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Forest degradation, not loss, drives widespread avian population declines

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1 **Abstract**

2

3 In many regions of the world, forest management has reduced old forest and simplified forest
4 structure and composition via reliance on monoculture tree plantations. We hypothesized that
5 such forest degradation has resulted in long-term habitat loss for forest-associated bird species of
6 eastern Canada (130,017 km²) which, in turn, has affected bird population declines. Back-cast
7 species distribution models revealed that despite little change in overall forest cover, breeding
8 habitat loss occurred for 66% of the 54 most common species from 1985-2020. This habitat loss
9 was strongly associated with population declines for 72% of species, as quantified in an
10 independent, long-term dataset. Since 1985, net forest bird abundance has declined in this region
11 by an estimated 33-104 million birds due to habitat loss alone. The effects of forest degradation
12 may therefore be a primary cause of biodiversity decline in managed forest landscapes.

13 Most conservation policy has focused on reducing deforestation, and this approach remains
14 fundamental to many conservation strategies. Effects of forest loss on global biodiversity are
15 well-known and directly measured¹ and often used as estimates of biodiversity decline². Forest
16 degradation is also expected to be a key driver of biodiversity decline and is a component of
17 broad-scale biodiversity agreements (e.g., Aichi Biodiversity Targets in the Convention on
18 Biological Diversity, REDD+ [Reducing Emissions from Deforestation and Forest
19 Degradation]). However, forest degradation has been much more challenging to measure and
20 there have been few attempts to quantify its effects on species' population trends across entire
21 regions^{3,4}.

22
23 From a biodiversity standpoint, forest degradation is defined as the reduction or loss of
24 biological complexity in forest ecosystems^{5,6}. Forest management alters forest complexity most
25 commonly in two important ways; first, due to harvesting, managed forests tend to be younger
26 than under a natural disturbance regime⁷, with potential implications for species associated with
27 mature or old-growth forests⁸. Second, because tree plantations tend to yield more wood per area,
28 managers are increasingly converting native forests to plantations⁶. Unlike most natural forests,
29 plantations tend to be comprised of only one or two tree species. Plantation area is expected to
30 rise as they are increasingly considered "natural climate solutions"⁹. Such changes in age-class
31 structure and forest composition may occur without any overall loss in forest cover, and have
32 thus been largely ignored⁴. Nevertheless, quantifying forest degradation is of critical importance
33 to understanding biodiversity responses in regions where timber harvest and regrowth
34 predominates (e.g., Canada, western US, Scandinavia, Russia)¹⁰.

35
36 The importance of quantifying forest degradation effects is particularly critical considering
37 recent findings by the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES)
38 that the planet is facing a biodiversity crisis¹¹. Causes of population declines remain poorly
39 understood for many species. For instance, recent work has quantified widespread avian
40 population declines¹², but researchers are still searching for the mechanisms driving these losses.
41 Hypotheses explaining avian population dynamics include habitat loss on the wintering
42 grounds¹³, direct effects of toxic chemicals¹⁴, and climate change effects throughout the annual
43 cycle^{15,16}. However, the hypothesis that population declines, for birds or other taxa, are driven by
44 forest degradation and resultant breeding habitat loss, remains largely untested. This lack of
45 robust testing is likely for two methodological reasons. First, changes in forest composition and
46 age-class structure are more challenging to detect than forest loss¹⁷. Second, it is well known that
47 species have different habitat requirements, which often do not correspond to coarse, human-
48 defined land-cover categories¹⁸.

49
50 Here, we used species distribution models with Landsat TM reflectance bands as predictor
51 variables¹⁹ to quantify habitat amount for each of the most common 54 forest-dependent bird
52 species in the Acadian Forest of eastern Canada (130,017 km²). Since Landsat has been available
53 since 1985, then enabled us to back-cast habitat model predictions to quantify habitat change for
54 each species over 35 years (1985-2020). Under the hypothesis that changes in forest degradation
55 is driving population declines, we predict that we would see (1) little net change in total forest
56 area (due to the rates of forest regeneration matching forest harvest), (2) reductions in breeding
57 habitat across forest-associated species, particularly those associated with mature native forest
58 which is under pressure from timber harvest, and (3) links between habitat loss and long-term

59 bird population trends – as quantified in an independent dataset (the Breeding Bird Survey²⁰).
60 These links between habitat change and populations are not necessarily a given, and several
61 alternative hypotheses are possible. First, initial habitat may have been underutilized, in which
62 case individuals initially occur at low population density and then pack into remaining habitat as
63 it declines over time²¹. Second, over a 35-year period, bird habitat preferences could relax or
64 shift via behavioral plasticity or strong evolutionary selection pressure exerted by habitat loss²².

65
66 The effects of habitat loss should be particularly severe when habitat amount is low^{23,24}.
67 Alternatively, some species may exhibit rapid population declines even at low levels of initial
68 habitat loss¹. Although these alternative hypotheses have been tested using space-for-time
69 studies²⁵ to our knowledge no studies have tested whether species' populations exhibit threshold
70 behavior during the process of habitat loss over the long-term. We formally tested this
71 'extinction threshold hypothesis' using long-term habitat change predictions, along with
72 independent data on bird population trends. We predicted that populations in landscapes with the
73 lowest amount of habitat at the beginning of our time series should experience the strongest
74 negative effect of further habitat loss.

75
76

77 **Results**

78

79 The Acadian Forest of eastern Canada has shown a pervasive signal of forest change since 1985
80 (Fig. 1), despite a relatively stable trend in total forest cover (Fig. 2A). Since 1985, >3 million ha
81 have been clearcut (Fig 1A), with most of this area now occupied by either tree plantations (Fig.
82 1A, B, D) dominated by single tree species²⁶ or a mix of early successional tree species (Fig. 1B).
83 This pattern of forest harvest followed by rapid regeneration appears to be common across many
84 forest regions of North America (e.g., central Canada, southeastern US, western US; Fig. 1C)¹⁰,
85 and can be considered forest degradation in that these practices simplify forest structure, reduce
86 tree species diversity, and truncate old forest age classes⁷.

87

88 Overall, species distribution models (SDMs) using Landsat reflectance bands as predictors
89 performed well for most species when tested on 50% independent hold-out data (Fig. S1; \bar{x} Area
90 Under the Curve (AUC)=0.69 [range: 0.58 – 0.86]) and when tested on training data (\bar{x}
91 AUC=0.74 [range: 0.61 – 0.91]). This model performance is high considering the fine spatial
92 scale of predictions (30 m² pixels); SDMs therefore provided reliable estimates of habitat
93 distributions for all 54 species.

94

95 Back-cast distribution models revealed habitat declines occurred for 66% of species during 1985-
96 2020; 93% of species exhibited habitat reductions over the past decade (Figs. 2, S2). Species
97 showing the greatest decreases in habitat were Golden-crowned Kinglet (*Regulus satrapa*; -38%)
98 and Blackburnian Warbler (*Setophaga fusca*; -33%, Movie M1), with 7 species showing habitat
99 declines >25% (Fig. 3). Most species with strongly declining habitat are associated with mature
100 forests²⁷ (Fig. 3A, B) which is consistent with forest degradation due to harvesting of mature
101 forest. Indeed, clearcut harvest alone was strongly associated with habitat declines for all mature-
102 forest-associated species (Fig. S3). Fifteen species exhibited habitat increases, and most (14/15)
103 of these tend to be associated with young or immature forests (Fig. 4A and 4B).

104

105 We tested the hypothesis that habitat loss affected bird population declines using Breeding Bird
106 Survey Data (BBS)²⁸ for the Maritime Provinces (see Methods). First, we used SDMs to quantify
107 habitat change (1985-2019) in landscapes surrounding BBS routes ($N=90$; see Methods). We
108 then used Bayesian hierarchical models²⁰ to test whether SDM-predicted habitat loss or gain in
109 each given year of the time series drove population changes for each species along each route.
110 Importantly, BBS data are entirely independent of our SDMs, so this test also represents a strong
111 validation of our habitat models (18). Bayesian models revealed a strong effect of habitat loss or
112 gain on population abundance (Fig. 4). Abundance changes for all but three species tracked
113 annual habitat change with 80% posterior distributions that did not include zero (vertical line in
114 Fig. 4A). Habitat change significantly affected population change for 48 species (>0.9 posterior
115 probability; Fig. 4B).

116
117 Given this strong association between habitat and population changes for most species, we
118 estimated the net number of breeding individuals lost due to habitat loss from 1985-2020 using
119 published accounts of territory sizes for each species²⁷ (see Table S1). Across all species, back-
120 cast species distribution models (SDMs) indicate that 28,215,247 ha (282,153 km²) of habitat has
121 been lost, equating to a loss of between 16,779,704 and 52,243,938 breeding pairs (33,559,408 –
122 104,487,876 individuals; Supporting Methods, Table S1). One might expect that forest
123 degradation, rather than resulting in broad-scale declines across species, is simply causing
124 species turnover from mature forest bird species to young-forest associates. However, it is
125 important to note that we quantified *net* bird decline from an unbiased list of the 54 most
126 common forest bird species in eastern Canada. This list included both early and late successional
127 species. Such net bird declines could be due to the fact that (1) even some early seral species are
128 losing habitat (perhaps due to conversion from diverse early successional forest to single-species
129 plantations) and (2) in this region, more species occupy older forests than regenerating forests.

