversity by determining minimum-area breeding requirements for Neotropical migrants such as Wood thrush and Ovenbird, and to identify landscape and vegetation features that support viable breeding populations [17] [18]. There is an opportunity to compare populations of these bird species with changing forested land areas over the years to identify correlation and subsequent impacts on the species. This research therefore aims to determine the impact that changes in forested land areas in Virginia, have had on Wood Thrush and Ovenbird populations.

2. Material and Methods

2.1. Study Area

Out of the more than 900 bird species that can be found in North America, Virginia provides natural habitat for about 400. Virginia serves as either a permanent or transitory home to approximately 45% of the bird species in America, out of which Virginia's Wildlife Action Plan has identified about 96 species to have declining populations [19]. Virginia's land cover is approximately 60% forestland, including both pine and hardwood forests. Mountainous areas, especially in the Appalachian region, contain tracts of various coniferous species and hardwoods such as hickory and oak. Virginia's very high avian diversity is due to varied habitats found in its varied physiographic regions—Coastal Plain, Piedmont, Appalachian Plateau, Blue Ridge and Valley and Ridge [20]. Virginia's oak-hickory and oak-pine communities offer favorable habitat for both Ovenbirds and Wood Thrush.

2.2. Breeding Bird Survey

Initiated in 1966, the North American Breeding Bird Survey (BBS) is an international monitoring program, jointly coordinated by the USGS Patuxent Wildlife Research Center and the Canadian Wildlife Service, to track the status and trends of North American bird populations. With 88 survey routes in Virginia, buffers with differing radii were created around each of them and the numbers of birds detected at each survey route in 2001, 2006 and 2011, were used in this analysis.

2.3. Data Analysis

Five buffers of different radii were created around each survey route; 25 miles, 20 miles, 15 miles, 5 miles and 1 mile (Figure 1). Three National Land Cover Dataset satellite images with a 30 by 30 m resolution were used, each representing 2001, 2006 and 2011. Forest patches in Virginia were classified as either "Core", "Connected" or "Fragmented" depending on neighboring pixels surrounding forest pixels (Figure 2). "Core" forests include pixels that are completely surrounded by other forest pixels while forest pixels surrounded by more than 60% but less than 100% forest pixels are labelled "Connected". "Fragmented" forest areas include forest pixels surrounded by less than 60% other forest pixels.

Virginia's topographic slopes were classified into 8 groups (Table 1), with 1 being the most gentle slope (between 0% and 2.5%) and 8 being very steep (above 60%). Virginia's five physiographic regions (Appalachian Plateaus, Blue Ridge, Valley and Ridge, Piedmont and Coastal Plain) were overlaid as a vector dataset (Figure 3) on each of the 5 maps of Virginia representing the 5 different buffer zones used in the study. Slope and physiographic regions were examined because of their potential to affect forest fragmentation and also influence Wood Thrush and Ovenbird populations.

Using the Repeated Measures ANOVA in the R software, the hypothesis that the population means of the wood thrush and ovenbird do not change between 2001 and 2011, was made. In this design, the independent variable is time and the different levels are 2001, 2006 and 2011. The treatment variables are three different forest types—Core, Connected and Fragmented; 8 slope categories and 5 physiographic regions. The Markov Chain Monte Carlo Generalized Linear Mixed Models (MCMCglmm) package with a Poisson distribution was used and a Bayesian data analysis model with a 95% probability interval was employed.

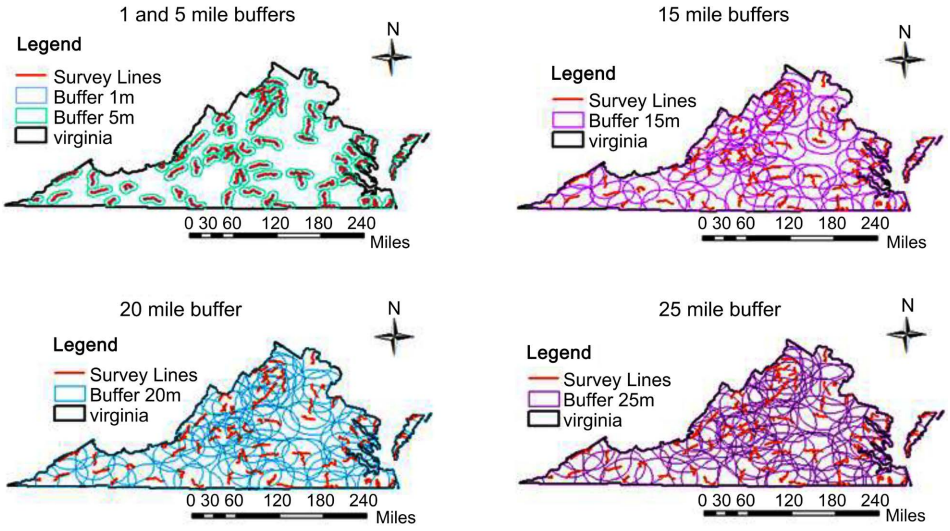

Figure 1. Map of Virginia showing survey routes and buffer zones created around them. While the 1 and 5 mile buffers have very lttle intersections, the 15, 20 and 25 mile buffers are more complicatedly intersected.

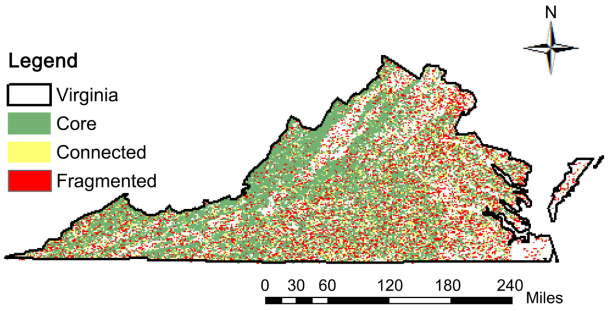

Figure 2. Map of Virginia in 2001 showing 3 forest classes; Core, Connected and Fragmented. Two other maps (not shown) showing the same forest classes were made for 2006 and 2011 to show forest fragmentation and connectivity.

