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Forest degradation, not loss, drives widespread avian population declines

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Abstract

In many regions of the world, forest management has reduced old forest and simplified forest structure and composition via reliance on monoculture tree plantations. We hypothesized that such forest degradation has resulted in long-term habitat loss for forest-associated bird species of eastern Canada (130,017 km$^2$) which, in turn, has affected bird population declines. Back-cast species distribution models revealed that despite little change in overall forest cover, breeding habitat loss occurred for 66% of the 54 most common species from 1985-2020. This habitat loss was strongly associated with population declines for 72% of species, as quantified in an independent, long-term dataset. Since 1985, net forest bird abundance has declined in this region by an estimated 33-104 million birds due to habitat loss alone. The effects of forest degradation may therefore be a primary cause of biodiversity decline in managed forest landscapes.
Most conservation policy has focused on reducing deforestation, and this approach remains fundamental to many conservation strategies. Effects of forest loss on global biodiversity are well-known and directly measured and often used as estimates of biodiversity decline. Forest degradation is also expected to be a key driver of biodiversity decline and is a component of broad-scale biodiversity agreements (e.g., Aichi Biodiversity Targets in the Convention on Biological Diversity, REDD+ [Reducing Emissions from Deforestation and Forest Degradation]). However, forest degradation has been much more challenging to measure and there have been few attempts to quantify its effects on species’ population trends across entire regions.

From a biodiversity standpoint, forest degradation is defined as the reduction or loss of biological complexity in forest ecosystems. Forest management alters forest complexity most commonly in two important ways; first, due to harvesting, managed forests tend to be younger than under a natural disturbance regime, with potential implications for species associated with mature or old-growth forests. Second, because tree plantations tend to yield more wood per area, managers are increasingly converting native forests to plantations. Unlike most natural forests, plantations tend to be comprised of only one or two tree species. Plantation area is expected to rise as they are increasingly considered “natural climate solutions.” Such changes in age-class structure and forest composition may occur without any overall loss in forest cover, and have thus been largely ignored. Nevertheless, quantifying forest degradation is of critical importance to understanding biodiversity responses in regions where timber harvest and regrowth predominates (e.g., Canada, western US, Scandinavia, Russia).

The importance of quantifying forest degradation effects is particularly critical considering recent findings by the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES) that the planet is facing a biodiversity crisis. Causes of population declines remain poorly understood for many species. For instance, recent work has quantified widespread avian population declines, but researchers are still searching for the mechanisms driving these losses. Hypotheses explaining avian population dynamics include habitat loss on the wintering grounds, direct effects of toxic chemicals, and climate change effects throughout the annual cycle. However, the hypothesis that population declines, for birds or other taxa, are driven by forest degradation and resultant breeding habitat loss, remains largely untested. This lack of robust testing is likely for two methodological reasons. First, changes in forest composition and age-class structure are more challenging to detect than forest loss. Second, it is well known that species have different habitat requirements, which often do not correspond to coarse, human-defined land-cover categories.

Here, we used species distribution models with Landsat TM reflectance bands as predictor variables to quantify habitat amount for each of the most common 54 forest-dependent bird species in the Acadian Forest of eastern Canada (130,017 km²). Since Landsat has been available since 1985, then enabled us to back-cast habitat model predictions to quantify habitat change for each species over 35 years (1985-2020). Under the hypothesis that changes in forest degradation is driving population declines, we predict that we would see (1) little net change in total forest area (due to the rates of forest regeneration matching forest harvest), (2) reductions in breeding habitat across forest-associated species, particularly those associated with mature native forest which is under pressure from timber harvest, and (3) links between habitat loss and long-term...
These links between habitat change and populations are not necessarily a given, and several alternative hypotheses are possible. First, initial habitat may have been underutilized, in which case individuals initially occur at low population density and then pack into remaining habitat as it declines over time\textsuperscript{21}. Second, over a 35-year period, bird habitat preferences could relax or shift via behavioral plasticity or strong evolutionary selection pressure exerted by habitat loss\textsuperscript{22}.

The effects of habitat loss should be particularly severe when habitat amount is low\textsuperscript{23,24}. Alternatively, some species may exhibit rapid population declines even at low levels of initial habitat loss\textsuperscript{1}. Although these alternative hypotheses have been tested using space-for-time studies\textsuperscript{25} to our knowledge no studies have tested whether species’ populations exhibit threshold behavior during the process of habitat loss over the long-term. We formally tested this ‘extinction threshold hypothesis’ using long-term habitat change predictions, along with independent data on bird population trends. We predicted that populations in landscapes with the lowest amount of habitat at the beginning of our time series should experience the strongest negative effect of further habitat loss.

**Results**

The Acadian Forest of eastern Canada has shown a pervasive signal of forest change since 1985 (Fig. 1), despite a relatively stable trend in total forest cover (Fig. 2A). Since 1985, >3 million ha have been clearcut (Fig 1A), with most of this area now occupied by either tree plantations (Fig. 1A, B, D) dominated by single tree species\textsuperscript{26} or a mix of early successional tree species (Fig. 1B). This pattern of forest harvest followed by rapid regeneration appears to be common across many forest regions of North America (e.g., central Canada, southeastern US, western US; Fig. 1C)\textsuperscript{10}, and can be considered forest degradation in that these practices simplify forest structure, reduce tree species diversity, and truncate old forest age classes\textsuperscript{7}.

Overall, species distribution models (SDMs) using Landsat reflectance bands as predictors performed well for most species when tested on 50% independent hold-out data (Fig. S1; \(\bar{\text{Area Under the Curve (AUC)}}=0.69\) [range: 0.58 – 0.86]) and when tested on training data (\(\bar{\text{AUC}}=0.74\) [range: 0.61 – 0.91]). This model performance is high considering the fine spatial scale of predictions (30 m\(^2\) pixels); SDMs therefore provided reliable estimates of habitat distributions for all 54 species.

