frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 22 July 2025
DOI 10.3389/fevo.2025.1511265

OPEN ACCESS

EDITED BY
Darren Norris,
Universidade Federal do Amapá, Brazil

REVIEWED BY
Wayne C. Zipperer,
Forest Service (USDA), United States
Suresh Chandra Subedi,
Norfolk State University, United States

*CORRESPONDENCE
Daniel S. Cooper
dan@cooperecological.com

RECEIVED 14 October 2024
ACCEPTED 23 June 2025
PUBLISHED 22 July 2025

CITATION
Cooper DS (2025) Avian turnover at Harvard Forest, Massachusetts, USA, 1948-2016.
Front. Ecol. Evol. 13:1511265.
doi: 10.3389/fevo.2025.1511265

Avian turnover at Harvard Forest, Massachusetts, USA, 1948-2016

Daniel S. Cooper[1,2]*

[1]Ornithology Department, Natural History Museum of Los Angeles County, Los Angeles, CA, United States, [2]Resource Conservation District of the Santa Monica Mountains, Calabasas, CA, United States

Multi-decadal datasets from systematic surveys of birds are rarely published, despite their potential to yield important information about local changes in the environment over time. I compare bird surveys at Harvard Forest in central Massachusetts, USA, between 1993 and 2016 with two unpublished annotated bird checklists from the area (1948 and 1970), along with data from other long-term bird survey sites in New England, and regional community science data. While a handful of breeding species at the Harvard Forest are common each year, species turnover has been constant, with roughly a third of bird species found one survey year and not the other. I list 18 species that have apparently colonized Harvard Forest as breeding species after 1948, and 16 that have declined since then, including two to the point of extirpation. I also note several examples of phylogenetic replacements in the recent vs. historical avifauna. More colonizing species than declining species are at their northern range limit rather than their southern limit in southern New England, and more migratory species appear to be declining than colonizing. More colonizing species favor forest interior than declining ones, and nearly all declining species are associated with edge/early-successional habitats or are considered habitat generalists. The majority of species to have colonized Harvard Forest since 1948 show positive statewide population trends, and none showed a loss in the number of breeding bird atlas blocks occupied between the 1970s and the 2000s. I identify three declining or extirpated species, Ruffed Grouse, Eastern Whip-poor-will, and Olive-sided Flycatcher, as particularly deserving of conservation attention. Long-term, site-scale monitoring is essential to detect the impact of local forest management techniques, which at Harvard Forest has included the creation of experimental clear-cuts, the loss of conifer plantations, and the continued maturation of the mixed hardwood forest.

KEYWORDS
change, avian, Massachusetts, community, time

Introduction

Long-term datasets are key to understanding ecological change over time, and can help clarify our role in effecting these changes (Magurran et al., 2010, Knapp et al., 2012). Conspicuous and diverse, birds make ideal subjects for long-term monitoring and detection of environmental change (Collins, 2001). Studies of species turnover and other measures of community change done on various spatiotemporal scales have long provided insight into the patterns to be expected from ongoing fluctuations and shifts in climate and vegetation succession and management (e.g., Holmes, 2007; Hitch and Leberg, 2007; DeLuca and King, 2017; Neate-Clegg et al., 2021; Craig, 2023). They may also be used to develop restoration priorities and goals for projects attempting to restore lost habitats (e.g., Cooper, 2008). In North America, regional and continent-scale avian monitoring programs such as the USGS Breeding Bird Survey ("BBS"), and more recently, community-science programs such as eBird have been used to detect continent-scale population change (e.g., James et al., 1996; Goetz et al., 2014; Schipper et al., 2016; Rosenberg et al., 2019). Each of these methods has different drawbacks; those reliant on passive data collection rather than standardized methodology tend to have records clustered near populated areas and popular birding sites, though with enough participation spread across a large enough region, these issues can be statistically overcome. Data from standardized, longitudinal population surveys are rare for all but a handful of taxa and sites, but have the advantage of providing quantitative data based on repeated observations by trained observers, even where early data are fragmentary (Curtis and Robinson, 2015).

Though many excellent short-term avian-habitat studies have been made in the forested habitats of the Northeastern U.S. (e.g., DeGraaf et al., 1998), longer-term datasets from this ecoregion are few. Among the exceptions are work by ornithologists at Hubbard-Brook Experimental Forest in central New Hampshire who pioneered research on neotropical migrant birds in the 1960s (e.g., Holmes and Sherry, 1988, 2001), which continues today. Elsewhere, McNulty et al. (2008) compared bird survey results from the 1950s from Huntington Wildlife Forest in New York's Adirondack Mountains with contemporary surveys, and bird monitoring at Yale-Myers Forest in northeastern Connecticut has been ongoing since the 1980s (see Hanle et al., 2020; Craig, 2023). Such site-based studies are essential to validate regional population trends (Walsh and Servison, 2017), and to detect contrasting patterns that can be explained by local land use, informing management.

Continent-wide analyzes have suggested that in recent decades, woodland birds have been generally increasing and grassland birds decreasing, with declines in abundance driven by drops in numbers of the most abundant species (Schipper et al., 2016). The Northeastern U.S. has seen widespread and continued reforestation in rural areas such as around Harvard Forest (Foster et al., 1998), which would presumably favor forest-interior species. However, this has occurred alongside the proliferation of both insect pests (Tingley et al., 2002; Barker Plotkin et al., 2024) and non-native understory plants in the region (Jenkins et al., 2008) which continue to transform this landscape. These habitat changes have impacted avian trends, but inconsistently so. For example, from surveys in Connecticut and Rhode Island, 2001-2008, Craig (2017) reported forest interior species more associated with increases, and edge/successional species with declines. However, in a longer-term study of breeding birds in Connecticut, Craig et al. (2022) found that the "seven most strongly increasing species were variously distributed forest interior and edge/successional-associated species". Furthermore, the differing survey and analytical methods and timeframes used for local studies have confounded interpretation.

Regional trends surely play a role in habitat-associated population changes, but directionality is inconsistent, and trends often contradictory at the local level, or between study sites (see Craig, 2023). For example, at Hubbard-Brook Experimental Forest in New Hampshire, Holmes and Sherry (2001) reported an overall numerical decline of breeding birds since the late 1960s, and reported far more forest-associated species decreasing than increasing. In their upstate New York study area, McNulty et al. (2008) also found more species to exhibit a drop in relative abundance than an increase since the 1950s. Yet, Craig et al. (2022) found that overall population density *increased* between their survey years (1985 to 2019), even as diversity levels remained constant.

