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BREEDING FOREST BIRDS OF NORTHEASTERN CONNECTICUT SHOW A LONG TERM POPULATION INCREASE AND HIGH SPECIES TURNOVER

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Abstract. North American birds have declined by 29% over 48 years, with declines occurring across species and biomes. To examine population patterns at a local scale, we investigated species and population shifts in a forest bird community in northeastern Connecticut. We did so in relation to its changing environments, focusing on patterns consistent with the effects of climate change and habitat manipulation. In 1985, we established survey routes primarily in the intensively managed Yale-Myers experimental forest, which we repeated in 2018 and 2019. Species richness varied little from the initial survey to the recent ones, although population density increased by 24% after 1985. Turnover in species composition exceeded 50%. The five most strongly declining species were northerly distributed, forest interior inhabitants, whereas the seven most strongly increasing species were variously distributed forest interior and edge/successional-associated species. Some species experienced increases by invading new habitats, whereas at least one appeared to decline due to interspecific competition. Expected effects of climate change on populations were consistent with some findings, but habitat effects appeared related to a greater number of shifts. However, much contrary data indicated that these factors were not alone in driving community change. This bird community may best be thought of as a dynamic assemblage that represents the sum of individualistic responses to environmental and perhaps stochastic factors.

North American birds are reported to have declined by 29% over 48 years, with declines occurring across a variety of species and biomes (Rosenberg et al. 2019). However, population declines are rarely uniform across ranges and examination of continent-wide population trends often show complex patterns of increase and decrease (James et al. 1996, Villard and Maurer 1996, Sauer et al. 2017). Processes driving population and range shifts are potentially many and may include both density dependent and density independent factors. Chief among these are thought to be climatic (Hitch and Leberg 2007) and structural habitat (Goodale et al. 2009, Duguid et al. 2016, Hanle et al. 2020) change, which may themselves be

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related (Whitaker 2017), although disease (May 1995, Friend et al. 2001), defoliation (Bell and Whitmore 1997, Gale et al. 2001), weather (Haggerty and Morton 2014), competition (Confer and Larkin 1998), species adaptations (Bearhop et al. 2005, Kubisch et al. 2013), changes in food availability (Barber and Marquis 2008), and stochastic effects (Craig and Klaver 2012, Taheri et al. 2016) also play roles. Moreover, for Neotropical or even shorter distance migrants, such factors are not only of consequence on breeding grounds but also on migratory routes and wintering grounds (LaSorte et al. 2017), with winter survivorship contributing to observed North American population patterns (Rappole and McDonald 1994).

Evidence that climate change is driving bird population and range shifts, particularly ranges receding or expanding north, is reported for North America (Hitch and Leberg 2007, Covino et al. 2020) and Europe (Thomas and Lennon 1999, but see Taheri et al. 2016). Climate change is evident even at regional scales, with Connecticut's annual mean temperatures rising 1.7 °C since 1900 (NOAA 2020). However, despite its warming climate, Connecticut's forest composition is still more driven by land-use history than climate change (Ashton et al. 2015).

Connecticut's forests have generally not succeeded to southerly-associated species but rather to ones more typical of northern forests (Alerich 1999, Butler 2017), although some species typical of the Southeast have increased (Craig 2017, Lefland et al. 2018). Connecticut's second-growth forests are now maturing, with some stands beginning to exhibit later-successional forest structures similar to old-growth, whereas early successional habitats have progressively declined in occurrence (Alerich 1999, Butler 2017). The character of Connecticut's forests is also continually changing in response to pests and disease (Wharton et al. 2004). Hence, at scales below continental ones, responses of forest birds to changing conditions are likely to be complex.

To investigate how its forest bird community has changed over time at a regional scale, we studied populations in the Northeast Uplands ecoregion of Connecticut (Dowhan and Craig 1976)—a tongue of higher elevation landscape with forest cover more northern-associated than in the rest of eastern Connecticut. As such, a variety of forest bird species have historically been at or near their southern range limit there (Craig 2017), making them potentially sensitive indicators of the effects of climate change. Quantitative bird surveys began in this region in 1985, so a long-term perspective exists on the status of its forest birds. Because annual variability in bird communities tends to be high, the importance of such a long-term perspective in elucidating processes driving patterns is well known (Collins 2001).

Our goal in this study was to determine, based on a 34-year perspective, the degree to which the regional forest bird community has changed and to what extent regional environmental alteration appears responsible for driving such change. We particularly sought evidence that might relate to the region's warming climate and changing habitat structure. Because the region's forests are extensive and maturing and because the study area's forests have been managed for earlier successional habitats, we predicted that bird species associated with these habitats should be differentially increasing. However, we also sought to identify community patterns that were consistent with explanations other than climate and habitat. Our findings should, thus, provide a regional perspective that assists with understanding larger continental trends.

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^2 and have the lowest temperatures (mean summer = 21°C, mean 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 1981–2010 Climate Normals). Forest covers about 70% of the region (Alerich 1999, CLEAR 2020). Based on measurements made at 75 stations by Craig (2017), forests are 21% oak-dominated, 11% mixed deciduous, 44% conifer-central hardwood, 3% pine-oak, 18% pure conifer and 2% mixed cover.

This study took place in and adjacent to the Yale-Myers Forest, a research and demonstration forest (41.95° N, 72.12° W). Within the roughly 15,000 ha ecoregion, Yale-Myers Forest covers 3,213 ha, or about 30% of the region's forest. Since the 1950s, forest stands have been treated through improvement cuts followed by commercial crown thinning. Crown thinning involves treatments to the canopy where growing space is cleared around selected crop trees, usually oak (Ashton and Kelty 2018). Since 1990, thinning has been conducted in at least one stand/year, with the total extent of stands thinned from 1990 to 2005 being about 690 ha (Ashton et al. 2015).

