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#### THE ECOLOGICAL VALUE OF SPRUCE PLANTATIONS IN MASSACHUSETTS

A Thesis Presented by

CALVIN RITTER

Submitted to the Graduate School of the

University of Massachusetts Amherst in partial fulfillment

of the requirements for the degree of

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May 2020

Environmental Conservation

#### THE ECOLOGICAL VALUE OF SPRUCE PLANTATIONS IN MASSACHUSETTS

A Thesis Presented

by

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#### ABSTRACT

# THE ECOLOGOCAL VALUE OF SPRUCE PLANTATIONS IN MASSACHUSETTS MAY 2020 CALVIN RITTER, B.S., UNIVERSITY OF MASSACHUSETTS AMHERST M.S., UNIVERSITY OF MASSACHUSETTS AMHERST Directed By: Professor David I. King & Professor Stephen DeStefano

The establishment of monoculture plantations of exotic tree species is common practice for supplementing native timber stocks. Such plantations typically provide inferior habitat for wildlife compared to native forest, which may result in a net reduction in biodiversity. However, some studies report that plantations may increase net biodiversity at the landscape scale by introducing novel habitats or supplementing existing natural forests. Using point count surveys, I examined six mature Norway spruce (*Picea abies*) plantations in western Massachusetts in 2016 and 2017 to evaluate bird use of these habitats relative to native forest stands. Count data were analyzed using N-mixture models to correct for imperfect detection, providing more accurate estimates of true abundance. Our findings showed that overall species richness for spruce plantations was not significantly lower than that of native forest habitats. Redbreasted nuthatch (*Sitta canadensis*) and golden-crowned kinglet (*Regulus satrapa*) were most abundant in spruce plantations. Conifer dependent species such as Blackburnian warbler (*Setophaga fusca*) and brown creeper (*Certhia americana*), were

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significantly more abundant in spruce plantations relative to native deciduous, hemlock, and mixed stands. Species that heavily associate with broadleaf habitat were rarely observed in spruce plantations. Species that associate with eastern hemlock habitat, such as Blue-headed vireo (*Vireo solitarious*) and black-throated green warbler (*Setophaga virens*) were observed using spruce plantations at similar levels as eastern hemlock stands. These results demonstrate that Norway spruce plantations can provide suitable habitat for native species associated with conifers, which is significant given projected continued decline of eastern hemlock in response to the hemlock wooly adelgid (*Adelges tsugae*). Although large-scale conversion of native forest to plantations would likely lead to a loss in biodiversity, land managers could be justified in allowing small-scale plantations to persist without suffering negative impacts to native biodiversity.

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#### **CHAPTER 1**

#### PLANTATIONS AND BIODIVERSITY

As global demand for timber rises and humans expand into previously undeveloped areas, the worlds' forested lands become increasingly imperiled. Deforestation rates have increased steadily over recent decades leading to large losses in the amount of forested land cover worldwide. Recent global assessments estimate this net loss of forest to be 0.13% annually (FAO 2015). Natural forests, those that regenerated without human planting and therefore represent a closer approximation of true native ecosystems, are faced with the highest rates of deforestation, which currently amounts to 0.24% annually (FAO 2015). Reforestation efforts help mitigate the loss of forested land cover; however, a majority of reforestation comes in the form of planted and managed forests. Plantations, which are planted forests characterized by evenly spaced, single aged trees consisting of one or two species, are widespread and often differ dramatically from natural forests in terms of structure, species composition, and disturbance regimes (Hanowski et al. 1997, Carnus et al. 2006, Demarais et al. 2017). The loss of natural forests has widespread implications for wildlife species that depend on the resources and habitat they provide, yet the timber industry continues to adopt plantation production due to its capacity for higher resource production and efficiency (Noormets et al. 2015). As natural forests decline, planted forests are increasing at a rate of 1.84% annually (FAO2015), meaning that planted forests, including plantations, become more prevalent each year and account for a higher

percentage of total forested area worldwide (Keenan et al. 2015*a*). This trend of increased reliance on managed plantations is expected to increase over time (Alcamo et al. 2005, Wade et al. 2019). Remaining tracts of natural forests will become smaller and more fragmented (McGill et al. 2015) and thus plantations will make up a progressively larger proportion of the ranges of native wildlife species. Therefore, understanding the dynamics between plantations and wildlife is of great importance for the preservation of biodiversity in working forests.