It is also unclear how much habitat – or our interpretation of habitat – can impact bird populations, and on what scale. Increasingly, population trends are framed as species' hypothesized response to climate change (e.g., Walsh and Servison, 2017), rather than as a response to habitat change (which has long dominated bird conservation narratives). While climatic warming appears to have an impact on many certain species' distributional shifts, the effect has been inconsistent across taxa (Martins et al., 2024). Still, patterns may be detected at the local level; Craig et al. (2022) reported the "five most strongly declining species" between 1985 and 2018/2019 in Connecticut survey sites were "northerly distributed", suggesting a retreat toward cooler climes.

Despite a long and productive publication record on forest ecology, information on the avifauna (and vertebrates in general) from Harvard Forest is lacking. During the summer of 1993, while in the Research Experience for Undergraduates (REU) program, I conducted the first systematic baseline breeding bird survey at Harvard Forest in north-central Massachusetts. Since the initial effort, I returned to Harvard Forest as a Visiting Researcher three more times to repeat the survey, in 2011, 2013 and 2016. My dataset may be compared directly with two historical, unpublished annotated lists of birds observed at the Harvard Forest and vicinity dating to the 1940s (described below). More recent data from the Massachusetts Breeding Bird Atlas project (Massachusetts Audubon Society (MAS), 2008) and the Breeding Bird Survey (Sauer et al., 2020), plus community science data such as that uploaded to online platforms such as eBird (www.ebird.org), can all be used to augment findings from Harvard Forest over the past 80 years.

Specifically, my study asks:

- Has overall avian species diversity at Harvard Forest increased or decreased over time?
- What bird species have been gained/lost over the past decades, and why?
- Are these trends similar to those found at comparable forest sites in the region, and are they reflective of regional trends?

Insight from this work may be compared with data from more established local bird-monitoring sites, as well as community-science (observational) data to inform ongoing and future habitat manipulation to benefit birds and avian diversity at Harvard Forest and elsewhere in the region.

Methods

Study area

The Prospect Hill Tract of the Harvard Forest lies within the Quabbin Reservoir Watershed (Massachusetts Department of Conservation and Recreation, 2007), covering 364 hectares/900 acres in Worcester County, north-central Massachusetts, US (Figure 1). Established in 1907, Harvard Forest supports a mix deciduous and coniferous woods, including oak-maple forest, conifer plantations, and natural spruce and hemlock bogs, with a variety of small, scattered wetlands (Jenkins et al., 2008). It is nearly encircled by disused dirt logging roads, and crisscrossed with footpaths and old stone walls, a reminder of its history as a complex of farms, pastures and woodlots. Since the early 1800s, when most of the land was cleared, these areas have grown back to contiguous woodland. While most of the land is forested, wetlands provide limited open habitat, as does an area of c. 8.5 ha/21 acres maintained as pasture lawn, or ornamental landscaping around the Forest headquarters, and several experimental clearings where trees have been selectively removed as part of forest manipulation experiments since the 1990s. It is now a combined LTER/NEON site (Parizek, 2018); the "Long-term Ecological Research" (LTER) program was launched in 1980 by the National Science Foundation to support long-term research projects in Ecology, and now boasts 28 sites, mainly in North America, including four in the northeastern U.S (LTER Network, 2022). NSF introduced the related "National Ecological Observation Network" (NEON) program in 2011, which now has 81 sites across the U.S (SanClements et al., 2020).

Major landuse changes at Harvard Forest include the Hurricane of 1938, which resulted in widespread tree blow-down throughout New England (Spurr, 1956), including at Harvard Forest. In the decades since the hurricane, plantations of non-native conifers, mainly red pine (*Pinus resinosa*), were established, such that by the early 2000s, 125 acres/50 ha of plantations remained. By the time of my 1993 survey, red pine was a dominant tree on the Prospect Hill Tract, recorded on 13 of 67 (19.4%) survey points sampled, and the 4th-ranked tree by biomass (as measured by trunk diameter), after red maple (*Acer rubrum*), "snag" (various dead trees), and red oak (*Quercus rubra*). In 2008, Harvard Forest released a plan to begin harvesting (selectively logging) 80 acres/32 ha of the remaining 125 acres of pine plantation, which was accomplished between 2008-2010 (O'Keefe et al., 2008). This resulted in the appearance of three discrete brushy clearings (of 1, 3 and 6 ha) just prior to my 2011 resurvey, which were being used as study plots by researchers. These logged areas regenerated quickly, with most supporting young forest at various stages of regrowth by the 2016 survey; six survey points were within 100 meters of these clearings, so their impact may have been detected on the post-2008 bird surveys. Vegetation surveys were not repeated in subsequent bird surveys due to time limitations.

Historical bird data from Harvard Forest

Contemporary surveys may be compared with a unique data source, a 1948 annotated checklist (unavailable online or published) by Earl E. Smith of birds observed by the author and his wife (Rhea Smith) from 12 June to 30 Nov. 1948[1]. Smith used a larger study area than mine, taking in several large ponds and swamps outside the Prospect Hill Tract. A second historical dataset was produced by Hopkins and Hopkins[2], another couple who recorded birds on the forest from Oct. 1, 1968 to Aug. 2, 1969. However, as they explain in their manuscript, they arrived unfamiliar with North American birds, having spent the prior 13 years in Africa. Still, their observations of certain (easily-identified) species serve some use for comparison.

Smith's observations from Harvard Forest in 1948 were from a landscape that had been decimated by a major hurricane just ten years prior. His account of Chestnut-sided Warbler (*Setophaga pensylvanica*) is illustrative of this. Terming it "the most common warbler of the Forest", Smith noted "the large areas of brush which cover the blow-down of the hurricane make an ideal habitat for this species." Chestnut-sided Warblers were still present and likely breeding during my surveys, but were detected at fewer than 15% of survey points each survey year (1993-2016), and outnumbered in detection frequency by *eight* other wood-warbler species during the same period. Similarly, Wood Thrush (*Hylocichla mustelina*) was noted by Smith as being a "summer resident of the forest" with "the three thrushes, hermit, wood and veery, during June and the first part of July would join in an evening chorus of pure melody." By 1993, Wood Thrush was recorded only around the Forest headquarters, in 2011 it was found just incidentally, and it was missed altogether in 2016. These qualitative observations are crucial in understanding the nuance of community change beyond numerical counts.