Also after 1990, shelterwood cutting occurred sporadically until 1999, after which it was conducted annually. Shelterwood refers to a regeneration treatment that harvests 50–80% of basal area and leaves large, evenly-spaced trees to act as a source of seed for new recruitment, shade and protection of the regenerating stand. The tree canopy is harvested in stages to allow more shade tolerant species to establish in the understory. These residual trees may be harvested 10−20 years after initial cutting and once

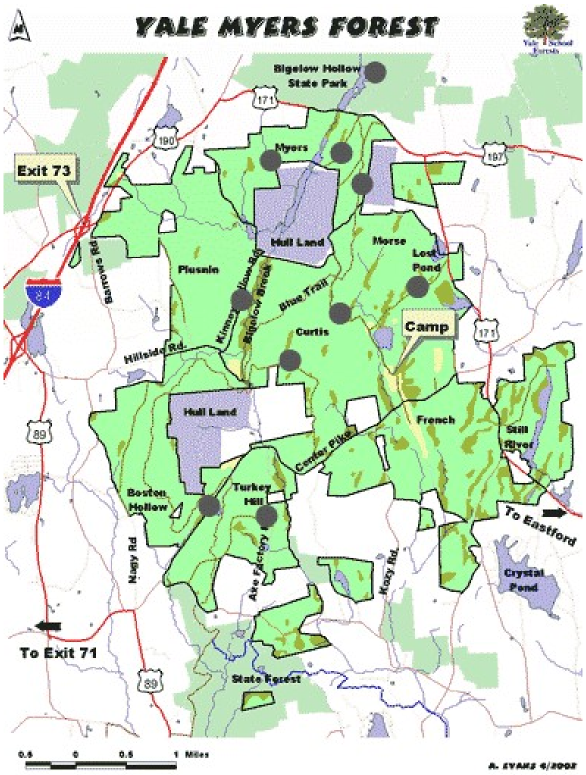

FIG. 1. Study areas in Yale-Myers Forest, Tolland and Windham counties, Connecticut, with transect locations (1985, 2018−2019) represented by centrally located dots.

regeneration has been established. Shelterwood treatments can be considered ‘‘irregular” by leaving additional structures behind (reserves) that remain uncut after the final removal of parent trees. Reserves can include snags or living trees of differing species and size classes that provide supplementary wildlife habitat and food (e.g., older cavity trees, trees that provide soft and hard mast, evergreens that provide thermal cover). Reserves can occur singly or be strategically arranged in groups across the harvest treatment (Smith et al. 1997). The practice of shelterwood cutting did not occur before 1990 because the forest was largely even-aged, with no stands considered mature (80–120 years of age). By 2006, shelterwoods covered ca. 380 ha. These types of forest management yielded a landscape with habitats from early successional to mature forest.

Bird surveys. In 1985, we established 10 survey routes that generally followed old logging roads or roads through the forest interior. Nine of these were mostly within Yale-Myers Forest and one traversed an adjacent state park, all primarily in the town of Union (Fig. 1). We initially measured the 1.6 km routes with a distance measuring wheel and recorded on maps key landmarks along them, although by 2018 we converted beginning and ending landmarks to global positioning system-determined coordinates.

Along each route between 25 May and 1 July, the height of the local breeding season, we performed duplicate surveys using the strip census protocol of Emlen (1977). We repeated the 1985 surveys in 2018 and 2019 using the same procedure of plotting on maps the position of all birds encountered to 60 m from each side of a route. We walked these routes after first light at about 1.2 kph on days of low wind and no precipitation.

Because of the long period between surveys performed by a single observer, detection ability could have declined for high-pitched vocalizers, notably the Blackburnian Warbler (*Setophaga fusca*). To test this, we divided our mapped observations for this species into those made at <30 and >30 m and compared the frequency of observations in these categories in 1985 vs. 2018–2019.

In 1985, we prepared field maps of each survey transect to document transect landmarks for future resurvey and also locations where forest openings with earlier successional growth occurred. To compare these initial measurements with present conditions, we again delineated locations with earlier successional growth on the same base maps prepared in 1985, using satellite imagery to refine boundaries on all maps. Maps did not show a continuum of effects but rather fell into three qualitative categories: 1) those with minimal change, 2) those with moderate change, 3) and those with extensive change.

Analysis. Emlen’s (1977) method does not account for the decline in detectability of birds with distance and thus produces problematic estimates of absolute population density (Buckland et al. 2001, Carrascal et al. 2008). Hence, in analyses we used our original counts as measures of relative abundance. To compute species richness, we counted all species associated with forest habitats even if they appeared just beyond the 60 m distance in order to give a more complete assessment of species present. Indeed, observations demonstrated that home ranges of such peripheral birds generally brought them later within the 60 m. However, in abundance analyses, we used observations only from within the 60 m boundary, with abundance defined as counts of individuals/transect.

Based on Craig’s (2017) quantitative evaluation of habitat use by Connecticut forest birds, we 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), we 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 < ± 0.4. In addition, we classified species as to their North American range using 2011–2015 range maps from Sauer et al. (2017): 1)

TABLE 1. Within- and between subject repeated measures tests of annual and transect hifts in breeding bird species’richness and abundance at Yale-Myers Forest.

	F	**df**	***P***
Species richness			
Within-subject			
Multivariate			
Years	2.76	2,9	0.12
Years x transect	0.78	18,20	0.7
Univariate			
Years	1.16	1.2, 12.4	0.32
Years x transect	0.491	1.2, 12.4	0.88
Between subject			
Transect	3.49	9,10	0.03
Species abundance			
Within-subject			
Multivariate			
Years	26.55	2,9	<0.01
Years x transect	3.91	18,20	<0.01
Univariate			
Years	28.98	2,20	<0.01
Years x transect	4.62	18,20	<0.01
Between subject			
Transect	8.12	9,10	<0.01
Species turnover	29.49	2,27	<0.01
Species richness vs. habitat change			
Within-subject			
Multivariate			
Years	2.56	2,13	0.12
Years x change	1.2	4,28	0.33
Univariate			
Years	1.46	2,28	0.25
Years x change	1.87	4,28	0.14
Between subject			
Habitat change	0.71	2,14	0.51
Species abundance vs. habitat change			
Within-subject			
Multivariate			
Years	6.38	2,13	0.01
Years x change	3.02	4,28	0.03
Univariate			
Years	8.33	2,28	<0.01
Years x transect	4.17	4,28	0.01
Between subject			
Habitat change	3.42	2,14	0.06

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). For these categories, we computed the number of species in each of these groups and the size of population increases and decreases in 1985–2018, 1985–2019 and 2018–2019. We computed proportionate change among categories in year-year comparisons by separately dividing increases and decreases by total population change. In assessing findings for individual species, we made further use of BBS data and data from other literature sources. When results for individual species provided additional evidence for the relationship between population patterns and potential causal factors, we report these under the heading of species accounts. We also computed species accumulation curves for each year of the study, with accumulation based on the chronology of surveys, in order to assess the completeness of community sampling.

We examined patterns in species richness, abundance, temporal population shifts and species turnover, with turnover calculated by summing the species gained and lost and dividing this number by the total species pool for the years of comparison. This yielded three sets of turnover values: 1985−2018, 1985−2019 and 2018−2019. Because we gathered data at the same sites over a series of years, the data were repeated measures. Hence, when required, we employed repeated measures analysis of variance in examining results. When sphericity assumptions were violated, we employed epsilon adjustments to evaluate significance of results. We entered habitat category, continental population trend, continental range and Yale-Myers Forest population trends (increase vs. decrease) into models as between-subject effects. In these and other tests, we 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, we employed data transformations to normalize data and stabilize variances. When assumptions remained poorly met, we employed Friedman and Wilcoxon related samples nonparametric tests. We used SPSS 15 (SPSS 2006) to perform tests.

