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Habitat loss on the breeding grounds is a major contributor to population declines in a long-distance migratory songbird

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Complete List of Authors:	Hallworth, Michael; National Zoological Park, Migratory Bird Center Bayne, Erin; University of Alberta Mckinnon, Emily; York University, Love, Oliver; University of Windsor, Biological Sciences Tremblay, Junior; Environment Canada Drolet, Bruno; Environment Canada région du Québec Ibarzabal, Jacques; Université du Québec Van Wilgenburg, Steven; Environment Canada Marra, Peter; Smithsonian Institution, Migratory Bird Center
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1 **Habitat loss on the breeding grounds is a major contributor to population declines in a**
2 **long-distance migratory songbird**

3 Michael T. Hallworth^{1*}, Erin Bayne², Emily McKinnon³, Oliver Love³, Junior A. Tremblay⁴,
4 Bruno Drolet⁴, Jacques Ibarzabal⁵, Steven Van Wilgenburg⁶, and Peter P. Marra^{1,7}

5 ¹ Migratory Bird Center, Smithsonian Conservation Biology Institute. Washington, D.C. 20008,
6 U.S.A.

7 ² University of Alberta, Alberta, Canada

8 ³ University of Windsor, Ontario, Canada

9 ⁴ Environment and Climate Change Canada, Québec, Canada

10 ⁵ Université du Québec à Chicoutimi, Saguenay, Canada

11 ⁶ Environment and Climate Change Canada, Saskatchewan, Canada

12 ⁷ Department of Biology and McCourt School of Public Policy, Georgetown University, 37th
13 and O Streets NW, Washington, DC 20057, USA

14 * Corresponding Author: mhallworth@gmail.com

15 Michael T. Hallworth - <https://orcid.org/0000-0002-6385-3815>

16 Erin Bayne - <https://orcid.org/0000-0002-0679-4521>

17 Olive Love - <https://orcid.org/0000-0001-8235-6411>

18 Emily McKinnon - <https://orcid.org/0000-0003-3631-0644>

19 Junior A. Tremblay - <https://orcid.org/0000-0003-4930-0939>

20 Jacques Ibarzabal - <https://orcid.org/0000-0002-8724-8038>

21 Steven Van Wilgenburg - <https://orcid.org/0000-0002-6742-4567>

22 Peter P. Marra - <https://orcid.org/0000-0002-0508-7577>

23 Abstract

24 Many migratory species are declining and for most, the proximate causes of their declines
25 remain unknown. For many long-distance Neotropical migratory songbirds, it is assumed habitat
26 loss, on breeding or non-breeding grounds is a primary driver of population declines. We
27 integrated data collected from tracking technology, community science and remote sensing data
28 to quantify migratory connectivity, population trends, and habitat loss. We quantified the
29 correlation between forest change throughout the annual cycle and population declines of a long-
30 distance migratory songbird, the Connecticut warbler (*Oporornis agilis*, observed decline: -
31 8.99% yr⁻¹). Migratory connectivity (MC), the geographic link between populations during two
32 or more phases of the annual cycle, was stronger between breeding and autumn migration routes
33 (MC = 0.24 ± 0.23) than between breeding and non-breeding locations (MC = -0.2 ± 0.14).
34 Different Connecticut warbler populations tended to have population-specific fall migration
35 routes but overlapped almost completely within the northern Gran Chaco ecoregion in South
36 America. Cumulative forest loss within 50km of breeding locations and the resulting decline in
37 the largest forested patch index was correlated more strongly with population declines than forest
38 loss on migratory stopover regions or on wintering locations in South America, suggesting that
39 habitat loss during the breeding season is a driver of observed population declines for the
40 Connecticut warbler. Land-use practices that retain large, forested patches within landscapes will
41 likely benefit breeding populations of this declining songbird, but further research is needed to
42 help inform land-use practices across the full annual cycle to minimize the impacts to migratory
43 songbirds and abate on-going population declines.

44 **Keywords:** Connecticut warbler, Conservation, Migration, Migratory Connectivity, Remote
45 Sensing

46 **Introduction**

47 More than half of migratory bird species in North America are experiencing population
48 declines [1]. For most species the drivers of these declines remain unknown. Migratory
49 populations cross multiple geo-political boundaries and use various habitat types throughout
50 their journeys making it difficult to identify when and where population limitation occurs and to
51 determine the proximate causes of decline. A primary obstacle for conservation of most
52 migratory populations is that migratory connectivity, i.e. where specific populations migrate
53 throughout the annual cycle, is not well understood and therefore limits our ability to identify the
54 threats they face [2,3], and their impacts on fitness and survival [4].

55 Habitat modification and loss is likely a major contributing factor to on-going avian
56 population declines [5]. By removing, converting, or modifying essential habitat, migratory
57 populations may be directly and indirectly impacted in a variety of ways [6,7] depending on
58 where within a species range the habitat alteration occurs. Habitat loss on breeding areas may
59 increase breeding densities within remaining habitat in the short-term, which in turn results in
60 decreased fecundity via density-dependent mechanisms, ultimately decreasing population size
61 [8]. In non-breeding areas, habitat loss may contribute to population declines either directly [9]
62 or indirectly through carry-over effects [10]. Habitat loss at key locations (i.e. stopovers) during
63 migration may limit populations by reducing migratory preparedness and increasing competition
64 for limited food resources [11–13]. Finally, a combination of these factors are likely operating
65 simultaneously. Identifying where and when mortality occurs during the annual cycle remains a
66 major priority but is an elusive goal because of challenges in tracking migratory birds as they
67 move across landscapes.

68 The advent of tracking technology has provided enormous insights into the annual
69 movements of migratory organisms [14]. For large bodied species like waterbirds and shorebirds,
70 tracking technology has identified areas to focus conservation efforts [12]. However, for small
71 bodied birds, tracking technology capable of revealing migratory movements throughout the
72 annual cycle became available only relatively recently [15–17]. Miniaturized tracking
73 technology has been used to better understand species distributions [18], identify where
74 individuals and populations go throughout the year [19], determine critical stopover locations
75 during migration [20], and measure the strength of migratory connectivity [21,22]. Few studies,
76 however, have used tracking information to better understand how habitat degradation in key
77 areas is correlated with on-going population declines [6,7,12,23]. For many long-distance
78 Neotropical migrants, a primary cause of decline is assumed to be habitat loss and it is often
79 assumed to occur outside of the breeding season, either along migratory routes [24] or during the
80 non-breeding season [9].