Contemporary bird and plant surveys

In 1993, I established and surveyed 82 fixed-radius points spread across the entire Prospect Hill tract, selected to cover as much accessible area of the forest as possible, using rock wall and trail intersections as markers. Points were situated 100–350 meters apart, and visited three times at least a week apart between 5:00 and 9:30 am from 8 June to 9 July. Counts lasted 10 minutes each, and birds heard or seen were only counted once (to the extent possible), and classified as being in "Zone A" (<50 meters of the observer) or "Zone B" (50–100 meters away from the observer). Birds detected >100 meters away, those flying over, and those encountered between points that were not recorded on survey points were recorded in incidental notes for each survey (due to the dense structure of the forest, far more birds were heard than seen while

1 Smith, E.E. 1948. Preliminary list of birds of the Harvard Forest. Earl E. Smith, Harvard Forest, Nov. 30, 1948.

2 Hopkins, B. and J. Hopkins. 1970. Some notes on the birds of Harvard Forest. January 1970. Unpublished report.

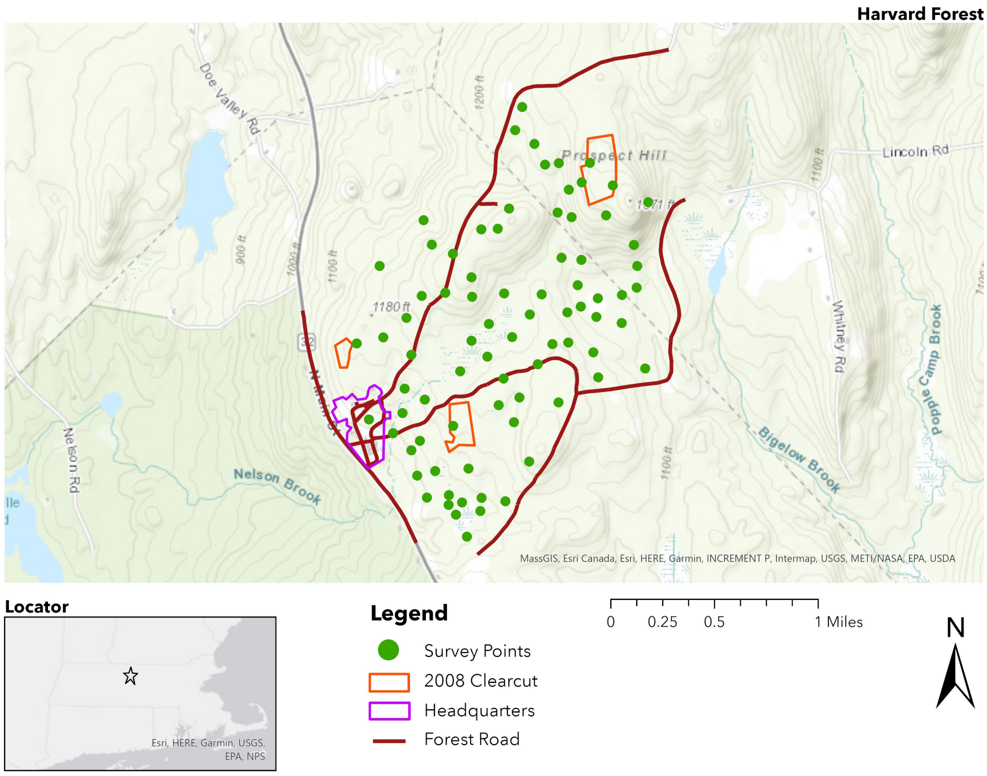

FIGURE 1
Location of survey points within the Prospect Hill Tract of Harvard Forest used 1993-2016. Not all points were used every year (depending on local conditions), and some were dropped or added (see text).

conducting point counts). All data was single-observer (Cooper), and because most avian detections were aural, and I felt confident in my identification abilities, I did not calculate visual vs. non-visual detections separately, but pooled all observations from all points (within Zone A) for this analysis.

This survey was repeated three more times, in 2011, 2013 and 2016, following the same protocol as faithfully as was feasible, but with only June visits in these years. Due to time constraints, surveys only employed 2 visits in 2011 (76 points) and 2013 (76 points), and single visits to each of 70 points in 2016. Unless noted, I dropped counts made in July (only done in 1993) because only June counts were conducted in subsequent years, and many bird species truncate their singing by mid-summer, focusing instead on raising young. I include notes on single-visit point count surveys of the adjacent former Petersham Country Club (Motzkin, 2014) from 2016 to inform my analysis of species turnover.

In 1993, I conducted vegetation surveys at 67 points. A 0.1-acre circle was established at each point using two 22-meter ropes crossed at the center/survey point. Within this circle, I recorded the diameter at standard height (DSH) of every tree with DSH of more than 4 cm (other measurements were taken, such as canopy cover, but those data have been lost and are not included in this analysis). A total of 5,174 trees and large shrubs were measured on the vegetation surveys, comprising 37 species (an additional three "species" cannot be identified and may have been mis-spellings; the full names are unknown).

Species richness and community composition

Though no single standard exists for calculating change in bird species diversity of a site over time, several comparative efforts involving repeated summer bird surveys of managed forests spanning more than one decade (e.g., Holmes and Sherry, 2001; Curtis and Robinson, 2015; Craig et al., 2022). For comparing species diversity over time, I used the R package "vegan" (v. 2.6-8) to compare overall species diversity across years (n=4 years) using the Shannon-Weaver index, which tends to be more sensitive to the gain and loss of rare species, and thus may pick up differences influenced by newly-colonizing and nearly-extirpated taxa. I calculated detection frequency for each survey year, based on the percentage of points surveyed that year where each species was recorded, expressed as a value from 0-1. This approach did not factor in a species' abundance at each point, due to the variation in number of visits per point each year (n = 1–3 visits/point), and the brevity of each visit.

Species trends over time

I analyzed individual species trends over time in two main ways. Qualitatively, I compared historical accounts from the area (notes from E. E. Smith, 1948 and those of Hopkins and Hopkins, 1970) with detection frequency and incidental observations from the 1993–2016 surveys (including my own observational data from the Petersham Country Club). I also compared these results to community science data from the Massachusetts BBA (which includes regional trends from BBS data over the past c. 60 years) and eBird records.

To quantify change in relative abundance over time, I identified a group of the most frequently-recorded species as those detected on a minimum of 10% of the survey points (n = 7 points per year) in at least one year to analyze. I used linear regression to compare slopes of detection frequency across the four years of the survey, and compared these findings to those from comparable study sites in the region. Bird species nomenclature follows Chesser et al. (2024).

