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RESPONSE OF BIRD POPULATIONS TO LONG-TERM CHANGES IN LOCAL VEGETATION AND REGIONAL FOREST COVER

MARY L. BUCHANAN,[1,3] ROBERT A. ASKINS,[1,4] AND CHAD C. JONES[2]

ABSTRACT.—We analyzed data from a woodland site for a 59-year period to determine whether changes in bird populations are related to changes in the diversity and relative abundance of woody plant species even when vegetation structure, degree of forest fragmentation in the surrounding landscape, and regional changes in bird populations are taken into account. Principal component analyses generated vegetation factors encompassing variables such as total basal area, shrub density, basal area of common tree species, and measures of tree and shrub species diversity. We also calculated a forest edge/ forest area index based on GIS analysis of the landscape within 2 km of the study site. Poisson regression models revealed relationships between these covariates and population changes for 19 bird species and for seven groups of species characterized by similar migration strategies or habitat requirements. All groups of habitat specialists showed a positive relationship with the first vegetation factor, which indicates that they declined as total basal area and dominance of oaks and maples increased and as tree and shrub diversity decreased. This suggests that floristic diversity may be important for determining habitat quality. Bird species associated with the shrub layer and with hemlock stands showed positive relationships with the second vegetation factor, suggesting that the recent decline in eastern hemlocks (*Tsuga canadensis*) because of hemlock woolly adelgid (*Adelges tsugae*) had an adverse impact on these species. Forest migrants, shrub-layer specialists, long-distance migrants and permanent residents showed negative relationships with the forest edge/forest interior index, indicating that conservation efforts to protect bird communities should take the wider landscape into account. The strongest relationship for most species and species groups was with the first vegetation factor, which suggests that species composition and diversity of trees and shrubs may be especially important in determining abundance of many forest bird species. *Received 26 June 2015. Accepted 4 February 2016.*

Key words: bird population declines, forest birds, forest fragmentation, hemlock decline, tree species composition.

Long-term monitoring of populations at particular study sites can provide new insights about the main drivers of population change, particularly if the environment within and around the site is monitored. For example, repeated bird censuses at several sites in eastern North America not only provided the initial evidence that Neotropical migratory birds were declining but also suggested two hypotheses to explain these declines (reviewed in Askins 2002). Severe population declines were attributed either to loss of winter habitat or to forest fragmentation in the region around the study site. Loss of habitat in non-breeding areas was a logical hypothesis because breeding habitat in the study areas had been carefully protected, and habitat fragmentation was a reasonable hypothesis because the temperate-zone study sites were in urban or suburban areas with recent loss of forest cover. These competing hypotheses triggered hundreds of studies that focused on winter habitat

requirements of Neotropical migrants or on the impact of forest fragmentation and edge effects on forest specialists. As a result, we now have a much better understanding of the complex interplay of breeding and non-breeding habitats in determining population dynamics of migratory forest birds (Holmes 2007).

One of the studies that contributed to the initial concern about population declines in Neotropical migrants was a standardized census of birds in the Connecticut College Arboretum that was initiated in 1953 (Butcher et al. 1981). In contrast to most long-term bird censuses in eastern North America, this study was done in conjunction with an intensive study of vegetation change at the same site (Niering and Goodwin 1962), permitting analysis of relationships between population changes in birds and changes in vegetation structure and plant species composition. Although populations of migratory forest birds are clearly affected by regional changes in landscape cover and by availability and quality of habitat in migratory stopover and wintering areas, they are also affected by the structure and composition of forest vegetation at potential breeding sites. Most analyses of the relationships between avian communities and vegetation have focused on

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vegetation structure, emphasizing both vertical structural elements such as canopy height and density of multi-tiered vegetation layers, and horizontal structural elements such as stem density and distribution of canopy gaps (reviewed in Fuller et al. 2012). There is growing interest in the role of floristic composition of the vegetation, however, and models that incorporate both structural and floristic variables have revealed emergent relationships between certain bird species and vegetation that were not evident in purely structural models (Hewson et al. 2011), indicating that floristics should not be ignored. Of course, just as it has been difficult to tease apart the effects of changes in breeding and winter habitat on migratory bird populations (Holmes 2007), it will also be difficult to assess the relative effects of floristic changes and other local and regional changes in breeding habitat on bird populations.

A number of recent studies indicated that changes in the presence and abundance of particular plant species lead to corresponding shifts in avian populations. Not all of these differences can be explained entirely by structural factors; in a study area in Pennsylvania, total abundance of birds in oak-dominated forests was higher than in maple-dominated forests even though the two forest types did not differ significantly in terms of vegetation structure (Rodewald and Abrams 2002). Also, a comparison of 47 Breeding Bird Census sites revealed significant correlations between bird species composition and tree species composition in forests in eastern North America even after geographic location and overall forest structure were taken into account (Lee and Rotenberry 2005). Shifts in floristic composition of a forest over time may therefore drive (or at least influence) changes in the composition and diversity of the avian community within the forest.

In-depth studies of insectivorous birds in Hubbard Brook Experimental Forest in New Hampshire indicated that while much of the variability among foraging guilds can indeed be explained by vegetation height and foraging substrate (e.g., ground, bark, foliage), differential use of plant species also accounts for some of the finer differences among species (Holmes et al. 1979). Different plant species have morphological characteristics that may affect avian foraging opportunities, such as branching pattern, leaf arrangement, and foliage density. Additionally, plant species may differ in terms of available food resources, as in the case for yellow birches (*Betula alleghaniensis*) in Hubbard Brook Forest, which support higher densities of lepidopteran larvae than do other tree species. Robinson and Holmes (1984) determined that species such as the American Redstart (*Setophaga ruticilla*) and Philadelphia Vireo (*Vireo philadelphicus*) encounter and attack prey more often in yellow birches than would be expected based solely on the frequency of these trees, probably because of high insect density and leaf accessibility. Moreover, Gabbe et al. (2002) observed selective foraging on particular tree species in 12 of the 13 avian species studied in floodplain forests in Illinois. Many of the birds with stronger preferences for particular tree species, such as Scarlet Tanagers (*Piranga olivacea*) and Cerulean Warblers (*Setophaga cerulea*), were among less common bird species, suggesting that more selective bird species may have greater difficulty finding suitable breeding sites, which may limit population size and distribution.

We analyzed standardized data on changes in both bird and woody plant populations between 1952 and 2012 in a study site in the Connecticut College Arboretum. Our main goal was to determine whether changes in bird populations are predicted by changes in the composition and diversity of woody plant species even when the structure of the forest vegetation, degree of forest fragmentation in the surrounding landscape, and regional changes in bird populations are also considered.