RESULTS

Community trends. We recorded 79 forest-associated species during this investigation. Species accumulation curves demonstrated from their slopes reaching essentially zero after addition of species from the 5th of 10 transects that we achieved virtually complete sampling of community composition.

Species richness (Fig. 2) varied little among years although survey transects differed in richness. In contrast, abundance measures (Fig. 3) differed among years and transects and displayed a year x transect interaction, with Bonferroni comparisons demonstrating that 2018 and 2019 mean abundances

TABLE 2. Breeding bird species richness and community abundance for Yale-Myers Forest transects undergoing low (n = 2), medium (n = 4) and high (n = 4) levels of conversion from mature forest to earlier successional habitats from 1985 to 2018–2019.

	1985		2018		2019	
	Mean	SD	Mean	SD	Mean	SD
Species richness						
Low	27.8	2.2	24.3	1.9	26.5	3.7
Medium	26.6	6.1	30.0	4.2	30.0	3.7
High	27.8	6.2	28.9	6.2	30.5	4.4
Population density						
Low	64.5	5.3	70.8	8.4	59.5	5.9
Medium	60.4	6.1	81.3	11.1	87.0	8.7
High	71.0	13.9	79.0	16.2	82.3	11.0

at transects were 24% greater than 1985 ($P < 0.001$, Table 1) but they did not differ from each other ($P = 0.99$, Table 1). However, variance in abundance estimates increased after 1985. Turnover in species composition was above 50% in comparisons of 1985 with both 2018 and 2019, although it was still 36% between 2018 and 2019. Examination of turnover values showed differences among years, with Bonferroni comparisons revealing that 2018–2019 turnover was less than that of 1985–2018 and 1985–2019 ($P < 0.01$; Table 1, Fig. 4). These latter two values did not differ ($P = 0.40$, Table 1).

Comparison of the extent of earlier successional habitats in 1985 vs. 2018–2019 showed that, although species richness remained constant overall, it tended to increase at sites with greater conversion to earlier successional habitats, although not significantly so (Table 1,2). Abundance, in contrast, showed significant differences among years and a year x habitat change interaction (Table 1,2), with particularly 2018 and 2019 transect counts having higher abundances at sites with more earlier successional habitat.

Species trends. Examination of temporal changes in detectability of the Blackburnian Warbler demonstrated that in 1985 observations were 54 and 46% (n = 35) for birds detected at < or >30 m, respectively. In 2018–2019, they were 59 and 41% (n = 22), respectively. These differences were not significant (Wilcoxon $z = -0.42$, P = 0.67). The smaller 2018–2019 samples corresponded to the species' strong Northeastern population decline during this time (Sauer et al. 2017).

Forest interior and particularly edge/successional species were by far the most frequently occurring at Yale-Myers Forest. Species that were continentally declining were also those comprising the greatest proportion of Yale-Myers species. Most species were not near their range periphery in Connecticut and the fewest species were near their northern range limit (Table 3).

Forest interior and edge/successional species undergoing population increases at Yale-Myers Forest accounted for 39% of the species pool. However, 32% of species associated with these habitats declined. Of these latter 24 species, only three were southern range limit species with continental population trends that suggested climate change could account for the declines. Of the remaining 21 species, an additional six had local declines coincident with continental declines, leaving 15 species for which local declines had no clear relationship to habitat, climate or continental trend (Table 3).

Species at their southern range limit undergoing population declines and species at their northern range limit undergoing population increases accounted for 25% of the species pool. However, of these 19 species, only six showed trends coincident with larger continental trends. Moreover, 13 range limit species had population shifts opposite to those predicted by a climate change hypothesis and the largest groups of increasing and decreasing species, 24% and 16% respectively, were not near their range limit (Table 3).

Of continentally increasing and decreasing species, 28% of Yale-Myers Forest species had the same trends. Of these 21 species, eight increasing species were associated with interior forest and edge/successional habitats, one increasing generalist was near its northern range limit and three decreasing species were near southern range limits. The nine remaining species with population trends not potentially accounted for by climate and habitat provided evidence for population shifts being solely related to continental trends (Table 3).

Population trends. Original data for Yale-Myers Forest populations showed that the 2018–

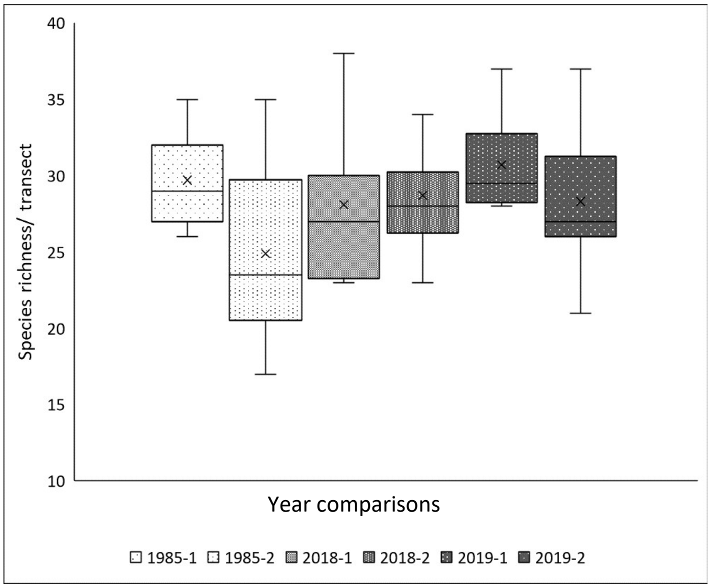

FIG. 2. Repeated measures of species richness estimates at the Yale-Myers Forest, Tolland/Windham counties, Connecticut, for 1985, 2018 and 2019 (*n* = 10) showing mean (x), median (-), standard deviation (shaded) and range (T).

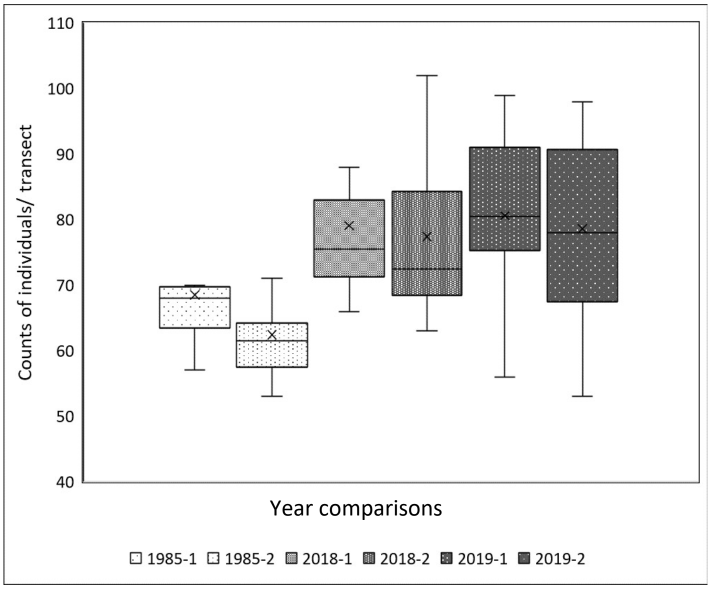

FIG. 3. Repeated measures of community abundance estimates for the first (e.g., 1985−1) and second (e.g., 1985−2) sets of annual surveys in 1985, 2018 and 2019 (*n* = 10) at the Yale-Myers Forest, Tolland/Windham counties, Connecticut.

