



The 30-YEAR Bird Study

The role of Maine's
commercial forests for
regional and national
bird conservation,
1992-2022

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Cover Photo

Landscape: Looking north toward Chesuncook Lake in the background, photo by J. Hagan

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Photo by J. Hagan



Executive Summary

North American breeding bird populations have declined by an estimated three billion individuals, or almost 30%, since 1970. Habitat loss and degradation are considered the primary drivers of declines. Maine's commercial forest landscape is the largest contiguous tract of intact (non-developed) forest east of the Mississippi and forms the heart of the largest globally significant Important Bird Area in the lower 48 states. What role does this 10-million-acre (4-million ha) area play in regional and national scale bird conservation today?

In this report, we answer this question by replicating an extensive study of birds and forestry we conducted 30 years ago in a 588,000-acre (234,000 ha) commercial forest landscape in the Moosehead Lake region of northcentral Maine. In 2021 and 2022, we surveyed the study area using the exact same methods we used in the early 1990s. Forest practices have changed in Maine since the early 1990s, changing forest types, age classes, and thus bird habitat. For example, clearcutting has declined since the 1990s and partial cutting has increased. Many paper mills now prefer hardwood to softwood, affecting forest types on the landscape. How have these changes, in turn, affected bird populations—positively or negatively—in the last 30 years?

Given the alarming backdrop of national declines in many forest birds, we were surprised to find that 33 (70%) of the 47 species we had sufficient data to analyze showed *increases* in abundance in the last 30 years. This is in stark contrast with trends reported in the Breeding Bird Survey (BBS) for the same timeframe. Instead, the BBS dataset showed that 35 (75%) of the species we analyzed declined both regionally and continentally since the early 1990s. Such a striking difference in results suggests that somewhat different forces are at play in the commercial forest of Maine relative to the rest of the Atlantic Northern Forest Bird Conservation Region (Region 14) and North America.

We estimated the abundance of each of 47 species in the landscape by multiplying the density of each species (birds per unit area) by the amount of each of nine broad forest types and age classes, ranging from clearcuts to late-successional forest. As expected, the amount of clearcut area in the study area declined by about 50% since the 1990s. Mature forest area also declined, most dramatically for mature softwood. Various partial harvesting methods increased, as expected. The amount of young regenerating forest and residual forest (with some overstory retained) greatly increased in the last 30 years. Interestingly, species abundance increases in the study area were driven more by changes in density (changes in birds per unit area) than by changes in the amounts of the nine broad forest types we studied. Many of the 47 species appear to be remarkably flexible in their use of forest types and age classes. We do not yet understand why so many species increased in density, but our results suggest the commercial forest of Maine is functioning as a large, landscape-scale refugium for birds, upholding National Audubon's designation of northern Maine as a globally significant Important Bird Area.

Despite the widespread increases, 14 species (30% of 47) decreased in abundance in the study area in the last 30 years, and thus merit closer examination. Is there something commercial forestry could do differently to support these species better?

Of the 14 species that declined in our study area, the same 14 were also decreasing regionally in the BBS dataset, and 13 of the 14 were decreasing continentally. Of these 14, three species stand out: Canada Warbler, Blackburnian Warbler, and Winter Wren. None of these species are endangered, but the Canada Warbler is a species of Special Concern in Canada. The Canada Warbler uses all forest types and age classes, but is often associated with small, shrubby wet areas within various forest age classes and types. We suspect that habitat loss on the wintering grounds may be driving the declines we detected in our study area. The Canada Warbler has a relatively limited winter range in the highlands of the South American Andes, which has experienced significant deforestation. The Blackburnian Warbler prefers mature and late-successional forest, which declined significantly in our study area. However, it too has a small winter range in the mountainous region of northwestern South America. If wintering ground habitat is limiting these species' populations, there may be little we can do on the breeding grounds to reverse the declines we observed. Not knowing the causes of

declines, to support Blackburnian Warbler conservation it will be important to keep late-successional forest in the greater breeding area landscape. Finally, the Winter Wren showed a dramatic decline in our study area in the last 30 years. This species winters in the southeastern U.S. It is also known to be associated with large fallen logs and root mounds for nesting. The study area could be losing some of the Winter Wren's key habitat structure in Maine because of the shift to a younger forest today. This points to the role of retention of large trees in harvest areas to produce a continual supply of this type of structure, which can be important to many species, especially cavity-nesting birds and not just Winter Wrens.

Finally, we explored the potential of LiDAR (light detection and ranging) data to generate bird species distribution models for Maine. We used the publicly available airborne LiDAR data from 2016-2019 to generate a forest canopy height model for a 1.8-million-acre (724,000 hectares) area of northcentral Maine centered on our study area. Using eight LiDAR-derived canopy metrics and our point count survey data, we developed species distribution models for selected species. Birds are tightly associated with forest structure and composition, and LiDAR is excellent at characterizing forest structure at a very fine scale. We show that LiDAR has enormous potential for generating hectare-resolution species distribution maps across very large areas. This tool could help us understand how different types of forest ownership in Maine (e.g., a mix of public and private) support the full array of forest bird species.

In summary, the commercial forests of Maine have become even more important for bird conservation in the last 30 years. The area appears to function as a "counterweight" to declines for many species at the larger regional and continental scales. Indeed, the continued loss of older forest age classes in the private commercial forest of Maine is a long-term conservation concern. However, since the original 1990s study, we have seen significant increases in private forest ownership for conservation purposes in the last 30 years (e.g., The Nature Conservancy, Appalachian Mountain Club, Northeast Wilderness Trust). This evolution of ownership could mitigate the shift to a younger forest on private commercial forest lands. Moreover, large working-forests easements put in place since the 1990s study ensure that large tracts of bird habitat will endure far into the future. Altogether, in the face of ongoing human development and continental declines in bird populations, all types of forest ownership in northern Maine are serving as an important sanctuary for birds.

Photo by J. Hagan



INTRODUCTION

North American breeding bird populations have declined by an estimated three billion individuals, or almost 30%, since 1970 (Rosenberg et al. 2019). Habitat loss and degradation are considered the primary drivers of declines. Maine's commercial forest is the largest contiguous tract of intact (non-developed) forest east of the Mississippi. It forms the heart of the largest globally significant *Important Bird Area* in the lower 48 states (National Audubon Society 2023). What role does this enormous 10-million-acre (4-million-ha) working-forest landscape play in this continental bird conservation story?

In the early 1990s, we conducted an expansive study of forestry and birds in the commercial forests of Maine (Hagan et al. 1997). To help answer the question above, we replicated the entire 1990s study in 2021 and 2022, thirty years after the original study was conducted. To replicate the study, we used the exact same methods of surveying birds in the exact same study area in the greater Moosehead Lake region of Maine. The comparison of the two studies, separated by three decades, could give us insight into the role Maine's commercial forests are playing today in both regional and national bird conservation.

Much has changed in Maine's commercial forest in the last thirty years, making the replication of the early 1990s study even more interesting. For example, in the early 1990s when the original study was conducted, clearcutting was (and had been) the prevailing harvest method in Maine's commercial forest (Fig. 1, MFS 1992 2023). The extensive clearcutting in the 1970s and 1980s had been prompted by a large spruce budworm outbreak that was decimating Maine's spruce and fir forests (Irland et al. 1988, Soloman et al. 2006). Clearcutting became a strategy for salvaging vulnerable or diseased trees (Fig. 2). At the same time, some landowners

were increasingly turning to intensive forestry that involved converting hardwood stands on rich, well-drained soils, to fast-growing softwood plantations. Confounding this strategy, in the late 1990s and early 2000s, many pulp mills converted to hardwood pulp instead of softwood pulp for papermaking. Manufacturing interest in softwood shifted to sawtimber instead of pulpwood.

In addition to the technological shifts in papermaking, there was a sociological shift that affected how Maine's commercial forests were managed. A growing public aversion to clearcutting was manifested in a 1995 ballot referendum to ban clearcutting in Maine (Hagan 1996). Though the referendum did not pass (it came close with 47% of the vote), it was a wake-up call regarding public perceptions of forest practices. Landowners shifted to various partial cutting approaches, in part to respond to public sentiment about clearcutting (see Fig. 1).

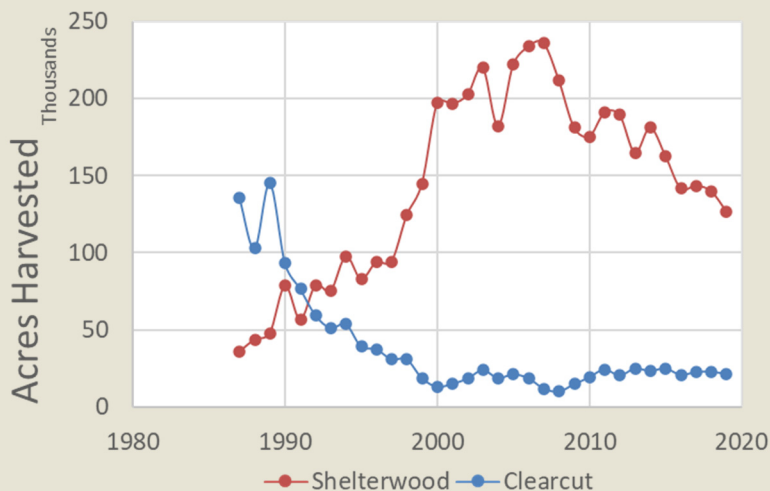


Figure 1. The number of acres harvested by clearcutting and shelterwood from 1987 to 2019 in Maine (MFS 1992, 2022). Clearcutting declined precipitously after the timber salvage operations associated with the 1970s and 1980s spruce budworm outbreak. Also, the public expressed dislike for the extensive clearcutting through a 1995 ban-clearcutting referendum that came close to passing.



Figure 2. The “Great Ragmuff Clearcut” in township T4R14 in 1993. This clearcut was over 15,000 contiguous acres and took a decade to create during and after the spruce budworm outbreak of the 1970s. Our 1990s study showed that the Ragmuff clearcut, and clearcuts in general, were important habitat for many early-successional bird species. (Photo by J. Hagan)

Thirty years ago, our original study showed that different forest types and age classes were used by different species. All forest types, including clearcuts, provided valuable habitat for species of conservation concern (Hagan et al. 1997). Many other researchers have since confirmed this observation for other managed forest landscapes in the eastern U.S. (see reviews in Duflot et al. 2022, Akresh et al. 2023). It is impossible to talk about any stand type or harvest method as “good” or “bad” for birds unless viewed through the lens of a particular species (Crawford et al. 1981). The Lincoln’s Sparrow and the Blackburnian Warbler, both species of conservation concern, would disagree about what constitutes “good” forest practices.

However, studies of forestry effects on bird conservation have been mixed. For example, a recent study in Atlantic Canada suggested that large scale declines in many bird species were a result of forest degradation (Betts et al. 2022). These authors argued that it was not forest loss that was leading to regional bird declines, but rather the simplification of natural forest stands through conversion to plantations and to younger, even-aged forest.

Considering the renewed national concern for bird populations, in combination with the changes in Maine’s forest over the past 30 years described above, we set out to understand how Maine’s commercial forest is, or is not, contributing to bird

An increase in many bird species in the 2020s was the most surprising result of replicating the 1990s study.



Figure 4. Two-person bird survey team conducting a point count (Ben Shamgochian (left) and Sage Levy (right)). (photo by J. Hagan)

We used timber stand maps from both study periods to stratify survey points across the range of forest types and age classes in the landscape. Because there are over 100 different unique stand types in most forest classification systems, we had to create a simplified stand classification system to estimate species density in relation to bird habitat. We called these forest types “Superclasses” (Table 1). Results are reported according to Superclass. Our sampling across Superclasses was roughly balanced in both studies (Table 1).

We estimated the species abundance in the study landscape by multiplying a species’ density within a Superclass by the total acres of that Superclass in the entire 588,000-acre study area, as derived from Geographic Information System (GIS) stand maps from each study period. We consider our estimates of abundance an index because we are effectively sampling only singing males with the standard point count method. Regardless, the field and analytical methods were identical for the two study periods, making our metrics directly comparable.

We compared our estimated changes in abundance in our study area to Breeding Bird Survey (BBS) trends for Region 14 (Atlantic Northern Forest) and for North America. We used BBS population trends for the period 1993 to 2021, the same window of time represented by our two studies. We downloaded trend data from the BBS web site (Sauer et al. 2022). We also compared abundance changes within our study area to Partners In Flight (PIF) conservation scores (Will et al. 2020). PIF scores range from 5 to 25, with higher numbers indicating greater conservation concern. PIF scores integrate five different elements, including population size, range extent, and threats on the breeding and wintering grounds, into a single conservation number.

Table 1. Nine forest Superclasses used in this study to evaluate how birds were using the landscape, and number of points surveyed in the 1990s and 2020s studies in each Superclass.

Habitat Superclass	Description	Points Surveyed	
		1990s	2020s
Clearcut (CC)	Clearcuts in the last 5 years with dominant vegetation less than 2 m tall.	34	59
Regeneration (Regen)	Young sapling and pole timber 6-20 years after a clearcut.	53	55
Residual	Young scrubby regrowth 0-20 years following a partial cut, including shelterwoods.	32	48
Mid-age Hardwood	Mid-age stands with > 75% hardwood trees, generally 10-18 m tall.	34	39
Mid-age Mixedwood	Mid-age stands with 25-50% hardwood and 25-50% softwood trees, generally 10-18 m tall.	51	49
Mid-age Softwood	Mid-age stands with > 75% softwood trees, generally 10-18 m tall.	45	64
Mature Hardwood	Mature stands with > 75% hardwood trees, generally 18+ m tall.	49	42
Mature Mixedwood	Mature stands with 25-50% hardwood and 25-50% softwood trees, generally 18+ m tall.	42	35
Mature Softwood	Mature stands with > 75% softwood trees, generally 18+ m tall.	47	31
TOTALS		387	422

We also measured an array of tree and shrub layer vegetation characteristics in 10x50-m plots centered on the point count station to determine whether forest Superclasses were structurally and compositionally similar between the two study periods.

Finally, we explored the ability of LiDAR (light detection and ranging) data to generate species distribution models built on our point count data. Airborne LiDAR data from 2016-2019 are publicly available for our study area. LiDAR generates a three-dimensional “point cloud” representation of the forest. We derived a canopy height model (“digital surface model,” or DSM) from this point cloud using ARCGIS Pro for a 1.8M-acre (724,000-ha) area that included our study area. The canopy DSM likely captures a lot of the structure of what a bird sees when it settles in a forest stand. We derived eight LiDAR metrics to describe each of the 1.8M acres. We then used presence-only data for selected bird species and the species distribution model MaxEnt (Phillips et al. 2004, Hijmans et al. 2023) in the R programming language (R Core Team 2023) to evaluate the ability of LiDAR to produce habitat maps.

RESULTS

We recorded 3,196 birds within a 50-m radius at 387 point count stations in the 1990s study and 4,771 birds within a 50-m radius at 422 point count stations in the 2020s study. Adjusted for effort, that represented 8.3 birds detected per circle in the 1990s and 11.3 birds detected per circle in the 2020s, a 37% increase. This increase in bird density is the main story to emerge from replication of the 1990s study.

