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CONNECTICUT COLLEGE

Department of Biological Sciences

Responses of Forest Bird Populations to Long-term Changes in Local Vegetation and Regional Forest Cover

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Abstract

Bird and vegetation surveys have been conducted periodically in the Connecticut College Arboretum since the 1950s, permitting analysis of long-term relationships of bird populations with the structure and floristic composition of the vegetation and with forest cover changes in the surrounding region. Principal component analyses created vegetation factors encompassing variables such as total basal area, basal area of common tree species, and tree diversity, and created a forest fragmentation factor based on GIS analysis of the landscape within 2 kilometers of the study site. Poisson regression models revealed relationships between these factors and population changes for twenty individual species and seven groups of ecologically similar species, most of which have declined sharply since the 1980s.

Most habitat and migrant groups showed a strong negative relationship with the first vegetation factor, which positively correlates with increasing total basal area and dominance of oaks and maples but negatively correlates with tree and shrub diversity, suggesting that floristic diversity may be critical for determining habitat quality. All groups showed at least a slight positive relationship with the second vegetation factor, which is related to eastern hemlock basal area, suggesting that the recent decline in hemlocks due to hemlock woolly adelgid has had adverse impacts on the forest bird community. All groups except short-distance migrants showed a negative relationship with the landscape factor measuring forest fragmentation, suggesting that conservation efforts to protect bird communities should take the wider landscape into account. The strongest relationship in most cases was with the first vegetation factor.

Introduction

Perhaps one of the most eloquent acknowledgments of the complexity of the natural world can be found in John Muir's book *My First Summer in the Sierra*, published in 1911:

> *"When we try to pick out anything by itself, we find it hitched to everything else in the Universe."*

Ecological research at its most fruitful seeks to illuminate the "hitchings" of the universe, throwing light upon the connections and interactions that make up functional ecosystems. Efforts at ornithological research, such as the present study, therefore benefit from including non-avian variables that may have important effects on the structure of an avian community. Habitat quality has a bearing on nearly every aspect of a bird's life, determining whether or not it will find adequate food, shelter from predators, and a place to nest. Good quality habitat takes on particular importance during the breeding season (Fuller, 2012), influencing reproductive success and the chances of a viable population continuing into the future.

In this study, I seek to examine the relationships among multiple features within and around a forest in southeastern Connecticut and the populations of birds that breed there in the summer. By comparing changes in local vegetation and regional forest cover to changes in local bird abundance over time, associations between habitat features and bird abundance may be revealed, providing information to guide future management and conservation decisions. At the forest patch scale, previous research has indicated the potential importance of structural components such as the closed canopy typically found in maturing forests or the denser shrub layers found under more open canopies (Fuller et al., 2012). The floristic composition of the canopy and understory layers has emerged as a more recent subject of interest in the literature surrounding bird ecology, as greater vegetative diversity has been linked to greater abundance of birds (Twedt et al., 1999). Dramatic floristic changes such as the rapid loss of eastern hemlock (*Tsuga canadensis*) in recent years may therefore produce significant impacts on avian communities (Tingley et al., 2002). Changes in forest cover and fragmentation at a landscape scale can also impact bird populations through increased predation and brood parasitism in edge habitats (Thompson et al., 2002). Examining these factors and their respective influences upon local bird populations, particularly when these populations are viewed in the context of wider regional trends, may show how much each of these components adds to the overall picture of habitat quality for breeding birds. Long-term research in the Bolleswood Natural Area of the Connecticut College Arboretum provides an opportunity to do just that.

The Bolleswood Natural Area

The Bolleswood Natural Area, a ~65-hectare portion of the larger Connecticut College Arboretum in New London, Connecticut, was established as both a preserve and research site to provide insight into the natural cycles and progressive changes of an ecosystem largely undisturbed by humans (Niering and Goodwin, 1962; Small et al., 2005). The Bolleswood Natural Area was delineated in 1952, and since then has been left to the dynamic forces of nature, receiving little active management from humans (Small et al., 2005).

Breeding bird censuses in the 23.1-hectare hemlock-hardwood study area of the Bolleswood Natural Area have been regularly conducted since 1953, offering an uncommon and useful opportunity to study patterns in bird populations over a long period of time (Askins and Philbrick, 1987). Such long-term data are valuable for detecting slow changes that might not otherwise be apparent. To underscore the value of long-standing and regularly updated data, one need look no further than previous research comparing results from annual monitoring projects like the Breeding Bird Census in the United States and the newer Breeding Bird Survey (established in 1966) in the United States and Canada, as declines in six mature forest migrant species were reflected only in data from 1940-1995, and not in data from 1966-1995 (King et al., 2006). The data set from the Bolleswood Natural Area may therefore reveal long-term shifts in bird populations that would go undetected in shorter-term studies.

Furthermore, the Bolleswood Natural Area is especially valuable as a research site because vegetation data have also been collected periodically since 1953, allowing long-term avian and vegetation data for the same study site to be analyzed concurrently. Despite the continued collection of both bird and vegetation data, there has not been a scientific paper related to these studies published for over twenty years (Askins and Philbrick, 1987), and the last Connecticut College Arboretum Bulletin pertaining to these studies was published in 1990 (Askins, 1990). There is therefore a need for an updated analysis of these data in order to take into account changes from the past few decades. The main goal of this study was to use avian and vegetation data from the Connecticut College Arboretum to explore a wide range of factors that contribute to the relationship between birds and their habitat, including floristic factors like the basal area of selected tree species and overall tree species diversity, as well as structural variables such as total tree basal area, percent cover of the shrub layer, and ground cover.

Forest Floristics and Bird Communities

Prior analyses of the relationships between avian communities and vegetation have predominantly focused on vegetation structure, examining vertical structural elements such as canopy height and multi-tiered vegetation layers as well as horizontal structural elements like stem density and distribution of canopy gaps (Fuller et al., 2012). There is growing interest, however, in the role of floristic composition – the types of plant species present in a given area. A large-scale study of forest sites in Great Britain recently highlighted the importance of this dimension, as bird communities appeared to respond to both structural and floristic components of forest habitat (Hewson et al., 2011). Moreover, models that incorporated structural and floristic variables revealed emergent relationships between certain bird species and vegetation that were not evident in purely structural models (Hewson et al., 2011), indicating that although the bulk of scholarly attention has been directed at structural variables, floristics ought not to be ignored.

Also, a number of recent studies have indicated that changes in the presence and abundance of plant species may lead to corresponding shifts within avian populations. Not all of these differences can be explained entirely by structural factors: in one Pennsylvania study, total abundance of birds in oak-dominated forests was higher than in maple-dominated forests even though the two forest types were not deemed significantly different in terms of habitat structure (Rodewald and Abrams, 2002). Specific subsets of bird communities may respond differentially to vegetation differences as well. For example, bark-foraging species like woodpeckers and species that consume or cache acorns are more common in oak-dominated forests than in forests dominated by maple, suggesting that associations between particular bird species and particular plant species may be driven by foraging needs (Rodewald and Abrams, 2002).

In-depth studies of insectivorous birds in the Hubbard Brook Forest in New Hampshire, in which birds were categorized into "guilds" based on their foraging patterns, have indicated that while much of the variability among foraging guilds can indeed be explained by vegetation height and foraging substrate, differential use of plant species also accounts for some of the finer differences among guilds (Holmes et al., 1979). Holmes et al. offer an explanation for this observation that highlights the connection between vegetation structure and floristic composition, noting that different plant species have morphological differences 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 of the yellow birches (*Betula alleghaniensis)* in the Hubbard Brook Forest, which supported higher densities of Lepidoptera larvae than did other tree species (Holmes et al., 1979). Robinson and Holmes (1984) determined that species such as the Philadelphia Vireo (*Vireo philadelphicus*) and American Redstart (*Setophaga ruticilla*) encounter and attack prey more often in yellow birches than would be expected solely based on the frequency of these trees in the Hubbard Brook Forest, likely because of their high insect density and leaf accessibility.

Bird communities in the floodplain forests in Illinois likewise reflect the importance of tree species for foraging behavior. Gabbe et al. (2002) observed selective foraging on particular tree species in twelve out of the thirteen avian species studied, revealing that many species of birds have definite preferences when it comes to foraging substrate. The less common birds observed in this study, such as the Scarlet Tanager (*Piranga olivacea*) and Cerulean Warbler (*Setophaga cerulea*), tended to have stronger foraging preferences. This is perhaps not surprising, as it suggests that more selective species may have more difficulty finding suitable habitat, which may limit population size.

Research on avian communities on a broader scale in North America has also supported the premise that floristics are a consistent factor for predicting the composition of bird communities. Data from the continent-spanning Breeding Bird Census have revealed significant correlations between bird species composition and tree species composition in eastern forests, even after geographic location and overall forest structure were taken into account (Lee and Rotenberry, 2006). Shifts in floristic composition of a forest over time may therefore drive (or at least influence) shifts in avian communities within the forest.

What this suggests for the present study is that the relative abundances of specific dominant plant species in the Connecticut College Arboretum likely have a role in determining habitat use by birds that goes beyond the vertical and horizontal structure of the forest layers. One goal for this study was therefore to identify major shifts in the vegetation assemblage in the Connecticut College Arboretum since 1953 that may have had a corresponding impact upon the avian community. These vegetation changes may be detected and measured through variables such as basal areas of dominant woody species.

Previous studies have indicated a positive correlation between the diversity of woody species in a specific location and the diversity and abundance of birds (Twedt et al., 1999). In a forest with high tree species diversity, chances are good that bird species with specific habitat requirements will find their preferred foraging substrate, whereas a homogenous forest of comparable area and vegetation structure but lacking preferred tree species may not be suitable habitat for the more selective bird species (Gabbe et al, 2002). It is therefore worthwhile to assess changes in the woody plant species diversity of the study area.

In addition to overall diversity, several tree species were chosen for specific scrutiny. Among these species were red maple (*Acer rubrum*) and several oak species (*Quercus alba, Quercus coccinea, Quercus rubra, Quercus velutina*, all included in a single "oak" category), as observations of forests in the eastern United States have revealed that historically oak-dominated forests have begun to give way to more shade-tolerant species, particularly red maple, with potential ripple effects on bird communities (Rodewald and Abrams, 2002). Yellow birch (*Betula alleghaniensis*) is another promising candidate for analysis, since previous research has indicated its importance as a source of Lepidoptera larvae (Holmes et al., 1979).

The Role of Eastern Hemlock

Perhaps one of the most significant floristic changes in the past few decades, in both the Connecticut College Arboretum and in eastern forests in general, has been the decline of the eastern hemlock (*Tsuga canadensis*). The hemlock serves as another reminder of the connections between floristic identity and vegetation structure, as its unique qualities shape the physical configuration of a forest in ways that other tree species do not. Hemlocks typically form dense stands, creating a heavily shaded microclimate with acidic, nutrient-poor soil; as a result, the shrub layer beneath a hemlock stand is often sparse (Ellison et al. 2005). Streams that flow through hemlock forests also tend to have more stable base flows and temperature than those flowing through deciduous forests (Ellison et al. 2005). For these reasons, eastern hemlock is considered a foundation tree species, as its presence can define and stabilize the conditions in an ecosystem (Ellison et al. 2005). Additionally, hemlocks provide foraging and nesting sites for birds at multiple heights, as hemlock trees retain their lower branches more than other species of conifers (Becker et al., 2008). The evergreen nature of eastern hemlock likewise adds to its wildlife value, as it provides a source of seeds and foliage insects throughout the winter for species such as American Goldfinch (*Spinus tristis*) and Evening Grosbeak (*Coccothraustes vespertinus*) (Yamasaki et al., 1999). Only a few other evergreen tree species were recorded in the Bolleswood Natural Area of the Connecticut College Arboretum (*Pinus resinosa, Pinus strobus, Juniperus virginiana,* and *Chamecyparis thyoides),* none of which occurred in abundance, suggesting that hemlock's role as an evergreen in the Bolleswood Natural Area is unique. Previous research has revealed that approximately 96 species of birds in New England have been observed using hemlock trees; of these, a limited number are specialists that heavily associate with hemlocks and the distinctive habitat conditions they support (Yamasaki et al., 1999).

Unfortunately, the eastern hemlock population is under siege from an invasive pest, the hemlock woolly adelgid (*Adelges tsugae*), which began attacking hemlocks in the southeastern United States in the 1950s and has since spread over much of the eastern hemlock's range (Kizlinski et al. 2002). Eggs of the adelgid can be transported easily by wind or carried by birds and mammals, making it difficult to stop the insect's expansion (Small et al., 2005). Eastern hemlocks have shown little resistance to the adelgid, which feeds on parenchyma cells in the xylem tissue (Becker et al., 2008); within four to fifteen years of adelgid infestation, afflicted hemlocks usually die (Ellison et al., 2005). Hemlock woolly adelgid first appeared in the Bolleswood Natural Area of the Connecticut College Arboretum in 1987, and by 2002 over 80% of the hemlock stems had died, reducing basal area of live hemlock trees in hemlock-dominated study plots by 75% (Small et al., 2005). Small et al. (2005) predicted the complete loss of live hemlock stems by 2006. Prior to the adelgid's arrival, hemlock dominance in the Bolleswood Natural Area had been on the rise, accompanied by black oaks (*Quercus velutina*) as a co-dominant species. The adelgid's invasion has thus been a critical turning point in the history of the forest at this site.

Hemlocks do not rebound easily from disturbance due to their slow growth and re-generation rates, shallow roots, and low seed viability (Small et al., 2005). Eventually, hardwood tree species such as oaks, maples, and birches become established in the sites where hemlocks once stood, but these species do not create the same type of microclimate that the hemlocks fostered (Ellison et al. 2005). Black birch (*Betula lenta*) in particular has been commonly observed sprouting up in dead hemlock stands, although this species' limited tolerance for shade suggests that it may not be a permanent replacement capable of withstanding shade-tolerant competitors as the forest canopy fills in (Lovett et al. 2006). Over time, the loss of the hemlocks is expected to produce a more homogenous forest composition (Tingley et al., 2002). Both black and yellow birch increased in basal area and density in the Bolleswood Natural Area after the decline of the hemlocks, and other hardwood species such as black oaks (*Quercus velutina*) and American beech (*Fagus grandifolia*) took on increased importance as well (Small et al., 2005). Sapling density and shrub layer richness also rose as hemlocks declined, and nine new species of shrubs and vines became established in the area for the first time, including several non-native invasive species.

The loss of the hemlock trees and its attendant impacts on canopy floristics and shrub layer composition fundamentally alter the qualities of the forest habitat. Previous studies have indicated that a habitat change of this magnitude leads to marked responses from the forest inhabitants, including birds. Certain species reliant upon hemlock trees may be displaced, while those preferring early-successional habitat may move in (Tingley et al., 2002). The relatively rapid loss of the hemlock population in the Bolleswood Natural Area of the Connecticut College Arboretum likewise may have triggered changes in the avian community, suggesting that special attention should be paid to population changes after 1992, by which point significant defoliation of hemlock trees had already occurred; complete tree mortality was a slower process, reaching a 45% mortality level in 1997 (Small et al., 2005).

In addition to examining changes in the bird community as a whole, it is worthwhile to pay particular attention to bird species known to be hemlock associates, which may show especially strong responses to hemlock decline in the Arboretum. Previous research has identified species meeting this criterion (Tingley et al., 2002, Becker et al., 2008); those that have appeared in the Arboretum in the years since 1953 include the Acadian Flycatcher (*Empidonax virescens*), Black-throated Green Warbler (*Setophaga virens*), Louisiana Waterthrush (*Parkesia motacilla*), Ovenbird (*Seiurus aurocapilla*), and Hermit Thrush (*Catharus guttatus*). Similarly, species that may benefit from the decline of the hemlock – such as those that thrive under more open canopies or increased shrub density – may show population increases as forest conditions become more favorable to their preferences. The scientific literature surrounding hemlock ecosystems has also identified a number of species that may fall into this category, including species that benefit from canopy gaps like Eastern Wood-Pewee (*Contopus virens*) (Becker et al., 2008) and species that benefit from dense shrub layers like Hooded Warbler (*Setophaga citrina*) (Tingley et al., 2002). Observing both the hemlock associates and the species that might benefit from hemlock decline (the "hemlock decline winners," as it were) for particular patterns may shed light on their relationships with the eastern hemlock, adding to a body of knowledge that may equip ecologists and conservationists for a future in which hemlock woolly adelgid continues to spread.

Vegetation Structure and Bird Populations

As mentioned earlier, the floristic composition of an ecosystem and its structural configuration are fundamentally linked, and floristic changes (such as hemlock decline) can affect the vegetation structure of a forest, by, for example, creating canopy gaps or altering light conditions so that more ground cover can grow. Even when floristic changes are not a factor, the structures of canopy and shrub layer vegetation mutually influence each other. Dense shrubs can shade out regenerating canopy trees, while the microclimate and light infiltration conditions created by the canopy layer in turn affect the configuration of the shrub layer (Fuller et al., 2012). As the bulk of the scientific literature surrounding avian ecology and habitat use has highlighted the role of vegetation structure, structural criteria such as total basal area and shrub layer percent cover were included in this analysis in order to produce a more complete picture of the factors shaping the relationship between birds and their habitat.

The structure of the shrub layer in particular is worthy of focused attention, both because of its potential responsiveness to hemlock decline and because of its importance to many bird species experiencing long-term population declines in the eastern United States, such as the Gray Catbird (*Dumetella carolinensis*), a shrubland generalist, and the Hooded Warbler (*Setophaga citrina*), a shrub-layer specialist (Tingley et al., 2002; Askins et al., 2007). Shrubland generalists may be found in both the shrub layer of forests and in open expanses of shrubland, whereas shrub-layer specialists are typically restricted to shrub layers beneath forest canopies or in small canopy gaps. Shrub cover can provide sheltered nesting sites and can influence the availability of food sources such as insects, snails, and seeds; in general, abundance and species richness of birds are higher in areas where shrubs are present (Fuller et al., 2012).

The impact of shrub layer presence and structure on avian communities is reflected in the broad patterns of bird communities that predictably follow successional changes in a forest. In the process of forest succession, a site that has been cleared by some disturbance (artificial or otherwise) initially supports a suite of low-stature plant species that thrive in open spaces; over time, saplings mature into trees, the canopy closes, and the shade-intolerant vegetation from the early successional stage is reduced to a sparser understory (Fuller et al., 2012). Clearly discernible changes in avian communities accompany forest succession, as early successional bird species present during the stage of open canopy and dense shrub layers no longer have suitable habitat once the closing canopy shades out the lower vegetation. These early successional species of birds may return, however, if the site is cleared again.