130
131 We also quantified overall population trends for 54 species of forest birds using data from the
132 BBS (Fig. 5). These estimates give the total magnitude of population changes which include, but
133 are not limited to, habitat loss or gain effects. Thirty-nine of the 54 species examined (72%) are
134 in population decline (defined as having 95% credible intervals that do not bound zero). The
135 magnitude of the declines for 15 forest bird species is severe ($>5\%/year$). It is notable that most
136 species exhibiting both habitat loss *and* population declines are mature-forest associates (Fig.
137 3A; bottom left quadrant, dark green dots), with mature-forest species exhibiting the greatest
138 habitat losses (Hierarchical regression, $\hat{\beta} = -16.66$ [6.32 SE]; Fig. 3B, see SI Methods ‘Habitat
139 Associations’).

140
141 BBS declines are not restricted to mature-forest species; several species in rapid population
142 decline are early seral species (e.g., Canada warbler [*Cardellina canadensis*], Lincoln’s Sparrow
143 [*Melospiza lincolni*], Mourning Warbler [*Geothlypis Philadelphia*]; Fig. 3A bottom right
144 quadrant). Despite the fact that these species have gained habitat over 35 years, their populations
145 continue to decline. Only three species (Black-capped Chickadee [*Poecile atricapillus*], Hairy
146 Woodpecker [*Leuconotopicus villosus*], and Ruby-throated Hummingbird [*Archilochus*
147 *colubris*]) are increasing in abundance. Populations of these species increased despite evidence
148 of habitat decline (Fig. 3A; top left quadrant) – perhaps because each benefit from anthropogenic
149 habitats and supplemental food. Importantly, habitat changes from 1985-2019 along BBS routes
150 were representative of changes at the scale of the entire region for most species (Fig. S4), so

151 BBS population trends are highly likely to reflect population trends at the regional scale. This
152 contrasts to the 1965-1985 period when habitat changes along routes differed markedly from the
153 broader region²⁹.

154
155 We also modeled BBS population trends over the past 10 years, as this is the period of
156 importance for informing listing decisions under the Committee on the Status of Endangered
157 Wildlife in Canada (COSEWIC). Nine species have exhibited population declines >30% over 10
158 years (Fig. S5), which meets the criterion for consideration as “Threatened” under COSEWIC
159 Criterion A2³⁰.

160
161 We found support for the hypothesis that the effects of habitat loss are particularly severe in
162 landscapes with low habitat amounts. The model testing for a statistical interaction between
163 initial habitat amount in landscapes surrounding BBS routes and annual habitat loss was
164 generally well supported across species; the effect of habitat loss was strongest when habitat
165 surrounding routes had already been reduced to a low level prior to 1985 (Fig. S6).

166
167 **Discussion**
168
169 Overall, our results support the hypothesis that forest degradation from 1985 to 2020 has resulted
170 in pervasive declines in bird habitat. Forest changes have included conversion from mixed-
171 species forests to single-species conifer-dominated plantations, and clearcutting old forests
172 without equivalent regrowth into old age classes. Notably, over the same time period, forest
173 cover changed very little, and harvest practices in this region are considered “sustainable” from a
174 wood production standpoint³¹.

175
176 The habitat changes we observed were strongly associated with long-term population changes for
177 most forest bird species in our study and appear to be driving severe population declines (Figs. 4,
178 S4) in several species, including those associated with mature forest (e.g., Bay-breasted Warbler
179 [*Setophaga castanea*], Blackburnian Warbler, Boreal Chickadee [*Poecile hudsonicus*], Winter
180 Wren [*Troglodytes hiemalis*]). Populations of four mature-forest associated species are declining
181 at rates >30% over the past 10 years (Fig. 4), which is a rate consistent with ‘threatened’
182 COSEWIC status. We recommend extending the approach we used here to model habitat and
183 habitat change across eastern North America, which encompasses most of the ranges of species
184 in this study. This analysis could be of great importance to future listing decisions.

185
186 The strong link between habitat change in landscapes surrounding BBS routes and bird
187 population changes indicates that SDMs are highly predictive of bird population trends. This
188 finding has two important implications; first, it means that broad-scale habitat loss in landscapes
189 beyond the BBS routes is driving region-wide population declines. Second, in eastern Canada, at
190 least, this constitutes evidence that breeding habitat loss due to forest degradation is a primary
191 cause of observed widespread population declines in birds (Rosenberg et al. 2019).

192
193 For several species, rates of population decline seemed to outpace rates of habitat decline
194 (compare x- and y-axes in Fig. 3A). For instance, Blackburnian Warbler populations have
195 experienced a ~70% decline over 35 years (4.5%/year; Fig. 4B), but only 33% of habitat has
196 been lost. One explanation for this apparent mismatch is that populations show particularly

197 strong declines at low habitat amounts, which supports the ‘extinction threshold’ hypothesis²³.
198 Indeed, our results indicate that the effect of habitat loss is much greater in landscapes with low
199 habitat amounts (Figure S5). The mechanism for such threshold effects could be due to habitat
200 fragmentation³²; once patches shrink below the size of an individual territory, it is likely to have
201 higher rates of local extinction. Disconnected patches are also less likely to be colonized³³.

202
203 However, the mismatch between population versus habitat declines could signal that additional,
204 non-habitat-related factors are compounding declines³⁴. In support of this idea, several species
205 that are gaining, or at least not losing, habitat are in strong population decline according to the
206 BBS (e.g., Canada warbler, Lincoln’s sparrow, Philadelphia vireo [*Vireo philadelphicus*]). Our
207 results do not preclude the well-known effects of wintering ground habitat loss¹³, climate
208 change^{15,35}, mortality on migration¹⁵, contaminants¹⁴, or intensification of plantation management
209 practices³⁶. Population declines in species associated with regenerating forest are particularly
210 cryptic because habitat amount for these species tends to be increasing (except for Olive-sided
211 Flycatcher [*Contopus cooperi*], which exhibited habitat declines of ~18% over 35 years). One
212 hypothesis is that populations of birds that prefer early seral stages, despite having potentially
213 more habitat, are declining due to climate change over the past three-and-a-half decades (~1°C
214 increase over 30 years;³⁷). Given that such stand types are likely warmer due to more open and/or
215 shallow canopies³⁸, any increases in ambient temperatures are likely to be more severe in
216 plantations and naturally regenerating forest than it is in mature forest, which would exert
217 physiological stresses and potentially have population consequences on birds³⁴. This effect could
218 be magnified by the fact that several early seral species are more associated with young
219 coniferous forest – which is typically found further to the north in Boreal forests²⁶.

220
221 More subtle mechanisms for habitat loss due to forest degradation reported in this study would
222 likely have remained undetectable without a species-specific habitat modeling approach¹⁹. Given
223 that no two species associate with identical habitats¹⁸, our model enabled us to quantify habitat
224 on a species-specific basis and then track habitat change over multiple decades (since 1985, the
225 origin of Landsat). If we had used generic, human-defined cover types (e.g. “forest” or “mature
226 forest”) as predictor variables, species-specific patterns in habitat change would have been
227 obscured. Similar approaches could be applied in other regions and for other taxa, if species
228 spatial distribution data are available.

229
230 Several lines of evidence support forest management as a driver of forest degradation rather than
231 alternative mechanisms (e.g., climate-mediated forest decline, natural disturbance). First, our
232 habitat models did not include climate data, so the reflectance changes from satellite imagery
233 used in our SDMs were predominantly due to forest compositional changes. Although climate
234 (e.g., interannual differences in precipitation) can cause subtle differences in reflectance (leaf
235 color) over time, most changes in the magnitude of reflectance are due to changes in forest
236 composition or cover rather than effects of climate³⁹. Indeed, if the observed habitat declines
237 were due to climate effects or natural disturbance, we would expect to see parallel habitat
238 declines in protected areas, which we did not (Fig. S7). Second, species exhibiting the greatest
239 declines in habitat are those most strongly associated with mature forest (Fig.3 A, B) – which is
240 the primary target of timber harvest. Indeed, amount of area clearcut was strongly associated
241 with habitat loss across the region in each year, for mature-forest-associated bird species (Fig.
242 S3). Third, it is well established that large-scale intensive forest management practices in this

243 region have resulted in substantial increases in single-species tree plantations (Fig. 1A)²⁶. In
244 areas that have not been planted, ingrowth of shade-intolerant hardwoods and balsam fir (*Abies*
245 *balsamea*) predominate; these replace original shade-tolerant deciduous and coniferous species
246 (Fig. 1B) and are unlikely to be succeeded by such species given current truncated harvest
247 rotations. We predict that similar effects of forest change could be prevalent in other temperate
248 forests globally that are heavily managed for timber production (e.g., southeastern USA, Pacific
249 Northwest USA, Chile, Scandinavia). These regions show little net loss of forest cover but high
250 rates of forest reductions and regrowth (e.g., Fig. 1C)¹⁰, which is symptomatic of intensive forest
251 management with potential for forest degradation.