For the 1990s and 2020s studies combined, we detected 88 bird species within the 50-m radius point count circles—73 species in the 1990s study and 75 species in the 2020s study. We did not detect 13 species in the 2020s study that we detected in the 1990s study (see Appendix A). We detected 15 species in the 2020s study that we did not detect in the 1990s study. Most of these species occurred at very

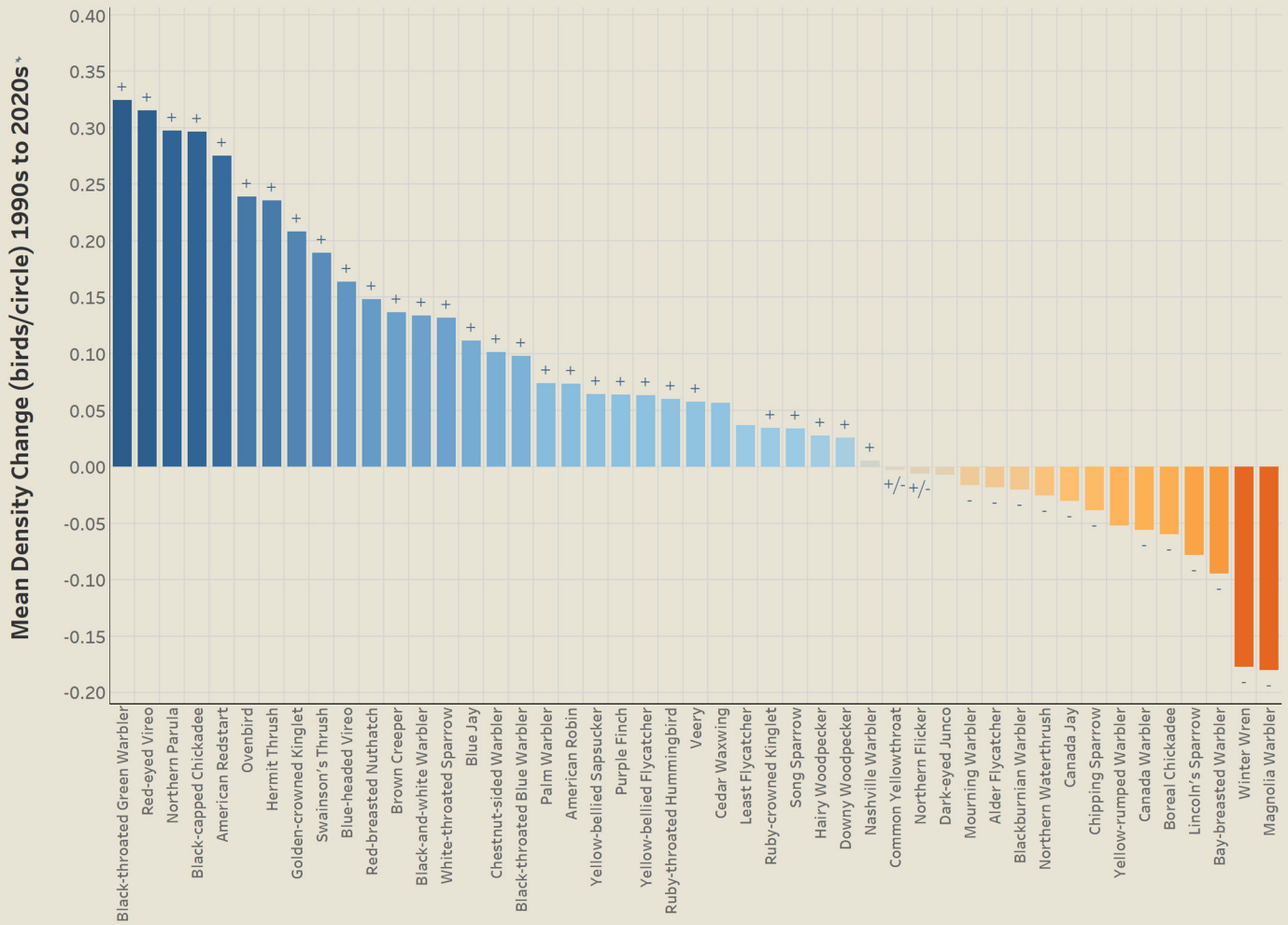


Figure 5. Change in average density (birds per circle) between the 1990 and 2020s studies. 70% of species increased (blue bars) and 30% of species decreased (orange bars). Species that significantly changed ($P < 0.05$) in one or more Superclasses are depicted with '+' (increased), '-' (decreased), or '+/-' for both increased and decreased, depending on the Superclass.

low densities, so meaningful interpretation is limited. However, we expected some species' ranges to have shifted in relation to climate change over the past 30 years—some shifting into our study region (e.g., Eastern Bluebird) and others shifting out (e.g., Tennessee Warbler).

Bird Species Density Changes

We restricted our analyses of density change to 47 species that occurred at 3% or more of the point count stations in *either* study period. Statistical analyses of species that occur at low densities, such as birds of prey, or that are not detected well with the point count method (e.g., owls), are not possible.

Of these 47 species analyzed, 33 species (70.2%) increased in density (birds per circle) and 14 species (29.8%) decreased in density since the 1990s study (Fig. 5). Based on the “three billion birds lost” paper in *Science* in 2018 (Rosenberg et al. 2019), we expected to find mostly declines in density, not increases. For whatever reasons (see Discussion), there were more singing individuals per unit area of many species in the 2020s study relative to the original 1990s study.

Figure 6. Examples of two species that increased in density (birds per circle) between the 1990s and 2020s studies across the 9 Superclass forest types (see Table 1). (a) American Redstart, and (b) Black-and-White Warbler

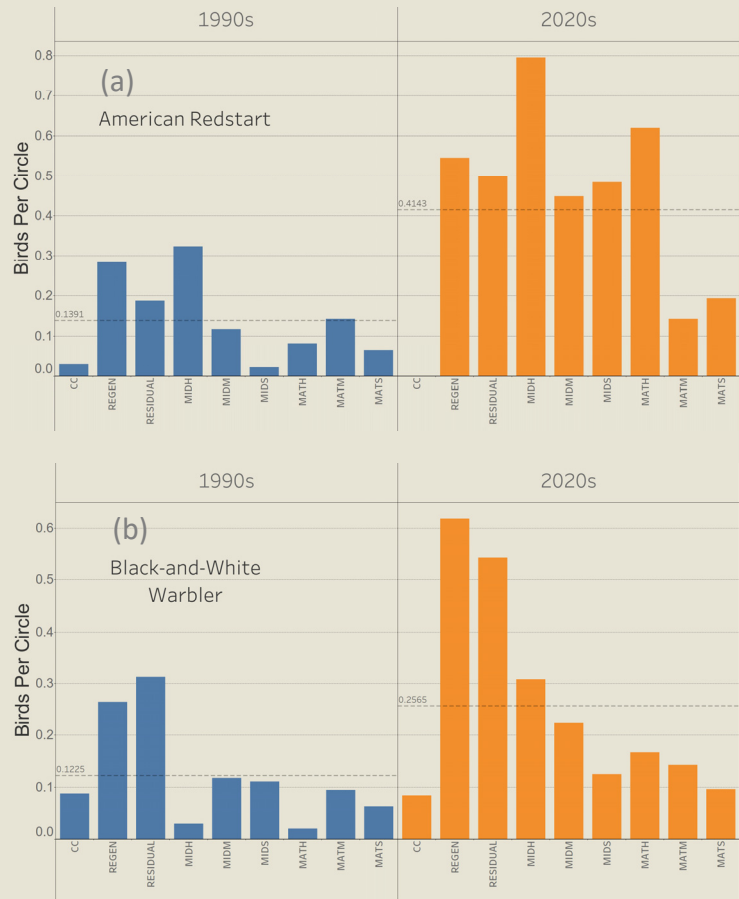
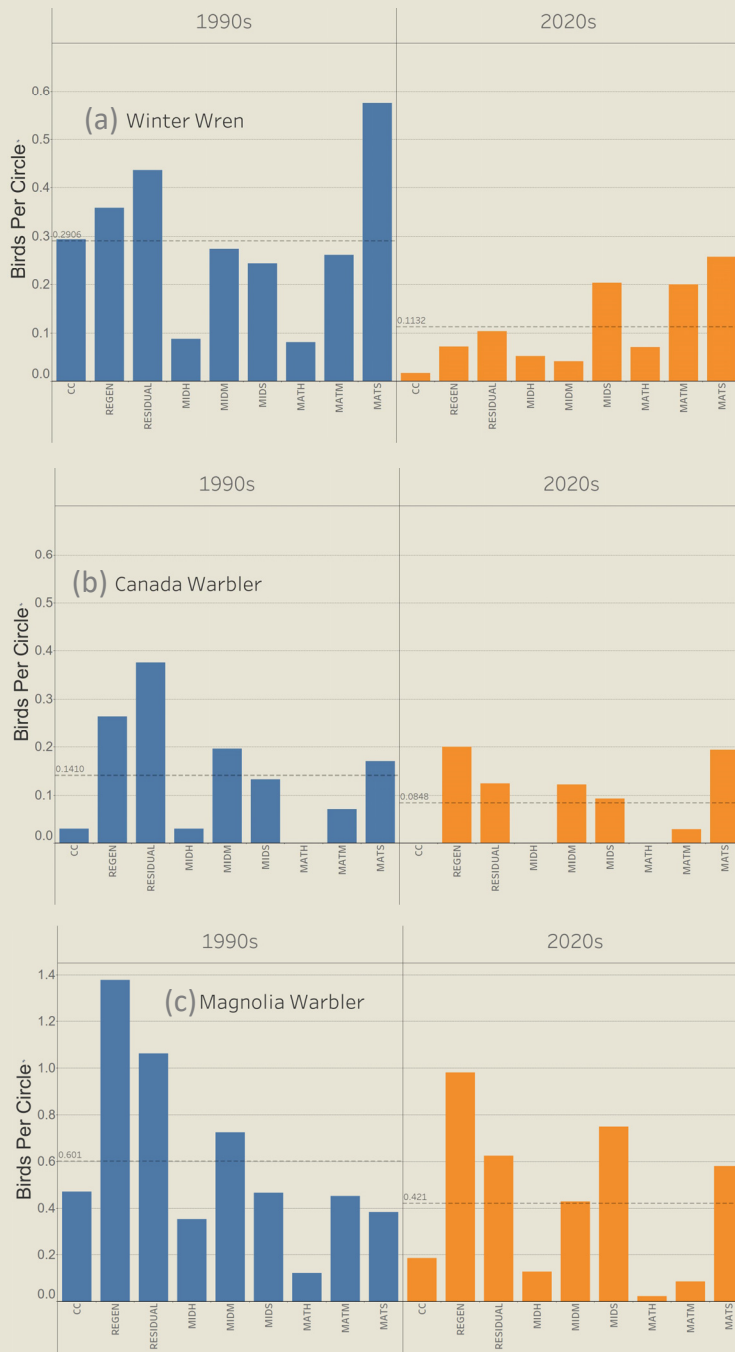


Figure 6 shows two examples of species that increased in density between the two study periods. The American Redstart (Fig. 6a) tends to be found in regenerating and early mid-age forest (saplings and young pole timber) but can be found in all Superclasses. Redstart density increased across all Superclasses by an average of more than *two-fold* (Fig. 6a). That is, we detected more than twice as many Redstarts per point count circle in the 2020s study relative to the 1990s study. This indicates that (1) the array of forest types was still serving as quality habitat, or even higher quality habitat, for this species, and/or (2) whatever has been driving increases in this species was broadly at play across the landscape, or even across the entire species' range. The American Redstart winters mostly in the Caribbean.

We saw another large increase in density in Black-and-White Warblers (Fig. 6b). Again, more than twice as many Black-and-White Warblers were detected per circle than in the 2020s study. Note that their use of the nine Superclasses stayed much the same; they increased across the board, like the American Redstart. The Black-and-White Warbler winters in Florida, Central America, and northern South America. What is causing these large increases in density, across all Superclasses?

While most species showed some increase in density relative to the 1990s, about one-third decreased in density (see Fig. 5). Three representative examples are the Magnolia Warbler, Winter Wren, and Canada Warbler (Fig. 7). On average, Winter Wren density decreased by 61% across all Superclasses (Fig. 7a). Canada Warblers decreased in density by an average of 40% across all Superclasses (Fig. 7b). Magnolia Warbler decreased in average density by 30% (Fig. 7c) and showed the

Figure 7. Examples of three species that declined in density (birds per circle) between the 1990s study and 2020s study across the 9 Superclass forest types (see Table 1). (a) Winter Wren, (b) Canada Warbler, and (c) Magnolia Warbler.



largest absolute decline in abundance of all species. The Magnolia Warbler merits mentioning because it prefers Regeneration, like the American Redstart, which, by contrast, showed dramatic increases in the landscape. The contrast with the Redstart suggests that the Magnolia Warbler may be experiencing some stressor elsewhere during its annual life cycle that manifested as lower densities in our study area. We should have seen an increase, based on the Redstart results. These species are found in most of the Superclasses (Fig. 7a-c). Do these large declines in density translate into declines in abundance in the study landscape? We take a closer look at declining species later in this report.

Habitat Change, 1990s vs. 2020s

The important conservation question of this study was ‘how is the commercial forest landscape today supporting birds relative to 30 years ago?’ To estimate the number of birds of each species in the entire study landscape, we need two pieces of information: (1) a species’ average density in each of the nine forest Superclasses for the 1990s and 2020s, and (2) the amount of each Superclass in the landscape in each time period. We addressed the density question in the previous section.

We used GIS stand maps from the 1990s and current-day stand maps from the 2020s to calculate the amount of each Superclass in the study landscape (~588,000 acres, 234,000 ha) for each study period.

As anticipated, the area in Clearcut declined between the study periods (-47%) (see Fig. 8). This resulted from a shift away from clearcutting in the 1990s, partly because of public opposition to clearcutting and partly because of the end of the spruce budworm salvage harvests of the 1980s. As a result, species that strongly prefer clearcut (e.g., Lincoln’s Sparrow, Mourning Warbler) would be expected to decline in the study landscape, assuming their densities (birds/circle) stayed the same.

By contrast, the amount of Regen in the landscape more than doubled (a 129% increase). Unless bird densities declined dramatically (e.g., Magnolia Warbler, see Fig. 7c), we would expect the abundance of a species that prefers Regen to greatly increase in the study landscape since the 1990s.

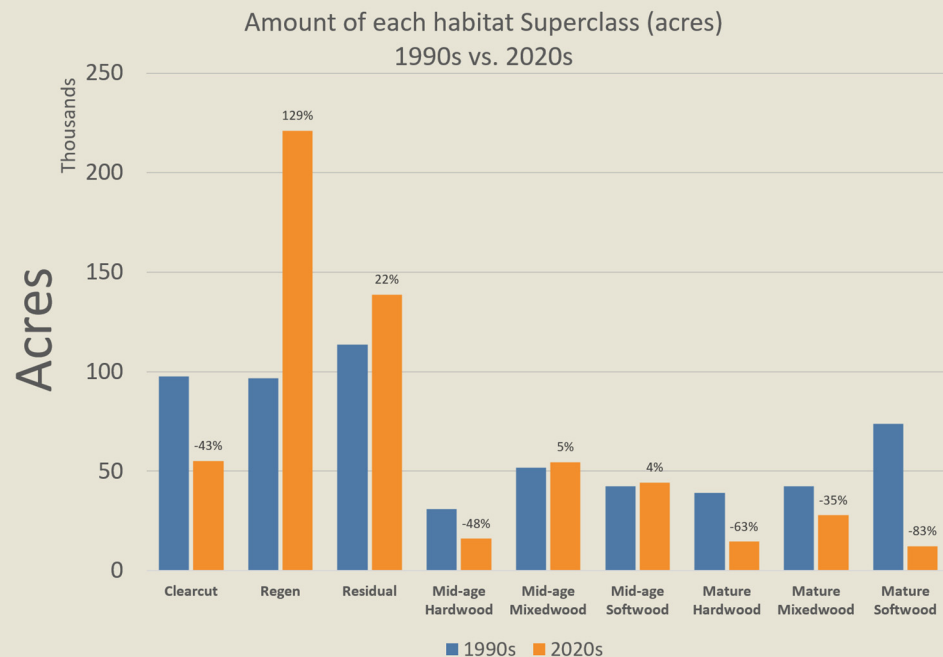


Figure 8. Amount of each habitat Superclass in the study area for each study period. Percents over the orange (2020s) bars indicate the percent change in the Superclass in the 2020s relative to the amount in the 1990s.

Residual, a forest type characterized by post-harvest retention of overstory trees, increased by 27% since the early 1990s. We expected a larger increase in Residual because of the shift to partial harvesting since the early 1990s. It may be that many of the initial shelterwood harvests of the 1990s have now received the final overstory removal harvest, moving them into our Regen Superclass (which lacks a dominant overstory). This may explain the large increase in Regen in the study area.

Mid-age Hardwood declined by 48%, but Mid-age Mixedwood and Mid-age Softwood remained about the same. The decline in Mid-age Hardwood may be a result of the conversion from hardwood to softwood plantations that occurred during the Scott Paper Co. ownership of the early 1990s.

Finally, as suspected, the study area lost significant amounts of forest in all three mature age classes (Fig. 8), but especially Mature Softwood. Dominant trees in these mature stands were generally at least 80 years old, and over 100 years old in many stands. While these older stands are ecologically valuable, they generally represent a financial opportunity cost for commercial landowners. Such mature stands are often harvested to put the stand on a more optimal financial rotation. These older stands remain in the modern-day landscape because of inaccessibility, or for a non-timber value, such as a deer wintering habitat (for the softwood and mixed wood stands). Or they may be designated as high-conservation-value stands to meet sustainable forestry certification guidelines. Nevertheless, we saw large declines in these age classes in our study area over the last 30 years.

Overall, the picture is one of a younger forest in the 2020s relative to the 1990s, despite the decline in clearcutting over the years. We discuss the implications for bird abundance change in the next section.