Table 1. Topographic slope categories used in this analysis.

Slope Categories	Slope Percentage (%)
1	0 - 0.5
2	>0.5 - 2
3	>2 - 5
4	>5 - 9
5	>9 - 15
6	>15 - 30
7	>30 - 60
8	Over 60

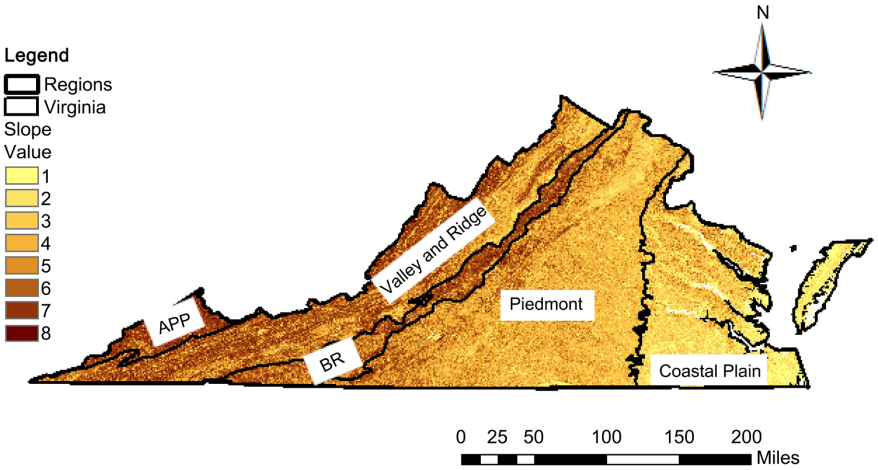

Figure 3. Map of Virginia showing the five physiographic regions (Appalachian Plateaus = APP, Blue Ridge = BR, Valley and Ridge, Piedmont and Coastal Plain) and 8 slope categories. Slope group 1 is very gentle and becomes steeper from 1 to 8 with 8 being the steepest.

Since all the treatment variables were calculated as percentages, they all add up to 100 and thus, one treatment of each variable had to be excluded from the model. Each treatment variable chosen for exclusion is based on a model selec-

tion from different combinations. Specifically, a deviance information criterion (DIC) is calculated from MCMCglmm with a lower DIC number identifying a better model. For the 3 forest types, only connected and fragmented forest types were included in the model because changes between 2001 and 2011 for these two were significant. These two forest types make up the research focus on forest fragmentation and connectivity. For the physiographic regions, a comparison of the combinations of ABCD, ABCE, ACDE, ABDE, and BCDE is made with Appalachian Plateau, Blue Ridge, Coastal Plain, Piedmont and Valley and Ridge represented by the letters A, B, C, D and E respectively. For the eight slope categories, the combinations of 1234567, 1234568, 1234578, 1234678, 1235678, 1245678, 1345678, and 2345678 are compared with each figure representing a slope category. The three year time periods and the 2 forest types are included in the model and run separately for Wood Thrush and Ovenbird multiple times, to identify which model has the lowest DIC. For the Ovenbird model, the model excluding the Appalachian Plateau and Slope category 3 had the lowest DIC and was therefore chosen. The model excluding the Appalachian Plateaus and Slope Category 2 was chosen for the Wood Thrush model. With the number of iterations, burnin and thinning set at 80,000, 10,000 and 10, respectively, the model was run with traceplots drawn for both fixed and random effects in the model.

3. Results

Between 2001 and 2011, populations of both Wood Thrush and Ovenbirds species have declined. On the average, the lowest numbers of Wood Thrush and Ovenbird species detected in each survey route have not gone any lower than previous years. However, the highest numbers detected in each survey route have varied considerably between 2001 and 2011 (**Figure 4**). The average number of Ovenbirds recorded per survey route in 2001 was approximately 13, compared to 12 in 2011. There is a more a drastic change among Wood Thrushes as the average number recorded per route in 2001 was 13 but declined to 7 by 2011.

Table 2 shows the significance of changes in forest fragmentation in Virginia between 2001 and 2011 in the various buffers. Whereas, changes in connected and fragmented forests are significant in the 15, 20 and 25 mile buffer radius, only connected forests are significant in the 5 mile buffer radius. Changes in core forests are not significant between 2001 and 2011. Generally, the trends are similar at all buffer sizes, with core forest declining and both connected and fragmented forest increasing (**Figures 5-9**), although these trends were statistically significant only for the latter two forest types at larger scale buffer sizes.

Using the 1 mile buffer radius, Ovenbird numbers were significantly lower in fragmented forest compared to other forest types, and significantly higher in the Coastal Plain physiographic region than in all the other regions (**Table 3**). Also, slope categories 2, 5 and 8 have negative relationships with Ovenbird numbers, whereas 1, 3, 4, 6 and 7 have positive relationships. Only the negative relationship with slope category 5 (9% - 15%) was significant. Ovenbird numbers did not differ significantly between time periods (**Table 3**). Wood Thrush abun-

dance was significantly lower in 2011 than in 2001 (Table 4). Within the 1 mile buffer radius, the only environmental variable that had a sizeable effect on Wood Thrush numbers was the slope category 4 variable (Table 4). Results using the 5 mile buffer were identical to those for the 1 mile buffer (Table 5 and Table 6).