81 The Connecticut warbler (*Oporornis agilis*) is a medium sized (~15g), insectivorous ground
82 foraging warbler that breeds in boreal forest [25]. Most of the population breeds in the boreal
83 forests of Canada but they also breed in northern regions (Michigan, Minnesota, and Wisconsin)
84 of the United States. Based on an annual, standardized breeding bird survey, the Connecticut
85 warbler has been experiencing on-going population declines (1.4% year⁻¹; [26]) with a total
86 population decline of 62% since the breeding bird survey began in 1966 [26]. Little information
87 is available about their annual phenology (i.e., migration timing), life history, migratory routes or
88 the non-breeding distribution [27]. Here, we tracked Connecticut warblers throughout their
89 range, to 1) identify the strength of migratory connectivity for distinct breeding populations with
90 varying population trends and 2) correlate remotely sensed habitat loss in the identified areas

91 with population trend data. After identifying where Connecticut warblers were throughout the
92 year, we extracted habitat loss estimates from breeding, migratory stopover and non-breeding
93 locations to determine how habitat loss and fragmentation within those regions correlated with
94 observed trends during the breeding season. By including habitat loss and fragmentation metrics
95 at regions throughout their annual cycle in a single analysis, we were able to draw inference
96 about the relative contribution of habitat loss occurring throughout their range to population
97 declines. If habitat loss throughout the annual cycle contributes to on-going declines, we
98 predicted that populations experiencing the highest amount of habitat loss would also be
99 experiencing the most severe population declines.

100 **Methods**

101 *Defining 'natural' populations*

102 The North American breeding bird survey is a large scale, annual survey used to monitor
103 the status and trends of North American bird populations [26]. We used breeding bird survey
104 data [26] to delimit 'natural' populations following Rushing et al. [28]. All breeding bird survey
105 routes located within the breeding distribution of Connecticut warblers were included. Survey
106 routes that occurred within 250km of the breeding range were also included resulting in 90
107 survey routes. We summarized route-level counts of Connecticut warblers conducted more than
108 three times from 1966-2017. We estimated route-level relative abundance and trend estimates
109 between 2000-2017. 'Natural' populations were identified using clustering based on the
110 Euclidean distance between route locations, estimated route-level abundance and trend estimates
111 [28].

112 *Light-level geolocation*

113 Archival light-level geolocators (geocator hereafter) were deployed on Connecticut
114 warblers within four distinct populations across their breeding range (Fig. 1). Individuals were
115 captured using mist nets and a simulated territorial intrusion where a conspecific song was
116 played from a speaker to elicit a territorial response. Birds aggressively responded and
117 approached the speaker and would usually get captured in the mist net. Once captured, standard
118 morphometric measurements were taken and individuals were fit with a geocator and released.
119 Geolocators were recovered the following breeding season. We recovered 9 geolocators from
120 returning Connecticut warblers from across their breeding range (Québec: n = 2 of 12,
121 Minnesota: n = 1 of 10, Manitoba: n = 4 of 29, Saskatchewan: n = 0 of 6, Alberta: n = 2 of 29).
122 We were unable to assess whether geolocators impacted the return rates in this study but a recent
123 meta-analysis [29] and previous findings [21] suggest geolocators have no appreciable effect on
124 survival of similarly sized species. All tags collected data long enough to characterize the
125 location of the stationary non-breeding season to identify where breeding populations wintered.
126 Some tags failed during the middle of the non-breeding season (n = 4, mean failure date: 04
127 April, sd: 16.85 days) limiting our analyses to autumn migration and the non-breeding season.
128 Once recovered, ambient light-levels recorded by the geolocators were transformed into
129 estimated geographic coordinates using the solar/satellite geolocation for animal tracking
130 (SGAT) package [30,31] in R [32] (see supplemental information for more detail).

131 *Migratory Connectivity*

132 We estimated the strength of migratory connectivity (MC) during three phases of the annual
133 cycle to better understand Connecticut warbler biology and assess how critical phases of the
134 annual cycle are geographically linked [22]. First, we used the geocator information to
135 determine the strength of MC between breeding locations and their first major stopover location

136 prior to making long-distance movements over water migrating south in the fall. We then
137 estimated MC between the breeding season and locations where individuals made landfall
138 following their over water flights. Finally, we estimated the strength of MC between breeding
139 and non-breeding seasons. We were unable to test whether the MC values differed significantly
140 between the phases of the annual cycle because the estimates are not independent. We used
141 500km x 500km target regions that included the eastern coastal regions of the United States and
142 Canada, the Caribbean basin and northern South America and the entirety of South America for
143 pre-flight, post-flight and non-breeding seasons respectively (Fig. S1). For the non-breeding
144 season, we used a grid that encompassed the entirety of South America because very little is
145 known about the non-breeding distribution of this species [25,27]. We estimated MC using the
146 estMC function available in the MigConnectivity package [33] in R (version 3.4.1 [32]). We used
147 the target regions identified for each population to estimate the influence of habitat loss during
148 critical stopover regions and the non-breeding season on observed breeding season declines.

149 *Habitat loss & fragmentation*

150 We summarized the amount of habitat loss per year (2000-2017) within 50km of breeding
151 bird survey routes to determine whether on-going declines can be attributed to habitat loss on the
152 breeding grounds. We chose a 50km radius around each breeding bird survey route to ensure the
153 entire route (~40 km) was included. In addition, for populations where we tracked individuals (n
154 = 4 populations), we used locations determined from geolocators to identify specific geographic
155 areas to quantify habitat loss during each phase of the annual cycle. We quantified cumulative
156 habitat loss through time for distinct regions we were able to identify using geolocators. Because
157 of the uncertainty associated with light-level geolocation [34], those regions included stopover
158 locations prior to and following large water crossings and the stationary non-breeding season in

159 South America. We used a weighted average to summarize habitat loss within the 500km x
160 500km regions identified for each population from 2000 to 2017 to determine whether habitat
161 loss correlates with population declines observed during the breeding season. We used the
162 estimated probability that a population used a particular 500km x 500km region derived from the
163 MC metric to calculate a weighted average (Fig. S1). We assumed that individuals from our
164 sampling locations were representative of the larger population and that the general location of
165 stopover and stationary non-breeding location remained the same among years for the different
166 populations. Finally, we included the total amount of habitat loss throughout the annual cycle by
167 summing breeding, stopover, and non-breeding forest loss. Habitat loss was summarized from
168 the Global Forest Change data set (version 1.6; [35]) using Google Earth Engine [36].