252
253 Overall, our results point to broad-scale declines in forest birds of the Acadian Forest of eastern
254 Canada. For most species we assessed, these declines are driven by habitat loss that is primarily
255 due to forest degradation rather than forest loss. We expect that similar consequences for
256 biodiversity may hold in other intensively managed forests of the world. This mechanism for
257 bird population declines would have been invisible using coarse, human-defined categories of
258 ‘habitat’ (i.e., forest cover)¹⁸.

259
260 If maintaining non-declining populations of forest birds is the goal, conservation measures that
261 halt the alteration of habitat, particularly in diverse, older forests, will be necessary. Future
262 conservation efforts will be most effective if they maintain relatively high proportions of habitat,
263 as such landscapes appear less susceptible to further population declines. Of course, this may
264 come at the expense of wood production, but potentially less so with forest-landscape zoning that
265 maintains reserves, ecological forestry and strategic, and spatially limited intensive
266 management⁴⁰.

267 **Materials and Methods**

269 **Bird Data**

270
271
272 We selected 54 species of birds that were designated as forest associated by Partners in Flight
273 (PIF 2021) and had sufficient data in the Maritimes Breeding Bird Atlas (MBBA) point count
274 dataset⁴¹ to facilitate distribution modeling ($N > 200$ individual location records). Between 2006
275 and 2010, avian point counts (Ralph et al. 1995) were conducted at 12,272 points across three
276 Canadian provinces: New Brunswick, Nova Scotia, and Prince Edward Island (Fig. S9). These
277 provinces represent the core of the Acadian Forest in Canada and encompass $> 130,000 \text{ km}^2$ ⁴².
278 Point counts were conducted from May 29 to July 3, no earlier than 30 minutes before sunrise
279 and no later than 5 hours after sunrise. Counts were 5-minutes long, and species were recorded
280 within an unlimited radius. Points were located to ensure maximum coverage of Breeding Bird
281 Atlas squares⁴¹; the coverage goal was to complete 10-15 point counts in each 10 km^2 atlas
282 square. Most points were randomly placed along roads, but a small proportion (8.4%; $N=1034$)
283 were conducted off-road. These points were placed $> 100 \text{ m}$ from roads and were spaced $> 300 \text{ m}$
284 apart.

285 **Remote-sensing Data**

288 We followed the methods of Shirley et al (2013)¹⁹ to model species as a function of six visible
289 Landsat bands that we used as predictor variables in our SDMs. Using Google Earth Engine, we
290 obtained cloud-free spectral surface reflectance from Landsat collection 1 Tier 1 from 2006 to
291 October 2010 building and testing SDMs. In addition, we used reflectance bands to create
292 harmonic fitting to capture the cyclical reflectance change due to vegetation phenology and
293 disturbance. Landsat data are collected at 30 m pixel resolution. We used the CCDC (Continuous
294 Change Detection and Classification) algorithm⁴³ in Google Earth Engine to fit each six Landsat
295 spectral bands in the form of:

$$296 \quad R_t = A_0 + B_0 t + \sum_{k=1}^3 \left\{ A_k \cos\left(\frac{2\pi}{T} kt\right) + B_k \sin\left(\frac{2\pi}{T} kt\right) \right\}$$

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

308

309 **Species Distribution Models**

310

311 We used Maxent implementation in Google Earth Engine (equivalent of version 3.4.4)⁴⁴ to
312 construct presence-only SDMs for the occurrence of 54 forest-associated species. Bird
313 occurrence data were from the MBBA, and predictor variables constituted only the remotely
314 sensed variables described above. Maxent uses presence-only data to predict species distributions
315 based on maximum entropy theory. The algorithm estimates a probability distribution for species
316 occurrence that is closest to uniform while still subject to environmental constraints (in this case
317 Landsat predictor variables). We generated a random sample of 10,000 pixels from the study
318 area to serve as background samples ('pseudoabsences'). Points sampled along roads were
319 jittered up to 180m to the most proximate forest patch to the point-count location. The SDMs
320 were constructed in Google Earth Engine, using the linear, product and quadratic feature types
321 provided by Maxent. The observation samples were split into equal 50% datasets which served
322 as training and validation data for all species. A regularization multiplier was optimized by
323 iterating the beta parameter from 0.1 to 2.0 for all 54 species separately, and the beta parameter
324 with the highest Area Under the Receiver Operating Characteristics Curve (AUC) value for
325 validation dataset were picked to create the final maxent model. We evaluated distribution
326 models using AUC derived from predictions on the independent validation data. The value of
327 AUC ranges from 0 to 1⁴⁵. An AUC value of 0.50 indicates that the model did not perform better
328 than random, whereas a value of 1.0 indicates perfect discrimination. Finally, we acquired
329 Landsat images and calculated predictor variables (see Remote Sensing Data above) for the
330 1985-2020 period and used SDM models to back-cast species distributions predictions across for
331 each species across the entire region in each year (e.g., Fig. 2 B-F). The Google Earth Engine

332 scripts for Landsat data analysis (CCDC) and Maxent models are available at
333 <https://figshare.com>.

334

335 **Breeding Bird Survey Data and Population Trends**

336

337 To test whether habitat change, measured using back-cast SDMs, predicted population trends we
338 compiled forest bird population data from the Canadian Breeding Bird Survey²⁸ between 1985-
339 2019 within the boundary of the Maritime Provinces of Canada (New Brunswick, Nova Scotia,
340 Prince Edward Island), which represents the core of the Acadian Forest in Canada and
341 encompasses >130,000 km². The BBS consists of a set of routes, each 40 km in length, along
342 secondary roads surveyed annually by trained observers since 1966 (not all routes were surveyed
343 every year). Observers stopped at 50 regularly spaced locations within each landscape and
344 recorded the species of every bird observed during 3-minute surveys. We combined data at each
345 stop to provide the total number of individuals of each species seen during each year within a
346 landscape. We quantified habitat change for each species in each year within 200 m diameter
347 buffer landscapes along each of the 90 routes (i.e., 40 km x 200 m areas) and used this change as
348 the main effect in our models. A positive effect of habitat gain or a negative effect of habitat loss
349 on population changes in each year would constitute strong, independent validation of our habitat
350 models and evidence that habitat change affect population size.

351

352 We modeled trends in 54 bird populations using a modified version of the hierarchical model
353 described by Sauer and Link (2011)²⁰. The BBS data have a complex nested structure, with
354 counts within years, within landscapes for individual species. There are several well-known
355 limitations of these data; counts tend to be overdispersed, observers have different skill levels
356 and can change among years, and some species are more difficult to detect in an observer's first
357 year of surveying. The model described by Sauer and Link (2011)²⁰ attempts to address these
358 limitations while simultaneously accounting for the complex and hierarchical structure of the
359 data. The basic form of this model is an overdispersed Poisson regression with a covariate for
360 year, which provides inference of trends in bird abundance within each surveyed landscape. As
361 these models control for, but do not correct, observer bias the model provides an index of
362 abundance, rather than true abundance of birds in each landscape. We used several different
363 model structures to investigate 1) population trends by species, 2) the effect of habitat change
364 along each route by species, and 3) the effect of initial habitat amount in mediating the effect of
365 habitat loss on abundance. For all models we used the survey data from 1985 to 2019 with all 90
366 BBS survey routes in the provinces of New Brunswick, Nova Scotia, and Prince Edward Island
367 (see SI Methods).

