

RESEARCH ARTICLE

Insights from five decades of monitoring habitat and breeding populations of American woodcock

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Abstract

1. Habitat loss and degradation are contributing to severe declines in many North American bird species. For American woodcock *Scolopax minor* ('woodcock'), loss of preferred young forest habitat matrices are generally attributed as the primary drivers of range-wide population declines in eastern North America, but regional patterns in abundance or habitat availability have not been assessed in Nova Scotia, the northeastern-most portion of the range.

2. Our objectives were to (a) identify regions of similar trends over the past five decades, (b) evaluate spatiotemporal relationships in the effect of habitat availability on abundance across the province and (c) provide recommendations for woodcock management priorities in Nova Scotia to target local population declines.

3. Using 50 years of standardised surveys and habitat measures, we investigated woodcock population trends and local habitat availability by applying a novel spatially-explicit model with Integrated Nested Laplace Approximation.

4. Province-level declines were primarily driven by losses of breeding woodcock in the north and south of the province, while the central region experienced growth. The proportion of area around a survey route comprised of clear-cut, harvested forest was the most important habitat feature of nine potential explanatory variables to affect abundance, where higher levels of clear-cut area predicted higher abundance, particularly in the last 15 years (increase from two to 10 birds on average as the amount of clear-cut area increased from zero to 28%).

5. Historically, habitat for species requiring open areas and regenerating forests would be established through periodic natural disturbance. Today, it is impractical for these processes to occur unimpeded, thus commercial timber harvests and proactive habitat management are necessary to ensure habitat availability. For woodcock in Nova Scotia, partnering with both the local forest products industry and wider national and international habitat management initiatives to provide habitat in the southern and northern regions of the province could be key to improving the population status both locally

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and ultimately range wide. The temporally and spatially extensive surveys used here provide a remarkably comprehensive avian monitoring dataset. Coupled with modern analytical tools, our study system serves as an example of how long-term avian survey efforts are capable of informing management regionally to achieve broader conservation targets.

KEYWORDS

American woodcock, avian monitoring, clear-cut harvest, forestry, habitat availability, management, population decline

1 | INTRODUCTION

Recent findings report that North America has lost more than one in four birds in the last 50 years, where habitat loss or degradation have been key drivers for many species (NABCI Canada, 2019; NABCI US, 2019; Rosenberg et al., 2019). Long-term monitoring schemes have proven crucial to provide the data required in gaining broad insights into avian trends in relation to ecological traits (Reif, 2013; Rosenberg et al., 2019). Continued efforts applying advanced, spatially explicit, analytical approaches to comprehensive time series of abundance and habitat are urgently needed to identify conservation and management priorities for target groups and species (Rosenberg et al., 2019).

American woodcock *Scolopax minor* (herein 'woodcock') share the worrisome trends emerging continentally across avian guilds, showing declines range-wide across eastern North America (Seamans & Rau, 2018). However, the relationship between human influence on the landscape and abundance is challenging to disentangle for species like the woodcock with highly specialised, disturbance-dependent niches (Hunter, Buehler, Canterbury, Confer, & Hamel, 2001). Woodcock are forest birds with particular breeding habitat requirements, thriving in local landscapes comprising young, moist woodlands with high stem density interspersed with clearings. Loss and degradation of preferred young forest matrices are generally attributed as the primary drivers of range-wide declines (Masse, Tefft, & McWilliams, 2014; McAuley, Keppie, & Whiting, 2013).

The most recent assessments of woodcock populations document long-term continental-scale declines since standardised monitoring protocols (called the American Woodcock Singing Ground Survey or 'SGS') began in 1968, with a higher magnitude of decline in the Eastern Management region in particular (around 1% per year; Saunders et al., 2019; Seamans & Rau, 2018). Roy et al. (2019) showed that the SGS population indices across the five Canadian provinces where woodcock regularly breed (Ontario, Quebec, New Brunswick, Prince Edward Island and Nova Scotia) experienced a slow, overall, total decline of 70% between 1975 and 2015.

While a number of landscape changes have likely contributed to range-wide woodcock declines, including suppression of fire, maturation of forests, agricultural intensification and urbanisation (McAuley, Keppie, & Whiting, 2013), assessing habitat change at a finer spatial scale could help elucidate the effect of local habitat availability on

woodcock abundance (Roy et al., 2019). In the province of Nova Scotia, recent assessments of SGS population indices indicated a decline of 0.9% per year between 1968 and 2017, with a slowing but steady decline of 0.39% per year over the more recent 10 year period of 2007–2017 (Seamans & Rau, 2018). SGS have been conducted continuously over the past 50 years, with excellent spatial coverage across the entire province. These data provide unique opportunities to assess how regional population trends contribute to the province-wide trend, and how localised habitat alteration and forest management practices may be influencing populations.

In this study, we investigated spatial patterns in woodcock population trends and associated changes in local habitat availability across the province of Nova Scotia. The latter analysis uses a novel application of spatially explicit, Bayesian approximation methods that generate parameter estimates and a latent Gaussian field to address spatial correlation with the Integrated Nested Laplace Approximation (INLA) approach (e.g. Bivand, Gomes-Rubio, & Rue, 2015). Our objectives were to (a) identify regions of similar long-term population trends over the past 50 years, (b) evaluate potential spatial and temporal relationships in the effect of habitat availability on woodcock abundance across the province and (c) based on our findings, provide spatially explicit recommendations for both future research priorities and land management practices in Nova Scotia to target local declines with the goal of ultimately improving the province-wide population trend.