Back-cast distribution models revealed habitat declines occurred for 66% of species during 1985-2020; 93% of species exhibited habitat reductions over the past decade (Figs. 2, S2). Species showing the greatest decreases in habitat were Golden-crowned Kinglet (\textit{Regulus satrapa}; -38\%) and Blackburnian Warbler (\textit{Setophaga fusca}; -33\%, Movie M1), with 7 species showing habitat declines >25\% (Fig. 3). Most species with strongly declining habitat are associated with mature forests\textsuperscript{27} (Fig. 3A, B) which is consistent with forest degradation due to harvesting of mature forest. Indeed, clearcut harvest alone was strongly associated with habitat declines for all mature-forest-associated species (Fig. S3). Fifteen species exhibited habitat increases, and most (14/15) of these tend to be associated with young or immature forests (Fig. 4A and 4B).
We tested the hypothesis that habitat loss affected bird population declines using Breeding Bird Survey Data (BBS)\textsuperscript{28} for the Maritime Provinces (see Methods). First, we used SDMs to quantify habitat change (1985-2019) in landscapes surrounding BBS routes ($N=90$; see Methods). We then used Bayesian hierarchical models\textsuperscript{20} to test whether SDM-predicted habitat loss or gain in each given year of the time series drove population changes for each species along each route. Importantly, BBS data are entirely independent of our SDMs, so this test also represents a strong validation of our habitat models (18). Bayesian models revealed a strong effect of habitat loss or gain on population abundance (Fig. 4). Abundance changes for all but three species tracked annual habitat change with 80% posterior distributions that did not include zero (vertical line in Fig. 4A). Habitat change significantly affected population change for 48 species ($>0.9$ posterior probability; Fig. 4B).

Given this strong association between habitat and population changes for most species, we estimated the net number of breeding individuals lost due to habitat loss from 1985-2020 using published accounts of territory sizes for each species\textsuperscript{27} (see Table S1). Across all species, backcast species distribution models (SDMs) indicate that 28,215,247 ha (282,153 km\textsuperscript{2}) of habitat has been lost, equating to a loss of between 16,779,704 and 52,243,938 breeding pairs (33,559,408 – 104,487,876 individuals; Supporting Methods, Table S1). One might expect that forest degradation, rather than resulting in broad-scale declines across species, is simply causing species turnover from mature forest bird species to young-forest associates. However, it is important to note that we quantified net bird decline from an unbiased list of the 54 most common forest bird species in eastern Canada. This list included both early and late successional species. Such net bird declines could be due to the fact that (1) even some early seral species are losing habitat (perhaps due to conversion from diverse early successional forest to single-species plantations) and (2) in this region, more species occupy older forests than regenerating forests.

We also quantified overall population trends for 54 species of forest birds using data from the BBS (Fig. 5). These estimates give the total magnitude of population changes which include, but are not limited to, habitat loss or gain effects. Thirty-nine of the 54 species examined (72%) are in population decline (defined as having 95% credible intervals that do not bound zero). The magnitude of the declines for 15 forest bird species is severe ($>5\%/year$). It is notable that most species exhibiting both habitat loss and population declines are mature-forest associates (Fig. 3A; bottom left quadrant, dark green dots), with mature-forest species exhibiting the greatest habitat losses (Hierarchical regression, $\hat{\beta} = -16.66$ [6.32 SE]; Fig. 3B, see SI Methods ‘Habitat Associations’).

BBS declines are not restricted to mature-forest species; several species in rapid population decline are early seral species (e.g., Canada warbler [Cardellina canadensis], Lincoln’s Sparrow [Melospiza lincolni], Mourning Warbler [Geothlypis Philadelphia]; Fig. 3A bottom right quadrant). Despite the fact that these species have gained habitat over 35 years, their populations continue to decline. Only three species (Black-capped Chickadee [Poecile atricapillus], Hairy Woodpecker [Leuconotopicus villosus], and Ruby-throated Hummingbird [Archilochus colubris]) are increasing in abundance. Populations of these species increased despite evidence of habitat decline (Fig. 3A; top left quadrant) – perhaps because each benefit from anthropogenic habitats and supplemental food. Importantly, habitat changes from 1985-2019 along BBS routes were representative of changes at the scale of the entire region for most species (Fig. S4), so
BBS population trends are highly likely to reflect population trends at the regional scale. This contrasts to the 1965-1985 period when habitat changes along routes differed markedly from the broader region.29

We also modeled BBS population trends over the past 10 years, as this is the period of importance for informing listing decisions under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Nine species have exhibited population declines >30% over 10 years (Fig. S5), which meets the criterion for consideration as “Threatened” under COSEWIC Criterion A2.30

We found support for the hypothesis that the effects of habitat loss are particularly severe in landscapes with low habitat amounts. The model testing for a statistical interaction between initial habitat amount in landscapes surrounding BBS routes and annual habitat loss was generally well supported across species; the effect of habitat loss was strongest when habitat surrounding routes had already been reduced to a low level prior to 1985 (Fig. S6).

Discussion

Overall, our results support the hypothesis that forest degradation from 1985 to 2020 has resulted in pervasive declines in bird habitat. Forest changes have included conversion from mixed-species forests to single-species conifer-dominated plantations, and clearcutting old forests without equivalent regrowth into old age classes. Notably, over the same time period, forest cover changed very little, and harvest practices in this region are considered “sustainable” from a wood production standpoint.31

The habitat changes we observed were strongly associated with long-term population changes for most forest bird species in our study and appear to be driving severe population declines (Figs. 4, S4) in several species, including those associated with mature forest (e.g., Bay-breasted Warbler [Setophaga castanea], Blackburnian Warbler, Boreal Chickadee [Poecile hudsonicus], Winter Wren [Troglodytes hiemalis]). Populations of four mature-forest associated species are declining at rates >30% over the past 10 years (Fig. 4), which is a rate consistent with “threatened” COSEWIC status. We recommend extending the approach we used here to model habitat and habitat change across eastern North America, which encompasses most of the ranges of species in this study. This analysis could be of great importance to future listing decisions.

The strong link between habitat change in landscapes surrounding BBS routes and bird population changes indicates that SDMs are highly predictive of bird population trends. This finding has two important implications; first, it means that broad-scale habitat loss in landscapes beyond the BBS routes is driving region-wide population declines. Second, in eastern Canada, at least, this constitutes evidence that breeding habitat loss due to forest degradation is a primary cause of observed widespread population declines in birds (Rosenberg et al. 2019).

For several species, rates of population decline seemed to outpace rates of habitat decline (compare x- and y-axes in Fig. 3A). For instance, Blackburnian Warbler populations have experienced a ~70% decline over 35 years (4.5%/year; Fig. 4B), but only 33% of habitat has been lost. One explanation for this apparent mismatch is that populations show particularly
strong declines at low habitat amounts, which supports the ‘extinction threshold’ hypothesis. Indeed, our results indicate that the effect of habitat loss is much greater in landscapes with low habitat amounts (Figure S5). The mechanism for such threshold effects could be due to habitat fragmentation; once patches shrink below the size of an individual territory, it is likely to have higher rates of local extinction.Disconnected patches are also less likely to be colonized.