169 Habitat fragmentation often accompanies habitat loss and total habitat loss may not capture
170 the influence that habitat fragmentation has on population declines. Therefore, in addition to
171 habitat loss we quantified metrics that best describe habitat fragmentation within each landscape
172 described above by calculating percentage of forest cover (PLAND), edge density (ED), patch
173 density (PD), number of habitat patches (NP), largest patch index (LPI), total core area (TCA),
174 and core area index (CAI) metrics [37] using the LandscapeMetrics R package [38]. We
175 removed highly correlated fragmentation metrics ($r > 0.75$) to reduce redundancy (see
176 supplemental information, Fig S5) resulting in three biologically relevant metrics used to
177 describe fragmentation within the landscapes. Those included largest patch index (LPI) which is
178 an area to edge metric, number of patches (NP) which describes the number of patches within the
179 landscape and total core area (TCA) which describes the amount of core area (non-edge habitat)
180 within a landscape [38]. We defined edge as habitat within 90m of a patch boundary.

181 We coupled relative abundance and trend estimates derived from breeding bird survey data
 182 with habitat loss and fragmentation within geographic regions used during different phases of
 183 annual cycle identified with tracking technology to assess where within the annual cycle habitat
 184 loss has the greatest impact on Connecticut warbler populations. Using a Bayesian framework,
 185 we first identified where within the annual cycle habitat loss had the greatest impact on breeding
 186 populations. Specifically, we modeled observed counts (y) at each breeding bird survey location
 187 i , within the ‘natural’ population pop , in each year t following

$$188 \quad y_{i,t} \sim \text{Poisson}(\lambda_{i,t})$$

$$189 \quad \log(\lambda_{i,t}) = \alpha_{pop_i} + \beta_{pop_i} * t + \beta'_{pop_i} * X_{i,t} + \beta_{obs} * naive_{i,t} + \omega_{i,t} + \varepsilon_{pop_i,t}$$

190 where β' indicates a vector of beta estimates. X represents a vector of covariates composed of
 191 cumulative habitat loss within 50km of the breeding bird survey routes, habitat loss at stopover
 192 locations pre and post Atlantic flights, habitat loss during the non-breeding season and the
 193 summation of habitat loss experienced throughout the annual cycle (breeding, stopover, and non-
 194 breeding). β_{obs} is a parameter to account for naive observers during their first survey year [28].
 195 ω and ε are observer and route-level random effects, respectively. We then fit a separate but
 196 similar model that included the habitat fragmentation parameters to better understand how
 197 fragmentation resulting from habitat loss and/or conversion impacts breeding populations. We
 198 used the same model structure, but the covariate vector included the fragmentation metrics LPI,
 199 NP and TCA for each landscape.

200 We used Gibbs variable selection (see [39]) to determine the relative importance of
 201 habitat loss or habitat fragmentation during different stages of the annual cycle. We modeled the
 202 β estimates as a joint distribution with an indicator variable γ [39]. As the MCMC updates, γ

203 takes a value of 1 if the associated variable is included in the model and 0 if not [44]. Therefore,
204 summarizing the posterior distribution of γ provides an unbiased estimate of variable
205 importance. We used the posterior mean of γ to evaluate the relative importance of habitat loss
206 and landscape fragmentation occurring throughout the annual cycle on breeding season
207 abundance. Models were run in JAGS (Just Another Gibbs Sampler; [40]) accessed through R via
208 the jagsUI package [41]. We ran 3 chains of 100000 iterations with an initial burn-in period of
209 50000 iterations following an adaptation phase of 10000 iterations. We thinned every 15th
210 iteration leaving 9999 draws from the posterior distribution from which we drew our inference.
211 We assessed model fit using a posterior predictive Chi-square goodness of fit test statistic [42].
212 Both habitat loss and habitat fragmentation models adequately fit the data as indicated by a
213 Bayesian p-value of 0.451 and 0.383, respectively (Fig. S4).

214 **Results**

215 *Population trends*

216 Across their range, the Connecticut warbler population declined by -8.99% (95% CI = -
217 15.53 : -2.7) per year between 2000-2017 and is composed of eight 'natural' populations (Fig.
218 1.). Trend estimates indicate that all 'natural' populations are declining with mean trend
219 estimates ranging from -12.48% to -5.02% per year. The 95% credible interval for nearly half of
220 the 'natural' populations (n = 3 of 8) did not include zero indicating a statistically significant
221 decline (see Fig. 1.). Although the 95% credible interval overlapped zero for 5 of the 8 'natural'
222 populations, between 88.42 and 99.97 percent of all samples drawn from the posterior
223 distribution (n = 9999) were negative trend estimates.

224 *Migratory Connectivity*

225 Connecticut warblers from the four tracked populations initiated fall migration in August
226 (Aug. 19 ± 5.28 days) and arrived on the east coast of North America in early September
227 (Sept. 10 ± 6.63 days). All but one Connecticut warbler made long-distance over water flights
228 from the east coast of North America on their way to South America. Individuals spent $10.5 \pm$
229 2.31 days on stopover prior to departing over the Atlantic in early October (Oct. 10 ± 5.82 days).
230 Mean flight time over the Atlantic Ocean was approximately 3 ± 0.65 days. Upon arrival to the
231 stopover in the Caribbean or South America, Connecticut warblers stayed on average $10.71 \pm$
232 2.43 days. They arrived on their stationary non-breeding grounds in early November (Nov. $09 \pm$
233 3.52 days), 81.5 ± 5.23 days after departing their breeding locations.

234 Connecticut warblers tended to have population specific stopover areas prior to and
235 immediately following their long-distance flights over the Atlantic. The strength of migratory
236 connectivity was stronger between breeding and fall stopover sites (stopover pre-Atlantic: $MC =$
237 0.24 ± 0.23 , stopover post-Atlantic: $MC = 0.31 \pm 0.23$) than it was between breeding and non-
238 breeding grounds ($MC = -0.2 \pm 0.14$). Most individuals spent the stationary non-breeding season
239 in an overlapping region of South America which includes southwestern Brazil, eastern Bolivia
240 and northern Paraguay (Fig. 2).

241 *Habitat loss & fragmentation*

242 Habitat loss occurred within breeding, migratory stopover and stationary non-breeding areas
243 used by Connecticut warblers. The annual rate of habitat loss was greatest within the non-
244 breeding regions in South America (mean = -0.16 ; range = -0.21 to -0.11 % $^{-yr}$) followed by
245 stopover regions pre Atlantic crossing (mean = -0.13 ; range = -0.24 to -0.03 % $^{-yr}$), the breeding

246 season (mean = -0.1; range = -0.13 to -0.06 % ^{-yr}), and finally stopover regions post Atlantic
247 crossing (mean = -0.05; range = -0.08 to -0.02 % ^{-yr}; Fig. 3).