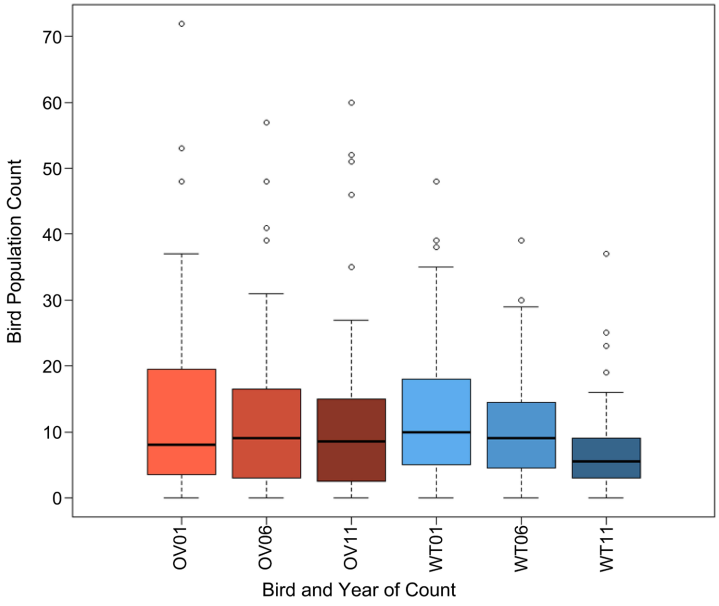

Figure 4. Populations of Ovenbirds and Wood Thrushes between 2001 and 2011. The red shades represent Ovenbird populations while the blue shades represent Wood Thrush populations. Between 2001 and 2011, the average number of individuals per survey route of Wood Thrush have declined.

Table 2. Changes in forest types from 2001 and 2011 in the different buffer regions.

BUFFER	FOREST TYPE	SIGNIFICANCE
1 mile	Core	0.7557
	Connected	0.7254
	Fragmented	0.7945
5 mile	Core	0.7318
	Connected	2.2e−16
	Fragmented	0.3778
15 mile	Core	0.6799
	Connected	2.2e−16
	Fragmented	5.503e−05
20 mile	Core	0.6644
	Connected	2.1e−16
	Fragmented	1.833e-06
25 mile	Core	0.5134
	Connected	2.3e−16
	Fragmented	2.431e−08

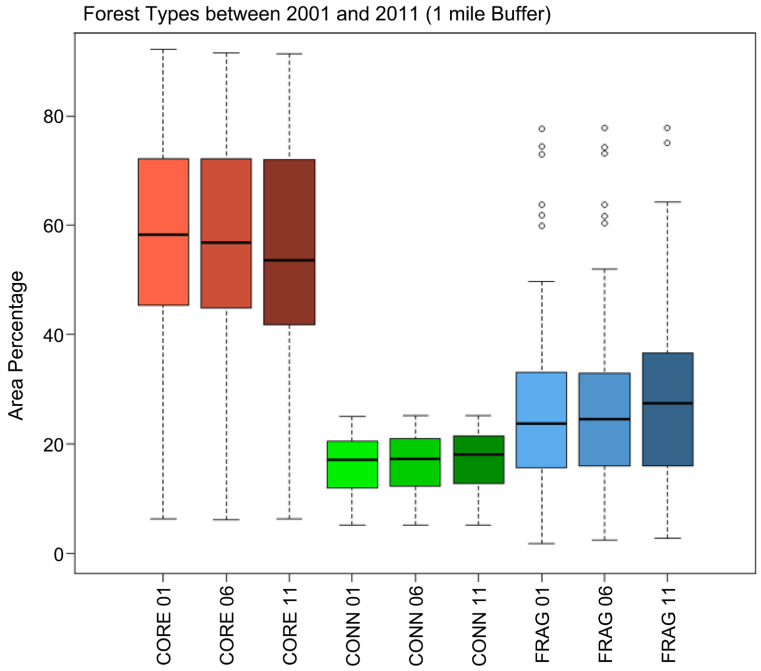

Figure 5. Changes in forest fragmentation in Virginia between 2001 and 2011 using a 1 mile buffer radius. While Core forest (red shades) generally declined between 2001 and 2011, both Connected (green shades) and Fragmented (blue shades) forest increased.

Table 3. Significant variables affecting Ovenbird populations in 1 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	2.312304	−3.61887	8.57661	0.447714
as.factor (2006)	−0.00619	−0.18303	0.166347	0.938571
as.factor (2011)	0.008696	−0.17462	0.201517	0.912571
Connected Forest	0.016077	−0.07289	0.113797	0.736571
Fragmented Forest	−0.05995	−0.09557	−0.01782	**0.002**
Blue Ridge	−0.00398	−0.01709	0.01071	0.564857
Coastal Plain	0.025478	0.003107	0.046312	**0.017429**
Piedmont	0.000837	−0.0157	0.020092	0.937429
Valley and Ridge	−0.00514	−0.02004	0.010505	0.489714
Slope1	0.024155	−0.02714	0.074963	0.343429
Slope2	−0.0481	−0.12879	0.036577	0.252
Slope4	0.065938	−0.06455	0.209657	0.336286
Slope5	−0.06706	−0.12555	−0.01046	**0.023143**
Slope6	0.012682	−0.08375	0.109229	0.792286
Slope7	0.033509	−0.02592	0.094083	0.263143
Slope8	−0.03242	−0.25165	0.185129	0.765143