Species Abundance Changes

With the densities of each species in each Superclass in each study period, and the amount of each Superclass in each study period, we estimated the number of birds of each species in the landscape. Remember that we were mostly detecting singing territorial individuals, so our numerical estimates of abundance essentially estimate the number of singing individuals. If all singers had a mate, we could multiply by 2. But since this multiplication wouldn't change the relative number of each species, we use the estimated abundance of singing territorial individuals as an index of abundance.

We estimated abundance in each time period with the following equation.

$$\text{Species Abundance} = \sum_{i=1}^9 \text{Species density } (d_i) \times \text{forest Superclass area } (a_i)$$

Appendix A shows the estimated change in abundance of each of the 47 species analyzed. The Red-eyed Vireo, a common species in the 1990s and the 2020s studies, increased the most—by over 100,000 individuals. The Red-eyed Vireo is a forest species but not of conservation concern either regionally or continentally. The American Redstart increased by over 93,000 individuals, partly a result of the large

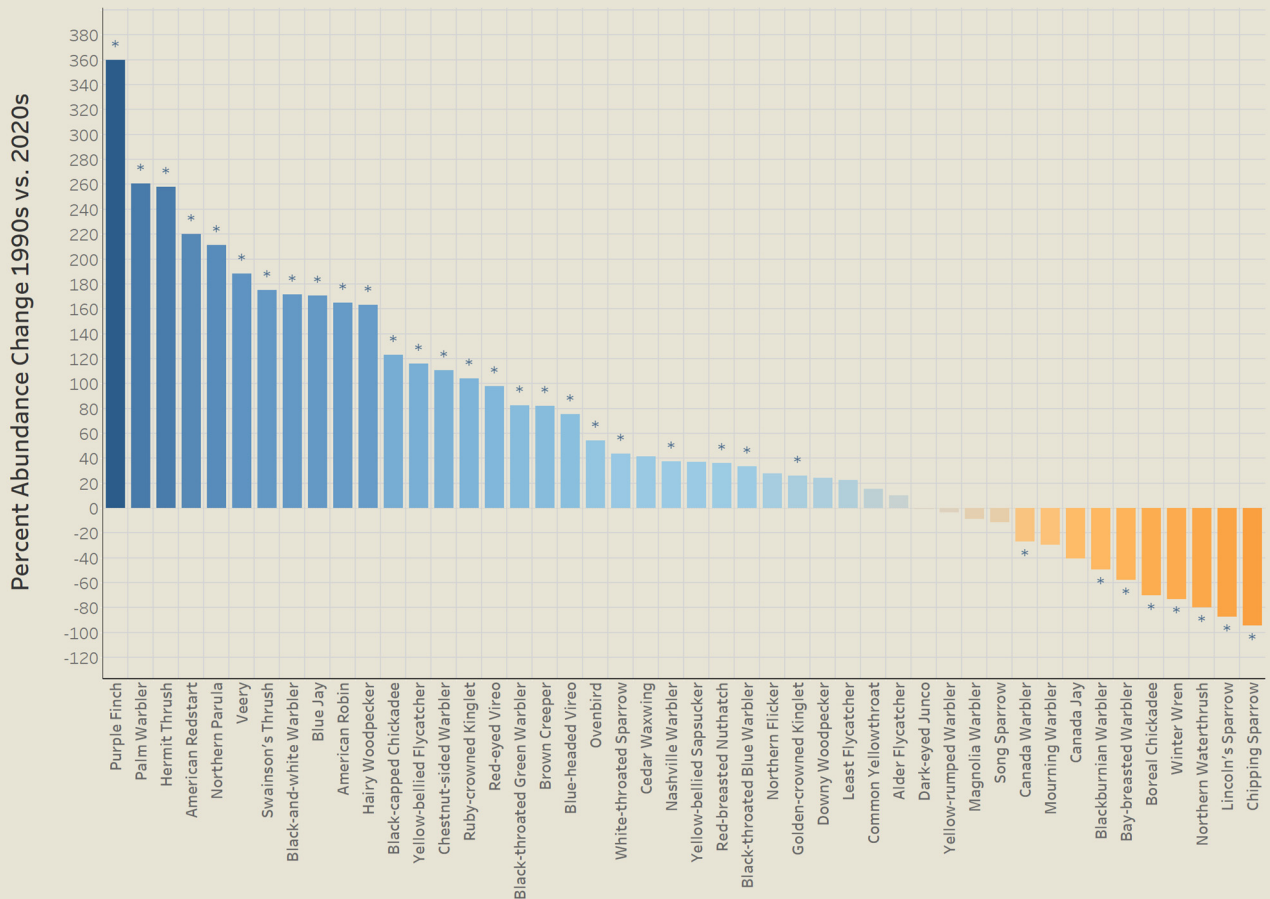


Figure 9. Change in absolute abundance of 47 species in the study area between the 1990s and the 2020s. Abundance is the product of density times area of forest Superclasses. Compare to density changes in Fig. 5. Species that significantly changed in abundance ($P < 0.05$) are indicated by '*'. (Ruby-throated hummingbird is not shown because it increased by 1,143%).

increase in density since the 1990s, but also because of the large increase in its preferred habitat, Regen. Abundance changes are correlated with density changes because abundance is generated from density estimates.

Driven largely by density declines, a minority of species also decreased in abundance in the landscape. While we can celebrate the increases in abundance from a regional and continental bird conservation perspective, the declines merit careful scrutiny. We do not want species of conservation concern to decrease significantly in commercial forests if we can help it. Because so many of these species migrate out of our region in the winter, we know factors beyond the control of forest landowners can affect populations. Still, we need to pay attention to these species and understand their habitat requirements and ecology as best we can.

Two species that declined the most in the study landscape were the Winter Wren and the Blackburnian Warbler. We discuss declining species in more detail in the Discussion. The Blackburnian Warbler prefers older forest but will use mid-age forest to a lesser degree. The Winter Wren uses all forest Superclasses but specializes on dead wood.

What drove changes in abundance—density or habitat availability?

Although we cannot know for certain the ecological causes of changes in abundance, we can at least parse out the relative roles of changes in density (birds per unit area) vs. change in habitat availability in the study area. We assessed the relative roles of these two parameters by calculating 2020s abundances as if density had not changed for any species (i.e., we used 1990s densities and 2020s habitat availability to calculate hypothetical 2020s abundances). Then, we compared the true 2020s abundances to these numbers. The difference in abundance in these two calculations tells us how much abundance change was driven by density change vs. change in amount of habitat.

The percent of abundance change due to density change alone is shown in Appendix A. For 18 species (of 47 analyzed), their abundance change due to density change was 100%. That is, though habitat amounts changed as shown in Figure 8, density changes fully explained the change in abundance in the landscape. For only six species did density change explain less than 50% of the change in abundance (Appendix A). This means that, for most species, it was their change in density, not changes in forest types and age classes, that drove abundance changes. This begs the question of what was driving density change in so many species, both increases and decreases in density? We revisit this question in the Discussion.

Changes in Superclass did not affect most species' abundances because most species use multiple Superclasses, and thus are relatively insensitive to changes in the amount of any particular Superclass (see Figs. 6 and 7 for examples). The exceptions are species that used only one or two Superclasses, such as the Lincoln's Sparrow (it only used Clearcut and Regen). This species declined both because of a loss of Clearcut area *and* a simultaneous decline in density (even within Clearcut). An analog for an older forest species is the Blackburnian Warbler, which prefers older forest age classes, declined in the study area, and also showed a decline in density. These two species, which prefer different ends of the forest age-class distribution, exemplify how two very different species can both decline in the landscape at the same time.

Species changes in relation to regional and continental trends

A central question of this study was to understand how the large commercial forest in Maine may be contributing to regional and national bird declines, or, as we discovered, countering many declines. To answer this question, we plotted the proportional change in abundance of each species in our landscape between the 1990s study and 2020s study against national and regional population trends of each species between 1992 and 2021, as determined by the Breeding Bird Survey.

There was a poor relationship between population abundance changes in our study area in the last 30 years and Breeding Bird Survey (BBS) trends at a continental scale (see Appendix A for numbers). Figure 10 shows which species decreased or increased in our study area in relation to their continental (Fig. 10a) and regional (Fig. 10b) BBS trends.

In fact, the inconsistency in trends between our study area and both continental and regional BBS trends was striking (Table 2). For example, 74.5% of 47 species we analyzed were decreasing at a continental scale using BBS data, but only 30% were decreasing in our study area using our survey data. Conversely, in the BBS dataset

Changes in density (birds per unit area) drove most changes in abundance, rather than changes in the amount of habitat.

Table 2. Relationship between the number of species declining or increasing between 1993 and 2021 in our study area vs. continental and Region 14 Breeding Bird Survey trends.

		Continental		
		# Decreasing	# Increasing	TOTALS
Our Study Area	# Decreasing	13	1	14 (29.8%)
	# Increasing	22	11	33 (70.2%)
	TOTALS	35 (74.5%)	12 (25.5%)	47

		Region 14		
		# Decreasing	# Increasing	TOTALS
Our Study Area	# Decreasing	14	0	14 (29.8%)
	# Increasing	21	12	33 (70.2%)
	TOTALS	35 (74.5%)	12 (25.5%)	47

for the same time period, only 25.5% of species were increasing continentally but 70% were increasing in our study area with our own survey data.

The same pattern was true at the regional scale (Table 2). In the BBS dataset for 1993 to 2021, 74.5% of the species were declining at the regional scale (albeit a slightly different mix of species from the continental trends).

This paradoxical *inverse* relationship between BBS trends and our data suggests different forces are at play in our study area relative to the region and the continent. Or, whatever is going on regionally and nationally is mostly not mirrored in our study area. Our study area seemed to be functioning as a geographic unit with different population patterns. Keep in mind that while our study area was quite large for a field-based project (588,000 acres, 234,000 ha), it is still a very small part of the region, and certainly of the continent.

There were a handful of species that were declining both nationally and in our study area: Canada Warbler, Mourning Warbler, Song Sparrow, Canada Jay, Bay-breasted Warbler, Blackburnian Warbler, Lincoln’s Sparrow, Boreal Chickadee, Chipping Sparrow, and Yellow-rumped Warbler (see lower left quadrant in Fig. 10a). Many of these same species were also declining in Region 14 (see lower left quadrant in Fig. 10b). The Canada Warbler stands out in both the continental and regional graphs as a species declining the fastest, at both scales. We discuss some of the species of concern in our study area in the Discussion.

One species decreasing in our study area but increasing nationally and regionally may merit further examination—the Winter Wren. We need to understand ‘why,’ and if there is anything we can do together as conservation biologists and forest managers to reverse the trends in the commercial forest. If the factors driving these changes are outside of our region (and control), there may be nothing we can do but continue to provide diverse forest types and age classes for habitat.

Another lens through which we can examine conservation significance is to compare changes in abundance in our study area with Partners in Flight species conservation scores. Relying on a team of experts, in combination with myriad

The paradoxical difference between our results and Breeding Bird Survey trends suggests that different forces are at play in Maine’s commercial forest.

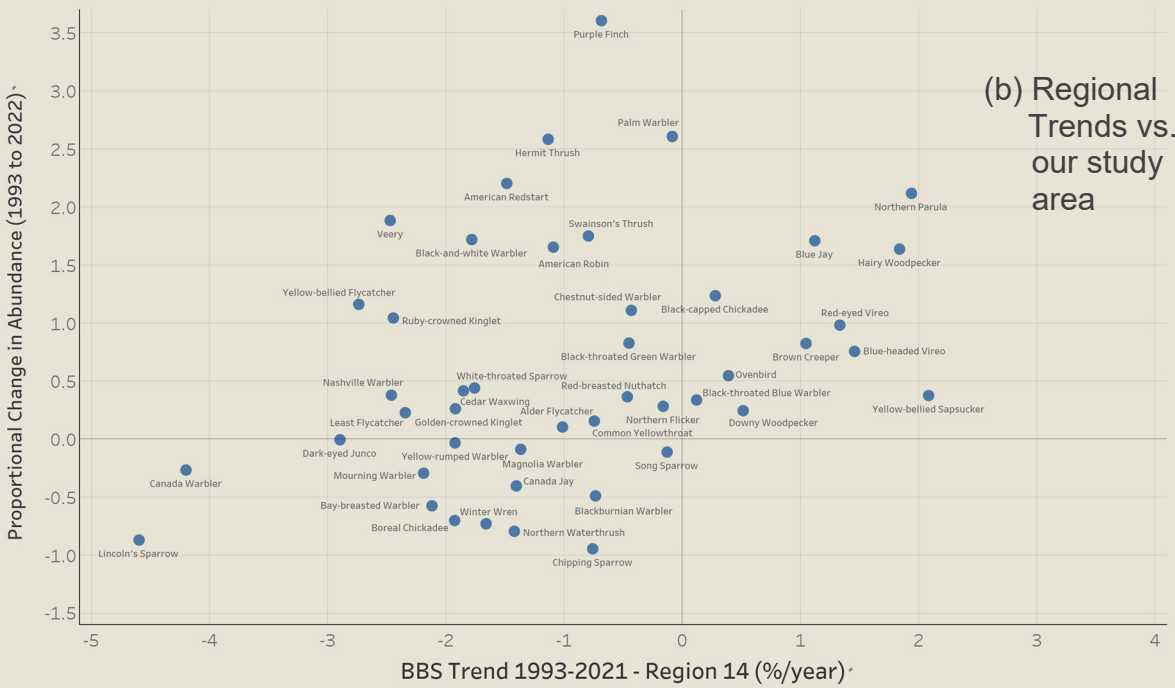
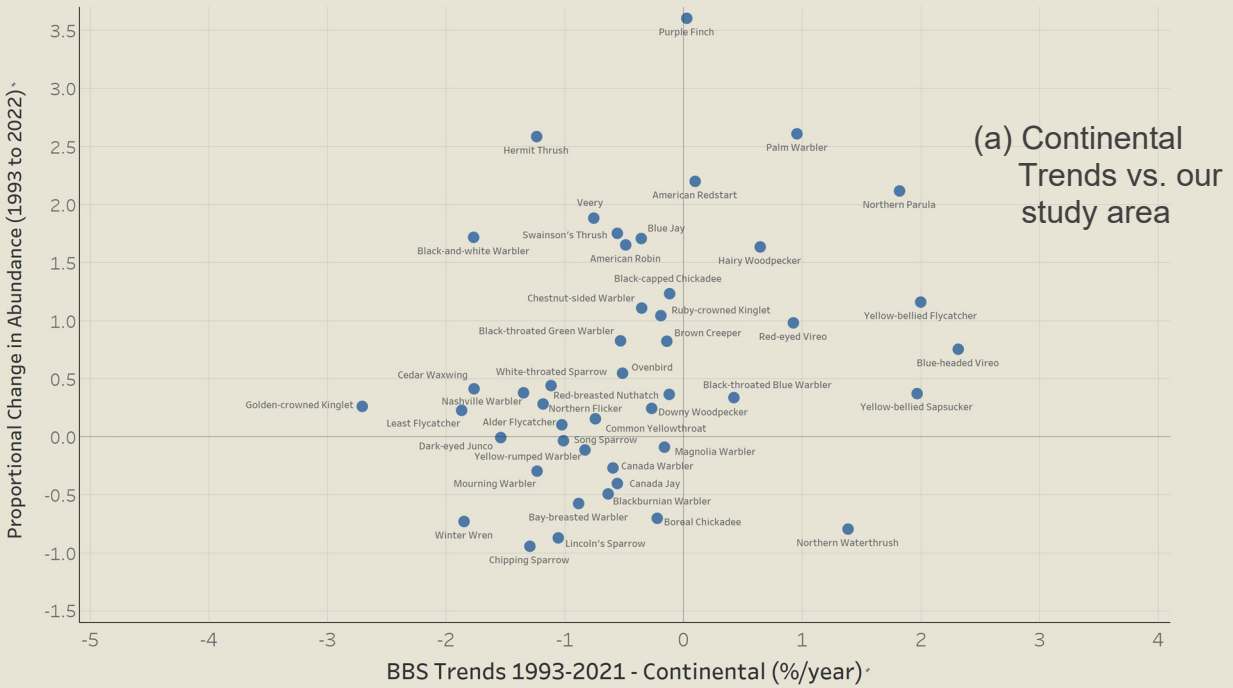


Figure 10. Annual population trends of 47 species based on Breeding Bird Survey (a) **continental** trends and (b) **regional** trends, in relation to abundance changes between the 1990s and 2020s studies. The species in the lower left quadrant of each graph show those declining in our study and continentally and/or regionally. These species merit careful scrutiny for possible management action.

varied sources of data about population change and threats on the breeding and wintering grounds, PIF scores are a composite conservation score for each species ranging from 5 to 25 (a '5' represents low conservation concern and '25' represents high concern). PIF scores are generated for each species at both a continental scale and a regional scale. The scores can differ depending on breeding or wintering range threats.

