Biological Conservation 302 (2025) 110934

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Increased bird abundances over 30 years in an extensive commercial forest landscape

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ARTICLE INFO

Keywords:
Bird declines
Commercial forestry
Maine
Wabanaki-Acadian Forest
Habitat selection
Working forest
Production forest
Forest birds
Forest management
Bird community

ABSTRACT

Habitat loss and degradation are considered the primary drivers of continental bird declines. We replicated an extensive study of forest bird populations conducted 30 years ago in a 238,000-ha commercial forest landscape in northern Maine (USA). The two study periods straddle a landscape-scale transition in forest ownership and management. We found that 55 % of the 47 species we had sufficient data to evaluate showed increased landscape-scale abundances since 1993, while another 28 % had not significantly changed. This is in stark contrast to trends reported in continental and regional Breeding Bird Survey data over the same period. Interestingly, abundance increases were driven primarily by changes in population densities within and across forest types, suggesting a greater role of flexible habitat selection than has been previously documented in this assemblage. The changes we observed suggest that the mosaic of commercial and preserved forest in northern Maine is providing an important reservoir of breeding bird habitat, and might be partially offsetting declines at broader spatial scales.

1. 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 primary factors in these declines, especially among forest-breeding passerines (Rosenberg et al., 2019). Commercial forestry has been widely identified as a driver of habitat loss and degradation (Betts et al., 2022; Imbeau et al., 2001; Pohlman et al., 2023), but has also been shown to be capable of maintaining or enhancing bird habitat quality (Akresh et al., 2023; Duflot et al., 2022; Reif et al., 2022). Indeed, whether forest management effects are characterized as net positive or negative for forest birds may depend on the region (Drapeau et al., 2016), timescale (Demarais et al., 2017), and species of focus (Akresh et al., 2023). Landscapes where commercial forestry is a dominant land-use may also hold high value for bird conservation. For instance, within the conterminous U.S., Maine's > 4 million ha of commercial, public, and preserved forestland comprise the largest undeveloped forest east of the Mississippi River, and the largest globally significant Important Bird Area (National Audubon Society, 2024). Consequently, gaining a more nuanced understanding of how the management of commercial forest landscapes impacts breeding habitat is an important component of determining the role of these landscapes in forest bird population changes.

A central component of any examination of forestry effects on bird populations is the type of tree harvest being used (Betts et al., 2021). Previous authors have contrasted lower-intensity methods such as partial harvesting with higher-intensity methods such as clearcutting and plantations (e.g., Belair and Ducey, 2018; Eggers et al., 2022; Gresh and Courter, 2022). However, several important caveats complicate these comparisons. First, the tradeoff between intensification and scale means that favoring lower-intensity over higher-intensity harvest may necessitate larger overall areas of annual disturbance (Betts et al., 2021, Fig. 1a). Next, as we illustrate in this study, landscape-level transitions between management regimes are likely to favor different subsets of a bird assemblage. Such phenomena have been little studied. Finally, the

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https://doi.org/10.1016/j.biocon.2024.110934
Received 8 July 2024; Received in revised form 24 October 2024; Accepted 10 December 2024

responses of a bird assemblage to changing forest management may also depend on geographically variable (e.g., Crosby et al., 2019) and species-specific characteristics such as sensitivity to habitat area (Brotons et al., 2003; Heikkinen et al., 2004) and distribution (Häkkilä et al., 2018), reliance on fine-scale habitat features (Andersson et al., 2018), and associations with different successional stages of forest (e.g., Akresh et al., 2023; Hagan et al., 1997; Rolek et al., 2018; Titterington et al., 1979).

This study presents a unique opportunity to address these limitations, by examining spatial and temporal change in bird habitat and populations across a large commercial forest landscape on either side of a major transition in forest practices. Our study landscape was managed primarily for timber production for over a century, but widespread turnover in landownership, manufacturing technology, and public perception of forestry facilitated significant shifts in forest management over the past three decades. Since 1990, the combination of a receding spruce budworm (*Choristoneura fumiferana*) outbreak (Gunn et al., 2019; Irland et al., 1988; Legaard et al., 2015; Scott et al., 2023) and public pressure to regulate clearcut sizes (Hagan, 1996) shifted the predominant harvest method in Maine commercial forests from clearcutting to various partial harvesting regimes (Fig. 1a). Additionally, the shorter-term management horizons of many new forestland owners, as well as changing sawlog markets (Irland, 2000; Legaard et al., 2015), disincentivized post-harvest treatments and planted stand establishment. Overall, the result of the past 30 years of silvicultural change within our focal landscape has been a large-scale shift from clearcuts with relatively uniform tree regeneration to partial cuts with regeneration staggered by subsequent harvests (Legaard et al., 2015).

We were specifically interested in how these changes in land management affected forest bird abundance and habitat use in the region. To address this, we measured forest-type-specific bird densities and landscape-scale abundances in 2021–22, using the same survey methods, forest-type classifications, and areal extent as a study conducted in 1992–93 (Hagan et al., 1997), to which we had access to the raw data. We also evaluated change over time in the distribution and extent of different forest types. Our specific aims were to: 1) compare

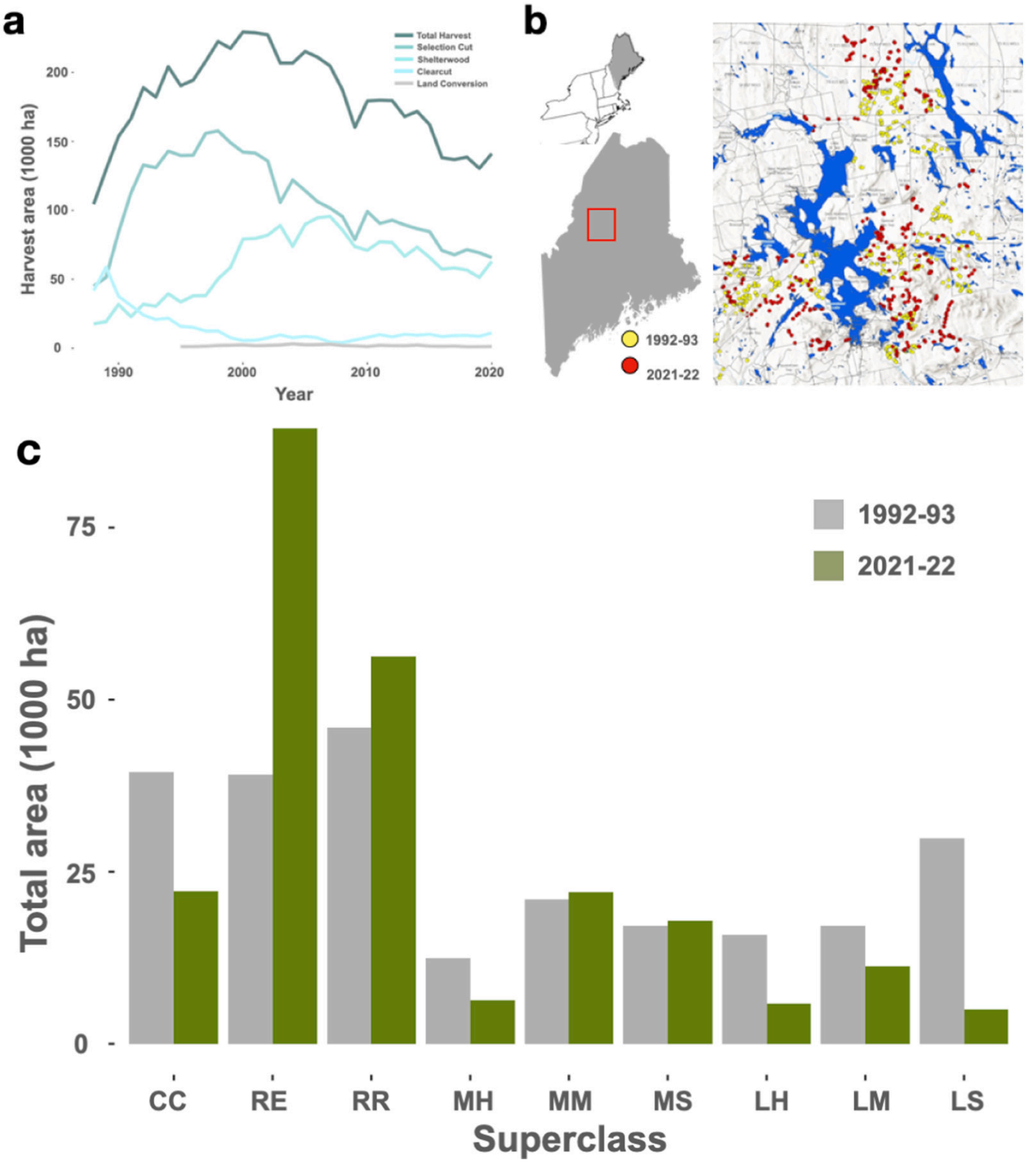

Fig. 1. a. Trends in tree-harvest practices in Northern Maine commercial forests, usig data from Maine Forest Service annual reports (https://www.maine.gov/dacf/mfs/publications/annual_reports.html, accessed Nov 1, 2023). b. Map of focal study area in Northern Maine with survey points from 1992-93 (yellow) and 2021-22 (red). c. Changes in total area (ha) of each Superclass from 1992-92 (gray) to 2021-22 (green) within the ~238,000 ha focal landscape. Superclass codes and definitions can be found in Table 1. 1992-93 data from Hagan et al. (1997).

estimated landscape-scale abundances of each forest bird species between the two time periods, incorporating changes in the distribution and extent of each forest type, 2) characterize changes in population densities over time within forest types for each species, 3) examine relationships between abundance changes and species functional guilds (foraging, nesting, and migratory), and 4) evaluate these changes in the context of continental and regional population change over the same time period in Breeding Bird Survey data. To our knowledge, no previous study has examined repeated bird survey and forest type distribution data over time at this spatial extent within North American commercial forests.