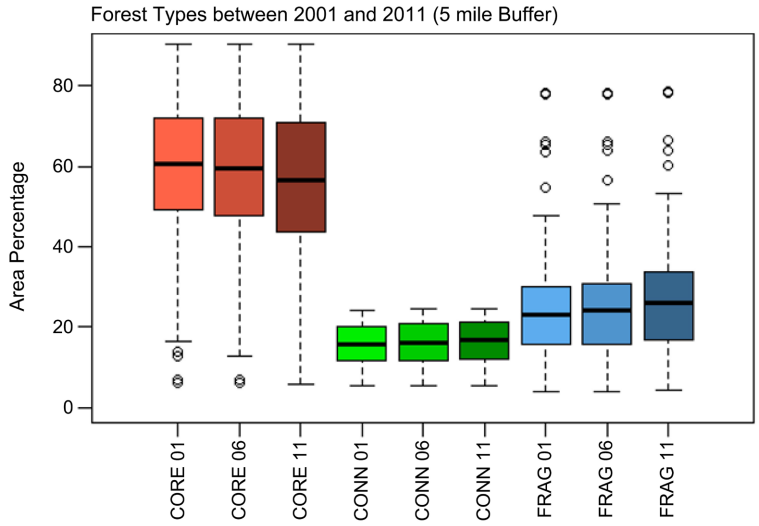

Figure 6. Changes in forest fragmentation in Virginia between 2001 and 2011 using a 5 mile buffer radius. While Core forest (red shades) declined between 2001 and 2011, both Connected (green shades) and Fragmented (blue shades) forest increased.

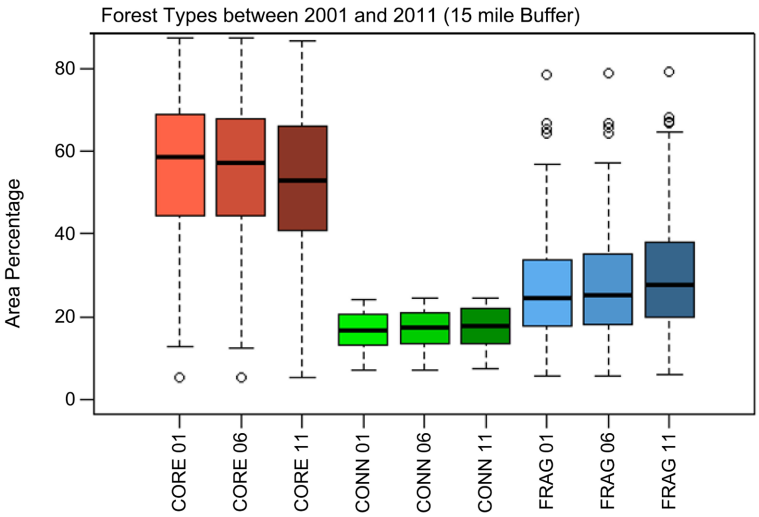

Figure 7. Changes in forest fragmentation in Virginia between 2001 and 2011 using a 15 mile buffer radius. While Core forest (red shades) declined between 2001 and 2011, both Connected (green shades) and Fragmented (blue shades) forest increased.

The Coastal Plain region had significantly higher numbers of Ovenbirds using the 15 mile buffer (Table 7), and again, Wood Thrush numbers were lower in year 2011 (Table 8). None of the variables analyzed had a significant relationship to Ovenbird numbers using the 20 mile buffer, and for Wood Thrush, the only significant variable again was the year, 2011 having significantly lower numbers than 2001 (Table 9 and Table 10). Using a 25 mile buffer radius around the survey routes, Wood Thrush numbers were significantly lower in year 2011 compared to 2001 (Table 11 and Table 12).

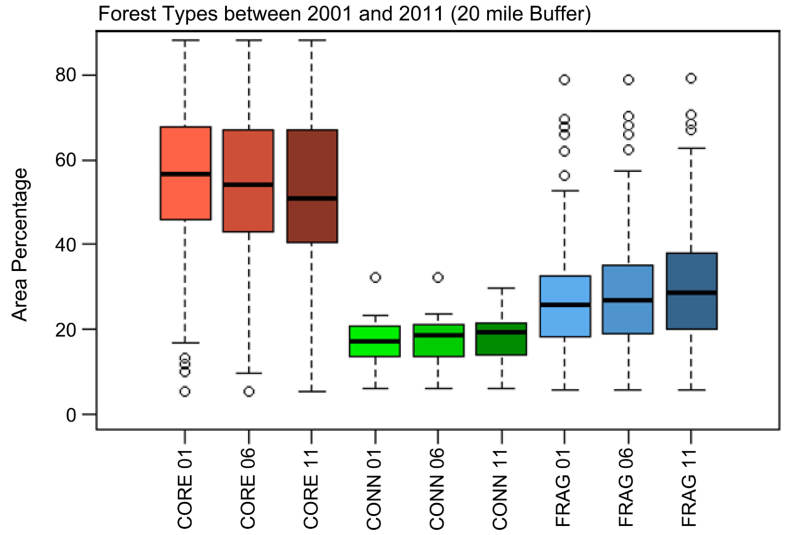

Figure 8. Changes in forest fragmentation in Virginia between 2001 and 2011 using a 20 mile buffer radius. While Core forest (red shades) declined between 2001 and 2011, both Connected (green shades) and Fragmented (blue shades) forest increased.