Results

The four seasons of contemporary point counts (1993, 2011, 2013 and 2016) yielded 5,712 records of 84 bird species, and an c. 10 additional species were observed incidentally (see Supplemental Data). Restricting the point count data to only those species detected within 50 m of the survey point ("Zone A") and dropping July counts yielded c. 2,924 records of 72 species, which comprise the dataset used for analysis here. A total of 94 species have been recorded on eBird checklists from the "Harvard Forest" Hotspot based on 54 submitted checklists as of 2 Sept. 2024[3]. The five most frequently-encountered birds on the Harvard Forest point counts (1993-2016) were: Ovenbird (*Seiurus aurocapilla*) (detected at a mean of 87.8% of survey points per year), Red-eyed Vireo (*Vireo olivaceus*) (59.9%), Pine Warbler (*Setophaga pinus*) (34.9%), Black-capped Chickadee (*Poecile atricapillus*) (30.0%) and Scarlet Tanager (*Piranga olivacea*) (29.3%). Two additional species made the top 10 most common species in each of the four survey years: Black-throated Blue Warbler (*Setophaga caerulescens*) (29.2%) and Black-throated Green Warbler (*Setophaga virens*) (26.6%). An additional 30 species were recorded on surveys in all four years, which comprise the "core breeding songbird community" at Harvard Forest (see Supplementary Table S1 in Supplementary Material for complete list).

Species turnover since 1948

As summarized in Table 1, Harvard Forest has seen 18 species colonize as breeders since 1948; during the same period, nearly as many have declined or become extirpated here (n=16) (see also Supplementary Table S1). Overall species turnover at Harvard Forest between survey years (as measured by Craig et al., 2022) was fairly high (mean = 0.315; 17–23 species gained or lost of a total of 55–69 present in the species pool each of the four survey years), and this value has varied little since 1993 (range: 0.302-0.333). Based on species representation on the survey points (presence/absence), overall species diversity has been stable across the study area since 1993, with Shannon-Weaver indices similar from year to year (range: 3.243 – 3.509). This stability is reflected in phylogenetic groups, in that a similar number of representatives have colonized vs. declined for several groups, including Galliformes (i.e., Wild Turkey *Meleagris gallopavo* colonized, Ruffed Grouse *Bonasa umbellus* declined), Accipitrids, Corvids and Parulids (Table 1). Other groups were off by just one or two species in this phylogenetic replacement (e.g., two Picids colonized, one declined).

The relationship of habitat preference, geographic position within range, and migratory status of species increasing or declining resists generalization, as counter-examples abound. However, some patterns since 1948 include the preponderance of species at their northern range limit in southern New England among the colonizing species (n=6), vs. those facing declines or extirpation here (n=1, Eastern Towhee *Pipilo erythrophthalmus*). Species at their southern range limit were represented in both the colonizing/increasing and the declining/extirpated species (Table 1).

More migratory species at Harvard Forest appear to have declined than colonized since 1948 (12 vs. 7, long-distance and short-distance migrants combined; Table 1). Looking at habitat association, more colonizing species at Harvard Forest favor forest interior (n=9) than declining/extirpated ones (n=2), and nearly all declining/extirpated species are associated with edge/early-successional habitats, or are considered habitat generalists (Table 1). However, looking at point count data since 1993, forest-interior species show both positive and negative trends, and those associated with early-successional habitat appear to have generally increased in this latter timeframe, with just two (Common Yellowthroat *Geothlypis trichas* and Song Sparrow *Melospiza melodia*) having declined (Table 2).

Comparing Harvard Forest data with regional patterns, most breeding bird species to have colonized Harvard Forest since 1948 were also found to be increasing statewide, as measured both by range expansion (i.e., change in Atlas blocks since the 1970s) as well as in numerical abundance, as shown by BBS data (both summarized in species accounts in BBA2[4]) (Table 1). They include taxa expanding into central Massachusetts from various directions, and associated a variety of habitat types, defying easy generalization (e.g., Wild Turkey, Red-bellied Woodpecker *Melanerpes carolinus*, Brown Creeper *Certhia americana*, and Northern Cardinal *Cardinalis cardinalis*). Some of these trends have been watched for decades (Veit and Petersen, 1993), while others, such as the (re-)invasion of Red-bellied Woodpeckers in the region, are much more recent (mid-1990s on).

Colonizing species show a mean 46.2% increase in occupied atlas blocks since the 1970s, and none showed a loss in the number of blocks occupied between the 1970s and the 2000s. Conversely,

3 See https://ebird.org/hotspot/L1239372; note that the Hotspot location shown in eBird (as of Sept. 2024) is pinned several km to the south of the Harvard Forest headquarters and Fisher Museum, which has probably reduced the number of checklists submitted from the Forest due to confusion over its location.

4 Species accounts published online: https://www.massaudubon.org/our-work/birds-wildlife/bird-conservation-research/breeding-bird-atlases/find-a-bird.

TABLE 1 Species turnover at Harvard Forest since 1948 (see Supplementary Table S1, and Supplemental Material for complete notes).

	BBA	BBS	Range/Migratory Status	Habitat
COLONIZED SINCE 1948				
Wild Turkey (*Meleagris gallopavo*)	97.9	+	Core/Resident	Edge/successional
Red-shouldered Hawk (*Buteo lineatus*)	29.2	+	Northern limit/Resident	Forest interior (Generalist)
Ruby-thr Hummingbird (*Archilochus colubris*)	41.7	+	Core/LDM	Generalist
Common Raven (*Corvus corax*)	70.8	+	Southern limit/Resident	Generalist
Tufted Titmouse (*Baeolophus bicolor*)	60.4	+	Northern limit/Resident	Generalist
Red-breasted Nuthatch (*Sitta canadensis*)	33.3	+	Southern limit/Resident	Forest interior
White-br. Nuthatch (*Sitta carolinensis*)	16.7	+	Core/Resident	Forest interior
Brown Creeper (*Certhia americana*)	33.3	+	Southern limit/Resident	Forest interior
Golden-cr. Kinglet (*Regulus satrapa*)	10.4	+	(Southern limit)/Resident	(Forest interior)
House Finch (*Carpodacus mexicanus*)	52.1	+	(Northern limit)/Resident	(Generalist)
No. Waterthrush (*Parkesia noveboracensis*)	29.2	+	Southern limit/LDM	Forest interior
Pine Warbler (*Setophaga pinus*)	81.3	+	Core/SDM	Forest interior
Northern Cardinal (*Cardinalis cardinalis*)	56.3	+	Northern limit/Resident	Edge/successional
Indigo Bunting (*Passerina cyanea*)	12.5	n/a	(Core)/LDM	(Edge/successional)
COLONIZED SINCE 1993				
Yellow-b. Sapsucker (*Sphyrapicus varius*)	66.7	+	Southern limit/SDM	Generalist (Forest interior)
Red-b. Woodpecker (*Melanerpes carolinus*)	66.7	+	Northern limit/Resident	Forest interior (Generalist)
Great Crested Flycatcher (*Myiarchus crinitus*)	37.5	n/a	Core/LDM	Generalist
Prairie Warbler (*Setophaga discolor*)	35.4	–	(Northern limit)/LDM	(Edge/successional)
DECLINED SINCE 1948				
Ruffed Grouse (*Bonasa umbellus*)	39.6	–	Southern limit/Resident	Edge/successional
Red-tailed Hawk (*Buteo jamaicensis*)	31.3	+	Core/Resident	Edge/successional
E. Whip-poor-will (*Caprimulgus vociferus*)	4.2	–	Core/LDM	Edge/successional
Northern Flicker (*Colaptes auratus*)	6.3	–	Core/SDM	Edge/successional
Olive-s. Flycatcher (*Contopus cooperi*)	-2.1	–	(Southern limit)/LDM	(Edge/successional)
Least Flycatcher (*Empidonax minimus*)	6.3	–	Southern limit/LDM	Edge/successional
American Crow (*Corvus brachyrhynchos*)	12.5	+	(Core)/Resident	(Generalist)
Gray Catbird (*Dumetella carolinensis*)	0	+	Core/SDM	Edge/successional
Wood Thrush (*Hylocichla mustelina*)	-4.2	–	Core/LDM	Forest interior (Edge/successional)
American Robin (*Turdus migratorius*)	2.1	–	Core/SDM	Edge/successional
Purple Finch (*Carpodacus purpureus*)	8.3	–	Southern limit/Resident	Edge/successional
Eastern Towhee (*Pipilo erythrophthalmus*)	0	–	Northern limit/SDM	Edge/Successional
American Redstart (*Setophaga ruticilla*)	-10.5	n/a	Core/LDM	Edge/successional
Magnolia Warbler (*Setophaga magnolia*)	4.2	+	Southern limit/LDM	Generalist (Forest interior)
Chestnut-s, Warbler (*Setophaga pensylvanica*)	2.1	–	Southern limit/LDM	Edge/Successional
Rose-br. Grosbeak (*Pheucticus ludovicianus*)	18.8	–	Core/LDM	Edge/successional