As mentioned above, eastern hemlock mortality has important implications for the structure of vegetation below the dying canopy. As shrub layers beneath hemlock stands tend to be sparse (Ellison et al. 2005), the decline of the eastern hemlock in the Arboretum has likely led to an increase in shrub density. Previous studies of hemlock decline in Connecticut and Massachusetts have revealed significantly higher shrub, vine, and herbaceous cover in sites damaged by hemlock woolly adelgid than in undamaged hemlock stands; damaged sites also had higher seedling and sapling densities than undamaged sites (Kizlinski et al. 2002). Mountain laurel (*Kalmia latifolia*) in particular became significantly more abundant in sites of high hemlock mortality (Tingley et al., 2002). These changes in the forest understory are due in large part to the increase in light infiltration after the loss of the dense evergreen canopy previously maintained by the hemlocks (Kizlinski et al. 2002). The Bolleswood Natural Area has followed this pattern, showing increased sapling density and shrub layer richness in the years after hemlock mortality reached near-completion (Small et al., 2005). One might reasonably expect, given the clear connections between avian communities and forest successional stages, that the gaps in the canopy and the increase in shrub layer caused by the decline of the hemlocks in the Bolleswood Natural Area will create habitat conditions more suitable to bird species that prefer open canopies and dense shrub layers, such as the Hooded Warbler, rather than birds that prefer late successional habitat. However, the successional clock of the forest will not be fully set back, as the hardwood trees in the Bolleswood Natural Area remain unaffected by the adelgid. The resulting canopy – partially open, but with mature trees still standing – may produce effects upon bird communities similar to those caused by timber management practices like selective cutting and group cutting, rather than the open expanse created by clearcutting on a larger scale (Askins, 2014).

However, although the Bolleswood Natural Area has been affected by storms and now the hemlock woolly adelgid, it has been largely protected from major artificial disturbance since its establishment. The forest has therefore been steadily maturing over time, particularly in the sections dominated by hardwoods, which may be reflected in variables such as total basal area; this gradual maturation may also have impacts upon the bird community.

Landscape-Level Factors and Wider Bird Populations Trends

Though fine-scale features of habitat such as floristics, basal area, and shrub and ground cover density are vital to avian territories within a forest, previous research has also indicated that the microhabitat scale may not be sufficient to account for selection of specific areas by birds. A habitat patch is only one part of a wider landscape, in which other habitat patches are also either present or absent, near or far, large or small. In order to fully understand the relationship between avian communities and habitat, it may be necessary to take, as it were, a "birds-eye view."

Wider landscape scales and variables, including characteristics like the percent of non-forested land surrounding a study site and the number of forest patches in the proximate area, may be more relevant for species that typically cover more ground, such as crows, jays, and certain woodpeckers (McFaden and Capen, 2002). However, McFaden and Capen, who studied birds and vegetation at multiple scales in the White Mountain National Forest of New Hampshire and Maine, also found a significant relationship between landscape-level variables and the abundance of certain smaller birds with more confined territories such as the Eastern Wood-Pewee (*Contopus virens*) and the Wood Thrush (*Hylocichla mustelina*). These birds may choose a general area of suitable habitat based upon landscape variables, and then may choose more specific sites within that area based on microhabitat variables.

Changes in the wider landscape also have important ramifications for predation and brood parasitism rates, both of which impact avian reproductive success and ultimately avian abundances. Forest fragmentation in particular, which can be roughly measured through the percent of forest cover within a given radius around a study site, has been linked to increased predation in numerous studies of forest birds (Thompson et al., 2002). The effect of landscape-level forest fragmentation will influence the strength of the edge effect on a local level. The "edge effect" refers to the higher rates of predation that commonly occur in edge habitat, such as the transition zone between a forest and a field. These higher predation rates may be due to increased predator density and richness near edges or to foraging patterns of predators that favor edges as traveling corridors (Thompson et al., 2002). Generalist nest predators like raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and Blue Jays (*Cyanocitta cristata*) are more common in landscapes with high fragmentation, leading to stronger edge effects in the habitat patches within these landscapes.

Brown-headed Cowbirds (*Molothrus ater*), a common brood parasite in eastern North America, are also more abundant in landscapes that have highly fragmented forests (Thompson et al., 2002). Cowbirds feed in open areas, such as meadows, roadsides, and agricultural lands, but parasitize the nests of forest birds. Forests without much fragmentation therefore have little open space to support feeding cowbirds and so will have lower rates of brood parasitism, whereas fragmented forests near cleared areas will likely have robust cowbird populations in close proximity that can take advantage of the forest bird population, leading to higher rates of brood parasitism.

Previous studies of the Bolleswood Natural Area itself have indicated the importance of forested land in the region surrounding the study site. Avian species categorized as forest interior specialists decreased from 66% of the total observed breeding pairs in 1953 and 1955 to 38% in 1976 (Butcher et al., 1981), during the same period that human development was reducing the amount of forest in the vicinity of the study area; subsequent increases in the long-distance migrant population between 1982 and 1985 occurred at the same time as nearby forest expanded (Askins and Philbrick, 1987). Thus, this previous research suggests that the extent to which the Bolleswood Natural Area is isolated from nearby forested land has a significant effect upon certain guilds within the forest bird community.

Ultimately, landscape patterns may lead to constraints on the quantity and quality of habitat patches within the landscape, thereby affecting the options available to birds selecting a microhabitat (Thompson et al., 2002). The potential array of habitat options offered by a particular landscape is of paramount importance for bird populations. Studies of Black-throated Blue Warblers (*Setophaga caerulescens*), considered representative of migratory passerines in eastern forests by Holmes (2007), have revealed that site suitability significantly influences the chances of survival and reproductive success. Therefore, it is important to incorporate this dimension of bird-landscape interaction by including a measure of surrounding forest cover among the variables used for analyzing trends in Arboretum bird populations, whether in the general forest bird community, specific subsets within that community, or selected species.

Including this landscape context adds depth to the results of this study, along with the recognition that the Bolleswood Natural Area does not exist in a vacuum. In addition, comparing population patterns of the birds within the Arboretum to regional trends in bird populations in southern New England allows changes in the avian community to be placed in an even wider context. If population trends within the Bolleswood Natural Area reflect those observed across southern New England as a whole, it is likely that natural or anthropogenic forces are influencing avian communities at a level beyond the scope of the Connecticut College Arboretum and its immediate surrounding landscape. If this is the case, the Bolleswood Natural Area may be representative of larger phenomena of regional or continental significance. Previous research in the Hubbard Brook Forest of New Hampshire has compared avian population trends from small study sites to statewide patterns measured by the Breeding Bird Survey coordinated by the U.S. Fish and Wildlife Service, establishing a precedent for this approach (Holmes and Sherry, 1988). Analyzing data from site-specific plots alongside broader regional data incorporates advantages from both data sets – the consistency and precision of small-scale censuses and the wider perspective of the state surveys (Holmes and Sherry, 1988). Therefore a goal of this study is to compare avian population patterns from the Bolleswood Natural Area to patterns observed in the Breeding Bird Surveys for Connecticut.

Objective of this Study

In a nutshell, then, the aim of this study is to examine the long-term trends in both the avian and plant communities in the Bolleswood Natural Area, seeking to determine the floristic and structural variables that impact the composition of the bird community or subsets within it. Accompanying this broad goal are several specific queries, such as how the population trajectories of specific bird groups have changed over time; how these changes relate to structural and floristic changes within the Bolleswood Natural Area such as forest maturation and tree species diversity; how the decline of the eastern hemlock has contributed to forest and avian community changes, particularly by impacting the relative dominance of tree species and the density of the shrub layer; and how changes in the surrounding landscape and regional bird populations can be integrated into the overall picture. In this study, I focus on two data sets spanning different ranges of years: one data set encompassing all years since the start of the bird surveys in 1953 to the most recent survey in 2012, and one set encompassing the years from 1982 to 2012. There are several reasons for this division. Prior to 1982, the bird censuses were conducted by a variety of researchers, whereas the surveys since 1982 have all been supervised by Professor Robert Askins of Connecticut College. As different observers may record and interpret data differently, Professor Askins' constant presence has likely led to more consistency in census methods and data interpretation since 1982. This fact, in addition to the increased frequency of surveys since Professor Askins' arrival, suggests that the data from 1982-2012 may be more reliable than the data gathered prior to 1982. Furthermore, the vegetation surveys in the Bolleswood Natural Area have been conducted by different researchers over the years, and shrub cover data has only been collected since 1982. Therefore examining the years from 1982-2012 separate from the full data set from 1953-2012 allows the inclusion of this variable in my analysis. The results of this study should provide the most recent installment of insights on bird populations changes drawn from the Bolleswood

Natural Area, building upon previous publications on this long-term study (Butcher et al., 1981; Askins and Philbrick, 1987).

Developing a fuller understanding of the relationship between vegetation and avian communities could help to direct and inform conservation efforts in the future, as bird populations face changing habitats due to invasive species infestations, climate change, and the inherently dynamic nature of ecosystems. Previous studies in the Bolleswood Natural Area have highlighted the importance of habitat quality to bird populations, noting that changes in habitat can lead to the local extinction of certain species (Butcher et al., 1981). Avian responses to eastern hemlock decline in particular may be useful for predicting ecosystem changes and identifying species of conservation concern as the hemlock woolly adelgid continues to spread. After conducting my analyses, I hope to determine whether the results of this study have any implications for conservation, such as which vegetation factors are most strongly correlated with robust bird abundance and diversity. These inferences may help to direct conservation efforts in the future to maximize their value for preserving avian communities.

Methods

Study Site

The study site is a 23.1-hectare forest in the ~65-hectare Bolleswood Natural Area of the Connecticut College Arboretum in New London, CT (Askins and Philbrick, 1987). The Bolleswood Natural Area is located 6.4 kilometers north of the Long Island Sound and covers terrain of varying elevation, including a series of ledges and a ravine; its highest point is 61 m in elevation (Niering and Goodwin, 1962; Small et al., 1995). In 1962 the

Bolleswood Natural Area was categorized as a primarily oak-hemlock forest (Niering and Goodwin, 1962), but since then the site has undergone dramatic hemlock decline since the arrival of the hemlock woolly adelgid in 1987 (Small et al., 1995).

Bird Census Methods

Twenty-nine breeding bird surveys have been conducted in the Bolleswood Natural Area since 1953. Although these surveys have not occurred at strictly regular intervals, there have been at least two surveys per decade up to the present. The frequency of these surveys increased after 1982, with particularly good coverage in the 1980s and 1990s (Table 1.). Most of the bird data used in the present study were recorded by previous researchers over the past sixty years; I personally participated in the twenty-ninth breeding bird survey in 2012.

In each survey, spot-mapping methods were used to determine the abundance and approximate location of territories of breeding birds at the site (Askins and Philbrick, 1987). The Williams Spot-Mapping Method was chosen for the first surveys, and has been used in subsequent surveys for the sake of consistency (Butcher et al. 1981). During survey years, approximately ten censuses were conducted between mid-May and mid-July, all taking place between 5:00 am and 8:00 am Eastern Daylight Time (Askins and Philbrick, 1987). Territorial birds tend to be most vocal during this time, and the distinctive songs specific to each species allow researchers to identify species by ear. As each bird was identified, its approximate location was marked on a handheld map of the study site. Dotted lines were used to indicate locations where multiple individuals of the same species were heard simultaneously because this information was especially helpful for mapping territorial boundaries. Combining the results of multiple surveys within a season for each species made it possible to determine territory boundaries for breeding birds and then count the number of territories for that species in a given year.

To organize my approach and better understand changes in the bird community, I divided bird species into categories based on habitat specialization, migratory patterns, and relationship to eastern hemlock. The habitat specialization categories used in this study are "migratory forest specialists", and "early successional or shrub-layer"; each label refers to the type of habitat needed to meet a particular species' requirements (Table 2). Habitat categories were determined using tables on habitat use by different species in DeGraaf and Yamasaki (2001). As in previous studies of this bird community, birds were likewise divided into the following groups based on migratory patterns: long-distance migrants, which overwinter in the Neotropics; short-distance migrants, which overwinter in the southern temperate zone or subtropics; and permanent residents, which overwinter in the Bolleswood Natural Area (Butcher et al. 1981; Askins and Philbrick, 1987) (Table 2). I also consulted the scientific literature about avian relationships to eastern hemlock (Tingley et al., 2002; Becker et al., 2008) to identify hemlock associates among the bird species found in the Bolleswood Natural Area, as well as those species that might benefit from hemlock decline, as discussed in the introduction, thereby creating two additional habitat-based categories within the set of breeding bird species found in the Bolleswood Natural Area.

Table 1. Years in which bird surveys and/or vegetation surveys were completed in Bolleswood Natural Area.

Years of Bird Surveys	Years of Vegetation Surveys
1953	1952
1955	
1959	
1961	1962
1964	
1973	1972
1976	
1982	1982
1983	
1984	
1985	
1986	
1987	
1988	
1989	
1990	
1991	
1992	1992
1993	
1994	
1995	
1996	
1997	
1999	
2000	
2002	2002
2007	
2009	
2012	2012

Table 2. Bird species in groups categorized by habitat and migratory patterns. Migratory forest specialists and early-successional/shrub-layer species categorized based on reference to DeGraaf and Yamasaki (2001). Hemlock categories are based on Tingley et al., 2002, and Becker et al., 2008). Migratory categories are based on Askins and Philbrick, 1987.

Migratory Forest Specialists	Early-Succesional & Shrub-Layer	Hemlock Associates	Hemlock Decline Winners
Acadian Flycatcher	American Redstart	Acadian Flycatcher	American Goldfinch
Black-and-white Warbler	Black-billed Cuckoo	Black-throated Green Warbler	Brown-headed Cowbird
Black-throated Green Warbler	Blue-winged Warbler	Hermit Thrush	Downy Woodpecker
Blue-gray Gnatcatcher	Brown Thrasher	Louisiana Waterthrush	Eastern Wood-Pewee
Broad-winged Hawk	Carolina Wren	Ovenbird	Great Crested Flycatcher
Eastern Wood-Pewee	Chestnut-sided Warbler		Hairy Woodpecker
Great Crested Flycatcher	Common Yellowthroat		Hooded Warbler
Louisiana Waterthrush	Eastern Towhee		Red-eyed Vireo
Ovenbird	Gray Catbird		Scarlet Tanager
Red-eyed Vireo	Hooded Warbler		Tufted Titmouse
Red-shouldered Hawk	House Wren		Veery
Scarlet Tanager	Northern Cardinal		White-breasted Nuthatch
Wood Thrush	Prairie Warbler		Wood Thrush
Worm-eating Warbler	Veery		
	White-eyed Vireo		
	Worm-eating Warbler		
	Yellow-billed Cuckoo		

Long-Distance Migrants	Short-Distance Migrants	Permanent Residents
Acadian Flycatcher	American Robin	American Crow
American Redstart	Brown-headed Cowbird	American Goldfinch
Baltimore Oriole	Common Yellowthroat	Barred Owl
Black-and-white Warbler	Eastern Phoebe	Black-capped Chickadee
Black-billed Cuckoo	Eastern Towhee	Blue Jay
Black-throated Green Warbler	Gray Catbird	Carolina Wren
Blue-gray Gnatcatcher	House Wren	Downy Woodpecker
Blue-winged Warbler	Mourning Dove	Fish Crow
Broad-winged Hawk	Northern Flicker	Hairy Woodpecker
Chestnut-sided Warbler	Red-winged Blackbird	Northern Cardinal
Eastern Wood-Pewee	White-eyed Vireo	Red-bellied Woodpecker
Great Crested Flycatcher		Red-shouldered Hawk
Hermit Thrush		Tufted Titmouse
Hooded Warbler		White-breasted Nuthatch
Louisiana Waterthrush		
Ovenbird		
Pine Warbler		
Prairie Warbler		
Red-eyed Vireo		
Scarlet Tanager		
Veery		
Wood Thrush		
Worm-eating Warbler		
Yellow-billed Cuckoo		

Vegetation Methods

In the early 1950s, Niering and Goodwin (1962) established four east-west transects spanning the Bolleswood Natural Area; three additional offsets cross land that was previously used as agricultural fields, although these offsets are not included in the bird survey area analyzed here , as this "old field" site is treated as a separate study area (Goslee et al., 2005). The permanent transects are 122 meters apart and 6 meters wide; each is divided into two rows of 3 x 3 meter quadrats. There are a total of 890 numbered quadrats subject to periodic surveys in the Bolleswood Natural Area (Goslee et al., 2005); only 750 are included in the study area for this analysis, as the "old field" site is not included in the forest site examined here. Vegetation surveys were conducted every ten years between 1952 and 2012 (Table 1.). All herbs, shrubs, saplings, and trees present in each quadrat were identified and recorded during each survey (Niering and Goodwin, 1962). Each plant was assigned to one of the following height classes: A, B, C, D (Table 3.) For the purposes of this study, Height Class A encompasses the forest canopy and high shrubs, whereas Height Class B includes intermediate shrubs. Plants in Height Classes C and D were not included in this analysis.

Table 3. Vegetation height classes as outlined by Niering and Goodwin (1962).

Height Class Label	*Heights Included in Class*	*Vegetation Type*
A	> 6 feet (~2 m)	Forest canopy and high shrubs
B	2 feet – 6 feet (~0.6 – 2 m)	Intermediate shrubs
C	2 inches – 2 feet (~5 cm - 0.6 m)	Low shrubs and herbs
D	< 2 inches (~ 5cm)	Very low shrubs and herbs

Additional data gathered during some surveys include basal area measurements for trees tall enough to have a DBH (diameter at breast height, typically measured on stems at a height of 1.37 m) for all years, frequency counts for tree and shrub species for all years, and percent shrub cover for surveys in the years after and including 1982. Fieldwork for each vegetation survey was primarily accomplished by a different set of botany students during each census (Goslee et al., 2005), so not all variables were recorded consistently over the full span of the long-term survey. In particular, the lack of consistent percent cover data for the shrub layer makes it difficult to assess changes in this variable prior to 1982. Intermediate and high shrub specimens were not always distinguished from one another to the same degree throughout the years, so these categories were combined into a "high + intermediate" category for all shrub cover higher than 2 ft.

On the basis of previous research on floristics and bird habitats (discussed in the introduction), I selected several species or groups of species for analysis: red maple, collective oak species (composed of black oak, red oak, white oak, and scarlet oak), black birch, yellow birch, and eastern hemlock. For each of these species or group of species, I used basal area (m^2/hectare) as a measure of species dominance in the forest canopy.

In order to evaluate tree species diversity, I calculated diversity values for each year using the Inverse Simpson's Diversity Index for measurements of basal area for all tree species. The equation for the Inverse Simpson's Diversity Index is as follows:

$$D = 1 / \Sigma p_i^2$$

where p_i represents the proportion of a specific species' basal area to the total basal area from all tree species (Gurevitch et al., 2006). This index measures species diversity on a scale starting at 1 and increasing until it reaches the maximum of species included in the data set. Twenty-three tree species have been recorded in the Bolleswood Natural Area since 1952. Similar diversity values for the shrub layer were calculated by applying the Inverse Simpson's Diversity Index to data on shrub species frequency in the transect quadrats.

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

Diversity of Migratory Forest Specialists

I calculated the diversity of the migratory forest specialist species using the same Inverse Simpson's Diversity Index that I used for assessing tree and shrub diversity. I chose to focus on only migratory forest specialists for this part of the project so that potential increases in generalist species, which would be included in a diversity index of the entire bird community, would not mask potential changes in specialist species. I then compared the diversity of the migratory forest specialists to tree species diversity, as the forest canopy is presumably most relevant to the needs of this habitat group.