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Figures

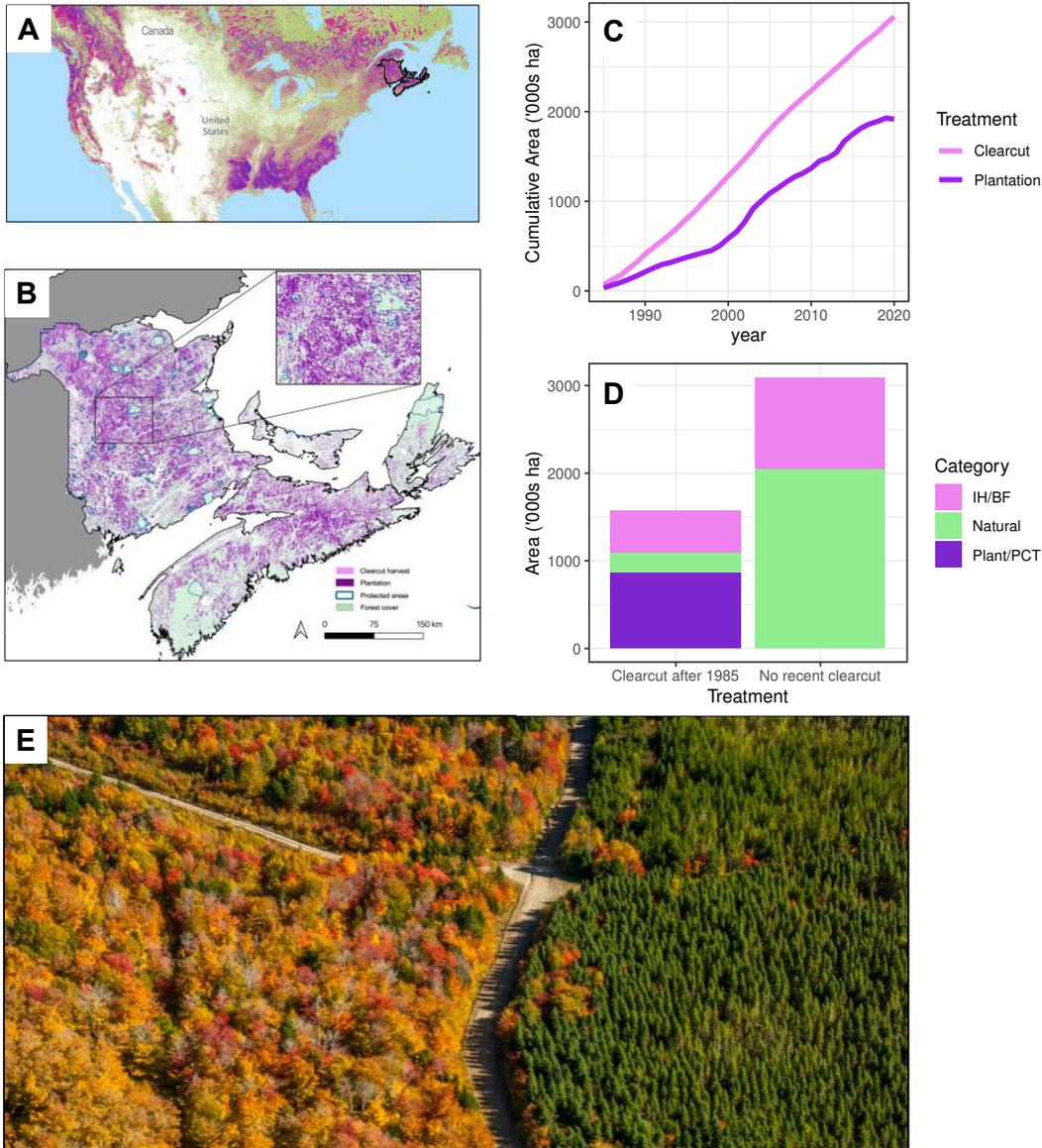


Fig. 1 **A** Study area in context of other regions of North America that have similar rapid rates of forest loss (pink), then gain (purple) – which is likely a signal of commercial forest harvest followed by rapid regeneration. Panel **B** shows cumulative clearcut disturbance (pink) across the Maritime 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.

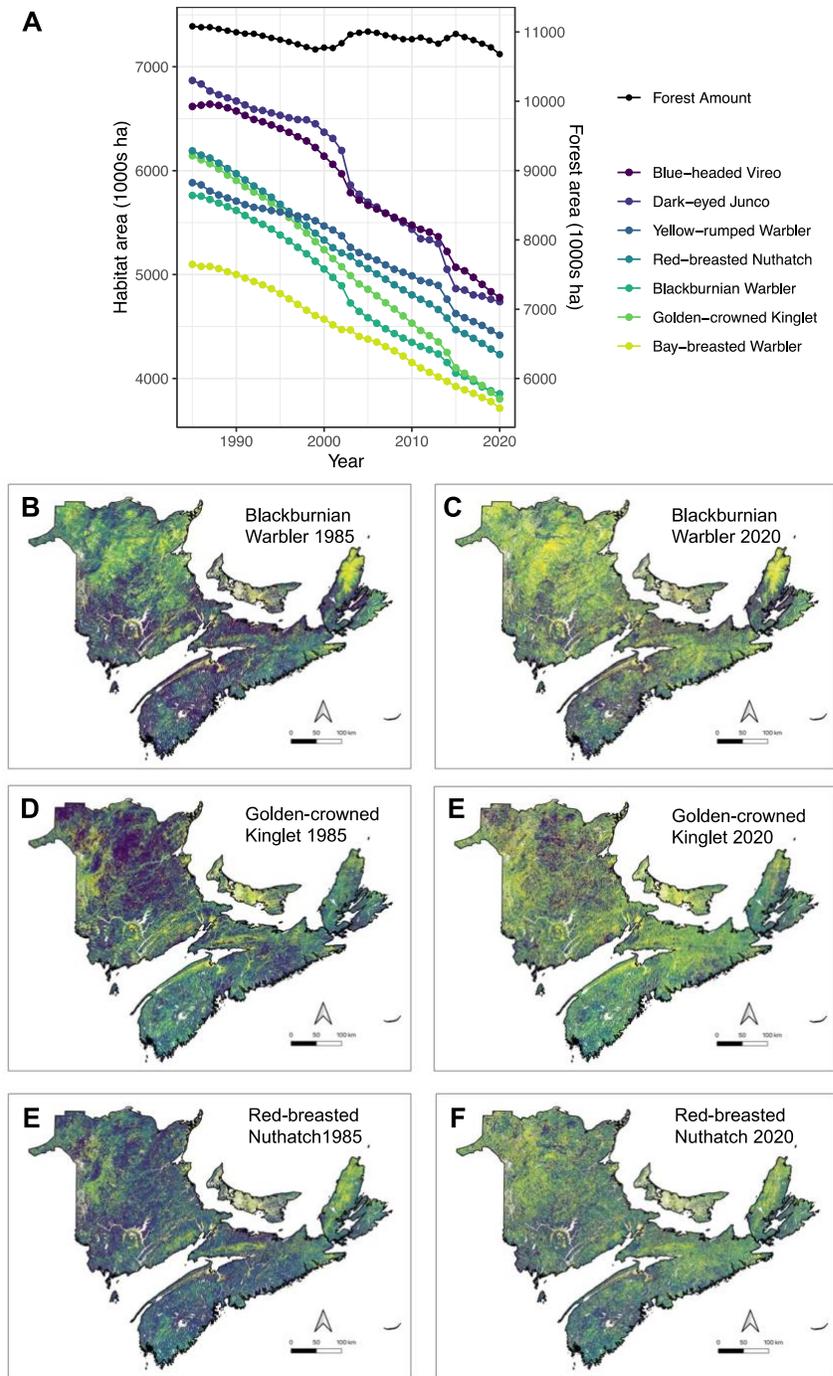


Fig. 2 A. Habitat trends (1985-2020) for the seven bird species exhibiting the greatest population declines according species distribution models (SDMs). All of these species are mature-forest associated (see Fig. 4a, 4b). Over the same time interval, total forest cover did not decline (black line), 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.

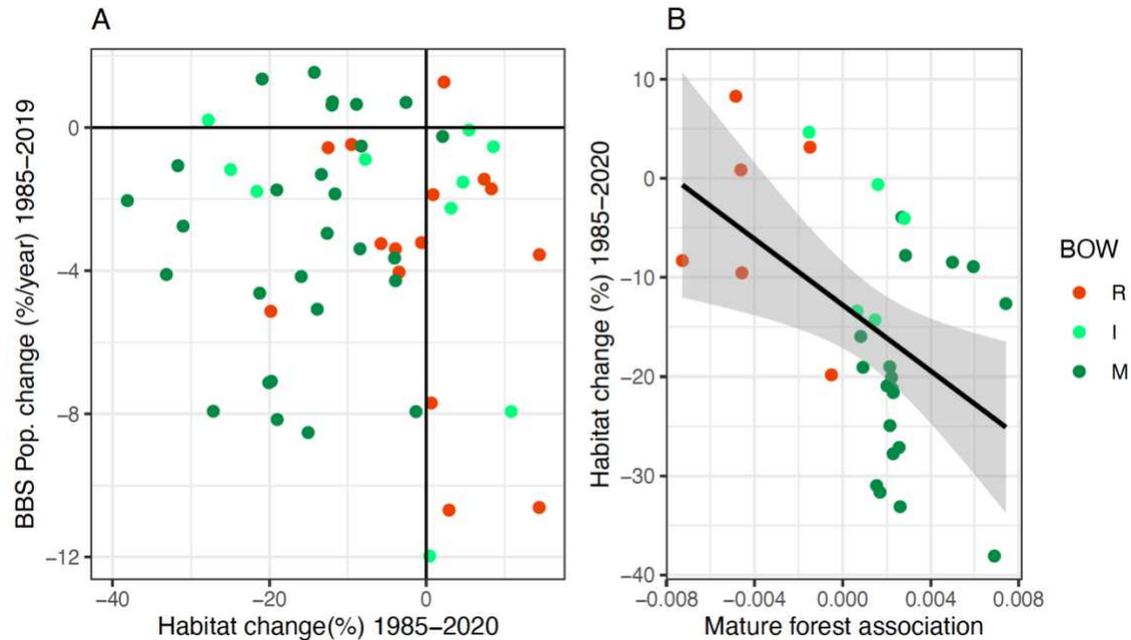


Fig. 3A Relationship between habitat change, estimated from species distribution models and independently derived estimates from the North American Breeding Bird Survey (BBS) for the Acadian Forest. Bird species of mature forests (M; green dots) exhibit the greatest habitat loss; this is generally reflected 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).