However, the mismatch between population versus habitat declines could signal that additional, non-habitat-related factors are compounding declines. In support of this idea, several species that are gaining, or at least not losing, habitat are in strong population decline according to the BBS (e.g., Canada warbler, Lincoln’s sparrow, Philadelphia vireo [Vireo philadelphicus]). Our results do not preclude the well-known effects of wintering ground habitat loss, climate change, mortality on migration, contaminants, or intensification of plantation management practices. Population declines in species associated with regenerating forest are particularly cryptic because habitat amount for these species tends to be increasing (except for Olive-sided Flycatcher [Contopus cooperi], which exhibited habitat declines of ~18% over 35 years). One hypothesis is that populations of birds that prefer early seral stages, despite having potentially more habitat, are declining due to climate change over the past three-and-a-half decades (~1°C increase over 30 years). Given that such stand types are likely warmer due to more open and/or shallow canopies, any increases in ambient temperatures are likely to be more severe in plantations and naturally regenerating forest than it is in mature forest, which would exert physiological stresses and potentially have population consequences on birds. This effect could be magnified by the fact that several early seral species are more associated with young coniferous forest— which is typically found further to the north in Boreal forests.

More subtle mechanisms for habitat loss due to forest degradation reported in this study would likely have remained undetectable without a species-specific habitat modeling approach. Given that no two species associate with identical habitats, our model enabled us to quantify habitat on a species-specific basis and then track habitat change over multiple decades (since 1985, the origin of Landsat). If we had used generic, human-defined cover types (e.g., “forest” or “mature forest”) as predictor variables, species-specific patterns in habitat change would have been obscured. Similar approaches could be applied in other regions and for other taxa, if species spatial distribution data are available.

Several lines of evidence support forest management as a driver of forest degradation rather than alternative mechanisms (e.g., climate-mediated forest decline, natural disturbance). First, our habitat models did not include climate data, so the reflectance changes from satellite imagery used in our SDMs were predominantly due to forest compositional changes. Although climate (e.g., interannual differences in precipitation) can cause subtle differences in reflectance (leaf color) over time, most changes in the magnitude of reflectance are due to changes in forest composition or cover rather than effects of climate. Indeed, if the observed habitat declines were due to climate effects or natural disturbance, we would expect to see parallel habitat declines in protected areas, which we did not (Fig. S7). Second, species exhibiting the greatest declines in habitat are those most strongly associated with mature forest (Fig. 3 A, B)—which is the primary target of timber harvest. Indeed, amount of area clearcut was strongly associated with habitat loss across the region in each year, for mature-forest-associated bird species (Fig. S3). Third, it is well established that large-scale intensive forest management practices in this
region have resulted in substantial increases in single-species tree plantations (Fig. 1A)\textsuperscript{26}. In areas that have not been planted, ingrowth of shade-intolerant hardwoods and balsam fir (\textit{Abies balsamea}) predominate; these replace original shade-tolerant deciduous and coniferous species (Fig. 1B) and are unlikely to be succeeded by such species given current truncated harvest rotations. We predict that similar effects of forest change could be prevalent in other temperate forests globally that are heavily managed for timber production (e.g., southeastern USA, Pacific Northwest USA, Chile, Scandinavia). These regions show little net loss of forest cover but high rates of forest reductions and regrowth (e.g., Fig.1C)\textsuperscript{10}, which is symptomatic of intensive forest management with potential for forest degradation.

Overall, our results point to broad-scale declines in forest birds of the Acadian Forest of eastern Canada. For most species we assessed, these declines are driven by habitat loss that is primarily due to forest degradation rather than forest loss. We expect that similar consequences for biodiversity may hold in other intensively managed forests of the world. This mechanism for bird population declines would have been invisible using coarse, human-defined categories of ‘habitat’ (i.e., forest cover)\textsuperscript{18}.

If maintaining non-declining populations of forest birds is the goal, conservation measures that halt the alteration of habitat, particularly in diverse, older forests, will be necessary. Future conservation efforts will be most effective if they maintain relatively high proportions of habitat, as such landscapes appear less susceptible to further population declines. Of course, this may come at the expense of wood production, but potentially less so with forest-landscape zoning that maintains reserves, ecological forestry and strategic, and spatially limited intensive management\textsuperscript{40}.

**Materials and Methods**

**Bird Data**

We selected 54 species of birds that were designated as forest associated by Partners in Flight (PIF 2021) and had sufficient data in the Maritimes Breeding Bird Atlas (MBBA) point count dataset\textsuperscript{41} to facilitate distribution modeling (N>200 individual location records). Between 2006 and 2010, avian point counts (Ralph et al. 1995) were conducted at 12,272 points across three Canadian provinces: New Brunswick, Nova Scotia, and Prince Edward Island (Fig. S9). These provinces represent the core of the Acadian Forest in Canada and encompass \textgreater 130,000 km\textsuperscript{2}\textsuperscript{42}. Point counts were conducted from May 29 to July 3, no earlier than 30 minutes before sunrise and no later than 5 hours after sunrise. Counts were 5-minutes long, and species were recorded within an unlimited radius. Points were located to ensure maximum coverage of Breeding Bird Atlas squares\textsuperscript{41}; the coverage goal was to complete 10-15 point counts in each 10 km\textsuperscript{2} atlas square. Most points were randomly placed along roads, but a small proportion (8.4%; N=1034) were conducted off-road. These points were placed >100 m from roads and were spaced >300 m apart.

**Remote-sensing Data**
We followed the methods of Shirley et al (2013) to model species as a function of six visible Landsat bands that we used as predictor variables in our SDMs. Using Google Earth Engine, we obtained cloud-free spectral surface reflectance from Landsat collection 1 Tier 1 from 2006 to October 2010 building and testing SDMs. In addition, we used reflectance bands to create harmonic fitting to capture the cyclical reflectance change due to vegetation phenology and disturbance. Landsat data are collected at 30 m pixel resolution. We used the CCDC (Continuous Change Detection and Classification) algorithm in Google Earth Engine to fit each six Landsat spectral bands in the form of:

\[ R_t = A_0 + B_0 t + \sum_{k=1}^{3} \left\{ A_k \cos\left(\frac{2\pi T}{T} kt\right) + B_k \sin\left(\frac{2\pi T}{T} kt\right) \right\} \]

where \( R_t \) is surface reflectance at time \( t \) (represented as day of year) for a spectral band, \( A_0 \) is intercept, \( B_0 \) is the interannual trend (slope) of surface reflectance, \( A_k \) and \( B_k \) are the coefficients for intra-annual spectral change; \( k \) is temporal frequency of harmonic components (\( k = 1, 2, \) and 3). \( T \) represents the number of days in a year (\( T = 365.25 \)). CCDC detects where change occurs in the spectral trajectory. The advantage of this approach is that it capitalizes on (1) within-year changes in reflectance (e.g., differential rates of leaf out across tree species), and (2) among-year changes in reflectance caused by disturbance and regrowth, to add additional forest composition information to raw reflectance bands. The harmonic coefficients (8 coefficients) for each band (6 bands) as well as 6 root-mean-squared error from the harmonic fit from the fits were used as environmental variables in the Maxent model (54 variables; see Species Distribution Models below).