248 Connecticut warbler breeding abundance in 3 of 8 ‘natural’-populations was negatively
249 correlated with cumulative habitat loss within 50km of breeding locations (Fig. 4A) and was the
250 most important variable in the habitat loss model for 7 of the 8 populations. The effect of habitat
251 loss at stopover locations prior to and following crossing the Atlantic were not identified as
252 important contributors to Connecticut warbler abundance for any of the ‘natural’ populations
253 within our modeling framework ($\gamma < 0.25$). Cumulative habitat loss during the stationary non-
254 breeding season in South America was identified as a highly important variable affecting
255 abundance in the Alberta East breeding population ($\gamma = 0.97$) and slightly important ($0.5 > \gamma >$
256 0.25) for the remaining tracked populations (Ontario West: $\gamma = 0.37$; Northern U.S.: $\gamma = 0.39$;
257 and Québec: $\gamma = 0.4$). Habitat loss during the stationary non-breeding season was more important
258 than breeding habitat loss for the Northern U.S. population but was not statistically significant (β
259 = 0.15; 95% CI = -0.45 : 1.42, Fig. 4).

260 Habitat loss increased habitat fragmentation within the landscapes used by Connecticut
261 warblers throughout their annual cycle. Largest patch index (LPI) on the breeding grounds was
262 identified as an important variable in our fragmentation modeling framework, was positively
263 correlated with Connecticut warbler abundance and was statistically significant in nearly all
264 populations (Fig. 4). LPI was generally higher on the breeding grounds than within either
265 stopover region or on the stationary non-breeding grounds (Fig. 3). Despite the declines in total
266 core area (TCA) throughout the annual cycle, TCA was not identified as an important feature of
267 the landscape contributing to abundance on the breeding grounds (Fig. 4C). The number of
268 habitat patches (NP) within 50km of the breeding bird survey routes was identified as being

269 slightly ($\gamma > 0.25$, $n = 4$ of 8 ‘natural’ populations) to highly important ($\gamma > 0.75$, $n = 2$ of 8
270 ‘natural’ populations) for many of the sub-populations. Our modeling framework suggests that
271 the number of habitat patches (NP) during the stationary non-breeding period was more
272 important for abundance on the breeding grounds than the number of habitat patches within
273 landscapes that Connecticut warblers used during migratory stopover (Fig. 4D). The effect that
274 NP had on breeding abundance differed between the phases of the annual cycle. For example, the
275 number of habitat patches on the breeding grounds was positively correlated with breeding
276 abundance in the Saskatchewan ($\beta = 0.83$; 95% CI = 0 : 1.54) and Ontario West ($\beta = 0.85$; 95%
277 CI = 0.46 : 1.22) populations while the number of patches on the stationary non-breeding
278 grounds was negatively correlated with observed breeding abundance for the Québec ($\beta = -0.49$;
279 95% CI = -4.72 : 0.4) and Ontario West ($\beta = -0.75$; 95% CI = -3.52 : 0) populations. The number
280 of habitat patches during the stationary non-breeding period was positively correlated with
281 breeding ground abundance within the Alberta East population ($\beta = 0.54$; 95% CI = 0 : 3.79).

282 **Discussion**

283 Identifying the causes of population declines for migratory animals is an urgent yet
284 challenging objective for multiple reasons, not the least of which is we still lack essential
285 information on migratory connectivity for most species [2]. Here, we provide a framework that
286 integrates multiple data sources to identify where within the annual cycle environmental
287 perturbations impact migratory populations. Through the combined use of long-term community
288 science data (breeding bird surveys), tracking technology and remote sensing we found that
289 habitat loss and the resulting habitat fragmentation on the breeding grounds was most strongly
290 correlated with population declines for a steeply declining long-distance migratory songbird, the
291 Connecticut warbler.

292 The strength of migratory connectivity between breeding locations and key migratory
293 stopover regions was stronger than it was between breeding and non-breeding locations. Our
294 results suggest that during autumn, breeding populations use migratory routes unique to each
295 ‘natural’ population but winter in the same general region of South America. However, our
296 migratory connectivity inferences are based on tracking information from relatively few
297 individuals. The factors contributing to stronger migratory connectivity during fall migration are
298 unknown but profitable wind patterns may be responsible [43]. The synchronous timing of
299 departure (Oct. 10 ± 5.82 days) from eastern North America despite individuals breeding across
300 their range suggests that favorable wind patterns during long-distance over-water flights may
301 govern migration timing [44]. Prior to departing the east coast of North America individuals
302 spent on average 10.5 days on stopover. Although the need to maximize re-fueling rates is
303 important, the long duration on stopover may also indicate selection for favorable wind patterns
304 prior to making long-distance over-water flights [44].

305 Interestingly, several other steeply declining songbird species that breed in North America,
306 the Prothonotary warbler (*Protonotaria citrea*; [45]) and Purple Martin (*Progne subis*; [46])
307 exhibit similar patterns of migratory connectivity where populations migrate along different
308 routes but winter in the same general location. Such a pattern could arise if survival varies
309 geographically within the non-breeding distribution [4,47]. If survival varies markedly across the
310 distribution, more individuals wintering in high survival locations will return to the breeding
311 grounds resulting in weak migratory connectivity, i.e., the appearance that individuals from
312 across the breeding distribution winter in a similar geographic region. Further research is needed
313 to determine how spatial variation in survival across the annual cycle could influence observed
314 migratory connectivity patterns [4]. However, the analytical framework employed here could be

315 used to help identify where within the annual cycle migratory populations are limited and could
316 be used for any migratory species where adequate tracking data and survey data exist.

317 Combining tracking technology and remote sensing allowed us to identify how habitat loss
318 and fragmentation at different times and places in the annual cycle correlates with population
319 declines observed during the breeding season. Our findings, although based on relatively few
320 tracked individuals suggest that habitat loss and fragmentation on the breeding grounds is
321 strongly correlated with population declines. Connecticut warblers exhibit weak migratory
322 connectivity between breeding and stationary non-breeding seasons, as such our ability to detect
323 a habitat loss or fragmentation signal from the non-breeding grounds is likely diminished.
324 Furthermore, more data were available from the breeding grounds and at a finer spatial
325 resolution (Breeding Bird Survey) than from the non-breeding phases of the annual cycle. The
326 combination of archival tracking technology with inherent location uncertainty and relatively
327 few tracked individuals may have decreased our ability to detect the full extent of how non-
328 breeding season habitat loss and fragmentation impact Connecticut warbler abundance.
329 However, this study illustrates that tracking data combined with other data sources can improve
330 our understanding of the biology and threats to little-known species.