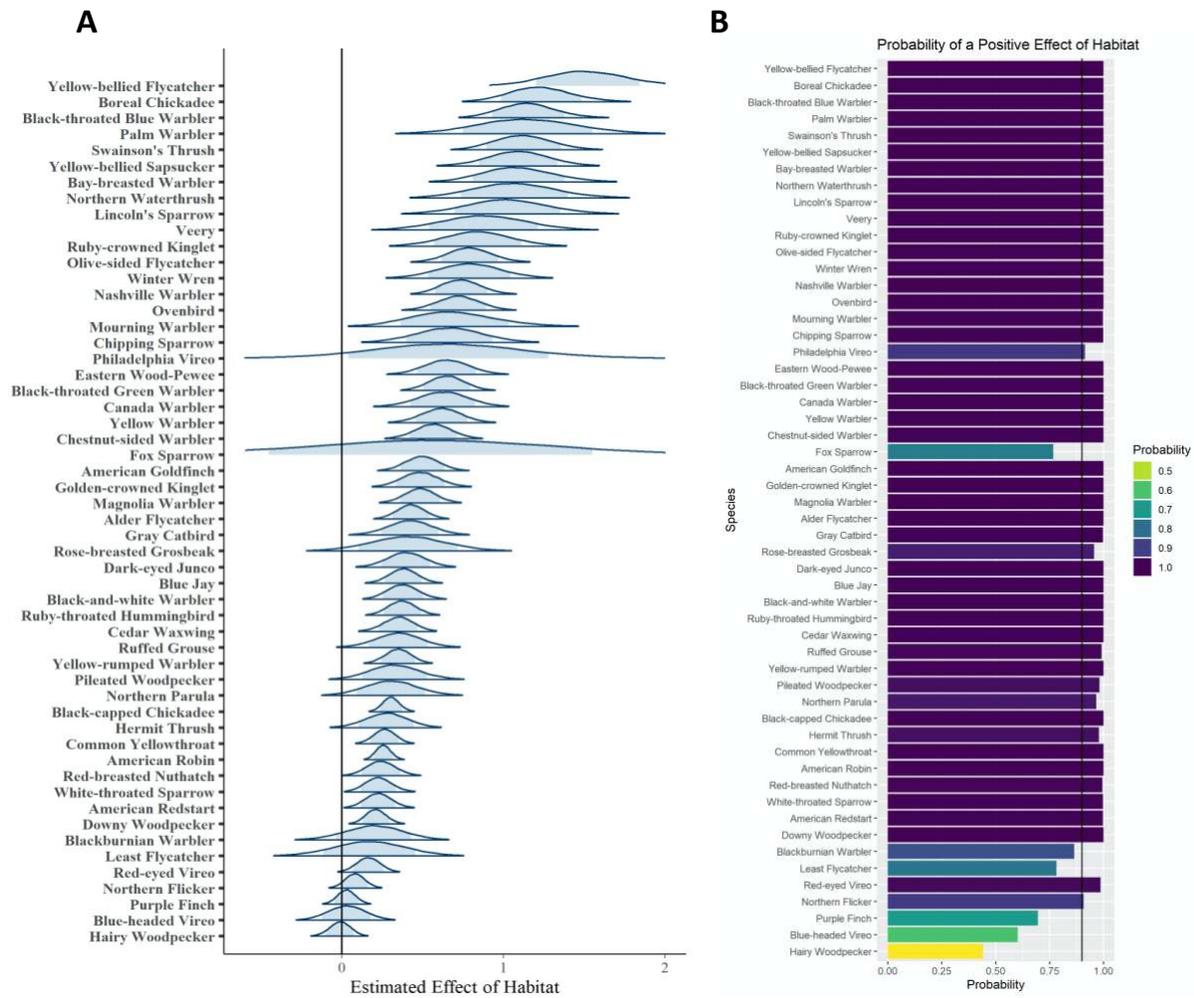


Fig. 4 Bayesian posterior distributions for the effects of SDM-modeled habitat gain or loss (x-axis) in a given year on bird abundance in the corresponding year, using Breeding Bird Survey data (A). Most species were strongly influenced by the effect of habitat change on abundance, which support the 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.

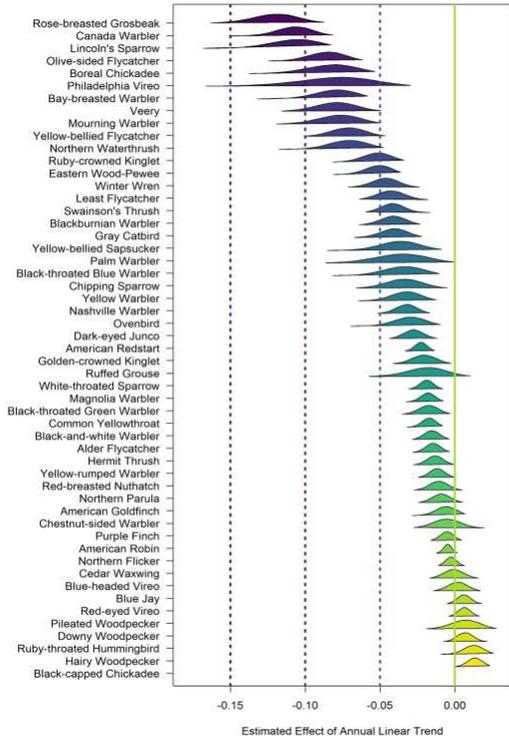
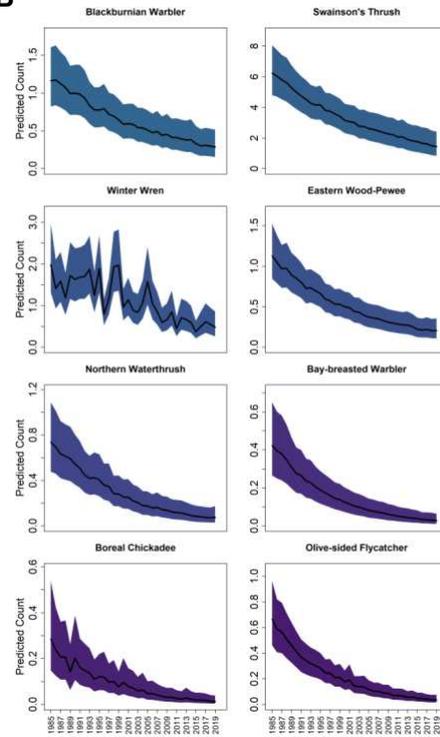
A**B**

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 JAGS¹ using the ‘rjags’ package², in the statistical software R³. 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 diagnostic⁴ 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,

$$\begin{aligned} y_{ijt} &\sim \text{Poisson}(\lambda_{ijt}) \\ \log(\lambda_{ijt}) &= \alpha_j + \gamma_t + \text{first.year}_{ij}\eta + \text{year}_{it}\beta_i + \epsilon_{ijt} \\ \alpha_j &\sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \\ \gamma_t &\sim \text{Normal}(0, \sigma_\gamma^2) \\ \beta_i &\sim \text{Normal}(\mu_\beta, \sigma_\beta^2) \\ \epsilon_{ijt} &\sim \text{Normal}(0, \sigma_\epsilon^2) \end{aligned}$$

where α_j are effects of unique route-observer combinations, γ_t are year effects, η 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)), β_i is the trend for route i (the variable year indicates the year of the survey for each route) and ϵ_{ijt} is general dispersion beyond that accounted for by the Poisson variance. The route-specific trends (β_i) arise from a distribution with mean μ_β and variance σ^2 representing the regional trend for the species, while α_j arise from a distribution with mean μ_α and variance σ^2 , representing the regional average route-observer effect. We used diffuse priors on our parameters as,

$$\mu_{\beta i}, \mu_{\beta \alpha i}, \eta \sim \text{Normal}(0, 10)$$

$$\sigma_{\beta}^2, \sigma_{\alpha}^2, \sigma_{\gamma}^2, \sigma_{\epsilon}^2 \sim \text{Gamma}(0.001, 0.001)^{-1}$$

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,

$$\begin{aligned} y_{ijt} &\sim \text{Poisson}(\lambda_{ijt}) \\ \log(\lambda_{ijt}) &= \alpha_j + \gamma_t + \text{first.year}_{ij}\eta + \text{habitat}_{it}\beta_i + \epsilon_{ijt} \\ \alpha_j &\sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \end{aligned}$$

$$\begin{aligned} \gamma_t &\sim \text{Normal}(0, \sigma_\gamma^2) \\ \beta_i &\sim \text{Normal}(\mu_\beta, \sigma_\beta^2) \\ \epsilon_{ijt} &\sim \text{Normal}(0, \sigma_\epsilon^2) \end{aligned}$$

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 μ_β 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,

$$\begin{aligned} y_{ijt} &\sim \text{Poisson}(\lambda_{ijt}) \\ \log(\lambda_{ijt}) &= \alpha_j + \gamma_t + \text{first.year}_{ij}\eta + \text{habitat}_{it}\beta_i + \epsilon_{ijt} \\ \beta_i &\sim \text{Normal}(\mu_\beta, \sigma_\beta^2) \\ \mu_{\beta_i} &\sim \beta_0 + \xi \times \text{init.hab}_i \\ \alpha_j &\sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2) \\ \gamma_t &\sim \text{Normal}(0, \sigma_\gamma^2) \\ \epsilon_{ijt} &\sim \text{Normal}(0, \sigma_\epsilon^2) \end{aligned}$$

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 β_0 is the effect of habitat change at mean initial habitat, while the parameter ξ is the effect of initial habitat, which modulates the route-level effect of habitat changes (β_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 (from⁵ 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)

91 these estimates concurred with the BNA accounts. In these cases of disagreement, we used the
92 local quantitative estimates for categorization. Finally, we checked these classifications with
93 existing habitat categories used by the New Brunswick Department of Natural Resources⁶ and we
94 found no discrepancies with our final categorization.