Abbreviations include “BBA” [Massachusetts Breeding Bird Atlas, indicating % change between 1974 and 2011 (MAS 2008)], “BBS” (Breeding Bird Survey Results, also available in Massachusetts Audubon Society (MAS), 2008), “LDM” (long-distance migrant) and “SDM” (short-distance migrant).

TABLE 2 Detection frequency and regression slope of the most widespread species (>10% of points per year) detected on Harvard Forest point counts (Zone A, June only, 1993-2016; % of points where detected, per survey year, visits pooled).

Species	1993	2011	2013	2016	Slope (SE)	HWF	HB	YMF	Ecological notes
Pine Warbler	12.2	44.7	50	32.9	0.802 (0.393)	n/a	n/a	Increasing	I, SDM
Red-eyed Vireo	45.1	61.8	71.1	61.4	0.552 (0.210)	0.000	-0.010*	Increasing	I, LDM
Ovenbird	78	85.5	94.7	92.9	0.401 (0.133)	-0.021***	0.013*	Increasing	I, LDM
Yellow-bellied Sapsucker	0	13.2	7.9	14.3	0.345 (0.111)	-0.028**	-0.028	Increasing	G, SDM
Scarlet Tanager	22	32.9	38.2	24.3	0.234 (0.262)	-0.023***	-0.023**	Increasing	I, LDM
Blackburnian Warbler	19.5	23.7	21.1	28.6	0.166 (0.113)	-0.002	-0.056**	Decreasing	I, LDM
Hairy Woodpecker	1.2	10.5	7.9	4.3	0.152 (0.129)	0.033**	-0.014	Decreasing	G, R
Chestnut-sided Warbler	8.5	9.2	14.5	12.9	0.119 (0.082)	-0.192***	n/a	Increasing	ES, LDM
Cedar Waxwing	3.7	10.5	9.2	4.3	0.094 (0.126)	n/a	n/a	Decreasing	ES, SDM
Gray Catbird	4.9	3.9	11.8	5.7	0.069 (0.139)	n/a	n/a	Increasing	ES, SDM
Black-thr. Blue Warbler	25.6	35.5	34.2	21.4	0.067 (0.275)	-0.005	0.002	Increasing	I, LDM
Eastern Towhee	4.9	2.6	7.9	7.1	0.048 (0.092)	n/a	n/a	Increasing	ES, R
Veery	17.1	2.6	17.1	24.3	0.031 (0.373)	n/a	0.009	Increasing	I, LDM
Blue Jay	12.2	22.4	7.9	12.9	0.024 (0.250)	-0.011	n/a	No trend	G, R
Brown Creeper	19.5	18.4	18.4	20	-0.008 (0.032)	0.102***	0.013	Decreasing	I, R
Hermit Thrush	13.4	9.2	25	5.7	-0.030 (0.344)	-0.006	-0.017	Decreasing	I, SDM
Common Yellowthroat	15.9	18.4	14.5	11.4	-0.063 (0.111)	n/a	n/a	Increasing	ES, SDM
Downy Woodpecker	7.3	2.6	11.8	1.4	-0.069 (0.190)	n/a	-0.055***	No trend	G, R
Tufted Titmouse	7.3	3.9	7.9	2.9	-0.077 (0.086)	n/a	n/a	Increasing	G, R
White-br. Nuthatch	7.3	11.8	9.2	0	-0.066 (0.204)	-0.008	-0.023*	No trend	I, R
Black-thr. Green Warbler	29.3	28.9	21.1	27.1	-0.105 (0.138)	-0.001	-0.023***	Decreasing	I, LDM
Northern Waterthrush	7.3	1.3	1.3	5.7	-0.107 (0.101)	n/a	n/a	No trend	I, LDM
Song Sparrow	7.3	3.9	3.9	2.9	-0.112 (0.009)	n/a	n/a	Increasing	ES, R
Canada Warbler	13.4	6.6	6.6	8.6	-0.166 (0.062)	-0.077***	n/a	Increasing	I, LDM
Winter Wren	13.4	5.3	11.8	5.7	-0.167 (0.124)	0.008	-0.012	No trend	I, R
Eastern Wood-pewee	25.6	18.4	21.1	18.6	-0.179 (0.054)	-0.082***	n/a	Increasing	I, LDM
Yellow-rumped Warbler	29.3	14.5	26.3	15.7	-0.299 (0.222)	0.033**	0.039**	Decreasing	I, SDM
Red-br. Nuthatch	24.4	13.2	17.1	14.3	-0.269 (0.084)	0.029*	n/a	Decreasing	I, R
Black-capped Chickadee	41.5	35.5	32.9	10	-0.562 (0.404)	-0.002	n/a	Decreasing	G, R
Black-and-white Warbler	37.8	7.9	19.7	17.1	-0.613 (0.277)	-0.042*	n/a	No trend	G, LDM
Blue-headed Vireo	39	11.8	28.9	7.1	-0.691 (0.367)	0.048***	-0.002	Decreasing	I, SDM

Abbreviations include “HWF” [Huntington Wildlife Forest Natural Area, Newcomb, NY (regression slopes from point count surveys 1954-63 and 1990-2000; see McNulty et al. 2008)], “HB” [Hubbard-Brook Experimental Forest, NH (regression slopes from area search survey 1969-1998; Holmes and Sherry, 2001)] and “YMF” [Yale-Myers Forest, Tolland and Windham counties, CT (trends from transect surveys in 1985, 2018 and 2019; Craig et al. 2022)].