2. Methods

2.1. Study area and survey design

Forest structure and bird surveys were conducted within a 238,000 ha, primarily commercial forest landscape embedded within the >4 million ha of commercial, private, and public forestland in northern Maine (45.733139 N, −69.527020 W; Fig. 1b), and exactly overlaying the focal area of the 1990s study (Hagan et al., 1997). The study area is in the Wabanaki - Acadian Forest ecoregion, which occupies a transition zone between northern hardwood forest and true boreal coniferous forest (Cox et al., 2024). To characterize the effects of shifting forest management on the distribution and amounts of bird habitat on this landscape, we categorized forests according to their age, composition, and canopy closure into nine coarse forest "Superclasses" (Table 1). These replicated the forest classification system of the earlier study (Hagan et al., 1997). To match the earlier study, we stratified bird survey points evenly across the nine Superclasses to obtain a representative sample of the composite bird community in each Superclass. To guide placement of survey points into the appropriate Superclasses, we used digitized timber stand maps from landowners and managers (LandVest, Huber Resources Corp., Weyerhaeuser Company, Appalachian Mountain Club, Maine Bureau of Public Lands in 2021–22; Scott Paper and Bowater Paper in 1992–93), which map the age, composition, and canopy closure of each stand.

2.2. Bird surveys

We conducted two, 10-min, 50 m fixed-radius, point counts at 422 locations across the breeding seasons (May–July) of 2021 and 2022, following the methods of Hagan et al. (1997). Each survey point was established at least 100 m from any road, and at least 200 m from other survey points to avoid double-counting individual birds. Surveys were conducted in the 5 h following 15 min before local sunrise on mornings with suitable weather conditions. During a given survey, the observer(s) recorded the species and mode of detection (seen/heard) of each individual bird, whether the bird detected was in or out of the 50 m-radius circle, and the minute the bird was first observed. If a bird was initially detected outside 50 m but moved within during the survey, we recorded the minute it entered the 50 m radius, and removed the outside record. We conducted one early-season (May 27–June 16) and one late-season (June 18–July 5) survey at each point, and shuffled the overall order and time of morning of surveys on the second visit. Early-season surveys were always conducted in pairs of observers to aid in standardizing observer distance estimations. We used laser rangefinders before and during counts to establish visual landmarks at 10 m increments out from the count center to improve estimation of the 50 m radius.

Table 1
Descriptions, names, and abbreviations (Code) of nine Superclasses representing each major forest type on the focal landscape.

Superclass	Code	Description
Clearcut	CC	Recent complete or nearly complete stand-removal harvest, ranging from bare ground and slash to young regeneration or planted saplings <2 m tall
Regeneration	RE	Young regenerating forest from heavy harvest treatment, with a dominant canopy height between 2 and 6 m
Residual Regeneration	RR	Regeneration with an additional overstory layer of sparse residual mid-age or mature trees from a previous selective-cut or shelterwood harvest
Mid-age Hardwood	MH	Forest with >75 % hardwood composition, dominant canopy height between 6 and 15 m
Mid-age Mixedwood	MM	Forest with 50–75 % hardwood or softwood composition, dominant canopy height between 6 and 15 m
Mid-age Softwood	MS	Forest with >75 % softwood composition, dominant canopy height between 6 and 15 m
Mature Hardwood	LH	Forest with >75 % hardwood composition, dominant canopy height > 15 m
Mature Mixedwood	LM	Forest with 50–75 % hardwood or softwood composition, dominant canopy height > 15 m
Mature Softwood	LS	Forest with >75 % softwood composition, dominant canopy height > 15 m

2.3. Vegetation surveys

To explore vegetation features related to bird densities, we measured a suite of structural and compositional variables at surveyed forest stands. Fine-grained changes in forest structure and composition, as well as their relationship to bird habitat selection, are explored elsewhere (Authors, unpublished results A; Authors, unpublished results B). Herein, we summarize measurements of selected vegetation parameters (Table 2), and relate these to coarse-scale shifts in habitat selection for the core bird species in our focal assemblage. Survey methods are detailed in Supplemental Materials.

2.4. Analyses

For each bird species, we determined densities at each point by the maximum count of individuals within 50 m across surveys, excluding flyovers and sub-adults (Hagan et al., 1997). The 47 species with a frequency of detection >0.03 (a natural break in the frequency distribution) in either the 1992–93 (Hagan et al., 1997) or 2021–22 datasets were selected for analyses of change in density and abundance in the study landscape. By examining densities within Superclasses, we determined coarse niche requirements for each species. By comparing landscape-level abundances between 30 years for each species, we assessed the degree to which changes in our landscape agreed with those at a broader scale.

To compare mean densities between Superclasses and study periods for a given species, we generated 83.4 % confidence intervals around each mean via bootstrapping, following the methods of Payton et al. (2003). A lack of overlap between these confidence intervals indicates a statistically significant difference at $\alpha = 0.05$ (Payton et al., 2003). We wrote a custom loop function in R to resample local population densities in 1000 bootstrap replicates and output the upper and lower bounds of the 83.4 % confidence interval for each study period-Superclass-species combination, using the boot and boot.ci functions in the "boot" R package (Canty and Ripley, 2024). To explore possible changes in species richness, we calculated Shannon's diversity indices for each Superclass in each time period, using the diversity function in the "vegan" R package (Oksanen et al., 2022), and compared these using Hutcheson *t*-tests at $\alpha = 0.05$. All analyses were conducted in R v4.3.2 (R Core Team, 2023).

We estimated landscape-level abundance (A) of each species in each time period as:

$$A = \sum_{i=1}^{9} d_i a_i$$

where d_i is mean population density and a_i is the area of Superclass *i*,

Table 2
Vegetation metrics derived from stand-level surveys used in this analysis and their descriptions.

Metric	Description
D_BAS	Basal area of standing deadwood ≥8 cm DBH within 10x50m quadrat
S_BAS	Basal area of live softwood* ≥ 8 cm DBH within 10x50m quadrat
H_BAS	Basal area of live hardwood* ≥ 8 cm DBH within 10x50m quadrat
N_S_live	Number of live softwood stems ≥8 cm DBH within 10x50m quadrat
N_H_live	Number of live hardwood stems ≥8 cm DBH within 10x50m quadrat
SimpDiv	Simpson's Diversity Index (n(n-1)/N(N-1)) of live woody stems <8 cm DBH, >0.5 m tall within 4x50m quadrat
N_0.5_1	Number of woody stems <8 cm DBH, 0.5-1 m tall within 4x50m quadrat
N_1_2	Number of woody stems <8 cm DBH, 1-2 m tall within 4x50m quadrat
N_2_4	Number of woody stems <8 cm DBH, 2-4 m tall within 4x50m quadrat
N_4_6	Number of woody stems <8 cm DBH, 4-6 m tall within 4x50m quadrat
N_6	Number of woody stems <8 cm DBH, >6 m tall within 4x50m quadrat
CANO_CLOS	Mean of canopy closure from a spherical densiometer reading at point center and either end of the 10x50m quadrat
SLAS	Percent slash cover within 50 m point count circle, in 10 % increments
LOG_scalar	Number of logs intersecting the 50 m transect line (2020s) or within the 10x50m quadrat (1990s), scaled to a percent of the maximum value
MEANTALL	Mean height of the four tallest trees within the 10x50m quadrat
AMBE_BAS	Basal area of American beech ≥8 cm DBH within 10x50m quadrat
YEBI_BAS	Basal area of yellow birch ≥8 cm DBH within 10x50m quadrat
RBSP_BAS	Basal area of red and black spruce ≥8 cm DBH within 10x50m quadrat
BAFI_BAS	Basal area of balsam fir ≥8 cm DBH within 10x50m quadrat
REMA_BAS	Basal area of red maple ≥8 cm DBH within 10x50m quadrat
SUMA_BAS	Basal area of sugar maple ≥8 cm DBH within 10x50m quadrat

* "Softwood" refers to coniferous tree species; "hardwood" to broadleaved deciduous species.

derived from timber-stand maps. We used the delta method function in the "msm" R package (Jackson, 2011) to compare abundances between study periods; this method estimates variance for a function of multiple random variables (Powell, 2007). From the variance of each estimated abundance, we calculated upper and lower bounds of an 83.4 % confidence interval as A ± 1.386Δ, where A is the estimated abundance and Δ is the delta-method-derived variance. A lack of overlap of confidence intervals between time periods indicated a statistically significant change in abundance for a given species.

