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## TEMPORAL CHANGE IN THE FOREST BIRDS OF NORTHEASTERN CONNECTICUT SHOWS PARTIAL CONCORDANCE WITH PREDICTED EFFECTS OF CLIMATE AND HABITAT CHANGE

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**Abstract.** I studied how a breeding forest bird community changed over 20 years in the largely undisturbed forests of the Northeast Uplands ecoregion of Connecticut to determine whether changes showed a relationship to predicted effects of climate change as well as to effects of habitat changes occurring over this period. Moreover, I wished to compare how changes documented at this regional scale compared with patterns observed at the continental scale and at a more local scale. I predicted that patterns detected would relate to the region's warming climate and maturing forests and that patterns would most closely resemble those of the continental scale. I gathered data via variable circular plot surveys performed at five 3.2 km-long transects, which I surveyed for two years each at the beginning and end of the study period. Species richness and community density varied little over time. However, long-term turnover in species composition was nearly 30%, supporting the view that bird communities are dynamic rather than static assemblages. Community density more closely resembled continental patterns and species with population trends coincident with continental trends were 1.6 times more than at the more local scale of the nearby Yale-Myers Forest. Species at their southern range limit undergoing population declines and species at their northern range limit undergoing population increases accounted for 26% of species, with four species showing the strongest population shifts having trends consistent with predicted effects of climate change. Forest interior species undergoing population increases and edge/successional species undergoing declines accounted for 36% of species. Moreover, increases were greater than decreases among forest interior populations. Furthermore, far more edge/successional species were declining than increasing. However, most populations undergoing changes were not associated with range limits. Moreover, 43% of species had population trends opposite to those predicted by a habitat hypothesis. The distributions and populations of community members may best be described as a consequence of a complex interplay of responses to multiple and sometimes conflicting factors and factors operating at differing environmental scales.

Climatic (Hitch and Leberg 2007) and structural habitat change and their interactions are among processes thought to affect population trends in breeding forest bird communities of regional landscapes (Goodale et al. 2009, Holmes and Sherry 2001, Duguid et al. 2016, Hanle et al. 2020) change, which may themselves be related (Whitaker 2017). However, patterns observed in population growth and de-

cline are related to the geographic scale of observation, as local habitat management might drive population phenomena at local scales, whereas wintering ground conditions or regional disease outbreaks might drive population phenomena at landscape scales (Wiens 1981, James et al. 1996, Bowler et al. 2021). In a previous investigation, Craig et al. (2022) determined that species richness varied little, abundance of individuals within the community increased by 24%, and species turnover exceeded 30% over 34 yr at the 3213 ha Yale-Myers Forest of

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Northeast Connecticut—a research and demonstration forest operated by the Yale University School of Forestry and Environmental Studies. Expected effects of climate change on populations (e.g., Rustad et al. 2014) were consistent with such findings as population declines of some species at their southern range limit and population expansions of others at their northern range limit, but such habitat effects as population growth among edge/successional-associated species in this highly managed location appeared related to a greater number of shifts. However, much contrary data such as boreal-associated species ranging south indicated that these factors were not alone in driving community change.

In this study, I expand the focus of Craig et al.'s (2022) investigation to the entire Northeast Uplands ecoregion of Connecticut—a ca. 15,000 ha tongue of high elevation, largely mature, extensively forested landscape with a more northern-associated forest cover than the rest of eastern Connecticut (Dowhan and Craig 1976). As such, some forest bird species have historically been at or near their range limits there (Craig 2017), making them potentially sensitive indicators of the effects of climate change. I compare results of this study with those of a study with a similar sampling effort at Yale-Myers Forest to determine whether this larger view offers insights into mechanisms driving long-term community change and the influence of scale of observation on observed community patterns.

I sought to determine the degree to which this regional breeding forest bird community has exhibited temporal change and to what extent changes in climate and habitat structure appeared related to such change. A warming climate may be expected to be associated with declining bird populations at their southern range limit and expanding populations at their northern limit, so I predicted that these patterns would be evident in this community. Moreover, because the Northeast Uplands' forests are extensive and maturing, with earlier successional habitat declining in occurrence (Alerich 1999, Butler 2017), I predicted that bird populations associated with forest interiors should be differentially increasing and those associated with edge/successional habitats should be decreasing. I also predicted that population trends in this region would more closely reflect those observed at the continental level than at Yale-Myers Forest, where local forest management practices produce more extensive earlier successional landscapes (Craig et al. 2022).

Connecticut's climate has indeed changed historically, with annual mean temperatures rising 1.7 °C since 1900 (NOAA 2020). However, Connecticut's forest composition has been demonstrated to be driven more by land-use history than climate change (Ashton et al. 2015). Connecticut's forests have generally not succeeded to southerly-associated plants but rather to shade-tolerant species more typical of

northern forests (Alerich 1999, Butler 2017), although some species typical of the Southeast have increased (Craig 2017, Lefland et al. 2018). Notably, the occurrence of the tulip poplar (*Liriodendron tulipifera*), near its northern range limit in the study area, has increased greatly in the forest canopy since the 1970s (R. Craig, M. Ashton, pers. obs.). The character of Connecticut's forests is also continually changing in response to pests and disease (Wharton et al. 2004). In brief, community change over time is a complex phenomenon related to multiple factors.

## METHODS

**Study areas.** Compared with the rest of eastern Connecticut, the Northeast Uplands have a sparse human population of 3.9–9.7 individuals/km<sup>2</sup> and have the lowest temperatures (mean summer = 21 °C, winter = –2 °C), shortest frost-free growing season of 150 days, annual mean rainfall of 123 cm and steeply hilly topography with elevations ranging from ca. 180 to 400 m (Dowhan and Craig 1976, NOAA 2020). Forest covers about 70% of the region (Alerich 1999, CLEAR 2020), which thus contains ca. 10,500 ha of forest that is 21% oak-dominated, 11% mixed deciduous, 44% conifer-central hardwood, 3% pine-oak, 18% pure conifer and 2% mixed cover (Craig 2017). Boundaries of the ecoregion as defined by Dowhan and Craig (1976) are strongly supported by measures of habitat characteristics mapped by Arvisais and Craig (2018).

**Bird surveys.** In initial surveys of Northeast Connecticut in 2001, I established 26 bird survey routes, five fell within the ecoregion. A table describing the location and characteristics of each of these is in Craig (2017). These five survey transects each traversed about 3.2 km for a total sample of ca. 16 km of forest—the same as that sampled at Yale-Myers Forest. I situated transects on public or private lands with public access, using a randomized block protocol to the extent practical based on parcel availability such that I chose sites at random from available parcels and placed single transects within individual blocks. During my original surveys, I restricted observations to between 20 May–5 July, the height of the local breeding season, to minimize any possible alteration of results due to temporal behavioral changes. I repeated these procedures for my 5 study sites in 2004, 2020 and 2021, which I visited once each year in random order.

I used the Variable Circular Plot (VCP) technique to survey. VCP has wide utility in evaluating populations over a variety of terrains, has a well-developed theoretical underpinning that accounts for differential detectability of species (Buckland et al. 2001, Thomas et al. 2010, Research Unit for Wildlife Population Assessment 2020) and has long been used for conducting large scale forest bird surveys (e.g., Scott et al. 1986, Camp et al. 2009, Linck et al.