**Species Distribution Models**

We used Maxent implementation in Google Earth Engine (equivalent of version 3.4.4) to construct presence-only SDMs for the occurrence of 54 forest-associated species. Bird occurrence data were from the MBBA, and predictor variables constituted only the remotely sensed variables described above. Maxent uses presence-only data to predict species distributions based on maximum entropy theory. The algorithm estimates a probability distribution for species occurrence that is closest to uniform while still subject to environmental constraints (in this case Landsat predictor variables). We generated a random sample of 10,000 pixels from the study area to serve as background samples (‘pseudoabsences’). Points sampled along roads were jittered up to 180m to the most proximate forest patch to the point-count location. The SDMs were constructed in Google Earth Engine, using the linear, product and quadratic feature types provided by Maxent. The observation samples were split into equal 50% datasets which served as training and validation data for all species. A regularization multiplier was optimized by iterating the beta parameter from 0.1 to 2.0 for all 54 species separately, and the beta parameter with the highest Area Under the Receiver Operating Characteristics Curve (AUC) value for validation dataset were picked to create the final maxent model. We evaluated distribution models using AUC derived from predictions on the independent validation data. The value of AUC ranges from 0 to 1. An AUC value of 0.50 indicates that the model did not perform better than random, whereas a value of 1.0 indicates perfect discrimination. Finally, we acquired Landsat images and calculated predictor variables (see Remote Sensing Data above) for the 1985-2020 period and used SDM models to back-cast species distributions predictions across for each species across the entire region in each year (e.g., Fig. 2 B-F).
scripts for Landsat data analysis (CCDC) and Maxent models are available at https://figshare.com.

Breeding Bird Survey Data and Population Trends

To test whether habitat change, measured using back-cast SDMs, predicted population trends we compiled forest bird population data from the Canadian Breeding Bird Survey between 1985-2019 within the boundary of the Maritime Provinces of Canada (New Brunswick, Nova Scotia, Prince Edward Island), which represents the core of the Acadian Forest in Canada and encompasses >130,000 km². The BBS consists of a set of routes, each 40 km in length, along secondary roads surveyed annually by trained observers since 1966 (not all routes were surveyed every year). Observers stopped at 50 regularly spaced locations within each landscape and recorded the species of every bird observed during 3-minute surveys. We combined data at each stop to provide the total number of individuals of each species seen during each year within a landscape. We quantified habitat change for each species in each year within 200 m diameter buffer landscapes along each of the 90 routes (i.e., 40 km x 200 m areas) and used this change as the main effect in our models. A positive effect of habitat gain or a negative effect of habitat loss on population changes in each year would constitute strong, independent validation of our habitat models and evidence that habitat change affect population size.

We modeled trends in 54 bird populations using a modified version of the hierarchical model described by Sauer and Link (2011). The BBS data have a complex nested structure, with counts within years, within landscapes for individual species. There are several well-known limitations of these data; counts tend to be overdispersed, observers have different skill levels and can change among years, and some species are more difficult to detect in an observer’s first year of surveying. The model described by Sauer and Link (2011) attempts to address these limitations while simultaneously accounting for the complex and hierarchical structure of the data. The basic form of this model is an overdispersed Poisson regression with a covariate for year, which provides inference of trends in bird abundance within each surveyed landscape. As these models control for, but do not correct, observer bias the model provides an index of abundance, rather than true abundance of birds in each landscape. We used several different model structures to investigate 1) population trends by species, 2) the effect of habitat change along each route by species, and 3) the effect of initial habitat amount in mediating the effect of habitat loss on abundance. For all models we used the survey data from 1985 to 2019 with all 90 BBS survey routes in the provinces of New Brunswick, Nova Scotia, and Prince Edward Island (see SI Methods).
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Conceptualization: MGB, ASH
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Writing—review & editing: all authors

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Data and materials availability: All data, code, and materials used in the analyses are available at https://figshare.com
Fig. 1A Study area in context of other regions of North America that have similar rapid rates of forest loss (pink), then gain (purple) – which is likely a signal of commercial forest harvest followed by rapid regeneration. Panel B shows cumulative clearcut disturbance (pink) across the Maritime provinces of eastern Canada from 1985-2020 along with the area that has been converted to plantations (purple). Panel C shows cumulative area clearcut and planted across the study area. Methods for mapping plantations and disturbance are given in the SI. Panel D shows the area of forest that has been clearcut since 1985 (left bar) for public land and private woodlots for a subset of the study area (New Brunswick; 72,908 km²), and forests that have not been clearcut since that date (right bar). Most forest cut since 1985 has been planted, or pre-commercially thinned to favor conifer species (purple bar) or has regenerated as shade-intolerant hardwood (IH) or balsam fir (BF); pink bar). In contrast, forest that has not been recently clearcut is comprised of shade-tolerant tree species (green bar). Intolerant hardwood/balsam fir stands in areas not recently harvested likely originated from clearcutting before 1985. Data in D were derived from the NB Forest Inventory (2010) so do not include changes over the past decade. Panel E shows native mixed deciduous/conifer forest (left) in relation to older conifer plantation forest (right) that replaced the original mixed forest.
Fig. 2 A. Habitat trends (1985-2020) for the seven bird species exhibiting the greatest population declines according species distribution models (SDMs). All of these species are mature-forest associated (see Fig. 4a, 4b). Over the same time interval, total forest cover did not decline (black line), indicating that habitat loss is a function of forest degradation rather than loss. B-F show predicted habitat distributions for three example species in 1985 and 2020 respectively; 25-33% of habitat (shown in blue, non-habitat is in yellow) has been lost over this period across the entire region. Habitat loss quantified using SDMs strongly predicted population trends for forest bird species.
Fig. 3A Relationship between habitat change, estimated from species distribution models and independently derived estimates from the North American Breeding Bird Survey (BBS) for the Acadian Forest. Bird species of mature forests (M; green dots) exhibit the greatest habitat loss; this is generally reflected in strongly negative population trends. Bird species associated with regenerating forest (R; red dots) tend to have stable or increasing habitat, but still show BBS population declines. B shows the relationship between quantitatively derived estimates of mature-forest association and habitat change from 1985-2020. Mature-forest associated species tend to be losing the most habitat in relation to immature (I; light-green dots) and regeneration-associated species. Successional stage categorizations (R, I, M) are from Birds of the World (BOW). Gray shading shows 95% credible intervals. Only a subset of species shown in B (those with quantitative data for mature forest associations).
Fig. 4 Bayesian posterior distributions for the effects of SDM-modeled habitat gain or loss (x-axis) in a given year on bird abundance in the corresponding year, using Breeding Bird Survey data (A). Most species were strongly influenced by the effect of habitat change on abundance, which support the hypothesis that bird population decline is driven at least partially, and often substantially, by breeding habitat loss. Panel B shows the posterior probability that habitat gain or loss had an effect on population change for 54 forest bird species.
Fig. 5 Population trend parameter estimates and posterior distributions for 54 species of forest birds derived from Bayesian models. 72% of species that are sufficiently common to model experienced population declines over 1985-2019. Panel B shows predicted linear population trends for 1985-2019 including annual variation estimated from Breeding Bird Survey data. Shaded purple areas reflect 95% credible intervals and reflect magnitude of species population declines shown in A. Populations of these eight mature-forest associated species have declined 60-90% over the period observed.
Supplementary Materials for