Given that abundance was a function of both per-Superclass densities and Superclass areas, a change in abundance over time could be the result of shifts in either component. Thus, to differentiate between these components and their relative effects, we generated a hypothetical abundance A_h for each species by keeping 1990s per-Superclass densities constant and multiplying by 2020s Superclass areas. We then calculated the proportional difference between A_h and observed 2020s abundance for each species. We considered this difference an index of the relative contribution of change in per-Superclass densities to abundance change over time, and capped the index at 1.0.

We also compared abundance changes in our study area to population trends reported at larger scales (Continental, and Bird Conservation Region (BCR) 14) across the same time period from Breeding Bird Survey (BBS) data (Sauer et al., 2022). Given that our data were from two short windows either side of this time period, we validated our comparisons to abundance trends using regional (BCR 14) data from 1992 to 93 and 2021–22. We divided the total count of each species by the number of BBS routes run across the region in a given year for 1992, 1993, 2021, and 2022. We then averaged these proportional abundances within study periods to obtain an estimate of abundance change between 1992 and 93 and 2021–22.

We used binomial generalized linear models to examine relationships between abundance change and functional guilds for each species using categorical guild identifiers as predictors. We evaluated six foraging guilds: insectivorous foliage gleaner, bark forager, aerial insectivore, ground insectivore, fruit or seed herbivore, and omnivore; five nesting guilds: midstory to canopy cup-nest, shrub cup-nest, cavity, ground, and stump/log; and three migratory guilds: long-distance, short-distance, and resident. Guild information came from Birds of the World species accounts (Billerman et al., 2022) supplemented with regional classifications from Azeria et al. (2011).

Although we used the same Superclass system as in the 1990s study (Hagan et al., 1997), shifts in forest management towards partial harvesting made classification of some contemporary stands more difficult, particularly for Regeneration and Residual Superclasses. Thus we evaluated and reconciled our categorizations between time periods using 21 vegetation parameters from our stand-level vegetation surveys at each point count location (Table 2). Most parameters were highly heteroscedastic, so we used weighted least squares regression (James et al., 2022) to determine differences in each parameter over time within each Superclass. Further information on model formulation and code can be found in the Supplemental Material.

3. Results

3.1. Forest cover and vegetation

Between 1992 and 93 and 2021–22, shifts in forest management within our focal region led to considerable differences in the relative amounts of each forest type (hereafter, "Superclass," see Table 1) on our focal landscape. Among the three early-successional Superclasses, Clearcut area was reduced by half, and the area of both Regeneration and Residual comparably increased (Fig. 2). During the same time period, all three late-successional Superclasses declined in area, while the amount of mid-age forest remained relatively stable (Fig. 1c).

Stand-level structure and composition were largely consistent among Superclasses over time, yet some important shifts occurred, particularly in early successional forest. Regeneration saw significant increases in softwood (coniferous) basal area (Fig. 2c), the number of softwood (Fig. 2d) and hardwood (deciduous) trees (Fig. S1b, Supp. Mat.), canopy closure (Fig. S1d, Supp. Mat.), and the number of woody stems in the two tallest height classes (Figs. 2f, S1h, Supp. Mat.), indicating an overall structural shift towards an older relative age. Residual experienced far fewer changes: only the canopy height and number of woody stems in the tallest shrub class significantly changed (Fig. 2b,f), and the small magnitude of change in both suggested these were not biologically meaningful shifts. In mid-age Superclasses, the most significant change occurred in the structure of the softwood canopy, with softwood basal area decreasing in Mid-Age Softwood (Fig. 2c), but number of woody stems >6 m and 4-6 m tall significantly increasing (Figs. 2f, S1h, Supp. Mat.). These shifts coincided with compositional change, with significant declines in the basal area of red and black spruce (Fig. 2i) and increases in the basal area of balsam fir (Fig. 2j). In mature forests, a similar compositional shift occurred between declining American beech (*Fagus grandifolia*) basal area (Fig. 2g) and increasing yellow birch (*Betula alleghaniensis*) basal area (Fig. 2h). Clearcut structure remained largely stable by the metrics generated in this study, with significant increases only in slash cover and canopy closure (Fig. S1c,d, Supp. Mat.), and significant but likely not biologically meaningful shifts in the

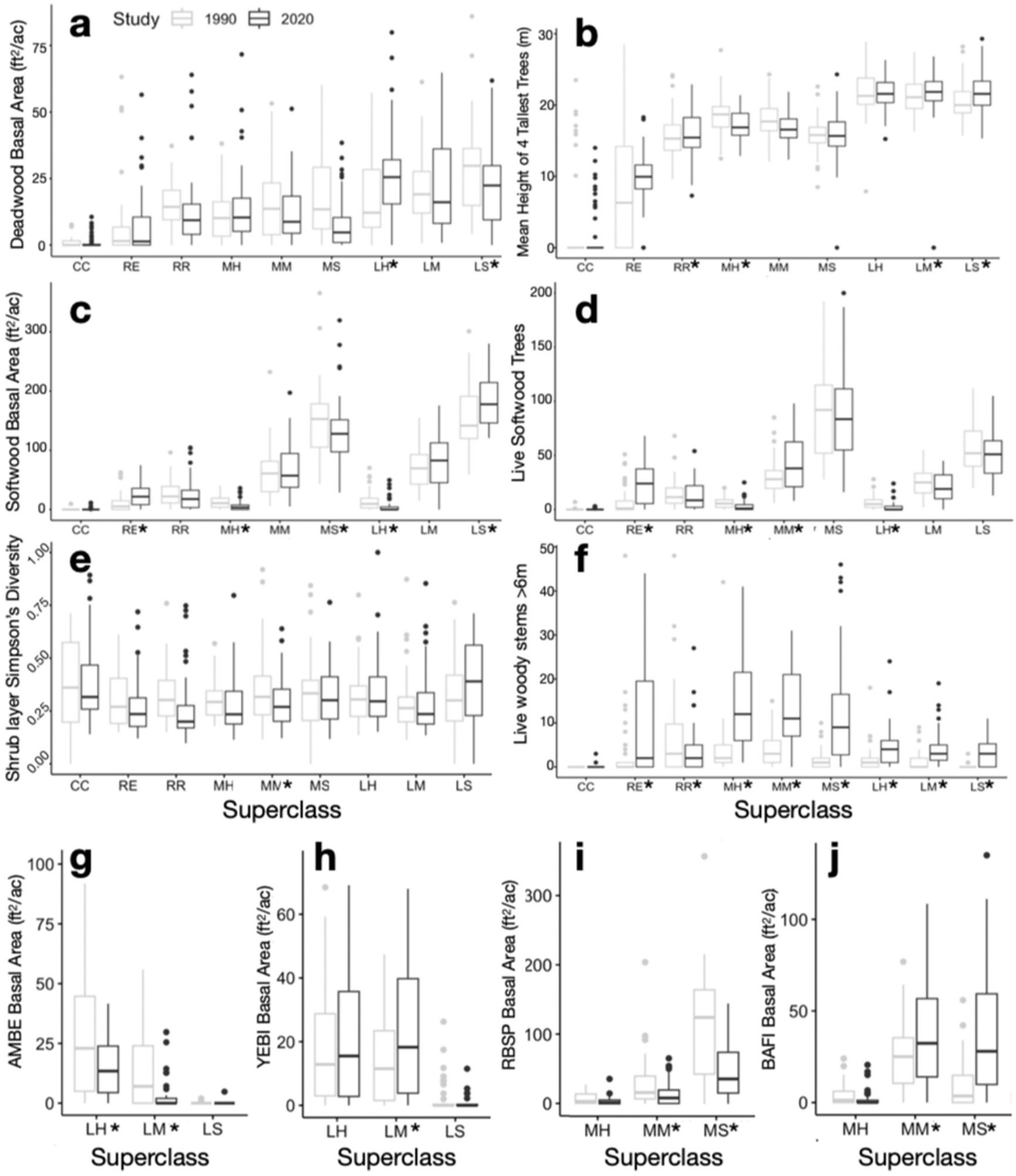

Fig. 2. Selected structural and compositional values within Superclasses between 1992-93 and 2021-22. Statistically significant differences (* $p < 0.05$) between time periods were determined by weighted least squares regression. Superclass codes can be found in Table 1. Among Superclass types, values are shown for a. standing deadwood basal area, b. mean height of the four tallest trees in a stand (a metric of canopy height), c. softwood basal area, d. number of live softwood stems at least 8 cm DBH, e. Simpson's Diversity Index of woody plants > 0.5 m tall, f. number of woody stems > 6 m tall, < 8 cm DBH. Tree-species-specific compositional trends are depicted for g. American beech (AMBE) and h. yellow birch (YEBI) in late successional Superclasses, and i. red and black spruces (RBSP) and j. balsam fir (BAFI) in mid-age Superclasses. Vegetation metrics are described in greater detail in Table 2, and boxplots for the remaining variables and Superclasses are depicted in Figs. S2, S3 (Supp. Mat.).

number of woody stems 2-4 m tall (Fig. S1g, Supp. Mat.), and balsam fir basal area (Fig. S2d, Supp. Mat.).