95
96 We examined the relationship between habitat change from 1985 - 2020 and mature forest
97 association (Fig. 3B) using linear regression with habitat change as the dependent variable. The
98 mature forest association has uncertainty associated with the estimates, so a simple regression
99 using the mean mature forest association estimate would deflate the uncertainty in this
100 relationship. Thus, we conducting this regression in a Bayesian framework, treating the true,
101 unobserved mature forest association as a random variable. We used the mean and standard error
102 of the estimated mature forest association to develop a prior on these values with mean equal to
103 the estimated mean and variance equal to the squared standard error. We fit models in JAGS,
104 running 4 chains each for 20,000 iterations, discarding the first 10,000 iterations as burn-in and
105 assessing convergence using the Gelman-Rubin diagnostic.

106

107 **Estimates of Loss/Gain in Bird Numbers**

108

109 To estimate the total number of birds lost or gained across the region from 1985-2020, we first
110 calculated net habitat loss or gain for each species. We gleaned territory size of each from the
111 Birds of North America Database⁷ and multiplied: habitat change x territory size. We made this
112 calculation for both the minimum territory size observed for each species, as well as the
113 maximum. Finally, we summed these values across all 54 species to provide lower (maximum
114 territory size) and upper (minimum territory size) bounds on the net change in bird numbers for
115 the Maritime provinces. The equation for this calculation is:

116

$$117 \sum_i ((H_{1985} - H_{2020}) \times T)$$

118

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

121

122 **Modeling Plantation Area and Clearcut Disturbance over Time**

123

124 Although forest inventory data for public land and small private woodlots are freely available for
125 New Brunswick, no such data exist for the entire study area, and are not available each year from
126 1985-2020. We therefore used a distribution modeling approach to predict and then backcast
127 plantations and disturbances, similar to our bird habitat SDMs. We used 97,627 samples of
128 known plantations >5 years since establishment as presence points, then extracted harmonic
129 coefficients as well as the synthetic spectral images corresponding to July 1 for years 1990,1995,
130 2000, 2005, 2010, and 2015. We used all 6 Landsat spectral bands (blue, green, red, nir, swir1,
131 and swir2). We held out 50% of the data (N=48,813) for model validation. Together with random
132 samples of 20,000 background locations were used for Maxent modeling. Regularization
133 optimizations were applied by comparing the AUC with varying beta from 0.1 to 2.0. The model
134 performance was not sensitive to regularization, so the default value of 1.0 was used. The
135 resulting model has an AUC of 0.872. We applied the Maxent predictions to all years from 1985
136 to 2020. A threshold (0.283) corresponding to equal sensitivity and specificity was chosen to

137 classify the map into plantations versus non-plantations. A spatial filter of a minimum mapping
138 unit of 11 pixels was applied to remove the scattered small patches from the final map, and we
139 masked the final plantation map using our disturbance map (see below) to ensure that no areas
140 that had not been clearcut were included as plantations.

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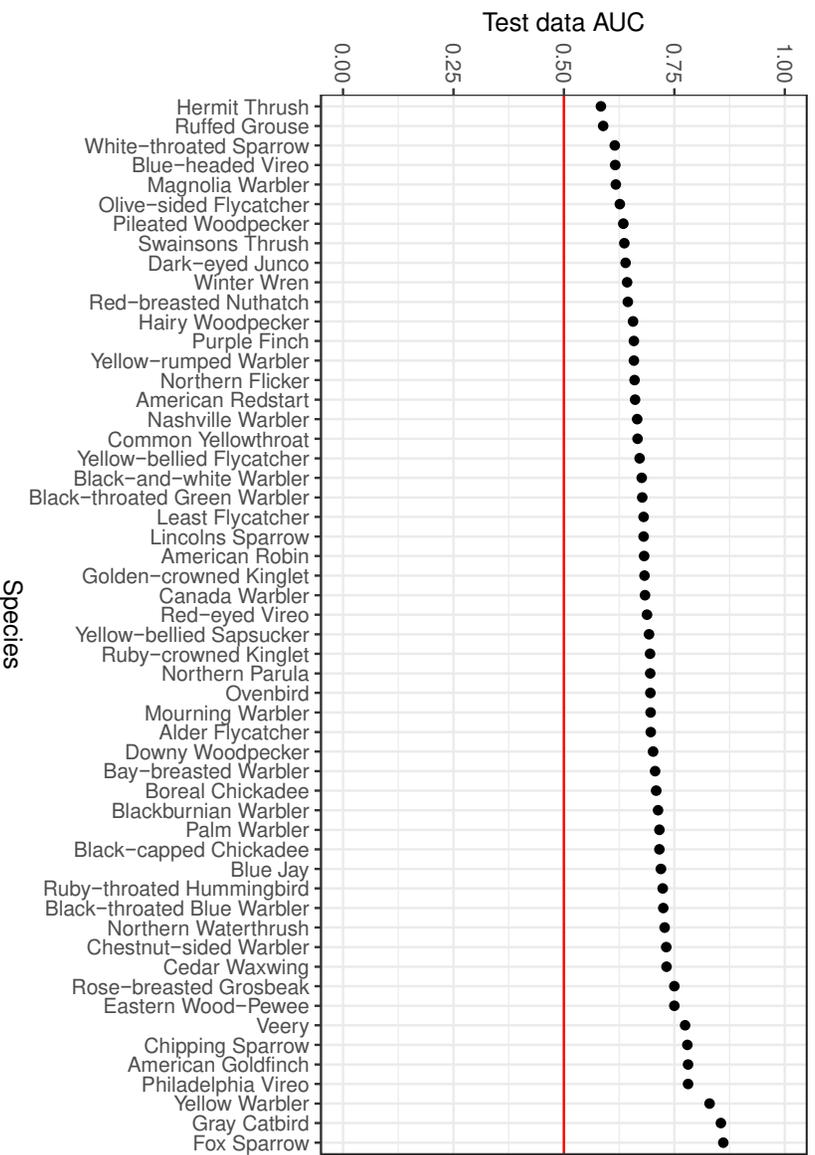


Fig. S1 Area Under the Receiver Operating Characteristic Curve (AUC) – a measure of model prediction success ranging from 0 – 1 (perfect predictions) for 54 forest bird species of the Maritime Provinces. AUCs were calculated using 50% of locations held-out as independent test data.



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.