Forest degradation, not loss, drives widespread avian population declines

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This PDF file includes:

Supplementary Methods
Figs. S1 to S8
Tables S1 to S2
References (1-7)

Other Supplementary Materials for this manuscript include the following:

Movie S1
Supplementary Methods

Breeding Bird Survey Models
We fit all models in JAGS using the ‘rjags’ package, in the statistical software R. We used four Markov Chain Monte Carlo (MCMC) chains for each model with random starting values. We optimized MCMC tuning with 1000 iterations and then sampled for 24000 iterations, discarding the first 2000 as a burn-in, and then thinned by discarding every other iteration, leaving a total of 11,000 iterations per chain. We assessed convergence by calculating the Gelman-Rubin diagnostic and examining trace plots of the posterior distributions of every parameter; no parameter diagnostics indicated lack of convergence.

Regional Trends
We investigated how bird counts have changed in the study period by modeling each species’ annual count at route \( i \), route-observer combination \( j \), and year \( t \) \((y_{ijt})\) as,

\[
\begin{align*}
y_{ijt} & \sim \text{Poisson}(\lambda_{ijt}) \\
\log(\lambda_{ijt}) & = \alpha_j + \gamma_t + \text{first.year}_{ij} \eta + \text{year}_{it} \beta_i + \epsilon_{ijt}
\end{align*}
\]

\[\begin{align*}
\alpha_j & \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \\
\gamma_t & \sim \text{Normal}(0, \sigma_\gamma^2) \\
\beta_i & \sim \text{Normal}(\mu_\beta, \sigma_\beta^2) \\
\epsilon_{ijt} & \sim \text{Normal}(0, \sigma_\epsilon^2)
\end{align*}\]

where \( \alpha_j \) are effects of unique route-observer combinations, \( \gamma_t \) are year effects, \( \eta \) is an effect of an observer being in their first year of conducting surveys (the variable first.year is an indicator (1 or 0) of when a route was observed for the first time by a specific observer and a zero otherwise; following Sauer and Link (2011)), \( \beta_i \) is the trend for route \( i \) (the variable year indicates the year of the survey for each route) and \( \epsilon_{ij} \) is general dispersion beyond that accounted for by the Poisson variance. The route-specific trends \( \beta_i \) arise from a distribution with mean \( \mu_\beta \) and variance \( \sigma_\beta^2 \) representing the regional trend for the species, while \( \alpha_j \) arise from a distribution with mean \( \mu_\alpha \) and variance \( \sigma_\alpha^2 \), representing the regional average route-observer effect. We used diffuse priors on our parameters as,

\[\begin{align*}
\mu_\beta, \mu_\alpha, \eta & \sim \text{Normal}(0,10) \\
\sigma_\beta^2, \sigma_\alpha^2, \sigma_\gamma^2, \sigma_\epsilon^2 & \sim \text{Gamma}(0.001,0.001)^{-1}
\end{align*}\]

Population Trend – Habitat Model
We investigated how bird counts have changed across the study period due to changes in habitat. We followed the same model structures as above, but replace year with the variable habitat as,

\[
\begin{align*}
y_{ijt} & \sim \text{Poisson}(\lambda_{ijt}) \\
\log(\lambda_{ijt}) & = \alpha_j + \gamma_t + \text{first.year}_{ij} \eta + \text{habitat}_{it} \beta_i + \epsilon_{ijt}
\end{align*}
\]

\[\begin{align*}
\alpha_j & \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)
\end{align*}\]
\[ y_t \sim \text{Normal}(0, \sigma^2_\gamma) \]
\[ \beta_i \sim \text{Normal}(\mu_\beta, \sigma^2_\beta) \]
\[ \epsilon_{ijt} \sim \text{Normal}(0, \sigma^2_\epsilon) \]

where ‘habitat’ is a normalized covariate (centered at zero and scaled to unit variance) of the amount of habitat available for each species in a route and year. The parameter \( \mu_\beta \) is the average effect of habitat across all routes. Prior distributions are defined similarly as the above models.

**Testing for Habitat Loss Thresholds**

We also investigated how habitat amount in the initial year (1985) mediated the effect of habitat change on bird abundance using the model,

\[ y_{ijt} \sim \text{Poisson}(\lambda_{ijt}) \]
\[ \log(\lambda_{ijt}) = \alpha_j + y_t + \text{first.year}_{ij} \eta + \text{habitat}_{it} \beta_i + \epsilon_{ijt} \]
\[ \beta_i \sim \text{Normal}(\mu_\beta, \sigma^2_\beta) \]
\[ \mu_\beta \sim \beta_0 + \xi \times \text{init.habitat}_i \]
\[ \alpha_j \sim \text{Normal}(\mu_\alpha, \sigma^2_\alpha) \]
\[ \gamma_t \sim \text{Normal}(0, \sigma^2_\gamma) \]
\[ \epsilon_{ijt} \sim \text{Normal}(0, \sigma^2_\epsilon) \]

where ‘habitat’ and ‘init.habitat’ are normalized covariates (centered at zero and scaled to unit variance within a species) of the amount of habitat available for each species in a route and year and the initial amount of habitat available to the species in the first year, respectively. The parameter \( \beta_0 \) is the effect of habitat change at mean initial habitat, while the parameter \( \xi \) is the effect of initial habitat, which modulates the route-level effect of habitat changes (\( \beta_i \)). Prior distributions are defined similarly as the above models. All Jags code is available at https://figshare.com/s/72d8da46d2041c984fdb.