3.2. *Bird species*

We detected 103 species on point-count surveys from 2021 to 22, of which 82 were detected at least once within the 50 m count radius (See Table S1, Supp. Mat. for full species list with scientific names). Within 50 m on point counts in 2021–22, we did not detect 12 species that were detected within at least one 50 m radius on the landscape in 1992–93, and we detected 16 species that were not detected in 1992–93 (Hagan et al., 1997). However, these differences were entirely among uncommon species: the maximum differences in detection frequency between years for this group of 27 species were in pine siskin (2 % of sites 1992–93, 0 % of sites 2021–22), and pine warbler (0 % sites 1992–93, 2 % of sites 2021–22). Additionally, six of 12 species undetected within 50 m in 2021–22 were detected at least once outside of the circles, and a further two, evening grosbeak and Tennessee warbler, were detected during site preparation in at least one site. In contrast, 15 of 16 undetected species within 50 m radii in 1992–93 were also undetected outside 50 m radii. Shannon's Diversity was significantly higher in five Superclasses in 2021–22 (Table S5, Supp. Mat.), but relative changes were small (Fig. 3).

3.3. Bird densities

Per-Superclass changes in density were highly variable across species (Fig. 4a,b). Among the 47 focal species, 24 (51 %) significantly increased in density in at least two Superclasses, while 7 (15 %) significantly decreased in density in at least two Superclasses. Changes in densities across species were distributed unevenly among Superclass types (Fig. 4c): Clearcuts and Mature Mixedwood had the fewest species with significant density change ($n = 10$), while more than twice as many species significantly changed density in Regeneration ($n = 21$) and Residual ($n = 22$). The direction of change was also distributed unevenly: half of the significantly changing species in Regeneration declined in this Superclass (n = 10), while less than a quarter of significant changes were negative in Residual ($n = 5$).

From the focal bird assemblage, we highlight six species to demonstrate the variety of changes in bird density that occurred within Superclasses from 1992 to 93 to 2021–22. Plots of per-Superclass density change for the remaining species can be found in the Supplemental Material. Red-eyed vireo (Fig. 5a) and northern parula (Fig. 5b) exhibited the most consistent increase in density across cover types, each significantly increasing in seven of nine forest Superclasses, while magnolia warbler (Fig. 5c) and winter wren (Fig. 5d) exhibited the most consistent density declines, each in five of nine Superclasses. Some species also displayed inconsistent shifts in densities: for example, white-throated sparrow significantly increased in density in three later-successional Superclass types (Fig. 5e), while Blackburnian warbler significantly declined in density in mid-age Superclasses, but significantly increased in Mature Mixedwood and Mature Softwood (Fig. 5f). Only five species showed no significant changes in density across all Superclass types: cedar waxwing, dark-eyed junco, downy woodpecker, least flycatcher, and yellow-rumped warbler (Fig. 4a).

3.4. Bird abundances

Changes in estimated landscape-scale abundances were similarly variable across bird species, but they were primarily positive: 26 of 47 (55 %) species significantly increased in abundance, 13 (28 %) showed no statistically significant change, while eight (17 %) significantly declined (Table 3, Fig. 6). Changes in density had a far more consistent influence on abundance change than did changes in Superclass area, the latter of which contributed >50 % to the abundance change for only six of 47 species (Table 3). This relative contribution appeared unrelated to the direction of abundance change: two each of these six species had significantly increased, significantly decreased, and not significantly changed in abundance since 1992–93 (Table 3). All three abundance changes occurred across foraging, nesting, and migratory guilds, such that none of these variables was a significant predictor of abundance change for a given species (Table S2, Supp. Mat.). Running separate GLMs for species with increasing and not significantly changing abundances improved model fit, but did not reveal any significant predictors (Tables S3, S4, Supp. Mat.). Sample size for significantly decreasing species was too small for the GLM to converge.

Abundance changes on our landscape showed no meaningful relationship to either regional (Fig. 7a) or continental (Fig. 7b) trends in BBS data (Spearman's correlation coefficient = 0.29, 0.23, respectively). Of the 26 species with significantly increasing abundances since 1992–93, 15 had decreased continentally, and 16 regionally over the same time period (Fig. 7a,b). However, of the eight species with significantly decreasing abundance, all had decreasing abundance trends at a continental scale, and seven at a regional scale (Fig. 7a,b). Changes in BCR 14 abundances between the two study periods were strongly correlated with BCR 14 abundance trends over the full time period (Spearman's correlation coefficient = 0.74, Fig. S3a, Supp. Mat.). As a result, changes in abundance within our focal landscape were similarly poorly correlated with concurrent abundance change for the region as a whole (Spearman's correlation coefficient = 0.11, Fig. S3b, Supp. Mat.).

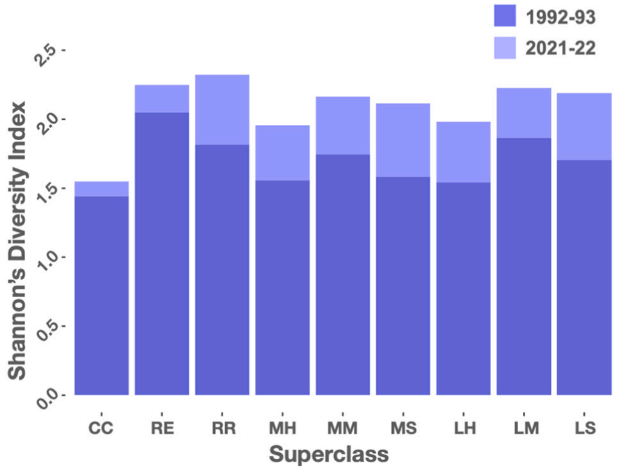

Fig. 3. Per-Superclass Shannon's Diversity of the complete bird species assemblage. Bars for 1992-93 and 2021-22 are overlaid. Shannon's Diversity significantly increased ($p < 0.05$) in five Superclasses (RE, RR, MS, LH, LS) via a Hutcheson t-tes (Table S4, Supp. Mat.). Superclass codes and definitions can be found in Table 1.

4. Discussion

Given widespread continental (Rosenberg et al., 2019) and regional (Betts et al., 2022; Pohlman et al., 2023) declines in many forest bird species, the landscape-scale abundance increases we observed since the 1990s study (Hagan et al., 1997) were unexpected. Over the past three decades, a majority (55 %) of the core 47 bird species of our focal assemblage significantly increased in landscape-scale abundance, while another 28 % did not significantly change. Over half of the increasing abundance trends on our landscape disagreed with concurrent negative trends for the same species at regional and continental scales. Increases in abundance occurred across migratory, nesting, and foraging guilds, also in contrast to broader-scale population declines in many forest-bird species, which have strong functional and phylogenetic components (e.g., continental declines in Parulid warblers and aerial insectivores, and increases in vireos and waterfowl since 1970: Rosenberg et al., 2019). We examine both methodological and mechanistic factors as potential drivers of these differences.

Two important differences exist between our survey methods and those used to generate continental-scale bird population trends. First, while North American Breeding Bird Survey (BBS) data offer the most comprehensive continental-scale picture of breeding bird abundance changes over time, considerable gaps exist in the spatiotemporal consistency of survey-route coverage (Roy et al., 2019). In particular, large, remote commercial forest landscapes such as our study area are sparsely covered. The resulting paucity of data on avian populations in remote landscapes often means that trends from better-covered survey routes are extrapolated onto areas with poorer coverage (Walker and Taylor, 2020; Will et al., 2021). Consequently, continental and regional patterns of abundance change might poorly reflect changes in these more sparsely surveyed areas.

Next, many previous studies (e.g., Betts et al., 2022; Hallman and Robinson, 2020), as well as large-scale datasets such as the BBS and Boreal Avian Monitoring Project (BAM, Sólymos et al., 2020), include point counts conducted along roadsides, which can allow for larger sample sizes (Huff et al., 2000). However, roadside surveys may produce different bird assemblages (Matsuoka et al., 2012; Sólymos et al., 2020) than do off-road counts, such as those we conducted, often through underrepresentation of more interior-associated species at roadside sites