METHODS

Study Site.—The study site is a 23.1-ha woodland located in the Bolleswood Natural Area of the Connecticut College Arboretum in New London, CT (Askins and Philbrick 1987). The Natural Area was originally established to facilitate long-term research in a woodland with no active management beyond trail maintenance. An exception to this policy was made with the completion of a deer fence around the study site in 1989 and subsequent culling of deer within the fence (G. D. Dreyer, pers. obs.). Also, an invasive plant, Japanese barberry (*Berberis thunbergii*), was

controlled in one small patch along the border of the study area.

The study area is located 6.4 km north of the Long Island Sound (41° 23′ N, 72° 07′ W) and covers terrain of varying topography, including a series of ledges and a ravine with an intermittent stream; its highest point is 61 m in elevation (Niering and Goodwin 1962, Small et al. 2005). It is bordered by a pond and a park-like plant collection area to the east, and wooded sections of the Arboretum to the southeast and west. A paved road on the north and a powerline corridor on the southwest separate the study area from other forested sections of the Arboretum.

In 1962, the study area was categorized as a primarily oak-hemlock forest (Niering and Goodwin 1962), but the site has undergone a severe decline in eastern hemlock (*Tsuga canadensis*) since the arrival of the hemlock woolly adelgid (*Adelges tsugae*) in 1987 (Small et al. 2005). The only non-forested areas within the study site are small areas of open water and low herbaceous and shrub vegetation in two small bogs (0.5 and 0.8 ha; Niering and Goodwin 1962).

Bird Census Methods.—Twenty-nine breeding bird surveys were conducted in the study area between 1953 and 2012. Although these surveys have not occurred at consistently regular intervals, there have been at least two surveys per decade; surveys were completed in 1953, 1955, 1959, 1961, 1964, 1973, 1976, 1982 to 1997, 1999–2000, 2002, 2007, 2009, and 2012. In each survey year, spot-mapping methods were used to determine the abundance of breeding birds (number of territories for each species) at the site (Svenson and Williamson 1969). When territories straddled the boundary of the study area, they were recorded as fractional territories (rounded to 0.5 or 1); territories that overlapped the study area by less than ~25% were not included in the analysis. Fractional territories were not recorded before 1973, which could result in slightly higher estimates of abundance during that period. Ten censuses were conducted during survey years except in 1953 and 1955, when seven and eight censuses were completed, respectively. Results of spot-mapping censuses are robust in the range of 7–10 censuses (Svensson 1978).

Censuses were conducted along four parallel north-south trails along the eastern and western edges and through the center of the study area.

Locations of birds were recorded on a map of the study area using stone walls, erratic boulders, rock ledges, and other permanent landmarks for orientation. All censuses were completed between mid-May and mid-July and between 0400 and 0700 Eastern Daylight Time (EDT) (Askins and Philbrick 1987).

Bird species were classified based on habitat and migration patterns (Table 1). We categorized bird species as migratory forest specialists (migratory species that primarily nest in mature forests) and shrub-layer specialists (species that nest in the shrub layer in the forest understory, forest edge, or shrubland openings) based on DeGraaf and Yamasaki (2001). We also grouped species that are associated with eastern hemlock (hemlock associates) and species that might benefit from hemlock decline ('hemlock decline winners'; Tingley et al. 2002, Becker et al. 2008). Species were categorized as long-distance migrants that overwinter in the Neotropics; short-distance migrants that overwinter in the southern temperate zone or subtropics; or permanent residents (Table 1; Askins and Philbrick 1987).

Vegetation Methods.—In 1952, Niering and Goodwin (1962) established four east-west transects spanning the study area. The permanent transects are 122 m apart and 6 m wide; each is divided into two rows of 3 × 3 m quadrats (750 total). Vegetation surveys were conducted every 10 years between 1952 and 2012. All herbs, shrubs, saplings, and trees present in each quadrat were identified during each survey (Niering and Goodwin 1962). Each plant was assigned to one of the following height classes: >2 m, 0.6–2 m, 5 cm–0.6 m, and <5 cm. Frequency of each tree and shrub species was calculated for each year as the number of quadrats in which the species occurred. Total shrub abundance was estimated using the sum of the frequencies for all shrub species. Diameter at breast height (DBH) was measured for all trees >1.37 m in height, and used to calculate basal area for each species.

On the basis of previous research on floristics and bird habitats (Holmes et al. 1979, Robinson and Holmes 1984, Gabbe et al. 2002, Rodewald and Abrams 2002, Tingley et al. 2002, Becker et al. 2008), we selected several tree species or groups of tree species for analysis: red maple (*Acer rubrum*), oaks (composed of black oak [*Quercus velutina*], red oak [*Q. rubra*], white oak [*Q. alba*],

and scarlet oak [*Q. coccinea*]), black birch (*Betula lenta*), yellow birch, and eastern hemlock. We used basal area (m^2/ha) as a measure of the abundance of each tree species in the forest canopy. We used total basal area of trees and total frequency of shrubs as measures of vegetation structure, because these are closely related to canopy height, tree canopy cover, and shrub cover. To evaluate tree species diversity, we calculated diversity values for each year using the Inverse Simpson's Diversity Index based on basal area (Gurevitch et al. 2006). Diversity values for the shrub layer were calculated by applying the Inverse Simpson's Diversity Index to data on shrub species frequency. Data on herbaceous plants were not included in the analysis of bird distributions.

Values for vegetation variables are available for seven years (1952, 1962, 1972, 1982, 1992, 2002, and 2012), while bird abundance values are available for 29 years, so we used linear interpolation to derive approximate values for vegetation variables for the years in which there were bird censuses but no vegetation surveys.

Measuring Forest Cover in the Surrounding Landscape.—We analyzed 1:10,000 aerial photographs using ArcGIS 10.2 (ESRI 2013) to assess changes in the amount and distribution of forest cover within 2 km of the study site. We first created a buffer zone polygon around the centroid of the study site. We obtained aerial photograph tiles of the buffer area from the years 1951, 1970, 1986, 1995, 2004, and 2012. We used aerial photographs from 1951–1995 from the online archives of the Map and Geographic Information Center (MAGIC, 2011). Georeferenced orthophotographs were available for 2004 and 2012 from Connecticut Environmental Conditions Online (Connecticut Department of Environmental Protection 2007, USGS 2013), and we used landmarks on these layers to georeference the earlier image tiles, creating links until we had achieved a root square mean error of <15 ft (4.6 m) for each image tile. All aerial photographs used the following projected coordinate system: NAD 1983 State Plane Connecticut FIPS 0600 Feet.