**Habitat Associations**

We used Birds of North America (BNA) to establish forest successional associations for each bird species. If BNA accounts indicated that a species was associated with “old” or “mature”, or “dead wood” we counted the species as a “mature-forest associate”. Alternatively, if the account indicated that the species was associated with “open”, “bog”, or “shrub” habitat (excluding mature species nesting in shrub understories) we classified the species as a “young-forest associate”. We also used an independent bird point count dataset (from\( ^5 \) to model all available species as a function of both deciduous and coniferous trees >20 cm in diameter. We used logistic regression with a binomial error distribution to model the presence or absence of each species as function of each of these variables. If species showed positive coefficients for either deciduous or coniferous large trees, we deemed these mature-forest associates. If a species’ model had a negative coefficient for both of these variables, we deemed it a young-forest associate. However, if confidence intervals overlapped zero, we categorized the species as a forest-age generalist. Only 30/54 species were sufficiently abundant in this dataset to yield model estimates; in all but three cases (Black-and-White Warbler, Swainson’s Thrush, Hermit Thrush)
these estimates concurred with the BNA accounts. In these cases of disagreement, we used the local quantitative estimates for categorization. Finally, we checked these classifications with existing habitat categories used by the New Brunswick Department of Natural Resources and we found no discrepancies with our final categorization.

We examined the relationship between habitat change from 1985 - 2020 and mature forest association (Fig. 3B) using linear regression with habitat change as the dependent variable. The mature forest association has uncertainty associated with the estimates, so a simple regression using the mean mature forest association estimate would deflate the uncertainty in this relationship. Thus, we conducting this regression in a Bayesian framework, treating the true, unobserved mature forest association as a random variable. We used the mean and standard error of the estimated mature forest association to develop a prior on these values with mean equal to the estimated mean and variance equal to the squared standard error. We fit models in JAGS, running 4 chains each for 20,000 iterations, discarding the first 10,000 iterations as burn-in and assessing convergence using the Gelman-Rubin diagnostic.

Estimates of Loss/Gain in Bird Numbers

To estimate the total number of birds lost or gained across the region from 1985-2020, we first calculated net habitat loss or gain for each species. We gleaned territory size of each from the Birds of North America Database and multiplied: habitat change x territory size. We made this calculation for both the minimum territory size observed for each species, as well as the maximum. Finally, we summed these values across all 54 species to provide lower (maximum territory size) and upper (minimum territory size) bounds on the net change in bird numbers for the Maritime provinces. The equation for this calculation is:

\[ \sum_i ((H_{1985} - H_{2020}) \times T) \]

Where \( H \) = habitat in each time period, and \( T \) = minimum, or maximum territory size for the \( i \)th species.

Modeling Plantation Area and Clearcut Disturbance over Time

Although forest inventory data for public land and small private woodlots are freely available for New Brunswick, no such data exist for the entire study area, and are not available each year from 1985-2020. We therefore used a distribution modeling approach to predict and then backcast plantations and disturbances, similar to our bird habitat SDMs. We used 97,627 samples of known plantations >5 years since establishment as presence points, then extracted harmonic coefficients as well as the synthetic spectral images corresponding to July 1 for years 1990,1995, 2000, 2005, 2010, and 2015. We used all 6 Landsat spectral bands (blue, green, red, nir, swir1, and swir2). We held out 50% of the data (N=48,813) for model validation. Together with random samples of 20,000 background locations were used for Maxent modeling. Regularization optimizations were applied by comparing the AUC with varying beta from 0.1 to 2.0. The model performance was not sensitive to regularization, so the default value of 1.0 was used. The resulting model has an AUC of 0.872. We applied the Maxent predictions to all years from 1985 to 2020. A threshold (0.283) corresponding to equal sensitivity and specificity was chosen to
classify the map into plantations versus non-plantations. A spatial filter of a minimum mapping
unit of 11 pixels was applied to remove the scattered small patches from the final map, and we
masked the final plantation map using our disturbance map (see below) to ensure that no areas
that had not been clearcut were included as plantations.
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Maritime Provinces. AUCs were calculated using 50% of locations held-out as independent test prediction success ranging from 0–1 (perfect predictions for 54 forest bird species of the Maritime Provinces. AUCs were calculated using 50% of locations held-out as independent test data.

Figure S1. Area Under the Receiver Operating Characteristic Curve (AUC) – a measure of model performance. The red line indicates the threshold for calling a location as positive (i.e., predicted presence).

Supplementary Figures and Tables
**Fig. S2** Habitat change (1985-2020) for 54 species of forest birds according to back-cast species distribution models. Transitions from green, through yellow, to red across cells indicate annual habitat loss. Sixty-six percent of species show net habitat loss over the full time period, and 93% lost habitat over the past 10 years.
Fig. S3. Relationship between area clearcut occurring in each species’ habitat in each year across the study area and habitat loss for each of 23 mature-forest associated species. Each dot represents a year (1985-2020). Clearcut area is the sum of t-1 and t (the year we quantified habitat loss because harvest can occur in winter before, and fall following the breeding season). Blue lines are regression lines and gray bands are 95% confidence intervals. Solid lines indicate the isometric (1:1) relationship between clearcuts and habitat loss. As expected, clearcutting within habitat is strongly associated with habitat loss, which indicates that ingrowth of new habitat has not compensated for by habitat loss (which would have obscured this relationship). Also, amount
clearcut is always greater than habitat loss, indicating that habitat decline is unlikely due to changes in Landsat reflectance bands caused by climatic factors. Species codes are provided in Table S1.
**Fig. S4.** Habitat trends within 100 m of BBS routes (red lines) versus the entire Maritimes region (green lines) for 54 species of forest birds. Habitat trends along BBS routes tend to reflect changes in the region except for a few species (e.g., Black-throated Blue Warbler).
Fig. S5 Ten-year population trend estimates for 54 species of forest-associated birds across the Maritime Provinces of Canada. Number below species names indicate the Bayesian posterior probability that the species is declining at a rate >30% over 10 years (9 species fall into this category, 4 of which are mature-forest associated).
Fig. S6 Effect of habitat amount in the landscape (200 diameter landscapes along 40 km long BBS routes; 800 ha) at the beginning of the study period on the strength of habitat loss effects on annual Breeding Bird Survey abundance. Each line represents a species, with colors indicating the strength of effect (red<-0.05, green=-0.05-0.05, grey=>0.05), and the histogram in top right showing the posterior distribution of the mean effect across all species. The black regression line and credible interval show the mean effect of habitat loss varying by amount of habitat at the beginning of the study period across all species (see ‘Testing for Habitat Loss Thresholds’). Note that the effect of habitat loss on bird populations is most severe when habitat amount is low, supporting the habitat threshold hypothesis.
**Fig. S7** Habitat distribution and change maps for two examples of mature-forest-associated species within and outside three national parks in eastern Canada (Fundy, Kouchibouguac, Kejimkujik National Parks) and the core area of the study region. Note that habitat loss (red) is common in landscapes surrounding parks, but largely absent within, indicating that the habitat loss we quantified is due to timber harvest, not climate-induced changes in Landsat reflectance, or natural disturbance. White areas indicate non-habitat.
Fig. S8 Study area and location of 12,272 Maritimes Breeding Bird Atlas (MBBA) survey locations (black dots), and Breeding Bird Survey (BBS) routes (orange lines). We used MBBA bird point counts (collected 2006-2011) to build species distribution (habitat) models, and we used long-term BBS routes (N=90) to test whether changes in habitat in landscapes surrounding these routes successfully predicted long-term population trends in 54 species of forest birds.
Table S1 Hectares of habitat lost (‘Loss’, 1985-2020) minimum (Min) and maximum (Max) reported territory sizes and estimated minimum and maximum number of birds lost (Min x Loss, Max x Loss) for 54 species of forest birds.