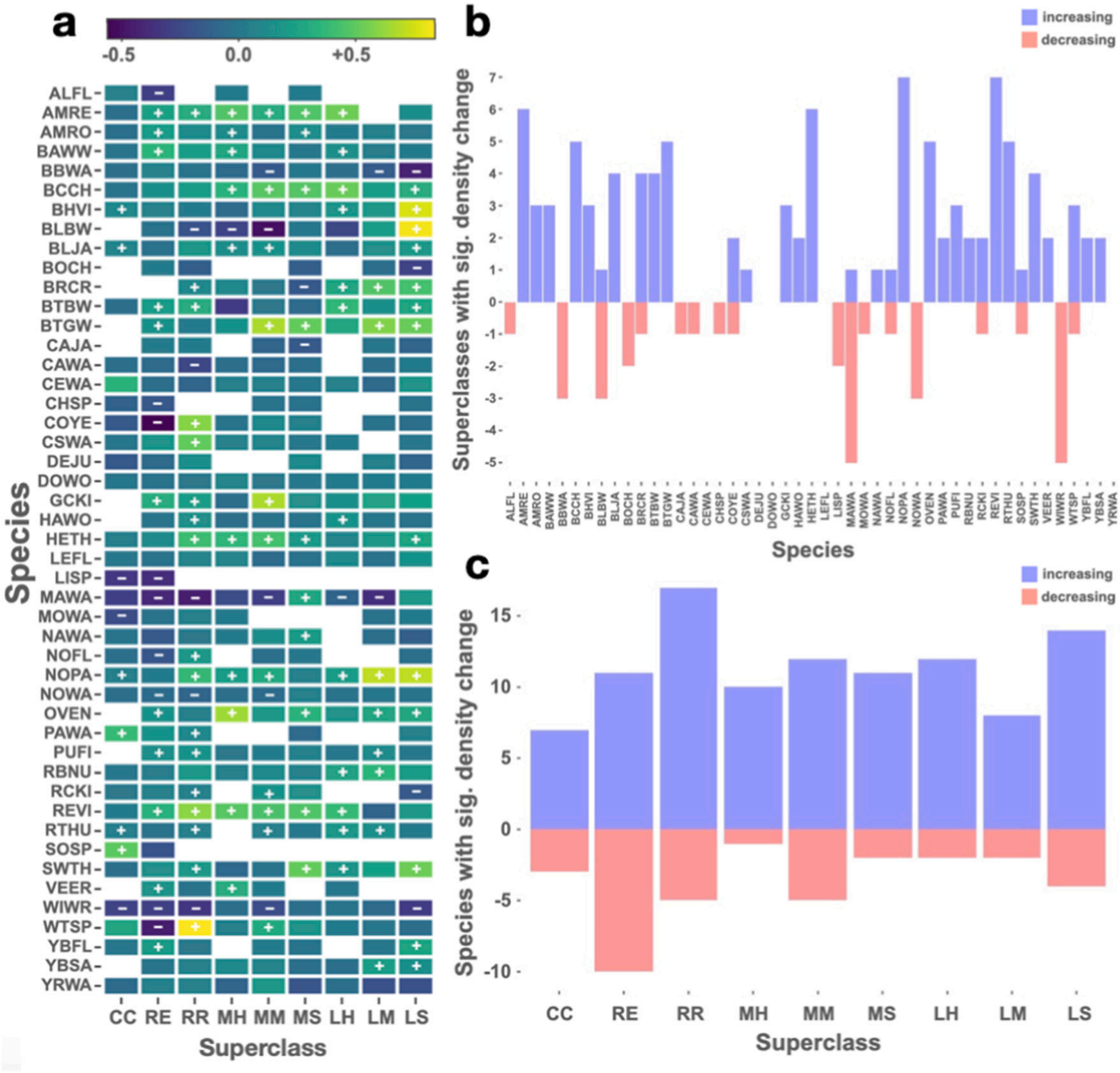

Fig. 4. a. Changes in per-Superclass density from 1992-93 to 2021-22 for each bird species in the core subset of 47 with a detection frequency > 0.03 across points in either study period. Significant increases are marked with a "+" symbol, and significant decreases with a "-" symbol. Blank spaces indicate Superclasses unoccupied by a species in both study periods. Superclass codes and definitions can be found in Table 1, common names associated with each bird species code can be found in Table 3, and a full list of species with common and scientific names can be found in Table S1 (Supp. Mat.). b. Number of Superclasses with significant increases or decreases in density for each bird species. c. Number of species exhibiting significant increases or decreases in density for each Superclass.

(Edenius and Elmberg, 1996). This may explain interregional differences in mean densities for particular species, but is unlikely to explain interregional differences in abundance changes, as both our off-road methods and those of roadside surveys have remained consistent in their design over time.

4.1. Potential drivers of abundance increase

Increases in abundance were explained largely by shifts in per-Superclass bird densities, rather than changing Superclass areas. Thus we considered that possible inflation of densities could have occurred through systematic differences in the methods or effectiveness of data collection in the 1990s (Hagan et al., 1997) versus the 2020s (this study). However, this does not appear to have been the case. First, we ensured that bird and plant survey methods were consistent with Hagan et al. (1997). We included multiple methodological controls for variability in between-species or between-observer detection, as recommended by previous authors (e.g., Elphick, 2008): A) each point was surveyed twice, B) early-season counts were conducted with multiple observers, C) all observers were given prior training to ensure a high level of proficiency in species identification and to standardize distance estimates.

In the broader regional context, the densities we observed were well within the range of variation reported by previous authors for northeastern passerine assemblages (e.g., Akresh et al., 2023). That some species significantly decreased in their densities, in particular the distinct and highly detectable winter wren (Matsuoka et al., 2012), further suggests that increases in other species were not the result of consistent inflation of densities by 2020s observers. Additionally, abundance changes of all directions were driven primarily by widespread change in density between cover types, including significant declines and shifts out of previously high-density Superclasses. Therefore we are confident that abundance changes represent true shifts in density and forest cover extent.

A reasonable null hypothesis for the primarily positive abundance changes we observed might be that these were the result of chance fluctuations in population size, or a response to stochastic events that affected many species in synchrony within a particular year, such as a severe drought or an overabundance of food. Both demographic and environmental stochasticity can affect wild bird population sizes on an

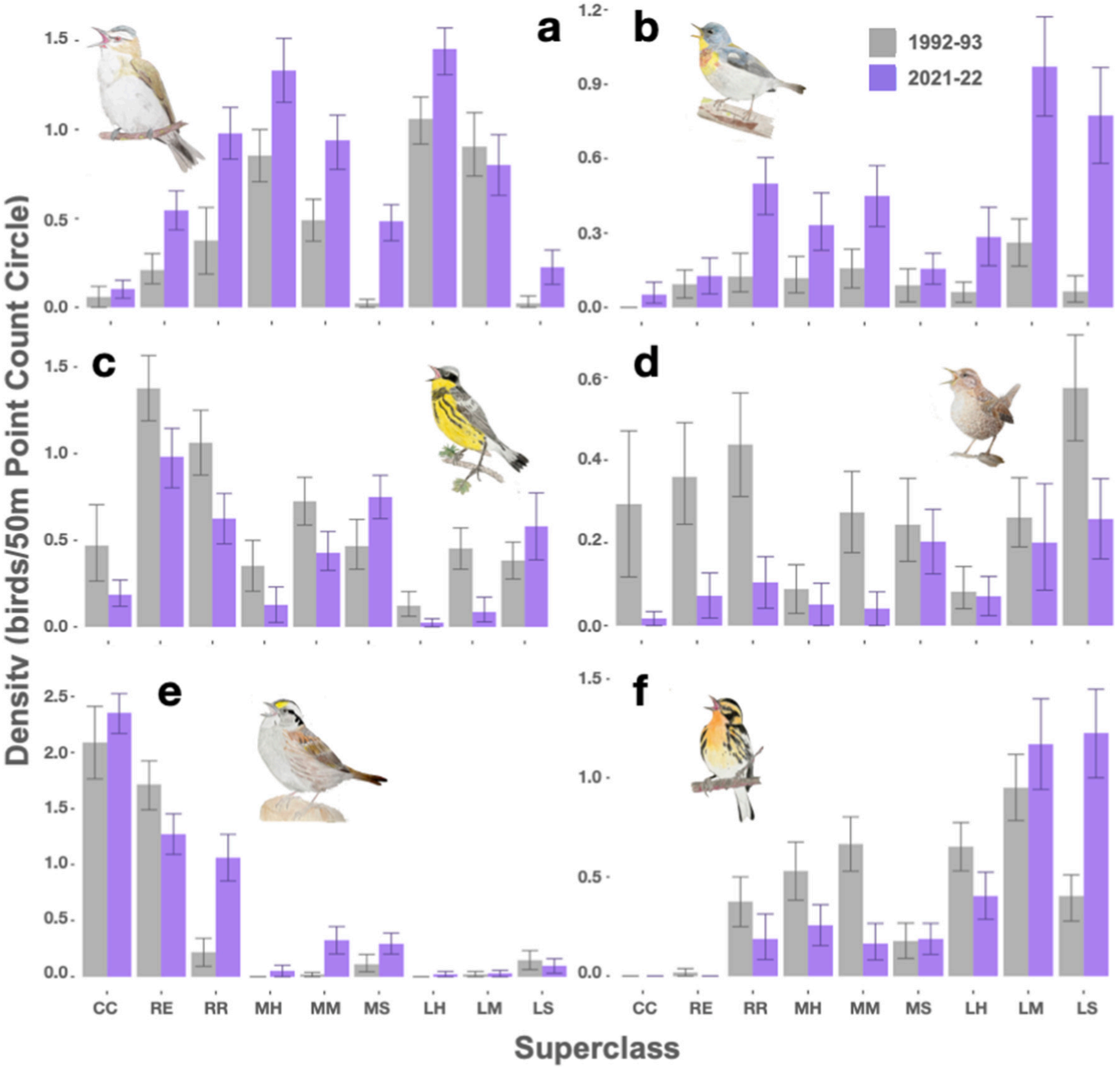

Fig. 5. Mean density per Superclass from 1992-93 to 2021-22 for six selected species. Red-eyed vireo (a.) and northern parula (b.) significantly increased in the most Superclasses (n = 7). Magnolia warbler (c.) and winter wren (b.) significantly decreased in the most Superclasses (n = 5). White-throated sparrow (e.) and Blackburnian warbler (f.) exhibited apparent broadening and narrowing of habitat associations, respectively. Error bars are 83.4% confidence intervals, where a lack of overlap is equivalent to significance $p < 0.05$. Superclass codes and definitions can be found in Table 1. Bird illustrations by Fen Levy.