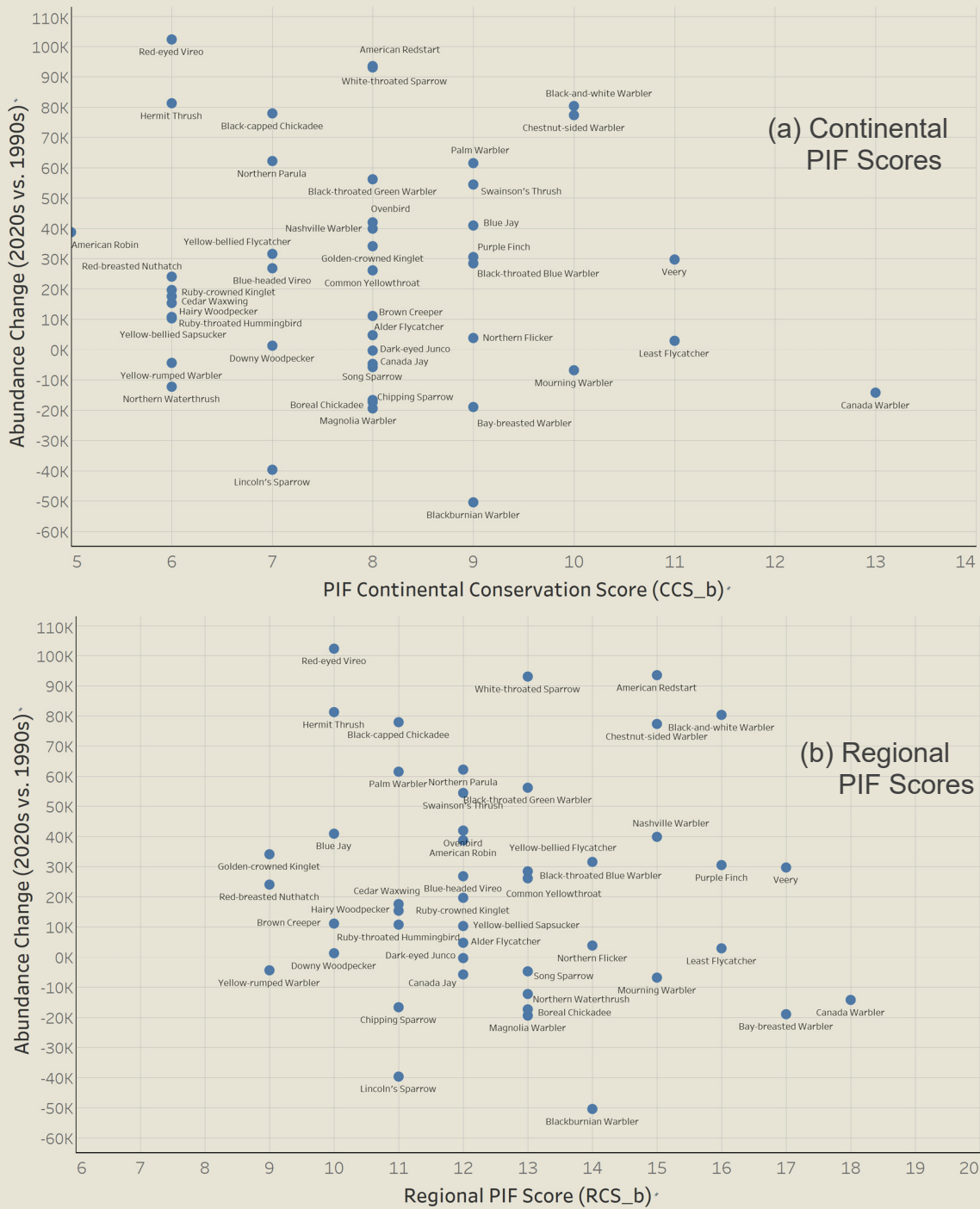


Figure 11. (a) **Continental** Partners in Flight species conservation scores (CCS_b) and (b) **Regional** Partners in Flight conservation scores (RCS_b) in relation to changes in abundance between our 1990s and 2020s studies. Higher PIF scores indicate greater concern (range 5 to 25). As with annual population trends in Fig. 10, there is no relationship between PIF scores and species changes in our study area.

As with the Breeding Bird Survey data, there was no relationship between abundance change in our study landscape and continental PIF scores or regional PIF scores (Fig. 11 a and b). That is, species of greater conservation concern both regionally and nationally showed no relationship to increases or decreases in our study area. One might hypothesize that species with higher conservation scores

would be more likely to be declining in our study area, but that was not the case. Still, one species that ranked high in conservation concern (score = 18), the Canada Warbler, also declined in our study area. Again, this is a species we need to understand better in relation to forest practices (see Discussion below).

Did forest types and age classes change since the 1990s study?

One of the motivations for replicating this study was because forest practices had changed in the study area (and Maine's commercial forest at large) since the 1990s study—more shelterwood harvests and less clearcutting today. Could these changes at the stand level affect bird populations, positively or negatively?

Although we used the same forest Superclass system for both the 1990s and 2020s studies, it was sometimes difficult to categorize stands using this system in the 2020s because of the more common shelterwood practices of today; these practices did not fit as neatly into our Superclass system developed for the 1990s study. Therefore, we used our ground vegetation surveys from each point count station in each study to understand if, and how, stand level composition and structure might have changed within Superclasses.

The most common forest metric used to describe a stand is live tree basal area (Fig. 12a). Live tree basal area increased significantly in Regen, partly because of extensive shelterwood harvesting. The increase in basal area in Regen could have made this Superclass more suitable for some bird species in the 2020s study. By contrast, live tree basal area declined in all three mid-age forest types. This probably reflected a younger forest, on average, in the 2020s study. Basal area decreased in Mature Hardwood but increased in Mature Softwood. Our ground vegetation data captured changes in forest practices since the original study.

Another forest metric especially interesting for wildlife, and birds in particular, is dead tree basal area. Dead trees are important to many primary and secondary cavity nesting birds. Dead tree basal area was either the same, or declined, since the 1990s, depending on the Superclass (see Fig. 12b).

A good metric of habitat diversity is coefficient of variation (CV) of tree diameters. In general, the greater the variety of tree sizes in a stand, the greater the vertical structural diversity within the stand. The CV of tree dbh's declined in the young and mid-age forest types but tended to increase in the mature forest types (Fig. 12c).

We also detected some compositional shifts in the forest between the study periods that could affect bird species. There was a large increase in basal area of balsam fir in the Mid-age Mixedwood and Mid-age Softwood stands, but a noticeable decrease in balsam fir in Mature Softwood (Fig. 13a). By contrast, spruce (spp.) decreased in Mid-age Mixedwood, and especially Mid-age Softwood (Fig. 13b). This reflected a shift to balsam fir following the extensive clearcutting during the spruce budworm outbreak of the 1970s and 1980s.

Among hardwoods, we did not see the increase in American beech that we expected (Fig.13c). This is good for forest products because of the beech bark disease and the poor-quality wood that results, but some bird species prefer beech for a foraging substrate (McKinley 2004). One of us (KA) is conducting a more thorough comparison of forest structure and composition between the two studies.

Overall, the study landscape of the 2020s was somewhat younger and smaller (in dbh) than the landscape of the 1990s study.

Figure 12. Selected structural changes in Superclasses (forest types) between the 1990s and 2020s studies.

- (a) live tree basal area
- (b) dead tree basal area
- (c) dbh coefficient of variation.

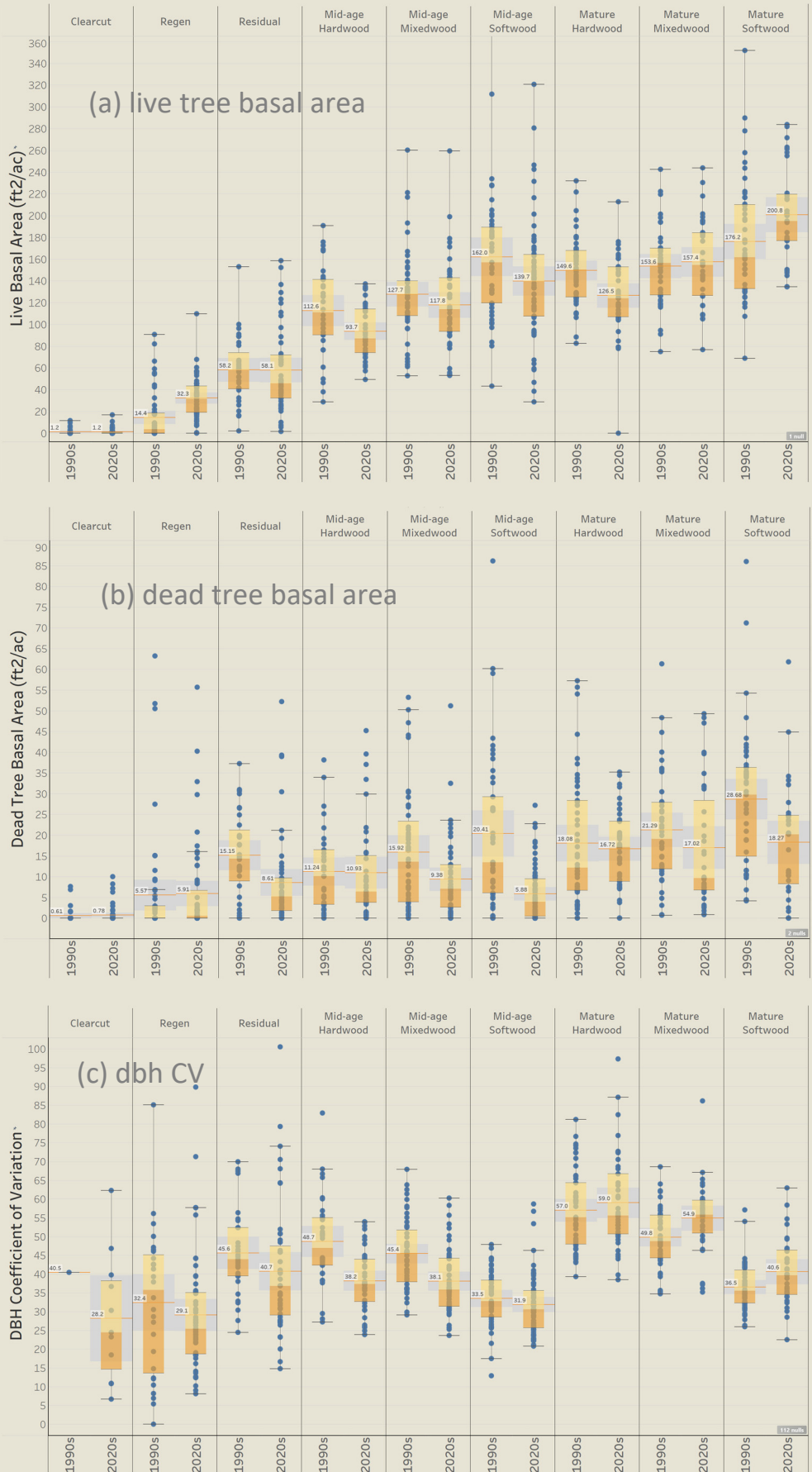


Figure 13. Selected tree species basal areas in Superclasses (forest types) between the 1990s and 2020s studies.

- (a) Balsam fir
- (b) Spruce (spp.)
- (c) American beech



Modeling species habitat availability with LiDAR

We also explored the potential of LiDAR to predict habitat availability for selected species. LiDAR can generate a relatively precise three-dimensional “picture” of the canopy surface (Fig.14). Canopy structure is important because we know many bird species cue on structure—some prefer mature closed canopy forest; others prefer openings in a tall canopy forest, and still others prefer a shorter regenerating forest. Publicly available LiDAR data contain all this structural information at a fine-scale resolution that traditional forest stand maps cannot reveal. While LiDAR is excellent at describing forest height and structure, it is not as effective at determining hardwood from softwood forest, which we know is important for many forest bird species. Still, hardwood and softwood forest have a different *physical* structure, and LiDAR can “see” some of that difference.

Figures 15 and 16 show estimates of the degree of habitat quality for two species, the Blackburnian Warbler and White-throated Sparrow, respectively, using the MaxEnt model and eight LiDAR metrics, for a 1.78-million-acre section of northcentral Maine centered on our study area. We chose these two species to demonstrate how a late-successional (Blackburnian Warbler) and early-successional species (White-throated Sparrow) “see” a different landscape. These two species demonstrate how it is impossible to produce habitat preferred by *all* species at the hectare scale, or even at the stand scale, simultaneously. Blackburnian Warblers and White-throated Sparrows will rarely be found in the same stand. It takes a landscape to provide habitat for the full array of bird species that naturally occur in northern Maine.

The MaxEnt model looks for hectares in the landscape that meet the same structural characteristics of the hectares in which we detected the species during our point count surveys. Because we tended to detect Blackburnian Warblers in late-successional forest, the MaxEnt model identified hectares with similar late-successional structure throughout the larger landscape as better quality (Fig. 15). Just because the forest composition and structure is suitable for a species does not guarantee the species will be found there. Rather, it means that, based on what we know, the forest type and structure is representative of what is suitable for the species.

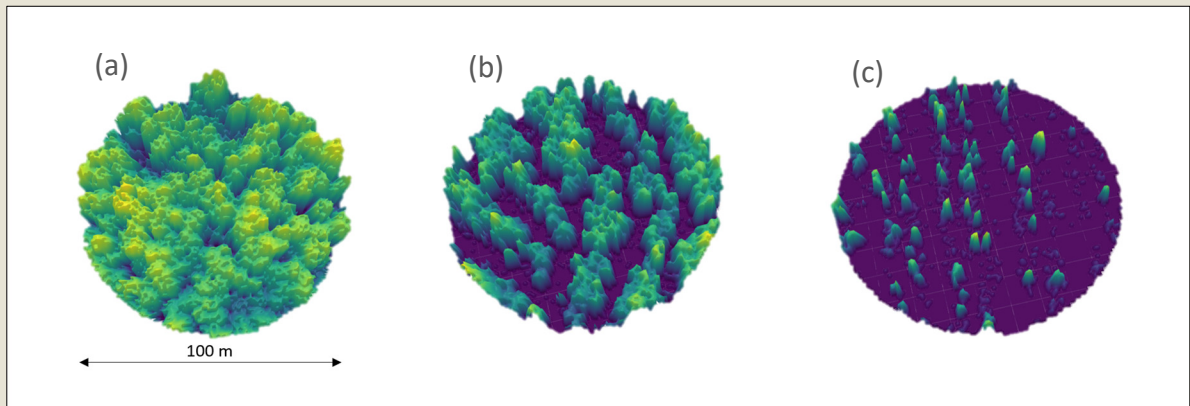


Figure 14. Examples of LiDAR canopy height models for three 50-m radius point count circles: (a) late-successional mixedwood, (b) strip-cut mid-age softwood, and (c) clearcut with remnant overstory. LiDAR metrics describe the structure of the stand in a way that cannot be captured by traditional ground vegetation plots.