With an estimated 50% of all terrestrial plant and animal species relying on forests for shelter or other resources (Hassan et al. 2005), preserving healthy forested areas is vital to maintaining biodiversity. As these ecosystems are removed and replaced with similar, yet functionally different plantations, many of the characteristics required to sustain plant and animal species may become inferior or absent all together. Forests consisting of diverse assemblages of native species with complex vegetation structures offer food, cover, breeding habitat, and other resources for a broad range of species (Macarthur and Macarthur 1961, Spies 1998). However, plantations are often characterized by their lack of structural and compositional diversity which has been shown to have a negative effect on biodiversity when directly compared to natural forests (Pawson et al. 2013, Castaño-Villa et al. 2019). The unique characteristics of plantations that are most commonly identified as being detrimental to biodiversity are homogenous age structure, increased disturbance regimes, high tree densities, reliance on exotic tree species, monoculture plantings, and lack of diverse understory structure and composition (Brockerhoff et al. 2009).

Plantations, especially those established for timber production, historically consisted of even-aged tracts of trees planted in dense, organized arrangements (Food and Agricultural Organization 2020). Once trees mature, they are clear-cut, and the process begins again (Lindenmayer and Franklin 2002). This system is ideal for maximizing the amount of wood mass that can be harvested but comes at the cost of eliminating any heterogeneity in age or species structure (Lindenmayer and Franklin 2002). Naturally regenerating forests undergo a constant cycling of older trees dying off and new seedlings replacing them. This dynamic age structure provides a diverse suite of habitat characteristics for wildlife (McKelvey 2015) such as saplings and young trees providing foraging for deer and sub-canopy cover for birds, and old and dead trees providing nesting cavities for woodpeckers. A plantation that only has trees of a single age class is only likely to support species that utilize that specific seral stage. In a comparison of even and uneven-aged planting of pine in Texas, Thill and Koerth (2005) observed that stands with more diverse age structure supported similar to higher bird abundance, species richness, and diversity. Even aged pine plantations in Florida, USA were shown to support birds communities that shifted from primarily grassland species shortly after planting, to shrubland species, and eventually mature forest species, yet at no time did the plantations support communities similar to those of naturally regenerated stands (Repenning and Labisky 1985). A possible explanation for this is that diverse age structures allow for more light penetration to the sub canopy leading to the formation of more complex understory structure (Decocq et al. 2004), a quality known to promote wildlife diversity given many species' affinity for specific structural features

(James and Wamer 1982). Un-even aged silviculture practices have been suggested as a way to offset or mitigate homogenous age structure in plantations in order to promote biodiversity. However, uneven-aged silviculture in plantations still results in the replacement of native tree species with native ones, and their effects on diversity have been mixed (Nolet et al. 2017).

One of the biggest factors that affects a plantation's influence on wildlife biodiversity is the species diversity of the planted trees. Monoculture planting, utilizing a single tree species within a plantation, remains prevalent in production forests (Keenan et al. 2015b) despite concerns of reductions in wildlife diversity (Hartley 2002, Nichols et al. 2006). Similar to even-aged stands, forest monocultures offer heterogenous habitat compared to natural forests which are often a mixture of species. This can negatively impact the number of unique species within a stand as well as their diverse interactions (Castaño-Villa et al. 2014). Monoculture plantations, on average, will support fewer habitat specialized wildlife species when directly compared to both natural mixed stands and polyculture plantations (Carnus et al. 2006, Stephens and Wagner 2007, lezzi et al. 2018) with species exhibiting narrow niche breadth being most impacted (Pryde et al. 2016). The incorporation of broadleaf trees into spruce monocultures in Sweden has been shown to increase stand level diversity of birds by attracting broad-leaf associated species without deterring conifer associated species (Felton et al. 2011). This positive response of interplanting broadleaf trees on biodiversity was also observed in herbaceous plants, lichens, and saproxylic beetles (Felton et al. 2010). Conversion of monoculture to polyculture plantations can have a

broad range of effects including increased light penetration (lezzi et al. 2018), diversification of vertical structure in the subcanopy (Bergner et al. 2015), and greater heterogeneity in herbaceous vegetation (Hartley 2002), all of which have been demonstrated to promote wildlife biodiversity.