For each year, we manually digitized polygons to outline the patches of forest cover present in the images. We included all tree-covered patches >1 ha. Digitizing at a consistent map scale of 1:10,000 helped minimize the effect of having aerial photographs with different resolutions. We then calculated the total forest area and the total amount of forest edge (excluding the buffer boundary) within 2 km of the center of the study area.

Statistical Analysis.—We assessed changes in species composition of woody plants by running a non-metric multi-dimension scaling (NMS) ordination using PC-Ord Version 6 on the 'slow and thorough' autopilot setting. Separate ordinations were conducted for all species of shrubs (using frequency) and for all species of trees (using basal area). Based on the criteria that each axis must be significant in Monte Carlo tests and must decrease overall stress in the model by at least 5 (McCune and Grace 2002), a two-dimensional solution was selected for trees (min stress = 0, $P = 0.012$) and a one-dimensional solution was selected for shrubs (min stress = 10.2, $P = 0.028$).

We used principal component analysis (PCA) in SPSS Version 21 (IBM Corp. 2012) to create factors that accounted for most of the variation in the 10 vegetation variables we had previously selected because they have been shown to be important for forest birds (Table 2). We included the shrub ordination scores as one of these ten variables, but chose to include the basal areas of specific tree species of interest rather than NMS ordination scores for trees to improve our ability to interpret results. To assess changes in forest cover in the region around the study area, we calculated a forest fragmentation index based on the ratio of total forest edge to total forest area within 2 km of the study area.

We used R statistical software Version 3.0.2 (R Core Team 2013) to analyze changes in bird populations with Poisson general linear models (GLM) using three independent variables—the first and second vegetation principal components, and the forest edge/forest area ratio. For each independent variable we used linear interpolation to produce values for each bird survey year and then standardized the variable prior to running GLM. The first vegetation factor was highly correlated ($r = 0.96$) with time (measured in years since the surveys began), so we did not include time as a separate independent variable.

We ran GLM for 19 common bird species, four groups of species categorized by habitat, and three groups of species categorized by migratory pattern. For each species or group of species, we ran models with every possible subset of independent variables ($n = 7$). We then used multi-model

TABLE 1. Species recorded as breeding residents in the Connecticut College Arboretum study area during at least 2 years between 1953 and 2012, showing habitat and migratory categories. Forest migrant = migratory forest specialist, Shrub specialist = species strongly associated with the shrub layer in either forest or shrubland habitat. Migratory group: Resident = permanent resident, Long = long-distance migrant (primarily winters in tropics), Short = short-distance migrant (primarily winters in temperate zone or subtropics). Relation to hemlock: DW = hemlock decline 'winner' (benefits from the decline of eastern hemlock), HA = hemlock associate. Species in bold had large enough sample sizes in the study area for statistical analysis of population change. Population trends for Connecticut (CT) are based on analysis of BBS data for all survey routes in the state (Field and Elphick 2012; C. R. Field unpubl. data).

Common name	Scientific name	Forest migrant	Shrub specialist	Migratory group	Relation to hemlock	Percent change per year	
						CT	Study area
Ruffed Grouse	*Bonasa umbellus*			Resident			
Red-shouldered Hawk	*Buteo lineatus*			Resident			
Broad-winged Hawk	*Buteo platypterus*	X		Long			
Mourning Dove	*Zenaida macroura*			Short			
Yellow-billed Cuckoo	*Coccyzus americanus*		X	Long			
Black-billed Cuckoo	*Coccyzus erythropthalmus*		X	Long			
Barred Owl	*Strix varia*			Resident			
Eastern Whip-poor-will	*Antrostomus vociferus*			Long			
Red-bellied Woodpecker	*Melanerpes carolinus*			Resident			
Downy Woodpecker	*Picoides pubescens*			Resident	DW		
Hairy Woodpecker	*Picoides villosus*			Resident	DW		
Northern Flicker	*Colaptes auratus*			Short			
Eastern Wood-Pewee	***Contopus virens***	**X**		**Long**	**DW**	nc[a]	nc
Acadian Flycatcher	*Empidonax virescens*	X		Long	HA		
Eastern Phoebe	*Sayornis phoebe*			Short			
Great Crested Flycatcher	***Myiarchus crinitus***	**X**		**Long**	**DW**	nc	nc
White-eyed Vireo	*Vireo griseus*		X	Short			
Red-eyed Vireo	***Vireo olivaceus***	**X**		**Long**	**DW**	+1.89	nc
Blue Jay	***Cyanocitta cristata***			**Resident**		−2.11	−1.90
American Crow	*Corvus brachyrhynchos*			Resident			
Fish Crow	*Corvus ossifragus*			Resident			
Black-capped Chickadee	***Poecile atricapillus***			**Resident**		+2.44	nc
Tufted Titmouse	***Baeolophus bicolor***			**Resident**	**DW**	+6.08	nc
White-breasted Nuthatch	***Sitta carolinensis***			**Resident**	**DW**	+2.64	nc
House Wren	***Troglodytes aedon***		**X**	**Short**		nc	−1.60
Carolina Wren	*Thryothorus ludovicianus*		X	Resident			
Blue-gray Gnatcatcher	*Polioptila caerulea*	X		Long			
Veery	***Catharus fuscescens***		**X**	**Long**	**DW**	nc	−1.06
Hermit Thrush	*Catharus guttatus*	X		Short	HA		
Wood Thrush	***Hylocichla mustelina***	**X**	**X**	**Long**	**DW**	−1.50	nc
American Robin	*Turdus migratorius*			Short			
Gray Catbird	***Dumetella carolinensis***		**X**	**Short**		nc	−1.49
Brown Thrasher	*Toxostoma rufum*		X	Short			
Ovenbird	***Seiurus aurocapilla***	**X**		**Long**	**HA**	nc	−1.95
Worm-eating Warbler	*Helmitheros vermivorum*	X	X	Long			
Louisiana Waterthrush	*Parkesia motacilla*	X	X	Long	HA		
Blue-winged Warbler	*Vermivora cyanoptera*		X	Long			
Black-and-white Warbler	***Mniotilta varia***	**X**		**Long**		nc	−1.99
Common Yellowthroat	***Geothlypis trichas***		**X**	**Short**		nc	nc
Hooded Warbler	***Setophaga citrina***		**X**	**Long**	**DW**	+7.12	−1.98
American Redstart	*Setophaga ruticilla*			Long			
Chestnut-sided Warbler	*Setophaga pensylvanica*		X	Long			
Pine Warbler	*Setophaga pinus*	X		Short			
Prairie Warbler	*Setophaga discolor*		X	Long			
Black-throated Green Warbler	*Setophaga virens*	X		Long	HA		
Canada Warbler	*Cardellina canadensis*		X	Long			
Eastern Towhee	***Pipilo erythrophthalmus***		**X**	**Short**		−4.32	−1.39
Scarlet Tanager	***Piranga olivacea***	**X**		**Long**	**DW**	nc	−2.96

TABLE 1.   Continued.