2 | MATERIALS AND METHODS

2.1 | Inferring population indices from singing ground surveys

The SGS is a standardised protocol used to estimate annual population indices for woodcock across their range (Seamans & Rau, 2018). The SGS exploits the conspicuous courtship display, whereby males repeatedly vocalise a series of loud 'peent' calls followed by an aerial display. These exhibitions are performed by males throughout spring dusk and dawn periods. Beginning in 1968, SGS route locations were chosen along secondary roads in the center of random 10-minute degree blocks within every state and province of the breeding range, totalling roughly 1,500 survey routes. Each route is 5.4 km long and consists

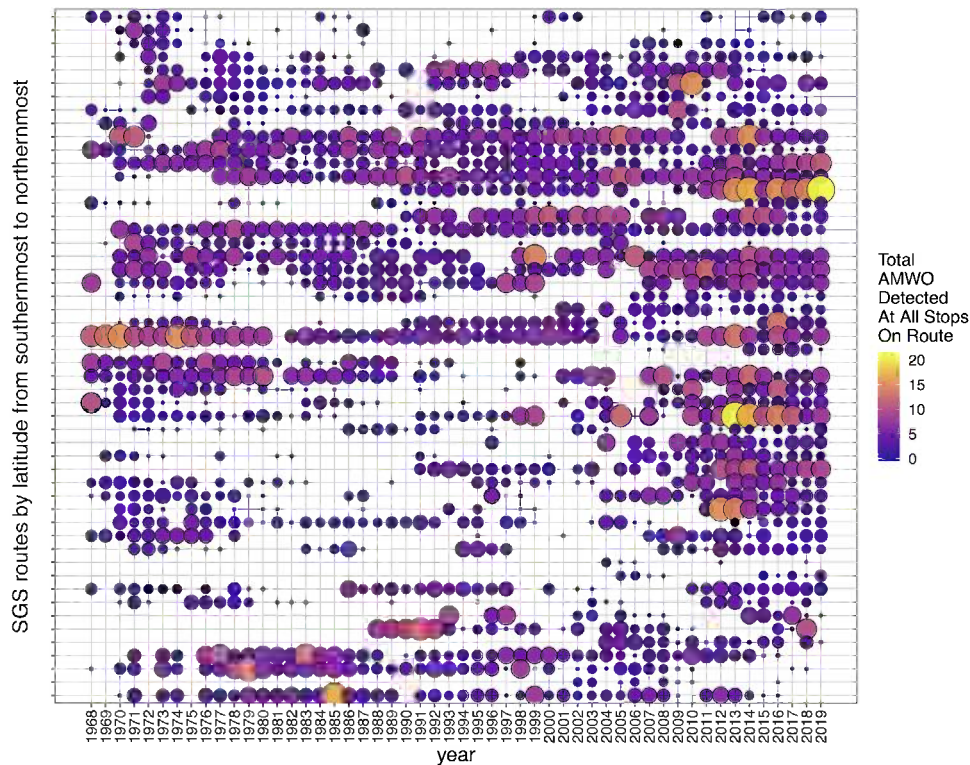


FIGURE 1 Total woodcock detected on 52 SGS routes surveyed across Nova Scotia, 1968–2019. Total detections depicted by colour (hotter = higher number detected) and circle size

of 10 listening stops spaced at 650 m apart to avoid detecting the same individuals at more than one stop. Surveys commence shortly after sunset during the peak spring courtship period at a given latitude. Observers record the number of individuals heard at each stop, and the total displaying males detected along the route serves as an index of local population abundance. The time of a survey relative to sunset and adverse weather conditions affect both displays and observer detection, and thus surveys are only conducted or deemed acceptable when conditions are within prescribed limits. If surveys on a given route fail to detect woodcock for two consecutive years, the route is not surveyed again for a period of 5 years (Seamans & Rau, 2018). All SGS data are archived by the U.S. Fish & Wildlife Service Department of Migratory Bird Management (USFWS Migratory Bird Data Center, 2019).

2.2 | Singing ground surveys in Nova Scotia

In Nova Scotia, 52 SGS routes have been active and geo-referenced during the period 1968 to 2019. The mean distance between nearest routes is 21.3 km (± 8 km standard deviation; range 3–43 km apart). Routes were initiated between 1968 and 2007 and have been surveyed for periods of 12–51 years (mean 43 years across routes). During this time, between 5 and 51 acceptable annual surveys have been recorded for each route, totalling 1,584 surveys conducted by 129 observers. Observers run their routes for as many consecutive years as possible

to reduce observer bias on trend estimates (Seamans & Rau, 2018); in Nova Scotia, the mean number of observers per route from 1968 to 2019 was low at six, ranging from 2 to 13.

2.3 | Estimating route-level trends in population indices

Initial examination of survey data over time revealed high variation across routes in both absolute abundance and change across the period 1968–2019 (Figure 1). Plotting indicated that spatial patterns in trends may be significant. To model the data at the route level, annual count (Poisson distribution, log-link) was regressed against survey year. We estimated parameters with INLA via the R-INLA package (<http://www.r-inla.org>). INLA is an extremely fast Bayesian approximation technique that integrates using a second-order Taylor expansion from the mode (Rue, Martino, & Chopin, 2009). It has become increasingly popular in ecology because of its speed, ease of use and functions for making Bayesian approximations from modelling latent Gaussian models (described below; Cosandey-Godin, Krainski, Worm, & Flemming, 2014; Gutowsky et al., 2020). For each model presented here, survey year was subtracted from the first survey year to give the intercepts a meaningful interpretation, that is, a baseline count estimate. The count coefficient for each route was plotted by the geographic coordinates to reveal temporal and spatial patterns. Credible intervals that overlapped zero were not considered important. Only routes with

10 or more years were included for the trend analyses (93% of routes, $n = 48$). All analyses were conducted in the R statistical environment (R Core Team, 2019).