In addition to the issue of planting monocultures or polycultures, foresters are also faced with the important decision of whether to utilize exotic or native tree species. This decision has equally significant implications for wildlife, as utilizing exotic trees can drastically reduce the amount habitat and other resources that native wildlife require. Exotic plantations have been widely used for timber production around the world despite criticisms of the potential effects on wildlife (Puettmann et al. 2009). Incorporating exotic trees into an ecosystem, especially as monocultures, introduces novel, and often inferior, habitat for native wildlife that evolved and adapted alongside native tree species and can eliminate and fragment remaining patches of valuable native habitat (Cossalter and Pye-Smith 2003). Previous studies have shown mixed results in terms of the effects exotic plantations can have on wildlife (Lindenmayer and Hobbs 2004). In a review of studies conducted within exotic tree plantations, Stephens and Wagner (2007) identified 10 cases in which plantations exhibited lower biodiversity, 5 studies with no differences, and 8 studies in which plantations supported higher biodiversity relative to nearby natural forests. One common trend is that of all the types of planted forests, exotic monoculture plantations tend to support the lowest levels of biodiversity and species abundances relative to native forest stands (Carlson 1986, Christian et al. 1998). Twedt et al. (1999) concluded that avian species richness,

diversity, and territory abundance were lower in cottonwood plantations when compared to native hardwood stands in southern North America with similar trends reported for hybrid poplar plantations in Minnesota, Wisconsin, and South Dakota (Hanowski et al. 1997). Other taxa have also been shown to experience diminished diversity and abundance in plantations including invertebrates in eucalypt and pine plantations (Ratsirarson et al. 2002) and mammals in pine plantations (lezzi et al. 2018). It should be noted, however, that exotic plantations that are established on already impoverished lands can promote biodiversity by creating forested habitat where it did not previously exist (Stephens and Wagner 2007, Brockerhoff et al. 2009). Another cause for concern is the vulnerability of monocultures to biotic disturbances such as pests and diseases, which could result in large losses of trees due to a lack of genetic variability or resistance within the host trees (Verheyen et al. 2016).

The assertion that plantations support lower species abundances and diversity (Zurita et al. 2006, Barlow et al. 2007) is typically based on a direct comparison to prime natural habitat (Stephens and Wagner 2007). This method of direct comparison, however, is becoming less common in favor of plantations (both native and non-native) that are established on already impoverished lands such as abandoned agricultural fields (Twedt et al. 1999), which can result in suitable habitat in areas that were previously lacking, leading to increased biodiversity at a landscape scale. Monocultures and exotic species can increase landscape level biodiversity when planted in smaller patches and incorporated into a mosaic of natural forests (Herbohn et al. 2000). Even when small amounts of native habitat are lost, a combination of natural and planted

forests can yield higher biodiversity across the landscape than native stands alone (Franklin and Forman 1987, Lindenmayer and Hobbs 2004, Pina et al. 2019) by introducing novel habitat types without removing significant cover of existing habitats (Gjerde and Sætersdal 1997, Donald et al. 1998). In situations where limited connectivity between remnant natural forests is compromised, plantations can act as steppingstones or corridors between fragments (Bett et al. 2016). Another method to promoting landscape level biodiversity within plantations is to allow small patches of natural forest to persist, scattered throughout the plantation in order to offer wildlife supplemental high quality habitat (Zurita et al. 2006, Azhar et al. 2013)

As demonstrated above there are many ways that plantations can be implemented, with varying effects on biodiversity. Although altering age structures, tree species and diversity, landscape characteristics, and management regimes can all have direct impacts on wildlife, they also indirectly effect biodiversity through alteration of forest structure. Variation and diversity in vertical and horizontal vegetation structure are perhaps the most important variables in terms of influencing bird biodiversity within plantation forests (Barlow et al. 2007, Bergner et al. 2015). Managing for variable age structure and precluding the formation of dense monotypic canopies promotes light penetration to the sub-canopy layers and positively influences the development of heterogenous vegetation structure (Barbier et al. 2008). Tree phenology, shade tolerance, and increased disease susceptibility were identified as likely drivers in an a increase in understory species diversity within mixed species stands when compared to monoculture stands in the northeastern United states (Himes and Puettmann 2020).