Species order follows slope values (at Harvard Forest) from positive to negative. Please refer to Supplementary Table S1 for Latin names. Abbreviations include “I” (forest interior), “G” (generalist), ES (edge/successional habitat), and “R” (resident).

*$P < 0.05$ **$P < 0.01$ ***$P < 0.0$ (from McNulty et al., 2008).

species that have been extirpated from Harvard Forest, or with apparent declines since 1948, show a much lower mean of increase in occupied blocks (7.4%), with many seeing a negative change in occupied blocks since the 1970s (and several with negative statewide population trends).

Comparisons with other sites

In comparison with other New England sites with long-term bird data, the core breeding bird community at Harvard Forest closely matches that reported from Yale-Myers Forest

(Goodale et al., 2009). Many of the population trends over time reported from Yale-Myers also match those of Harvard Forest, with similar species increasing (Yellow-bellied Sapsucker, Red-eyed Vireo, Ovenbird, Pine Warbler, and Scarlet Tanager) and decreasing (Blue-headed Vireo, Red-breasted Nuthatch, Black-capped Chickadee, Yellow-rumped Warbler).

By contrast, while both Hubbard-Brook Experimental Forest in New Hampshire and Huntington Wildlife Forest in New York shared some of the common breeding species with Harvard Forest, the trends of all three sites rarely matched (Table 2). It is possible that because both Hubbard-Brook and HWF reported their last surveys from 1998 and 2000, respectively, more contemporary trends may be different. Indeed, Holmes and Sherry (2001) noted that several of the most numerous species at Hubbard-Brook from 1969–1998 experienced significant negative population change through the 1990s, including Least Flycatcher and American Redstart (see also Holmes, 2007), leaving Ovenbird and Red-eyed Vireo as the most abundant breeding birds over multiple recent decades here (both Least Flycatcher and American Redstart are fairly rare at Harvard Forest today).

Discussion

The finding that overall species diversity (if not species makeup) has remained fairly constant at Harvard Forest since the mid-1900s, with a similar number of colonized vs. extirpated breeders (18 vs. 16), conforms to findings of Craig et al. (2022) in nearby northeastern Connecticut. The low annual rate of species turnover found at Harvard Forest – below that reported by Craig et al. (2022) for the Yale-Myers Forest – suggests even more stability over time here. Predicted northward expansion of southerly species due to climate change (see Walsh and Servison, 2017) appears to be underway, with more species near the northern edge of their range colonizing, rather than declining (of those where either pattern was noted). The suggestion that migratory species would be particularly vulnerable to extirpation (Holmes, 2007; McNulty et al., 2008), is supported by the finding that of the migratory species that have *either* colonized or declined at Harvard Forest, many more have declined or have become extirpated altogether.

The finding that more *colonizing* species at Harvard Forest since 1948 favor forest interior (n=9) than declining/extirpated ones (n=2), and nearly all of the latter group are associated with edge/early-successional habitats or are considered habitat generalists, is supported by research from other New England sites where forest interior species increased in the latter part of the 20th Century (e.g., Holmes and Sherry, 2001). However, habitat-associated trends at Harvard Forest since 1993 appear to be much more mixed, with forest-interior species showing both positive and negative trends. Several of the species with the most pronounced recent declines at Harvard Forest (Table 2) are conifer-dwelling species (e.g., Blue-headed Vireo *solitarius* and Yellow-rumped Warbler *Setophaga coronata*) that may be responding to more recent local loss/succession of conifer plantations to hardwoods, and possibly the death of eastern hemlocks due to wooly adelgid invasion (see Tingley et al., 2002). Since 1993, several species with positive trends are associated with edge/successional habitat (Table 2); however, the two declining (since 1993) species associated with these early-successional habitats, Common Yellowthroat and Song Sparrow, are both strongly associated with water and emergent wetland vegetation. Thus, it is possible that neither benefitted from the experimentally logged plots as much as upland species like Gray Catbird and Eastern Towhee.

Those species that appear to have declined at the Harvard Forest and that *also* show statewide negative (or non-positive) population trends could be candidates for continued monitoring, and as targets for future habitat management. These include Ruffed Grouse, Eastern Whip-poor-will (*Caprimulgus vociferans*), Northern Flicker (*Colaptes auratus*), Olive-sided Flycatcher (*Contopus cooperi*), Least Flycatcher (*Empidonax minimus*), Wood Thrush (*Hylocichla mustelina*), American Robin (*Turdus migratorius*), American Redstart (*Setophaga ruticilla*), Chestnut-sided Warbler (*Setophaga pensylvanica*), Eastern Towhee, Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Purple Finch (*Haemorhous purpureus*). While most of these species are still persisting in the vicinity of Harvard Forest, they tend to be restricted to early-successional habitat such as old field vegetation and the forest-clearing ecotone (including at the former Petersham County Club, Cooper, unpubl. data). However, both Eastern Whip-poor-will and Olive-sided Flycatcher, appear to be essentially extirpated as breeders from the larger Petersham area (various sources), and the former is considered a sensitive species at the state level[5]. Of the Ruffed Grouse, Smith wrote: "Many of these fine birds are present on the Forest and rarely is a trip in the field concluded without seeing or hearing several. Three broods were flushed in the summer consisting of 5 to 10 young." This decline of grouse may be fairly recent; in 1993, I noted that this species was seen "throughout", with an active nest (with eggs) on 5 June. However, by 2011, only a single bird was encountered, and it went unrecorded in 2013 and 2016 (eBird and iNaturalist only show a handful of records from the Petersham area). While not explicitly surveyed-for, the Eastern Whip-poor-will seems to have declined even earlier. It was recorded by Smith in 1948 as being "heard throughout the summer", yet none was heard during my surveys, despite spending several weeks each year staying in the same area of the Forest headquarters and taking regular dusk walks and being out pre-dawn for the point count surveys.