2020). I surveyed 15 points/transect at each study site—the maximum I could visit during the peak of morning bird activity (before 09:00 h). I recorded locations, elevations of points and horizontal distances between points with a Garmin Etrex global positioning device (Garmin, Inc. Olathe, KS). Routes began at ca. 05:15 h, lasted 3.5–4 hr each and were performed under conditions of low wind and negligible precipitation.

Survey routes primarily followed existing trails in order to travel expeditiously between points and to re-locate survey points easily. When no trails were present, I followed compass bearings through forest to subsequent points. Survey points were ca. 200 m apart, a distance that I empirically determined to minimize detecting the same bird from two successive points. In those few instances where I found a wide-ranging, loudly vocal individual to be detectable from two stations, I entered its presence into calculations for only the first station of encounter.

At each point, I estimated the horizontal distance at first detection to each bird detected. To help calibrate distance estimates, before surveys I placed colored plastic flagging at 10 m intervals to 70 m from one point along each route and periodically walked from a point to detected birds to verify distance estimates. I also plotted on topographic maps the location of distant birds so that I could directly measure from the map their distance from the sampling point. Furthermore, I relied on my long experience with distance sampling of forest birds to record accurately distances of individuals encountered (e.g., Craig 1996, Craig et al. 2003).

My sampling period at each station was eight minutes, a time often used in VCP surveys of forest birds (e.g., DeSante 1981, Camp et al. 2009, Linck et al. 2020). It was short enough to approximate an instantaneous count (minimize movement of birds), yet long enough to record adequately all birds present. On a few occasions I detected rarer bird species, particularly raptors, outside this sampling period. If I found no other individuals during the survey, I included the initial detection in my survey, reasoning that doing so yielded a more accurate representation of species richness.

Although I recorded all birds encountered regardless of habitat affiliation, in analyses I considered only those species associated with forest (Table S1). I broadly defined such species as those that inhabit 1) unbroken forest, 2) forest openings caused by tree fall or selective logging, 3) closed to partly open swamps and 4) forested river banks. These constituted principal habitat patch types within the broader category of forest landscape, with the last three often referred to as forest gaps. I did not include in detailed analyses species that were associated primarily with marshes, shrub swamps, extensive fields, open water, or species detected flying high overhead, whose presence was unrelated with the

forest environment. Hence, species like the Willow Flycatcher (*Empidonax traillii*) were associated exclusively with marsh shrubbery and were excluded from analyses.

**Habitat evaluation.** In addition to bird surveys, I measured six habitat variables at each survey point. Beginning in 2001 and repeated each year of the study thereafter, I visually evaluated habitat to a 70 m radius from each sampling station for: 1) forest type, 2) vegetation type, 3) moisture regime, 4) diameter of canopy trees at breast height (dbh), 5) canopy cover and 6) understory density. Following bird surveys, I re-visited each point each year of the study to verify these measurements. Details of habitat evaluation procedures are in Craig (2017). Briefly, I recorded a numerical category for each habitat measure. Forest type consisted of 3: 1) deciduous: <10% evergreen conifers, 2) mixed: 20–60% evergreen coniferous, 3) coniferous: >70% evergreen conifers. Vegetation types represented major associations of tree species encountered: 1) oak-dominated (e.g., oak-hickory-birch), 2) mesic/hydric mixed deciduous; e.g., maple-birch-ash, 3) conifer (hemlock-white pine)-northern hardwood, 4) pine-oak, 5) conifer (hemlock, plantation conifers, white pine), 6) mixed sites, e.g., half xeric oak, half hydric mixed deciduous. Moisture regimes were: 1) hydric, 2) mesic and 3) xeric. In practice, I distinguished swamp sites as hydric, dry ridges and sandy uplands as xeric and used mesic as a broader category describing intermediate situations. I divided prevailing canopy tree dbh into 3 categories: 1) young forest: <15 cm, 2) mature forest: >15–45 cm, and 3) old growth: >45 cm. I similarly divided canopy cover into 3 categories: 1) open: <40% cover, 2) semi-open: 50–60% cover, and 3) closed: >70% cover. I evaluated understory density for larger shrubs and saplings ca. 1–4 m tall rather than for low ground covers and herbaceous growth: 1) open: <20% cover; 2) moderate: 30–60% cover, and 3) dense: >70% cover. In addition to these measures made at the study sites, I assessed long-term USDA Forest Service data (USFS 2020) on tree volume and tree number for the state as a whole.

**Analysis.** I computed population densities with Distance 7.3 software (Thomas et al. 2010, Research Unit for Wildlife Population Assessment 2020), consulting also the protocols of Buckland et al. (2001) in selecting detection functions. Based on initial plots of species detection probability vs. detection distances, I grouped similar observations, often into 5–10 categories, with interval cut points placed between favored rounding distances to minimize data “heaping” and to improve robustness of density estimation. I explored the fit of detection data to six models recommended by Buckland et al. (2001): uniform/cosine, uniform/simple polynomial, half normal/cosine, half normal/hermite polynomial, hazard rate/cosine and hazard rate/simple polynomial. As also recommended by Buckland et al. (2001), I

TABLE 1. Repeated measures tests of annual shifts in species richness and community abundance (males/km<sup>2</sup>).

	<i>F</i>	<i>df</i>	<i>P</i>
Species richness			
Years	7.76	3,2	0.12
Species abundance			
Years	4.23	3,2	0.20

explored truncating detection data for individual species to eliminate the largest 5–10% of values, which can facilitate model fitting by eliminating outliers. When doing so improved model fit, I employed this technique. I sought a conventional distance sampling model that yielded a smooth curve with near 100% detection probability at the left shoulder, evaluated fit by visual inspection of plotted data, with Akaike’s Information Criterion and with chi-square goodness of fit tests and computed variance empirically. When species occurred in flocks, I performed analyses using clusters as the basis of density measurement. I used all distance measures obtained in this study as well as all gathered from my 2001–2009 surveys of Connecticut/Rhode Island forest birds (Craig 2017) in computing global detection functions (38,143 total detections), as large samples produce the most accurate detection functions and, thus, density estimates. In reporting results for community densities, I divided density estimates by two for species in which males and females were equally likely to be encountered before summing them with densities of those species represented by solely singing males. Doing so improved comparability among the study sites by accounting for any differences among them in the prevalence of densities represented by both sexes.