Understory vegetation structure was systematically removed within pine plantations in Chile, resulting in significant declines in medium-sized mammal abundance (Simonetti et al. 2013). Retention of understory vegetation has also been linked to increased mammal abundances in pine plantations in Argentina (Lantschner et al. 2011), Chile (Saavedra and Simonetti 2005), and Australia (Lindenmayer et al. 1999). Another important consideration in plantation ecology is the management regime being implemented. Plantations that are maintained for high timber yields and have short rotation times will undergo frequent disturbances that will be detrimental to many wildlife species and preclude mature forest structure from developing (Patterson et al. 1995, Carnus et al. 2006). In a study looking at Norway spruce plantations in Europe, Baguette et al. (1994) found that plantations supported impoverished bird communities for the first 30 years after planting, after which species richness reached levels similar to that of surrounding native beech stands. Selective thinning is a common alternative to clearcutting and can increase vegetation diversity in the sub-canopy layer allowing plantations to approach the complexity of natural forests (Jason and Nick 2008, Cheng et al. 2017).

The relationship between plantation forests and biodiversity is complex and dependent on a number of variables. Although early research used the term "green deserts" to describe plantations (Horák et al. 2019), the term has become less accurate as plantation forestry evolved over the past few decades. Shifts towards more sustainable practices have helped mitigate many of the negative impacts of planted forests. Although plantations, especially production forests, rarely exceed natural stands in terms of biodiversity metrics, there are a number of management options available

that can greatly reduce the gap. Additionally, the impact of plantations is better assessed on a broader landscape scale and their value to biodiversity needs to be examined on a case by case basis.

#### **CHAPTER 2**

#### THE ECOLOGOCAL VALUE OF SPRUCE PLANTATIONS IN MASSACHUSETTS

#### 2.1 Introduction

Total forested area has decreased globally over the past decade (FAO 2015). Although some losses are mitigated through reforestation efforts, there remains a net annual loss of 0.13%. Furthermore, natural forests are in decline and most reforestation is achieved through the implementation of planted forests, which are increasing at a rate of 1.84% annually (FAO 2015). This loss of natural forest and subsequent replacement with planted forest has implications for wildlife species that depend on forested habitats. Planted forests, such as plantations, can differ greatly from surrounding natural forests (Carnus et al. 2006) in terms of simplified vegetation structure, vegetation composition, and age structure (Hanowski et al. 1997). Also, production plantations are subjected to disruptive management regimes such as clearcutting and high density planting (Carnus et al. 2006) that negatively affect wildlife (Demarais et al. 2017). Despite the potential adverse effects planted forests can impose on wildlife (Castaño-Villa et al. 2019), timber production and other ecosystem services such as erosion control have historically been the primary motivating factor for the establishment of such plantations, especially those utilizing monocultures and exotic tree species (Brockerhoff et al. 2009, Pawson et al. 2013). However, concerns about unprecedented increases in species decline and extinction rates due primarily to habitat

loss (Groombridge 1992) and climate change (Parmesan et al. 2003) have resulted in the emergence of more sustainable and ecologically conscious forestry practices to better support conservation objectives (Puettmann et al. 2009, D'Amato et al. 2017). Such practices include implementing management regimes that diversify the sub-canopy layers, creating complex vertical and horizontal structure (Dickson and Segelquist 1979, Carnus et al. 2006), relying more heavily on native tree species to support associated native fauna (Castaño-Villa et al. 2019), polyculture planting to provide a wider breadth of habitat niches (Kerr 1999), and integration with the surrounding landscapes to improve connectivity and colonization between native habitat patches (Laurance and Bierregaard 1997, Castaño-Villa et al. 2019). The degree to which biodiversity is impacted can also depend on plantation size, composition, characteristics of adjacent habitat, and the needs of native flora and fauna (Hartley 2002, Quine and Humphrey 2010).

The removal of native forest habitat and subsequent replacement with nonnative or monoculture plantations has been shown to result in an overall net reduction in biodiversity within that stand, but not all plantations involve the large-scale removal of native habitats and their impact on biodiversity is dependent on a number of variables (Stephens and Wagner 2007). For example, monoculture Norway spruce (*Picea abies*) plantations in western Norway were shown to have a positive net effect on landscape-level biodiversity when incorporated into a mosaic of pine stands (Gjerde and Sætersdal 1997, Christian et al. 1998). Humphrey et al. concluded that various nonnative conifer plantations in the United Kingdom provided suitable habitat for many

non-vertebrate and fungal species, resulting in an overall positive contribution to the UK biodiversity action plan (2002).