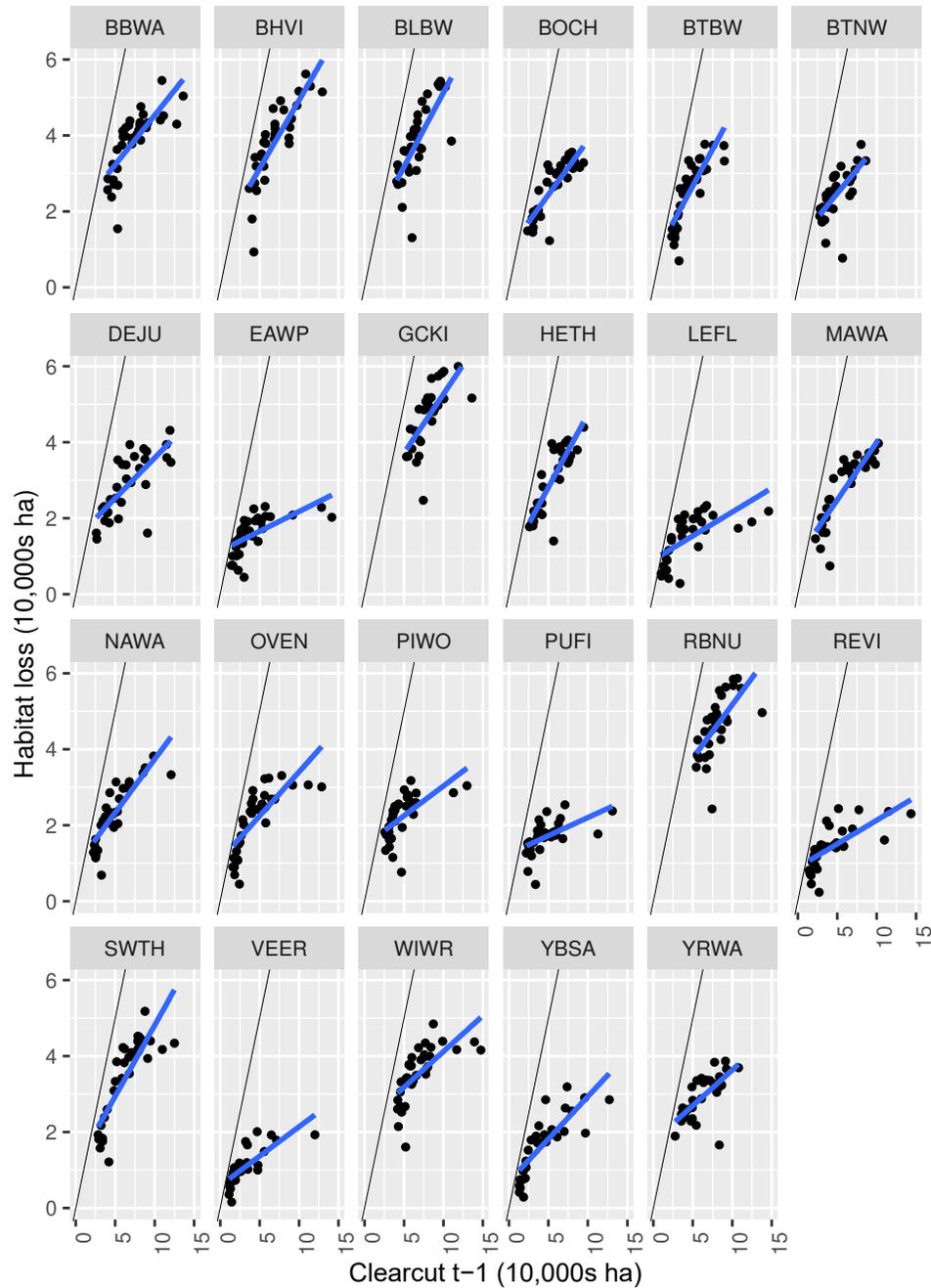


Fig. S3. Relationship between area clearcut occurring in each species’ habitat in each year across the study area and habitat loss for each of 23 mature-forest associated species. Each dot represents a year (1985-2020). Clearcut area is the sum of t-1 and t (the year we quantified habitat loss because 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.

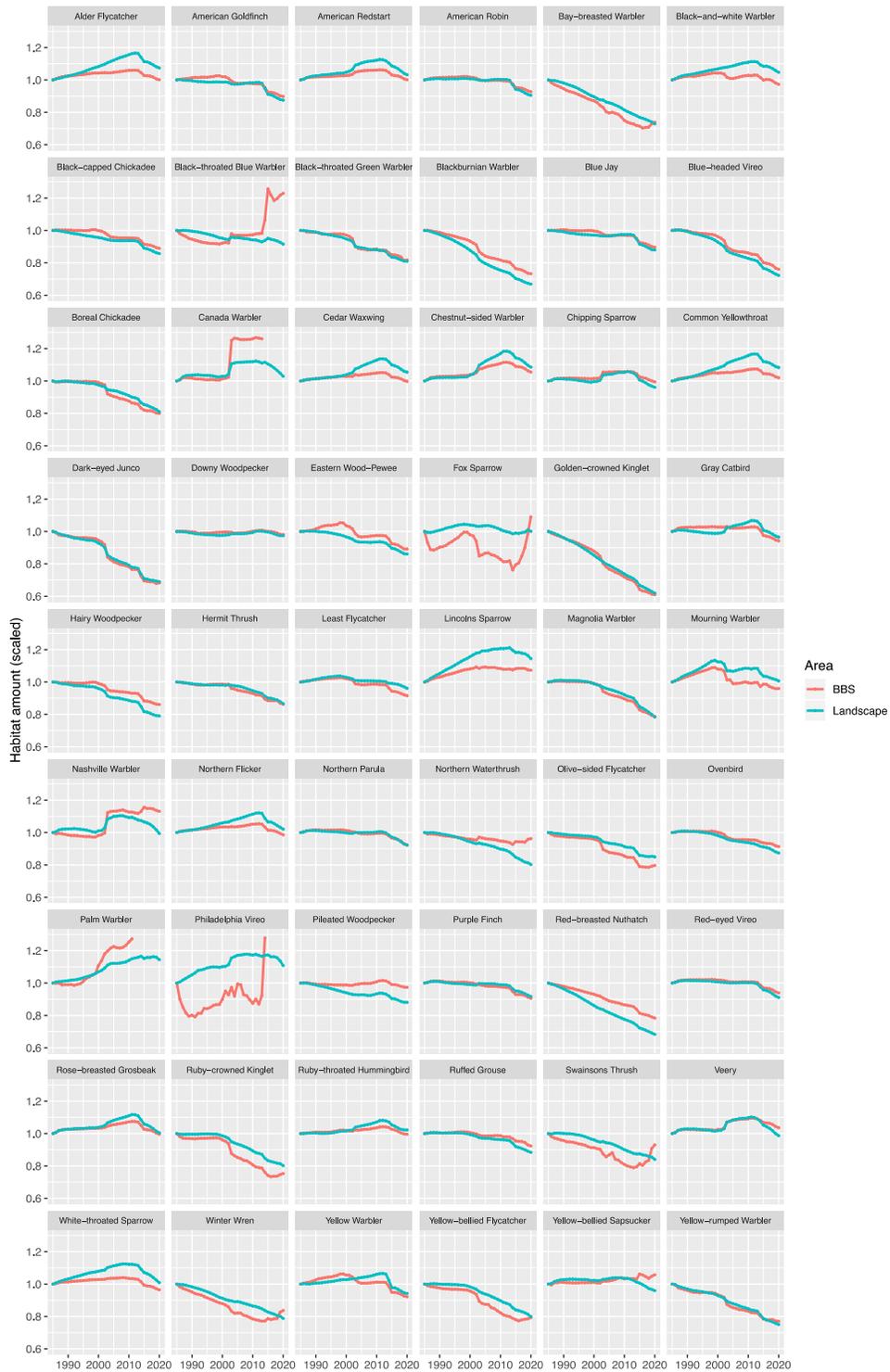


Fig. S4. Habitat trends within 100 m of BBS routes (red lines) versus the entire Maritimes region (green lines) for 54 species of forest birds. Habitat trends along BBS routes tend to reflect changes in the region except for a few species (e.g., Black-throated Blue Warbler).

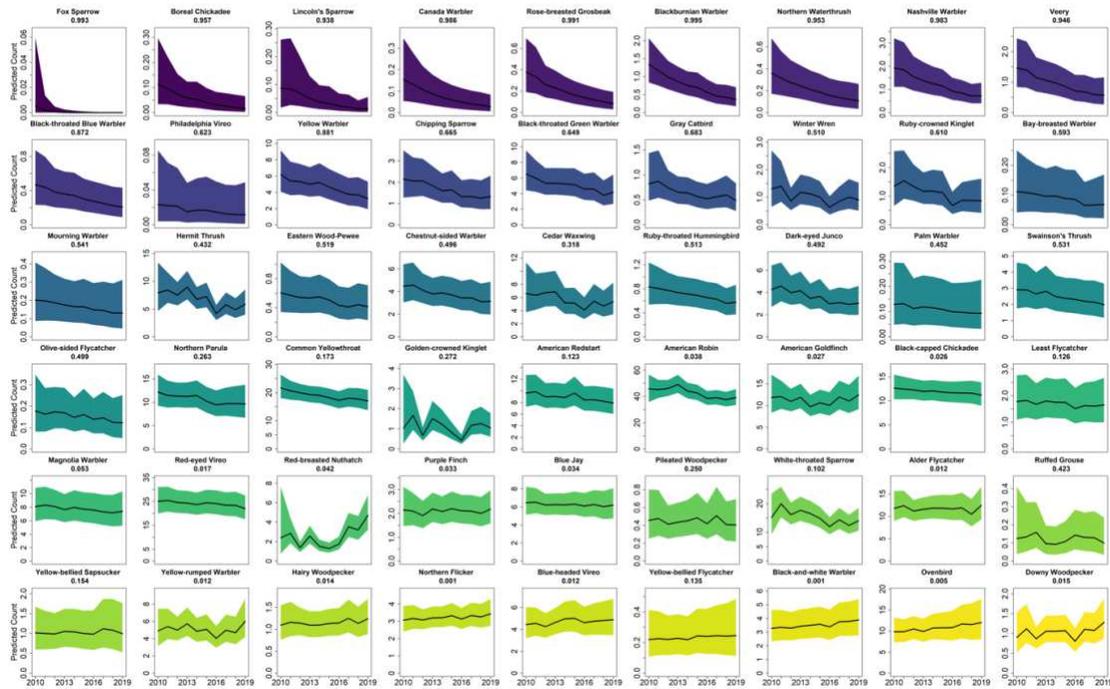


Fig. S5 Ten-year population trend estimates for 54 species of forest-associated birds across the Maritime Provinces of Canada. Number below species names indicate the Bayesian posterior probability that the species is declining at a rate >30% over 10 years (9 species fall into this category, 4 of which are mature-forest associated).