Measuring Forest Cover in the Surrounding Landscape

Previous research in the Connecticut College Arboretum in the 1980s indicated that the amount of forest cover within 2 kilometers in the landscape surrounding the Arboretum was positively related to the abundance of long-distance migratory bird species (Askins and Philbrick, 1987). More recent advances in aerial photography and mapping technology, particularly Geographic Information Systems (GIS), have improved the accuracy of landscape analysis. I therefore decided to analyze aerial photographs using ArcGIS 10.2 to assess changes in the amount of forest cover over the years within 1, 2, and

5 kilometers of the Connecticut College Arboretum. My goal was to digitize polygons representing areas of forest cover, based on aerial photographs examined at 1:10,000 scale, in order to measure changes in forest cover surrounding the study site.

I first created a buffer zone polygon of 5 kilometers around a shapefile of the Arboretum from the Connecticut College GIS data collection (and later repeated this step to create 1 km and 2 km buffers, using the outline of the Arboretum boundaries as the initial polygon to be buffered). I then obtained aerial photograph tiles of the buffer area from the years 1951, 1970, 1986, 1995, 2004, and 2012. I acquired the photographs from 1951-1995 from the online archives of the Map and Geographic Information Center (MAGIC) at the University of Connecticut, using their Aerial Photography Centerpoint Indices. From these indices, I obtained a patchwork of aerial photo tiles covering my chosen buffer zone in each year, but these images were not yet georeferenced. Georeferenced orthophotographs were available for the years 2004 and 2012 from Connecticut Environmental Conditions Online (CT ECO), and I was able to use these layers to georeference the other image tiles. All aerial photographs analyzed in this project used the following projected coordinate system: NAD 1983 StatePlane Connecticut FIPS 0600 Feet.

To georeference the photographs from 1951, 1970, 1986, and 1995, I first identified the photograph tiles needed to cover the region encompassing the study area and fit each image to its approximate location relative to the Arboretum. The aerial photograph layer from 2012 already had accurate spatial information, so I used this layer as my base for comparison while creating new links to georeference the images from the years without sufficient spatial data. Essentially, I located landmarks on the aerial photographs from earlier years and linked them to landmarks that were still visible in 2012, so that the GIS software would display them where they belonged on the map, a necessary prerequisite for further analysis. For each image tile that I georeferenced, I created links for at least four points within the image, and continued creating links until I had achieved a root square mean (RMS) error of less than fifteen feet.

After I had georeferenced all of the aerial photographs and assembled them in a mosaic to cover the 5-kilometer buffer zone around the Arboretum, I began to digitize polygons to outline the patches of forest cover present in the images, so that the area of forest cover could be compared over the years. Digitizing at a consistent map scale of 1:10,000 helped minimize the effect of having different aerial photographs with different resolutions. For each polygon I created, I also created several new points both inside and outside the polygon, and assigned them attributes of “forest” or “not forest” so that each polygon could later be identified and its classification double-checked. Some forest polygons had interior areas without forest (such as a field surrounded by forest), which I excised from the outer forest polygons to ensure planar enforcement, so that no polygons would overlap and no areas would be counted twice. I then reviewed the “forest” or “not forest” labels for my final polygons to ensure that each polygon only fell into one category, thereby checking logical consistency. I then calculated the total forest area in square meters for each year to be consistent with the other metric measurements used in this study. I defined “forest patch” as tree-covered areas larger than 10,000 square meters, and so excluded any polygons less than 10,000 square meters from the total forest area measurement. For each year, I also counted the number of forest patches (again excluding those less than 10,000 square meters), and calculated the average patch size in square meters.

Breeding Birds Survey

Data from the Connecticut portion of the North American Breeding Bird Survey were obtained from the University of Connecticut Ornithology Research Group's CTBirdTrends website and through correspondence with Chris Field. These data contained the statewide trends for individual bird species from 1966-2009, and noted whether or not these trends were significant (Field and Elphick, 2012).

Statistics

I assessed the overall composition of the bird community over time by running non-metric multi-dimension scaling (NMS) ordinations using PC-Ord Version 6 on the "slow and thorough" autopilot setting. Two ordinations were conducted: one including data from 1953 to 2012 and one including data from 1982-2012 to focus on the most recent and most thorough data, as mentioned earlier. Prior to running these ordinations, bird species that had not appeared more than once in the selected census years were removed from the data set. Two-dimensional models were selected as the best solution for both the data set from 1953 onward and from 1982 onward, using the criteria that each axis must be significant in Monte Carlo tests and must decrease overall stress in the model by at least 5.

Principal component analysis reduces the number of variables used in a statistical model while preserving as much information as possible, so I used PCA in SPSS to create factors that accounted for most of the variation in vegetation patterns caused by the numerous variables I had previously selected. This allowed me to reduce the number of vegetation variables (both floristic and structural) to two principal components (Table 4.). I also used principal component analysis in SPSS to create a single landscape factor that took into account total forest area in the 2 km buffer zone, the number of forest patches in that area, and the average patch size, in order to produce a variable measuring forest fragmentation.

For the analysis of the data from 1953 to 2012, I ran general linear models that focused on three independent variables – the first vegetation principal component, the second vegetation principle component, and the landscape factor created to measure forest fragmentation. I standardized all the independent variable values and used linear interpolation to produce values for each bird survey year before proceeding to the general linear models. The first vegetation factor was highly correlated (0.971) with time (measured in years since the surveys began), so I did not include time as a separate independent variable. For the analysis of the data from 1982 to 2012, I considered including percent shrub cover as an independent variable, but found that this was not necessary because shrub percent cover was highly correlated (0.973) with the first vegetation factor. Therefore the models for the 1982-onward data focused on the same three variables as the 1953-onward models, and the first vegetation factor in these models can be understood to also be a good indicator of patterns in shrub cover.

I performed Poisson general linear models using R statistical software for 20 common bird species, four groups of species categorized by habitat, and three groups of species categorized by migratory pattern. For each general linear model, I originally included all three selected independent variables – the first two vegetation factors and the landscape factor. I then used the dredge tool in R to rank potential variants of the general linear model using all possible subsets and combinations of independent variables, and selected the model with the lowest AICc value to find the best fit, generating intersect and regression coefficients . AICc values were calculated rather than AIC values to take into account the relatively small sample size. I also used linear regression models to test the relationship between the ordination scores produced by my initial data explorations using PC-Ord and the same three independent variables as the general linear models.

A few models representing individual species or species groups were overdispersed, (defined for my purposes as having a ratio of residual deviance: degrees of freedom that was greater than 1.3). For these cases, since the Poisson Distribution was no longer an adequate fit, I calculated Quasi AIC values to determine the best model.

To compare the trends of bird species in the Arboretum to the statewide trends reflected in the results of the Connecticut Breeding Bird Surveys, I ran Poisson regression models for each species and group again for the years from 1964-2009, using time as the only independent variable. From these models, I determined which species had significant increases or declines in population in the Bolleswood Natural Area over this time period (and which species had no significant trends over time), which I could then compare to the trends for these species in the statewide surveys.

To get a sense of whether or not tree species diversity is associated with the diversity of the migratory forest specialists that use the canopy layer, I tested the significance of the association between species diversity of migratory forest specialists and tree diversity by using bivariate correlation in SPSS to produce a Pearson correlation coefficient.

Results

Patterns in the Overall Bird Community

Exploratory NMS ordinations provided an overview of the bird community in the Bolleswood Natural Area in each survey year since 1953 and since 1982. For the data set from 1953-2012, a two-dimensional model gave the best fit (minimum stress = 10.627; p = 0.0040, Sorenson Cumulative R^2 = .937). A two-dimensional model also gave the best fit for the 1982-2012 data set (minimum stress = 11.212; p = 0.0040, Sorenson Cumulative R^2 = .916). In the ordination graphs for both data sets (Figure 1, Figure 2), a chronological pattern is discernible for Axis 1 scores, but not as clear for Axis 2 scores, indicating that the bird community is likely responding both to the maturation of the forest over time and to other additional factors not as closely linked to time. The next stages of the analysis helped to identify and test possibilities for these factors.

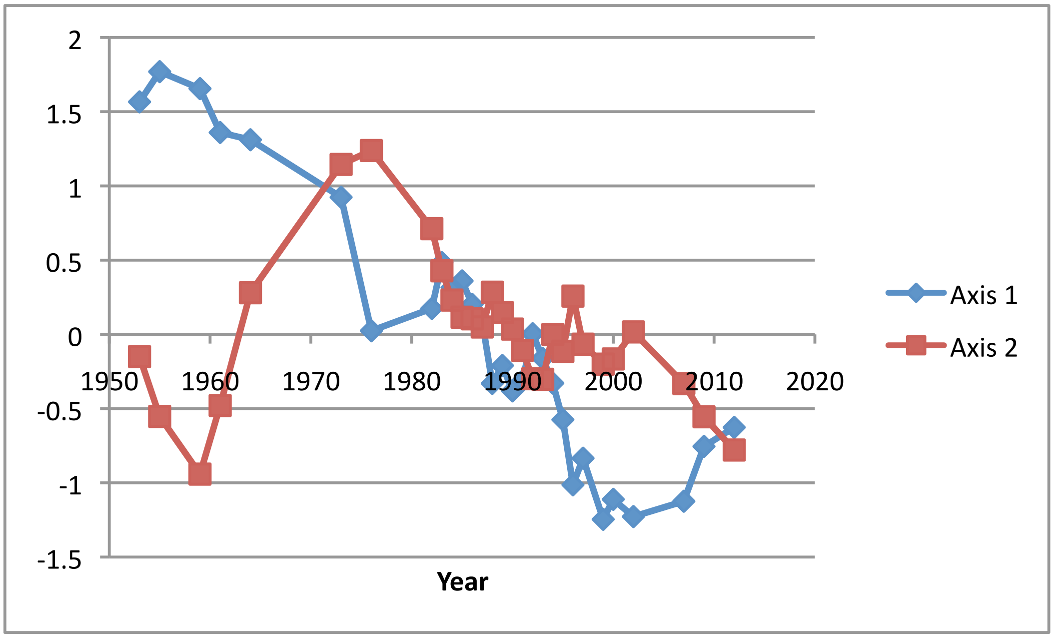

Figure 1. Changes in NMS ordination scores for bird survey years from 1953 - 2012.

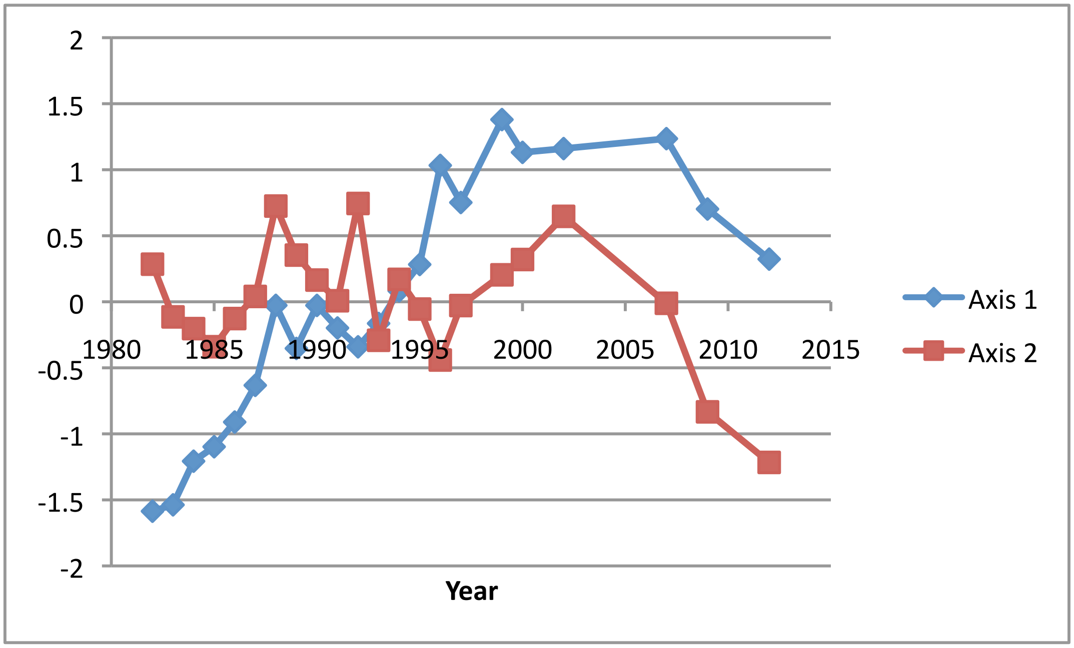

Figure 2. Changes in NMS ordination scores for bird survey years from 1982 - 2012.

Total bird abundance sharply declined in the 1970s, increased again in the 1980s, and has strongly declined since then to even lower levels (Figure 3.). Diversity of migratory forest specialist species as measured by Inverse Simpson's Index has fluctuated widely throughout the study period since the 1950s (Figure 4.).

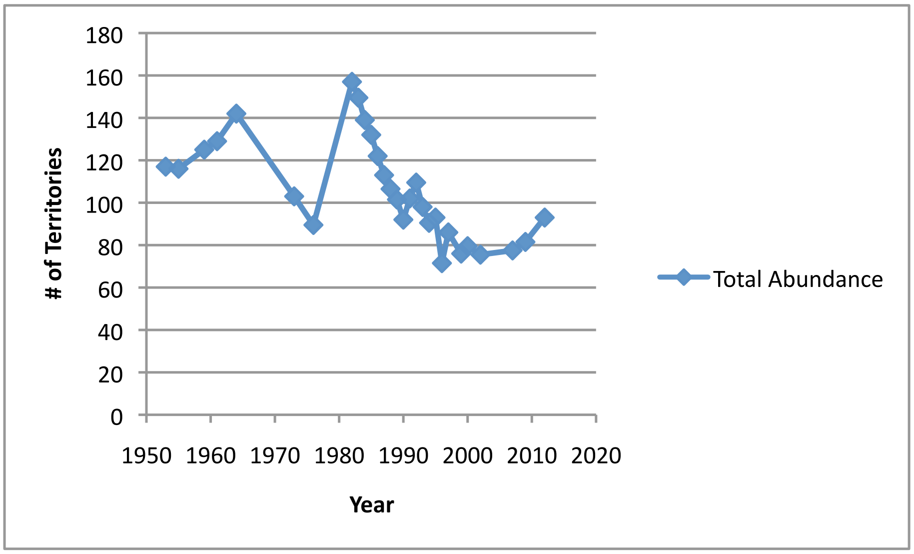

Figure 3. Changes in total bird abundance over time.

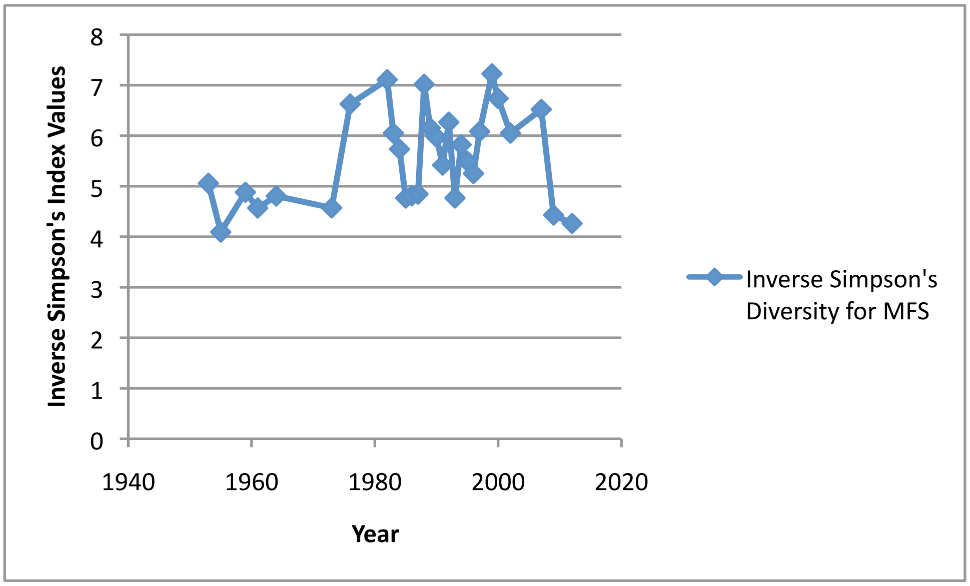

Figure 4. Diversity of migratory forest specialist species over time, as measured by Inverse Simpson's Diversity Index.

Species Groups Over Time

All habitat specialization and migratory pattern groups showed a decline in the 1970s (Figures 5-11) but appeared to recover by the early 1980s. Migratory forest specialists, early-successional and shrub-layer species, hemlock associates, long-distance migrants, and short-distance migrants have all declined fairly steadily and steeply since the 1980s. Hemlock decline winners and permanent residents do not appear to have declined as sharply.

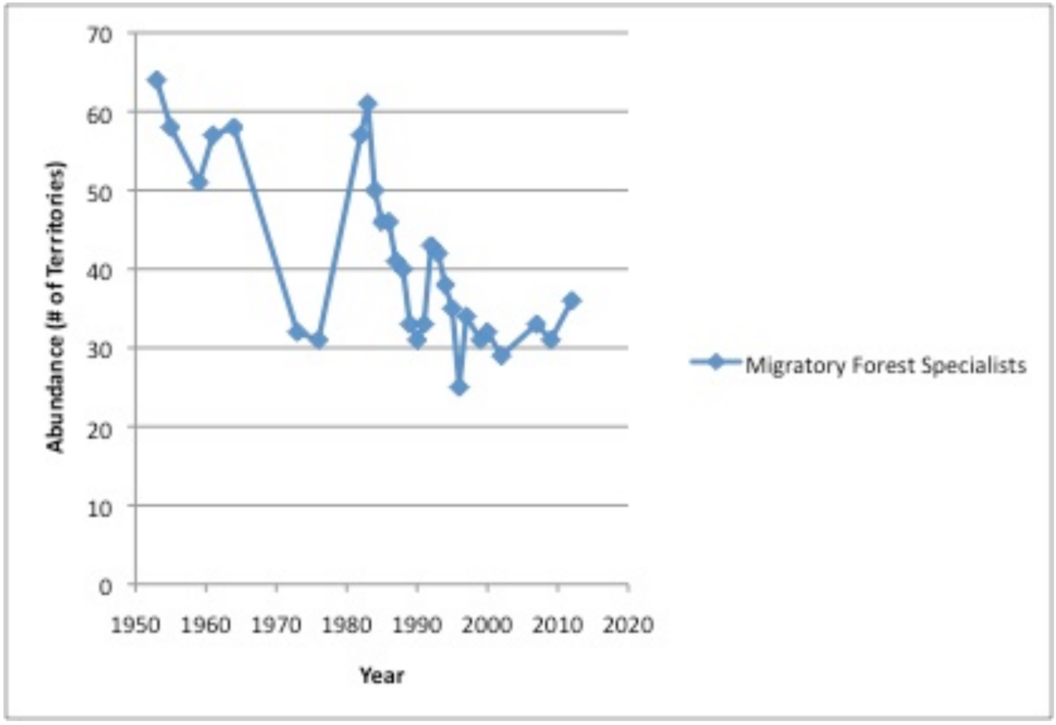

Figure 5. Changes in the total population of migratory forest specialists between 1953 and 2012.