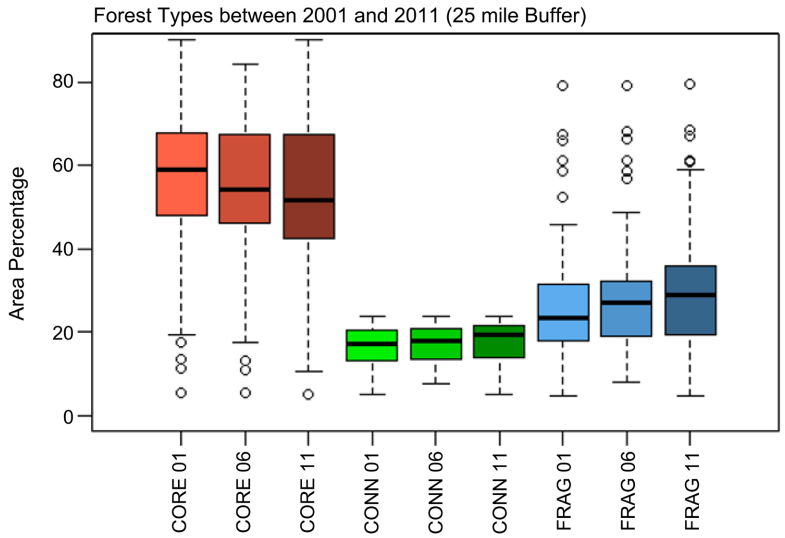

Figure 9. Changes in forest fragmentation in Virginia between 2001 and 2011 using a 25 mile buffer radius. While Core forest (red shades) declined between 2001 and 2011, both Connected (green shades) and Fragmented (blue shades) forest increased.

4. Discussion

Many studies such as [3] [21] hypothesized that population declines in migratory specialist species such as the Ovenbird and Wood Thrush, were caused by reduction and isolation of their breeding habitats. The three forest classes in this analysis, Core, Connected and Fragmented were categorized based on surrounding pixels and the connectivity of those pixels and as such, capture the forest conditions important to the Wood Thrush and Ovenbird.

Table 4. Significant variables affecting Wood thrush populations in 1 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	0.93577	−4.99489	6.933566	0.764
as.factor (2006)	−0.12754	−0.29067	0.047477	0.137143
as.factor (2011)	−0.5801	−0.75966	−0.37993	**0.000143**
Connected Forest	−0.07986	−0.17886	0.025016	0.130286
Fragmented Forest	0.017619	−0.02669	0.058456	0.413143
Blue Ridge	−0.00038	−0.01717	0.015061	0.960857
Coastal Plain	0.019287	−0.00554	0.04202	0.115143
Piedmont	0.007039	−0.01115	0.027924	0.472857
Valley and Ridge	0.005529	−0.01166	0.022874	0.507143
Slope1	−0.00413	−0.06304	0.053	0.897714
Slope3	−0.01805	−0.10938	0.0726	0.692857
Slope4	0.086443	−0.01114	0.192908	**0.091714**
Slope5	−0.04252	−0.14857	0.077147	0.454857
Slope6	0.02756	−0.04696	0.098633	0.457143
Slope7	0.013383	−0.06267	0.09279	0.726
Slope8	0.061436	−0.18213	0.285244	0.596571

Table 5. Significant variables affecting Ovenbird populations in 5 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	1.484353	−8.24956	10.85013	0.76171
as.factor (2006)	−0.01121	−0.18269	0.174739	0.9
as.factor (2011)	−0.01102	−0.22352	0.183804	0.91771
Connected Forest	0.028748	−0.08609	0.161252	0.65343
Fragmented Forest	−0.04882	−0.09575	−0.00208	**0.04486**
Blue Ridge	0.004797	−0.01596	0.025751	0.666
Coastal Plain	0.035169	0.007757	0.062695	**0.00743**
Piedmont	0.00395	−0.01841	0.028955	0.76571
Valley and Ridge	0.003563	−0.01886	0.024633	0.75629
Slope1	0.019131	−0.05742	0.098037	0.62514
Slope2	−0.07822	−0.24494	0.094051	0.36086
Slope4	0.099043	−0.11767	0.308045	0.36286
Slope5	−0.10699	−0.19288	−0.01996	**0.014**
Slope6	0.00806	−0.14285	0.157487	0.91314
Slope7	0.043097	−0.05303	0.14831	0.39686
Slope8	−0.01976	−0.34875	0.282534	0.91857

Table 6. Significant variables affecting Wood thrush populations in 5 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	4.125226	−5.62165	14.21436	0.41
as.factor (2006)	−0.13946	−0.32323	0.038706	0.134
as.factor (2011)	−0.52958	−0.73731	−0.31121	**<1e-04**
Connected Forest	−0.03348	−0.14655	0.081077	0.571
Fragmented Forest	−0.02275	−0.07091	0.02435	0.351
Blue Ridge	−0.00412	−0.02452	0.016293	0.681
Coastal Plain	0.007754	−0.02102	0.034935	0.583
Piedmont	0.000503	−0.02198	0.024129	0.96
Valley Ridge	0.001423	−0.02061	0.021977	0.898
Slope1	−0.0029	−0.11185	0.105045	0.955
Slope3	−0.05254	−0.21237	0.11144	0.512
Slope4	0.060702	−0.04611	0.172105	0.284
Slope5	−0.05155	−0.22741	0.126136	0.577
Slope6	−0.01197	−0.10921	0.083783	0.79
Slope7	−0.00373	−0.13764	0.127423	0.957
Slope8	−0.04415	−0.33095	0.229077	0.752

Table 7. Significant variables affecting Ovenbird populations in 15 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	3.467754	−10.0534	16.6905	0.6046
as.factor (2006)	−0.06856	−0.24851	0.098066	0.4509
as.factor (2011)	−0.15539	−0.36273	0.054095	0.1497
Connected Forest	0.084142	−0.06021	0.233762	0.2591
Fragmented Forest	−0.00302	−0.05952	0.055117	0.9191
Blue Ridge	0.01478	−0.02645	0.054716	0.4757
Coastal Plain	0.042148	−0.00211	0.086049	**0.0657**
Piedmont	0.018718	−0.0222	0.060505	0.3609
Valley and Ridge	0.022316	−0.01584	0.058204	0.24
Slope1	−0.06002	−0.16521	0.039055	0.2354
Slope2	−0.14053	−0.36105	0.081191	0.212
Slope4	−0.06048	−0.38022	0.244216	0.7097
Slope5	−0.04499	−0.18405	0.097581	0.5194
Slope6	−0.10631	−0.33892	0.12738	0.3674
Slope7	0.04625	−0.09564	0.190542	0.5174
Slope8	−0.10376	−0.41371	0.201941	0.4983