Of particular interest are those species with mixed trends across sites in New England, as local studies can elucidate subtle trends not detected on statewide or regional monitoring programs. From a management perspective, these may also be those species most responsive to changes in forest management, such as species that may move into experimentally logged tracts, or which may be persisting in unusual habitats such as red pine plantations surrounded by extensive hardwood forest. Examples of species showing increases at Harvard Forest over time, yet declines or

5 https://www.mass.gov/info-details/list-of-endangered-threatened-and-special-concern-species#birds.

static trends statewide, include Great Crested Flycatcher (*Myiarchus crinitus*), Indigo Bunting (*Passerina cyanea*) and Prairie Warbler (*Setophaga discolor*), all of which have increased at the Forest in the past decades, likely aided by local experimental habitat manipulation. See Supplementary Table S2 for notes on regional trends.

Of course, with such different methodologies employed (transects vs. point counts vs. territory mapping), it may not be possible to generalize and extract numeric trends from one study and expect it to match the other. Analysis of different datasets can also present significant analytical challenges within the same study; for Harvard Forest data, the different numbers of points visited in different years, the low number of years (n = 4), and the different number of visits per year (1, 2 or 3), limit the interpretation of actual abundance and trends. As with any such study, a trade-off exists between dropping points and visits to increase standardization and avoid bias (e.g., if a particular microhabitat type was better represented one year vs. others), or retaining them to increase the amount of available data to interpret, and to capture rare species that might be particularly data-rich (e.g., a bird associated with an age-class of clearing that might be nearing extirpation as the forest grows in and matures).

It is also possible that more species have increased at Harvard Forest, but the brief descriptions (i.e., without numerical counts) from the pre-1993 period (e.g., "summer resident in forest") make this determination is difficult. "Observer perception" can influence impressions of abundance, and may have influenced the Smith (1948) dataset; for example, any guest at Harvard Forest staying at the headquarters will hear American Robins singing continuously from well before dawn to sunset; yet away from developed areas, robins are rare in the forest interior and the natural wetlands, as seen in the point count data. So, while they may (still) seem like a "common resident of the forest", determining exactly where they were common, and how numerically common they were, is not possible from the data. Of note, Smith's references to "the Forest" included large expanses of wooded swamp habitat (e.g., Tom Swamp), as well as large clearings and other habitats and other open habitats lacking on the Prospect Hill Tract. And, a relatively large number of species were recorded (this study) in very small numbers in each year, in some cases with only a single pair or two likely present around the main headquarters, which (now) provides the largest open habitat approximating the early pasture habitat in the area (horse-grazed through summer) (Supplementary Table S1).

Finally, some increases and colonizations may be unreliable as trends in cases where the number of territorial birds continues to be small, such as with Alder Flycatcher (*Empidonax alnorum*), found on territory in 2011 and 2013, but on only two points located at a unique swamp habitat; or Nashville Warbler (*Leiothlypis ruficapilla*) and Northern Parula (*Setophaga americana*), recorded as territorial singletons in 1993 and 2016, respectively, but seemingly not fully colonized as breeders. Still, while colonizations are usually fairly straightforward – either the species was listed by earlier authors, or detected on point counts, or not – declines and even extirpations are less clear-cut, since a rare species may be persisting, and may even be common, in areas not visited on modern surveys (particularly given that the "study area" in 1948 extended well beyond the boundaries of the Prospect Hill tract used as the 1993–2016 study area). This is particularly true for species found in secondary growth and open areas, given how the forest has matured in and around the study area in the seven decades since the 1948 accounts of Smith.

From a management perspective, replicating these open habitats could be a way to encourage historically-present species to return, or to augment their populations (assuming this is a goal). The experimental forest clearings established since the initial 1993 survey may have led to the "bounce-back" of species like Least Flycatcher and Chestnut-sided Warbler, as well as the arrival of species like Prairie Warbler and Indigo Bunting which were not found as breeders historically. Assuming these interventions do not remove sensitive/rare habitats (particularly if they remove non-native plantations), they could be expanded as a management tool to create a more complex mosaic of habitats of different age classes. Habitat data was not a major component of this study, and I hope this publication may raise awareness of these important data sets for future analysis.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this study was based on passive (listening) surveys of birds in a forest; no close contact with animals was involved.

Author contributions

DC: Writing – original draft, Writing – review & editing.

Funding

The author(s) declare that no financial support was received for the research and/or publication of this article.

Acknowledgments

I thank the NSF REU program for the opportunity to conduct original research as an undergraduate in 1993, under the direction of Richard Lent. The entire staff of Harvard Forest was welcoming and supportive throughout the internship, and I particularly wish to thank David Foster for his encouragement both during the internship and on my return visits. Laurie Chiasson and Audrey Barker Plotkin helpfully facilitated my resurveys, as did Oscar Lacwasan who immediately recognized me when I appeared taking predawn coffee 18 years later. I thank Çağan Şekercioğlu and Monte Neate-Clegg for encouraging me to finally write this up, Mark Ashton and Robert Craig for advising me on current information and data, and Isabella Isles for assistance in producing the map.

Conflict of interest

The authors declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1511265/full#supplementary-material

References

Barker Plotkin, A., Orwig, D. A., MacLean, M. G., and Ellison, A. M. (2024). Logging response alters trajectories of reorganization after loss of foundational tree species. *Ecol. Appl.* 34. doi: 10.1002/eap.2957

Chesser, R. T., Billerman, S. M., Burns, K. J., Cicero, C., Dunn, J. L., Hernández-Baños, B. E., et al. (2024). Check-list of North American Birds. Available online at: https://checklist.americanornithology.org/taxa/ (Accessed September 25, 2024).

Collins, S. (2001). Long-term research and the dynamics of bird populations and communities. *Auk* 118, 583–588. doi: 10.1093/auk/118.3.583

Cooper, D. S. (2008). The use of historical data in the restoration of the avifauna of the Ballona Wetlands, Los Angeles County, California. *Nat. Areas J.* 28, 83–90. doi: 10.3375/0885-8608(2008)28[83:TUOHDI]2.0.CO;2

Craig, R. J. (2017). "Forest birds of Connecticut and Rhode Island," in *Bird Conservation Research* Contribution 23 (Pomfret, CT: Arts and Academic Publishing).