2019 comparison had smaller population shifts than did those of 1985–2018 or 1985–2019 (Friedman χ^2 = 13.15, df = 2, $P < 0.01$). Otherwise, proportionate data showed patterns similar to those of original data and use of proportionate data facilitated parametric analyses, so we use proportions in the analyses that follow. For forest interior, edge/successional and generalist species, 2018–2019 comparisons of population increases vs. decreases (Fig. 5) were similar but both 1985–2018 and 1985–2019 had greater increases than decreases. Species associated with the three habitat categories differed in the extent of their population shifts, with Bonferroni tests showing that forest interior species had greater shifts than edge/ successional species (P = 0.05, Table 4) and both underwent greater shifts than did generalists ($P <$ 0.01, Table 4). Population increases were also greater than decreases overall, with forest interior and

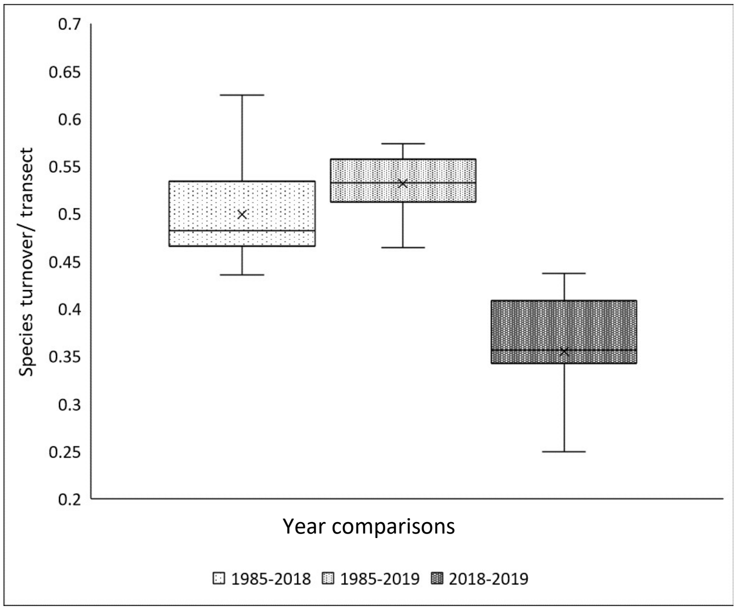

FIG. 4. Repeated measures of species turnover estimates at the Yale-Myers Forest, Tolland/Windham counties, Connecticut, for 1985, 2018 and 2019 ($n = 10$), with turnover calculated by summing the species gained and lost and dividing this number by the total species pool for the years of comparison.

edge/successional populations differentially showing increases, whereas generalists had increases similar to decreases (Table 4).

Examination of Yale-Myers Forest population increases vs. decreases in relation to continental population trends (Fig. 6) showed the 2018–2019 comparison had greater decreases than did those of 1985–2018 or 1985–2019. However, population increases were greater than decreases overall and continentally increasing and decreasing populations both differentially increased at Yale-Myers Forest. An interaction occurred as well among year comparisons, continental trends and Yale-Myers population shifts primarily because greater population declines occurred in 2018 –2019 for continentally increasing and decreasing species (Table 4).

Investigation of Yale-Myers Forest population increases vs. decreases in relation to geographic ranges (Fig. 7) again demonstrated that 2018–2019 comparisons had lower increases but higher decreases than those of 1985–2018 and 1985–2019. Moreover, populations shifts differed among ranges, with Bonferroni tests showing that populations at their northern range limit had the lowest shifts and centrally distributed populations had the greatest ($P < 0.01$, Table 4). Population increases were greater than decreases overall and particularly species not near their range limit had more strongly increasing populations. An interaction among year comparisons, ranges and Yale-Myers Forest population shifts also occurred, primarily due to population shifts being less for increasing species and greater for declining species in 2018– 2019.

Species accounts. The 2nd through 5th most strongly declining species at Yale-Myers Forest were all northerly-distributed and interior forest-associated. The Brown Creeper (*Certhia americana*) and Blackburnian Warbler are continentally stable but declining in the Northeast. The Blue-headed Vireo (*Vireo solitarius*) is increasing continentally and in the Northeast, whereas the Yellow-rumped Warbler (*Setophaga coronata*) has little continental trend but is increasing in the Northeast (Sauer et al. 2017).

Of the 1st through 4th most strongly increasing Yale-Myers Forest species, all of which are associated with interior forest, the centrally distributed Red-eyed Vireo (*Vireo olivaceus*) is increasing continentally but shows inconsistent Northeastern trends, the northerly distributed Veery (*Catharus fuscescens*) is declining continentally and in the Northeast, the centrally distributed, historically rare (Craig 2017) Pine Warbler (*Setophaga pinus*) is increasing at all scales and the centrally distributed Ovenbird (Seiurus *aurocapilla*) shows little continental trend and is declining in the Northeast (Sauer et al. 2017). Notably, the Pine Warbler, absent from Yale-Myers Forest in 1985 but now the second commonest forest warbler, appears to have invaded eastern Connecticut from southeastern coastal plain populations (Craig 2017).

The 5th, 6th and 8th most strongly increasing Yale-Myers Forest species were all early succession-

TABLE 3. Breeding bird species totals for Yale-Myers Forest habitat associations, continental ranges and continental trend associations.

	Total species	**Increase Yale-Myers**	**Decrease Yale-Myers**	**No change**
Habitat association				
Interior	30	14	12	4
Edge/successional	34	16	12	6
Generalist	12	5	3	4
Continental range				
Southern limit	24	9	11	4
Northern limit	13	8	4	1
Central	39	18	12	9
Continental trend				
Increase	25	12	7	6
Decrease	32	17	9	6
No change	19	6	11	2

al habitat-associated. The southerly distributed Eastern Towhee (*Pipilo erythropthalmus*) is declining continentally and in the Northeast, the centrally distributed Gray Catbird (*Dumatella carolinensis*) is stable continentally and in the Northeast and the northerly distributed Chestnut-sided Warbler (*Setophaga pensylvanica*) is declining continentally and in the Northeast (Sauer et al. 2017).