| Species                  | Code  | Loss (ha) | Min (ha) | Max (ha) | Min. lost | Max. lost |
|--------------------------|-------|-----------|----------|----------|-----------|-----------|
| Alder Flycatcher         | ALFL  | 302.278   | 0.20     | 3.00     | 100,759   | 1,511,390 |
| American Goldfinch       | AMGO  | -496,899  | NA       | NA       | NA        | NA        |
| American Redstart        | AMRE  | 143,888   | 0.39     | 1.00     | 143,888   | 368,944   |
| American Robin           | AMRO  | -461,831  | 0.11     | 0.84     | -549,799  | -4,198,462|
| Bay-breasted Warbler     | BBWA  | -1,384,012| 1.50     | 1.50     | -922,675  | -922,675  |
| Black-and-white Warbler  | BAWW  | 217,677   | 1.93     | 3.57     | 60,950    | 112,870   |
| Black-capped Chickadee   | BCCH  | -686,409  | 1.50     | 5.30     | -129,511  | -457,606  |
| Black-throated Blue Warbler | BTBW | -382,489  | 1.00     | 4.00     | -95,622   | -382,489  |
| Black-throated Green Warbler | BTNW | -1,094,419| 0.25     | 0.90     | -1,216,021| -4,377,674|
| Blackburnian Warbler     | BLBW  | -1,908,373| 0.40     | 1.10     | -1,734,885| -4,770,933|
| Blue Jay                 | BLJA  | -557,514  | NA       | NA       | NA        | NA        |
| Blue-headed Vireo        | BHVI  | -1,838,962| 3.00     | 3.00     | -612,987  | -612,987  |
| Boreal Chickadee         | BOCH  | -895,580  | 5.00     | 5.00     | -179,116  | -179,116  |
| Canada Warbler           | CAWA  | 118,590   | 0.24     | 0.80     | 148,238   | 494,127   |
| Cedar Waxwing            | CEWA  | 209,893   | NA       | NA       | NA        | NA        |
| Chestnut-sided Warbler   | CSWA  | 315,671   | 0.40     | 1.10     | 286,973   | 789,176   |
| Chipping Sparrow         | CHSP  | -137,187  | 0.20     | 1.00     | -137,187  | -685,937  |
| Common Yellowthroat      | COYE  | 370,919   | 0.20     | 2.20     | 168,600   | 1,854,597 |
| Dark-eyed Junco          | DEJU  | -2,129,036| 1.31     | 1.96     | -1,086,243| -1,625,218|
| Downy Woodpecker         | DOWO  | -113,816  | 4.40     | 5.50     | -20,694   | -25,867   |
| Eastern Wood-Pewee       | EAWP  | -565,774  | 2.20     | 7.70     | -73,477   | -257,170  |
| Fox Sparrow              | FOSP  | 1,993     | 0.25     | 1.00     | 1,993     | 7,971     |
| Golden-crowned Kinglet   | GCKI  | -2,340,504| 0.34     | 1.60     | -1,462,815| -6,965,785|
| Gray Catbird             | GRCA  | -96,834   | 0.32     | 0.41     | -236,180  | -302,606  |
| Hairy Woodpecker         | HAWO  | -1,164,827| 0.65     | 1.50     | -776,551  | -1,792,041|
| Hermit Thrush            | HETH  | -815,713  | 0.72     | 3.34     | -244,225  | -1,129,796|
| Least Flycatcher         | LEFL  | -192,566  | 0.11     | 0.43     | -447,829  | -1,750,604|
| Lincolns Sparrow         | LISP  | 497,618   | 1.43     | 2.00     | 248,809   | 348,333   |
| Magnolia Warbler         | MAWA  | -1,267,549| 0.51     | 1.05     | -1,207,190| -2,485,391|
| Mourning Warbler         | MOWA  | 25,130    | 0.50     | 0.65     | 38,662    | 50,260    |
| Nashville Warbler        | NAWA  | -26,507   | 1.10     | 1.10     | -24,098   | -24,098   |
| Northern Flicker         | NOFL  | 93,575    | 50.00    | 111.00   | 843       | 1,872     |
| Northern Parula          | NOPA  | -388,443  | 0.08     | 0.65     | -597,605  | -4,855,539|
| Northern Waterthrush      | NOWA  | -866,875  | 0.80     | 1.50     | -591,250  | -1,108,594|
| Olive-sided Flycatcher   | OSFL  | -814,650  | 10.00    | 40.00    | -20,366   | -81,465   |
| Ovenbird                 | OVEN  | -646,331  | 0.48     | 0.83     | -781,536  | -1,349,333|
| Palm Warbler             | PIWA  | 539,477   | 0.70     | 13.70    | 39,378    | 770,681   |
| Philadelphia Vireo       | PHVI  | 251,573   | 0.50     | 4.00     | 62,893    | 503,146   |
| Pileated Woodpecker      | PIWO  | -619,808  | NA       | NA       | NA        | NA        |
| Purple Finch             | PUFU  | -439,157  | 62.50    | 83.33    | -5,270    | -7,027    |
| Red-breasted Nuthatch    | RBNU  | -1,960,231| 0.20     | 10.00    | -196,023  | -9,801,154|
| Red-eyed Vireo           | REVI  | -432,886  | 0.86     | 3.71     | -116,681  | -503,355  |
| Rose-breasted Grosbeak   | RBGR  | 14,645    | 0.34     | 1.30     | 11,265    | 43,072    |
| Ruby-crowned Kinglet     | RUKI  | -1,023,415| 1.10     | 6.00     | -170,569  | -930,378  |
| Ruby-throated Hummingbird| RTHU  | 88,815    | NA       | NA       | NA        | NA        |
| Species                  | Loss          | Min (ha) | Max (ha) | Min. Lost  | Max. Lost  |
|--------------------------|---------------|----------|----------|------------|------------|
| Ruffed Grouse           | RUGR -598,188| 2.10     | 2.30     | -260,082   | -284,851   |
| Swainsons Thrush        | SWTH -952,748| 2.10     | 2.10     | -453,689   | -453,689   |
| Veery                   | VEER -43,794  | 0.10     | 2.00     | -21,897    | -437,937   |
| White-throated Sparrow  | WTSP 42,618   | 0.99     | 3.26     | 13,073     | 43,049     |
| Winter Wren             | WIWR -1,240,884| 1.90     | 2.10     | -590,897   | -653,097   |
| Yellow Warbler          | YEWA -177,218 | 0.20     | 0.78     | -227,203   | -886,092   |
| Yellow-bellied Flycatcher| YBFL -1,025,003| 0.75     | 1.00     | -1,025,003 | -1,366,671 |
| Yellow-bellied Sapsucker| YBSA -175,882 | 0.81     | 3.10     | -56,736    | -217,139   |
| Yellow-rumped Warbler   | YRWA -1,467,292| 0.45     | 0.80     | -1,834,115 | -3,260,648 |
| **Males lost**          | **-28,215,247**|          |          | **-16,779,704**| **-52,243,938**|
| **Individuals lost**    | **-33,559,408**|          |          | **-104,487,876**|
Table S2. Habitat categorizations for 54 forest bird species based on logistic regression model estimates ($\hat{\beta}$) and standard errors (SE) predicting the occurrence of each species as a function of trees >20 cm diameter (an indicator of older forest; see ‘Habitat Associations’), as well as Birds of North America (BNA) species accounts. ‘Age class’ is the final designation of each species into regenerating (R), immature (I), and mature (M) categories. Model estimates with ‘NA’ are species with insufficient data.