interannual basis (Stegen et al., 2013; Storch et al., 2023; Virkkala, 1991), and thus present a challenge for interpreting population change over time from disjunct samples. It is not clear without interpolating data between our two study periods how likely this would be for our large assembly of species. However, both the magnitude of abundance increases and their consistency across functional guilds in our focal assemblage suggest that chance fluctuations, alone, were not responsible for the patterns we observed. We are also unaware of any major single-year climatic stressors that occurred during surveyed years, and neither study period was within a peak of the spruce budworm cycle, which would represent unusually high regional food abundance across the forest bird assemblage. Moreover, stochastic variability in population size is often rooted in, or at least difficult to disentangle from deterministic factors (Stegen et al., 2013). For example, within temperate and boreal forests, habitat alteration can be a driver of short-term landscape-scale population fluctuations (Virkkala, 1991) in addition to longer-term or wider-scale change (Betts et al., 2022). For these reasons, we focus primarily on deterministic hypotheses for observed abundance change.

We propose a variety of mechanistic hypotheses for these patterns that could be explored by future studies. First, species may have recovered from previous declines, as might occur following a period of decreased habitat quality (Askins and Philbrick, 1989; but see Schrott et al., 2005). This does not appear to be the case in our study, as densities increased across all forest Superclasses and among species with a range of Superclass associations. Additionally, we might expect sensitivities to habitat change to be consistent among functional guilds (Valente and Betts, 2019), as has been reported for cavity nesters (Doyon et al., 2005; Lešo et al., 2019) and bark foragers (Doyon et al., 2005), or associates with particular habitat types (Halstead et al., 2019), but no such relationships were detected in our assemblage. Finally, although corroborating data are limited, some species may experience “natural” continent-wide fluctuations in population size on multi-decadal timescales, irrespective of habitat change in a particular area (Hill and Hagan, 1991; Sillett et al., 2000; Townsend et al., 2016).

Second, changes in food supply could influence both adult survival and breeding success. Insectivorous birds, which make up the majority of our focal assemblage, have shown significant declines at broad geographic scales (Reif and Hanzelka, 2020; Rosenberg et al., 2019), concurrent with declines in global insect abundance and richness (Cardoso et al., 2020). However, Drummond (2022) found that insect populations had remained relatively stable in Maine over a similar period to that between our studies, with moderate community turnover.

Table 3

Functional guild membership of bird species and proportional contributions of per-Superclass density (relative to Superclass area) to abundance change (1992–93 to 2021–22) on the focal landscape for 47 core species of the focal assemblage (those with a detection frequency ≥ 0.03 in either study period). Species codes are used in Figs. 4,6, and 7. Scientific names can be found in Table S1 (Supp. Mat).

Code	Species	Abundance Change*	Migratory Guild**	Foraging Guild**	Nesting Guild**	Habitat with Peak 1992–93 Density	Habitat with Peak 2021–22 Density	Contribution of Density to Abundance Change (%)***
ALFL	Alder flycatcher	no Δ	LDM	hawk	shrub	RE	RE	100
AMRE	American redstart	+	LDM	glean	shrub	MH	MH	78.5
AMRO	American robin	+	SDM	generalist	shrub	CC	RE	93.8
BAWW	Black-and-white warbler	+	LDM	bark	log	RR	RE	82.9
BBWA	Bay-breasted warbler	–	LDM	glean	tree	LS	MS	17.1
BCCH	Black-capped chickadee	+	RES	generalist	cavity	RR	MM	80.66
BHVI	Blue-headed vireo	+	SDM	glean	shrub	LM	LS	100
BLBW	Blackburnian warbler	–	LDM	glean	tree	LM	LS	66.9
BLJA	Blue jay	+	RES	generalist	tree	RE	RR	66.0
BOCH	Boreal chickadee	–	RES	generalist	cavity	LS	MS	25.6
BRCR	Brown creeper	no Δ	RES	bark	tree	MS	LS	100
BTBW	Black-throated blue warbler	+	LDM	glean	shrub	MH	LH	100
BTGW	Black-throated green warbler	+	LDM	glean	tree	LH	LM	98.5
CAJA	Canada jay	no Δ	RES	generalist	tree	LS	LS	72.5
CAWA	Canada warbler	–	LDM	glean	shrub	RR	RE	100
CEWA	Cedar waxwing	no Δ	SDM	plant	shrub	RE	CC	9.7
CHSP	Chipping sparrow	–	SDM	ground	shrub	RE	CC	100
COYE	Common yellowthroat	no Δ	LDM	glean	shrub	CC	CC	82.5
CSWA	Chestnut-sided warbler	+	LDM	glean	shrub	CC	RR	77.7
DEJU	Dark-eyed junco	no Δ	SDM	ground	log	CC	RR	67.3
DOWO	Downy woodpecker	no Δ	RES	bark	cavity	MH	MH	6.7
GCKI	Golden-crowned kinglet	+	RES	glean	tree	LS	LS	100
HAWO	Hairy woodpecker	+	RES	bark	cavity	RE	RR	68.6
HETH	Hermit thrush	+	SDM	generalist	ground	RE	MH	81.5
LEFL	Least flycatcher	no Δ	LDM	hawk	tree	LH	LH	100
LISP	Lincoln's sparrow	–	LDM	ground	shrub	CC	CC	100
MAWA	Magnolia warbler	no Δ	LDM	glean	shrub	RE	RE	100
MOWA	Mourning warbler	no Δ	LDM	glean	ground	CC	RR	59.9
NAWA	Nashville warbler	+	LDM	glean	ground	RE	RE	7.8
NOFL	Northern flicker	no Δ	SDM	ground	cavity	RE	RR	100
NOPA	Northern parula	+	LDM	glean	tree	LM	LM	95.3
NOWA	Northern waterthrush	–	LDM	ground	log	RR	MS	100
OVEN	Ovenbird	+	LDM	ground	ground	LH	MH	86.0
PAWA	Palm warbler	+	SDM	ground	ground	RE	RE	63.0
PUFI	Purple finch	+	RES	plant	tree	LS	RR	100
RBNU	Red-breasted nuthatch	+	RES	bark	cavity	LS	LS	100
RCKI	Ruby-crowned kinglet	+	SDM	glean	tree	MS	MS	100
REVI	Red-eyed vireo	+	LDM	glean	tree	LH	LH	90.8
RTHU	Ruby-throated hummingbird	+	LDM	plant	tree	RE	LH	87.5
SOSP	Song sparrow	no Δ	SDM	ground	shrub	CC	CC	100
SWTH	Swainson's thrush	+	LDM	ground	shrub	MM	LS	87.8
VEER	Veery	+	LDM	ground	ground	MH	MH	69.7
WIWR	Winter wren	–	SDM	ground	log	LS	LS	96.6
WTSP	White-throated sparrow	+	SDM	ground	shrub	CC	CC	35.1
YBFL	Yellow-bellied flycatcher	+	LDM	hawk	ground	MS	LS	100
YBSA	Yellow-bellied sapsucker	no Δ	SDM	bark	cavity	LH	LM	94.9
YRWA	Yellow-rumped warbler	no Δ	SDM	glean	tree	MS	MS	100

* Abundance change, positive (+), negative (–), or not significantly changing (no Δ), from 1992 to 93 to 2021–22, calculated from total areas of habitat Superclasses and densities within each Superclass for each species. Migratory, foraging, and nesting guild information for each species gleaned from Birds of the World accounts (Billerman et al., 2022), suppemented by a review by Azeria et al. (2011). Migratory guilds comprise resident (RES), short-distance migrant (SDM), and long-distance migrant (LDM) species. Foraging guilds include omnivorous (generalist), bark-gleaning (bark), ground foraging (ground), foliage-gleaning (glean), hawking (hawk), and herbivorous, or primarily foraging for fruits, seeds, or nectar (plant). Nesting guilds include cup-nesters separated by canopy stratum (ground, shrub, and tree), cavity nesters (cavity), and ground-level nesters dependent on decaying stumps or downed wood (log).

*** Relative contribution of density (versus Superclass area) to abundance change calculated as the expected abundance with 2021–22 per-superclass densities under the assumption of no change in superclass areas; contributions >100 scaled to 100.