2.4 | Characterising habitat around SGS routes

A buffer area of 1 km around the length of each SGS route (Supp. Fig. 1) was chosen to represent the habitat available to the local woodcock breeding population. Buffer generation and habitat extraction was completed using a geographic information system (ArcGIS version 10.5, ESRI, Redlands, CA, USA). Because SGS routes follow secondary roads, routes are not always linear and resulted in slightly variable buffer sizes around each route (mean $13.4 \text{ km}^2 \pm 0.7 \text{ SD}$). Habitat variables were assessed as proportions of the buffer area to reduce the influence of non-linear routes. A 1-km buffer was chosen based on known movements of woodcock within a breeding season. Males can have multiple singing grounds within home ranges varying in size from 0.01 km^2 to 4.75 km^2 ($n = 52$ individuals tracked for ≥ 25 days; Masse et al., 2014), while females tend to nest in close proximity to singing grounds ($< 90 \text{ m}$ away; McAuley, Keppie, & Whiting, 2013). A 1-km buffer zone of total area of $12\text{--}16 \text{ km}^2$ then represents numerous habitat mosaics of forest and non-forest land cover available to the males (and potential associated females) detected along the length of the route for all breeding season activities including courtship, roosting, nesting and feeding. This spatial extent allows us to capture responses of local woodcock populations to changes in landscape composition over time, but precludes inferences about responses at an individual level (e.g. site selection, survival, fecundity) to environmental factors at a finer spatial resolution.

Habitat variables within buffers around each route were characterised from publicly available Forest Inventory Program (FIP) data collected by the Nova Scotia Department of Lands and Forestry (NSDLF; Nova Scotia Department of Lands and Forestry, 2018). The FIP is designed to monitor changes in Nova Scotia's forests over time using inventory cycles informed by two complementary measurement systems: permanent forest inventory plots and aerial photo and satellite imagery interpretation. The first inventory cycle (Cycle 1) is representative of the period 1985–1993, Cycle 2 represents 1994–2004, and Cycle 3 has been continuously updated since 2005 thus representing conditions between 2005 and 2019. The GIS dataset for each inventory cycle delineates all land area in Nova Scotia into two general land-cover types, forest or non-forest polygons, each with extensive attribute data. Relevant available habitat attributes for this study include 'forest' polygons designated as the following: clear-cut (stands that have been completely cut where any residuals comprise $< 25\%$ canopy closure with little or no indication of regeneration), successional forest (stands in the 'establishment phase' with age < 25 year and mean canopy height $0\text{--}6 \text{ m}$), young forest (stands age $26\text{--}40$ year with canopy mean height $7\text{--}11 \text{ m}$), shrubland (dry areas containing $< 75\%$ alder canopy closure, $> 25\%$ woody plants, and $< 25\%$ other tree cover), and generally forested (i.e. all 'forest polygons' combined, or all areas not designated as 'non-forest'). Relevant 'non-forest'

polygons included those designated as active agriculture (areas of hay field, pasture, tilled crop or orchard), old regenerating field (areas of field with regrowth of tree canopy closure $< 25\%$ and height $< 1 \text{ m}$), wetland (areas of poor drainage consisting of ericaceous plants, sphagnum and other mosses, with $< 25\%$ stunted tree cover) and urban/developed (areas used primarily as residential or industrial including structures, streets, sidewalks, parking lots, golf courses, parks, cemeteries, etc.). The proportion of area comprised of each of these habitat variables within the route buffer was extracted for the three FIP cycle periods, resulting in nine habitat variables for each route representing each of the three time periods (example provided in Supp. Fig. 1).

2.5 | Evaluating the influence of habitat availability across Nova Scotia

The relative importance of habitat variables was first examined using boosted regression trees (BRT; Friedman, 2001) to model woodcock abundance (route level means for each inventory cycle time period) to the set of nine explanatory habitat variables for each of the three periods. BRT differs from traditional regression in that many models (i.e. trees) are fit and combined to optimise predictive performance. Additionally, BRT is able to cope with complex interactions, non-linearity and outliers (Elith, Leathwick, & Hastie, 2008). Classification trees, as performed here, fit regions with the most probable class. Recursive binary splits are used to grow trees until a stopping criterion is reached.

BRTs were fitted with the R packages *dismo* (Hijmans, Philips, Leathwick, & Elith, 2017) and *gbm* (Ridgeway, 2017), which prune trees through cross-validation (Hastie, Tibshirani, & Friedman, 2009). We used 10-fold internal cross validation on a dataset of response and predictor variables associated with each route (Jarnevich, Stohlgren, Kumar, Morissette, & Holcombe, 2015). Two learning rates, two bag fractions and five tree complexities were tested for a total of 20 models with 1,000 trees each. The model with the lowest deviance was pruned to remove predictors based on k -fold cross validation and a procedure similar to backwards model selection that identifies the order in which low contributing predictors should be removed based on the mean change in deviance and standard error (Elith et al., 2008; Hijmans, Tibshirani, & Friedman, 2017). While BRT fits woodcock abundance for each habitat variable, anticipated spatial correlation was expected in the response variable. Therefore, BRT was used only to identify the top predictor variables for a generalised linear mixed model (GLMM) capable of incorporating spatially correlated random effects.