Other species once largely or entirely absent at Yale-Myers Forest but now present include the centrally distributed Sharp-shinned Hawk (*Accipiter striatus*), the northerly distributed Nashville Warbler (*Oreothlypus ruficapilla*) and the southerly distributed Warbling Vireo (*Vireo gilvus*), Worm-eating Warbler (*Helmitheros vermivorum*), Cerulean Warbler (*Setophaga cerulea*) and Kentucky Warbler (*Geothlypis formosa*). The northerly distributed Red-breasted Nuthatch (*Sitta canadensis*), the commonest nuthatch at Yale-Myers Forest in 1985, was infrequent by 2018−2019. The Cerulean Warbler, declining over much of its range (Sauer et al. 2017), is shifting its range by expanding into southern New England, where it is moving into its maturing, extensive forests (Craig 2017)—its preferred habitat (Buehler 2013).

DISCUSSION

Individual species examined at multiple geographical scales (Appendix 1) provided additional evidence for the relationship between population patterns and potential causative agents. The northerly distributed habitat generalist Black-capped Chickadee (*Poecile atricaipila*) has undergone a continent-wide and Northeastern (Sauer et al. 2017) breeding population increase, yet it experienced the strongest decline of any species at Yale-Myers Forest, with the decline averaging 40%. During the same period, its larger, southerly distributed generalist relative, the Tufted Titmouse (*Baeolophus bicolor*) also undergoing a continental and Northeastern increase, went from being largely absent to quadrupling its numbers and experiencing the 7th largest population increase. This same phenomenon occurred when the titmouse first invaded northwestern Connecticut (Loery and Nichols 1987).

The boreal forest-associated Yellow-bellied Sapsucker (*Sphyrapicus varius*) has also undergone a continent-wide and Northeastern (Sauer et al. 2017) population increase. Although historically a rare Connecticut breeder of open swamps into the early 1970s, it expanded its habitat use to include mature conifer-hardwood upland forest in northwestern Connecticut, where it is now the commonest woodpecker (Craig 2017). When first detected summering in northeastern Connecticut in 2001, it occupied open swamp habitat (Craig 2017). It has similarly expanded to conifer-hardwoods at Yale-Myers Forest, where it has undergone the 9th largest population increase. Notably, during this same period the continentally increasing Hairy Woodpecker (*Picoides villosus*), although seemingly ecologically unlike the sapsucker, has declined since 1985.

Still another species that has clearly expanded its habitat use is the Common Raven (*Corvus corax*). Confined primarily to remote core forests in far northern portions of the Northeast into the 1970s, (Boarman and Heinrich 1999), its populations expanded south into Connecticut during the 1980s. It now occurs south to the coast and occupies a range of Connecticut forests from conifer-hardwood to oak-dominated and most recently has expanded into agricultural and urban landscapes (Craig 2017). In contrast, the Blackburnian Warbler's Northeastern

TABLE 4. Within- and between-subject repeated measures tests of temporal population shifts among breeding bird species' habitat associations, continental population trends and continental ranges at Yale-Myers Forest.

	F	**df**	***P***
Habitat-associated population shifts			
Within-subject effects			
Multivariate			
Year comparisons	0.30	2,5	0.75
Year x habitat association	1.62	4,12	0.23
Year x population shift	5.81	2,5	0.05
Year x habitat x population	1.97	4,12	0.16
Univariate			
Year comparisons	0.19	1.07,6.45	0.7
Year x habitat association	1.51	2.15,6.45	0.26
Year x population shift	9.17	1.07,6.45	0.02
Year x habitat x population	1.80	2.15,6.45	0.19
Between-subject effects			
Habitat association	116.60	2,6	<0.01
Population increase/decrease	52.20	1,6	<0.01
Habitat x population	19.14	2,6	<0.01
Continental population trend-associated population shifts			
Within-subject effects			
Multivariate			
Year comparisons	0.94	2,5	0.45
Year x continental trend	2.23	4,12	0.13
Year x population shift	38.55	2,5	<0.01
Year x trend x population	3.83	4,12	0.03
Univariate			
Year comparisons	0.84	2,12	0.45
Year x continental trend	8.51	4,12	<0.01
Year x population shift	38.45	2,12	<0.01
Year x trend x population	7.54	4,12	<0.01
Between subject effects			
Continental trend	2.02	2,6	0.21
Population increase/decrease	166.33	1,6	<0.01
Trend x population	67.72	2,6	<0.01
Geographic range-associated population shifts			
Within-subject effects			
Multivariate			
Year comparisons	0.58	2,5	0.6
Year x geographic range	1.54	4,12	0.25
Year x population shift	22.56	2,5	<0.01
Year x range x population	3.81	4,12	0.03
Univariate			
Year comparisons	0.72	2,12	0.51
Year x geographic range	1.05	4,12	0.42
Year x population shift	22.33	2,12	<0.01
Year x range x population	15.53	4,12	<0.01
Between subject effects			
Geographic range	82.31	2,6	<0.01
Population increase/decrease	33.46	1,6	<0.01
Range x population	12.81	2,6	0.01

decline has been coincident with the dramatic decline of Connecticut's Red Pine (*Pinus resinosa*) stands. It was formerly a regular inhabitant of Red Pine at Yale-Myers Forest (R. Craig pers. obs.). Also notably, populations of the increasing Eastern Towhee (Bell and Whitmore 1997) as well as the successional-associated Yellow-billed (*Coccyzus americanus*) and Black-billed Cuckoos (*C. erythropthalmus*) profit from outbreaks of gypsy moths (Gale et al. 2001), and particularly eastern Connecticut had the second largest state outbreak in 2017–2019 (Stafford III 2020).

We found an increase in community abundance that was nearly as large as that reported for continental population declines. Community species richness varied little over time, which itself raises questions about whether there is an upper limit to the number of species that the Yale-Myers Forest system can support. Furthermore, a greater than 50% turnover occurred in species composition, with species rare or absent in 1985 frequent by 2018–2019 and species frequent in 1985 rare or absent by 2018–2019. Differences computed for multiple community measures were less for 2018–2019 comparisons than for those of 1985–2018 or 1985–2019, indicating that progressive community change occurred. Moreover, variance among transect abundances increased after 1985, apparently as a consequence of increased habitat heterogeneity at eight of 10 study sites. Such substantial shifts support Craig's (2005) proposition that bird communities are dynamic rather than static assemblages, with a region's communities changing continually over time. Similarly, since the last ice age, plant species in eastern North America have responded individualistically to changing conditions, such that plant associations with no contemporary counterparts have appeared and disappeared (Prentice et al. 1991, Jablonski and Sepkoski 1996), and principal community members have invaded and receded from areas due to a host of ecological factors (Davis 1998, Fuller 1998).