Common name	Scientific name	Forest migrant	Shrub specialist	Migratory group	Relation to hemlock	Percent change per year	
						CT	Study area
Northern Cardinal	***Cardinalis cardinalis***		**X**	**Resident**		**+4.62**	**nc**
Rose-breasted Grosbeak	*Pheucticus ludovicianus*			Long			
Red-winged Blackbird	*Agelaius phoeniceus*			Short			
Brown-headed Cowbird	***Molothrus ater***			**Short**	**DW**	**nc**	**nc**
Baltimore Oriole	*Icterus galbula*			Long			
American Goldfinch	*Spinus tristis*			Resident	DW		

[a] No change: $P < 0.05$ for regressions of population trends for BBS data for Connecticut; time does not improve the model for GLM analyses of data from the study area.

weighted averages to calculate coefficients for each of the independent variables using the MuMIn package in R (Bartón 2013). Model weights were determined by comparing AIC*c* values. AIC*c* values were used rather than AIC to correct for small sample size. For models that were overdispersed (residual deviance/degrees of freedom >1.3), we used Quasi AIC (QAIC) values to determine the model weights. Because averaging unstandardized coefficients is problematic in the presence of multicollinearity, we first standardized the coefficients in each model using the partial standard deviation (Cade 2015). Importance values for each independent variable are often calculated by summing the weights of individual models that contain that variable, but recent analyses suggests that these values poorly represent the actual contribution of independent vari-

ables (Galipaud et al. 2014). Consequently, we used relative importance values based on the ratio of standardized coefficients within each set of weighted models as recommended by Cade (2015). Thus, the most important variable is given a value of one.

We compared population trends in our study area with those from Breeding Bird Survey (BBS) routes in Connecticut (Sauer et al. 2008). BBS data for Connecticut routes were obtained from Field and Elphick (2012) and C. R. Field (unpubl. data). Connecticut BBS routes provide an appropriate measure of regional population trends because the state is mostly wooded and is dominated by one forest type (central hardwood forest). To determine which species had increasing or declining populations in the study area, we ran Poisson regression models for each species and group of species for censuses between 1964 and 2009 (the time period corresponding to the BBS data) using time as the only independent variable. Because we were interested in overall trends, we used the identity link in Poisson regression so that coefficients indicate predicted change in abundance per year. Species or groups for which adding time as a variable did not reduce AIC*c* or QAIC were considered to have no significant change in abundance during 1964–2009. We then compared population trends in the study area to trends for these species in the statewide surveys during the same time period. We only included species with a sufficient sample size in the Arboretum censuses (an average of ≥ 2 individuals per year for the period 1964–2009).

We calculated the Pearson correlation coefficient between tree species diversity and both abundance and species diversity of migratory

TABLE 2.   Factor loadings for principal component analysis (PCA) of 10 vegetation variables. Three components were extracted, but only the first two (which account for 85% of the variance) are included here.

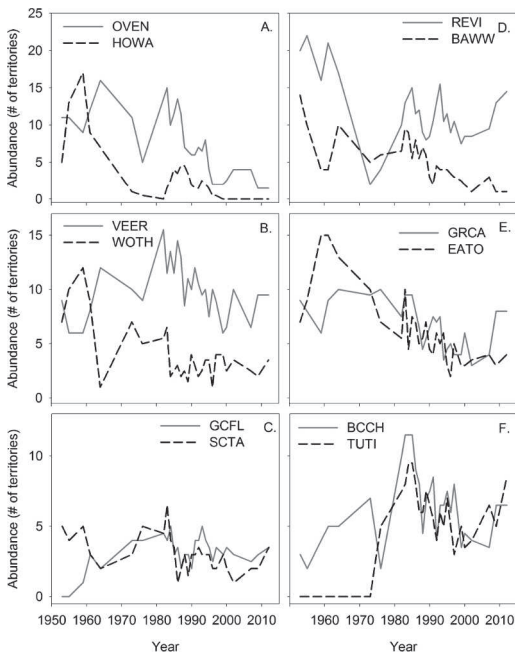| Vegetation variables	Component	
	1	2
Total shrub frequency	0.084	0.37
Shrub ordination axis 1	0.98	−0.10
Basal area (m²/ha)		
Red maple	−0.98	0.16
Yellow birch	0.85	−0.36
Black birch	−0.69	0.64
Oak spp.	−0.98	0.20
Eastern hemlock	−0.24	−0.91
Total basal area	−0.96	−0.21
Simpson's Diversity Index		
Trees	0.89	0.40
Shrubs	0.30	0.36

FIG. 1. Population changes in 12 bird species with the highest cumulative abundance during the 29 census years. (A) and (B) Shrub-layer and forest-floor species (Ovenbird [OVEN] Hooded Warbler [HOWA], Veery [VEER], and Wood Thrush [WOTH]. (C) Canopy species (Great Crested Flycatcher [GCFL] and Scarlet Tanager [SCTA]). (D) Canopy and subcanopy species (Red-eyed Vireo [REVI] and Black-and-white Warbler [BAWW]). (E) Shrub-layer specialists (Gray Catbird [GRCA] and Eastern Towhee [EATO]). (F) Habitat generalists (Black-capped Chickadee [BCCH] and Tufted Titmouse [TUTI]).
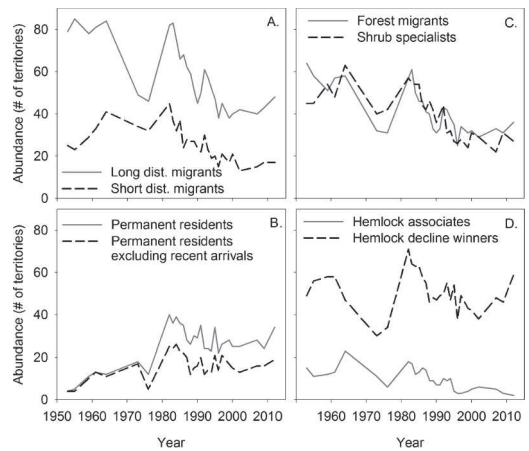

FIG. 2. Population changes in (A) long-distance and short-distance migrants, (B) all permanent residents and permanent residents excluding 'Recent Arrivals,' which are those species first recorded in the study area after the 1950s because they colonized southern New England as their geographical ranges expanded northward (Red-bellied Woodpecker, Tufted Titmouse, Carolina Wren, and Northern Cardinal; Appendix 4), (C) migratory forest specialists and shrub-layer specialists, (D) species that are associated with eastern hemlock and species that are known to increase after the decline of eastern hemlock stands ('hemlock decline winners').

forest specialists (Inverse Simpson's Diversity Index based on the abundance of different species). We chose to focus only on migratory forest specialists so that potential increases in generalist species, which would be included in a diversity index of the entire bird community, would not mask population changes in species that depend on forests.