331 Tracking data were only available during autumn migration and the stationary non-
332 breeding season, as such our findings do not consider the role of habitat loss in regions used
333 during spring migration on population dynamics. Connecticut warblers undertake large over-
334 water flights during southward migration in autumn [27], and it is possible they use alternate
335 routes during their journey north in spring and are impacted by habitat loss in regions not
336 included in our analyses. However, community science (also referred to as citizen science)
337 observations submitted to eBird suggest that Connecticut warblers migrate primarily through the

338 Caribbean Basin and into eastern North America as they migrate north in the spring - the same
339 general regions used during fall we identified with light-level geolocators (Fig. S5). That said,
340 the evidence that habitat loss and resulting fragmentation on the breeding grounds is most
341 strongly correlated with on-going declines suggests it is likely an important contributing factor in
342 population declines.

343 Little is known about the basic biology of Connecticut warblers despite on-going population
344 declines (~ 70% decline since 1966). For example, information as fundamental as the non-
345 breeding distribution and patterns of habitat use are essentially undescribed in the scientific
346 literature [25,27]. The primary wintering locations identified here encompassed the northern
347 Gran Chaco ecoregion, a region including southern Brazil, eastern Bolivia, and northern
348 Paraguay, further south than previously thought although few observations and captures from
349 that region exist [25]. The Gran Chaco ecoregion is a global deforestation hotspot [35,48] and
350 lost >20% of its forest between 1985 and 2013 (142,000km²; [48]). Deforestation rate in the
351 region has increased substantially since 2000 [48]. Remotely sensed land cover data indicate the
352 region is dominated by savanna (37.28%), and grassland (23.65%) ecosystems. However, the
353 forested areas within the region where Connecticut warblers winter are comprised of deciduous
354 broadleaf (12.79%) and evergreen broadleaf (7.77%) forest types. Agriculture is common in the
355 region with croplands encompassing about 5% (4.39%) of the landscape. Commodity driven
356 deforestation and shifting agricultural practices are the dominant causes of permanent forest loss
357 in the region [49]. Continued expansion and further encroachment of agriculture could pose a
358 threat to these forested areas in future [48,50]. Inherent location uncertainty associated light-level
359 geolocation [34] precluded us from inferring habitat associations during the winter period.
360 However, the forested areas in southern Brazil, eastern Bolivia and northern Paraguay appear to

361 support Connecticut warblers from across their breeding range. Therefore, continued forest loss
362 in the region will likely impact Connecticut warbler populations across their breeding
363 distribution. Currently, over 4,300 square kilometers of protected areas exist in the region where
364 they wintered including portions of the forested regions.

365 The breeding range of Connecticut warblers falls primarily within warm continental and
366 subarctic ecoregions, but specific habitat requirements differ across their breeding range [51]. In
367 the northwestern portion of their breeding distribution, they breed in upland aspen (*Poplar sp.*)
368 stands [52,53] while across most of their distribution they breed in wet, tamarack (*Larix laricina*)
369 / black spruce (*Picea mariana*) [54], and jack pine (*Pinus banksiana*) stands [55]. Cumulative
370 habitat loss within 50km of breeding bird survey routes had stronger effects on population
371 declines in areas where they breed in wet, tamarack / black spruce and jack pine stands. While
372 the underlying mechanism contributing to the observed differences between forest types are not
373 well understood, the potential regeneration time of the forest structure to a state needed for
374 successful reproduction may differ depending whether they breed in wet, tamarack stands or
375 upland aspen woodlands and may contribute to on-going population declines.

376 Habitat loss and the resulting fragmentation on the breeding grounds is strongly correlated
377 with observed population declines for the Connecticut warbler. Our findings suggest that large
378 intact forest patches within the landscape are positively correlated with Connecticut warbler
379 abundance. Therefore, Connecticut warbler populations would likely benefit from land
380 management practices that retain large, intact forest patches within the landscape. Although the
381 specific causes of habitat loss were not identified here, conversion of forest to agriculture
382 [56,57], peat mining [58] and forestry practices are common in the region and have impacts on
383 breeding bird species. Curtis et al. [49] found that forestry and wildfire are the primary sources

384 of forest cover loss within the warm continental and subarctic ecoregions in North America, but
385 most of these losses will recover with subsequent tree regrowth. However, these disturbances
386 affect forest age structure and composition that may result in habitat loss for the Connecticut
387 warbler. Forestry within the northern temperate / boreal forest is an important industry. In
388 Canada, where the vast majority of Connecticut warblers breed, the forestry industry employs
389 over 200,000 people and accounts for over 7% of all Canadian exports totaling over \$25 billion
390 for the Canadian economy [59]. As such, without some immediate policy action for habitat
391 protection, the continued harvesting of forest products and resultant change in forest age
392 structure and composition will continue and may further influence declines of this poorly known
393 species.

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401 E.M., J.T., B.D., J.I., & P.P.M. conducted field work. M.T.H. conducted the analyses and wrote
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404 **Data Availability** – Movement data associated with the manuscript can be found in
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567

568 **Tables**

569 Table 1. β coefficients between forest loss during different phases of the annual cycle and Connecticut warbler abundance on the
 570 breeding grounds. Connecticut warbler ‘natural’ populations were identified following [30]. Mean β correlations are shown along with
 571 the 95% credible interval in parenthesis. Zero values are reported outside of the breeding season for ‘natural’ populations with no
 572 tracking data. The number of Breeding Bird Survey routes the comprise the ‘natural’ population are reported in parentheses.