Table 8. Significant variables affecting Wood thrush populations in 15 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	−0.4672	−10.064	9.424537	0.9337
as.factor (2006)	−0.15083	−0.33825	0.034535	0.1103
as.factor (2011)	−0.56545	−0.77371	−0.34914	**<1e-04**
Connected Forest	−0.02856	−0.14554	0.093548	0.644
Fragmented Forest	−0.00731	−0.05442	0.04058	0.7691
Blue Ridge	0.018125	−0.01233	0.049467	0.2457
Coastal Plain	0.02916	−0.0047	0.063506	**0.0966**
Piedmont	0.015938	−0.01562	0.046651	0.3057
Valley and Ridge	0.017606	−0.01184	0.045381	0.2283
Slope1	0.01662	−0.10633	0.133381	0.7937
Slope3	−0.02133	−0.19763	0.138442	0.802
Slope4	0.096409	−0.03033	0.231501	0.14
Slope5	−0.0371	−0.23824	0.154172	0.712
Slope6	−0.00238	−0.12029	0.111673	0.9651
Slope7	0.046688	−0.08547	0.180339	0.5011
Slope8	0.015631	−0.18666	0.200825	0.8697

Table 9. Significant variables affecting Ovenbird populations in 20 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	3.56E+00	−1.04E+01	1.77E+01	0.61
as.factor (2006)	−6.74E−02	−2.38E−01	1.09E−01	0.454
as.factor (2011)	−1.40E−01	−3.37E−01	7.45E−02	0.187
Connected Forest	9.42E−02	−3.53E−02	2.14E−01	0.135
Fragmented Forest	−8.80E−03	−5.25E−02	3.52E−02	0.693
Blue Ridge	1.95E−04	−4.04E−02	3.82E−02	0.984
Coastal Plain	2.64E−02	−1.82E−02	7.18E−02	0.253
Piedmont	9.10E−03	−3.46E−02	5.22E−02	0.674
Valley and Ridge	9.54E−03	−2.36E−02	4.27E−02	0.559
Slope1	−4.86E−02	−1.56E−01	5.36E−02	0.357
Slope2	−1.03E−01	−3.45E−01	1.25E−01	0.381
Slope4	−6.79E−02	−3.56E−01	2.49E−01	0.653
Slope5	−8.27E−03	−1.33E−01	1.11E−01	0.891
Slope6	−1.19E−01	−3.37E−01	1.23E−01	0.299
Slope7	1.05E−01	−5.57E−02	2.81E−01	0.213
Slope8	−3.30E−01	−8.24E−01	1.68E−01	0.193

Table 10. Significant variables affecting Wood thrush populations in 20 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	−1.78E+00	−1.08E+01	7.49E+00	0.694
as.factor (2006)	−1.55E−01	−3.31E−01	3.68E−02	**0.0971**
as.factor (2011)	−5.74E−01	−7.78E−01	−3.53E−01	**<1e-04**
Connected Forest	−2.78E−02	−1.35E−01	8.17E−02	0.6089
Fragmented Forest	−4.90E−03	−4.25E−02	3.52E−02	0.8037
Blue Ridge	−3.64E−04	−2.81E−02	2.98E−02	0.9737
Coastal Plain	8.92E−03	−2.27E−02	3.87E−02	0.5629
Piedmont	9.88E−04	−2.81E−02	3.16E−02	0.952
Valley and Ridge	1.44E−03	−2.29E−02	2.59E−02	0.8983
Slope1	6.26E−02	−5.30E−02	1.83E−01	0.2954
Slope3	7.81E−02	−9.27E−02	2.55E−01	0.3646
Slope4	−1.47E−03	−1.01E−01	9.86E−02	0.9786
Slope5	1.06E−01	−7.30E−02	2.93E−01	0.26
Slope6	−7.62E−03	−1.07E−01	8.83E−02	0.8611
Slope7	1.03E−01	−6.20E−02	2.66E−01	0.2051
Slope8	−1.45E−01	−4.73E−01	1.72E−01	0.368

Table 11. Significant variables affecting Ovenbird populations in 25 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	7.177702	−3.11725	18.50138	0.196
as.factor (2006)	−0.09856	−0.27941	0.083868	0.2963
as.factor (2011)	−0.19009	−0.39012	0.019169	**0.0706**
Connected Forest	0.078469	−0.02307	0.18533	0.136
Fragmented Forest	0.003198	−0.03549	0.043324	0.874
Blue Ridge	−0.01595	−0.04746	0.017702	0.336
Coastal Plain	0.005291	−0.02798	0.038473	0.7429
Piedmont	−0.01234	−0.04632	0.021749	0.4694
Valley and Ridge	0.001566	−0.02575	0.029716	0.9109
Slope1	−0.07414	−0.15675	0.008259	**0.0791**
Slope2	−0.12348	−0.29995	0.060605	0.1794
Slope4	−0.07567	−0.3133	0.177085	0.5346
Slope5	−0.08293	−0.19051	0.017675	0.1111
Slope6	−0.05211	−0.21792	0.110791	0.5263
Slope7	−0.04928	−0.15866	0.062672	0.3829
Slope8	−0.0496	−0.16776	0.070577	0.4066

Table 12. Significant variables affecting Wood thrush populations in 25 mile buffer.