Based on Craig’s (2017) quantitative evaluation of habitat use by Connecticut forest birds, I divided species into those associated with one of three habitat categories: 1) forest interior, 2) forest edge and successional habitats and 3) generalists. Using Breeding Bird Survey (BBS) data (Sauer et al. 2017), I also classified species into those showing continental population 1) increases, 2) decreases or 3) little change since 1966, with the latter defined as a BBS population trend of  $< \pm 0.4$ . In addition, I classified species as to their North American range using 2011–2015 range maps from Sauer et al. (2017): 1) species for which 90% of the range east of the Rocky Mts., excluding an Appalachian Mountain range extension, was north of Connecticut, 2) ones for which 90% of this eastern range was south of Connecticut, and 3) ones for which Connecticut was within the core of the range ( $< 90\%$  of range to the north or south). As I had previously done for Yale-Myers

Forest (Craig et al. 2022), for all these categories I computed the number of species in each of these groups and the size of population increases or decreases for 2020–2004, 2020–2001, 2021–2004, 2021–2001, 2020–2021 and 2001–2004. I computed proportionate change among categories in year–year comparisons by separately dividing increases and decreases by total count change. When results for species provided evidence for a relationship between population patterns and additional potential causative agents, I report these under the heading of Species Trends.

I examined patterns in species richness—the sum of all forest bird species encountered, community density—the sum of computed densities for all forest species encountered, temporal community population shifts and species turnover for the years of the study, with turnover calculated by summing the species gained and lost and dividing this number by the total species pool for the years of comparison. Hence, in these instances I tested the null hypotheses that temporal effects on species richness, community density and species composition did not occur. I also computed species accumulation curves for each year of the study in order to assess the completeness of community sampling.

Because I gathered data at the same sites over a series of years, they were repeated measures. Hence, when required, I employed repeated measures analysis of variance in examining results. In the case of species richness and community density analyses under the heading of Habitat and Community Trends, I entered years into models as a within-subject factor. Individual transect measures were observations within years. In analyses presented under the heading of Population Trends below, I entered habitat category, continental population trend or continental range as well as study site population trends (increases vs. decreases) into models as between-subject factors. I also grouped year-year comparisons into short- (2001–2004, 2020–2021) and long-term (2020–2001, 2020–2004, 2021–2001, 2021–2004) comparisons to facilitate repeated measures analysis, entering these as a within-subject factor and having year-year comparisons function as observations within categories.

In these instances, I tested the null hypotheses that no temporal effects occurred in habitat occupancy, relationships to continental population trends or relationships to continental ranges. In these and other tests, I checked the fit of data to model assumptions with data plots, frequency histograms, normal Q-Q plots, residual plots, Levene’s homogeneity of variance tests, Shapiro-Wilk normality tests and Mauchly’s W test. When assumptions were violated, I employed square root transformations to normalize data and stabilize variances. When assumptions remained poorly met, I employed Friedman related samples nonparametric tests.

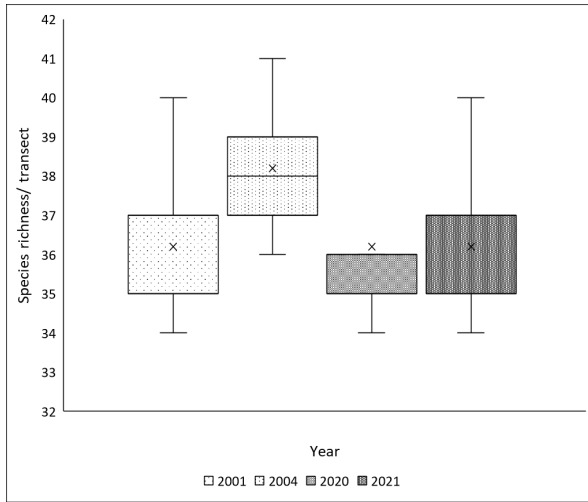


FIG. 1. Repeated measures of species richness estimates at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut, for 2001–2021 species richness/transect showing mean (x), median (—), standard deviation (shaded) and range (T).

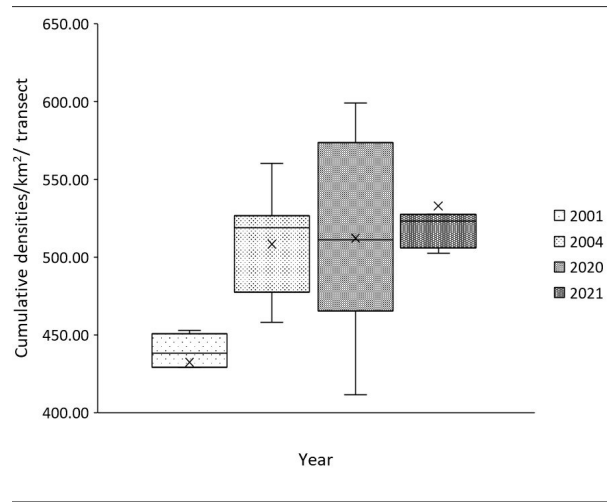


FIG. 2. Repeated measures of 2001–2021 mean community density as measured by the sum of densities of all species encountered/transect at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut.

In investigating trends from 2001–2004 with those of 2020–2021 under the heading of Species Trends, I limited comparisons to those where total detections for a species were  $\geq 5$ , as examination of the data indicated that differences encountered below this level might be due to chance. Above this number, population differences encountered corresponded well with observations from Craig (2017) and Craig et al. (2022). To obtain an overall view of the contribution of individual species to total population changes from 2001–2004 to 2020–2021, for each species I summed computed densities for all 2020 and 2021 transects and subtracted the values obtained by the summed densities for 2001 and 2004. Positive values indicated density increases and negative values indicated density declines. I divided these by the sum of all 2001–2004 to 2020–2021 density changes to obtain the proportionate change.

**RESULTS**

**Habitat and community trends.** Compilation of habitat measures showed only nominal change since 2001, with forests now averaging slightly more open (2001–2004 =  $2.67 \pm 0.22$  vs.  $\pm SD_{2020-2021} = 2.66 \pm 0.20$ ; Friedman  $\chi^2 = 6.85$ ,  $df = 3$ ,  $P = 0.08$ ), deciduous (2001–2004 =  $1.93 \pm 0.46$  vs.  $\pm SD_{2020-2021} = 1.90 \pm 0.47$ ; Friedman  $\chi^2 = 5.37$ ,  $df = 3$ ,  $P = 0.15$ ) and with more understory cover (2001–2004 =  $2.15 \pm 0.13$  vs.  $\pm SD_{2020-2021} = 2.18 \pm 0.16$ ; Friedman  $\chi^2 = 1.39$ ,  $df = 3$ ,  $P = 0.71$ ).

I recorded 73 forest-associated species during this investigation (Appendix). Species accumulation

curves demonstrated that by the 3<sup>rd</sup> of five transects virtually all species present had been detected, indicating nearly complete sampling of species composition. Repeated measures analysis of species richness and community density (Fig. 1, Table 1) showed non-significant variation among years. In contrast, species turnover (Fig. 3) on individual transects showed a difference among years (Friedman  $\chi^2 = 11.82$ ,  $df = 5$ ,  $P = 0.04$ ), with 2001–2004 primarily responsible for this by differing most from other year-year comparisons in having lower turnover, although both short-term comparisons ranged lower but had greater variance than longer-term ones. Turnover was high particularly for long-term comparisons, averaging 38.9%, although even short-term turnover averaged 30.6% (Fig. 3, Table 1, Appendix). Moreover, even when I compared long-term turnover for the entire species pool of the five study sites, it still averaged 29.7%.