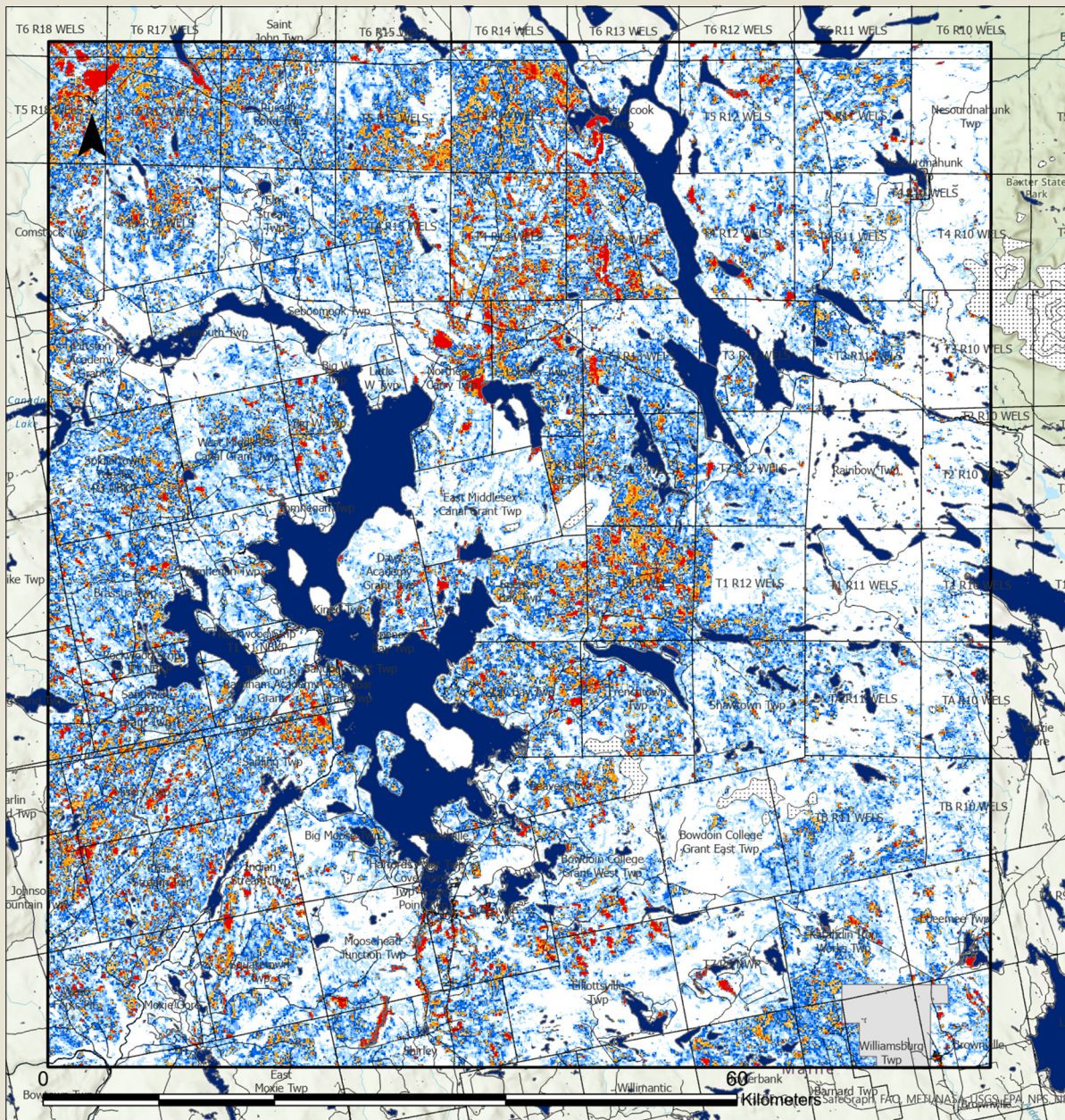


Figure 15. Habitat suitability map for the Blackburnian Warbler, as generated from LiDAR data and MaxEnt species modeling software. Warmer colors (reds and oranges) depict more suitable habitat based on where we detected Blackburnian Warblers on our point count surveys. Cooler colors (blues to pure white) show where this species is less likely to be found.

For the Blackburnian Warbler habitat map, the warmer colors (reds and oranges), which indicate more suitable forest structure and composition, tend to occur on public lands that have a mandate for protection of multiple values, from wood production to species conservation. Note the red colors around Big Spencer Mountain, an ecological reserve, near the center of Fig. 15, and the reds and oranges (higher suitability) concentrated in the center right, on The Nature Conservancy and Bureau of Parks and Lands forests. It may be that a mix of private conservation

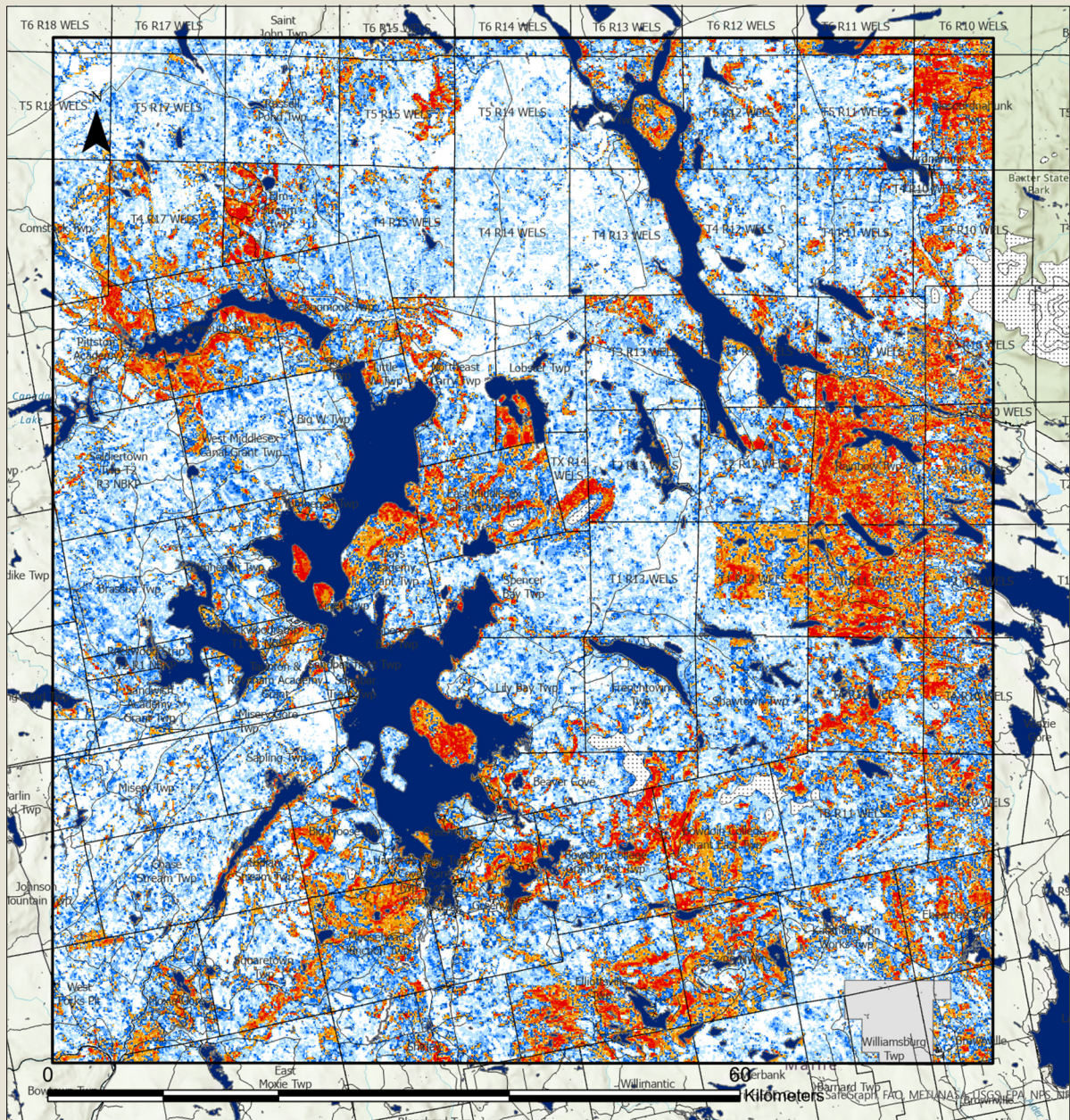


Figure 16. Habitat suitability map for the White-throated Sparrow, as generated from LiDAR data and MaxEnt species modeling software. Warmer colors (reds and oranges) depict more suitable habitat based on where we detected White-throated Sparrows on our point count surveys. Cooler colors (blues to pure white) show where this species is less likely to be found. Compare this map to the Blackburnian Warbler map in Fig. 15. These two species prefer quite different habitats.

forest and public forest will be needed to provide Blackburnian Warbler habitat over the long term.

By contrast, the White-throated Sparrow prefers early-successional forest. The LiDAR-derived habitat map for the White-throated Sparrow (Fig. 16) is almost the inverse image of the habitat map for the Blackburnian Warbler (Fig. 15). For the White-throated Sparrow, the early-successional forest age-classes are critical. These young forest conditions tend to occur on private commercial forestland.

DISCUSSION

Given the reported widespread continental (Rosenberg et al. 2019) and regional (Betts et al. 2022) declines in many forest bird species, we were surprised to see so many apparent *increases* in abundance in the commercial forest of Maine since the original 1990s study. Although a few species showed declines and warrant more careful examination (see below), most species showed increases in our study area, irrespective of larger-scale declines. Our results suggest that Maine's commercial forest may be helping counter population declines at these larger scales. This is a small but good-news story for bird conservation.

One reason many species have seemed to do well in our study area in the past 30 years may be because of their plasticity in forest type use. Some species were found using all nine Superclass types, from Clearcuts to the mature forest types. Even species that had their highest densities in mature forest still used mid-age forest, and Regen and Residual, of which there was an abundance in the study landscape. Most species, therefore, were not very sensitive to changes in the amounts of the Superclasses in the landscape.

Our results stand in contrast with a recent, analogous study of forest bird trends across the border in the Maritimes of Canada (Betts et al. 2022). In that study, which spanned approximately the same timeframe (1985-2020) as our study, the authors described widespread declines in forest birds. The authors attributed declines to forest degradation resulting from the conversion of natural forest to plantations for forest products.

One striking example of a difference between the two studies is population changes in the Golden-crowned Kinglet, a mid-age to mature softwood species. In the Betts et al. study, Golden-crowned Kinglets were projected to have decreased by 38% between 1985 and 2020. By contrast, we estimated Golden-crowned Kinglets *increased* by 26% in our study area. In fact, Golden-crowned Kinglets had high densities in the current-day, overstocked, 40-year-old softwood stands that resulted from the massive spruce budworm clearcutting of the 1970s and 1980s.

On the other hand, both studies reported declines in the Blackburnian Warbler, a species that prefers more mature forest. The Blackburnian Warbler decreased by 33% in the Betts et al. study and by 49% within our study area. The decline in our study area was caused by the loss of mature forest stands and a shift in bird density among Superclasses. Interestingly, the average density (birds per circle) remained about the same as in the 1990s study. There was simply less of its preferred habitat in the 2020s landscape.

The contrast with the study by Betts et al. (2022) is curious. Several factors could be at play. The methods of the two studies were quite different. For example, Betts et al. relied on point counts at a single point in time and then back-calculated and forward-calculated abundances based on habitat availability as derived from Landsat data from 1985 and 2020. By contrast, we conducted point counts in the early 1990s and then again in the 2020s, using actual bird densities from the respective time periods to estimate abundance change. We also used forest stand maps from each time period to estimate habitat availability. Stand maps, which are generated from stand classifications of high-resolution aerial photography, provide finer detail on forest types and age classes than the Landsat imagery (30-m pixel

Our results suggest that Maine's commercial forest may be helping counter population declines at these larger scales.

resolution) used by Betts et al. Also, Betts et al. point counts were mostly roadside, whereas all our counts were inside the forest type of interest and away from road edges that might affect the bird species detected.

We cannot know if these differences in methods explain the different results of the two studies. It is also possible bird trends in Maritime Canada really were different from Maine. Maine has experienced very different forest practices than the Canadian Maritimes. Maine has relatively little plantation forestry compared to the Maritimes, at least partly because of public resistance to intensive plantation forestry in Maine. Some of the timberland investment management organizations (TIMOs) that bought Maine's commercial forest in the 1990s and early 2000s had less interest in investing in plantation forestry or silviculture than previous landowners because they did not plan to own the forest for the long term when such investments would pay off. While long-term forest productivity might have suffered as a result, bird populations mostly did not. In fact, it appears most species have done well in the commercial forests of Maine over the past 30 years.

Another recent study of birds and silviculture in the Penobscot Experimental Forest found little effect of two expanding-gap silvicultural treatments on bird assemblages over the last 25 years but did note declines in abundance across all treatments (Pohlman et al. 2023). The authors speculated that bird declines in their 1,681-ha study area were driven by widespread regional population declines rather than by harvest effects. The Pohlman et al. study used territory spot-mapping to evaluate bird communities, an appropriate method for a more localized and intensive study. By contrast, using the point count method, we covered a much larger landscape (238,000 ha, 588,000 ac). Our much larger sampling of a much greater diversity of forest types and age classes may have contributed to the differences in trends detected between the two studies.

Rolek et al. (2018) studied bird species associated with spruce-fir forest across Northern New England, including Maine's commercial forest. They found that various conventional silvicultural treatments in even-aged softwood stands, such as precommercial thinning and herbicide spraying, enhanced spruce-fir associated bird species over the long term.

Differences between our study results and those of the Breeding Bird Survey (BBS) could be explained by at least two factors. First, there are few BBS survey routes in the commercial forest of Maine because BBS surveys depend on volunteers, and this part of Maine is remote. Therefore, BBS data may not be a good indicator of bird trends in our study area. Second, BBS routes are roadside surveys, which are efficient but not as accurate as our off-road surveys of birds within a forest type of interest.

Notwithstanding the Betts et al. paper discussed above, forest management has routinely been shown to support diverse bird communities (e.g., Dufлот et al. 2022, Akresh et al. 2023), as did our original study in the 1990s (Hagan et al. 1997). We reiterate this widespread observation in our current study, but this time documenting many increases in abundance in a commercial forest over the long term.

Why are so many species increasing in the commercial forest of Maine?

We do not know the answer to this question. We ruled out significant difference in the 1990s and 2020s field crews' abilities to identify birds by song. Both crews were

well-trained in bird identification by sound and sight. Moreover, some species are simply hard to get wrong by sound—e.g., Ovenbird, Black-throated Blue Warbler, Swainson’s Thrush—or by distance from observer. Reasonably well-trained observers are not likely to miscount these species. Furthermore, if the 2020s field crew were somehow superior birders, they still found some species *less* abundant than in the 1990s. We conclude that increasing species really did increase between the 1990s and 2020s. Why?

Because our results were so unexpected, we offer some hypotheses that perhaps others might test with further research.

ONE: The bird attractor hypothesis: One possibility for the increased densities of birds in our study area is immigration into the commercial forests from other areas. This could occur through two different pathways: conspecific attraction during spring breeding site selection, and prospecting-based dispersal at the end of the breeding season. Both can result in shifting of individuals across large areas (regions). For both behaviors, individuals could be drawn from long distances away from their breeding or natal sites of the previous year. This hypothesis depends on some yet unknown cues that make the commercial forests of Maine attractive to birds relative to surrounding regions.

At the end of the breeding season, individuals sometimes “prospect” for breeding habitat over hundreds of kilometers, especially adults with a failed breeding season (Reed et al. 1999, Pärt & Doligez 2003, Cooper & Marra 2020, Ciaglo et al. 2021, Oro et al. 2021). If New Brunswick, for example, is deteriorating in habitat quality (Betts et al. 2022), it could be that individuals reared in New Brunswick are settling in Maine. Also, individuals will select a breeding territory near other conspecifics (Betts et al. 2008, Swift et al. 2023). Birds returning from migration in the spring may be inclined to settle in Maine’s commercial forest where there is a high density of conspecifics. This could be a positive feedback loop where “the rich get richer.” That is, habitat that already has singing territorial males attracts others to settle, at least until the habitat becomes saturated and can no longer accommodate additional breeding individuals.

In addition, individuals that have been successful breeders are likely to return to the same area in subsequent years, even to the same hectare of forest (e.g., Holmes and Sherry 1992, Schlossberg 2009). If the commercial forest of Maine is highly productive, it could lead to an ever-increasing population, again, recognizing the habitat will eventually become saturated. It could be that the commercial forests of Maine are producing large numbers of offspring, which, over time, would lead to an ever-expanding population. It may be that the respective species’ habitats were not saturated in the 1990s and were able to accommodate greater densities of most species if breeding success was consistently high over time. And/or, habitat increased in quality for some species over the last 30 years.

TWO: The food supply hypothesis: Most forest birds in our study area depend on lepidopteran larvae (caterpillars) for food (the early-successional species, such as White-throated Sparrow and Lincoln’s Sparrow depend more on seeds.) We know bird populations respond to changes in abundance of their prey (e.g., Darveau et al. 1997). In our region, forest birds are especially responsive to outbreaks of the spruce budworm (Vernier et al. 2009, Venier and Holmes 2010). The densities of some bird species can increase 2 to 5 times during insect outbreaks (Kendeigh 1947; Morris et al. 1958; Sanders 1970; Holmes et al. 2009; Venier et al. 2009). There has been evidence of increased spruce budworm abundance in recent years,

Why are so many species showing increases in Maine’s commercial forest?

especially 2019 (Parisio 2022), but nothing like the last massive outbreak of the 1970s. It is unlikely that the recent uptick in the spruce budworm could have caused such large increases in bird abundance in our 2020s study. A recent evaluation of long-term arthropod population trends in Maine revealed no major declines in insects (Drummond 2022). It may be that the prey base for birds in the commercial forest of Maine is healthy relative to other parts of the country. Abundance and richness of forest lepidopterans decrease more significantly with clearcutting than with partial harvesting (Summerville and Crist 2006). Perhaps the shift from clearcutting in the 1990s to partial harvesting today supports a greater lepidopteran food supply for birds. Further research would be needed to explore the food supply hypothesis.