RESULTS

Changes in the Bird Community Over Time.— Many of the most common species of birds in the study area showed overall population declines during the 59 years of the study (Fig. 1, Table 1). Several habitat and migratory groups showed substantial population declines in the study area during the 1970s but appeared to recover by the early 1980s (Fig. 2). However, long-distance and short-distance migrants declined since the 1980s (Fig. 2A). In contrast, permanent residents increased substantially (Fig. 2B). This increase was evident even when we excluded new colonists that were only observed in the study area following northward range expansions into southern Connecticut. Migratory forest specialists and shrub-layer specialists both showed long-term declines (Fig. 2C). Hemlock associates showed a long-term decline and hemlock decline winners fluctuated (Fig. 2D).

Changes in Vegetation.—Principal component analysis reduced 10 vegetation variables to two principal components accounting for 85% of the variance (Table 2). The first principal component was strongly and negatively associated with the basal areas of red maple and oak species, and with total basal area of all tree species. The first component also was strongly and positively associated with basal area of yellow birch, overall tree species diversity, shrub ordination axis 1, and total shrub frequency. This same pattern is clear in

TABLE 3. Correlation coefficients between non-metric multi-dimension scaling (NMS) ordination axes and variables used in the analysis of changes in bird populations. Separate NMS ordinations were run on basal area of all species of trees and frequency of all species of shrubs. Significant relationships are shown in bold font.

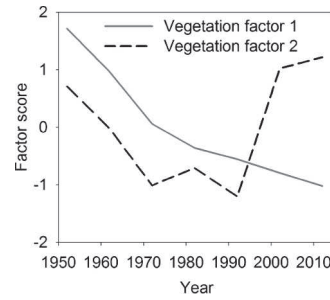| Variable	Shrub axis 1	Tree axis 1	Tree axis 2
Yellow birch	**0.84***	**−0.78***	−0.55
Red maple	**−0.99****	**0.94****	0.30
Black birch	−0.71	0.55	0.69
Eastern hemlock	−0.17	0.43	**−0.82***
Oak spp.	**−0.99****	**0.92****	0.32
Total basal area	**−0.93****	**0.99****	−0.06
Tree diversity (Simpson's Index)	**0.83***	**−0.96****	0.21
Shrub diversity (Simpson's Index)	0.17	−0.24	0.32
Total shrub frequency	0.76*	**−0.83***	0.25
Shrub axis 1	1	**−0.95****	−0.21
Tree axis 1	**−0.95****	1	0
Tree axis 2	−0.21	0	1

* $P < 0.05$.
** $P < 0.01$

FIG. 3. Changes in the two vegetation principal components between 1952 and 2012. Factor 1 is negatively correlated with measures of forest maturation such as total basal area and basal areas for oaks and red maple, while Factor 2 is negatively correlated with basal area of eastern hemlock.

the results of the first NMS ordination axis for trees (Table 3), which are based on data from all species of trees. The first vegetation principal component decreased during the entire 60 years of the study (Fig. 3), indicating a progressive shift to larger trees, a sparser shrub layer, and a less-diverse tree canopy dominated more by oaks and maples (Table 2, Appendix 1). NMS ordinations also indicate a progressive shift in species composition of both shrubs and trees during this period. The shrub ordination axis showed a relatively steady decline over time, reflecting a shift in species composition of the shrub layer (Appendix 1D). The frequency of many common shrub and vine species such as *Gaylussacia baccata*, *Hamamelis virginiana*, *Rubus* spp., *Smilax rotundifolia*, *Toxicodendron radicans,* and *Vaccinium corymbosum* were positively correlated with the scores for the shrub ordination axis (Appendix 2), indicating that they declined during the 60 years of the study.

The second vegetation component was strongly and negatively associated with basal area of eastern hemlock. A strong relationship with basal area of eastern hemlock also characterizes the second axis for trees in the NMS vegetation ordination (Table 3). The second vegetation principal component declined until the early 1990s and then increased sharply (Fig. 3), reflecting the rise and subsequent fall in the dominance of eastern hemlock in the study area (Appendix 1B).

Changes in Regional Forest Cover.—Although specific areas within the 2-km buffer changed from forest to non-forest or vice versa, the total area of forest cover did not change substantially between 1951 and 2012, never fluctuating by >10% from its maximum. In the years covered by this study, the forest edge/forest area index reached its highest point in the 1970s, and then declined fairly steadily except for a temporary and smaller spike in the 1990s (Appendix 1F). Although many forested areas were cleared in the region after 1951, the woodland areas to the north of the study area became more extensive and continuous between 1951 and 2012 (Appendix 3) because of growth of forest on abandoned farmland (Goodwin 1991).

Relationship between Bird Community and Vegetation and Landscape Factors.—Importance values derived from regression models revealed which variables or combination of variables best explained changes in abundance of particular bird species or groups of species (Table 4). All species groups except permanent residents had a positive relationship with the first vegetation factor, indicating a decrease in their abundance over time as the maturing forest became more dominated by larger trees and by oaks and red maple (variables which are correlated with lower factor scores for

TABLE 4. Results of analyses of changes in the abundance of the 19 most common species of birds in the study area, and of seven groups of species characterized by similar habitat requirements or migratory strategies. Bird populations were analyzed with Poisson general linear models using three independent variables: the first and second factors from a principal component analysis of vegetation factors (Vegetation Factors 1 and 2), and the ratio of forest edge/forest area in the 2-km radius area around the study area (Edge Index). The coefficient for each variable is following by its relative importance value (in parentheses) based on the ratio of standardized coefficients within each set of weighted models. Residual deviance is for the full model with all variables included.