**Population trends.** Repeated measures analysis of variance showed that forest interior, edge/successional and generalist populations had increases greater than decreases (Fig. 4, Table 2). Moreover, the three habitat categories differed, with forest interior populations having greater shifts than edge/successional ones and generalists and edge/successional having greater shifts than generalists. Short- vs. long-term population trends did not differ overall, although increasing populations were greater than decreasing in both short- and long-term population trends. In addition, forest interior and generalist populations averaged having greater changes when

TABLE 2. Repeated measures tests of temporal population shifts among species habitat associations, continental population trends and continental ranges.

	<i>F</i>	<i>df</i>	<i>P</i>
Forest occupancy-associated population shifts			
Within-subject effects			
Short- vs. long-term trend	0.01	1,6	0.94
Trend x population shift	2.55	1,6	0.16
Trend x habitat association	6.72	2,6	0.03
Trend x population x forest	7.16	2,6	0.03
Between-subject effects			
Population shift	10.73	1,6	0.02
Forest occupancy association	31.96	2,6	<0.01
Population x forest occupancy	3.26	2,6	0.11
Continental population trend-associated population shifts			
Within-subject effects			
Short- vs. long-term trend	<0.01	1,6	0.99
Trend x population shift	1.56	1,6	0.26
Trend x continental trend	2.08	2,6	0.26
Trend x population x continental	4.19	2,6	0.07
Between subject effects			
Population shift	23.60	1,6	<0.01
Continental trend	0.76	2,6	0.51
Population x continental	5.05	2,6	0.05
Geographic range-associated population shifts			
Within-subject effects			
Short- vs. long-term trend	0.11	1,6	0.75
Trend x population shift	0.64	1,6	0.46
Trend x geographic range	2.58	2,6	0.16
Trend x population x range	3.36	2,6	0.11
Between subject effects			
Population shift	9.85	1,6	0.02
Geographic range	35.02	2,6	<0.01
Population x range	1.89	2,6	0.23

undergoing long-term changes. (Fig. 4, Table 2).

Repeated measures examination of population increases vs. decreases with respect to continental trends showed that increases averaged greater than decreases, although no differences occurred between short- vs. long-term population trends (Fig. 5, Table 2). Moreover, the interaction of continental trends, increases vs. decreases and short-vs. long-term trends showed that increases and decreases were similar for continentally stable populations whereas increases were greater than decreases for other continental categories (Fig. 5, Table 2).

Repeated measures examination of population

increases vs. decreases with respect to geographical ranges showed that increases were greater than decreases (Fig. 6, Table 2). Moreover, differences occurred among the ranges with the smallest shifts occurring among populations at their southern range limit and the greatest occurring among those that were centrally distributed. I also found no overall difference between short- vs. long-term population trends in relation to geographic range (Fig. 6, Table 2).

**Species trends.** Of the 53 species with >5 observations, forest interior and particularly edge/successional species were by far the most frequently

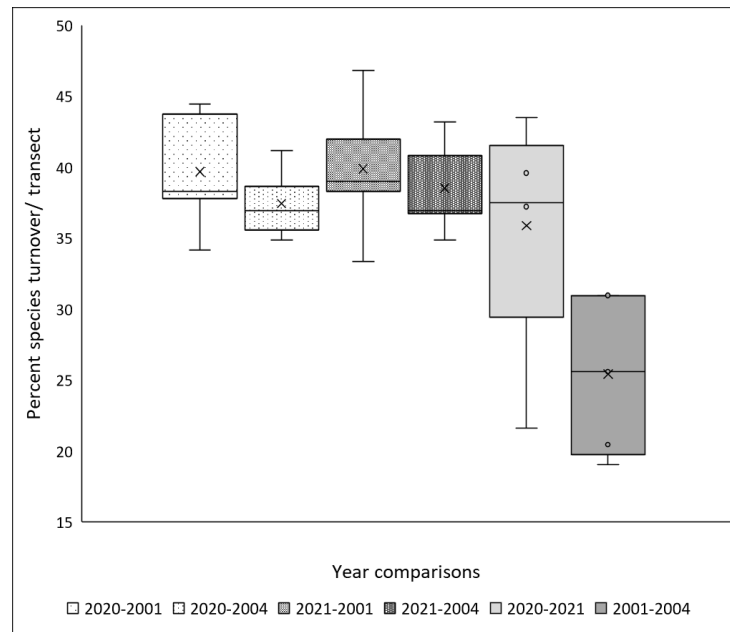


FIG. 3. Repeated measures of species turnover estimates at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut, for 2001–2021 year-year comparisons, with turnover calculated for each transect by summing the species gained and lost and dividing this number by the total species pool for the years of comparison.

occurring. Continentally declining species were also slightly more frequent than increasing species. Moreover, most species were not near their range periphery in Connecticut and the fewest species were near their northern range limit (Table 3, Appendix).

Forest interior species undergoing population increases and edge/successional species undergoing declines accounted for 36% of species. In contrast, 43% of species had trends opposite to those of predicted habitat effects. Of these latter 23 species, 15 had population trends consistent with continental trends or expected climate effects, leaving eight species trends not accounted for by habitat, continental trends or climate (Table 3, Appendix).

Species at their southern range limit undergoing population declines and species at their northern range limit undergoing population increases accounted for 26% of species. In contrast, 17% of species had trends opposite to those of predicted climate effects. Of these latter nine species, seven had population trends consistent with continental trends or expected habitat effects, leaving two species trends not potentially accounted for by habitat, continental trends or climate. The largest groups of increasing and decreasing species were not near their range limit (Table 3, Appendix).

Of continentally increasing and decreasing populations of species, 36% had the same local trends. In contrast, 28% of species in this study had trends opposite to these. Of the latter 15 species, seven had

population trends consistent with expected range or habitat effects, leaving six species trends not potentially accounted for by habitat, continental trends or climate. (Table 3, Appendix).

Examining patterns among the top 15 species undergoing the greatest population changes also proved instructive (Fig. 7). The six increasing species of the 15 accounted for 71% of all increases. Most had continentally increasing populations and four were forest interior species. None were near their northern range limit. Notably, the northerly-distributed, forest interior-inhabiting but continentally declining Veery (*Catharus fuscescens*) underwent the 3<sup>rd</sup> greatest population increase.

The remaining nine species of the top 15 were all declining and accounted for 68% of all declines. Five of the nine were also forest interior species, with the remaining edge/successional-associated. However, only three of these were continentally declining and only three were near their southern range limit. Notable among declining species were the most steeply declining, northerly distributed Black-throated Green Warbler (*Setophaga virens*) and centrally distributed Scarlet Tanager (*Piranga olivacea*), both forest interior species, neither of which is declining continentally. Moreover, the edge/successional American Goldfinch (*Spinus tristis*), Cedar Waxwing (*Bombycilla cedrorum*), Brown-headed Cowbird (*Molothrus ater*) and American Robin (*Turdus migratorius*) experienced among the

TABLE 3. Species totals for the Northeast Uplands habitat, continental range and continental trend associations.