R-INLA contains functions to construct Gaussian random fields (GRFs) that allow for parameter estimation in relation to complex spatial structures (Beguín, Martino, Rue, & Cumming, 2012; Bivand et al., 2015; Lindgren, Rue, & Lindström, 2011). GRFs are estimated using Matérn correlation solved by a stochastic partial differential equation on an irregular grid, that is, mesh (Bivand et al., 2015). The mesh is a series of non-overlapping triangles (edges and vertices) created using

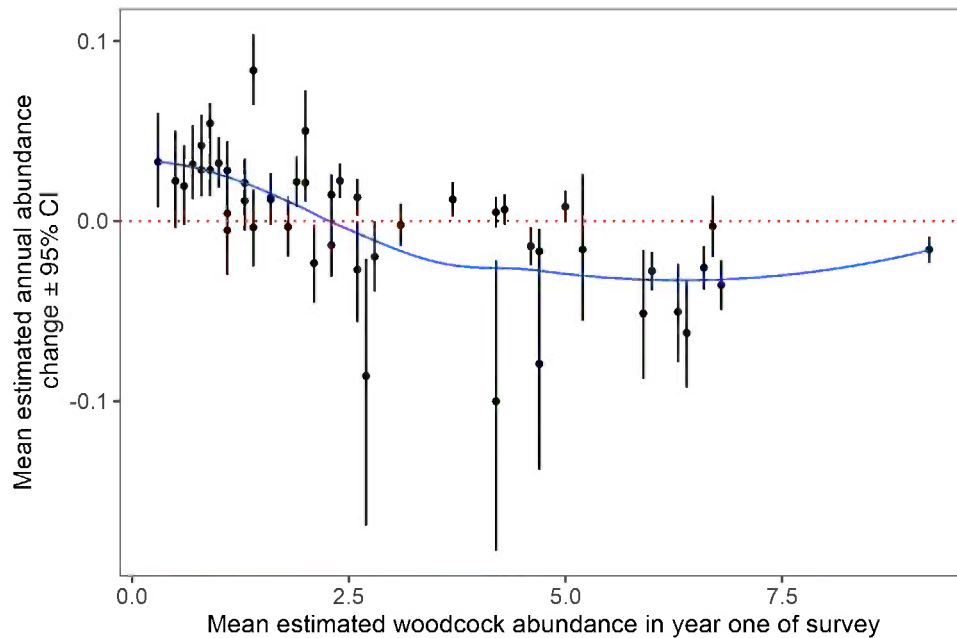


FIGURE 2 Slope (y-axis) and intercept (x-axis) \pm 95% credible interval from annual count (Poisson distribution, log-link) regressed against survey year for each SGS route in Nova Scotia. The x-axis was transformed to show change in annual abundance relative to the expected number of woodcock in the first year of the survey whereas the y-axis remains on the natural log scale to indicate the relative rate of expected change (i.e. approximating the annual per cent change). The dashed red horizontal line shows where credible intervals overlap zero

functions of the R-INLA package. Our mesh was generated from a GIS shapefile plus an extended domain to avoid boundary effects (i.e. an increase in variance near the edge of the mesh) that can arise from the stochastic partial differential equation approach of GRF estimation (Blangiardo & Cameletti, 2015). Our model was a normally distributed GLMM with route-level mean abundance for each inventory cycle time period as the response, the top habitat variables found by the BRT (proportion of clear-cut area and urban/developed area within a route buffer), time period, all interactions, and the locations of sampling routes as the spatially correlated random effects. Two-way and three-way interactions were estimated to test for complex relationships among the variables identified by the BRT.

3 | RESULTS

3.1 | Route-level trends in abundance

Our trend analysis showed that there were 32 routes with a 95% probability of either an increasing ($n = 17$) or decreasing ($n = 15$) trend in woodcock abundance since the first surveys were completed (Figure 2). Plotting the coefficients spatially showed similar trends for routes in relatively close proximity, including for routes without a trend through time. For example, abundance decreased across much of the southwestern routes and increased in the central parts of the province (Figure 3). Patterns indicated that trends in woodcock abundance at the route level were non-independent, with distinct regions of similar but opposite trends.

3.2 | Influence of habitat availability on abundance

The BRT with the lowest deviance had a tree complexity of four, learning rate of 0.01 and a bag fraction of 0.75. Simplifying the top model indicated that only two variables were important (i.e. per cent relative influence) based on their standard error and deviance compared to a model with all habitat predictors. Proportional area of clear-cut (27.2%) and urban/developed habitat (26.7%) were identified as important variables to explain woodcock abundance (Figure 4).

The mesh for Nova Scotia contained 1,977 vertices (Figure 5a). Correlation among routes diminished below 10% at 26.3 km. Several terms were important, including the intercept (representing time period 1), time period 3, the two-way interactions between clear-cut and time period 3 and the three-way interaction between urban, clear-cut and time period 2 (Table 1). Neither clear-cut (%) nor urban area (%) environments alone explained woodcock abundance; however at the average value for per cent urban area (mean: $3.7\% \pm 4.0$ SD, range: 1.5–28.5%) woodcock abundance increased considerably in the third time period (Figure 6). During the third time period, woodcock numbers increased from two to ten birds on average as the amount of clear-cut area increased from zero to 28% (Figure 6). While a decrease occurred in woodcock abundance as the per cent of urban environment increased, the trend was not different from zero (Table 1). Approximately 40% of the variation in woodcock abundance was explained in the spatial random field (Figure 5b). The GRF indicated a latent process showing the strongest effects on abundance in the northcentral and northeastern regions of the province (Figure 5-b).