Species/group	Vegetation factor 1	Vegetation factor 2	Edge index	Null deviance	Residual deviance
Red-eyed Vireo	0.213 (1.00)	0.096 (0.45)	−0.140 (0.66)	50.9	25.2
Veery	−0.030 (0.24)	−0.130 (1.00)	−0.088 (0.68)	18.0	11.2
Ovenbird	0.320 (0.91)	−0.350 (1.00)	−0.082 (0.24)	73.6	31.0
Gray Catbird	0.113 (1.00)	−0.108 (0.95)	0.062 (0.55)	20.1	14.9
Eastern Towhee	0.259 (1.00)	−0.169 (0.65)	0.155 (0.60)	46.0	15.3
Black-capped Chickadee	−0.114 (0.54)	−0.167 (0.79)	−0.211 (1.00)	34.0	19.7
Black-and-white Warbler	0.349 (1.00)	−0.276 (0.79)	−0.151 (0.43)	52.4	20.2
Tufted Titmouse	−0.484 (0.83)	−0.160 (0.27)	−0.583 (1.00)	80.8	20.8
Wood Thrush	0.284 (1.00)	0.055 (0.19)	0.165 (0.58)	41.9	21.8
Scarlet Tanager	0.140 (1.00)	−0.085 (0.61)	0.044 (0.31)	16.2	13.3
Great Crested Flycatcher	−0.395 (1.00)	−0.164 (0.42)	0.126 (0.32)	21.2	8.8
Hooded Warbler	0.468 (1.00)	−0.389 (0.83)	−0.165 (0.35)	115.7	30.5
Blue Jay	−0.006 (0.05)	−0.138 (1.00)	0.078 (0.56)	17.2	14.9
Northern Cardinal	−0.645 (1.00)	−0.135 (0.21)	−0.394 (0.61)	43.7	18.8
House Wren [a]	0.346 (0.48)	−0.716 (1.00)	0.311 (0.44)	93.8	57.6
Common Yellowthroat	0.130 (0.80)	−0.114 (0.70)	−0.163 (1.00)	14.6	10.3
Eastern Wood-Pewee	0.008 (0.03)	0.174 (0.69)	−0.253 (1.00)	20.9	14.4
Brown-headed Cowbird[a]	−0.764 (1.00)	−0.310 (0.41)	−0.361 (0.47)	62.3	40.9
White-breasted Nuthatch	−0.821 (1.00)	−0.132 (0.16)	−0.203 (0.25)	32.9	14.4
Forest migrants	0.171 (1.00)	−0.048 (0.28)	−0.074 (0.43)	86.9	31.9
Shrub-layer specialists[a]	0.166 (1.00)	−0.155 (0.94)	−0.026 (0.16)	91.4	39.1
Hemlock associates[a]	0.304 (1.00)	−0.302 (1.00)	−0.061 (0.20)	80.6	37.3
Hemlock-decline winners	0.111 (1.00)	−0.008 (0.08)	−0.108 (0.98)	47.0	28.6
Long-distance migrants[a]	0.197 (1.00)	−0.079 (0.40)	−0.066 (0.34)	145.4	40.8
Short-distance migrants	0.131 (0.67)	−0.195 (1.00)	0.093 (0.48)	73.0	34.7
Permanent residents	−0.191 (1.00)	−0.102 (0.54)	−0.139 (0.73)	105.3	30.2

[a] Model was overdispersed, so we used Quasi AIC rather than AICc to determine the model weights.

this principal component). High importance values for all of these species groups except short-distance migrants indicate that the first vegetation factor explained relatively more of the variability than either of the other two covariates.

Importance values for shrub-layer specialists, hemlock associates, and short-distance migrants showed a negative relationship with the second vegetation factor, indicating that they were more abundant in years with higher hemlock dominance (Table 4). The hemlock-associate group declined since the 1980s (Fig. 2D), and three out of five of its members – Acadian Flycatcher, Black-throated Green Warbler, and Hermit Thrush – vanished as breeding species (Appendix 4; see Table 1 for scientific names unless otherwise indicated). Also, Ovenbird has been present in recent years at only a

fraction of its previous abundance (Fig. 1, Appendix 4).

Hemlock decline winners and permanent residents showed a negative relationship with the forest edge/forest area index, indicating that they decreased when forest fragmentation increased (Table 4). While importance values for this variable were substantially lower for migratory forest specialists, shrub-layer specialists, hemlock associates and long-distance migrants, examination of the delta AICc values for these regressions indicate that they also decreased when forest fragmentation increased (Appendix 5). In contrast, short-distance migrants showed a positive relationship with the forest edge/area ratio.

Tree species diversity was negatively correlated with the diversity (Pearson coefficient = −0.369, *P*

= 0.049), but positively correlated with the abundance (Pearson coefficient = 0.472, $P = 0.010$), of migratory forest specialists.

Of the 19 bird species analyzed, 14 showed a strong relationship (indicated by importance values >0.7) to the first vegetation component (9 positive, 5 negative), while eight showed a strong relationship to the second vegetation component (all negative), and four showed a strong relationship to the forest fragmentation index (all negative) (Table 4). This suggests that although many species responded negatively to changes associated with forest maturation, some species responded positively. In addition, it suggests that some species responded negatively to the decline of eastern hemlock or to increases in forest fragmentation.

Comparison to Statewide Breeding Bird Surveys.—When comparing the population trends in the study area to statewide trends, we determined if local populations were faring better or worse than across the state. For example, a species that did not show appreciable change in the study area but increased substantially statewide fared 'worse' in the study area than in the state. Species that showed the same trend at both the state and local levels are likely responding to factors on a larger scale than the Arboretum study area and the surrounding 2-km zone.

Of the 19 species analyzed for population trends, nine species declined and no species increased in the study area (Table 1). Thirteen species showed different patterns in the study area than in the statewide surveys, 12 of which fared worse in the Arboretum study area. The exception was Wood Thrush, a migratory forest specialist, which declined on statewide BBS routes but showed no significant change in the study area. Of the 12 species that fared worse in the study area, four are migratory forest specialists, five are shrub-layer species, and three are generalized permanent residents

DISCUSSION

The picture that emerges from this analysis is that changes in the bird community are most strongly associated with the various vegetation variables associated with the first vegetation component. This factor had the highest importance value for 11 of the 19 species, and for all of the

migratory and habitat groups except short-distance migrants (Table 4). One caveat is that the first vegetation component is strongly correlated with time, so any unmeasured covariate that showed a consistent linear change over the 60 years of the study could potentially drive these changes in bird populations. Changes in forest fragmentation in the surrounding landscape and changes in the abundance of eastern hemlock generally had weaker associations with bird populations. We address these two secondary factors first and then discuss the first vegetation component.