	<b>Northeast Uplands</b>
Forest occupancy association	
Increase	
Interior forest	9
Edge/successional	9
Generalist	6
Decrease	
Interior forest	14
Edge/successional	10
Generalist	2
No change	
Interior forest	1
Edge/successional	1
Generalist	1
Continental range	
Increase	
Southern limit	5
Northern limit	8
Central	11
Decrease	
Southern limit	1
Northern limit	9
Central	16
No change	
Southern limit	1
Northern limit	2
Central	0
Continental trend	
Increase	
Increase	10
Decrease	9
No change	5
Decrease	
Increase	6
Decrease	9
No change	11
No change	
Increase	1
Decrease	1
No change	1

strongest declines.

Another among the top 15 species undergoing a notable population change was the northerly-distributed generalist Yellow-bellied Sapsucker (*Sphyrapicus varius*), which has also undergone a continent-wide population increase. Absent from the Northeast Uplands in 2001–2004, it has undergone the 6th largest population increase of species in the study area. The Common Raven (*Corvus corax*), although not one of the species with the greatest population shifts, is notable in having undergone a similarly explosive range expansion south over this time. Moreover, the southerly-distributed, forest interior-inhabiting Red-bellied Woodpecker (*Melanerpes carolinus*) occurred infrequently in the study area in 2001–2004 but underwent a 77% increase by 2020–2021.

## DISCUSSION

I observed that selective logging was principally responsible for individual sampling points becoming more open and that mortality of eastern hemlock (*Tsuga canadensis*) due to woolly adelgid (*Adelges tsugae*) infestation was related to points becoming more deciduous. Despite the general lack of temporal difference that I found, USDA Forest Service estimates of 1998–2019 Connecticut live tree volume (Alerich 1999, USFS 2020) showed a 28% increase whereas the number of live trees fell by 13%, indicating that Connecticut’s forests are trending toward more old growth-like conditions.

The breeding bird community of the Northeast Uplands ecoregion of Connecticut exhibited temporal change in some although not all parameters studied. Species richness and community density were relatively stable, as also found in other studies (Blowes et al. 2019), even though at the continental scale declines in populations are apparent across a variety of species and biomes (Rosenberg et al. 2019). Community stability was likely a reflection of the extensive and maturing forests of the region, which appear to provide the most suitable habitat for a variety of forest-dwelling species (Holmes et al. 1986, Robbins et al. 1989, Holmes and Sherry 2001). Indeed, in my ongoing studies on the effects of forest fragmentation on bird communities across southern New England, population densities of interior forest-associated species, particularly ground- and tree-nesting species, were consistently highest in those areas with the most extensive core (>100 m from edge) forest (R. Craig, unpubl. Data; see also Askins and Philbrick 1987, Zipkin et al. 2009). The detrimental effects of forest fragmentation on forest bird communities are well-documented (e.g., Dorazio et al. 2015, Farwell et al. 2020), and the deterioration of North America’s temperate forest biome across much of its extent (Thompson et al. 2002) is likely to be substantially responsible for the continental decline of forest-



associated bird species.

At the smaller scale of the more intensively managed Yale-Myers Forest portion of the region, I found a greater departure from continental trends, with clear increases in abundance occurring there (Craig et al. 2022). The conversion of forest to earlier successional landscapes that has occurred there has long been known to be associated with increasing bird population densities (Odum 1950, Kendeigh and Fawver 1981, Duguid et al. 2016). Similarly in my study, however, community population increases were greater than decreases for all habitat categories, geographic ranges and continentally population trends. Further evidence consistent with the larger scale of this study showing greater synchrony with continental patterns was that 36% of species had trends coincident with continental trends, which was 1.6 times more species than at Yale-Myers (Appendix).

Unlike richness and density, long-term species turnover for individual transects averaged 29.7%, over 20 years. The greater turnover of over 50% over 34 years for individual transects, or 30.4% for the entire species pool at Yale-Myers Forest, provided additional evidence that turnover has a temporal component, although in this case increasing availability of early successional habitats has contributed to the turnover. Such observations of substantial community turnover are similar to those noted over 30 years by Holmes and Sherry (2001) in a similarly extensive and maturing forest. Also similar to the Yale-Myers Forest portion of the study area, a 4700 ha area of temperate Polish old growth deciduous forest examined over 35 years, little change occurred in species richness and 69% of species showed population increases largely related to habitat change, although in this instance little change occurred in species composition (Wesolowski et al. 2010).

Evidence that community change was consistent with the expected effects of climate change in driving population and range shifts was present in several instances. Species at their southern range limit undergoing population declines and species at their northern range limit undergoing population increases accounted for 26% of species, virtually the same as that observed for Yale-Myers Forest (Craig et al. 2022). In particular, the strongest decline of any species was exhibited by the northerly-distributed Black-throated Green Warbler—a phenomenon also observed elsewhere in Connecticut (Comins et al. 2021). Moreover, the 4<sup>th</sup> and 6<sup>th</sup> strongest declines occurred among the northerly-distributed Dark-eyed Junco (*Junco hyemalis*) and Blackburnian Warbler (*S. fusca*). Furthermore, the 5<sup>th</sup> largest population increase occurred in the southerly-distributed Tufted Titmouse (*Baeolophus bicolor*). Notable also was the explosive increase of the southerly-distributed Red-bellied Woodpecker over

the course of this study. In addition, the continentally increasing Pine Warbler (*Setophaga pinus*), infrequently occurring in 2001–2004, was by 2020–2021 the 2nd most commonly encountered forest warbler, apparently invading eastern Connecticut from south-eastern coastal plain populations (Craig 2017). However, although such occurrences provide evidence consistent with a climate change hypothesis, alternative processes such as unmeasured changes in habitat, adaptive changes or anthropogenic effects might also account for these population patterns, and only further study is likely to distinguish among the alternative hypotheses.

Despite these findings, multiple observations were inconsistent with a climate change hypothesis. Most species and populations undergoing shifts were not associated with range limits. Moreover, unlike at Yale-Myers Forest (Craig et al. 2022), population shifts were least among those at their southern range limit. Evidence from individual species also showed strong departures with expected effects of climate change. The 3rd largest increase observed was by the northerly-distributed Veery. The 6<sup>th</sup> largest increase occurred in the Yellow-bellied Sapsucker, which has undergone an explosive range expansion south in the face of climate change. Similarly, eastern populations of the once northerly-distributed Common Raven have expanded south, again explosively. Still another example is that of the northerly-distributed Magnolia Warbler (*S. magnolia*), whose Northeastern populations have declined, although its small Northeast Uplands populations have been stable to increasing.

In all these instances for individual species, expansion into new habitats is likely responsible for driving increases, as particularly species near range limits are under selective pressure to adapt to local conditions (Liebl and Martin 2014). In the case of the traditionally second growth-associated Veery (Heckscher et al. 2020), based on large samples, Craig (2017) found no evidence for preference of younger forests or forest gaps. Moreover, the Yellow-bellied Sapsucker has expanded habitat use from edge/successional habitats to mature forest (Craig 2017, Craig et al. 2022). Similarly, the Northeastern population of the Common Raven has expanded from inhabiting remote core forests to occupying a variety of forested and non-forested habitats (Craig et al. 2022). In the case of the largely edge/successional-associated Magnolia Warbler (Dunn and Hall 2020), as of 2021 I observed that the species had expanded its local habitat use from solely successional habitats to mature forest, much as the larger populations in northwestern Connecticut had previously accomplished (Craig 2017).