Evidence consistent with climate change driving community change is that of population declines of species at their southern range limit and population increases of species at their northern range limit. That the five most strongly declining species were all northerly distributed provides supportive evidence, although only two of the top eight increasing species were southerly distributed. Our accounts of the decline of other less common northern-associated species and the invasion of the forest by more uncommon southern-associated species also suggests that climate change plays a role in driving community change. However, patterns related to population shifts of range limit species revealed that comparatively few species showed trends also reflective of larger continental trends and more species showed population patterns contrary to predictions than were consistent with them. Similarly, most species at the

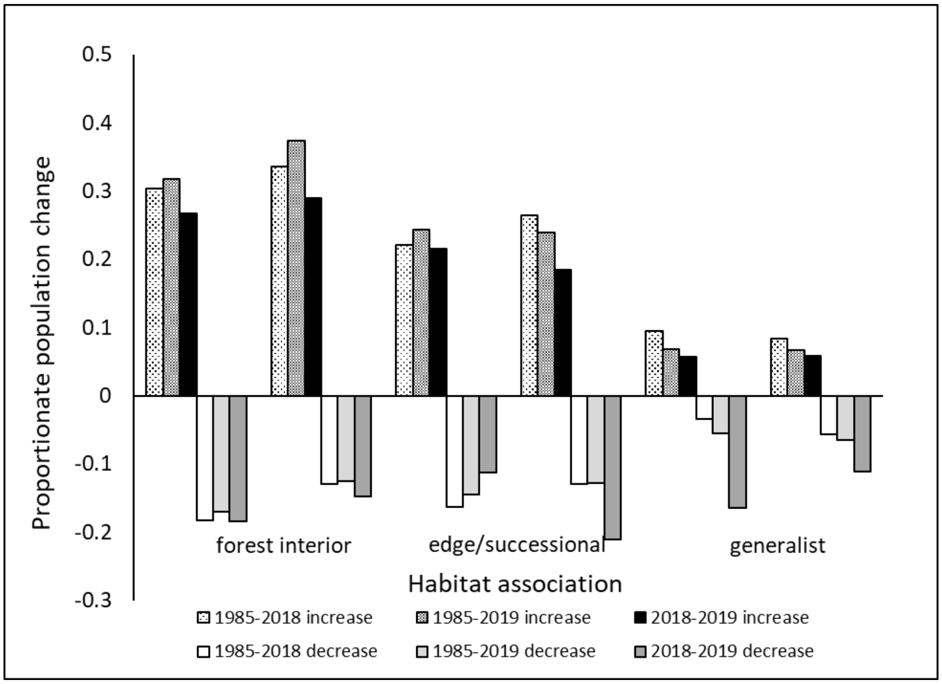

FIG. 5. Proportionate population shifts at the Yale-Myers Forest, Tolland/Windham counties, Connecticut, for three categories of habitat use: forest interior, edge/successional species, generalist.

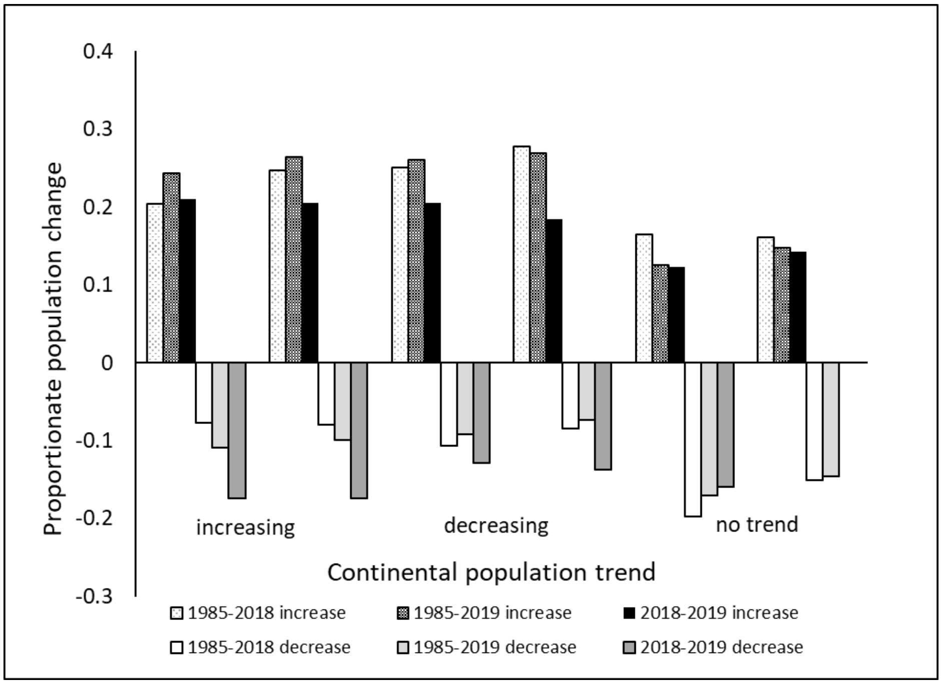

FIG. 6. Proportionate population shifts at the Yale-Myers Forest, Tolland/Windham counties, Connecticut, for three categories of continental population trend: increasing, decreasing, no trend.

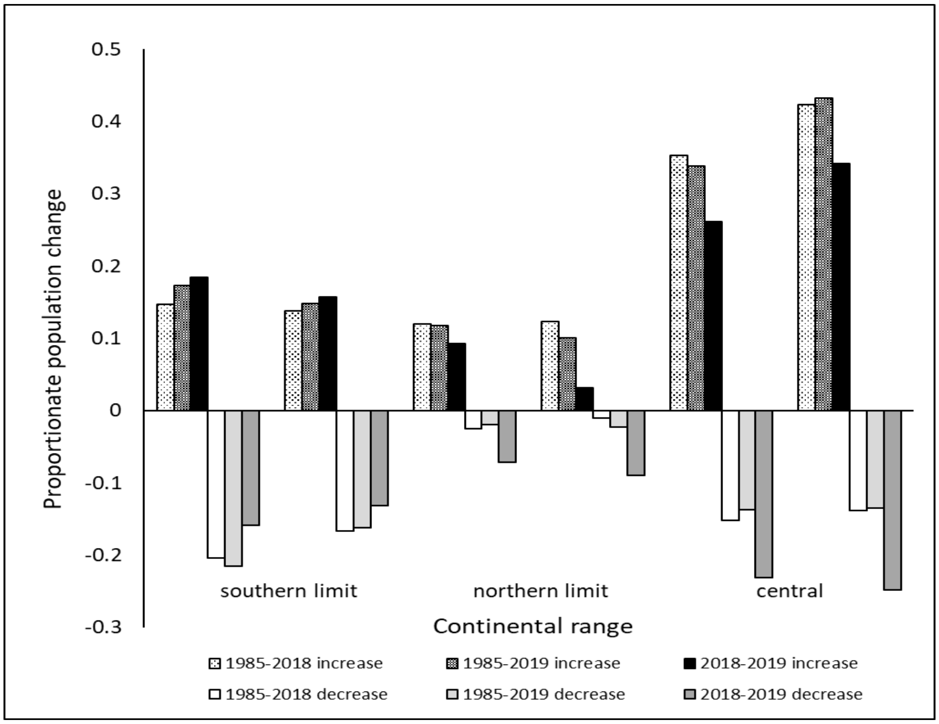

FIG.7. Proportionate population shifts for three categories of geographic ranges with respect to Connecticut: southern range limit, northern range limit, not near range limit.

highest elevation of the White Mountains, New Hampshire showed trends opposite to those predicted by climate change (DeLuca and King 2016). Moreover, most species undergoing population shifts were not near their range limit. Hence, climate change is clearly not the only agent driving community change.