‘Natural’ Population	Breeding	Pre-Atlantic	Post-Atlantic	Stationary non-breeding	Cumulative
Québec (n = 1)	-0.76 (-3.49 : 0.86)	-0.83 (-6.44 : 2.67)	-0.5 (-4.12 : 0.83)	-0.36 (-1.49 : 0.73)	-0.16 (-0.86 : 0.24)
Great Lakes (n = 5)	0.01 (-1.00 : 1.04)				
Ontario West (n = 26)	-0.04 (-0.43 : 0.30)	0.37 (-1.18 : 2.32)	-0.13 (-1.21 : 0.42)	0.39 (-0.73 : 1.87)	-0.01 (-0.31 : 0.25)
Northern U.S. (n = 13)	-0.36 (-0.80 : 0.04)	1.86 (-0.07 : 5.61)	0.19 (-0.27 : 1.20)	-0.22 (-2.43 : 0.88)	-0.05 (-0.76 : 0.48)
Alberta W. (n = 6)	-0.26 (-0.81 : 0.27)				
Alberta E. (n = 20)	-1.01 (-1.74 : -0.20)	0.11 (-1.09 : 1.32)	0.12 (-0.73 : 1.20)	1.09 (0.15 : 2.11)	-0.01 (-0.72 : 0.51)
Saskatchewan (n = 9)	0.14 (-0.40 : 0.70)				
Manitoba (n = 10)	-0.80 (-1.79 : 0.01)				

573

574 Table 2. β coefficients for three habitat fragmentation parameters, total core area (TCA), number of patches (NP) and largest patch
 575 index (LPI) throughout the annual cycle on Connecticut warbler abundance on the breeding grounds. The mean effect size along with
 576 the 95% credible interval are reported. β coefficients where the 95% credible interval does not include zero are indicated with bold
 577 font. The effect sizes outside the breeding season are reported as zero for ‘natural’ populations without tracking data.

Fragmentation Metric	Québec	Great Lakes	Ontario West	Northern U.S.	Alberta W.	Alberta E.	Saskatchewan	Manitoba
Total Core Area								
Breeding	1.03 (-0.5:7.28)	0.34 (-0.54:1.15)	0.33 (-0.5:1.09)	0.08 (-0.63:0.63)	0.40 (-0.08:0.93)	0.41 (0.06:0.78)	0.37 (-0.25:1.34)	0.19 (-0.43:0.69)
Pre-Atlantic	0		0	0		0		
Post-Atlantic	-1.68 (-10.48:4.62)		-2.72 (-9.44:0.36)	-0.24 (-0.49:-0.01)		-0.24 (-1.74:0.54)		
Stationary	2.72		0.65	-0.22		0.22		
Non-breeding	(-3.8:9.99)		(-5.76:5.3)	(-0.5:0.14)		(-2.21:4.48)		
Number of Patches								

Breeding	-0.47 (-4.53:1.31)	0.3 (-2.91:1.19)	0.03 (-0.84:0.8)	0.85 (0.46:1.22)	0.08 (-1.15:1.06)	0.29 (0.05:0.55)	0.89 (0.29:1.56)	0.39 (-1.74:0.81)
Pre-Atlantic	0.01 (0:0)		0 (0:0)	0.02 (0:0)		0 (0:0)		
Post-Atlantic	0.64 (-3.73:3.91)		-1.72 (-9.16:3.37)	0.63 (-0.73:2.26)		-0.16 (-1.02:0.86)		
Stationary	-2.11		-1.13	-2.09		2.29		
Non-breeding	(-7.29:2.69)		(-3.41:0.02)	(-3.98:-0.51)		(-0.23:4.53)		

Largest Patch

Index

Breeding	0.74 (-0.23:1.41)	0.71 (-0.19:1.29)	0.43 (-0.61:1.12)	0.76 (0.42:1.13)	0.79 (-0.02:1.5)	1 (0.46:1.59)	0.11 (-1.68:0.92)	0.85 (0.38:1.33)
Pre-Atlantic	0.13 (0:2.54)		-0.02 (0:0)	-0.02 (0:0)		0 (0:0)		
Post-Atlantic	-0.96 (-9.12:8.13)		1.95 (-5.39:21.17)	-0.07 (-1.02:2.05)		-0.37 (-2.61:1.35)		
Stationary	4.22		2.33	-0.14		-0.71		

Non-breeding (-2.52:13.24)

(-9.57:7.95)

(-0.53:0.57)

(-4.99:2.23)

579 **Fig. 1** The breeding distribution of the Connecticut warbler (gray polygon) is comprised of eight
580 'natural' populations. The breeding bird survey locations within each 'natural' population are
581 represented by different colors. The population trend and 95% credible interval are provided
582 alongside the abundance estimates for each 'natural' population. The population wide trend
583 estimate is also shown. The locations of light-level geolocator deployment are illustrated with a
584 black triangle. Image of Connecticut warbler drawn by David Sibley.

585 **Fig. 2** Breeding, autumn migratory stopover regions and non-breeding locations of Connecticut
586 warblers captured throughout their breeding distribution. The four 'natural' populations, the
587 median (colored circles) and 95% credible intervals for each location during autumn migration
588 are shown. The stationary non-breeding location of individuals is indicated with a grey filled
589 point. Sample sizes are shown in each panel. Each individual track is connected with a dotted
590 line to distinguish between individuals but does not represent the actual path traveled between
591 stopover locations. The underlying color ramp represents the uncertainty for the tracking
592 duration.

593 **Fig. 3** Habitat loss and fragmentation metrics across phases of the annual cycle of Connecticut
594 warblers. Cumulative forest loss (% change per year) is shown in the top row. The shaded area
595 around breeding season estimates represents the 95% CI for each 'natural' population. The colors
596 of the lines correspond to the 'natural' populations illustrated in Fig. 1. Although it appears in
597 some figures that fewer than four lines are present, three of the four populations wintered in the
598 same area and therefore have similar forest loss values. The three landscape fragmentation
599 metrics used in our analyses, largest patch index (LPI), total core area (TCA) and number of
600 forest patches (NP) are also shown. Landscape metrics were derived from the Global Forest

601 Change data set (version 1.6; [35]) using the LandscapeMetrics R package [38]. Note the
602 different scale of the y-axis in the breeding ground figures.

603 **Fig. 4** The relative importance of forest loss and forest fragmentation metrics on population
604 declines of Connecticut warblers (A) and the posterior distribution of the β coefficients (B).
605 Indicator values approximating 1 indicate the variable is highly important while values
606 approximating 0 indicate the variable is not important. The colors of the posterior distributions
607 correspond to the ‘natural’ populations illustrated in Fig. 1. Indicator variable and β estimates for
608 the effect of forest loss outside of the breeding grounds are shown for only the populations
609 tracked via light-level geolocators.