THREE: The habitat hypothesis: We documented some structural and compositional changes in the forest with our vegetation surveys. However, none of the changes we detected can explain such widespread increases in so many different bird species. Recall that most of the increases we observed derived from increases in density (bird per unit area), not changes in the forest types in the landscape. More birds were packing into a unit of area. Moreover, forest types and age classes did not change enough to account for a 2-fold or 3-fold increase in density, which some species showed. The greater area in Regen and Residual can explain changes in abundance in the overall study area, but not changes in density within a stand type. It is possible the shift to more balsam fir relative to spruce across the landscape could attract more individuals of certain species. Some bird species can have strong preferences for foraging substrate (Whelan 2001), distinguishing between spruce and fir, or between yellow birch and American beech (McKinley 2004).

FOUR: The dark skies hypothesis: Many bird species migrate at night and navigate by the stars (Emlen 1975). Therefore, light pollution from cities and towns that reduces the visibility of stars can make orientation difficult (McLaren et al. 2018). The 10-million acres of unorganized townships of Maine are unusually dark at night due to the lack of human infrastructure. The Appalachian Mountain Club's Maine Woods ownership northeast of Greenville, Maine has recently been designated as an [International Dark Sky Park](#), based on ambient light at night. The large dark area that results from such an extensive area of commercial forestry with essentially no human habitation could function as an attractor to migrating birds. Because birds settle just before sunrise, they may find this dark area filled with singing conspecifics and decide that this is a good place to set up a breeding territory.

All four of the hypotheses above are speculative. It is possible that all four work together to make the commercial forests of Maine a disproportionately more attractive area for birds relative to surrounding regions that have more human development.

What about the declining species?

While we can celebrate this good news story about bird conservation, we still need to understand the minority of species that might not be doing as well in a commercial forest landscape, for whatever reason(s).

When densities (birds per unit area) increased or decreased, the implication for abundance of that species in the landscape was significant. For example, the densities of the Winter Wren, Canada Warbler, and Magnolia Warbler all decreased, resulting in decreased abundances in the study landscape (see Appendix A). As

Multiple forces may be at play that make the commercial forest of Maine a disproportionately more attractive area for breeding birds.

opposite examples, densities of the American Redstart and Black-and-white Warbler increased by two- or three-fold, and so did their abundances.

What is interesting to understand is when habitat (Superclasses) remained abundant in the landscape but the species declined due to a decline in the number of birds per point count circle (i.e., density). If the habitat is present, but the birds are not, this suggests there are factors outside our study region, perhaps in their wintering areas, that are driving the declines in our study area. If true, there is nothing we can do within the commercial forest of Maine to create larger populations of those species. We need to be careful not to change forest practices in the expectation that we can increase populations when, in fact, forest breeding habitat is not what is limiting the species.

Below we take a closer look at selected species that declined in our study area. Whether we can or cannot do anything different with forestry that would make a difference for these species, it is good to understand that these species warrant a bit more scrutiny. Is there anything we could be doing that might increase these populations within the commercial forest of Maine?

Canada Warbler

The Canada Warbler is widely reported to be declining over the long-term across its breeding range (Fig 17) (Ball et al. 2016, Kirken et al. 2018, Wilson et al. 2018), but declines appear to have reversed since 2012 (COSEWIC 2020). As a result, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) downgraded this species from Threatened to Special Concern in 2020 (COSEWIC. 2020), but said lack of effective management could cause the species to be designated as Threatened again. This species prefers forest with a well-developed shrub layer near small wetlands (Hallworth et al. 2008). The average density (birds per circle) of this species has decreased by 40% in our study area since the 1990s, and the abundance in the landscape has decreased by about the same percentage. This is interesting because the species uses all Superclass types, with a slight preference for the younger Regen and Residual age classes. We suspect this species is cueing on shrubs and small wetlands more than forest age class. There has been no obvious reduction in Canada Warbler habitat in our study area since the 1990s, and yet the species showed a significant decline in density and abundance, consistent with other studies across its breeding range.

Therefore, it is more likely that the decline of Canada Warblers in our study area is a result of wintering habitat loss. The Canada Warbler winters on the slopes of the Andes in northwestern South America (Fig. 17). Between 1993 and 2009, the human "footprint" (i.e., impact) index increased by only 0.11% on the breeding grounds, but by 14% on the wintering grounds (Rodríguez Eraso et al. 2018). There is likely nothing forest managers in Maine can do to help the Canada Warbler if the primary factors causing the decline are on the wintering grounds (González-Prieto et al. 2017, Albert et al. 2020). Keeping Maine's forest as a working forest might be the best conservation we can do in our region for Canada Warblers (Westwood et al. 2020). Any effort to increase habitat would likely be futile ("Build it, but they likely will not come."). It is good for forest managers to understand the breeding habitat needs of the Canada Warbler, but business-as-usual forestry will likely maintain breeding habitat for this species.

It's important that we understand what might be causing declines in a minority of species.

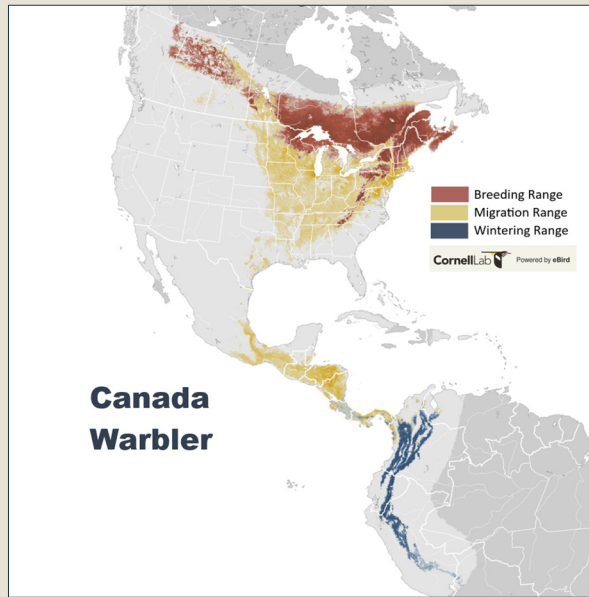


Figure 17.

Canada Warbler range map (left).
Photo: Macaulay Library
(ML133253451)

BBS Trend (Region 14): -4.2%/yr
BBS Trend (Continental): -0.6%/yr
Trend (this study): -26.5%/30 years

Winter Wren

In contrast to the Canada Warbler, the Winter Wren is a short-distance migrant that breeds in Maine but overwinters in the southeastern U.S. (Fig. 18). The Winter Wren decreased by 73% in our study area, in part because of an across-the-board decrease in density in all forest types (see Fig. 7a), but also because of a reduction of its most-preferred forest type, Mature Softwood. Note, however, it also uses younger forest types, including clearcuts. This species nests in existing cavities, downed trees, large, upturned root balls, stream banks, decaying logs, under tree bark, and in hanging moss (Hejl and Paige 1994). The species is associated with natural mature and old-growth forests throughout much of its range but can nest in any age-class of forest so long as the nesting structures described above are present (Hejl et al. 2020). However, such structures can diminish in younger forest. Given the shift to a younger forest in our study area, the Winter Wren could be declining because of loss of older forest structure.

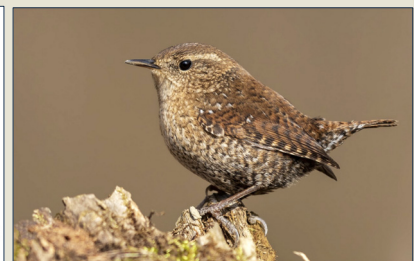
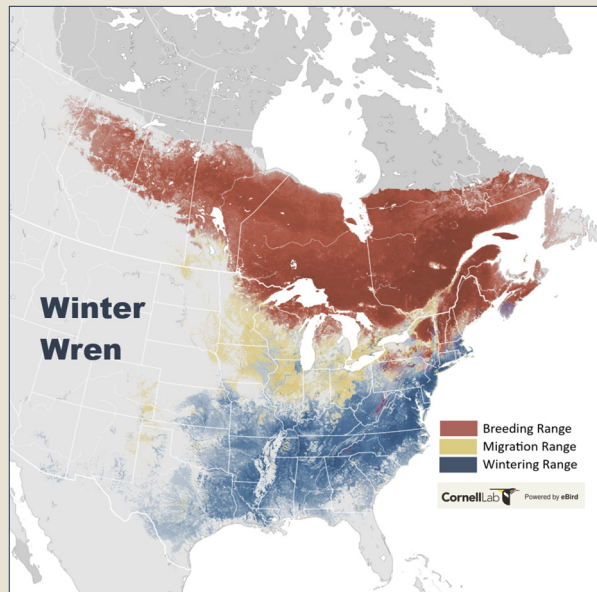


Figure 18.

Winter Wren range map (left).
Photo: Macaulay Library
(ML297982601)

BBS Trend (Region 14): -1.7%/yr
BBS Trend (Continental): -1.8%/yr
Trend (this study): -73.0%/30 years

However, the Winter Wren was increasing at both the regional and continental scales (see Appendix A). In this case, the decline in our study area ran in opposition to larger scale changes. Still, it makes sense that the shift to a younger forest in our study area might result in the local (study area) loss of breeding habitat structure. We support forest managers continuing to focus on retention of large trees (living, dead, and fallen) in stand-level management strategies. Often such management practices will have little or no financial impact on landowners, and yet support species such as the Winter Wren. Widespread snag retention and/or patch retention would help maintain Winter Wren habitat. While commercial forestry generates much early-successional habitat for species also of conservation concern, we need to pay attention to important forest structure that might be more difficult to retain in a shorter-rotation forest.

Blackburnian Warbler

The Blackburnian Warbler prefers mature mixedwood forest in Maine but can be found in pure softwood and pure hardwood stands as well (Young et al. 2005, Morse 2020). It is known to prefer older forest (Doepker et al. 1992). We found it also used mid-age forest but in lesser densities. This species is declining in Region 14 (-0.73%/year) and continentally (-0.63%/year). It declined in abundance in our study area by almost half (-49%), in part because it prefers mature forest types that greatly diminished in our study area over the last 30 years. Moreover, like the Canada Warbler, it has a fairly limited winter range centered mostly in the highlands of northern South America (Fig. 19). If it is experiencing significant habitat loss on both its wintering grounds and breeding grounds, this could be a species of increasing conservation concern. The best management strategy we can do on the breeding grounds is to maintain tall (mature) forest in the landscape, which can be a challenge in a commercial forest where shorter rotations better meet society's wood supply demands. To that end, we should understand the complementary role that public and private conservation lands might play in Maine to help mitigate declines in this species.

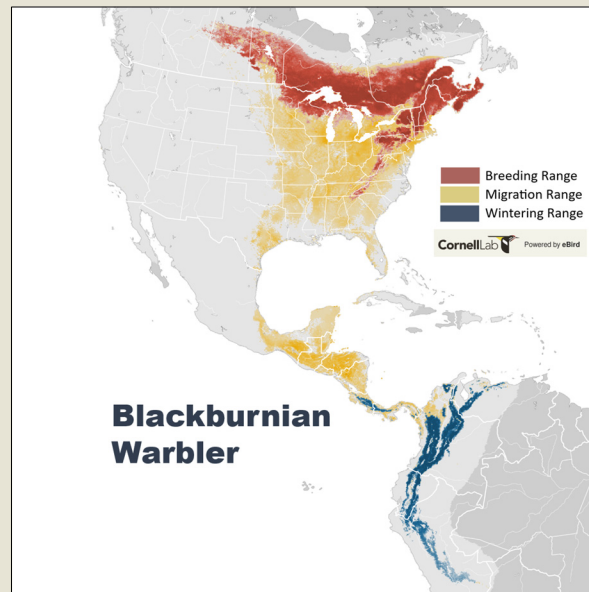


Figure 19.

Blackburnian Warbler range map (left).
 Photo: Macaulay Library
 (ML456215891)

BBS Trend (Region 14): -0.7%/yr
 BBS Trend (Continental): -0.6%/yr
 Trend (this study): -49.2%/30 years



Figure 20.

Lincoln's Sparrow range map (left).
Photo: Macaulay Library
(ML83887671)

BBS Trend (Region 14): -4.6%/yr
BBS Trend (Continental): -1.1%/yr
Trend (this study): -87.3%/30 years

Lincoln's Sparrow

The Lincoln's Sparrow is one of the most habitat-restricted species of the 47 we could analyze. It prefers recent (<5 years) clearcuts and is occasionally found in Regen. It declined in our study area by 87% since the 1990s, partly because of the loss of Clearcut area, but also because of more than a 50% decline in density, even in Clearcut forest. The Lincoln's Sparrow is declining continentally at -1.1%/year, and -4.6%/year in Region 14. However, because of its large range (Fig. 20), it is not considered a species of continental concern (Pandolfino et al. 2023).

The commercial forests of Maine are on the southern margin of this species' breeding range (Fig. 20). As with the Boreal Chickadee and Canada Jay, this species might be shifting its breeding range northward in response to climate change (Matthews et al. 2004). This would explain its lower densities even in its preferred clearcut habitat in our study areas. This is another example of how factors beyond our study area, or even beyond our region (e.g., global climate change), could be driving population change in our study area. If we want to try to maintain this species in Maine, clearcutting is the way to produce its preferred habitat. The key is to not reduce the mature forest habitat preferred by the Blackburnian Warbler (and others) for the purpose of creating more clearcuts for Lincoln's Sparrows.

Golden-crowned Kinglet

The Golden-crowned Kinglet in our study area increased by 25%, whereas it was projected to have lost 38% of its habitat over the same time period in the Canadian Maritimes (Betts et al. 2022). This species also declined both regionally (-1.9%/year) and continentally (-2.7%/year) in the Breeding Bird Survey data (1993-2021). This raises the question of why Golden-crowned Kinglets increased in our commercial forest study area over the last 30 years. In some sections of its range, it is a year-round resident, and in other areas it migrates to the southeastern U.S. for the winter (Fig. 21).

Altogether, in the face of ongoing human development and continental declines in bird populations, all types of forest ownership in northern Maine are serving as an important sanctuary for birds.

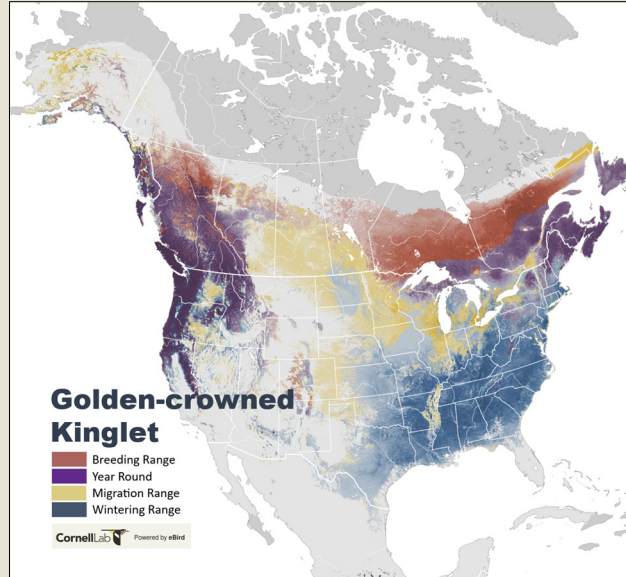


Figure 21.

Golden-crowned Kinglet range map (left).
Photo: Macaulay Library (ML189443171)

BBS Trend (Region 14): -1.9%/yr
BBS Trend (Continental): -2.7%/yr
Trend (this study): +25.9%/30 years

The Golden-crowned Kinglet is a canopy foraging and nesting species (Swanson et al. 2020). It prefers older softwood forest and is sensitive to moderate levels of harvesting (St. Laurent et al. 2008). However, in our study area, we found Golden-crowned Kinglets in about the same density in mid-age softwood forest as in mature softwood forest. Our study area contained a lot of mid-age softwood forest as a result of forest recovery after the spruce budworm outbreak and clearcut harvesting of the 1970s and 1980s. In addition, we saw an increase in density of Golden-crowned Kinglets in almost all Superclasses. As a result, the population of Golden-crowned Kinglets increased in our study landscape. This is another example where trends in Maine’s commercial forest appear different from neighboring New Brunswick and Nova Scotia.

Magnolia Warbler

The Magnolia Warbler is one of the most common species in our study landscape. It prefers Regen and Residual Superclasses, which were both abundant in the study landscape. We highlight this species because, despite its preference for young regenerating forest (Dunn and Hall 2020, Hagan et al. 1997), it still declined in abundance by 9% in our study area. In this case, the trends in our study area matched the direction of trend in the Breeding Bird Survey, -1.35%/year regionally, and -0.16%/year continentally.