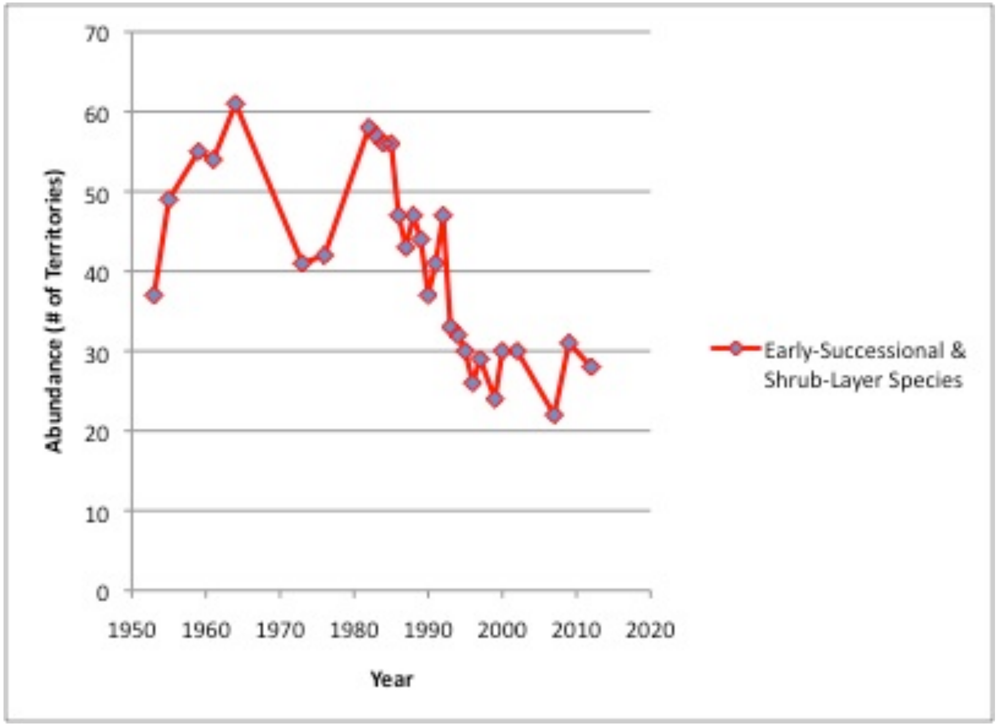

Figure 6. Changes in the total population of the early-successional and shrub-layer species group between 1953 and 2012.

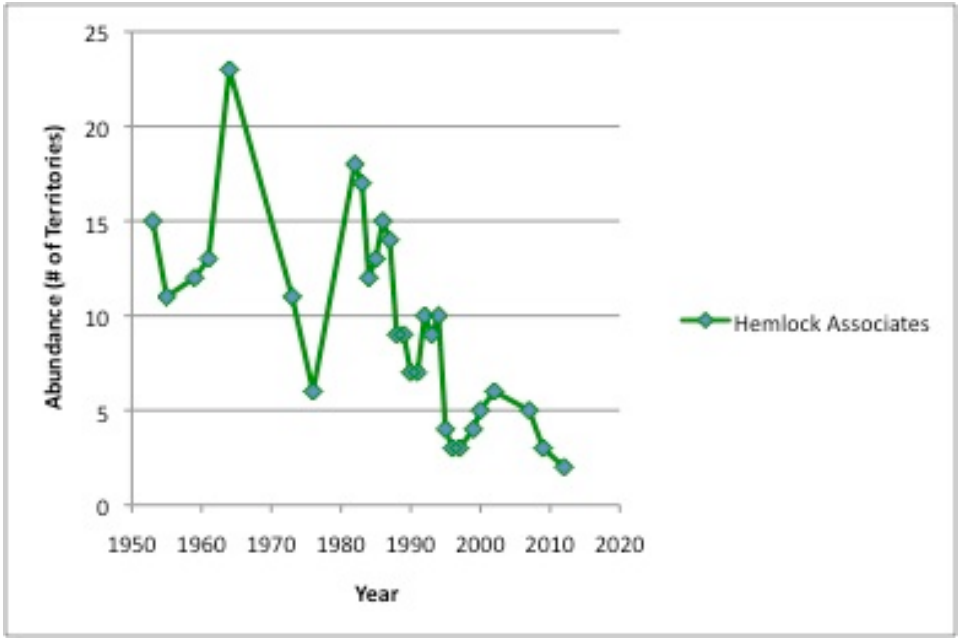

Figure 7. Changes in the total population of the hemlock associaties species group between 1953 and 2012.

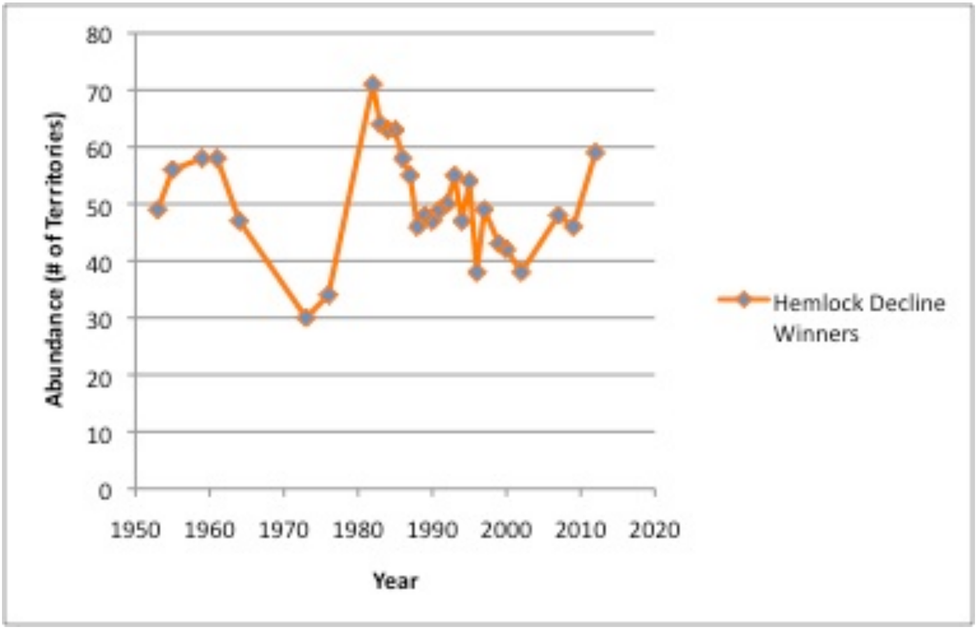

Figure 8. Changes in the total population of the hemlock decline winners species group between 1953 and 2012.

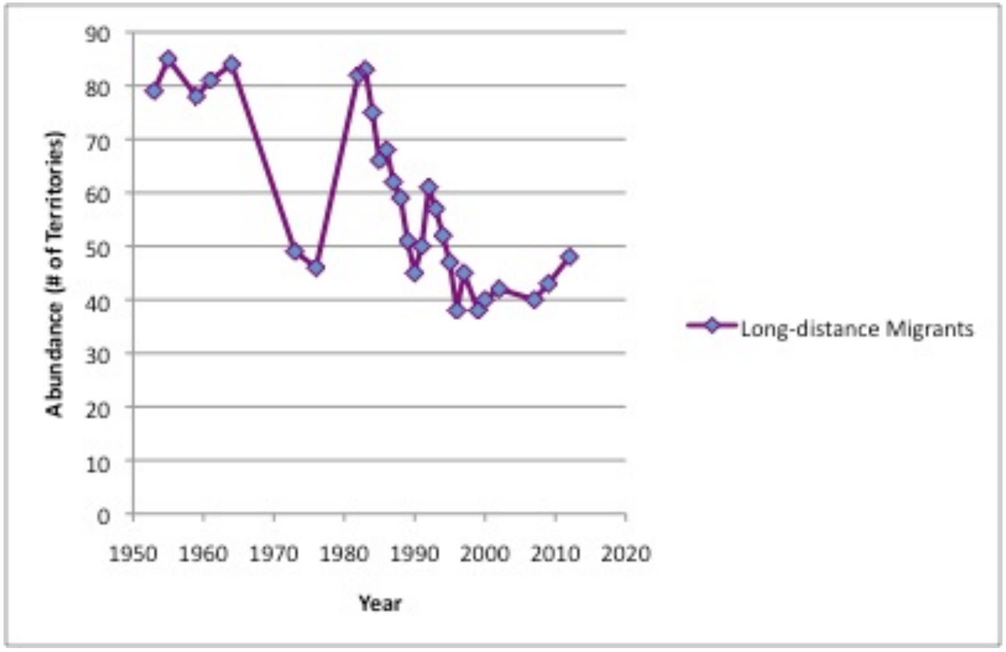

Figure 9. Changes in the total population of the long-distance migrant species group between 1953 and 2012.

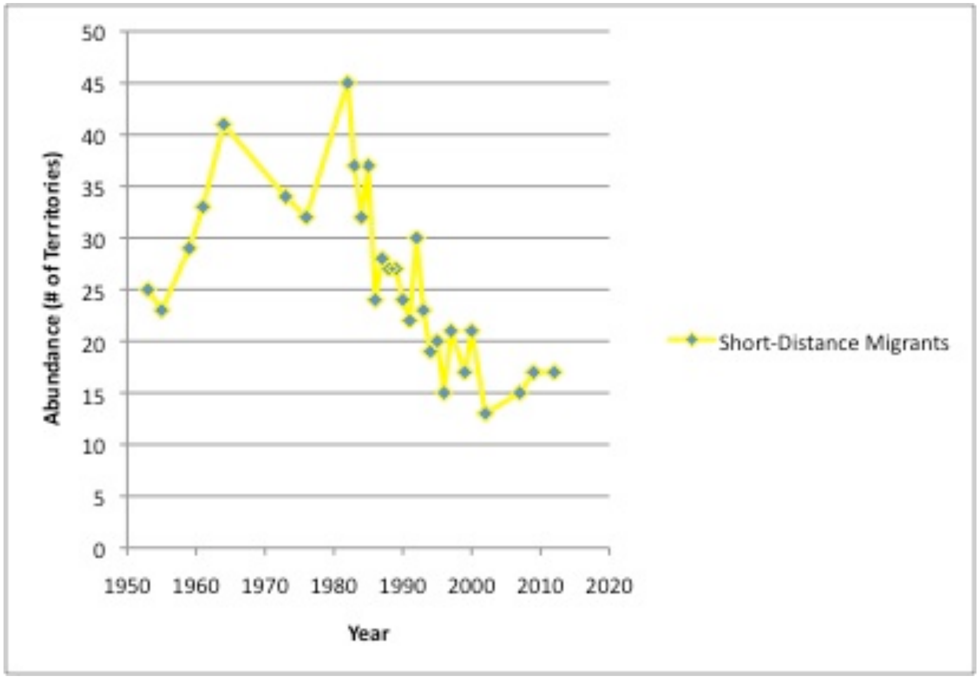

Figure 10. Changes in the total population of the short-distance migrant species group between 1953 and 2012.

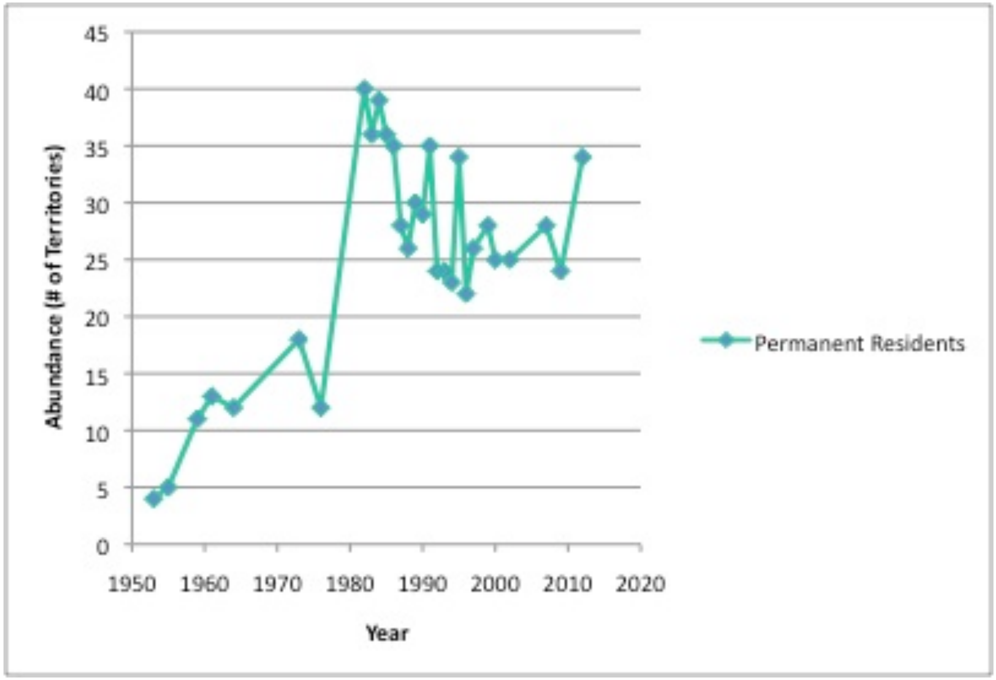

Figure 11. Changes in the total population of the permanent resident species group between 1953 and 2012.

Vegetation Factors

Principal component analysis reduced eight vegetation variables to two principal components accounting for 85% of the variance (Table 4). The first vegetation component was strongly and positively associated with the basal areas of red maple and oak species, as well as the total basal area; the same component was strongly and negatively associated with basal area of yellow birch and overall tree species diversity. The second vegetation component was strongly and positively associated with basal area of eastern hemlock. The first vegetation principal component increased throughout the study period, indicating increasing abundance of oak and maple trees and higher total basal area in the forest overall, but decreasing diversity and decreasing abundance of yellow birch (Figure 12). The second vegetation principal component increased until the early 1990s and then declined sharply, reflecting the rise and fall of the eastern hemlock population in the

Bolleswood Natural Area (Figure 12). These two components were later used as variables in general linear models.

Table 4. Component matrix for principal component analysis of eight vegetation variables from 1952-2012.

Component Matrix[a]

	Component	
	1	2
A.rubrum	.988	-.084
Quercus	.984	-.142
B.lenta	.727	-.607
B. alleghaniensis	-.876	.308
T.canadensis	.201	.966
Total Basal Area	.950	.292
InverseSimpson'sFor Trees	-.874	-.474
InverseSimpson'sForShrubs	-.240	-.203

Extraction Method: Principal Component Analysis.

a. 2 components extracted.

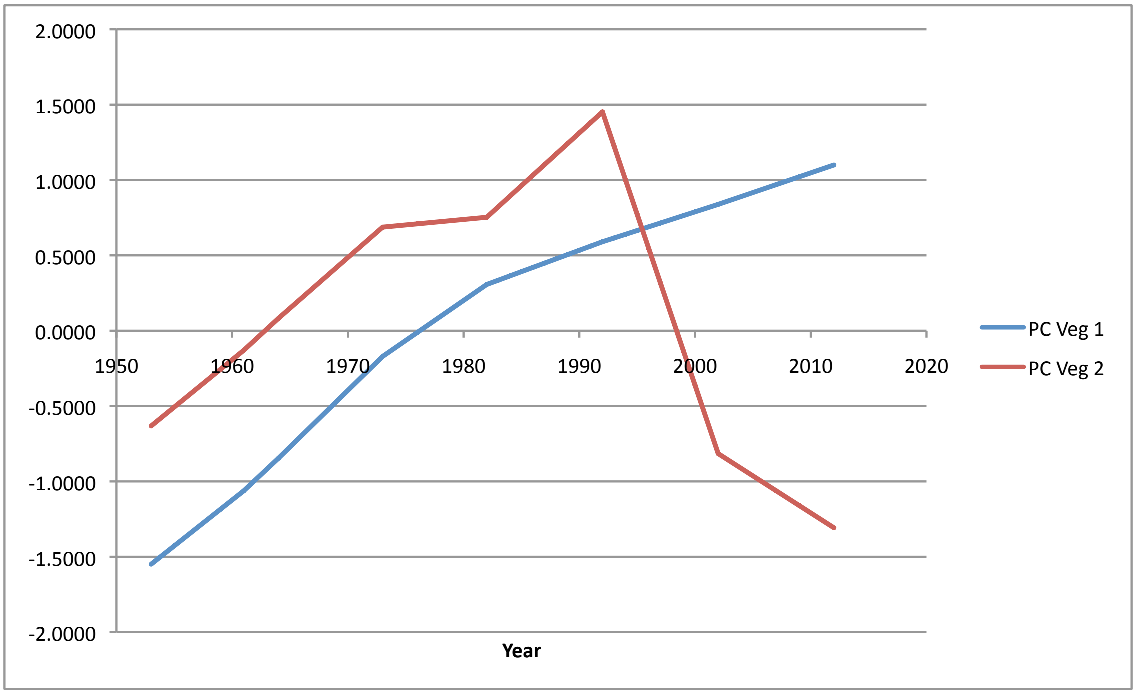

Figure 12. Changes in the two vegetation principal components over time.

Landscape Analysis

GIS analysis of the land within 2 km of the Arboretum's boundaries revealed that although specific areas within this zone changed from forest to non-forest or vice versa, the net area of forest cover did not change substantially in magnitude between 1951 and 2012, never fluctuating by more than 10% from its highest area (Figures 14, 15, 16). The number of forest patches increased from 1951 to 1970, and the average size of forest patches decreased during this period. Number of forest patches fluctuated in the 1980s and 1990s, and then trended downward after 1995; average patch size followed the inverse pattern, increasing after 1995 (Table 5.). PCA analysis using these three factors – total forest area, number of forest patches, and average forest patch size – produced a single landscape component accounting for 68% of the variance (Table 6.). Values for this factor were higher when forest parcels were more numerous and smaller, indicating that it is a measure of forest fragmentation. In the years covered by this study, this fragmentation factor reached its highest point in the 1970s, and has declined fairly steadily since except for a temporary and smaller spike in the 1990s (Figure 13). Patterns were similar at the 1 km and 5 km range, so I only used the 2 km buffer for subsequent analysis.

Table 5. Patterns in forest cover within 2 km of the Connecticut College Arboretum boundaries.

Year	Forest Cover (m^2)	Number of Forest Patches	Average Patch Size (m^2)
1951	12,716,457	62	205,104
1970	12,225,479	68	179,786
1986	11,627,107	54	215,317
1995	11,658,923	59	197,609
2004	12,000,084	55	218,183
2012	12,132,721	49	247,607

Table 6. Component matrix for principal component analysis of three landscape variables from 1951-2012.