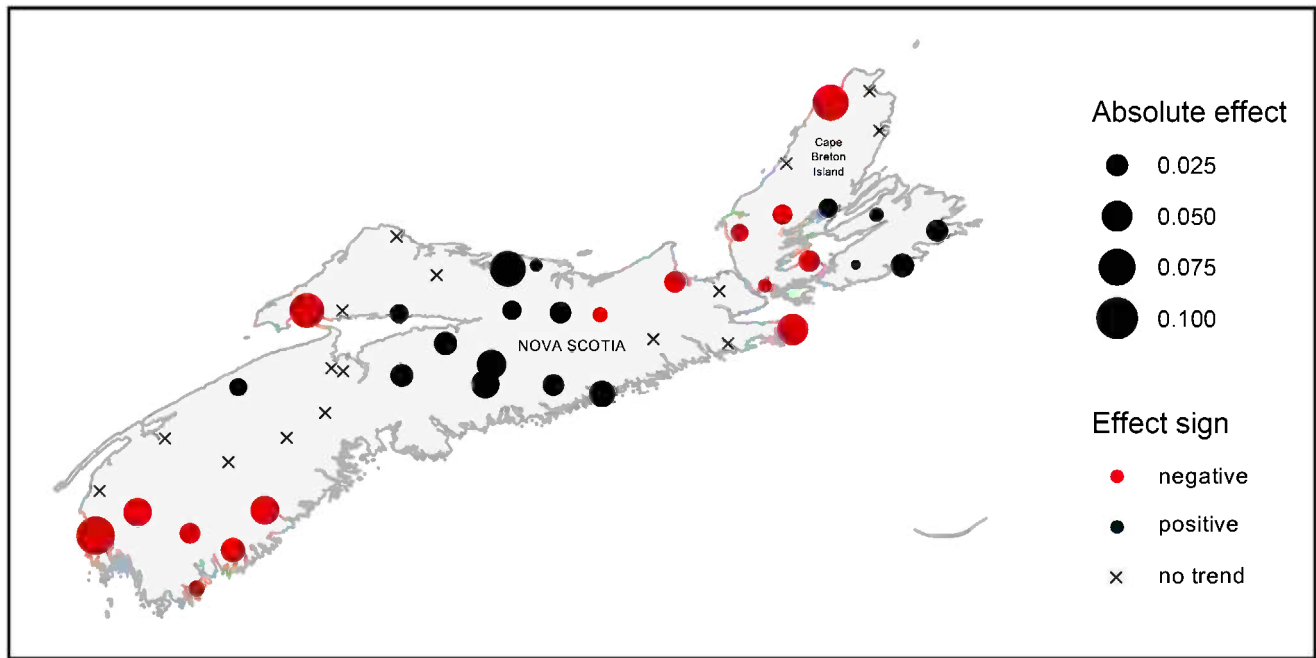


FIGURE 3 SGS route locations indicated by slopes (absolute effect) from each model (Poisson distribution, log-link) of annual woodcock abundance over time

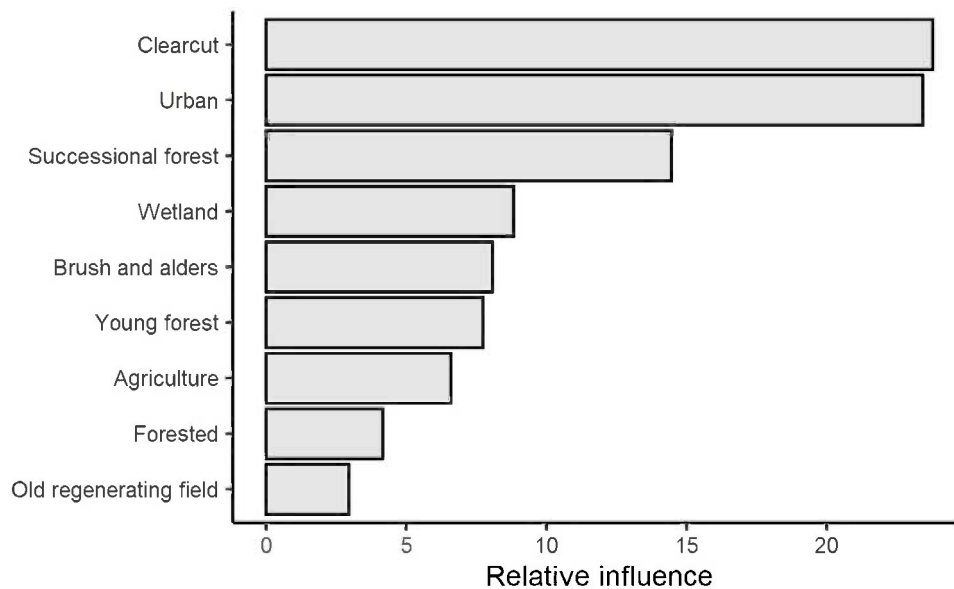


FIGURE 4 BRT results showing the relative influence of the nine habitat variables predicted to effect woodcock abundance

4 | DISCUSSION

We evaluated spatiotemporal patterns in woodcock population trends and associated changes in local habitat availability across the province of Nova Scotia, Canada, over five decades. To our knowledge, these analyses of population indices and habitat availability are unique in their spatial and temporal coverage for ground-nesting landbirds. We found clear spatial patterns in woodcock population trends. The province-wide decline reported by Seamans and Rau (2018) has been

mainly driven by populations in the north and south of the province, whereas the central region has experienced population growth. We found that the proportion of area around a survey route comprised of clear-cut, harvested forest was the most important habitat feature of nine potential explanatory variables to affect abundance, such that clear-cut area was positively correlated with abundance, particularly in the last 15 years. These findings help to guide the most effective management approach for addressing declining woodcock in Nova Scotia, and our novel approach is transferrable to other regions and species.