The Influence of Forest Fragmentation.—Although the most important predictor of the overall abundance of migratory forest specialists and long-distance migrants was the first vegetation factor, their abundance was also negatively associated with the amount of forest fragmentation (the ratio of forest edge to forest area) in the surrounding region. This is consistent with previous research demonstrating lower densities of migratory forest birds and higher nest predation and brood parasitism rates in highly fragmented landscapes (reviewed by Thompson et al. 2002).

Previous analyses of bird population changes in the Arboretum study area also reported a relationship between forest fragmentation and the abundance of migratory forest birds (Butcher et al. 1981, Askins and Philbrick 1987). Askins and Philbrick (1987) hypothesized that the decrease in forest migrants during the 1970s and a subsequent increase during the 1980s were associated with a corresponding decrease and then increase in forest cover in the area within 2 km of the study area. Our analysis of landscape forest cover, which was conducted using aerial photographs examined at a larger scale (1:10,000) than those used by Askins and Philbrick (1987) (1:12,000–1:20,000), did not show the substantial decrease in forest area within 2 km of the study area during this same time period. The use of more precise GIS technology with larger scale maps resulted in inclusion of forest patches that were too small to recognize using the methods of Askins and Philbrick (1987). Overall forest cover did not change substantially because forest losses resulting from suburban development were mostly offset by abandoned farm fields growing into forest patches. The earlier study captured the losses of larger areas but not the appearance of smaller patches of re-growth. These opposing processes resulted in a more fragmented

regional forest cover by the 1970s, however, with an increase in the ratio of forest edge to total forest area.

Many previous studies have used percent forest cover as a surrogate measure for fragmentation (see Thompson et al. 2002). However, this measure would not distinguish a landscape with a single large forest patch from a landscape with many small patches but the same total percent forest cover. Our forest fragmentation index was based on the total forest edge/total forest area ratio, so we were able to detect changes in habitat fragmentation even though the total forest area did not change substantially in the region surrounding the Arboretum. The resulting relationships with bird species and groups therefore appear to be a response to changes in the distribution of forest cover, not simply in the amount of cover. Larger patches of forest have a smaller ratio of edge to interior, and therefore suffer less from the 'edge effect,' the higher rates of predation and parasitism that occur in transitional habitat zones (Thompson et al. 2002).

Although the 1970s were characterized by increased levels of forest fragmentation around the study area, the forest around this site has become less fragmented since the 1970s. If local fragmentation were a major driving force behind changes in bird abundances, one would expect a positive impact, even if slight, on the bird populations as a result. By 1985, the rebound in bird abundances in the 1980s appeared to be linked to surrounding forest becoming less fragmented (Askins and Philbrick 1987). Data from subsequent years, however, indicate that this trend did not continue. All groups of bird species showed a net decline since the 1980s even though forest fragmentation stayed relatively low, suggesting that some negative change has outweighed the positive effects of low habitat fragmentation in the surrounding region.

Populations of migratory forest specialists may have been affected more strongly if changes in forest fragmentation in the region around the study area had been greater. An analysis of breeding bird survey data from 46 forest tracts within 65 km of the Connecticut College Arboretum indicated that abundance was negatively related to the amount of forest in the region around study sites for 10 species of migratory forest specialists (Dorazio et al. 2015), including several species that did not

show a strong relationship with forest fragmentation in our analysis of long-term data from the Arboretum study site. The latter study encompassed sites in which forest cover within 2 km of the center of the study area ranged from 48–1200 ha, however, reflecting much greater differences in the degree of forest fragmentation than were observed at the Arboretum study site.

Impact of the Decline of Eastern Hemlocks.— The population of eastern hemlocks dropped dramatically after the arrival of hemlock woolly adelgid. Although hemlock was previously the most dominant species in the forest canopy in terms of stem density, basal area, and frequency, there were few surviving hemlocks in the study area by 2002 (Small et al. 2005). Not surprisingly, the hemlock associates showed the strongest relationship with the second vegetation principal component, rising in abundance as eastern hemlock became increasingly dominant in the forest canopy prior to the adelgid's arrival. The hemlock-associate group has been declining steadily since the 1980s, and three out of five of its members have disappeared as breeding species in the study area.

Surprisingly, the group of species that we had categorized as potential 'hemlock decline winners' based on previous research showed no relationship with the second vegetation component. This group includes flycatchers, which often perch on exposed snags while looking for food, and species such as Hooded Warbler and Veery that benefit from dense shrubs that develop in stands of dead trees (DeGraaf and Yamasaki 2001, Becker et al. 2008). Although the hemlock woolly adelgid arrived in the Connecticut College Arboretum in 1987, mortality did not begin to increase until after 1992, and subsequent changes in forest structure took even longer, which may explain the delayed response of this group of species (Small et al. 2005). Perhaps more importantly, the abundance of these species in the study area is determined by the characteristics of the understory, including areas where hardwoods were always dominant.

Disentangling the First Vegetation Principal Component: Declines Over Time.— The first vegetation principal component can be considered to represent the degree of forest maturation, with negative values associated with characteristics of mature forest (i.e., high values for total basal area and basal areas of oaks and red maple, and low

values for yellow birch basal area, tree diversity, and shrub abundance). This component is a good predictor of the abundance of every group of species, and of many individual species. Groups of species did not always respond to this vegetation factor in expected ways, however. Positive links between forest maturation and avian communities, particularly forest-specialist species, have been observed in prior studies. Gil-Tena et al. (2009) found forest maturation to be the most important factor influencing bird species in Mediterranean forests, noting that older forests tend to have a more complex vertical structure that provides better habitat for forest specialist species. Johnston and Odum (1956) showed that increasing ecological age in a forest tends to lead to an increase in bird population densities in forested regions with sufficient moisture. In contrast to what one would expect based on results of these earlier studies, however, our study showed that populations of migratory forest specialists declined substantially after the early 1980s even as the forest continued to mature.

The first principal component was strongly and positively linked to the Inverse Simpson's Index of tree diversity, and negatively related to the basal area of oaks and red maple. Thus the progressive decline in this principal component indicates a decline in tree diversity as oaks and red maple became more dominant. Although the species diversity of migratory forest specialists showed a negative correlation with tree species diversity, the total abundance of migratory forest specialists dropped as tree species diversity decreased. The presence of a variety of trees, even those that were never dominant in the canopy, may have provided a range of substrates for foraging and nesting, offering more resources to bird species with selective or uncommon preferences. Gabbe et al. (2002) noted that several species of trees most strongly preferred by foraging insectivores in floodplain forests of Illinois were relatively rare, suggesting that some less dominant canopy species may be disproportionately important in terms of habitat value for birds. As the canopy shifts towards increasing dominance of a few common tree species, bird species that use these relatively rare tree species may decline.