Evidence consistent with habitat driving population shifts is more extensive, with 39% of interior forest and edge/successional species experiencing population increases. The percent of forest that is mature—now over 70%—has increased steadily in Connecticut since the first 1952 survey, with less than a 10% decline in total forest area occurring over this time (Alerich 1999, Butler 2017). If we presume that many of the Northeast's species coevolved with the mature forest that covered much, although not all, of the prehistoric landscape (Foster 1998), evidence of which may be the greater reproductive success experienced by species inhabiting forest interiors (Donovan et al 1995, Tittler et al. 2006), then population increases by interior forest species likely reflect this adaptation, with greater population densities of such species (Holmes and Sherry 2001) resulting from high reproductive success in mature, extensive forest.

Additional evidence of such high success is the movement of typically mature forest species into the younger age class forests at Yale-Myers Forest reported by Duguid et al. (2016), suggesting that individuals from source (mature) habitats are overflowing to sink (earlier successional shrubland and shelterwood treatment) habitats, where reproductive success is typically less (Thompson and Nolan 1973, Probst and Hayes 1987, Weinberg and Roth 1998).

Evidence also comes from population patterns in successional habitats. Although these habitats have declined state-wide, their proportion at Yale-Myers Forest has grown since 1985 and the greatest abundance increases we observed were among edge/ successional species. Such habitats have long been known to support bird populations at greater densities than in more mature forests (Odum 1950, Kendeigh and Fawver 1981). Indeed, plots of decreasing stand age at Yale-Myers Forest were associated with increasingly greater bird species density (Duguid et al. 2016).

Observations contrary to habitat driving an abundance increase are that 27% of species associated with interior forest and edge/successional habitats had population declines not appearing to be related either to habitat or climate. Furthermore, some of the most strongly declining species were forest interior-associated. Habitat, then, also appears able to account for only a portion of population shifts.

Additional factors showing a relationship with observed population patterns include for at least some species the effects of interspecific competition and expansion of habitat use. Interspecific competition is strongly suggested in the decline of the Black-capped Chickadee. Similar evidence for competition influencing populations of species, particularly near their range limits, is known for other species (Gross and Price 2000). Moreover, habitat expansion appears evident for the Yellow-bellied Sapsucker, which has ranged south even in the face of climate change, as have such northerly distributed species as the Common Raven. Rapid adjustments of traits, including those related to shifts in geographic range, is well documented for birds (Johnson and Selander 1964, Yeh 2004, Bearhop et al. 2005). Whether climate change may be involved in forcing such change (Martin 2001) is as yet uncertain, but species near their range limit are known to be under selective pressure to adapt to conditions found there (Liebl and Martin 2014).

The re-emergence of bird predators within the Yale-Myers Forest ecosystem also raises the possibility that such species influence populations of prey species. The recently arrived but former resident Sharp-shinned Hawk has begun re-occupying northeastern Connecticut for the first time since its local population collapsed after the 1920s (Craig 2017), likely in part a consequence of the DDT era (Hickey 1969), although the species also may be profiting from the expansion of younger forest at Yale-Myers Forest—its preferred habitat (Bildstein and Meyer 2000). Similarly, the Cooper's Hawk (*A. cooperii*) has reappeared as a widespread breeder throughout southern New England, including being observed at Yale-Myers Forest in 2020, with populations in Connecticut and Rhode Island now estimated at 4,820 (Craig 2017). The Fisher (*Pekania pennanti*), a predator of birds and eggs long extirpated from Connecticut (Craig 1979), has also become widespread (M. Duguid pers. obs.) after first being recorded at the forest in 1987 (R. Craig pers. obs.).

Observations reported further indicate complicating issues in interpreting the changes seen in this community. Patterns observed at the continental level were not necessarily evident at the regional level of this study, with both continentally increasing and decreasing species differentially showing increases at Yale-Myers Forest. This indicates that regional factors override continental ones in determining population trajectory. Moreover, we report that more than one factor may produce the same population response of individual species, making it difficult to distinguish the causative agent responsible for yielding an observed pattern.

All this strongly suggests that, although certain suites of species may respond similarly to particular environmental changes, species in general tend to respond individualistically to their environment, depending upon their particular physiology and ecological requirements, which are themselves not necessarily constant. Moreover, phenomena occurring external to a specific geographic region may drive local populations. For example, for neotropical and even migrants to the Southeastern U.S., conditions on the wintering ground may well have contributed to some of the patterns observed in this study. Any individual species' population is a complex interplay of responses to multiple and sometimes conflicting factors and factors operating at differing environmental scales (Holt 1993). Moreover, given the typical population fluctuations that occur at range peripheries (Thompson and Nolan 1973, Marti 1997) and even annually (Collins 2001), such as between 2018 and 2019 species composition, simply annual settlement patterns of breeding individuals may drive some community dynamism. (James et al. 1996, Villard and Maurer 1996). Hence, the Yale-Myers Forest bird community may be best thought of as the sum of individualistic responses to environmental and perhaps also stochastic factors.

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Appendix 1.