Model Variables	Posterior Mean	Lower 95% CI	Upper 95% CI	pMCMC
Intercept (2001)	1.785281	−5.28637	8.534741	0.6106
as.factor (2006)	−0.17731	−0.35528	0.011997	**0.0671**
as.factor (2011)	−0.62222	−0.83117	−0.40189	**<1e-04**
Connected Forest	−0.01035	−0.10529	0.083357	0.8389
Fragmented Forest	0.011201	−0.02224	0.047492	0.516
Blue Ridge	0.005236	−0.02046	0.030702	0.6911
Coastal Plain	0.00516	−0.02083	0.03188	0.698
Piedmont	−0.00091	−0.028	0.025485	0.9437
Valley and Ridge	0.006333	−0.01654	0.028496	0.5843
Slope1	−0.00302	−0.09396	0.090905	0.9566
Slope3	−0.0251	−0.14994	0.102159	0.6934
Slope4	0.046048	−0.04494	0.146752	0.3377
Slope5	−0.02131	−0.1627	0.113956	0.7503
Slope6	−0.00197	−0.08227	0.078213	0.9571
Slope7	0.003322	−0.08225	0.086437	0.9354
Slope8	−0.00856	−0.07652	0.066563	0.8091

As our results show a significant increase in fragmented forests across all survey routes from 2001 to 2011, the decline in populations of Wood Thrush in Virginia over that period parallels an increase in forest fragmentation. Forest fragmentation leads to the creation of small forest patch sizes which limit the food resources available for the bird species. Thus, the link between the decline in Wood Thrush populations and forest fragmentation in Virginia is consistent with the findings of [22] who found a direct relationship between forest patch sizes, reproductive success, and return rates for Wood Thrushes in Delaware.

Our results indicate a modest decline in Ovenbird populations between 2006 and 2011, whereas Wood Thrush declined significantly and consistently between 2001 and 2011. Since forest fragmentation significantly affected Ovenbirds in the 1 and 5 mile buffers, our results are consistent with the results of [9] study suggesting that pairing success of Ovenbirds can be influenced by habitat fragmentation. Ovenbirds avoid forest fragments which might be the reason for their modest decline compared to the significant decline in Wood Thrush populations.

Core forest areas are important for buffering Wood Thrush and Ovenbird species from the incursions of predators as a result of the shield provided by the high and closed canopy structure with small canopy gaps [23]. However, our results show that the decline in core forest in Virginia is not significant. This means that the decline in Wood Thrush is caused by other factors such as in-

creased forest fragmentation leading to increased predation.

For many migrating interior forest specialists like the Ovenbird and Wood Thrush, although small habitat spaces are not appropriate for breeding, they serve as stopover habitats and corridors that link core forest patches together. Our results show that the change in connected forests in all the buffer regions is significant which is important for ensuring the persistence of healthy Wood Thrush and Ovenbird populations.

Reductions in populations of migrant habitat specialists such as the Ovenbird and Wood Thrush could be a result of increasing urban development which directly leads to increased rates of nest predation in forest fragments close to development sites, changes in habitat structure and composition, and consequently, avoidance of developed areas by birds due to human habitation [24] [25]. Among effects of urban development, are increases in numbers of domestic pets from nearby homes in the area, which are likely to disturb nesting birds [26] [27].

Our results show that at local scales (1, 5 and 15 mile buffer radius), fragmentation, slope and physiographic regions have significant effects on Wood Thrush and Ovenbird populations. At the regional scale (20 and 25 mile buffer radius), forest fragmentation has no effect either due to the fact that forests no longer dominate the matrix or the species do not respond to the landscape at these large scales. There was a similar trend in changes in core, connected and fragmented forest in every buffer area considered (**Figures 5-9**). Core forest areas declined from 2001 to 2011 while fragmented forest areas increased, demonstrating a general increase in forest fragmentation across Virginia. This means that a singular policy aimed at decreasing forest fragmentation can be effective across the entire state of Virginia. For instance, [28] showed that economic research can rely on a model of net benefits that reflects or emphasizes the fragmentation or pattern of the landscape, rather than individual species or specific locations within the landscape. However, given that effects of all variables considered in each buffer zone on the populations of wood thrush and ovenbird differ, it is important that more specific deliberations are made, with particular species in mind. For example in the 5 mile buffer, fragmented forests, the Coastal Plain region and slope category 5 have significant effects on Ovenbird populations but none of these factors have significant effects on Wood thrush populations in the same buffer. Hence, results are dependent on the species under focus and policy makers should be cautious in the application of generalized concepts to all species.

4.1. Specific Effects on Ovenbird Populations in Virginia

At local scales (*i.e.* 1 and 5 mile buffers), ovenbirds are less common in fragmented areas, more common in the Coastal Plain region and less common in slope category 5. BBS survey routes are roadside surveys which means that the count is influenced by conditions of forest edge areas. With a key result of forest

fragmentation being an increase in edge areas [29], fragmented forest types, usually characterized by small patch sizes and linear or irregularly shaped patches, are most likely present near survey routes where data on the birds are collected as they are more abundant near roads and pathways [29]. Therefore, roads likely create more negative impacts on forest interior species such as the Ovenbird, in the 1 and 5 mile buffer zones. The Ovenbirds' tendency to nesting only within forest interiors and rarely near forest edges is due primarily to lower habitat quality in forest edges such as reduced cover, nesting and foraging sites [30].

The Coastal Plain, a low-relief terraced region that stair-steps down gently towards the coast and covers about 21% of Virginia, has higher densities of Ovenbirds than the other regions in the 1, 5 and 15 mile buffer zones. The Coastal Plain can be divided into inner and outer sections based on topographic features with the outer Coastal Plain characterized by an undulating to a nearly flat landscape [31]. A line through the town of Suffolk north to Gloucester Courthouse and Westmoreland County on the Potomac roughly divides the inner and outer Coastal Plain. It is therefore important for future research on the effect of the Coastal Plain region on Ovenbird populations in Virginia to take into consideration the differences in characteristics of the inner and outer regions.