Craig, R. J. (2023). Temporal change in the forest birds of northeastern Connecticut shows partial concordance with predicted effects of climate and habitat change. *Wilson J. Ornith* 135, 467–479. doi: 10.1676/22-00043

Craig, R. J., Duguid, M. C., and Ashton, M. S. (2022). Breeding forest birds in northeastern Connecticut show a long-term population increase and high species turnover. *Wilson J. Ornith* 134, 27–42. doi: 10.1676/20-00129

Curtis, J. R., and Robinson, W. D. (2015). Sixty years of change in avian communities of the Pacific Northwest. e1152. doi: 10.7717/peerj.1152

DeGraaf, R. M., Hestbeck, J. B., and Yamasaki, M. (1998). Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. *For. Ecol. Man.* 103, 217–233. doi: 10.1016/S0378-1127(97)00213-2

DeLuca, W. V., and King, D. I. (2017). Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. *J. Ornith.* 158, 493–505. doi: 10.1007/s10336-016-1414-7

Foster, D. R., Motzkin, G., and Slater, B. (1998). Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* 1, 96–119. doi: 10.1007/s100219900008

Goetz, S. J., Sun, M., Zolkos, S., Hansen, A., and Dubayah, R. (2014). The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness. *Env. Res. Lett.* 9. doi: 10.1088/1748-9326/9/3/034013

Goodale, E., Lalbhai, P., Goodale, U. M., and Ashton, P. M. S. (2009). The relationship between shelterwood cuts and crown thinning and the abundance and distribution of birds in a southern New England Forest. *For. Ecol. Man.* 258, 314–322. doi: 10.1016/j.foreco.2009.04.020

Hanle, J., Duguid, M. C., and Ashton, M. C. (2020). Legacy forest structure increases bird diversity and abundance in aging young forests. *Ecol. Evol.* 10, 1193–1208. doi: 10.1002/ece3.5967

Hitch, A. T., and Leberg, P. L. (2007). Breeding distributions of North American birds moving north as a result of climate change. *Cons. Biol.* 21, 534–540. doi: 10.1111/j.1523-1739.2006.00609.x

Holmes, R. T. (2007). Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis* 149, 2–13. doi: 10.1111/j.1474-919X.2007.00685.x

Holmes, R. T., and Sherry, T. W. (1988). Assessing population trends of New Hampshire forest birds: local vs. *Regional Patterns Auk* 105, 756–768.

Holmes, R. T., and Sherry, T. W. (2001). Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk* 118, 589–609. doi: 10.1093/auk/118.3.589

James, F. C., McCulloch, C. E., and Wiedenfeld, D. A. (1996). New Approaches to the Analysis of Population Trends in Land Birds. *Ecology* 77, 13–27. doi: 10.2307/2265650

Jenkins, J. C., Motzkin, G., and Ward, K. (2008). The Harvard Forest Flora. *Invent. Anal. Ecol. Hist. Harvard For. Paper* 28, 266.

Knapp, A. K., Smith, M. D., Hobbie, S. E., Collins, S. L., Fahey, T. J., Hansen, G. J. A., et al. (2012). Past, present and future roles of long-term experiments in the LTER network. *BioScience* 62, 377–389. doi: 10.1525/bio.2012.62.4.9

LTER Network (2022).Decadal Review Report, National Science Foundation Long Term Ecological Research. Available online at: https://lternet.edu/documents/decadal-review-report-2022/ (Accessed September 25, 2024).

Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A., Scott, E. M., et al. (2010). Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *TREE* 25, 574–582. doi: 10.1016/j.tree.2010.06.016

Martins, P. M., Anderson, M. J., Sweatman, W. L., and Punnett, A. J. (2024). Significant shifts in latitudinal optima of North American birds. *PNAS* 121, e2307525121. doi: 10.1073/pnas.2307525121

Massachusetts Audubon Society (MAS) (2008). *Handbook for the Massachusetts Breeding Bird Atlas 2.* Available online at: https://www.massaudubon.org/content/download/8933/file/handbook.pdf (Accessed September 8, 2024).

Massachusetts Department of Conservation and Recreation (DCR) (2007).Quabbin Reservoir Watershed System: Land Management Plan 2007-2017. Available online at: https://www.mass.gov/files/documents/2018/01/22/quabbinlmp2007_0.pdf (Accessed September 25, 2024).

McNulty, S. A., Droege, S., and Masters, R. D. (2008). Long-term trends in breeding birds in an old-growth Adirondack forest and surrounding region. *Wilson J. Ornith* 120, 153–158. doi: 10.1676/07-032.1

Motzkin, G. (2014). Biodiversity Conservation on Agricultural Land: The Vegetation and Flora of Petersham Country Club, Harvard Forest, Petersham, MA. *Harvard Forest Paper* 30.

Neate-Clegg, M. H. C., Horns, J. J., Buchert, M., Pope, T. L., Norvell, R., Parrish, J. R., et al. (2021). The effects of climate change and fluctuations on the riparian bird communities of the arid Intermountain West. *Anim. Cons.* 25, 325–341. doi: 10.1111/acv.12755

O'Keefe, J., Plotkin, A., and Foster, D. (2008).The harvard forest land use master plan for the second century: Harvard Forest. Available online at: https://harvardforest1.fas.harvard.edu/files/HF-masterplan-exec-summary.pdf (Accessed September 25, 2024).

Parizek, C. D. (2018).NEON site level plot summary, harvard forest (HARV). Available online at: https://www.neonscience.org/field-sites/harv (Accessed September 25, 2024).

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., and Smith, P. A. (2019). Decline of the North American avifauna. *Science* 366, 120–124. doi: 10.1126/science.aaw1313

SanClements, M., and 10 co-authors. (2020). Collaborating with NEON. *BioScience* 79, 107. doi: 10.1093/biosci/biaa005

Sauer, J. R., Link, W. A., and Hines, J. E. (2020). The North American Breeding Bird Survey, Analysis Results 1966 - 2019. *U.S. Geol. Surv. Data Release*. Available online at: https://www.sciencebase.gov/catalog/item/5f1836a482cef313ed843104 (Accessed September 8, 2024).

Schipper, A. M., Belmaker, J., Dantas de Miranda, M., Navarro, L. M., Böhning-Gaese, K., Costello, M. J., et al. (2016). Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Global Change Biol.* 22, 3948–3959. doi: 10.1111/gcb.13292

Spurr, S. H. (1956). Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* 37, 443–451. doi: 10.2307/1930166

Tingley, M. W., Orwig, D. A., Field, R., and Motzkin, G. (2002). Avian response to removal of a forest dominant: consequences of hemlock wooly adelgid infestations. *J. Biogeog.* 29, 1505–1516. doi: 10.1046/j.1365-2699.2002.00789.x

Veit, R. R., and Petersen, W. R. (1993). *Birds of Massachusetts* (Lincoln, MA: Massachusetts Audubon Society).

Walsh, J. M., and Servison, M. S. V. (Eds.) (2017). *State of the Birds 2017: Massachusetts Birds and Our Changing Climate* (Lincoln, MA: Massachusetts Audubon Society).