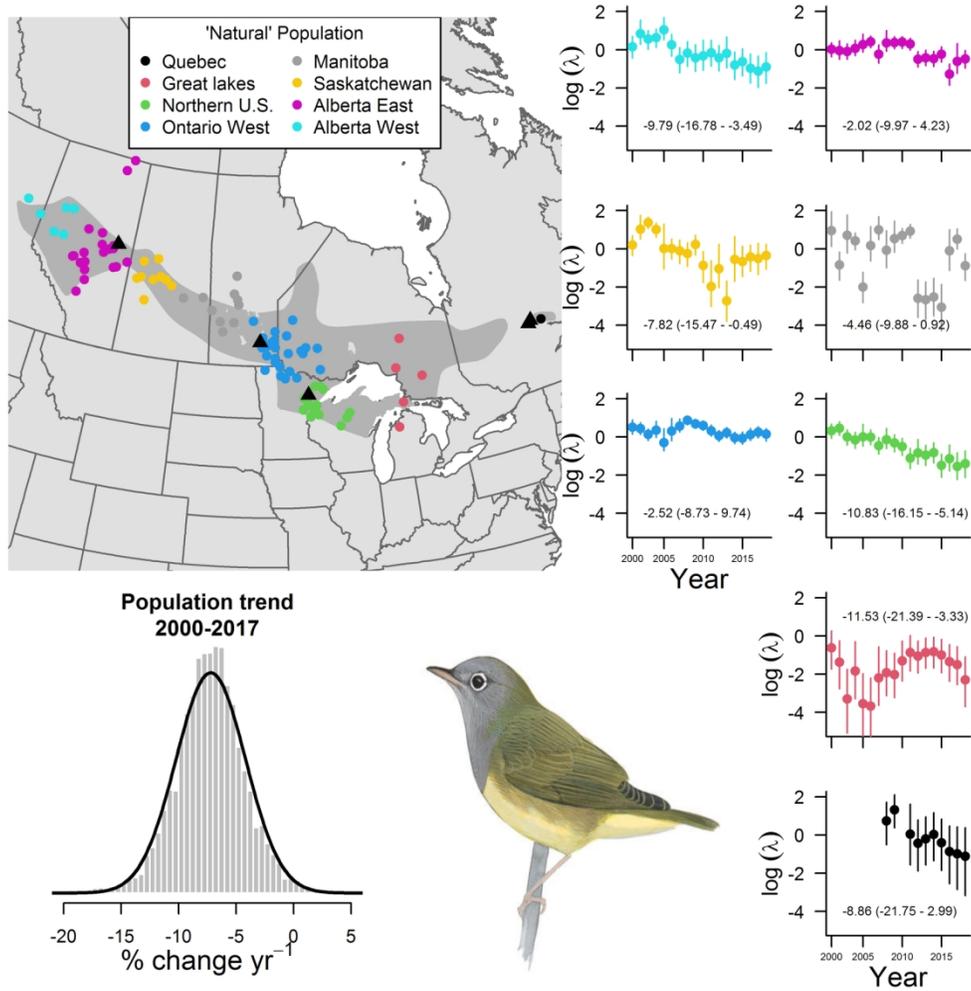


Fig. 1 The breeding distribution of the Connecticut warbler (gray polygon) is comprised of eight 'natural' populations. The breeding bird survey locations within each 'natural' population are represented by different colors. The population trend and 95% credible interval are provided alongside the abundance estimates for each 'natural' population. The population wide trend estimate is also shown. The locations of light-level geolocator deployment are illustrated with a black triangle. Image of Connecticut warbler drawn by David Sibley.

152x152mm (300 x 300 DPI)

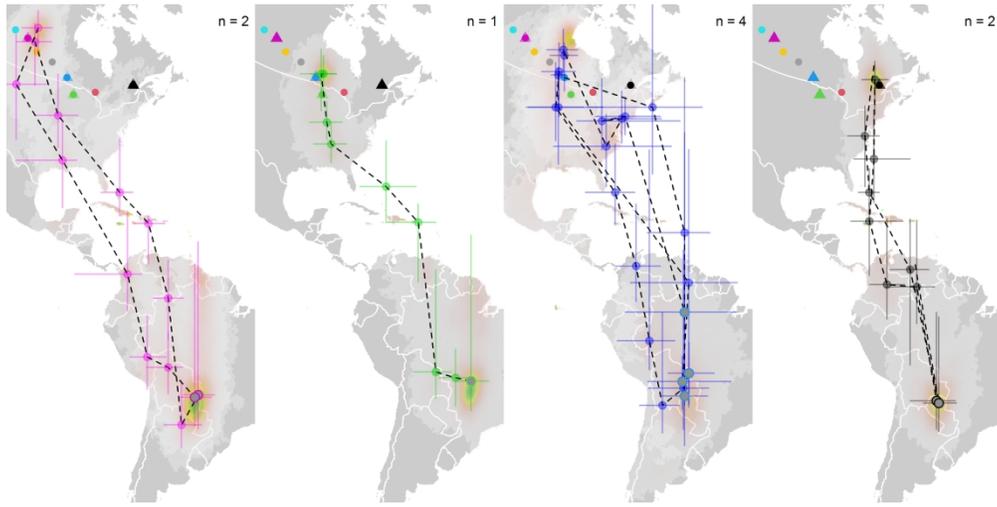


Fig. 2 Breeding, autumn migratory stopover regions and non-breeding locations of Connecticut warblers captured throughout their breeding distribution. The four 'natural' populations, the median (colored circles) and 95% credible intervals for each location during autumn migration are shown. The stationary non-breeding location of individuals is indicated with a grey filled point. Sample sizes are shown in each panel. Each individual track is connected with a dotted line to distinguish between individuals but does not represent the actual path traveled between stopover locations. The underlying color ramp represents the uncertainty for the tracking duration.