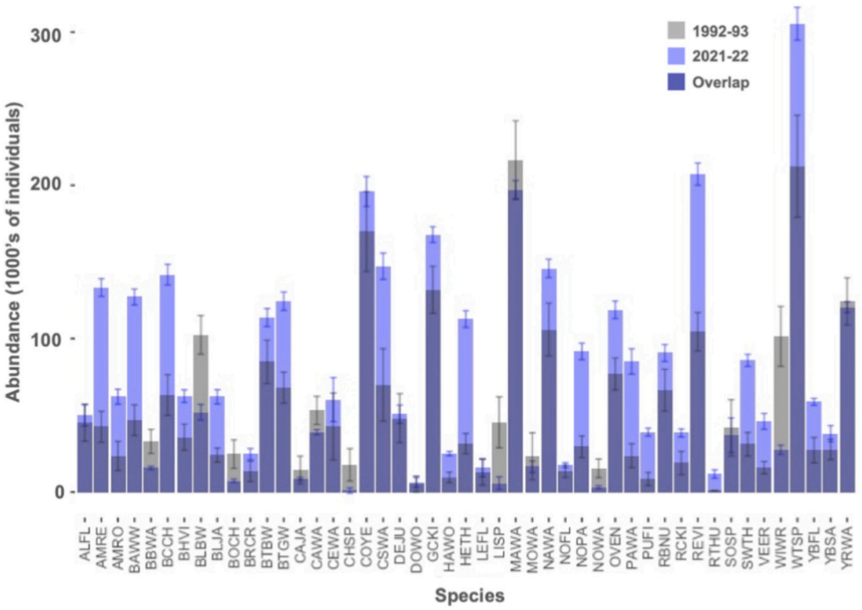

Fig. 6. Landscape-scale abundance from 1992-93 to 2021-22 for the core subset of the 47 bird species with detection frequency > 0.03 in either study period. Bars are overlaid such that dark purple indicates the lower of the two abundances. Error bars are 83.4% confidence intervals; a lack of overlap is equivalent to significance $p < 0.05$. Common names associated with each bird species code can be found in Table 3.

Additionally, insect populations may show varying responses to commercial forest management. For instance, abundance and richness of forest lepidopterans in commercial forests decrease significantly more strongly in response to clearcutting than to partial harvest (Summerville and Crist, 2008), and community composition recovers with regeneration (Fisher and Peterson, 2021). Lepidopteran larvae comprise a major portion of the breeding-season diets of many species in our focal assemblage (Miller et al., 2022; Morse, 1989), thus it is possible that the widespread shift from clearcutting to partial harvest and increases in regenerating forest since 1990 contributed to increased food availability within our focal region, and thus boosted reproductive success across the bird species assemblage over that time period.

Third, conspecific attraction could augment reproductive output and adult abundance through increased immigration (Reed and Dobson, 1993; Swift et al., 2023; Valente et al., 2021). Migratory species within our assemblage commonly use the presence of conspecifics that have already settled as a cue for habitat selection (Morse, 1989; Reed and Dobson, 1993; Swift et al., 2023; Valente et al., 2021), and this cue may outweigh vegetation structure (Betts et al., 2008). Thus, increasing populations in Maine commercial forests could recruit further individuals during spring migration. Additionally, many species that breed in this region prospect widely for new territory during post-breeding dispersal (Ciaglo et al., 2021; Cooper and Marra, 2020; Oro et al., 2021; Pärt and Doligez, 2003), which can influence settlement in subsequent breeding seasons. It is possible that breeders dispersing from elsewhere in the region could recognize higher reproductive success (Piper, 2011; Reed et al., 1999), habitat structural quality (Arlt and Pärt, 2008; Pärt et al., 2011) or food abundance (Côté et al., 2007; Moisan Perrier et al., 2021) in forests in our focal region and opt to settle there in subsequent years.

Finally, changes in forest structure and composition could have improved habitat quality for certain species. Since 1992–93, the functional mean age of Regeneration appears to have increased, with this Superclass exhibiting greater basal area and structural complexity. Thus, regenerating stands may now provide more suitable habitat for older-forest birds. Simultaneously, the mean age of Mid-aged Softwood appears to have decreased, with dominant woody plant mass shifting from softwood trees towards softwood saplings. This may have improved mid-aged forest habitat for some species, particularly boreal species associated with very dense young-to-mid-aged softwood. Finally, two major compositional shifts occurred across the landscape: the shift from American beech to yellow birch in mature forest, and the shift from red and black spruce to balsam fir in mid-aged forest. Multiple species within our focal bird assemblage have shown marked foraging preferences between balsam fir and spruce species (Morse, 1989; Régnière et al., 2021), and between yellow birch and American beech (McKinley, 2004). Thus, a landscape-scale compositional shift towards particular tree species might support density increases in associated bird species.

4.2. *Contrasts to nearby forest bird studies*

Interregional differences in bird abundance changes could also be explained by differences in forest management. For instance, planted forests are far more common in intensively managed Canadian Maritimes forests (Betts et al., 2022) than in adjacent northern Maine forests, which rely largely on natural regeneration after harvest. Natural regeneration produces denser stands with distinct herbaceous communities relative to planted forests (Gunn et al., 2019; Haughian and Frego, 2016), and thus may provide different habitat value to some species. Simplification of forest structure in planted stands has been linked to loss of important structural features for mature-forest birds (Eggers et al., 2022; Versluijs et al., 2017), and consequently is hypothesized to be a major driver of mature forest bird declines in the Maritimes (Betts et al., 2022).

Interestingly, multiple species identified as mature-forest-obligates in other studies from northeastern North America, including red-breasted nuthatch, golden-crowned kinglet, hermit and Swainson's thrushes, ovenbird, and blue-headed and red-eyed vireos (Betts et al., 2022; Guénette and Villard, 2005; Pohlman et al., 2023; Rolek et al., 2018; Schmiegelow et al., 1997), exhibited much broader habitat

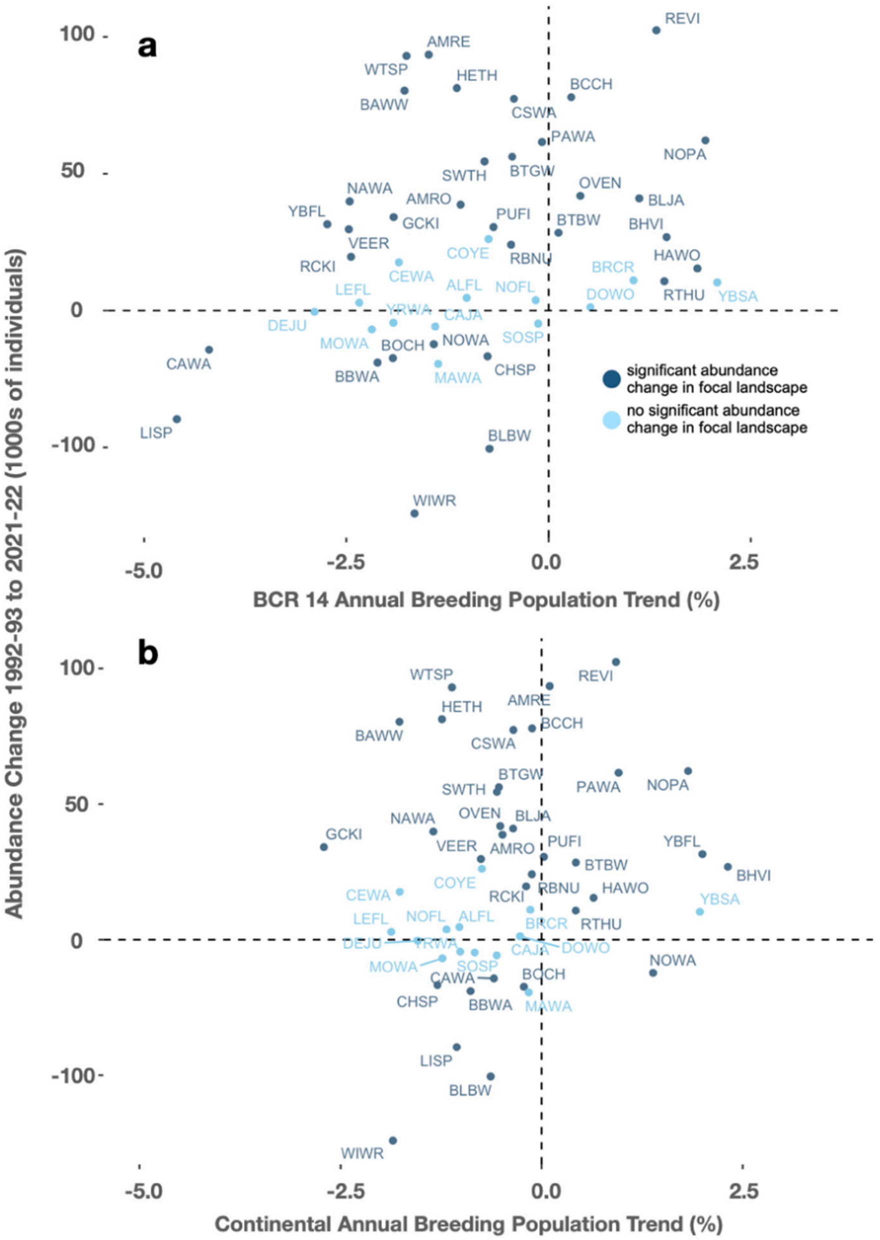

Fig. 7. Abundance change from 1992-93 to 2021-22 for each species in the core subset of 47 bird species (detection frequency > 0.03 in either study period) relative to proportional annual abundance trend over the same time period (1993-2021), derived from Breeding Bird Survey data for a. Bird Conservation Region 14, which included our study area, and b. North America. Where abundance change within the focal landscape was statistically significant, species are depicted in dark blue; non-significant changes are depicted in light blue. Common names associated with each bird species code can be found in Table 3.

associations in our focal landscape. It is unclear whether this apparent niche broadening is ephemeral, but our observations are not unique: other studies have reported members of this group of species using young forests in northern Maine (Collins, 1983; Hagan et al., 1997; Titterington et al., 1979) and showing strong relationships with partially harvested stands (Akresh et al., 2023).