Because preferred habitat appears to have increased in the study area, but the species decrease in abundance, we suspect the cause of declines in our study area to be a result of habitat loss or degradation along migration routes or on the wintering grounds (Fig. 22). This pattern is reminiscent of the Canada Warbler case study above, where habitat seemed to be plentiful, but the species declined in our landscape anyway. There could have been some unmeasured and unknown alteration of our Superclasses that led to a decline in habitat suitability and thus a decline in density and overall abundance, but given the generalist nature of this species, we suspect the cause might be outside our study area. We hope other researchers may explore this species in greater detail.

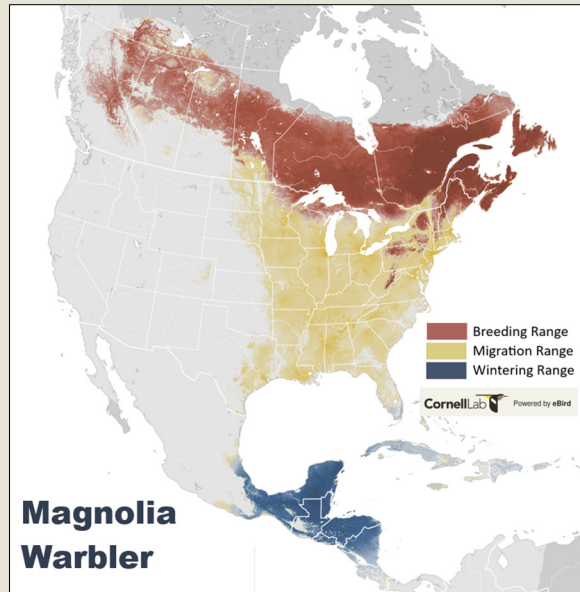


Figure 22.

Magnolia Warbler range map (left).
 Photo: Macaulay Library
 (ML160169121)

BBS Trend (Region 14): -1.4%/yr
 BBS Trend (Continental): -0.2%/yr
 Trend (this study): -9.05%/30 years

CONCLUSIONS

The commercial forests of Maine appear to be functioning as a large, landscape-scaled refugium for birds. Our results support the designation of the area as a globally significant Important Bird Area by the National Audubon Society. Within its bounds, our study area shows many species increases, in contrast with declines in other parts of the Atlantic Northern Forest region and North America. While bird conservation is not the primary goal of commercial forestry, we can all take satisfaction from knowing the commercial forests of Maine are contributing in a positive way to bird conservation at a large scale. Ten million acres of contiguous working forest doing good for bird conservation is something to celebrate when most of the global biodiversity news seems dire.

Despite the good news, we know factors beyond Maine can negatively affect species, especially migratory species that overwinter in the Neotropics. There may be nothing Maine forest managers can do other than continue to provide the array forest types and age classes that these species need for breeding. For smaller woodlot owners who want to manage their woodlots for birds, Maine Audubon's *Forestry for Maine Birds* is an excellent resource (Gallo et al. 2017).

We should pay careful attention to those species decreasing in our study area, and regionally and nationally as well. The most vulnerable forest types are older forest age classes and associated structures (e.g., large living and dead trees). It may be that a diversity of forest owners across the 10-million acres of unorganized territories, from private conservation organizations to multi-use public lands to more intensive commercial forest companies, is an effective strategy for providing the array of forest types and age classes that birds need. Moreover, the many conservation easements applied to commercial forest lands since our 1990s study will help ensure large tracts of bird habitat remain far into the future. Understanding more precisely how this mix of forest owners, acreages, and distributions across the vast unorganized territories of Maine would help us plan even better for bird conservation over the long term.

LITERATURE CITED

- Akresh, M.E., King, D.I., McInvale, S.L., Larkin, J.L. and D'Amato, A.W., 2023. Effects of forest management on the conservation of bird communities in eastern North America: A meta-analysis. *Ecosphere*, 14(1), p.e4315.
- Albert, S., Wolfe, J.D., Kellerman, J., Sherry, T., Stutchbury, B.J., Bayly, N.J. and Ruiz-Sánchez, A., 2020. Habitat ecology of Nearctic–Neotropical migratory landbirds on the nonbreeding grounds. *The Condor*, 122(4), p.duaa055.
- Ball, J.R., Sólymos, P., Schmiegelow, F.K., Hache, S., Schieck, J. and Bayne, E., 2016. Regional habitat needs of a nationally listed species, Canada Warbler (*Cardellina canadensis*), in Alberta, Canada. *Avian Conservation and Ecology*, 11(2), p.10.
- Betts, M.G., Hadley, A.S., Rodenhouse, N., and Nocera, J.J. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B: Biological Sciences* 275:2257–2263.
- Betts, M.G., Yang, Z., Hadley, A.S., Smith, A.C., Rousseau, J.S., Northrup, J.M., Nocera, J.J., Gorelick, N. and Gerber, B.D., 2022. Forest degradation drives widespread avian habitat and population declines. *Nature Ecology & Evolution*, 6(6), pp.709-719.
- Bird Conservancy of the Rockies. 2023. Avian Conservation Assessment Dataset, available online at: <https://pif.birdconservancy.org/>
- Ciaglo, M., Calhoun, R., Yanco, S.W., Wunder, M.B., Stricker, C.A., and Linkhart, B.D. 2021. Evidence of post-breeding prospecting in a long-distance migrant. *Ecology and Evolution* 11:599-611.
- Cooper, N.W. and Marra, P.P. 2020. Hidden long-distance movements by a migratory bird. *Current Biology* 30:4056-4062.
- COSEWIC. 2020. COSEWIC assessment and status report on the Canada Warbler *Cardellina canadensis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 54 pp. ([link](#))
- Crawford, H.S., Hooper, R.G. and Titterton, R.W., 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *The Journal of Wildlife Management*, pp.680-692.
- Doepker, R. V., R. D. Earle and J. J. Ozoga. (1992). Characteristics of Blackburnian Warbler, *Dendroica fusca*, breeding habitat in upper Michigan. *Canadian Field-Naturalist* 106:366-371
- Drummond, F., 2022. Evidence for Arthropod Decline in Maine. Unpublished report. Maine Audubon Society, Falmouth, Maine.
- Duflot, R., Fahrig, L. and Mönkkönen, M., 2022. Management diversity begets biodiversity in production forest landscapes. *Biological Conservation*, 268, p.109514.
- Dunn, E. H. and G. A. Hall (2020). Magnolia Warbler (*Setophaga magnolia*), version 1.0. In *Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.ezproxy.library.tufts.edu/10.2173/bow.magwar.01>
- Emlen, S.T., 1975. The stellar-orientation system of a migratory bird. *Scientific American*, 233(2), pp.102-111.
- Gallo, S., R. Bryan, A. Mahaffey, R. Morrill, D. Morgan, A. Shultz, S. Stockwell, and J. Wiley. 2017. *Forestry for Maine Birds: A Guidebook for Foresters Managing Woodlots "With Birds in Mind."* Maine Audubon Society, Falmouth, Maine. 131 pp.
- González-Prieto, A.M., Bayly, N.J., Colorado, G.J. and Hobson, K.A., 2017. Topography of the Andes Mountains shapes the wintering distribution of a migratory bird. *Diversity and Distributions*, 23(2), pp.118-129.
- Hagan III, J.M., 1996. Clearcutting in Maine: would somebody please ask the right question? *Maine Policy Review*, 5(2), pp.7-19.
- Hagan, J.M., McKinley, P.S., Meehan, A.L. and Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *The Journal of Wildlife Management*, pp.718-735.
- Hallworth, M., Benham, P.M., Lambert, J.D. and Reitsma, L., 2008. Canada warbler (*Wilsonia canadensis*) breeding ecology in young forest stands compared to a red maple (*Acer rubrum*) swamp. *Forest Ecology and Management*, 255(3-4), pp.1353-1358.
- Harris, J.B.C. and Haskell, D.G., 2007. Land cover sampling biases associated with roadside bird surveys. *Avian Conservation & Ecology*, 2(2).

- Hejl, S. J. and L. C. Paige. (1994). "A preliminary assessment of birds in continuous and fragmented forests of western redcedar/western hemlock in northern Idaho." In Interior cedar-hemlock-white pine forests: ecology and management., edited by D. M. Baumgartner, J. E. Lotan and J. R. Tonn, 189-197. 1993. Washington State Univ., Pullman: Spokane, WA.
- Hejl, S. J., J. A. Holmes, and D. E. Kroodsma (2020). Winter Wren (*Troglodytes hiemalis*), version 1.0. In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.ezproxy.library.tufts.edu/10.2173/bow.winwre3.01>
- Hijmans, R.J., Phillips, S., Leathwick, J. and Elith, J., 2023. dismo: Species Distribution Modeling. R package version 1.3-14. <<https://CRAN.R-project.org/package=dismo>>.
- Holmes, S.B., Sanders, C.J., Fillman, D., and Welsh, D.A. 2009. Changes in a forest bird community during an outbreak cycle of the spruce budworm in northwestern Ontario. *Bird Populations*, 9: 13–28.
- Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation, p. 563–575. In J. M. Hagan III and D. W. Johnston [eds.], *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C.
- Irland, L.C., Dimond, J.B., Stone, J.L., Falk, J., and Baum, E. 1988. The spruce budworm outbreak in Maine in the 1970's –assessment and directions for the future. *Maine Agric. Exp. Stn. Bull.* 819.
- Kendeigh, S.C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. *Biological Bulletin No. 1*. Ontario Department of Lands and Forests, Division of Research. 100 pp.
- Krikun, R.G., McCune, J.L., Bayne, E.M. and Flockhart, D.T., 2018. Breeding habitat characteristics of Canada Warblers in central Alberta. *The Forestry Chronicle*, 94(3), pp.230-239.
- Matthews, S. N., R. J. O'Connor, L. R. Iverson, and A. M. Prasad (2004). Atlas of climate change effects in 150 bird species of the Eastern United States. USDA Forest Service General Report NE-GTR-318.
- McLaren, J.D., Buler, J.J., Schreckengost, T., Smolinsky, J.A., Boone, M., Emiel van Loon, E., Dawson, D.K. and Walters, E.L., 2018. Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters*, 21(3), pp.356-364.
- McKinley, P., 2004. Tree Species Selection and Use by Foraging Insectivorous Passerines in a Forest Landscape. Ph.D. Dissertation. University of New Brunswick, Fredericton, New Brunswick. 141 pp.
- MFS 2022. 2021 Silvicultural Activities Report. (download all annual silvicultural reports from: https://www.maine.gov/dacf/mfs/publications/annual_reports.html)
- MFS 1992. 1992 Silvicultural Activities Report. Maine Forest Service, August, ME (download archived report from: https://digitalmaine.com/for_docs/125/)
- Morris, R.F., Cheshire, W.F., Miller, C.A., and Mott, D.G. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology*, 39(3): 487–494.
- Morse, D. H. (2020). Blackburnian Warbler (*Setophaga fusca*), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.ezproxy.library.tufts.edu/10.2173/bow.bkbwar.01>
- National Audubon Society 2023. National Audubon Society Important Bird Areas web page: <https://www.audubon.org/important-bird-areas>
- Oro, D., Bécarea, J., Bartumeus, F., and Arcos, J.M., 2021. High frequency of prospecting for informed dispersal and colonisation in a social species at large spatial scale. *Oecologia* 197:395-409.
- Pandolfino, E. R., E. M. Ammon, and K. W. Sockman (2023). Lincoln's Sparrow (*Melospiza lincolni*), version 2.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.ezproxy.library.tufts.edu/10.2173/bow.linspa.02>
- Parisio, M., 2022. Spruce Budworm in Maine: 2022 Summary Report. Maine Forest Service. Available online: https://digitalmaine.com/cgi/viewcontent.cgi?article=1295&context=for_docs
- Phillips, S.J., Dudík, M. and Schapire, R.E., 2004, July. A maximum entropy approach to species distribution modeling. In Proceedings of the twenty-first international conference on Machine learning (p. 83).
- Pohlman, C.K., Roth, A.M., Hartley, M.J., Hunter Jr, M.L., McGill, B.J. and Seymour, R.S., 2023. Experimental natural disturbance-based silviculture systems maintain mature forest bird assemblage long-term in Maine (USA). *Forest Ecology and Management*, 528, p.120630.

- R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reed, J.M., Bouludier, T., Danchin, E., and Oring, L.W. 1999. Informed dispersal: prospecting by birds for breeding sites. *Current Ornithology* 15:189-259.
- Rodríguez Eraso, N., Armenteras-Pascual, D. and Alumbrosos, J.R., 2013. Land use and land cover change in the Colombian Andes: dynamics and future scenarios. *Journal of Land Use Science*, 8(2), pp.154-174.
- Rolek, B.W., Harrison, D.J., Loftin, C.S. and Wood, P.B., 2018. Regenerating clearcuts combined with postharvest forestry treatments promote habitat for breeding and post-breeding spruce-fir avian assemblages in the Atlantic Northern Forest. *Forest Ecology and Management*, 427, pp.392-413.
- Rosenberg, K.V., A. Dokter, P. Blancher, J. Sauer, A. Smith, P. Smith, J. Stanton, A. Panjabi, L. Helft, M. Parr, and P. Marra. 2019. Decline of the North American Avifauna. *Science*, 366:120-124.
- Sanders, C.J. 1970. Populations of breeding birds in the spruce- fir forests of northwestern Ontario. *Can. Field Nat.* 84: 131–135.
- Sauer, J.R., Link, W.A., and Hines, J.E., 2022, The North American Breeding Bird Survey, Analysis Results 1966 - 2021: U.S. Geological Survey data release, <https://doi.org/10.5066/P9SC7T11>.
- Sauer, J.R., Pendleton, G.W. and Orsillo, S., 1995. Mapping of bird distributions from point count surveys. *Monitoring bird populations by point counts*, pp.151-160.
- Schlossberg, S., 2009. Site fidelity of shrubland and forest birds. *The Condor*, 111(2), pp.238-246.
- St-Laurent, M.H., Ferron, J., Haché, S. and Gagnon, R., 2008. Planning timber harvest of residual forest stands without compromising bird and small mammal communities in boreal landscapes. *Forest Ecology and Management*, 254(2), pp.261-275.
- Solomon, D.S., L. Zhang, T.B. Brann, and D.S. Larrick. 2003. Mortality patterns following spruce budworm infestation in unprotected spruce-fir forests in Maine. *Northern Journal of Applied Forestry* 20(4): 148-153.
- Summerville, K.S. and Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review1. *The Canadian Entomologist*, 140(4), pp.475-494.
- Swanson, D. L., J. L. Ingold, and R. Galati (2020). Golden-crowned Kinglet (*Regulus satrapa*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org.ezproxy.library.tufts.edu/10.2173/bow.gockin.01>
- Swift, R.J., Anteau, M.J., Ellis, K.S., Ring, M.M., Sherfy, M.H. and Toy, D.L. 2023. Conspecific density and habitat quality affect breeding habitat selection: Support for the social attraction hypothesis. *Ecosphere* 14(5), p.e4524
- Tallamy, D.W. and Shriver, W.G., 2021. Are declines in insects and insectivorous birds related?. *The Condor*, 123(1), p.duaa059.
- Venier, L., Pearce, J., Fillman, D., McNicol, D. and Welsh, D., 2009. Effects of spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on boreal mixed-wood bird communities. *Avian Conservation and Ecology*, 4(1).
- Venier, L.A. and Holmes, S.B., 2010. A review of the interaction between forest birds and eastern spruce budworm. *Environmental Reviews*, 18(NA), pp.191-207.
- Westwood, A.R., Lambert, J.D., Reitsma, L.R. and Stralberg, D., 2020. Prioritizing areas for land conservation and forest management planning for the threatened Canada warbler (*Cardellina canadensis*) in the Atlantic northern forest of Canada. *Diversity*, 12(2), p.61.
- Volpato, G.H., Lopes, E.V., Mendonça, L.B., Boçon, R., Bisheimer, M.V., Serafini, P.P. and Anjos, L.D., 2009. The use of the point count method for bird survey in the Atlantic forest. *Zoologia (curitiba)*, 26, pp.74-78.
- Whelan, C.J., 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology*, 82(1), pp.219-231.
- Will, T., J.C. Stanton, K.V. Rosenberg, A.O. Panjabi, A.F. Camfield, A.E. Shaw, W.E. Thogmartin, and P.J. Blancher. 2020. Handbook to the Partners in Flight Population Estimates Database, Version 3.1. PIF Technical Series No 7.1.