Component Matrix[a]

	Component
	1
Forest Cover	.428
Number of Parcels	.997
Average Parcel Size	-.931

Extraction Method: Principal Component Analysis.

a. 1 components extracted.

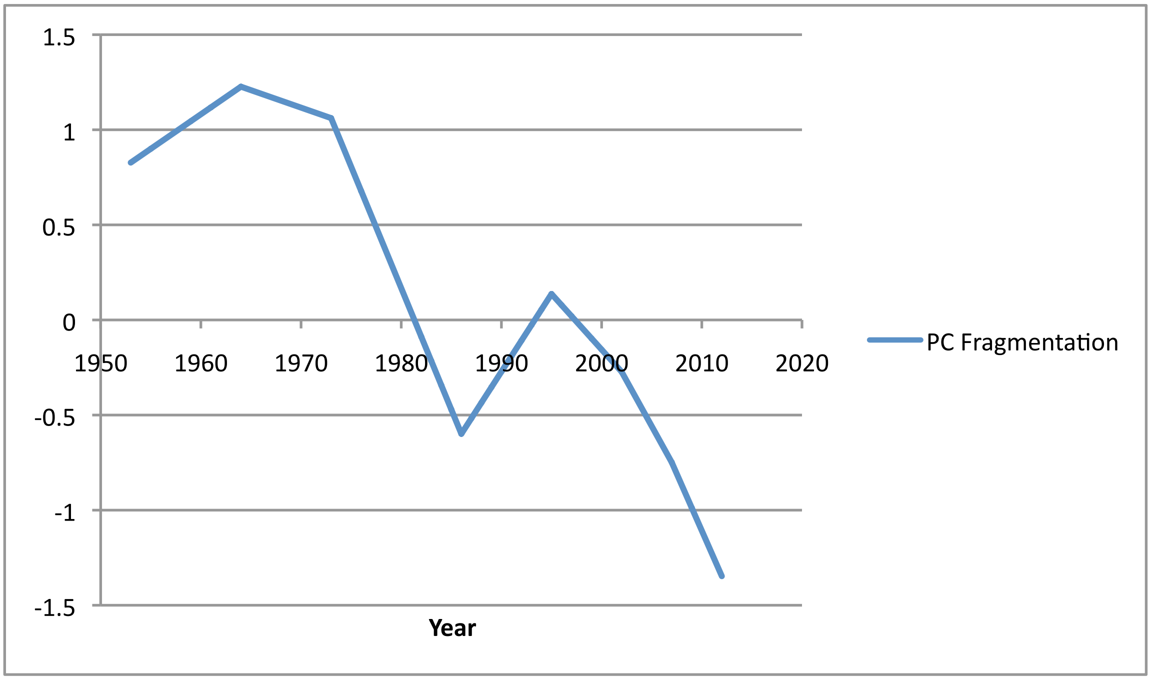

Figure 13. Changes in the fragmentation factor over time. Higher values indicate more fragmentation (and therefore less intact forest cover).

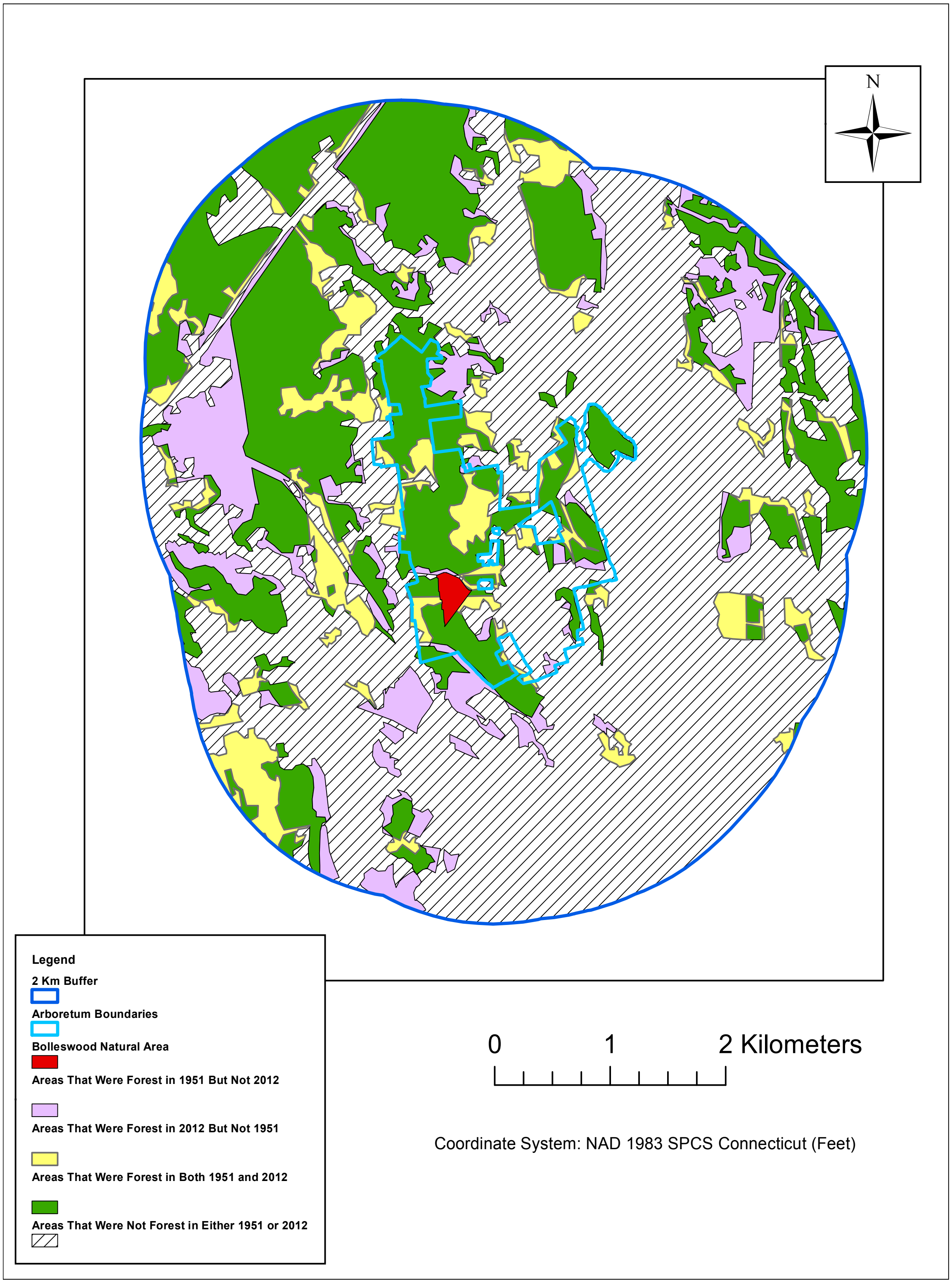

Figure 14. Changes in forest cover between 1951 and 2012 within 2 km of Arboretum boundaries.

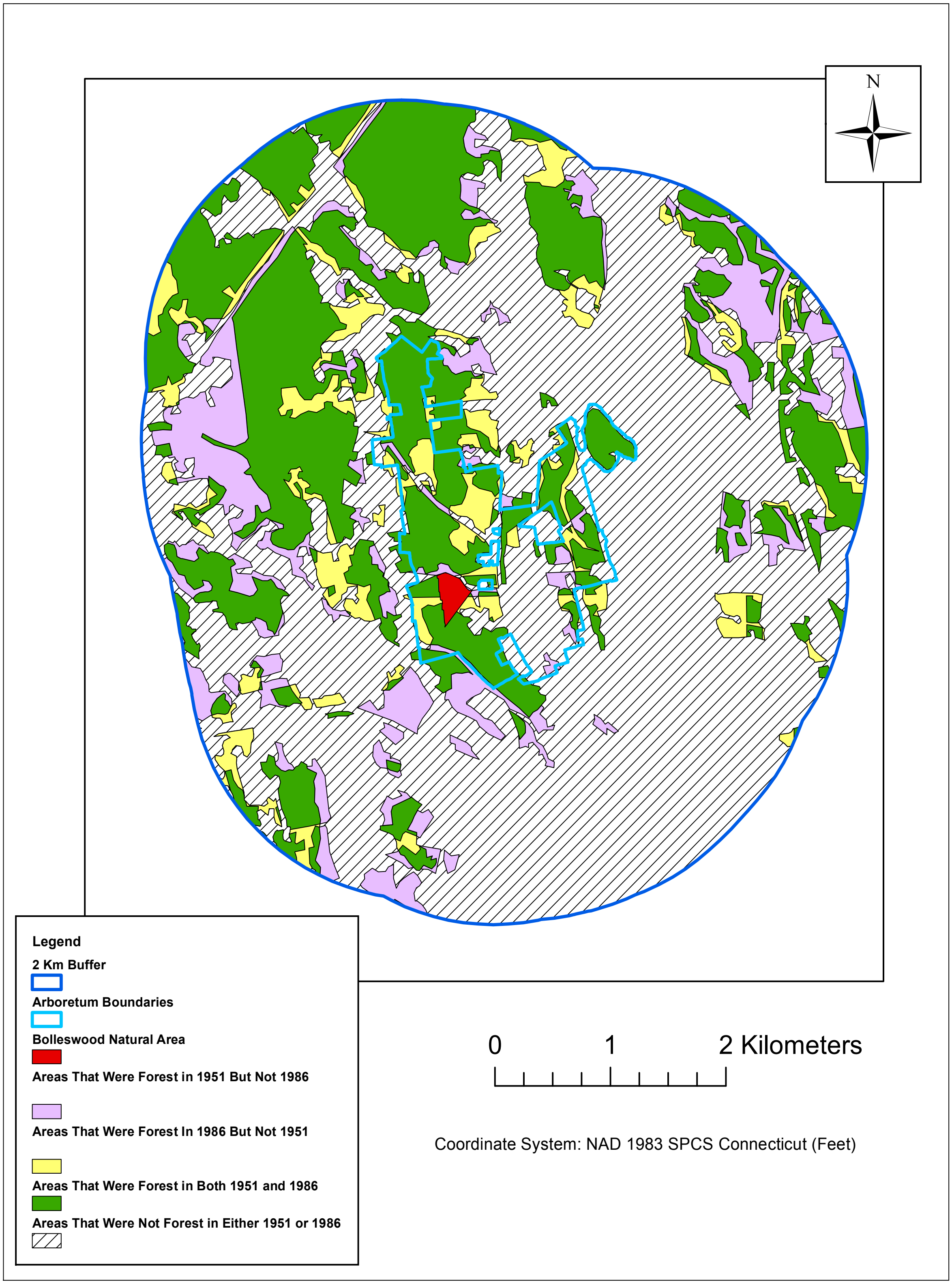

Figure 15. Changes in forest cover between 1951 and 1986 within 2 km of Arboretum boundaries.

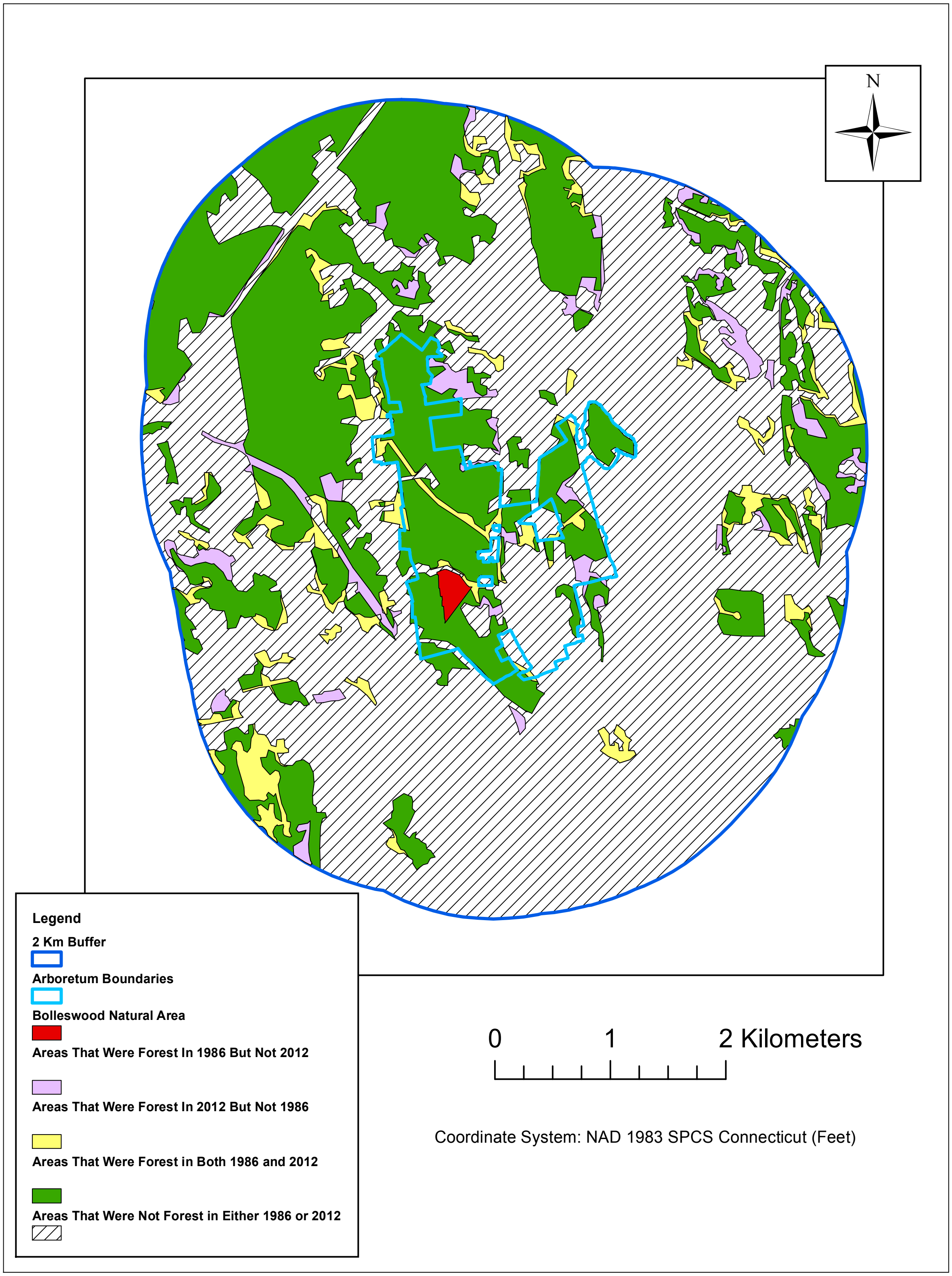

Figure 16. Changes in forest cover between 1986 and 2012 within 2 km of Arboretum boundaries.

Relationship Between Bird Community and Vegetation and Landscape Factors

A positive relationship with the first vegetation factor indicates that the bird species or group is associated with the increasing presence of red maple and oaks, as well as the increasing total basal area linked to the maturation of the forest over time; a negative relationship with this factor indicates that the bird species or group is associated with the presence of yellow birch and higher overall tree species diversity. A positive relationship with the second vegetation factor indicates that the bird species or group is more common in years with more hemlock dominance, whereas a negative relationship with this factor indicates higher abundance in the years with a lower hemlock presence, such as the years after adelgid-driven hemlock mortality had begun. A positive relationship with the landscape factor indicates that the bird or group is more common when the degree of forest fragmentation is higher, whereas a negative relationship indicates higher abundance when the forest is less fragmented.

In order to get an initial sense of potential relationships between bird abundances and the vegetation and landscape factors, I created basic X-Y scatter plots of the abundances of the habitat and migratory groups against the three PCA factors for both the 1953-2012 range (Figures 17, 18, and 19) and the 1982-2012 range of data (Figures 20, 21, 22), and then displayed only the trend lines. Nearly all groups showed a negative trend as the first vegetation principal component increased in both the 1953-2012 and 1982-2012 data sets, suggesting that they decreased at the same time as oak, maple, and total basal area increased in the forest; the permanent residents in the 1953-2012 data set were an exception, however, and showed a positive trend instead. Nearly all groups showed a positive trend with the second vegetation principal component factor, suggesting that these groups are more common in forests with higher hemlock basal area but have declined in the Bolleswood Natural Area at the same time as the hemlocks have declined; only the migratory forest specialists in the 1982-2012 data set appeared to show little relationship with this factor. The graphical relationships between groups and the landscape factor measuring forest fragmentation are not as consistent. Abundances of migratory forest specialists, early-successional and shrub-layer species, hemlock associates, long-distance migrants, and short-distance migrants all have higher abundances at higher forest fragmentation values in the 1953-2012 data set, as these groups have been declining even as forest fragmentation has declined in recent years. Permanent residents show a negative trend with increasing values for forest fragmentation, as do hemlock decline winners. In the 1982-2012 data set, all of the groups appear to be relatively unrelated to the forest fragmentation factor.

Subsequent regression models then revealed which of these relationships produce significant results for the data set from 1953-2012 and 1982-2012, and which variables or combination of variables have the most explanatory power. Some of the relationships visible in the simple abundance-versus-factor graphs are therefore less obvious or absent altogether in the regression results, indicating that the variability associated with these factors was already accounted for by other factors or was not strong enough to register as significant given the sample size.

Diversity of migratory forest specialists was negatively correlated with tree species diversity (Pearson coefficient = -.369, p = .049), although this relationship was not a strong one and only just registered as significant (Figure 23).