Species	Habitat preference	Geographic range	Geographic trend	Yale-Myers trend
Ruffed Grouse (*Bonasa umbellus*)	edge/successional	southern limit	decreasing	increasing
Wild Turkey(*Meleagrus gallipavo*)	edge/successional	core range	increasing	increasing
Mourning Dove (*Zenaida macroura*)	edge/successional	core range	decreasing	increasing
Yellow-billed Cuckoo (*Coccyzus americanus*)	edge/successional	northern limit	decreasing	increasing
Black-billed Cuckoo (*C. erythropthalmus*)	edge/successional	core range	decreasing	increasing
Ruby-throated Hummingbird (*Archilochus colubris*)	generalist	core range	increasing	increasing
Sharp-shinned Hawk (*Accipiter striatus*)	forest interior	core range	increasing	increasing
Red-shouldered Hawk (*Buteo lineatus*)	forest interior	northern limit	increasing	decreasing
Broad-winged Hawk *(B. platypterus*)	forest interior	core range	no trend	decreasing
Red-tailed Hawk (*B. jamaicensis*)	edge/successional	core range	increasing	no trend
Red-bellied Woodpecker (*Melanerpes carolinus*)	forest interior	northern limit	increasing	increasing
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	generalist	southern limit	increasing	increasing
Downy Woodpecker (*Picoides pubescens*)	generalist	core range	no trend	no trend
Hairy Woodpecker (*P. villosus*)	generalist	core range	increasing	decreasing
Northern Flicker (*Colaptes auratus*)	edge/successional	core range	decreasing	decreasing
Pileated Woodpecker (*Dryocopus pileatus*)	forest interior	core range	increasing	increasing
Eastern Wood Pewee (*Contopus virens*)	forest interior	core range	decreasing	increasing
Acadian Flycatcher (*Empidonax virescens*)	forest interior	northern limit	decreasing	decreasing
Least Flycatcher (*E. mimimus*)	edge/successional	southern limit	decreasing	no trend
Eastern Phoebe (*Sayornis phoebe*)	edge/successional	core range	increasing	no trend
Great-crested Flycatcher (*Myiarchus crinitus*)	generalist	core range	no trend	no trend
Yellow-throated Vireo (*Vireo flavifrons*)	edge/successional	northern limit	increasing	increasing
Blue-headed Vireo (*V. flavifrons*)	forest interior	southern limit	increasing	decreasing
Warbling Vireo (*V. gilvus*)	edge/successional	core range	increasing	increasing
Red-eyed Vireo *(V. olivaceus*)	forest interior	core range	increasing	increasing
Blue Jay (*Cyanocitta cristata*)	generalist	core range	decreasing	no trend
Common Raven (*Corvus corax*)	generalist	southern limit	increasing	increasing
Black-capped Chickadee (*Poecile atricapillus*)	generalist	southern limit	increasing	decreasing
Tufted Titmouse (*Baeolophus bicolor*)	generalist	northern limit	increasing	increasing
Red-breasted Nuthatch (*Sitta canadensis*)	forest interior	southern limit	no trend	decreasing
White-breasted Nuthatch (*S. carolinensis*)	Forest interior	core range	increasing	no trend
Brown Creeper (*Certhia americana*)	forest interior	southern limit	no trend	decreasing
House Wren (*Troglodytes aedon*)	edge/successional	core range	no trend	decreasing
Winter Wren (*T. hiemalis*)	forest interior	southern limit	increasing	no trend
Blue-gray Gnatcatcher (*Polioptila caerulea*)	generalist	northern limit	no trend	decreasing
Eastern Bluebird (*Sialia sialis*)	edge/successional	core range	increasing	no trend
Veery (*Catharus fuscescens*)	forest interior	southern limit	decreasing	increasing
Hermit Thrush (*C. guttatus*)	forest interior	southern limit	no trend	decreasing
Wood Thrush (*Hylocichla mustelina*)	forest interior	core range	decreasing	increasing

American Robin (*Turdus migratorius*)	edge/successional	core range	no trend	decreasing
Gray Catbird (*Dumatella carolinensis*)	edge/successional	core range	no trend	increasing
Cedar Waxwing (*Bombycilla cedrorum*)	edge/successional	core range	increasing	decreasing
Purple Finch (*Haemorhous purpureus*)	edge/successional	southern limit	decreasing	no trend
Pine Siskin (*Spinus pinus*)	edge/successional	southern limit	decreasing	decreasing
American Goldfinch (*Spinus tristis*)	edge/successional	core range	no trend	decreasing
Chipping Sparrow (*Spizella passerina*)	edge/successional	core range	no trend	decreasing
Dark-eyed Junco (*Junco hyemalis*)	forest interior	southern limit	decreasing	decreasing
White-throated Sparrow (*Zonotrichia albicollis*)	edge/successional	southern limit	decreasing	decreasing
Song Sparrow (*Melospiza melodia*)	edge/successional	core range	decreasing	increasing
Eastern Towhee (*Pipilo erythropthalmus*)	edge/successional	northern limit	decreasing	increasing
Baltimore Oriole (*Icterus galbula*)	edge/successional	core range	decreasing	decreasing
Brown-headed Cowbird (*Molothrus ater*)	edge/successional	core range	decreasing	no trend
Common Grackle (*Quiscalus quiscula*)	edge/successional	core range	decreasing	decreasing
Ovenbird (*Seiurus aurocapilla*)	forest interior	core range	no trend	increasing
Worm-eating Warbler (*Helmitheros vermivorum*)	forest interior	northern limit	increasing	no trend
Louisiana Waterthrush (*Parkesia motacilla*)	forest interior	northern limit	increasing	decreasing
Northern Waterthrush (*P. novaboracensis*)	forest interior	southern limit	decreasing	no trend
Blue-winged Warbler (*Vermivora cyanoptera*)	edge/successional	core range	decreasing	decreasing
Black-and-white Warbler (*Mniotilta varia*)	generalist	core range	decreasing	no trend
Nashville Warbler (*Oreothlypis ruficapilla*)	edge/successional	southern limit	decreasing	increasing
Kentucky Warbler (*Geothlypis formosa*)	forest interior	northern limit	decreasing	increasing
Common Yellowthroat (*Geothlypis trichas*)	edge/successional	core range	decreasing	increasing
American Redstart (*Setophaga ruticilla*)	edge/successional	core range	decreasing	decreasing
Cerulean Warbler (*S. cerulea*)	forest interior	northern limit	decreasing	increasing
Magnolia Warbler (*S. magnolia*)	generalist	southern limit	no trend	increasing
Blackburnian Warbler (*S. fusca*)	forest interior	southern limit	no trend	decreasing
Yellow Warbler (*Setophaga petechia*)	edge/successional	core range	decreasing	increasing
Chestnut-sided Warbler (*S. pensylvanica*)	edge/successional	southern limit	decreasing	increasing
Black-throated Blue Warbler (*S. caerulescens*)	forest interior	southern limit	no trend	increasing
Pine Warbler (*S. pinus*)	forest interior	core range	increasing	increasing
Yellow-rumped Warbler (*S. coronata*)	forest interior	southern limit	no trend	decreasing
Black-throated Green Warbler (*S. virens*)	forest interior	southern limit	increasing	decreasing
Canada Warbler (*Cardellina canadensis*)	forest interior	southern limit	decreasing	increasing
Scarlet Tanager (*Piranga olivacea*)	forest interior	core range	no trend	increasing
Northern Cardinal (*Cardinalis cardinalis*)	edge/successional	northern limit	no trend	increasing
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	edge/successional	core range	decreasing	increasing