- Wilson, S., Saracco, J.F., Krikun, R., Flockhart, D.T., Godwin, C.M. and Foster, K.R., 2018. Drivers of demographic decline across the annual cycle of a threatened migratory bird. *Scientific Reports*, 8(1), p.7316.
- Young, L., Betts, M.G. and Diamond, A.W., 2005. Do Blackburnian Warblers select mixed forest?: the importance of spatial resolution in defining habitat. *Forest Ecology and Management*, 214(1-3), pp.358-372.
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APPENDIX A. All species detected within 50-m radius point count circles in either the 1990s or the 2020s studies. See footnotes for header explanations. Rows in blue represent the 47 species analyzed. Rows in orange are species not analyzed due to low occurrence at point count stations.

#	Sp. Code	Species	Max. Density ^a		Max. Habitat ^b	Niche Breadth ^c	Abundance ^d		Abund. Change (%) ^e	Change Dir.	% Change Due to Density ^f	Continental		Region 14		Migration Status ^k
			1990s	2020s			Trend ^g	PIF Score ^h				Trend ⁱ	PIF Score ^j			
1	ALFL	Alder Flycatcher	0.64	0.35	Young Regen	4	45,233	49,900	10.3	INC	100.0	-1.02	8	-1.01	12	Netrop
2	AMRE	American Redstart	0.32	0.79	Mid-age Hardwood	8	42,517	135,995	219.9	INC	78.5	0.10	8	-1.48	15	Netrop
3	AMRO	American Robin	0.15	0.29	Young Regen	9	23,430	62,116	165.1	INC	93.8	-0.49	5	-1.09	12	Partial
4	BAWW	Black-and-white Warbler	0.31	0.62	Young Regen	9	46,819	127,146	171.6	INC	82.9	-1.77	10	-1.78	16	Netrop
5	BBWA	Bay-breasted Warbler	0.43	0.09	Mid-age Softwood	3	32,937	13,976	-57.6	DEC	17.1	-0.88	9	-2.12	17	Netrop
6	BCCH	Black-capped Chickadee	0.41	0.82	Mid-age Mixedwood	9	63,247	141,172	123.2	INC	80.7	-0.12	7	0.28	11	Resident
7	BHVI	Blue-headed Vireo	0.26	0.94	Mature Softwood	9	35,662	62,491	75.2	INC	100.0	2.32	7	1.46	12	Netrop
8	BLBW	Blackburnian Warbler	0.95	1.23	Mature Softwood	7	102,415	51,971	-49.3	DEC	66.9	-0.63	9	-0.73	14	Netrop
9	BLJA	Blue Jay	0.23	0.35	Residual Overstory	9	24,023	64,989	170.5	INC	66.0	-0.35	9	1.12	10	Partial
10	BOCH	Boreal Chickadee	0.28	0.14	Mid-age Softwood	2	24,685	7,341	-70.3	DEC	25.6	-0.22	8	-1.93	13	Resident
11	BRCR	Brown Creeper	0.2	0.58	Mature Softwood	7	13,458	24,510	82.1	INC	100.0	-0.14	8	1.05	10	Partial
12	BTBW	Black-throated Blue Warbler	0.85	1.12	Mature Hardwood	8	84,870	113,305	33.5	INC	100.0	0.43	9	0.12	13	Netrop
13	BTGW	Black-throated Grn Warbler	0.71	1.09	Mature Mixedwood	8	68,056	124,274	82.6	INC	98.5	-0.53	8	-0.45	13	Netrop
14	CAJA	Canada Jay	0.19	0.10	Mature Softwood	5	14,294	8,498	-40.6	DEC	72.5	-0.56	8	-1.40	12	Resident
15	CAWA	Canada Warbler	0.38	0.20	Young Regen	6	53,207	38,920	-26.9	DEC	100.0	-0.59	13	-4.20	18	Netrop
16	CEWA	Cedar Waxwing	0.28	0.49	Clearcut	8	42,646	60,259	41.3	INC	9.7	-1.76	6	-1.85	11	Partial
17	CHSP	Chipping Sparrow	0.17	0.03	Clearcut	1	17,662	963	-94.6	DEC	100.0	-1.30	8	-0.76	11	s.e. U.S.
18	COYE	Common Yellowthroat	1.74	1.58	Clearcut	6	169,883	195,997	15.4	INC	82.5	-0.74	8	-0.74	13	s.e. U.S.
19	CSWA	Chestnut-sided Warbler	0.59	0.79	Residual Overstory	8	69,840	147,179	110.7	INC	77.7	-0.35	10	-0.43	15	Netrop
20	DEJU	Dark-eyed Junco	0.35	0.20	Young Regen	6	48,062	47,643	-0.9	DEC	67.3	-1.54	8	-2.89	12	Partial
21	DOWO	Downy Woodpecker	0.09	0.18	Mid-age Hardwood	8	5,170	6,426	24.3	INC	6.7	-0.27	7	0.52	10	Resident
22	GCKI	Golden-crowned Kinglet	1.47	1.71	Mature Softwood	8	131,898	166,038	25.9	INC	100.0	-2.71	8	-1.92	9	Partial
23	HAWO	Hairy Woodpecker	0.08	0.19	Residual Overstory	6	9,437	24,853	163.4	INC	68.6	0.65	6	1.84	11	Resident
24	HETH	Hermit Thrush	0.26	0.54	Mid-age Hardwood	9	31,475	112,736	258.2	INC	81.5	-1.24	6	-1.13	10	s.e. U.S.
25	LEFL	Least Flycatcher	0.22	0.33	Mature Hardwood	8	12,841	15,729	22.5	INC	100.0	-1.87	11	-2.34	16	Netrop
26	LISP	Lincoln's Sparrow	0.53	0.2	Clearcut	1	45,400	5,780	-87.3	DEC	100.0	-1.06	7	-4.60	11	s.e. U.S.
27	MAWA	Magnolia Warbler	1.38	0.98	Young Regen	9	216,467	197,043	-9.0	DEC	100.0	-0.16	8	-1.37	13	Netrop
28	MOWA	Mourning Warbler	0.32	0.13	Residual Overstory	5	23,264	16,385	-29.6	DEC	59.9	-1.23	10	-2.19	15	Netrop
29	NAWA	Nashville Warbler	0.98	0.82	Young Regen	7	105,988	145,855	37.6	INC	7.8	-1.35	8	-2.46	15	Netrop
30	NOFL	Northern Flicker	0.19	0.21	Residual Overstory	3	13,533	17,323	28.0	INC	100.0	-1.18	9	-0.16	14	Partial
31	NOPA	Northern Parula	0.26	0.97	Mature Mixedwood	9	29,407	91,578	211.4	INC	95.3	1.82	7	1.94	12	Netrop
32	NOWA	Northern Waterthrush	0.09	0.11	Mid-age Softwood	3	15,340	3,103	-79.8	DEC	100.0	1.39	6	-1.42	13	Netrop
33	OVEN	Ovenbird	0.76	1.21	Mid-age Hardwood	8	76,958	118,861	54.5	INC	86.0	-0.51	8	0.39	12	Netrop
34	PAWA	Palm Warbler	0.4	0.56	Young Regen	5	23,616	85,157	260.6	INC	63.0	0.96	9	-0.08	11	s.e. U.S.
35	PUFI	Purple Finch	0.09	0.17	Residual Overstory	8	8,474	38,988	360.1	INC	100.0	0.03	9	-0.68	16	Partial
36	RBNU	Red-breasted Nuthatch	0.53	0.74	Mature Softwood	9	66,447	90,521	36.2	INC	100.0	-0.12	6	-0.46	9	Partial
37	RCKI	Ruby-crowned Kinglet	0.22	0.38	Mid-age Softwood	6	18,821	38,442	104.3	INC	100.0	-0.19	6	-2.44	12	s.e. U.S.
38	REVI	Red-eyed Vireo	1.06	1.45	Mature Hardwood	9	104,457	206,825	98.0	INC	90.8	0.93	6	1.33	10	Netrop
39	RTHU	Ruby-thr'd Hummingbird	0.02	0.19	Mature Hardwood	7	939	11,672	1143.2	INC	87.5	0.43	6	1.43	11	Netrop
40	SOSP	Song Sparrow	0.59	1.08	Clearcut	2	41,787	37,038	-11.4	DEC	100.0	-0.83	8	-0.13	13	Partial
41	SWTH	Swainson's Thrush	0.27	0.58	Mature Softwood	8	31,137	85,590	174.9	INC	87.8	-0.56	9	-0.79	12	Netrop
42	VEER	Veery	0.12	0.44	Mid-age Hardwood	5	15,800	45,523	188.1	INC	69.7	-0.75	11	-2.47	17	Netrop
43	WIWR	Winter Wren	0.57	0.26	Mature Softwood	9	101,518	27,442	-73.0	DEC	96.6	-1.85	8	-1.66	14	s.e. U.S.
44	WTSP	White-throated Sparrow	2.09	2.36	Clearcut	9	212,378	305,416	43.8	INC	35.1	-1.12	8	-1.76	13	s.e. U.S.
45	YBFL	Yellow-bellied Flycatcher	0.29	0.48	Mature Softwood	7	27,226	58,766	115.9	INC	100.0	2.00	7	-2.74	14	Netrop
46	YBSA	Yellow-bellied Sapsucker	0.22	0.4	Mature Mixedwood	8	27,669	37,959	37.2	INC	94.9	1.97	6	2.09	12	s.e. U.S.
47	YRWA	Yellow-rumped Warbler	1.02	0.84	Mid-age Softwood	8	124,331	119,919	-3.6	DEC	100.0	-1.01	6	-1.92	9	s.e. U.S.
48	AMBI	American Bittern	0.03	0	.	.	1,828	-	.	.	0.21	11	-1.90	15	s.e. U.S.	
49	BBCU	Black-billed Cuckoo	0.02	0	.	.	809	-	.	.	0.08	12	-0.32	15	Netrop	
50	BBWO	Black-backed Woodpecker	0.06	0	.	.	4,736	-	.	.	2.26	8	-0.55	15	Resident	
51	CORA	Common Raven	0.02	0	.	.	939	-	.	.	1.28	6	-0.05	11	Resident	
52	EVGR	Evening Grosbeak	0.06	0	.	.	5,275	-	.	.	-4.57	13	-8.60	18	Partial	

APPENDIX A (cont.)

#	Spp. Code	Species	Max. Density ^a		Max. Habitat ^b	Niche Breadth ^c	Abundance ^d		Abund. Change (%) ^e	Change Dir.	% Change Due to Density ^f	Continental		Region 14		Migration Status
			1990s	2020s			1990s	2020s				Trend ^g	PIF Score ^h	Trend ⁱ	PIF Score ^j	
53	GRCA	Gray Catbird	0.03	0	.	.	2,418	-	.	.	.	0.32	7	-0.22	13	Partial
54	PHVI	Philadelphia Vireo	0.06	0	.	.	4,878	-	.	.	.	2.66	8	-1.12	13	Netrop
55	PISI	Pine Siskin	0.15	0	.	.	9,411	-	.	.	.	-2.33	10	-11.50	13	Partial
56	SSHA	Sharp-shinned Hawk	0.05	0	.	.	1,043	-	.	.	.	0.39	7	0.11	10	Partial
57	TEWA	Tennessee Warbler	0.02	0	.	.	939	-	.	.	.	-3.08	8	-6.47	12	Netrop
58	TTWO	American 3-toed Woodpeck	0.06	0	.	.	2,428	-	.	.	.	2.68	8	-0.47	11	Resident
59	WIWA	Wilson's Warbler	0.15	0	.	.	9,799	-	.	.	.	-1.78	10	-3.44	10	Netrop
60	WOTH	Wood Thrush	0.02	0	.	.	523	-	.	.	.	-1.07	12	-6.40	15	Netrop
61	MODO	Mourning Dove	0	0.03	.	.	-	204	.	.	.	-0.62	6	1.03	7	Partial
62	AMWO	American Woodcock	0	0.02	.	.	-	482	.	.	.	0.22	11	0.00	16	Partial
63	INBU	Indigo Bunting	0	0.02	.	.	-	573	.	.	.	-0.90	8	0.64	8	Netrop
64	EABL	Eastern Bluebird	0	0.02	.	.	-	837	.	.	.	-0.75	6	1.25	8	Partial
65	SAVS	Savannah Sparrow	0	0.03	.	.	-	963	.	.	.	-2.31	8	-2.89	12	s.e. U.S.
66	GRHE	Green Heron	0	0.04	.	.	-	1,146	.	.	.	-1.73	12	-1.98	13	Partial
67	RECR	Red Crossbill	0	0.02	.	.	-	1,490	.	.	.	-1.27	8	2.13	10	Partial
68	AMCR	American Crow	0	0.02	.	.	-	2,071	.	.	.	-0.70	6	0.08	10	Partial
69	SWSP	Swamp Sparrow	0	0.02	.	.	-	2,071	.	.	.	1.13	6	0.99	11	Partial
70	FOSP	Fox Sparrow	0	0.02	.	.	-	3,560	.	.	.	-1.55	9	-5.46	12	s.e. U.S.
71	CHSW	Chimney Swift	0	0.02	.	.	-	3,916	.	.	.	-3.51	12	-2.09	14	Netrop
72	RUBL	Rusty Blackbird	0	0.04	.	.	-	4,141	.	.	.	-0.99	11	-2.34	13	s.e. U.S.
73	CMWA	Cape May Warbler	0	0.03	.	.	-	4,325	.	.	.	-0.14	10	0.59	17	Netrop
74	PIWA	Pine Warbler	0	0.13	.	.	-	5,332	.	.	.	-0.46	7	6.06	9	Partial
75	WWCR	White-winged Crossbill	0	0.05	.	.	-	6,785	.	.	.	1.80	6	-1.00	8	Partial
76	WBNU	White-breasted Nuthatch	0.02	0.03	.	.	484	1,881	.	.	.	1.27	6	1.25	9	Resident
77	SPGR	Spruce Grouse	0.02	0.02	.	.	809	2,071	.	.	.	2.36	7	-4.23	11	Resident
78	GCFL	Great Crested Flycatcher	0.03	0.03	.	.	1,828	410	.	.	.	0.14	7	-1.51	11	Netrop
79	SCTA	Scarlet Tanager	0.06	0.09	.	.	2,751	6,491	.	.	.	-0.37	11	-1.67	16	Netrop
80	PIWO	Pileated Woodpecker	0.02	0.04	.	.	2,756	4,087	.	.	.	1.40	7	2.67	11	Resident
81	EWPE	Eastern Wood-Pewee	0.03	0.07	.	.	2,762	2,846	.	.	.	-0.73	10	-1.78	14	Netrop
82	OSFL	Olive-sided Flycatcher	0.03	0.04	.	.	2,772	6,559	.	.	.	-1.70	12	-3.49	14	Netrop
83	TRSW	Tree Swallow	0.09	0.03	.	.	2,885	410	.	.	.	-1.34	9	-3.56	16	s.e. U.S.
84	BLPW	Blackpoll Warbler	0.09	0.02	.	.	3,237	3,916	.	.	.	-2.21	10	-2.07	13	Netrop
85	AMGO	American Goldfinch	0.11	0.17	.	.	5,633	7,296	.	.	.	-0.69	6	0.25	11	Partial
86	RBGR	Rose-breasted Grosbeak	0.06	0.18	.	.	6,147	6,206	.	.	.	-0.19	11	-3.57	17	Netrop
87	COGR	Common Grackle	0.06	0.06	.	.	6,209	2,309	.	.	.	-1.83	9	-1.59	11	Partial
88	RUGR	Ruffed Grouse	0.08	0.08	.	.	9,088	9,024	.	.	.	1.71	7	0.84	14	Resident

^a maximum density among all 9 Superclasses (birds detected per 50-m radius circles).

^b the Superclass in which the species showed its highest density. Uncommon species are too uncommon to assign a habitat.

^c niche breadth is defined as the number of Superclasses in which the species was detected within a circle in the 2020s study.

^d abundance is estimated by bird density x Superclass area for each study, 1990s and 2020s.

^e abundance change (%) is the percent change in abundance between the 1990s and 2020s studies.

^f percent change due to density is the percent change in abundance that can be explained by a change in density (birds per circle) rather than a change in habitat availability (i.e., change in area of each Superclass).

^g annual % change in continental population based on Breeding Bird Survey data.

^h Partners In Flight Continental Conservation Score (scores range from 5 to 25, with higher numbers indicating greater conservation concern).

ⁱ annual % change in the Region 14 population based on the Breeding Bird Survey data.

^j Partners In Flight Region 14 Conservation Score (scores range from 5 to 25, with higher numbers indicating greater conservation concern).

^k where the species resides in the winter.



Hannibal's Crossing
Golden Road