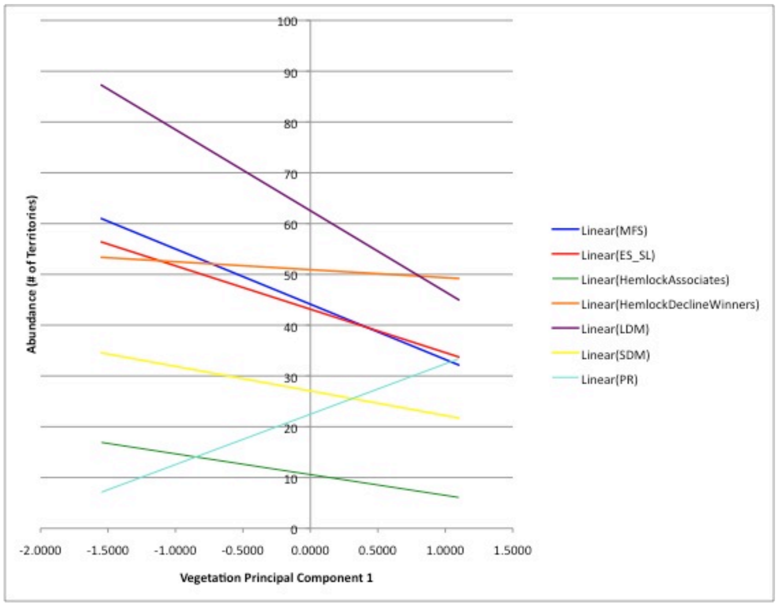

Figure 17. Scatter plot (trend line shown) of group abundances against scores for vegetation principal component 1, using the data from 1953-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

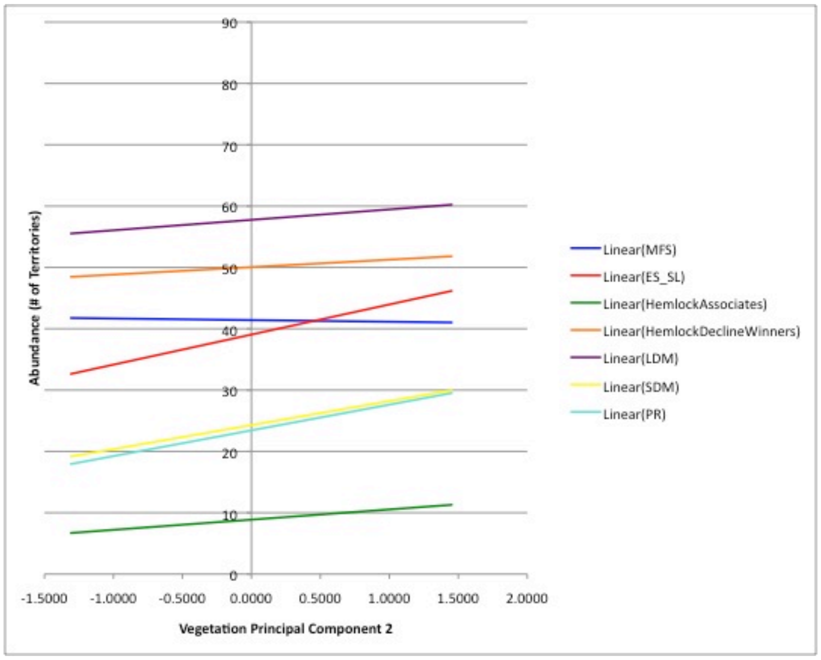

Figure 18. Scatter plot (trend line shown) of group abundances against scores for vegetation principal component 2, using the data from 1953-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

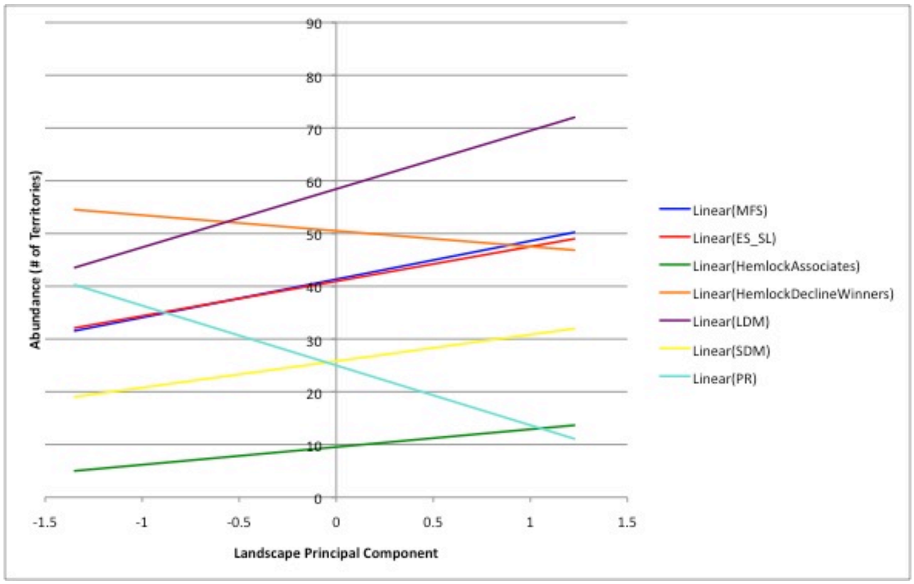

Figure 19. Scatter plot (trend line shown) of group abundances against scores for the landscape principal component, using the data from 1953-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

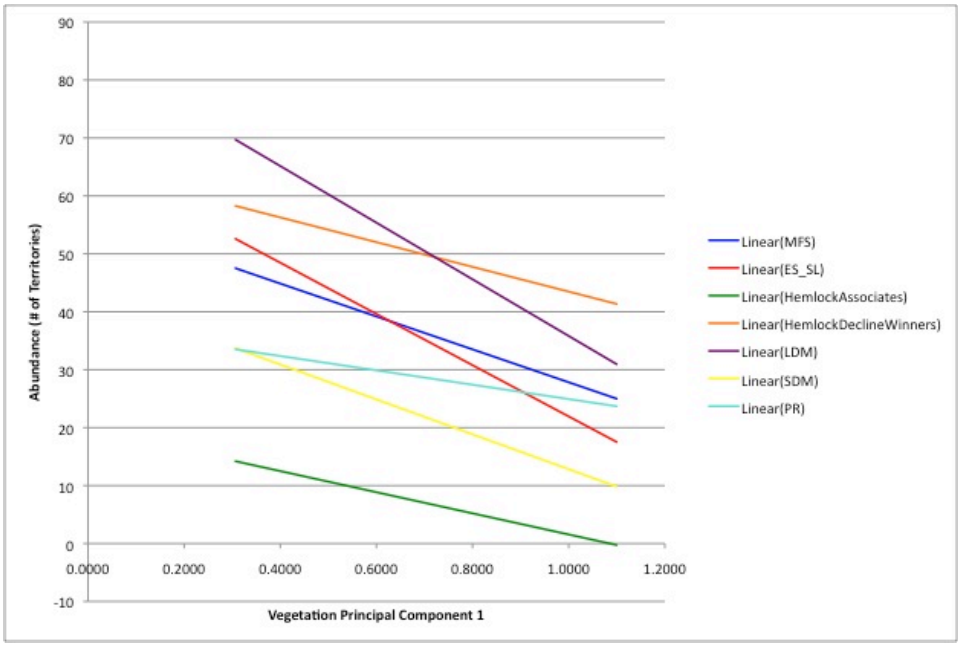

Figure 20. Scatter plot (trend line shown) of group abundances against scores for the vegetation principal component 1, using the data from 1982-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

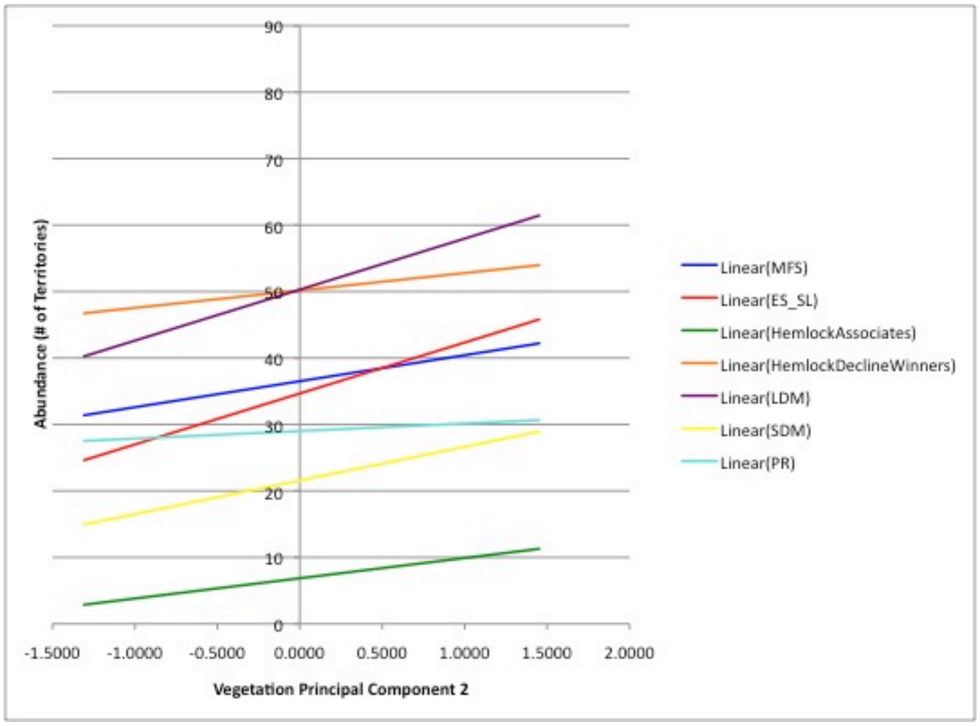

Figure 21. Scatter plot (trend line shown) of group abundances against scores for vegetation principal component 2, using the data from 1982-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

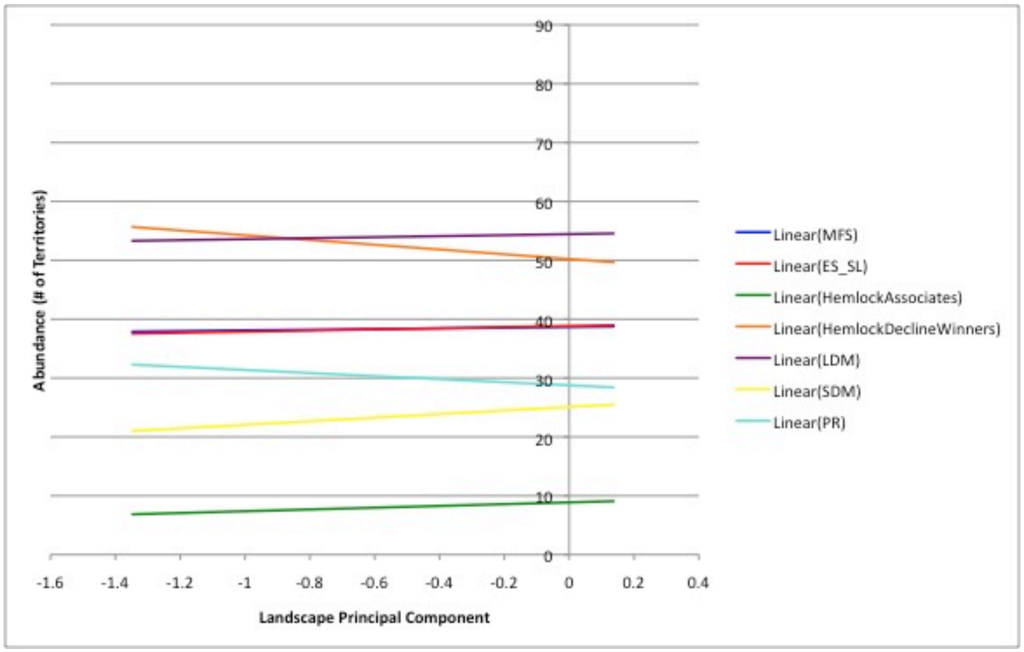

Figure 22. Scatter plot (trend line shown) of group abundances against scores for the landscape principal component, using the data from 1982-2012. (MFS = migratory forest specialists; ES_SL = early-successional & shrub-layer; LDM = long-distance migrants; SDM = short-distance migrants; PR = permanent residents).

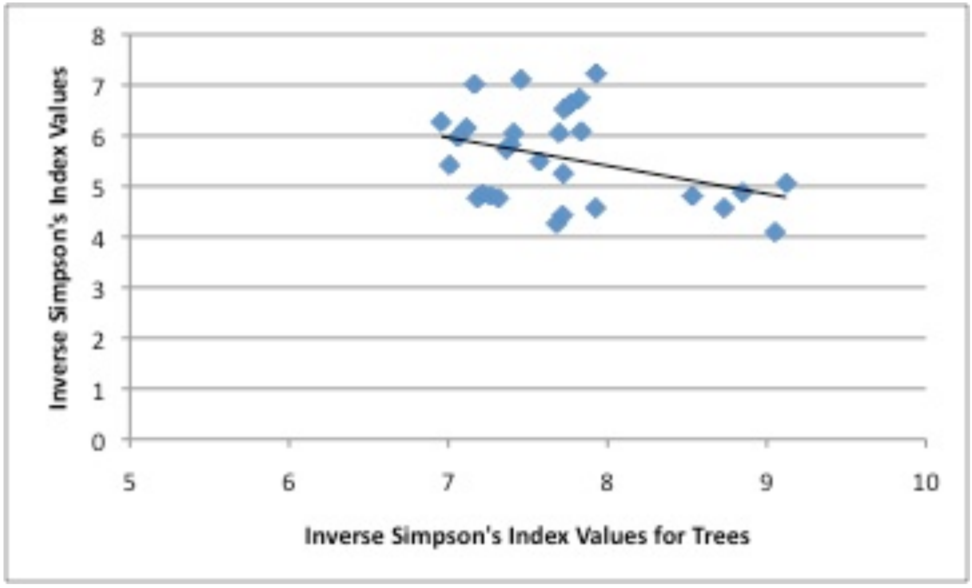

Figure 23. Diversity (as measured by Inverse Simpson's Diversity Index) of migratory forest specialist species versus diversity of trees over time in the Bolleswood Natural Area. Pearson's coefficient = -.369, p = .049.

The results of the Poisson regression for the 1953-2012 data are listed in Table 7. Of the twenty species selected for individual analysis, fourteen showed some relationship to the first vegetation component (six positive, eight negative), while nine showed some relationship to the second vegetation component (all positive), and six showed some relationship to the landscape factor measuring forest fragmentation (all negative). Three species showed no relationship to any of the three factors. Associations between species groups and the three factors were also revealed. Migratory forest specialists, early-successional and shrub-layer species, hemlock decline winners, long-distance migrants, and permanent residents all showed at least some relationship to all three factors, and in most cases showed the strongest association with the first vegetation component. Hemlock associates and short-distance migrants showed a relationship with only the two vegetation factors and not the landscape factor; both had a stronger relationship with the first vegetation component than with the second. All groups except permanent residents had a negative relationship with the first vegetation factor, indicating a decrease in abundance over time as the maturing forest became more dominated by oak and maple. All groups showed a positive relationship with the second vegetation factor, indicating that they were more abundant in years with higher hemlock dominance in the forest. Though not all groups were associated with the landscape factor, those that were showed a negative relationship, indicating that they decreased when forest fragmentation increased. Models also displayed connections between the ordination scores for the entire bird community over the years and the vegetation and landscape components (Table 9). The first axis was more strongly associated with the first vegetation component than with the other variables in its best-fit model, while the second axis was only associated with the second vegetation component.

The results of the Poisson regression for the 1982-2012 data are listed in Table 8. Of the twenty species selected for individual analysis, nine showed some relationship to the first vegetation component (all negative), while two showed some relationship to the second vegetation component (one positive, one negative), and five showed some relationship to the landscape factor measuring forest fragmentation (one positive, four negative). Seven species showed no relationship to any of the three factors. Migratory forest specialists and permanent residents showed relationships to both the first and second vegetation components; all relationships were negative, indicating population declines as the forest became more dominated by oak and maple and less dominated by hemlock, and both groups were more strongly associated with the first component than the second. Early-successional and shrub-layer species, hemlock decline winners, and long-distance migrants all showed negative relationships to both the first vegetation component (indicating lower populations as oak, maple, and total basal area increased) and the landscape factor (indicating lower populations when forest fragmentation was higher); only early-successional and shrub-layer species had a stronger relationship with the landscape factor than with the first vegetation component. Hemlock associates and short-distance migrants only showed a relationship with the first vegetation component; both relationships were negative, again suggesting population declines as the composition of the forest shifted toward increasing oak dominance and maple presence. The first bird ordination axis for this data range was associated with both the first vegetation component and the landscape component, whereas the second ordination axis was only associated with the landscape component (Table 10.).

Table 7. Results of Poisson regression for the 1953-2012 data set. Null Deviance values have 28 degrees of freedom. *QAIC values are included only for models that showed overdispersion. Four-letter codes refer to standardized codes for bird species. MFS refers to migratory forest specialists; ES_SL refers to early-successional and shrub-layer species; H. Associates refers to hemlock associates. H. Decline Winners likewise refers to hemlock decline winners; LDM refers to long-distance migrants; SDM refers to short-distance migrants; PR refers to permanent residents.

Species/Group	Intercept	Veg1	Veg2	Landscape	AICc	Null Deviance	Residual Deviance	QAIC*
REVI	2.463	-0.422	—	-0.290	158.4	50.9	27.9	—
VEER	2.301	—	0.132	—	137.7	18.0	13.4	—
OVEN	1.931	-0.627	0.406	-0.243	147.5	73.6	29.9	—
GRCA	1.958	-0.124	—	—	130.7	20.1	16.7	—
EATO	1.787	-0.389	0.146	—	128.6	46.0	16.9	—
BCCH	1.845	—	0.205	-0.213	132.8	34.0	19.9	—
BAWW	1.537	-0.703	0.353	-0.316	126.6	52.4	19.9	—
TUTI	1.267	0.510	0.349	-0.526	116.8	80.8	22.7	—
WOTH	1.383	-0.353	—	—	118.8	41.9	22.4	—
SCTA	1.155	—	—	—	104.2	16.2	16.2	—
GCFL	1.118	0.337	—	—	101.3	21.2	13.7	—
HOWA	0.404	-1.388	1.142	—	104.7	115.7	30.8	—
BLJA	1.099	—	—	—	103.5	17.2	17.2	—
NOCA	0.871	0.688	—	—	102.5	43.7	24.1	—
HOWR	0.721	-0.648	0.870	—	135	93.8	65.6	57.9
COYE	1.039	—	—	—	99.5	14.6	14.6	—
EAWP	0.816	—	—	-0.278	94.9	20.9	16.2	—
BHCO	0.519	0.851	0.384	—	108.4	62.3	40.8	70.1
WBNU	0.460	0.797	—	—	85	32.9	16.3	—
DOWO	0.194	0.951	—	—	78.5	33.0	15.9	—
MFS	3.700	-0.328	0.062	-0.172	200.4	82.6	30.4	—
ES_SL	3.687	-0.295	0.171	-0.133	208.3	93.3	38.8	138.1
H.Associates	2.161	-0.394	0.329	—	160	80.6	38.5	114.2
H.DeclineWinners	3.916	-0.207	0.053	-0.213	206.4	49.9	30.1	—
LDM	4.043	-0.348	0.100	-0.176	218.1	122.9	38.1	146.6
SDM	3.225	-0.179	0.187	—	191.6	71.6	38.3	128.8
PR	3.141	0.226	0.155	-0.203	187.4	126.2	34.2	140.1

Table 8. Results of Poisson regression for the 1982-2012 data set. Null Deviance values have 21 degrees of freedom. No models were overdispersed so no QAIC values were necessary. See Table 7 caption for explanation of species/group codes.