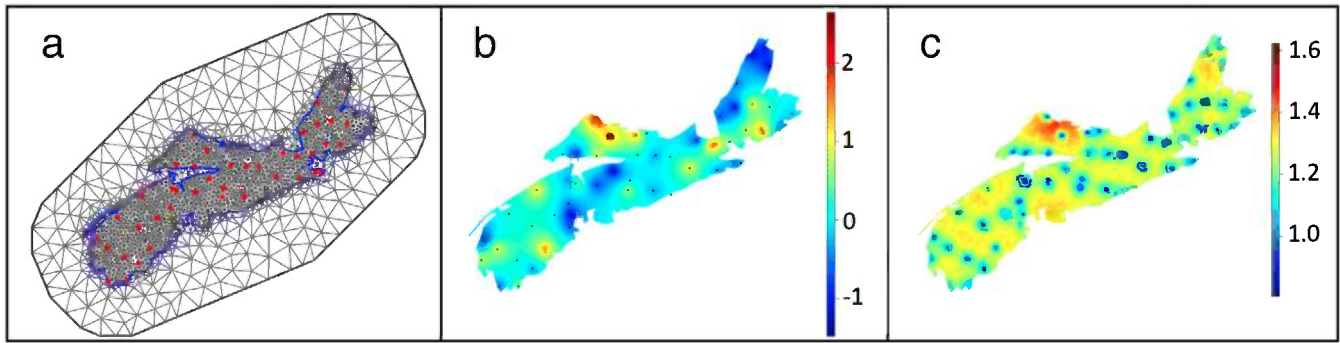


FIGURE 5 Panel a: Mesh of 1,977 vertices created by constrained refined Delaunay triangulation. Panel b: Posterior mean values of the GRF estimated for woodcock abundance across Nova Scotia. Panel c: Variation (SD) of the GRF estimated for woodcock abundance. Routes are indicated by red or black circles

TABLE 1 Fixed effects estimates from the GLMM for woodcock abundance in Nova Scotia. Credible intervals are the 2.5% and 97.5% quantiles. Important terms are indicated in bold. Hyperparameters were: $\kappa_{\text{spatial}} = 0.0002$, $\sigma_{\text{spatial}} = 1.24$; range = 26.3 km

| Term | Mean | 2.5% quantile | 97.5% quantile |
|-----------------------------------|---------------|---------------|----------------|
| Intercept | 2.492 | 1.851 | 3.122 |
| Time period 2 | -0.182 | -0.851 | 0.486 |
| Time period 3 | 0.850 | 0.111 | 1.580 |
| Urban | -0.278 | -0.808 | 0.0253 |
| Clear-cut | -0.223 | -0.848 | 0.404 |
| Urban × clear-cut | 0.356 | -0.099 | 0.811 |
| Urban × Time period 2 | -0.264 | -0.929 | 0.400 |
| Urban × Time period 3 | 0.837 | -0.302 | 1.962 |
| Clear-cut × Time period 2 | 0.607 | -0.314 | 1.531 |
| Clear-cut × Time period 3 | 1.642 | 0.821 | 2.456 |
| Urban × clear-cut × Time period 2 | -1.278 | -2.349 | -0.209 |
| Urban × clear-cut × Time period 3 | 0.325 | -1.131 | 1.767 |

4.1 | Influence of habitat on abundance

The proportion of clear-cut within a buffer area around a given SGS route was identified in the BRT as the most important factor explaining woodcock abundance. Importantly, polygons identified as clear-cut during a forest inventory would have been considered not yet regenerating at the time of survey, but the harvest and subsequent designation could have occurred at any point during an FIP inventory cycle (9–15 years). Thus, the amount of clear-cut area represents both freshly harvested plots and early regenerating areas (maximum of 14 years since harvest). Although the proportion of area represented by clear-cuts within a route buffer was relatively low with means of only 3.8–4.3% across the three time periods (equating to an average of ~500 m² of non-contiguous patches within a route buffer), there was a large degree of variation in proportion of clear-cut area among routes (Supp. Table 1). In addition, the proportion of successional young forest

was also identified as the third most important factor, despite not being retained in the best BRT model. The strong influence of clear-cut and to a lesser extent early successional forest on woodcock abundance aligns with the well-established habitat requirements of this species. For example, of 89 nests located in a National Wildlife Refuge in Maine, 44% were within clear-cuts ≤ 10 years old (McAuley, Longcore, Sepik, & Pendleton, 1996). It has been found that clear-cutting harvests, in strips or in patches, effectively creates woodcock breeding habitat for singing grounds and night-time roosting areas, and eventually for nesting and feeding cover (Kelley, Williamson, & Cooper, 2008; Williamson, 2010). Land management to support woodcock habitat, particularly for providing early-successional forest, also provides conservation benefits to an array of non-target bird species, making the woodcock an effective umbrella species for early-successional forest birds (Masse, Tefft, & McWilliams, 2015).

We expected that increases in urban area would have a negative effect on woodcock abundance, like urban development has had on many other landbird species (Marzluff, 2001). Few studies have considered the availability of urban area as a potential explanatory factor for woodcock abundance, as much of the work on breeding habitat preference has been carried out in areas that are actively managed or protected. Nelson and Andersen (2013) found that the amount of developed land was not strongly related to woodcock abundance in either Minnesota or Wisconsin, in contrast to the prediction that higher urban area would be associated with lower abundance. Throughout the Canadian range for woodcock, the steepest declines in the SGS population index occurred at the beginning of the survey in the late 1970s, while continued steady declines have persisted since the 1980s. It has been suggested that extensive land development through urbanisation occurred in the 1960s to 1970s, and accelerated in the 1980s in each Canadian province (Roy et al., 2019). Across the continental range for woodcock, accelerated urbanisation during this period in combination with changes in forestry and agricultural practises have been attributed to large-scale decreases in preferred woodcock habitat (i.e. conversion of wetlands, flatlands, flood plains, old fields, young forest (Roy et al., 2019; Steketee et al., 2015; Thogmartin, Sauer, & Knutson, 2007). Our data suggest this has not been the case in Nova Scotia, where province-wide urban/developed area increased by