Thus, it is possible that young forests in our focal region provide more suitable habitat for typically mature-forest species than do forests of similar age in the Canadian Maritimes. While we cannot draw this comparison directly without comparable vegetation data from other commercial forests, the structural changes we observed since the 1992–93 study (Hagan et al., 1997) within the Regeneration Superclass are intriguing in this regard. Regeneration saw a significant increase in canopy closure and the volume of live hardwood and softwood trees, all of which have been identified as important structural features for mature-associated species such as those noted above (Betts et al., 2022; Pohlman et al., 2023; Tremblay et al., 2018).

4.3. *Potential drivers of abundance decline*

Among the species with significant abundance declines since 1992–93, a combination of factors may be at work. Three of these species, bay-breasted warbler, boreal chickadee, and Lincoln's sparrow, are near the southern edge of their breeding distributions in our study area, thus their declines may be in part due to northward shifts out of our study area in response to climate change (e.g., Lehikoinen and Virkkala, 2016). Concurrent declines in these species at regional scales are consistent with this prediction (Virkkala, 2016).

External pressures such as sources of mortality during migration and loss of habitat on wintering grounds may also be drivers of abundance change in our study area, regardless of changes in breeding habitat (Calvert et al., 2009). In particular, we would expect an influence of this mechanism where abundance declines were consistent between our study and BBS data, or density declines occurred across cover types (Pohlman et al., 2023). For example, the Canada warbler is a species of conservation concern due to widespread population declines and vulnerabilities across the annual cycle (Céspedes and Bayly, 2019; Lambert and Faccio, 2005; Roberto-Charron et al., 2020). The alignment between significant Canada warbler declines within our focal landscape and strong declines at regional and continental scales suggests that non-breeding factors may have influenced the landscape abundance change (Wilson et al., 2018). However, Canada warbler densities significantly declined in only one forest Superclass, Residual, which was additionally surprising given that this forest type has been identified as preferred for this species in commercial forest landscapes due to its complex shrub layer structure (Lambert and Faccio, 2005). Thus unmeasured structural change(s) within this Superclass since 1992–93 could have led to lower breeding densities.

For species associated with specific habitat features strongly tied to mature forests, inconsistent availability of these features in younger forests coupled with mature forest loss could also lead to decline. For example, Blackburnian warblers showed the strongest associations with Mature Softwood forest of any species within our focal assemblage, and declined significantly in landscape-level abundance despite positive changes at regional and continental scales. Interestingly, the mature-forest-association of this species appears to be relatively recent: densities shifted significantly out of Mid-age Softwood and Mixedwood and into Mature Softwood since 1992–93. Concurrently, Mid-age Softwood stands became structurally younger: basal area of softwood trees declined while the number of stems in the two tallest young tree/shrub classes significantly increased. Whether these changes represented thresholds of habitat quality for Blackburnian warblers is as yet unknown, although Betts et al. (2022) hypothesized that habitat thresholds could explain the significant declines they estimated by backcasting for this species over a similar time period in Canadian Maritimes commercial forests.

4.4. Flexible habitat selection

We expected that changing areas of each Superclass from shifts in forest management since 1992–93 would influence bird populations, thus the predominance of density change rather than Superclass area as the driving factor in abundance changes was surprising. The overall degree of density change across species was far greater than expected: 42 of 47 species showed a significant density change in at least one Superclass. Moreover, patterns of density change were not uniform: across species, these included cross-habitat inflation or deflation of density, apparent niche broadening and narrowing, and shifts to new peak-density Superclasses. This suggests a greater possible role of flexible habitat selection in shaping avian assemblages in the Wabanaki - Acadian Forest than has been previously discussed (e.g., Betts et al., 2022). This presents an especially important caveat to consider when extrapolating current density-habitat relationships onto past or future landscapes (e.g., Hallman et al., 2021), as failing to account for spatio-temporal change in habitat associations could skew reported population changes. Previous authors have addressed potential issues with space-for-time substitution; for example, Betts et al. (2022) used BBS data to validate model projections from their own surveys. However, fixed habitat associations remain a standard assumption in species distribution modeling (Dormann, 2007; Taheri et al., 2021).

We explore flexible habitat selection in greater detail in a separate paper (Authors, unpublished results B), and so here we highlight how coarse shifts in density might interact with forest management to confer either vulnerability or resistance to landscape change for a particular species. Broadly, such shifts might reflect both changes to the fundamental niche of a species (e.g., a shift in the Superclass where a species has its highest density), or to the realized niche on our landscape due to some deterministic driver (e.g., niche broadening from spillover due to saturation of preferred habitat). We consider both to be forms of flexible habitat selection.

Localized density increases in subsets of Superclasses could indicate tracking changes in the distribution of important structural features, as we hypothesized might be the case for expected mature-forest associates that increased in younger forests. For example, the significant increase of expected Clearcut specialists white-throated sparrow, alder flycatcher, and common yellowthroat in the Residual Superclass, which expanded in area since 1992–93, allowed these species to maintain or increase their overall abundance even with the considerable decrease in Clearcut area. Similarly, despite declining significantly in density in five Superclasses, the maximum amount for the assemblage, magnolia warblers did not significantly decline in abundance, as they maintained their highest densities in Regeneration and Residual Superclasses, which increased in area. In contrast, winter wrens showed the steepest density declines in these two Superclasses, and the largest abundance decline over time, from an estimated 101,000 to 28,000 individuals. For this species, factors beyond our focal landscape may be reducing the pool of returning breeders, but loss of key habitat features such as downed deadwood or upturned root masses could also be contributing.

5. Conclusion

The unexpected abundance increases we observed are likely influenced by factors both within and beyond our focal landscape. However, the broad niche space exhibited by many species, particularly those restricted to mature forest in other primarily commercially managed landscapes, suggests that the mosaic of commercial and preserved forests in northern Maine may be providing higher habitat quality than that in nearby regions across multiple forest types. Monitoring increasingly limited forest types and age classes, especially late-successional forest and associated bird species, may be important for preventing future bird declines. Additionally, both the wide range of habitat associations across the assemblage and the prevalence of change in habitat association since 1992–93 suggest that flexible habitat selection may play a greater role than is often explored in studies of forest bird responses to management. Incorporating this understanding into future forecasting and backcasting models could improve their predictive power, and thus better guide bird conservation efforts.

CRediT authorship contribution statement

Fen S. Levy: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Conceptualization. **J. Michael Reed:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Peter S. McKinley:** Writing – review & editing, Methodology, Investigation, Conceptualization. **John S. Gunn:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Kelsi Anderson:** Writing – review & editing, Methodology, Investigation, Conceptualization. **John M. Hagan:** Writing – review & editing, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Funding

This work was funded by the National Fish and Wildlife Foundation, the UMaine Cooperative Forestry Research Unit, Maine Timberlands Charitable Trust, Tufts University, the National Council for Air and Stream Improvement, Maine Outdoor Heritage Fund, the UNH Cooperative Extension, and Weyerhaeuser Company.

Declaration of competing interest

The authors of this manuscript remain solely responsible for its content and conclusions.

Acknowledgements

Many people were key to making this ambitious project possible. The authors are grateful to all the forest managers and landowners who embraced repeating the early 1990s study, and provided electronic stand maps of the study area. In particular, the authors thank Henning Stabins (Weyerhaeuser), Eugene Mahar, Jim O'Malley, and Colton Burgess (Landvest), Trevor London and Lance Case (Huber Forest Resources), and Steve Tatko and Jenny Ward (Appalachian Mountain Club). The authors are especially grateful to Landvest, Huber Forest Resources, and Diane Bartley for field lodging in 2021 and 2022. The authors are grateful to the many diverse funders of this project (see below). The authors thank the Spatial Informatics Group – Natural Assets Laboratory (SIGNAL), and especially Operations Manager Amy Matthews for serving as the project's fiscal agent. Finally, this study could not have happened without the dedication of the 2022 field team: Ryan Andrews, Jude Dickerson, Josh Kolasch, Molly Lynch, Hannah Mirando, Ben Shamgochian, and Jalen Winstanley. The 2020s study would not have been possible without Manomet's support of the original 1990s study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110934.

Data availability

All data used in the analyses can be found at doi:https://doi.org/10.6084/m9.figshare.25883863. Data on annual harvest volumes in Maine by harvest type are available in Maine Forest Service reports (https://www.maine.gov/dacf/mfs/publications/annual_reports.html). Annual changes in Breeding Bird Survey data (for the Maine and Bird Conservation Region (BCR) 14) for focal species can be downloaded from the Partners In Flight Population Estimates Database (https://pif.birdconservancy.org/population-estimates-database/). All R code used in the analyses can be found at doi:https://doi.org/10.6084/m9.figshare.25883863.

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