Species/Group	**Intercept**	**Veg1**	**Veg2**	**Landscape**	**AICc**	**Null Deviance**	**Residual Deviance**
REVI	2.426	—	—	—	106.3	10.4	10.4
VEER	2.621	-0.564	—	—	103.4	12.6	6.7
OVEN	2.817	-2.178	—	—	94.9	57.4	11.6
GRCA	2.068	-0.774	—	-0.362	96	14.9	7.4
EATO	2.034	-0.909	—	—	87.4	14.5	7.4
BCCH	2.367	-0.788	—	—	99	18.5	10.6
BAWW	2.328	-1.964	—	—	82.1	32.4	7.0
TUTI	1.995	-0.710	—	-0.392	94	12.8	5.8
WOTH	1.199	—	—	—	79.8	11.3	11.3
SCTA	1.083	—	—	—	78.2	12.4	12.4
GCFL	1.278	—	—	—	75.6	4.4	4.4
HOWA	-0.526	—	1.354	-0.913	61	41.0	11.3
BLJA	1.068	—	—	—	75.9	10.1	10.1
NOCA	1.266	—	—	—	83.5	14.0	14.0
HOWR	2.392	-4.427	—	—	71.1	71.6	25.4
COYE	1.496	-0.903	—	—	74.9	10.5	6.4
EAWP	0.739	—	—	-0.392	71.3	8.5	5.4
BHCO	1.299	—	—	0.569	89	30.5	25.7
WBNU	0.916	—	—	—	71.6	9.1	9.1
DOWO	0.715	—	-0.258	—	67.7	11.2	7.5
MFS	4.117	-0.937	-0.133	—	143.6	43.2	16.0
ES_SL	4.024	-1.018	—	-0.195	136.8	71.6	9.6
H.Associates	2.939	-1.925	—	—	100.5	57.7	11.8
H.DeclineWinners	4.071	-0.421	—	-0.149	149.7	30.6	15.4
LDM	4.288	-0.801	—	-0.161	151.6	70.8	16.6
SDM	3.642	-1.012	—	—	128.2	55.3	14.0
PR	3.749	-0.705	-0.136	—	134.3	21.5	12.3

Table 9. Results of linear regression for the bird community ordinations from 1953-2012.

Ordination	Intercept	Veg1	Veg2	Landscape	Residual Std Err.	Multiple R^2	Adjusted R^2	F-statistic	p-value	AICc
Ord_1953_1	3.46E-06	-1.08E+00	1.94E-01	-2.70E-01	0.2978 on 25 df	0.901	0.8891	75.84 on 3 and 25 df	1.09E-12	20.3
Ord_1953_2	6.91E-06	__	2.32E-01	__	0.435 on 27 df	0.2272	0.1985	7.937 on 1 and 27 df	8.95E-03	38.9

Table 10. Results of linear regression for the bird community ordinations from 1982-2012.

Ordination	Intercept	Veg1	Veg2	Landscape	Residual Std. Err.	Multiple R^2	Adjusted R^2	F-statistic	p-value	AICc
Ord_1982_1	-1.183	3.075	__	0.700	0.3903 on 19 df	0.8341	0.8167	47.77 on 2 and 19 df	3.87E-08	28.2
Ord_1982_2	0.217	__	__	0.453	0.4011 on 20 df	0.2928	0.2574	8.279 on 1 and 20 df	9.31E-03	27.5

Several differences in results between the 1953-2012 models and the 1982-2012 models are clearly visible. The 1982-2012 data set depends on bird surveys that were more consistently and frequently conducted than the surveys between 1953-1982, so in this sense may be considered more reliable. Additionally, the first vegetation factor in the 1982-2012 data set can be viewed as a representation of shrub cover as well, since the shrub cover data gathered since 1982 are highly correlated with this component. This assumption cannot be made for the full 1953-2012 data set because shrub cover data were not reliably collected before 1982. However, the 1953-2012 data set reflects change over a longer span of time and has a larger sample size, so it may have a higher statistical power. The 1953-2012 regression models were more similar to the trendlines in their correlation scatter plots than the 1982-2012 regression models were to their respective correlation scatter plots. In the results from both data sets, the first vegetation component was almost always the factor with the strongest relationship with bird groups, and was the only factor to be associated in some way (usually negatively) with every habitat and migratory group. This suggests that the strength of this relationship is such that it is visible even over a shorter span of time and a smaller sample size, whereas some of the relationships between bird groups and the hemlock and fragmentation factors were not strong enough to appear in the models for this short-term data set.

Comparison to Statewide Breeding Bird Surveys

When comparing the population trends over time in the Bolleswood Natural Area to the population trends in the state of Connecticut, I primarily focused on how individual species fared at the Arboretum level compared to how they fared at a statewide level instead of whether their overall pattern was increasing, declining, or not significant. Therefore, a species that does not show any significant change in population in the Bolleswood Natural Area but increases in population in the state of Connecticut can be viewed as having done "worse" in the Arboretum than in the state, because the local population did not show the increase experienced by the overall statewide population. If a particular species declines in the Arboretum but does not show an appreciable change at statewide levels, it has likewise done worse in the Arboretum than in the state. Species that increased or declined at both the state and local levels are likely responding to factors outside the scope of the Bolleswood Natural Area (and in these cases, neither level can be said to have done better or worse than the other).

Relationships between time and abundance of species or groups of species (if there were any significant trends over time) in the Bolleswood Natural Area are shown in Table 11. Eight species and every group except hemlock decline winners and permanent residents showed a negative relationship with time, indicating that they have significantly declined in the Bolleswood Natural Area. One species, Downy Woodpecker (*Picoides pubescens*), had a positive association with time, indicating that it has increased significantly in abundance. Information about similar trends of species at the statewide level can be accessed on the CTBirdTrends website of the UCONN Ornithology Research Group (Field and Elphick, 2012).

Table 11. Results of Poisson regression for 1964-2009 data set, using time as the only independent variable. Null Deviance values have 23 degrees of freedom. QAIC values are included only for models that showed overdispersion.

Species/Group	Intercept	Time	AICc	Null Deviance	Residual Deviance	QAIC
REVI	2.371	__	130.9	28.98	28.981	101.7
VEER	2.391	-0.172	114.8	13.07	9.8431	__
OVEN	2.079	-0.632	122	62.76	29.03	95
GRCA	1.998	-0.347	104.2	18.69	9.732	__
EATO	1.808	-0.536	96.3	25.39	7.2376	__
BCCH	1.958	__	116.7	24.65	24.648	__
BAWW	1.667	-0.572	99.1	32.82	14.742	__
TUTI	1.742	__	118.5	35.97	35.967	76.7
WOTH	1.229	__	91.7	17.13	17.127	__
SCTA	1.085	__	85.2	13.60	13.6	__
GCFL	1.265	__	82.3	5.26	5.2563	__
HOWA	0.812	-0.724	87.7	45.64	32.918	61.6
BLJA	1.165	-0.295	86.2	14.43	11.644	__
NOCA	1.166	__	91.2	18.59	18.589	__
HOWR	1.110	-1.060	100	83.91	42.794	55
COYE	1.070	__	82.4	10.83	10.828	__
EAWP	0.829	__	79.2	16.29	16.285	__
BHCO	0.996	__	100.5	37.67	37.668	62.5
WBNU	0.792	__	78.1	14.84	14.844	__
DOWO	0.455	0.399	74	17.13	14.482	__
MFS	3.701	-0.213	171.9	54.20	35.937	108.4
ES_SL	3.749	-0.328	168.7	78.34	32.321	117.7
H.Associates	2.295	-0.604	127.9	67.03	29.054	99.4
H.DeclineWinners	3.899	__	184.6	45.15	45.146	94
LDM	4.058	-0.260	190.6	85.54	46.374	94.3
SDM	3.316	-0.403	145.9	65.61	20.26	__
PR	3.313	__	174.4	49.46	49.46	83.2

Of the twenty species selected for individual analysis, eight showed similar trends at both the local and regional scales over time. Downy Woodpecker (*Picoides pubescens*) increased significantly at both levels, while Eastern Towhee (*Pipilo erythrophthalmus*) and Blue Jay (*Cyanocitta cristata*) declined at both levels, and Scarlet Tanager (*Piranga olivacea*), Great Crested Flycatcher (*Myiarchus crinitus*), Common Yellowthroat (*Geothlypis trichas*), Eastern Wood-Pewee (*Contopus virens*), and Brown-headed Cowbird (*Molothrus ater*) all showed no significant trend at either level.

Twelve species showed different patterns in the Bolleswood Natural Area than in the statewide surveys (Table 12). Red-eyed Vireo (*Vireo olivaceus*), Black-capped Chickadee (*Poecile atricapillus*), Tufted Titmouse (*Baeolophus bicolor*), Northern Cardinal (*Cardinalis cardinalis*), and White-breasted Nuthatch (*Sitta carolinensis*) showed no significant change in the Arboretum but increased in the state of Connecticut. Veery (*Catharus fuscescens*), Ovenbird (*Seiurus aurocapilla*), Gray Catbird (*Dumetella carolinensis*), Black-and-white Warbler (*Mniotilta varia*), and House Wren (*Troglodytes aedon*) declined in the Arboretum but showed no significant change in the state. Hooded Warbler (*Setophaga citrina*) declined in the Arboretum but increased in frequency in the Breeding Bird Survey results. Wood Thrush (*Hylocichla mustelina*) showed no significant change in the Arboretum but declined statewide. Overall, eleven out of twelve of the species with differing patterns at the local and state levels fared worse in the Bolleswood Natural Area than in the state of Connecticut as a whole.

Of the twelve species that differed, four are migratory forest specialists; three of these species did worse in the Arboretum than in the state, and one (Wood Thrush) did better in the Arboretum. Five species are early-successional or shrub layer species, all of which did worse in the Arboretum than in the state. One species (Ovenbird) is a hemlock associate, and did worse in the Arboretum than in the state as a whole. Six species are hemlock decline winners, and all but one (Wood Thrush) fared worse in the Arboretum than in the state. Six species are long-distance migrants, and again, all but one (Wood Thrush) did worse in the Arboretum. Two species are short-distance migrants, both of which did worse in the Arboretum than in state. Four species are permanent residents; all of them did worse in the Arboretum than in the state of Connecticut as a whole.

Table 12. Comparisons between population trends in Bolleswood Natural Area and the Breeding Bird Surveys for Connecticut for those species that showed different trends at the two spatial levels. A status of "worse" indicates that the species either declined in the BNA while maintaining or increasing its population statewide, or that the species did not undergo a significant change in population in the Arboretum while its statewide population increased. Only one species, Wood Thrush, received a "better" status, indicating that its population within the BNA has not changed appreciably despite the species' statewide decline.

Species	**Status in BNA Compared to State-wide Trend**	**Presumed Habitat Specialty (if any)**	**Migratory Pattern**
Red-eyed Vireo	Worse	Forest specialist, Hemlock Decline Winner	Long-distance migrant
Black-capped Chickadee	Worse	—	Permanent resident
Tufted Titmouse	Worse	Hemlock Decline Winner	Permanent resident
Northern Cardinal	Worse	Early-Successional/Shrub Layer	Permanent resident
White-breasted Nuthatch	Worse	Hemlock Decline Winner	Permanent resident
Veery	Worse	Early-Successional/Shrub-layer, Hemlock Decline Winner	Long-distance migrant
Ovenbird	Worse	Forest specialist, Hemlock Associate	Long-distance migrant
Gray Catbird	Worse	Early-Successional/Shrub-Layer	Short-distance migrant
Black-and-White Warbler	Worse	Forest Specialist	Long-distance migrant
House Wren	Worse	Early-Succesional/Shrub-Layer	Short-distance migrant
Wood Thrush	Better	Forest Specialist, Hemlock Decline Winner	Long-distance migrant
Hooded Warbler	Worse	Early-Successional/Shrub-Layer, Hemlock Decline Winner	Long-distance migrant

Discussion

The picture that emerges from this analysis includes two secondary factors, forest fragmentation in the surrounding landscape and the decline of the eastern hemlock, whose associations with the bird community are noticeable but not especially powerful, and one main factor that encompasses many vegetative variables and has a more profound relationship on the bird community and groups within it. As the secondary factors are relatively straightforward and showed expected patterns, I shall address them first before moving on to the more complex factor that has stronger explanatory power for the decline of the birds in the Bolleswood Natural Area.

The Influence of the Landscape

The factor that measured forest fragmentation was not the strongest factor associated with bird species and groups, particularly in the years after 1982, but nevertheless produced a significant and expected response in many cases. All of the significant relationships between bird groups and the landscape principal component factor were negative, indicating that increasing forest fragmentation has a negative impact on bird abundance. This is consistent with the literature, as previous research has revealed higher predation and brood parasitism rates in highly fragmented landscapes (Thompson et al., 2002).

Many prior studies have used percent forest cover as a surrogate measure for fragmentation (Thompson et al., 2002). However, this measure would not distinguish between a landscape with one large forest patch and many small forest patches if the total percent cover was the same. My forest fragmentation index was based on forest area, the number of forest patches, and the average patch size. As a result, I was able to detect changes in fragmentation even though the net forest area did not change substantially in the area surrounding the Arboretum. The resulting relationships with bird species and groups, therefore, may be a response to changes in the division and layout of forest cover, not simply the amount of cover.

Butcher et al. (1981) found a significant association between habitat specialization and population changes in response to forest fragmentation in the Bolleswood Natural Area, and asserted that species who required forest interior habitat were more sensitive to fragmentation impacts. The migratory forest specialists in my study showed a negative association with fragmentation in the 1953-2012 data set, although this relationship was not as strong as for some of the other habitat groups; there was no significant relationship between the migratory forest specialists and the landscape factor for the 1982-2012 analysis. Askins and Philbrick (1987), working with data from the same study area, suggested that the decrease in bird abundance during the 1970s and subsequent increase during the 1980s was associated with a corresponding decrease and then increase in forest cover in the area within 2 km of the central point of the Bolleswood Natural Area. My analysis of the landscape forest cover from 1951-1970 was conducted using similar aerial photographs examined at a larger scale (1:10,000) than those used by Askins and Philbrick (1:12,000 – 1:20,000), and did not show the substantial decrease in forest area during this time period measured in their study, even when adjusted to cover the exact same zone. However, as mentioned earlier, the average size of patches decreased during this time and the number of forest patches increased. It is possible that the GIS technology used in my analysis and the scale at which I examined the aerial photographs allowed me to count forest patches that were too small to recognize using the methods of Askins and Philbrick, who cut out outlines of forest patches from tiled photographs and weighed the pieces to estimate area. My overall forest cover area measurements did not change significantly because forest losses due to development were mostly offset by small clearings growing into small forest patches; Askins and Philbrick's analysis might have captured the losses of larger areas but not the appearance of smaller re-growth. Additionally, the GIS technology used in my study may have allowed me to determine the identity of blurry patches more easily because overlaying GIS layers on top of each other can provide multiple ways of examining the same area. Both the approach used by Askins and Philbrick and my approach are also naturally subject to classification and positional errors, which may influence the degree to which our results differ.

The fact that changes in the bird populations were associated with both the forest cover measurements used by Askins and Philbrick (1987) and in many cases with my landscape factor (which primarily reflected the number and average size of patches and only slightly reflected total forest cover) suggests that bird populations respond to the division and size of forest patches, rather than the net area of forest cover in a given area. The small forest patches re-growing from small clearings, therefore, did not suit the bird community's needs as much as larger patches. Thus my results support Butcher et al.'s (1981) assertion that "large preserves are essential if species are to be saved."

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). Brown-headed Cowbird, a common brood parasite species, has been regularly observed in the Bolleswood Natural Area since

1982, and was the only species shown to have a positive relationship with the landscape factor measuring forest fragmentation in this study. Furthermore, the landscape factor was the only variable that registered a significant relationship with Brown-headed Cowbird abundances, suggesting that this species' presence depended more upon the level of forest fragmentation in a region than the habitat quality within the study site.

The Brown-headed Cowbird's ecological role has implications for the other bird species in the Bolleswood Natural Area as well, even those that did not show a significant relationship to the landscape factor. Though the abundance of mating pairs in these species may not be directly related to forest fragmentation, they are likely to be at greater risk of parasitism from cowbirds and may therefore have lower reproductive success. Likewise, nest predators such as raccoons and opossums are most common in highly fragmented landscapes, increasing the threat of reproductive failure (Thompson et al., 2002). This increased vulnerability may not necessarily be reflected in the abundance of territories in this study (which are recognized by songs from adult birds), although higher nest failure may cause some birds to not return to the study site in subsequent years and may affect the rate of settlement at the site by young birds.

The results of the Poisson regression make it clear that the level of forest fragmentation has not been the major driving force behind population changes for most of the species or groups of species over the entire time period covered in this study. Furthermore, although the 1970s were characterized by increased levels of forest fragmentation around the Bolleswood Natural Area (along with a drop in population for all the groups studied here), the forest around the Arboretum has for the most part been becoming less fragmented since the 1980s. 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. At the time of the 1987 analysis by Askins and Philbrick, the rebound in bird abundances in the 1980s appeared to be linked to the forest becoming less fragmented. The more recent data, however, does not show the continuation of this trend. Nearly all the groups of birds have shown a net decline since the 1980s, suggesting that some negative change has outweighed the potential gains from the landscape factor.

Impact of the Eastern Hemlock Decline

The hemlock woolly adelgid's effect was severe in the Bolleswood Natural Area, and the eastern hemlock population has dropped dramatically since the adelgid's arrival. Although the hemlock was previously the most dominant species in the forest canopy in terms of stem density, basal area, and frequency, there were very few surviving hemlocks in the Bolleswood Natural Area by 2002 (Small et al., 2005). Consequently, shrub species increased in abundance and richness, responding to the more open overstory and increased sunlight. One might expect certain predictable changes from the bird community in response to these vegetation changes, such as a decline in hemlock associate species, and an increase in species that thrive under open canopies and in dense shrub layers. Instead, every group of species in the 1953-2012 analysis showed a positive relationship with the second vegetation principal component, which is associated with increasing hemlock basal area, suggesting that they have suffered adverse effects from the hemlock decline.

Not surprisingly, the hemlock associates group, which was the smallest group tested in this analysis, showed the strongest association with this component in the 1953-2012 models, rising (albeit irregularly) in abundance as hemlock became increasingly dominant in the forest canopy prior to the adelgid's arrival. This group has been declining steadily since the 1980s, and three out of five of its members – Acadian Flycatcher, Black-throated Green Warbler, and Hermit Thrush – appear to have vanished from the Bolleswood Natural Area altogether. In recent years, Ovenbird has been present at only a fraction of its previous abundance, while Louisiana Waterthrush has maintained a consistent low-level presence of no more than two territories a year. Although the 1982-2012 models did not reflect a significant relationship between the hemlock associates group and eastern hemlock basal area, these data covered a shorter span of years and included fewer surveys; additionally, the patterns of the first two vegetation factors are negatively correlated for these years, so much of the variation may be reflected in the first factor. The 1953-2012 models therefore provide a more reliable long-term picture of the hemlock trajectory and response of associated species.

The group of species that I had categorized as potential "hemlock decline winners" showed a very slight positive relationship with the principal component measuring hemlock basal area in the 1953-2012 models, and no relationship at all in the 1982-2012 models. This is a surprising result, given the ecological niches of these species. Flycatchers often perch on exposed snags while looking for food, while species such as Hooded Warbler and Veery benefit from dense shrub layers (DeGraaf and Yamasaki, 2001; Becker et al., 2008). Downy Woodpeckers did show a negative relationship with the second principal component factor in the 1982-2012 model, indicating that they are more common in the years with lower hemlock basal area, but were the only species to do so. Woodpeckers benefit from standing dead trees, which provide good sites for excavating cavities and foraging (Becker et al., 2008). Hemlock decline winners as a group tended to decrease during the 1980s and 1990s, but have been on the increase since the survey in 2002. Although the hemlock woolly adelgid arrived in the Bolleswood Natural Area in 1987, mortality did not begin to increase until after 1992, which may explain the delayed response of this bird group. Further surveys in future years may reveal a continuing upward trend, which might produce a significant inverse relationship between hemlock basal area and the abundance of hemlock decline winners in a future study with a larger sample size.