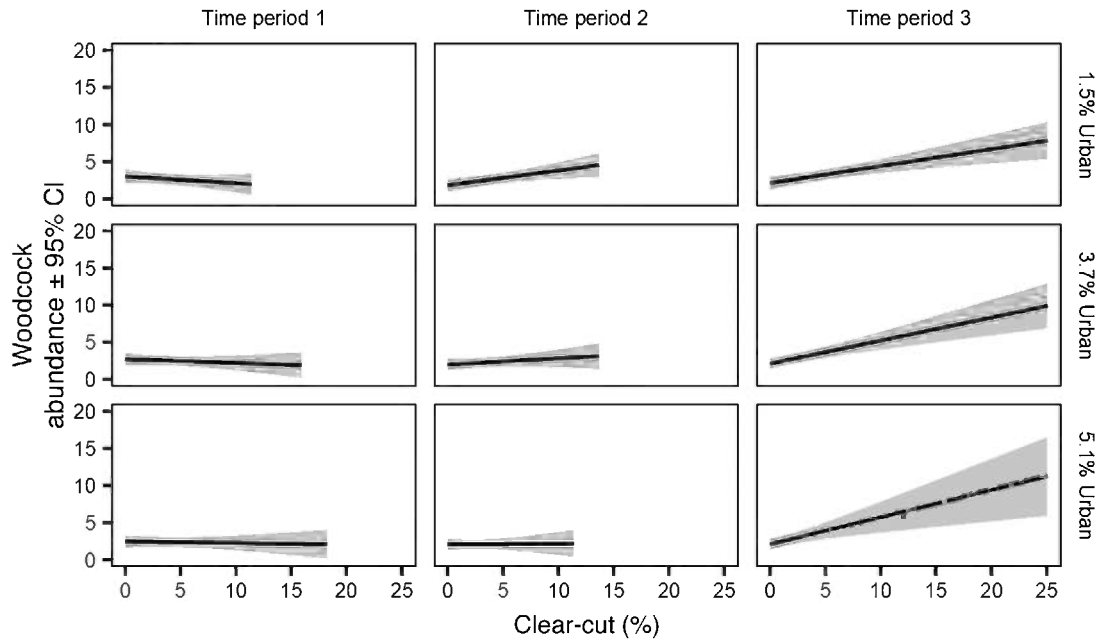


FIGURE 6 Predicted woodcock abundance relative to proportion of route buffer area comprised of clear-cut and urban/developed areas along SGS routes of Nova Scotia in each of three forest inventory cycle periods (1: 1985–1993, 2: 1994–2004 and 3: 2005–2019). Predicted values of clear-cut area from the GLMM were generated under the mean value of urban area (middle panes) and the first and third quantile of urban area (top and bottom panes)

only 0.3% from 1985 to 2004 and has remained stable since (Supp. Table 1).

Urbanisation is often equated to the creation and expansion of major urban centres with high population density or industrial activity, typically combined with the loss of old fields and early successional habitats from development (Marzluff, 2001). Based on examination of urban/developed polygons within SGS route buffers in Nova Scotia, urban areas identified in this study are more typically single or small groups of homes along secondary roads in regions considered more rural, where large yards and/or fields are associated with each urban property. Nova Scotia is one of Canada's most rural provinces, where 43% of the population live in communities with populations of less than 1,000 and < 400 people per km² (Gibson, Fitzgibbons, & Nunez, 2015). Consequently, we interpret that urbanisation and urban areas along SGS routes in Nova Scotia actually represent two different processes. While the proportion of urban area around a given SGS route was identified in the BRT as the second most important factor explaining woodcock abundance, it is not surprising that the effect was only important as an interaction with clear-cut area and time period.

Why are the effects of habitat on woodcock abundance strongest in the last inventory cycle (2005–2019) compared to the weak effects in the second cycle (1994–2004) and even more so compared to the first cycle (1985–1993)? We speculate that one possible latent factor at play may have been a decrease in harvest pressure. Management of game species can benefit from an integrated approach considering the multi-dimensional complexity of factors influencing population dynamics. Combining harvest and habitat management decisions has recently been emphasised for North American waterfowl stocks (Osnas et al.,

2014) exemplified by a case study from the declining Northern pintail *Anas acuta* (Mattsson et al., 2012). For the closely related and similarly declining Eurasian woodcock *Scolopax rusticola*, local population dynamics in wintering populations were strongly influenced by regional differences in hunting regimes (Peron et al., 2012; Prieto et al., 2019). A recent analysis of trends in woodcock population and harvest in Canada identified a significant downturn in harvest trends beginning in 2004, with subsequent continuing significant declines in harvest levels from 2006 to 2010 (Roy et al., 2019). Multiple consecutive years of reduced harvesting pressure may have allowed suppressed population numbers to respond to preferred habitat availability with a reduced effect of direct removal of individuals. Unfortunately, data on the spatial distribution of hunting intensity over time across the province are not presently available, and therefore it is not possible to assess potential localised impacts on SGS route-level trends.

4.2 | Regions of growth and decline

Our analysis identified clear spatial patterns in regions of growth, decline and stability across the province. Specifically, surveyed populations in the central and northwestern regions of the mainland and in eastern Cape Breton Island have mostly been growing or stable since surveying began in 1968. Over the same time period, populations in the Cape Breton uplands and in the southwestern end of the province have seen significant declines. Areas of stable long-term population trends were also identified, particularly in the northwestern mainland and areas of northern Cape Breton Island. The temporal resolution of

the available habitat dataset is much more coarse than the population index time series, meaning a fine-scale spatiotemporal investigation of the response of woodcock populations to habitat availability is not currently possible. Further, our analysis indicates that a latent variable explains 40% of the variation in population trends, with strong effects in particular regions of the province. For example, the routes in the northcentral area of the mainland have both shown overall stable population index trends at relatively high levels of abundance. Throughout the survey period, this localised region has experienced relatively high abundance and high variability (e.g. routes supporting a mean of 6.4 males and a maximum of 15). Latent Gaussian models are increasingly being used in ecology (Zuur, Ieno, & Saveliev, 2017; Beguin et al., 2012), in part because of their ability to incorporate spatial correlation and reveal potentially unmeasured processes (Pavanato, Mayer, Wedekin, Engel, & Kinas, 2018; Redding et al., 2019; Selwood, Clarke, McGeoch, & Nally, 2017). For example, a similar modelling approach identified a latent process affected fisheries biomass estimates in one particularly productive region of Ontario (Gutowsky et al., 2019). It is plausible that unique circumstances with unmeasured and important habitat variables exist in localised regions of Nova Scotia (e.g. harvest pressure or habitat variables not identified as most important by BRT). Thus, our analysis identifies the influence of measured and unmeasured habitat variables that warrant further investigation.