During the Civil War, most of the old forests in the Coastal Plain were destroyed for lumber construction and firewood for the armies [32]. With about 46% of the Coastal Plain forested, urban development in large cities like Roanoke, Newport News and Norfolk has led to broad-scale forest fragmentation [31]. Currently, only 13% of the Coastal Plain region consists of unfragmented natural lands with high ecological integrity, with these areas limited to only the Great Dismal Swamp and the Fort A. P. Hill Military Reservation [33]. This suggests that higher numbers of Ovenbirds occur in the Coastal Plain region despite high levels of fragmentation. However, there are natural mixed communities of the longleaf pine (*Pinus palustris*) and pond pine (*Pinus serotine*) woodlands that are largely restricted to the southern part of the Coastal Plain [31]. With Ovenbirds having a preference for mixed-pine hardwood ecosystems [34], it is typical for this region to have a significant positive effect on ovenbird populations.

Slope category 5 representing areas with slope percent greater than 9 but less than 15, has a significant negative relationship to Ovenbird numbers in the 1 and 5 mile buffer zones. For aesthetic and site drainage purposes as well as lower construction costs, most residential and road constructions are carried out in areas with grades between 10% and 15% slope. Thus, the relationship to slope category 5 may be due to greater residential development in such areas. As one moves further from the survey routes, in the 20 and 25 m buffer zones, there is increased possibility of finding areas with steeper slopes and therefore, the Slope 5 variable becomes less significant. Our results show that Ovenbirds are more responsive at the local scale compared to the regional scale.

[3] argued that despite low fecundity success of Ovenbird populations in small forest fragments, a system of interacting subpopulations allows for local sink populations to persist as a result of immigration from other source populations. As such, the overall dynamics of source-sink systems are not necessarily impacted by poor reproductive success in forest fragments at larger scales especially if the birds avoid those small fragments [3]. This might be why none of the variables in the 25 m buffer analysis, had a significant effect on Ovenbird populations.

4.2. Significant Effects on Wood Thrush Populations in Virginia

In the smallest buffer analyzed in this study, the 1 m buffer, Slope category 4 had a sizeable, albeit insignificant relationship to Wood Thrush abundance. Slope 4 represent areas with slope percent between 5% and 9%. According to [35], prime agricultural lands are characterized by slopes between 0% and 5% because they have low erosion hazards and are not prone to risks of damaging overflow. This means that forested lands with slopes in this category are more prone to agricultural conversion. Through the process of convective pre-heating, wildfires generally advance as slopes become steeper [36]. As a result, it is highly likely that medium slopes, between 5% and 9%, present ideal conditions for mature forests in Virginia which might be why this slope category has a positive relationship to Wood Thrush numbers in Virginia in areas close to survey routes.

The year 2011 has a significant negative relationship to Wood Thrush abundance at all buffer sizes analyzed, and the year 2006 also has a negative relationship to Wood Thrush in the 20 and 25 m buffer zones. This is best interpreted as indicating a decline in Wood Thrush populations in Virginia over the study period from 2001 to 2011 rather than indicative of annual variation. That Wood Thrushes are not less common in fragmented forest than core forest suggests they do not avoid forest fragments, rendering their populations susceptible to adverse effects of fragmentation on their reproduction and survival. If the year effects instead represent annual variation, one possible cause of their variation is drought, which reduces availability of food resources for birds, making them more susceptible to predation and starvation [37]. According to the US Drought Monitor for Virginia, the state experienced severe to exceptionally severe droughts between 2007 and 2009. While drought severity reduced to abnormally dry conditions after 2009, Virginia again experienced severe drought in the latter months of 2010. These drought conditions might be responsible for a decline of Wood Thrush numbers being evident in 2006 and 2011.

Only in the 15 m buffer did the Coastal Plain region have a sizeable positive relationship to Wood Thrush abundance. The large composition of mixed-pine woodlands in the Coastal Plain region of Virginia can be a contributing factor to the positive significant effect of this region on Wood Thrush populations. [38] found a positive correlation between mixed forests with high pine concentration and Wood Thrush populations. [39] reported that the South Atlantic Coastal

Plain has one of the largest forested floodplains and the largest remnants of former longleaf pine and woodland ecosystems.

5. Conclusions

The study shows that populations of Wood Thrush and Ovenbird in Virginia decreased between 2001 and 2011, forest fragmentation increased over this period, and that Ovenbirds are less common in forest fragments than in core forests. Increased fragmentation could account for the significant decline in Wood Thrush since our results show that they do not avoid fragments whereas Ovenbirds avoid forest fragments and have therefore only declined moderately. This study also demonstrates how habitat conditions affect populations of Wood Thrush and Ovenbird. For example, slope has a significant effect on Wood Thrush and Ovenbird populations because it determines the intensity of development in an area. The Coastal Plain region harbors larger numbers of Wood Thrush and Ovenbird than other physiographic regions in Virginia as its mixed forested lands with high pine concentrations provide an ideal habitat for both the Wood Thrush and Ovenbird.

The study identifies factors whose consideration may allow policy makers to make more effective decisions to increase Ovenbird and Wood Thrush populations in Virginia. In particular, use of differing buffer zones showed that these species respond to their environment at relatively small (1 -5 miles) spatial scales. The trace plots of our results show effectiveness of our model in identifying the effects of multiple variables over a time gradient. Thus, our model can be replicated and improved by other studies to ensure that effective decisions are made to improve bird populations.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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