| Species                     | $\hat{\beta}$ | SE  | BNA | Age class |
|-----------------------------|---------------|-----|-----|-----------|
| Alder Flycatcher             | NA            | NA  | R   | R         |
| American Goldfinch           | NA            | NA  | R   | R         |
| American Redstart            | -0.001        | 0.001 | R  | I         |
| American Robin               | -0.005        | 0.001 | R  | R         |
| Bay-breasted Warbler         | 0.003         | 0.001 | M  | M         |
| Black-and-white Warbler      | -0.002        | 0.001 | I  | I         |
| Black-capped Chickadee       | 0.001         | 0.001 | I  | M         |
| Black-throated Blue Warbler  | 0.005         | 0.001 | M  | M         |
| Black-throated Green Warbler | 0.001         | 0.001 | M  | M         |
| Blackburnian Warbler         | 0.003         | 0.001 | M  | M         |
| Blue Jay                     | NA            | NA  | I   | M         |
| Blue-headed Vireo            | 0.002         | 0.001 | M  | I         |
| Boreal Chickadee             | 0.002         | 0.001 | M  | M         |
| Canada Warbler               | NA            | NA  | R   | R         |
| Cedar Waxing                 | NA            | NA  | R   | I         |
| Chestnut-sided Warbler       | NA            | NA  | R   | I         |
| Chipping Sparrow             | NA            | NA  | R   | R         |
| Common Yellowthroat          | -0.005        | 0.002 | R  | R         |
| Dark-eyed Junco              | 0.002         | 0.001 | M  | M         |
| Downy Woodpecker             | NA            | NA  | I   | M         |
| Eastern Wood-Pewee           | NA            | NA  | I   | M         |
| Fox Sparrow                  | NA            | NA  | R   | R         |
| Golden-crowned Kinglet       | 0.007         | 0.001 | M  | M         |
| Gray Catbird                 | NA            | NA  | R   | R         |
| Hairy Woodpecker             | 0.002         | 0.001 | M  | M         |
| Hermit Thrush                | 0.001         | 0.001 | I  | M         |
| Least Flycatcher             | 0.003         | 0.001 | M  | M         |
| Lincolns Sparrow             | NA            | NA  | R   | R         |
| Magnolia Warbler             | 0.002         | 0.001 | M  | I         |
| Mourning Warbler             | NA            | NA  | R   | R         |
| Nashville Warbler            | 0.002         | 0.001 | I  | R         |
| Northern Flicker             | NA            | NA  | R   | M         |
| Northern Parula              | 0.003         | 0.001 | M  | I         |
| Northern Waterthrush          | NA            | NA  | M   | M         |
| Olive-sided Flycatcher       | NA            | NA  | M/R | M         |
| Ovenbird                     | 0.007         | 0.001 | M  | M         |
| Palm Warbler                 | NA            | NA  | R   | R         |
| Philadelphia Vireo           | NA            | NA  | R   | I         |
| Pileated Woodpecker          | NA            | NA  | M   | M         |
| Purple Finch                 | -0.007        | 0.003 | R  | M         |
| Red-breasted Nuthatch        | 0.002         | 0.001 | M  | M         |
| Red-eyed Vireo               | 0.006         | 0.001 | M  | M         |
| Rose-breasted Grosbeak       | NA            | NA  | I   | I         |
| Ruby-crowned Kinglet         | -0.001        | 0.001 | R  | R         |
| Ruby-throated Hummingbird    | NA            | NA  | R   | R         |
| Ruffed Grouse                | NA            | NA  | I   | M         |
| Swainsons Thrush             | 0.001         | 0.001 | M  | M         |
| Veery                        | NA            | NA  | I   | M         |
| White-throated Sparrow       | -0.005        | 0.002 | R  | R         |
| Winter Wren                  | 0.002         | 0.001 | M  | M         |
| Yellow Warbler               | NA            | NA  | R   | R         |
| Species                  | Value1 | Value2 | Sex1 | Sex2 |
|-------------------------|--------|--------|------|------|
| Yellow-bellied Flycatcher| 0.002  | 0.001  | M    | M    |
| Yellow-bellied Sapsucker| 0.003  | 0.001  | I    | M    |
| Yellow-rumped Warbler    | 0.002  | 0.001  | M    | I    |
Movie S1.
Animation showing species distribution model using Landsat TM bands for blackburnian warbler \((Setophaga fusca)\) in each year of our study (1985-2020) for the Maritime Provinces of Canada. Habitat for this mature-forest associated species (delineated in blue) declined 33\% over the period observed. This habitat change was driven primarily by clearcutting without sufficient habitat regeneration (due to tree species composition changes and age-class truncation), and was a strong predictor of population declines in this species.