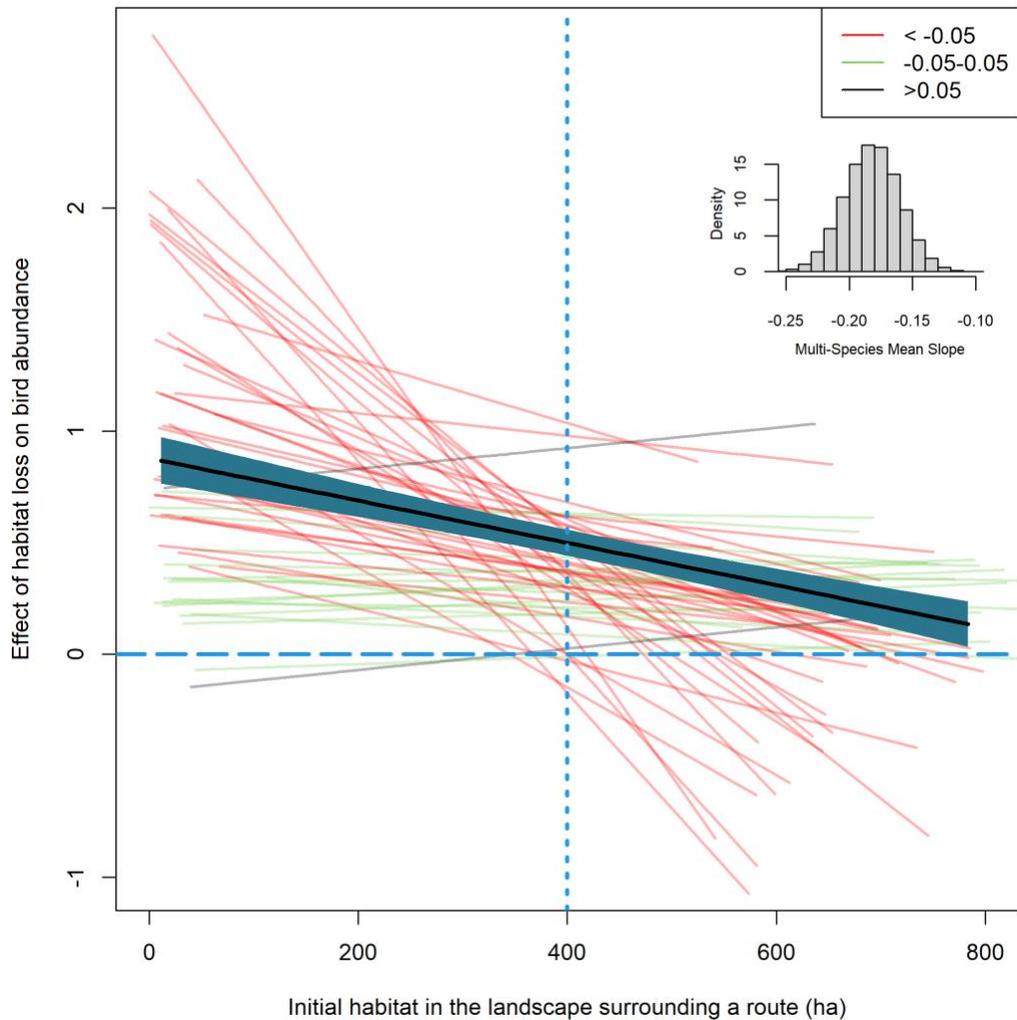
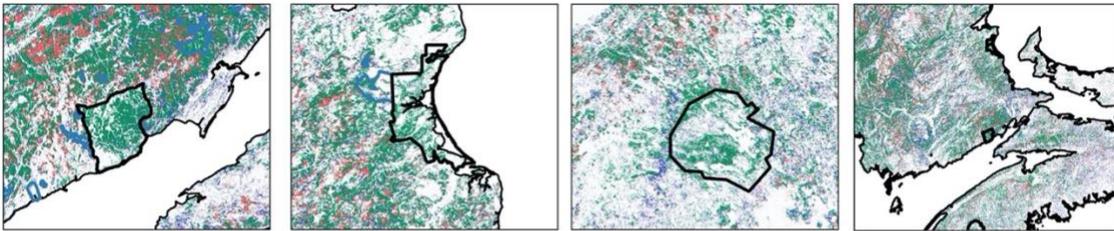


Fig. S6 Effect of habitat amount in the landscape (200 diameter landscapes along 40 km long BBS routes; 800 ha) at the beginning of the study period on the strength of habitat loss effects on annual Breeding Bird Survey abundance. Each line represents a species, with colors indicating the strength of 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.

Black-throated Blue Warbler



Blackburnian Warbler

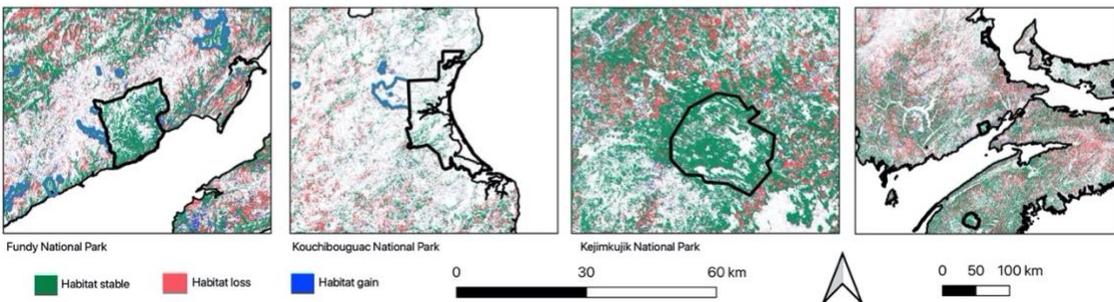


Fig. S7 Habitat distribution and change maps for two examples of mature-forest-associated species within and outside three national parks in eastern Canada (Fundy, Kouchibouguac, Kejimikujik National Parks) and the core area of the study region. Note that habitat loss (red) is common in landscapes surrounding 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.

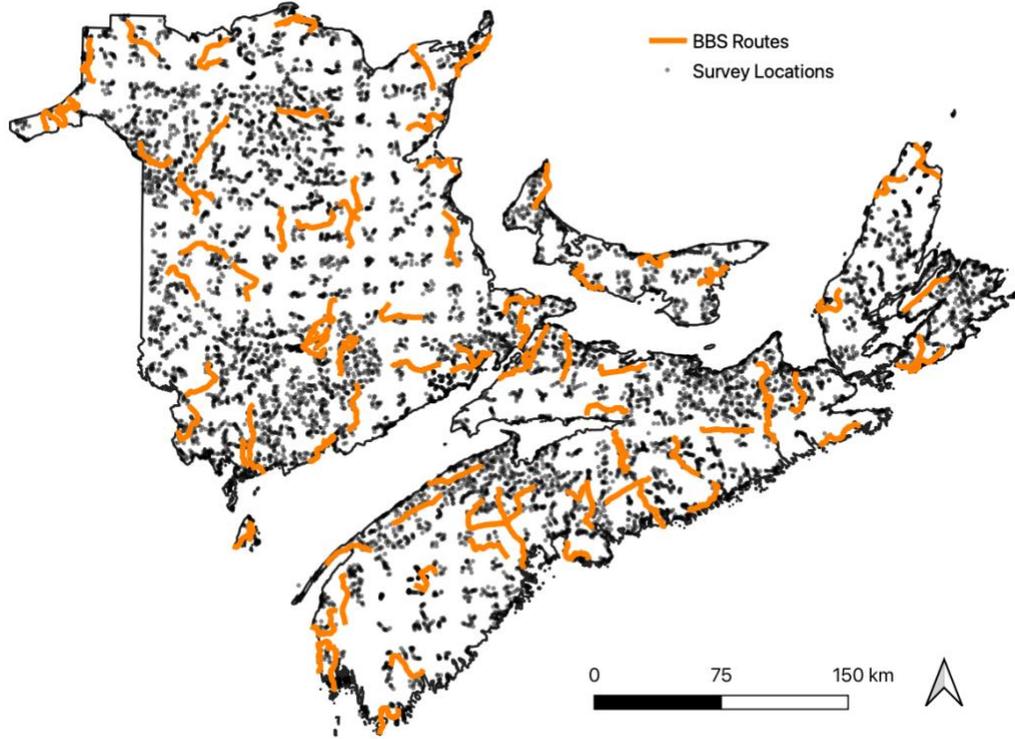


Fig. S8 Study area and location of 12,272 Maritimes Breeding Bird Atlas (MBBA) survey locations (black dots), and Breeding Bird Survey (BBS) routes (orange lines). We used MBBA bird point counts (collected 2006-2011) to build species distribution (habitat) models, and we used long-term BBS routes (N=90) 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	-886,875	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	PUFI	-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 Waxwing	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

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.