Evidence consistent with habitat driving species and population shifts in the extensive and maturing forests of this study is that forest interior species un-

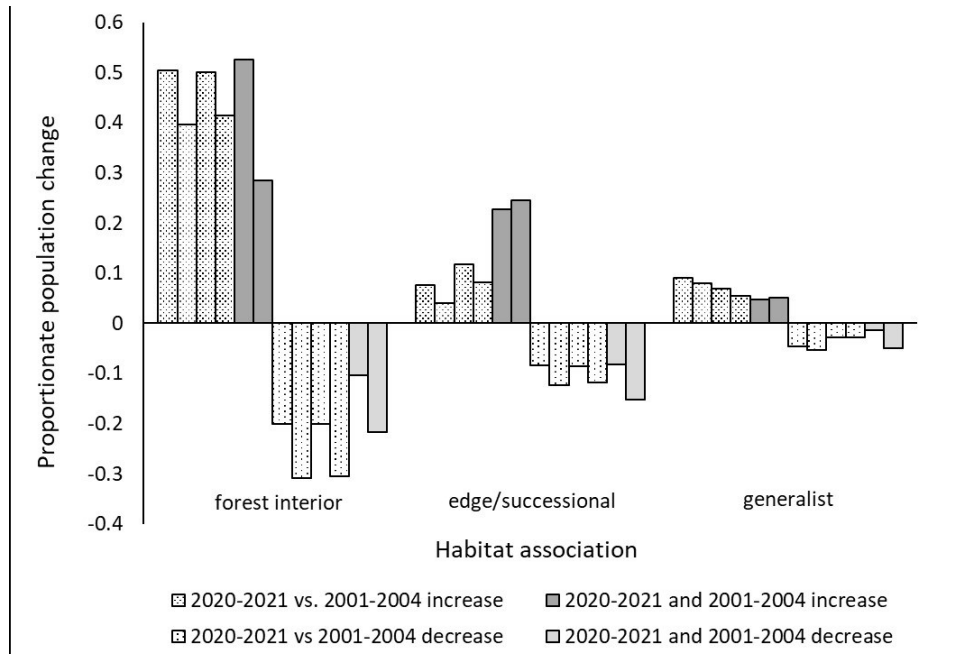


FIG. 4. Proportionate population shifts at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut for three categories of habitat use: forest interior, edge/successional species, generalist.

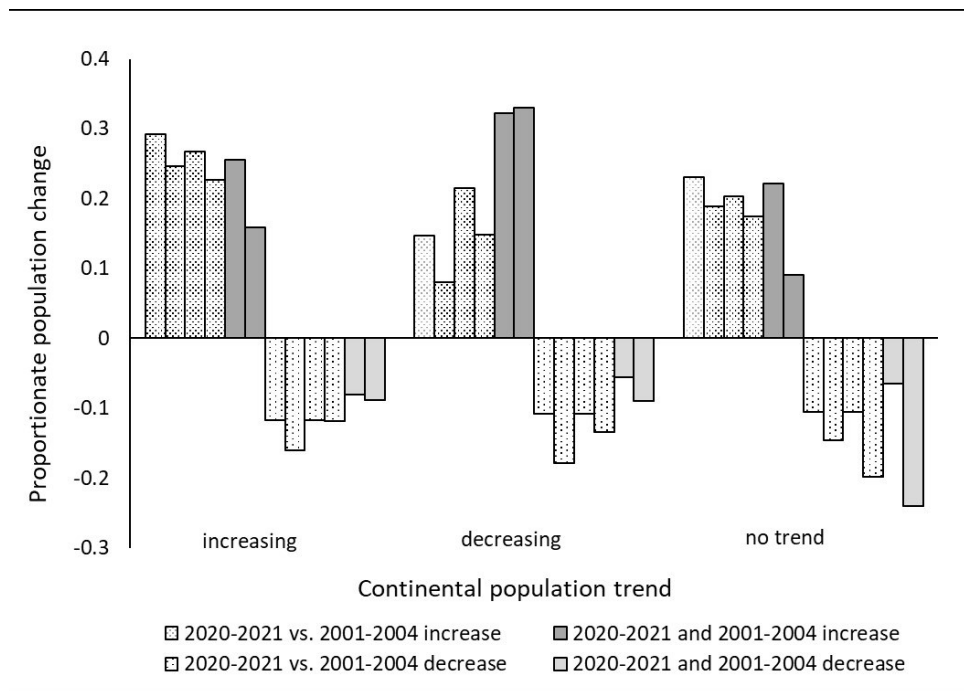


FIG. 5. Proportionate population shifts at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut for three categories of continental population trend: increasing, decreasing, no trend.

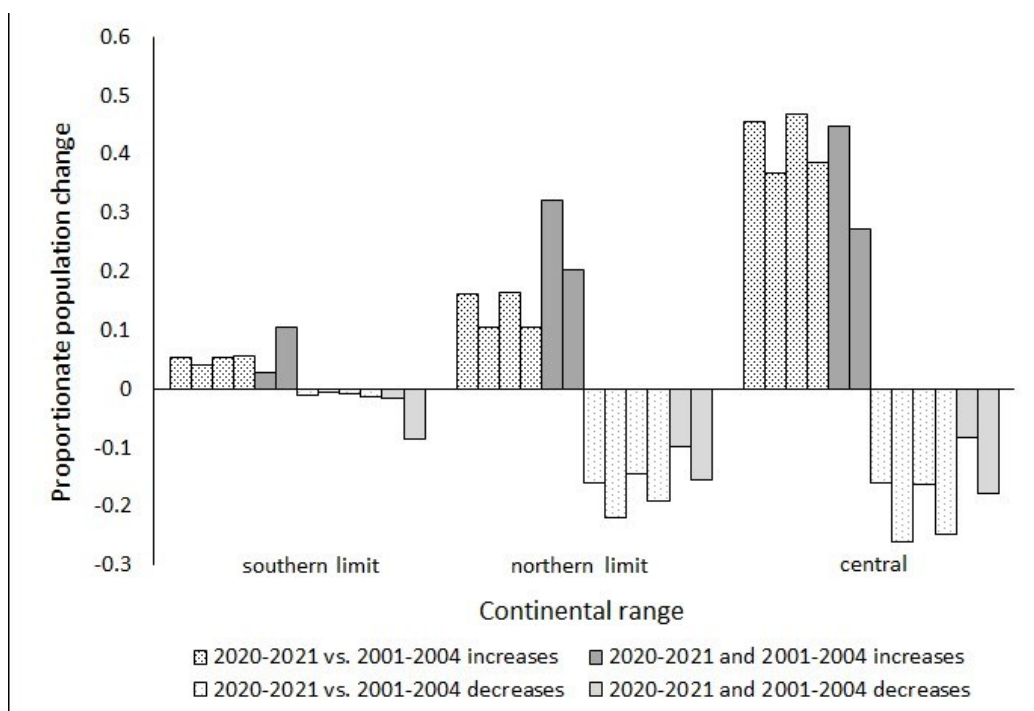


FIG.6. Proportionate population shifts at the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut for three categories of geographic ranges with respect to Connecticut: southern range limit, northern range limit, centrally distributed (not near range limit).

dergoing population increases and edge/successional species undergoing declines accounted for 36% of species. Moreover, increases were greater than decreases among forest interior populations. Furthermore, far more edge/successional species were declining than increasing. In contrast, in the more managed landscapes of Yale-Myers Forest a number of edge/successional species increased.