Ultimately, our approach has highlighted important regional patterns, but a more fine-scale annual analysis could identify local drivers of population trends. In particular, further efforts should be made to investigate the importance of habitat creation by clear-cutting practices over time in Nova Scotia. This may be possible because forestry data are available at a finer timescale than many other habitat variables and are more closely monitored than changes in other habitat factors. Future work could look at assessing clear-cut frequency and patch size at a yearly time step where data are available, for comparison of year-to-year and temporal lag effects on abundance. Careful monitoring of woodcock population size and productivity in areas where active management is undertaken is highly recommended.

4.3 | Recommendations for management priorities

Range-wide, the woodcock is an important species both economically, as a recreational gamebird, and as an ecological indicator of forest health and resources. In Canada and the United States, the woodcock is managed as a migratory species under the Convention for the Protection of Migratory Birds. In Nova Scotia, the woodcock is considered a priority bird species under the Regional Nova Scotia Bird Conservation Strategy, and a population objective of 50% increase has been set due to their consideration as a species of national/continental concern (Environment Canada, 2013). However, a targeted management plan does not exist in Canada. In the United States, a 'Woodcock Task Force' completed the American Woodcock Conservation Plan in 2008 (Kelley et al., 2008). Two key objectives of this plan were to halt population declines by 2012 and to achieve positive population growth by 2022. These goals were motivated by a desire to return populations

to densities that provide adequate opportunity for use of woodcock as a game resource. To accomplish this, recommendations were made to manage for early successional forest cover in clustered large patches of many square kilometres. In response to recommendations made in the Conservation Plan (Kelley et al., 2008), a large collaborative effort called the Young Forests Initiative (YFI) was launched covering all 17 states within the core breeding range (Weber & Cooper, 2019). This initiative is intended to benefit a suite of young forest-dependent wildlife, including songbirds, gamebirds, mammals and reptiles. Efforts to improve habitat availability have thus far failed to improve woodcock population status; declines persist, especially in the Eastern Management Region. Range-wide, it is well accepted that further improved habitat management is critical to stemming further losses.

Historically in Nova Scotia, preferred open areas and early successional habitats were established through periodic disturbance, particularly of mature forest, of which fire was the primary disturbance agent followed by wind (predominantly hurricanes) and insect infestation (e.g. outbreaks of spruce budworm), as well as disease and ice storm damage (Taylor et al., 2020). Today, it is impractical on many landscapes to allow most natural disturbance agents to act unimpeded, and therefore commercial timber harvests and other proactive habitat management at regular intervals is necessary to ensure the availability of required habitat (Dessecker & McAuley, 2001). Nova Scotia forest management is currently entering a new paradigm of 'ecological forestry' gaining popularity across Canada, where emphasis is placed on practises that emulate natural disturbance patterns (Taylor et al., 2020). Replication of natural disturbance needs to be carried out with careful consideration of the various juxtaposed habitat cover requirements of local species-of-concern, for example with woodcock where clearing size and proximity to other habitat type patches is critical. Our findings strongly support the recent recommendation to expand YFI work into Canada (Weber & Cooper, 2019), and the results of our study can provide guidance for where these efforts would be best spent and how cooperation with provincial forest managers could be vital.

5 | CONCLUSIONS

Using a latent Gaussian model, we captured dynamic, regional relationships between habitat and breeding population change for a declining species in eastern North America. Without this approach, it would be challenging to reveal abundance trends across a broad landscape. Other long-term and spatially extensive landbird surveys would benefit from a similar analytical strategy to guide conservation and management priorities. In 2008, it was estimated that Nova Scotia had lost 22% of singing males (9,049 individuals) since 1970, likely as a result of a decrease in small-diameter size class forests (Kelley et al., 2008). It had been suggested at that time that active management of roughly 730 km² of forestland for small-diameter size class is required to increase woodcock populations to historical levels. With continued population declines, this area is likely now higher. However, our spatially explicit analysis has shown that efforts to improve habitat availability should be targeted in the north and south of the province where populations

continue to decline. Fortunately, 14.4% of working forest in Nova Scotia is owned and maintained by the forest products industry with another 30.8% as Crown land, which could greatly aid in achieving these habitat goals towards sustaining regional woodcock populations (Lahey, 2018). Realising a positive population status for woodcock within Nova Scotia and beyond to their continent-wide range will require large-scale and long-term planning through more extensive provincial, national, and international partnerships focused on providing habitat for the suite of wildlife species dependent on young forests.

AUTHORS' CONTRIBUTIONS

S.E.G. designed the study and wrote the manuscript, L.F.G.G. conducted the analyses, M.L.M. and G.R.M. facilitated inception and collaboration of the study. All inputted to the manuscript and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENTS

All SGS data are archived and publicly available from the USFWS (USFWS Migratory Bird Data Center, 2019). All habitat data from the FIP are archived and publicly available from the NSDLF (Nova Scotia Department of Lands and Forestry, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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