One species whose population trajectory belied its hypothesized inclusion in the hemlock decline winner category was the Hooded Warbler. Interestingly, Hooded Warblers showed a relatively strong positive relationship with the component measuring hemlock basal area in the 1982-2012 models. This species' preference for dense shrub layers would suggest that its relationship with hemlocks should be an inverse one, as its abundance should increase as hemlock decreases and shrub cover grows denser. The abundance pattern of this species through time in the Bolleswood Natural Area reveals a peak of 17 recorded territories in the 1959, at which point hemlock basal area in the forest was still relatively low, followed by a plummet in the 1960s and 1970s, and then a slight increase in the late 1980s and early 1990s (right at the time the hemlocks were beginning to die en masse). However, the species has not been observed in the Bolleswood Natural Area since 1997, even as hemlock mortality has worsened and shrub cover has increased.

Potential explanations for this phenomenon include the possibility that an external factor has been adversely impacting this species' population on a scale larger than the Bolleswood Natural Area, leading to an overall decline even though the habitat in the Arboretum is seemingly improving for Hooded Warblers. However, no such decline is evident in the results of the Breeding Bird Survey in Connecticut since 1966, which indicate that Hooded Warblers have increased in the state, particularly after 1986 (Field and Elphick, 2012). Another possibility is that the canopy gaps caused by the decline of the hemlocks are in some way less suitable habitat for Hooded Warblers than canopy gaps in hardwood stands. Hooded Warblers at other sites are typically found in deciduous forests with canopies dominated by maple, beech, or oak, although hemlock is also sometimes present; these warblers often inhabit selectively logged forests due to the regular creation of canopy gaps (Chiver et al., 2011). The distribution of hemlocks and hardwoods in the Arboretum forest is not uniform, as Goodwin and Niering illustrated in their survey of the vegetation types in the Bolleswood Natural Area (1962). As the forest in the Bolleswood Natural Area matures over time in the absence of any logging, the basal area of hardwoods such as oaks and maples has increased, indicating that the canopy in the hardwood sections of the site is becoming increasingly closed. The increase in shrub cover in the Bolleswood Natural Area may therefore be primarily localized to dying hemlock stands, which may not be as attractive to Hooded Warblers. Additionally, Small et al. (2005) noted that some of the shrub species sprouting in the canopy gaps left by dying hemlock are invasive plant species, such as *Berberis thunbergii*, *Celastrus orbiculatus*, and *Lonicera japonica*, which were not present in the Bolleswood Natural Area prior to the hemlock decline. If the case of the Hooded Warbler is any indication, it seems that the ecological changes brought about by the decline of the eastern hemlock in the Bolleswood Natural Area, which might have been expected to benefit shrub-layer birds at the expense of mature-forest specialists, may in fact produce more nuanced and sometimes detrimental effects on shrub-layer species as well.

The groups of species tested in the 1953-2012 set of regression models showed a universally positive response to the second vegetation principal component, although the relationships for migratory forest specialists and hemlock decline winners were very slight. This suggests that all of these groups were faring better during the years in which live hemlock trees were more prevalent (or at least present) in the Bolleswood Natural Area, which does not bode well for bird abundances in a future in which the hemlock woolly adelgid continues to spread. Although the hemlock principal component was not the factor with the strongest influence on any of the species groups (including the hemlock associates), its universal relevance in the 1953-2012 analysis suggests that it (or a factor that co-varies with it) is nonetheless important as a secondary factor that has the potential to exacerbate declines caused by other variables.

Untangling the First Vegetation Principal Component: Declines Over Time

The results of the Poisson regression suggest that the first vegetation principal component – which is linked to basal areas of oak and maple, as well as total basal area, in addition to being highly correlated with time overall and shrub cover since 1982 – is the most significant predictor for every group of species, although not every individual species. These groups of species, however, have not been responding to this vegetation factor in the way that one might expect. I had anticipated a positive relationship for this factor for most of the bird groups studied – presumably, migratory forest specialists should benefit from the expansion of hardwood basal area over time, while early-successional and shrub-layer species, even though they require more open canopies, might find refuge in the increasing shrub cover in the gaps left by the dying hemlocks. 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 significant dynamic influencing specialist and generalist species in Mediterranean forests, noting that older forests tend to have a more complex vertical structure, which may provide better habitat for forest specialist species. Johnston and Odum (1956) suggested that increasing ecological age in a forest tends to lead to an increase in bird population density in forested regions with sufficient moisture.

The actual population trends of the species groups in the Bolleswood Natural Area, however, paint a far more worrisome picture. Total abundance of birds and abundance of most of the major species groups, whether categorized by habitat preference or migratory pattern, have sharply declined from a peak in the early 1980s, even as the forest has continued to mature.

Additionally, although it may appear as though permanent residents are faring better than the other groups, it should be noted that this group's population pattern has been inflated by the arrival of several species that did not previously inhabit the Bolleswood Natural Area due to northward expansion in these species' geographical ranges. Most notable among these are the Northern Cardinal, which was first observed in 1964 but did not show a strong presence until 1982, and the Tufted Titmouse, which arrived in 1976. The number of species in this group has therefore increased since the start of the bird surveys in 1953, and therefore the fact that the group's total abundance has not shown the same sharp decrease over time as most of the other groups is not as reassuring as it first appears. Additionally, Black-capped Chickadee, Tufted Titmouse, Northern Cardinal, and White-breasted Nuthatch, all of which are permanent residents, are doing worse in the Bolleswood Natural Area than in the state of Connecticut as a whole. This group should therefore not be exempted from conservation concerns. Many of the species in this group, and the other migratory groupings, are also included in the categories based on habitat preference, two of which – migratory forest specialists and early-successional/shrub-layer species – I will examine in detail.

The surprising results of the regression for local vegetation variables on the local populations of birds in the Bolleswood Natural Area makes it especially crucial to consult regional trends in forest bird population, as the birds of the Arboretum may be responding to factors beyond the boundaries of the Arboretum or the analyzed buffer zone. The results of the Breeding Bird Surveys in the state of Connecticut therefore shed some light on the matter and help to highlight which species might be showing population trends particular to the Bolleswood Natural Area site, and which species might simply be reflecting wider trends. Of the twenty species selected for individual analysis, twelve showed different population trends in the Arboretum than in the state of Connecticut; of these twelve, eleven species fared “worse” in the Arboretum than the state. This suggests that at least part of the observed decline in many species and species groups in the Bolleswood Natural Area is due to local factors, and is not simply a reflection of the species’ overall trajectory through time.

Untangling the First Vegetation Principal Component: The State of the Shrub-Layer

There were five early-successional or shrub-layer species that showed a different pattern in the Bolleswood Natural Area than in the state, and all five did worse in the Bolleswood Natural Area. This supports the previous conclusion from the specific case study of the Hooded Warbler that the shrub layer in the Bolleswood Natural Area, even though it has been increasing in cover since 1982, is not of adequate quality to sustain healthy populations of shrub-layer bird species. The introduction of new invasive shrub species such as *Berberis thunbergii*, *Celastrus orbiculatus*, and *Lonicera japonica* in the years since the hemlock decline, as described in Small et al. (2005), may be contributing to this inferior quality. Therefore, even though shrub species diversity as measured by Simpson's Inverse Diversity Index did show a slight increase in the years immediately after hemlock mortality became severe, there is no guarantee the increased richness created improved habitat. Additionally, shrub diversity in 2012 was lower than in 2002, suggesting that even this slight increase in richness was temporary. However, only 3.1% of the forest plots included in the study site contained an invasive shrub or vine in 2012 (although areas outside the forest are more heavily invaded), so their role in the shrub layer is likely not a dominant one.

Veery is another shrub-layer species that showed a significant, although slight, negative trend over time in the Bolleswood Natural Area but no such decline at the state level. Most of this decline, measured since 1964, has occurred in the years after 1982. This species prefers damp forests with dense understories, often in slightly disturbed habitats (Bevier et al., 2005), which suggests that the Bolleswood Natural Area should be increasingly suitable habitat, as many of the dying hemlock stands were in damp portions of the site and so the subsequent increase in shrub and sapling cover has led to denser understories in these areas since the 1990s (Small et al. 2005). Nevertheless, Veery populations are on the decline.

These unexpected population trends of species like Hooded Warbler and Veery, as well as the overall decline of the early-successional and shrub-layer species group, suggests that closer attention ought to be paid to the forest understory. It should be noted that the Bolleswood Natural Area is currently fenced to keep deer out of the forest, although this was not always true, so the overbrowsing that is common in many sites in the northeastern United States is likely not a major culprit here. Although data on percent cover of shrubs is not directly available for the years prior to 1982, the sapling density data listed in Small et al. (2005) provides some indication of the condition of the forest understory in the years since 1952. Sapling density decreased steadily from 1952 to 1982 at the same time as basal area of the dominant tree species increased. As increasing canopy cover would have presumably shaded out the understory, the density of the shrub layer likely followed the same trajectory as the saplings and decreased for most of this time period. Data on shrub frequency supports this conjecture. It is likely, therefore, that shrub cover in the Bolleswood Natural Area was on the decline from 1952 to 1982, and then soon afterward began to increase as hemlock mortality began and progressed. This would explain why shrub cover measured after 1982 was correlated so highly with the first vegetation principal component, which also tended to increase over this time period. Shrub frequency data suggests that despite this increase, the forest understory has not regained the density originally present in 1952, when the forest was recovering from the massive damage of a hurricane in 1938. It may therefore not be reasonable to expect shrub-layer birds to return to the Bolleswood Natural Area in their original numbers. Their steepening decline, however, is still mysterious in light of the shrub cover trends since 1982.

Because structural factors of density and frequency alone do not appear to satisfactorily explain these population trends, floristics may offer an explanation. A typical Hooded Warbler population in Pennsylvania occupies an understory with *Rubus sp., Prunus* *sp., Ribes cynosbati, Viburnum acerifolium*, and *Lindera benzoin*, whereas a population in southern Ontario likewise inhabits a shrub layer of *Viburnum acerifolium, Rubus sp*., and *Fraxinus, Prunus*, and *Acer* saplings (Chiver et al., 2011). Similarly, Veery territories in Wisconsin are found in dense shrub layers of *Corylus, Alnus, Viburnum, Cornus, Rubus, Vaccinium, Lonicera, Amelanchier, Salix,* and *Myrica* species (Bevier, 2005). 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 Bolleswood Natural Area at the start of the plant surveys, they have nearly all declined since, even as shrub cover in general has increased since 1982. Understory species on the rise include vine species like *Parthenocissus quinquefolia* and shrubs tolerant of damp soil like *Rhododendron periclymenoides,* as well as the invasive species mentioned earlier*,* but these species are not mentioned as much in the scientific literature as being associated with these shrub-layer birds.

Therefore, although structural factors like shrub cover and frequency appear to be trending in increasing directions, harkening back to an earlier time in the Arboretum's history when the understory was thicker, the composition of this understory is not the same as it used to be. Most of the bird species selected for individual analysis are insectivores, and floristic composition of the shrub layer can influence insect abundance and diversity. Butterfly richness and abundance in forests in northern Georgia was improved by the removal of an invasive privet species, and Hanula and Horn (2011) concluded that the insects were responding primarily to the amount of non-privet plant cover (a floristic component) rather than the increased openness of the canopy and greater availability of sunlight (structural components). A similar phenomenon may be at work in the Bolleswood Natural Area.

Untangling the First Vegetation Principal Component: Forest Maturation And Diversity

Migratory forest specialists, however, are likely not responding strongly to the changed composition of the understory, as they are often found in mature forests with closed canopies that have shaded out much of the shrub layer. However, the decline of this group suggests that the gradual maturation of the forest in the Bolleswood Natural Area, which I originally hypothesized would be a positive factor, may not actually be as favorable for bird populations as previously believed. In the absence of external factors driving down the population, I had assumed that forest specialist species would increase in abundance as the basal area of the forest increased and the canopy filled in. This assumption may need to be revisited in light of the results of this study.

The decline of the hemlocks likely complicated this maturation somewhat, as it did impact the total basal area, but the strength of the relationship between hemlock basal area and the bird abundances as measured by the Poisson regression models is for the most part not as strong as the other factors tested. Additionally, oak and red maple basal area has increased in recent decades, filling in some of the space left by the hemlocks so that the total basal area since the arrival of the woolly adelgid has only dipped slightly even as hemlock basal area plummeted. The strong associations between oak basal area, red maple basal area, and the first vegetation principal component make it clear that these hardwoods have been increasing their dominance in the Bolleswood Natural Area; oak species in particular now very much dominate the canopy. These shifts suggest that structurally – in terms of total basal area and thus likely canopy cover – the forest has mostly maintained a trend toward increased maturation, at least in the hardwood sections of the site.

The first vegetation principal component is a complex factor taking several vegetation variables into account. Examining these variables more closely reveals not only which aspects of the forest have increased over time, but also what has been lost, which may help to account for the collective decline of so many bird species and groups. The first principal component was strongly and negatively linked to tree diversity and somewhat negatively linked to shrub diversity, suggesting that the forest in the Bolleswood Natural Area has become more homogenous over time. This component was also strongly and negatively linked to basal area of yellow birch; data on tree species frequency confirms that yellow birch, despite a brief proliferation in 2002, has strongly declined in the forest overall.

As mentioned in the introduction, diversity of woody species in hardwood forests has been positively correlated with abundance and diversity of birds in previous studies (Twedt et al., 1999). Diversity of migratory forest specialists in the Bolleswood Natural Area showed a slight negative correlation with tree species diversity, which does not fit with this pattern. This correlation, however, is just barely significant and may be influenced by the other changes in both the forest and the bird community over the years, so this result does not necessarily mean vegetation diversity has had an impact on bird diversity at this site. Furthermore, abundance of this group as well as most of the others has dropped sharply as tree species diversity has decreased. The presence of a variety of trees, even those that never become dominant in the canopy, provides 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 tree most strongly preferred by foraging insectivores in Illinois floodplain forests 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 species, these rare but good-quality trees are likely to have less and less of a presence in the forest.

One candidate species for such a role is yellow birch. Previous research in the Hubbard Brook Experimental Forest in New Hampshire identified yellow birch as a particularly important resource for birds, as this species supported more Lepidoptera larvae than other tree species in the forest, leading several bird species to forage on yellow birch trees more frequently than would be expected based on the abundance of this species in the forest (Holmes et al., 1979). Lepidoptera larvae are a crucial food source for many species of insectivorous birds, including migratory forest specialist species that have shown declines in the Arboretum such as Black-and-White Warbler (Kricher, 1995). The strong negative relationship between yellow birch and the first vegetation principal component makes it clear that yellow birch has been declining at the same time as the majority of the bird groups studied. Although this is likely not the full story, as some insectivorous species are not faring worse in the Arboretum than in the state, it should nevertheless be flagged as a subject for further investigation.

In addition to yellow birch, the Bolleswood Natural Area has also undergone steep declines in several tree species that used to play non-dominant roles in the canopy, such as gray birch (*Betula populifolia*), hickories (*Carya sp.*), and flowering dogwood (*Cornus* *florida*). In this respect, the migratory forest specialists might be facing a situation similar to the shrub-layer species that cannot thrive in a shrub layer with the wrong species of shrubs, which might explain the simultaneous declines of both groups of birds despite their different structural habitat preferences.

Additional Areas for Research

Further investigations into the relationship between vegetative diversity and bird diversity would be worthwhile, as my preliminary comparison of migratory forest specialist diversity and tree diversity did not yield results as strong as my comparisons between vegetation factors and bird abundance.

Future research projects on population trends of invertebrates in the Bolleswood Natural Area, and particularly on relationships between invertebrate abundance and the presence of particular tree species, would shed more light on the possibility that problems with food sources are contributing to avian decline.

In addition to the role of food resources, larger-scale fragmentation may be a factor in need of further study. The landscape patterns noted in this study were similar at the 1-km, 2-km, and 5-km ranges, although only the 2-km values were used in the regression models. It is possible that the Arboretum birds are responding to changes in land cover over wider scales. Lloyd et al. (2005) found that land cover over a 20-km radius scale had more explanatory power for patterns in nest parasitism than edge or patch effects for 17 species vulnerable to parasitism from cowbirds. Likewise, 25 species in the same study showed an association between developed land within a 10-km radius and the rate of nest predation. Further research repeating these regression models using land cover variables over wider scales may therefore indicate whether the birds of the Bolleswood Natural Area show a similar relationship.

Conclusion and Conservation Implications

While many of the species present in the Bolleswood Natural Area are following similar population trajectories at this study site as in the rest of the state, the fact that eleven out of twelve of the species with differing trends are faring worse in the Arboretum than in Connecticut as a whole suggests that some local factor or factors have caused the Bolleswood Natural Area to be of inferior habitat quality for the bird community. 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 the migratory forest specialists nor the early-successional and shrub-layer species. The loss of eastern hemlock has negatively impacted most of the groups studied, although hemlocks have been declining across southern New England so this variable does not explain why certain population trends in the Bolleswood Natural Area are worse than in the state of Connecticut. The 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 overall vegetation diversity, as well as the particular losses of specific tree and shrub species that are especially utilized by birds, has emerged from this analysis as a possible contributing factor to the downward population trends.

Some of the results of this study lend themselves easily to clear conservation applications. The negative relationships between bird groups and forest fragmentation highlight the value of large preserves with small edge to interior ratios, especially because forest fragmentation as measured in this project was largely a function of number of patches and patch size rather than total forested area. The positive relationship between eastern hemlock and groups of bird species, especially but not only hemlock associates, likewise emphasizes the importance of this tree species and provides motivation for continued research and funding into control methods for the hemlock woolly adelgid, such as biological control using lady beetles (Askins, 2014).

As extensive damage to hemlock populations has already occurred, conservationists must also be prepared to salvage forest ecosystems in the wake of hemlock mortality. Careful attention must be paid to which tree and shrub species are filling in the gaps left by dying hemlock stands. This project suggests that the vegetation composition of the Bolleswood Natural Area post-hemlock-mortality has shifted towards a more homogenous array of species that may provide habitat of lesser quality than the habitat that existed in the early decades of the preserve's creation. These results highlight the importance of floristics in determining habitat quality for bird populations.

As a final note, this case study may also call into question the long-term value of the hands-off approach to maintaining wildlife preserves. The Bolleswood Natural Area has been left largely unmanaged since its creation. However, the long-term preservation of the area and protection from human interference has apparently not ensured the stable persistence of its avian populations. If this wait-and-watch approach is maintained and the vegetation patterns of the forest continue to shift towards increasing dominance of a few species, it seems likely that the population trajectories of most of the bird species and groups in the Bolleswood Natural Area will continue to decline.

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