Despite these consistencies, multiple patterns, including that 43% of species had population trends opposite those expected, were at odds with a habitat hypothesis, additional contrary observations come from individual species. Apart from species at their southern range limit, the forest interior-dwelling Black-and-white Warbler (*Mniotilta varia*) and Scarlet Tanager had among the strongest declines of any species. The decline of the Black-and-white Warbler is a widespread one in southern New England (Fink et al. 2022). Moreover, particularly the strong decline of the Scarlet Tanager in precisely the types of conditions it is thought to prefer (Mowbray 2020) and in which breeding success has been documented to be highest (Roberts and Norment 1999), indicates that habitat extent and maturation alone cannot account for all population trends of forest interior species. The fact that tanager declines did not also occur in the more managed landscape of Yale-Myers Forest

further suggests that our understanding of the species' habitat preference is incomplete. Craig (2017), again based on large samples, found conflicting patterns of habitat association when comparing habitat use by individuals vs. habitats characteristics where population densities were highest.

All these observations strongly indicate that no single factor is principally responsible for the extensive species and population changes observed in this study. Any individual species' distribution and population may best be described as the consequence of a complex interplay of responses to multiple and sometimes conflicting factors and factors operating at differing environmental scales (Holt 1993, Holmes and Sherry 2001, Craig et al. 2022). Hence, community patterns observed among the forest birds of Connecticut's Northeast Uplands ecoregion may be described as the sum of individualistic responses to environmental and perhaps also stochastic factors.

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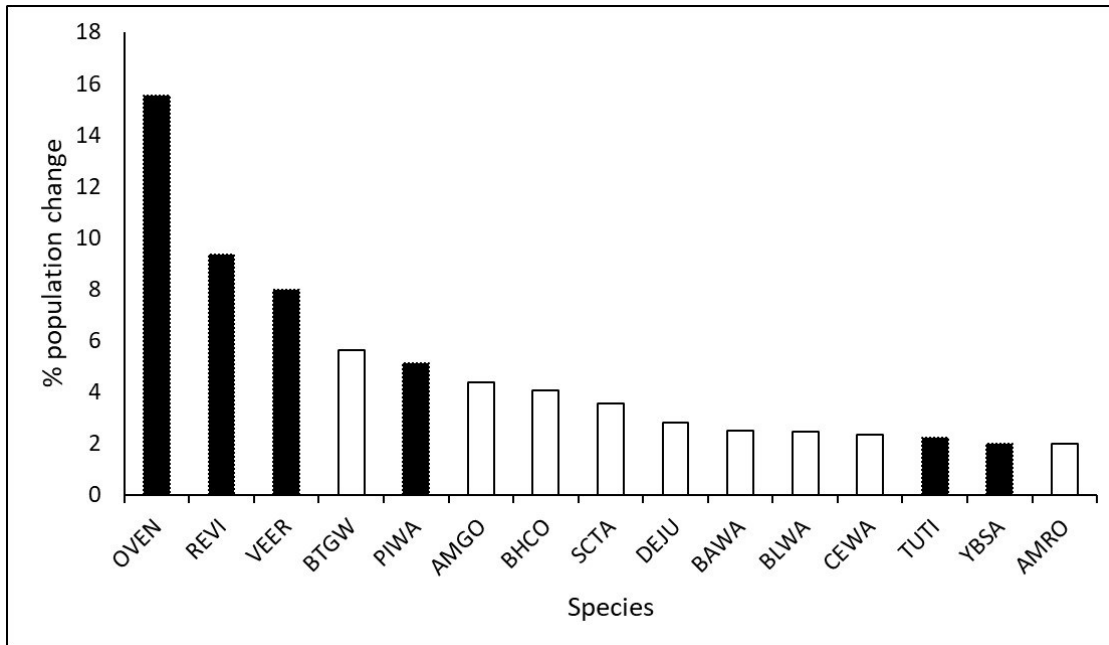


FIG. 7. The top 15 population shift percents for the Northeast Uplands ecoregion, Tolland/Windham counties, Connecticut. Species codes are U.S. Fish and Wildlife Service banding codes; black bars = increases, open bars = decreases.