At Hubbard Brook Experimental Forest in New Hampshire, yellow birch was a particularly important resource for birds, supporting more caterpillars and more foraging insectivorous birds than other tree species in the forest (Holmes et al. 1979). Notably at our study site, yellow birch has a strong negative relationship with the first vegetation principal component, and the average basal area of yellow birch declined during the same period in which forest migrants declined. In addition, several tree species that used to play non-dominant roles in the tree canopy or sub-canopy, such as gray birch (*Betula populifolia*), hickories (*Carya* sp.), and flowering dogwood (*Benthamidia florida*), have also declined (CCJ, unpubl. data).

Shrub frequency data indicate that the density of the understory declined from 1952–1972 (Hemond et al. 1983), which would explain the decline in shrub-dependent bird species during this period (Butcher et al. 1981). These species continued to decline from 1982 to 2012, however, even though shrub frequency generally increased during this period (Appendix 1E). Moreover, five of eight shrub-layer species did worse in the study area than on state BBS routes. Shrub frequency may have increased after 1982 as a result of completion of a deer fence around the study site in 1989, but it did not reach the density originally present in 1952 when the forest was still recovering from the massive damage to the tree canopy by a hurricane in 1938.

Because overall shrub density does not appear to satisfactorily explain these population trends, floristics may offer a better explanation. Perhaps shrub-layer specialists were not able to thrive in a shrub layer with the wrong species of shrubs. Populations of Hooded Warblers in northeastern North America are typically found in forests with an understory dominated by *Rubus* sp*., Ribes cynosbati, Viburnum acerifolium*, *Lindera benzoin*, and *Fraxinus, Prunus*, and *Acer* saplings (Chiver et al. 2011). Similarly, territories of Veeries in Wisconsin are found in dense shrub layers of *Corylus, Alnus, Viburnum, Cornus, Rubus, Vaccinium, Lonicera, Amelanchier, Salix,* and *Myrica* species (Paszkowski 1984). Although many of these understory species and genera (*Alnus, Amelanchier, Lindera benzoin, Myrica, Prunus* sp., *Rubus* sp., *Vaccinium*, and *Viburnum acerifolium*) were present in the study area at the start of the study, they have nearly all declined since then (Appendix 2; CCJ, unpubl. data). Changes in the composition of the shrub layer are reflected in

the relatively steady decline in scores for the shrub ordination axis. Many shrub species that are frequent in the study area show a significant positive relationship to this ordination axis indicating that they have declined. In contrast, invasive, introduced shrub and vine species such as *Berberis thunbergii*, *Celastrus orbiculatus*, and *Lonicera japonica* increased in the years since the hemlock decline (Small et al. 2005), but they still occurred in only 3.1% of the vegetation plots in 2012 (CCJ, unpubl. data).

Conclusions and Conservation Implications.— While many bird species are following similar population trajectories in the Connecticut College Arboretum study area and on BBS routes across Connecticut, 12 of 13 species with different trends fared worse in the Arboretum than in the statewide surveys. This suggests that some local factor or factors account for population declines in the study area. The increasing maturation of the hardwood sections of the forest, and the simultaneous increase in canopy gaps and shrub cover in the hemlock sections of the forest, appear to have benefited neither migratory forest specialists nor shrub-layer species. A decrease in fragmentation in the immediately surrounding landscape in recent decades has not stemmed the decline of most of the bird species and groups analyzed. A decrease in the diversity of woody plants, as well as losses of particular tree and shrub species that may be important for particular species of birds, are potential causes of these downward population trends that should be considered in future studies of bird populations.

Long-term monitoring of bird populations alone cannot be used to test hypotheses about habitat requirements or demographic processes. However, they are important for revealing questions for study and for generating new hypotheses about the causes of population changes. Just as earlier analyses of bird census data directed attention to the potential roles of habitat fragmentation and destruction of tropical wintering habitats in population declines of migratory forest birds (Holmes 2007), this study indicates that floristic composition of forest vegetation may be another key factor. This hypothesis could be tested, for example, by comparison of insect abundance and the frequency and success of foraging by birds on different species of plants (Holmes and Robinson 1981). Conservationists should also be aware of

the possibility that tree species such as yellow birch and eastern hemlock may be disproportionately important for some species of birds even when these tree species are not dominant components of the vegetation. The potential importance of the diversity and composition of woody plants is particularly important in light of widespread homogenization of tree species composition in eastern deciduous forest because of such factors as fire suppression, intense browsing of tree seedlings by white-tailed deer (*Odocoileus virginianus*), and the decline of particular species of trees after insect pests and pathogens have been introduced (Abrams 1998, Hall et al. 2002).

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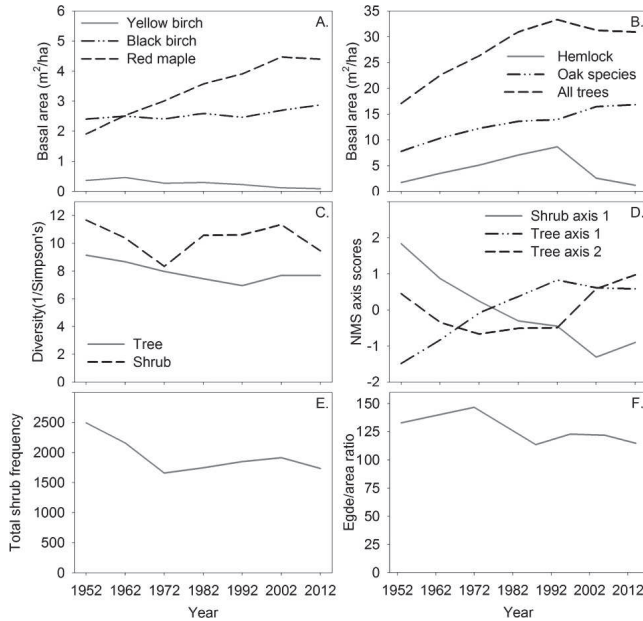
APPENDIX 1. Changes between 1951 and 2012 in (A) and (B) basal area of focal tree species and all trees; (C) species diversity (Inverse Simpson's Index) of trees and shrubs; (D) non-metric multi-dimension scaling (NMS) ordination axis scores for trees and shrubs; (E) total frequency of shrubs; and forest edge/forest area ratio for region within 2 km of the study site for the Connecticut College Arboretum study area. Focal tree species: yellow birch—*B. alleghaniensis*, black birch—*B. lenta*, red maple—*A. rubrum*, hemlock—*T. canadensis*, and oak species—*Quercus* spp.