203x101mm (300 x 300 DPI)

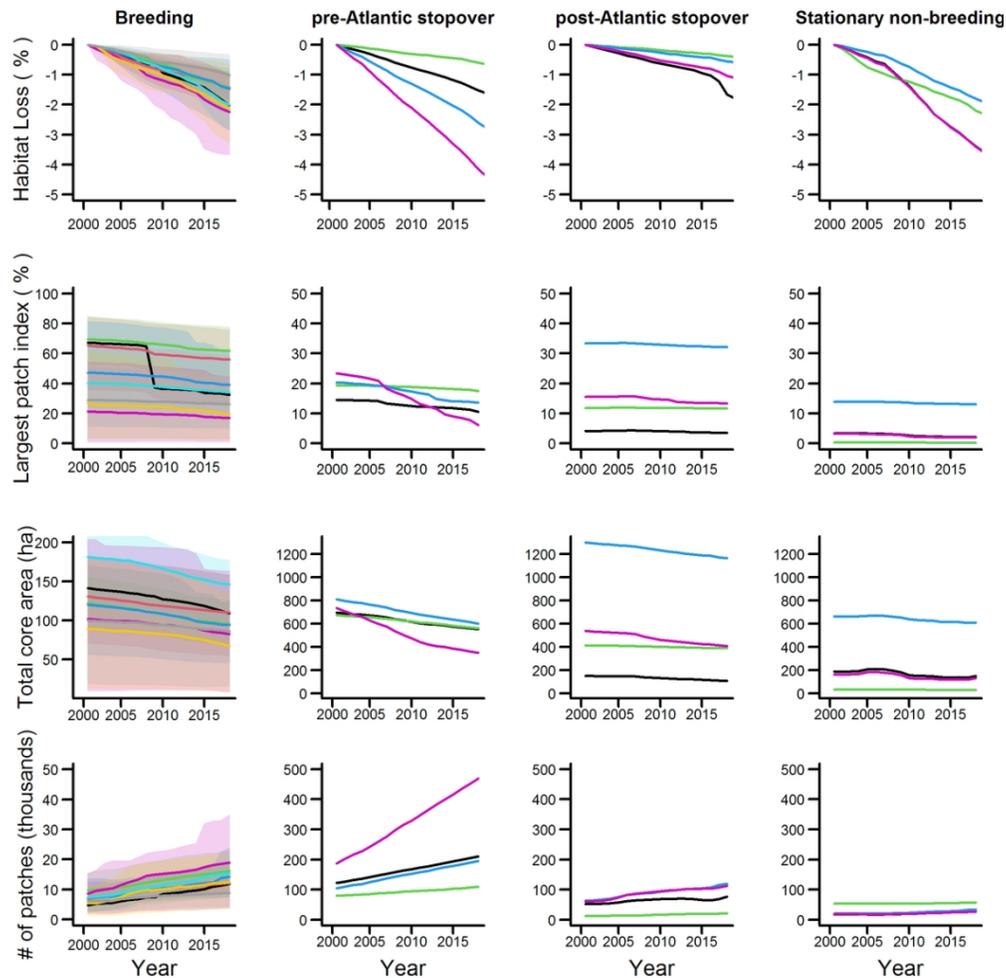


Fig. 3 Habitat loss and fragmentation metrics across phases of the annual cycle of Connecticut warblers. Cumulative forest loss (% change per year) is shown in the top row. The shaded area around breeding season estimates represents the 95% CI for each 'natural' population. The colors of the lines correspond to the 'natural' populations illustrated in Fig. 1. Although it appears in some figures that fewer than four lines are present, three of the four populations wintered in the same area and therefore have similar forest loss values. The three landscape fragmentation metrics used in our analyses, largest patch index (LPI), total core area (TCA) and number of forest patches (NP) are also shown. Landscape metrics were derived from the Global Forest Change data set (version 1.6; [35]) using the LandscapeMetrics R package [38]. Note the different scale of the y-axis in the breeding ground figures.

101x101mm (300 x 300 DPI)

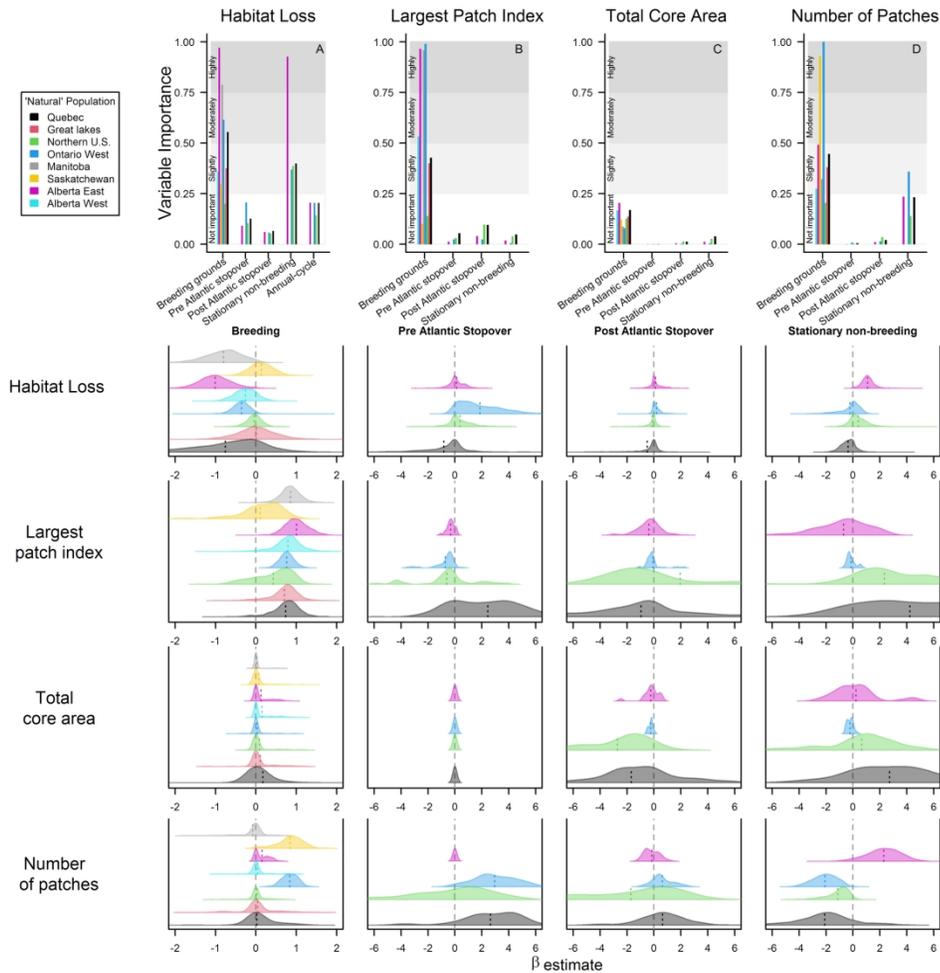


Fig. 4 The relative importance of forest loss and forest fragmentation metrics on population declines of Connecticut warblers (A) and the posterior distribution of the β coefficients (B). Indicator values approximating 1 indicate the variable is highly important while values approximating 0 indicate the variable is not important. The colors of the posterior distributions correspond to the 'natural' populations illustrated in Fig. 1. Indicator variable and β estimates for the effect of forest loss outside of the breeding grounds are shown for only the populations tracked via light-level geolocators.

203x203mm (300 x 300 DPI)