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Appendix	Species	Forest occupancy association	Geographic range	Continental trend	Northeast Uplands trend	Yale-Myers trend
	Ruffed Grouse ( <i>Bonasa umbellus</i> )	edge/successional	southern limit	decreasing	absent	increasing
	Wild Turkey ( <i>Meleagrus gallinavo</i> )	edge/successional	core range	increasing	rare	increasing
	Mourning Dove ( <i>Zenaida macroura</i> )	edge/successional	core range	decreasing	increasing	increasing
	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	edge/successional	northern limit	decreasing	rare	increasing
	Black-billed Cuckoo ( <i>C. erythrophthalmus</i> )	edge/successional	core range	decreasing	absent	increasing
	Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	generalist	core range	increasing	rare	increasing
	Sharp-shinned Hawk ( <i>Accipiter striatus</i> )	forest interior	core range	increasing	absent	increasing
	Cooper's Hawk ( <i>A. cooperii</i> )	forest interior	core range	increasing	rare	absent
	Northern Goshawk ( <i>Accipiter gentilis</i> )	forest interior	southern limit	decreasing	rare	absent
	Red-shouldered Hawk ( <i>Buteo lineatus</i> )	forest interior	northern limit	increasing	no trend	decreasing
	Broad-winged Hawk ( <i>B. platypterus</i> )	forest interior	core range	no trend	rare	decreasing
	Red-tailed Hawk ( <i>B. jamaicensis</i> )	edge/successional	core range	increasing	rare	no trend
	Red-bellied Woodpecker ( <i>Melanerpes carolinus</i> )	forest interior	northern limit	increasing	increasing	increasing
	Yellow-bellied Sapsucker ( <i>Sphyrapicus varius</i> )	generalist	southern limit	increasing	increasing	increasing
	Downy Woodpecker ( <i>Picoides pubescens</i> )	generalist	core range	no trend	increasing	no trend
	Hairy Woodpecker ( <i>P. villosus</i> )	generalist	core range	increasing	increasing	decreasing
	Northern Flicker ( <i>Colaptes auratus</i> )	edge/successional	core range	decreasing	decreasing	decreasing
	Pileated Woodpecker ( <i>Dryocopus pileatus</i> )	forest interior	core range	increasing	increasing	increasing
	Eastern Wood Pewee ( <i>Contopus virens</i> )	forest interior	core range	decreasing	decreasing	increasing
	Acadian Flycatcher ( <i>Empidonax virescens</i> )	forest interior	northern limit	decreasing	rare	decreasing
	Least Flycatcher ( <i>E. minimus</i> )	edge/successional	southern limit	decreasing	rare	no trend
	Eastern Phoebe ( <i>Sayornis phoebe</i> )	edge/successional	core range	increasing	decreasing	no trend
	Great-crested Flycatcher ( <i>Myiarchus crinitus</i> )	generalist	core range	no trend	decreasing	no trend
	Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	edge/successional	core range	decreasing	rare	absent
	Yellow-throated Vireo ( <i>Vireo flavifrons</i> )	edge/successional	northern limit	increasing	increasing	increasing
	Blue-headed Vireo ( <i>V. flavifrons</i> )	forest interior	southern limit	increasing	decreasing	decreasing
	Warbling Vireo ( <i>V. gilvus</i> )	edge/successional	core range	increasing	rare	increasing
	Red-eyed Vireo ( <i>V. olivaceus</i> )	forest interior	core range	increasing	increasing	increasing
	Blue Jay ( <i>Cyanocitta cristata</i> )	generalist	core range	decreasing	decreasing	no trend
	American Crow ( <i>Corvus brachyrhynchos</i> )	generalist	core range	no trend	decreasing	absent
	Common Raven ( <i>Corvus corax</i> )	generalist	southern limit	increasing	increasing	increasing
	Black-capped Chickadee ( <i>Poecile atricapillus</i> )	generalist	southern limit	increasing	increasing	decreasing
	Tufted Titmouse ( <i>Baeolophus bicolor</i> )	generalist	northern limit	increasing	increasing	increasing
	Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	forest interior	southern limit	no trend	rare	decreasing
	White-breasted Nuthatch ( <i>S. carolinensis</i> )	forest interior	core range	increasing	decreasing	no trend
	Brown Creeper ( <i>Certhia americana</i> )	forest interior	southern limit	no trend	decreasing	decreasing
	House Wren ( <i>Troglodytes aedon</i> )	edge/successional	core range	no trend	rare	decreasing
	Winter Wren ( <i>T. hiemalis</i> )	forest interior	southern limit	increasing	decreasing	no trend
	Blue-gray Gnatcatcher ( <i>Polioptila caerulea</i> )	generalist	northern limit	no trend	rare	decreasing
	Eastern Bluebird ( <i>Sialia sialis</i> )	edge/successional	core range	increasing	rare	no trend
	Veery ( <i>Catharus fuscescens</i> )	forest interior	southern limit	decreasing	increasing	increasing
	Hermit Thrush ( <i>C. guttatus</i> )	forest interior	southern limit	no trend	decreasing	decreasing
	Wood Thrush ( <i>Hylocichla mustelina</i> )	forest interior	core range	decreasing	decreasing	increasing
	American Robin ( <i>Turdus migratorius</i> )	edge/successional	core range	no trend	decreasing	decreasing
	Gray Catbird ( <i>Dumetella carolinensis</i> )	edge/successional	core range	no trend	decreasing	increasing
	Cedar Waxwing ( <i>Bombycilla cedrorum</i> )	edge/successional	core range	increasing	decreasing	decreasing

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Purple Finch ( <i>Haemorhous purpureus</i> )	edge/successional	southern limit	decreasing	rare	no trend
Pine Siskin ( <i>Spinus pinus</i> )	edge/successional	southern limit	decreasing	absent	decreasing
American Goldfinch ( <i>Spinus tristis</i> )	edge/successional	core range	no trend	decreasing	decreasing
Chipping Sparrow ( <i>Spizella passerina</i> )	edge/successional	core range	no trend	decreasing	decreasing
Dark-eyed Junco ( <i>Junco hyemalis</i> )	forest interior	southern limit	decreasing	decreasing	decreasing
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	edge/successional	southern limit	decreasing	absent	decreasing
Song Sparrow ( <i>Melospiza melodia</i> )	edge/successional	core range	decreasing	decreasing	increasing
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	edge/successional	northern limit	decreasing	decreasing	increasing
Baltimore Oriole ( <i>Icterus galbula</i> )	edge/successional	core range	decreasing	increasing	decreasing
Brown-headed Cowbird ( <i>Molothrus ater</i> )	edge/successional	core range	decreasing	decreasing	no trend
Ovenbird ( <i>Seiurus aurocapilla</i> )	forest interior	core range	no trend	increasing	increasing
Worm-eating Warbler ( <i>Helmitheros vermivorum</i> )	forest interior	northern limit	increasing	rare	no trend
Louisiana Waterthrush ( <i>Parkesia motacilla</i> )	forest interior	northern limit	increasing	increasing	decreasing
Northern Waterthrush ( <i>P. novaboracensis</i> )	forest interior	southern limit	decreasing	decreasing	no trend
Blue-winged Warbler ( <i>Vermivora cyanoptera</i> )	edge/successional	core range	decreasing	rare	decreasing
Black-and-white Warbler ( <i>Mniotilta varia</i> )	generalist	core range	decreasing	decreasing	no trend
Nashville Warbler ( <i>Oreothlypis ruficapilla</i> )	edge/successional	southern limit	decreasing	rare	increasing
Kentucky Warbler ( <i>Geothlypis formosa</i> )	forest interior	northern limit	decreasing	absent	increasing
Hooded Warbler ( <i>Setophaga citrina</i> )	edge/successional	northern limit	increasing	rare	absent
Common Yellowthroat ( <i>Geothlypis trichas</i> )	edge/successional	core range	decreasing	increasing	increasing
American Redstart ( <i>Setophaga ruticilla</i> )	edge/successional	core range	decreasing	no trend	decreasing
Cerulean Warbler ( <i>S. cerulea</i> )	forest interior	northern limit	decreasing	absent	increasing
Magnolia Warbler ( <i>S. magnolia</i> )	generalist	southern limit	no trend	no trend	increasing
Blackburnian Warbler ( <i>S. fusca</i> )	forest interior	southern limit	no trend	decreasing	decreasing
Chestnut-sided Warbler ( <i>S. pensylvanica</i> )	edge/successional	southern limit	decreasing	increasing	increasing
Black-throated Blue Warbler ( <i>S. caeruleascens</i> )	forest interior	southern limit	no trend	increasing	increasing
Pine Warbler ( <i>S. pinus</i> )	forest interior	core range	increasing	increasing	increasing
Yellow-rumped Warbler ( <i>S. coronata</i> )	forest interior	southern limit	no trend	decreasing	decreasing
Black-throated Green Warbler ( <i>S. virens</i> )	forest interior	southern limit	increasing	decreasing	decreasing
Canada Warbler ( <i>Cardellina canadensis</i> )	forest interior	southern limit	decreasing	increasing	increasing
Scarlet Tanager ( <i>Piranga olivacea</i> )	forest interior	core range	no trend	decreasing	increasing
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	edge/successional	northern limit	no trend	increasing	increasing
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	edge/successional	core range	decreasing	increasing	increasing
Indigo Bunting ( <i>Passerina cyanea</i> )	edge/successional	core range	decreasing	rare	increasing