Norway spruce is a common species used in monoculture plantations across North America due to its fast growth rate and ability to tolerate warmer temperatures and more acidic soils compared to other conifers (Tjoelker et al. 2007). In Massachusetts, where native spruce can be regionally rare or absent, Norway spruce plantations may supplement native forest stands by offering pure coniferous habitat. Norway spruce plantations are characterized by dense canopies of short needle vegetations and shady understories with sparse vegetation. These characteristics are similar to those of habitat provided by eastern hemlock (*Tsuga canadensis*), a conifer native to Massachusetts (DeGraaf and Yamasaki 2001). Eastern hemlock is in steep decline (Paradis et al. 2008) due to the hemlock woolly adelgid (Adelges tsugae), an invasive aphid-like insect, resulting in removal of pure hemlock stands (Small et al. 2016). Furthermore, the effects of climate change are likely to amplify the range and severity of adelgid infestations over the next century (Parker B. L. 1998, Paradis et al. 2008, Ellison et al. 2018), leading to decline in habitat availability for wildlife that use short-leaved conifer species for foraging and nesting (Yamasaki et al. 1999). As hemlock recedes, it is most commonly replaced by birch and other opportunistic deciduous species (Orwig et al. 2002) leading to a net reduction in available conifer habitat.

The ecological value of spruce plantations relative to their surrounding native forested habitats had not been assessed in Massachusetts. Given the idiosyncratic nature of plantations in terms of their contributions to local biodiversity, it is often unclear which actions should be taken to manage them in cases where promoting biodiversity is a priority. Understanding the relative value of a plantation as well as its role in a larger landscape context is necessary for land managers to make informed decisions about these habitats. Furthermore, the value of a particular habitat cannot be entirely described using common metrics like abundance and species richness. Some species may represent a higher level of conservation priority. The Partners in Flight (PIF) bird conservations scores offer a method of calculating conservation values for each bird species based on a suite of population metrics (Partners in Flight 2019), giving land managers a more objective method of comparing the conservation value of differing habitats. Additionally, birds are effective indicators of overall biodiversity due to their diversity, prevalence, and relatively high observability (Butler et al. 2012).

For this study, I was interested in examining the differences in bird compositions among Norway spruce plantations and native forest stands in Massachusetts. My primary objectives were to:

- Determine the bird species characteristic of Norway spruce plantations
- 2) Compare bird abundances and pooled PIF scores among Norway spruce plantations and native cover types in order to assess the role plantations serve in facilitating bird conservation goals within the study area and the region
- Compare bird communities among cover types, with an emphasis on the comparison between Norway spruce plantations and eastern

hemlock stands given the habitat similarities between the two to determine the extent to which Norway spruce could support species typical of hemlock stands in the face of continued hemlock decline.

#### 2.2 Study Area

I conducted my research during the 2016 and 2017 breeding seasons (May to August) at two separate sites in Massachusetts: one within the watershed of the Quabbin reservoir (Fig. 1), and a second at the Beartown State Forest (Fig. 2). The Quabbin watershed is located in central Massachusetts, USA (42.38° N, 72.36° W), is managed by the Massachusetts Department of Conservation and Recreation, Division of Water Supply Protection, and consists of ~ 38,445 ha of hardwood-conifer mixed forests. The second site, Beartown State forest in western Massachusetts (42.21 N, 73.23 W) is managed by the Massachusetts Department of Conservation and Recreation, State Parks and consists of mixed hardwood-conifer forest similar in composition to that found at the Quabbin site. Elevations ranged from approximately 175 – 325m at the Quabbin site, and 400 – 600m at the Beartown site. Nearly all the land within the Quabbin watershed had been formerly cleared for agriculture but was later abandoned and allowed to reforest throughout the late 1800s and early 1900s (Foster 1998). The Quabbin site is protected to maintain water quality within the adjoining reservoir, which was established in the 1930s through the impoundment of the Swift River. The Quabbin site encompassed a network of narrow dirt roads with locked gates to restrict public vehicle access. In addition to smaller trails, Beartown was

also accessible via a limited number of paved roads, which were open to the public. Both sites encompassed three Norway spruce plantations that occurred within a matrix of native forest cover types. It is worth noting that natural regeneration of Norway spruce was not occurring within these plantations and some trees were beginning wo die off naturally.

#### 2.3 Methods

#### 2.3.1 Point Selection

Initial selection of point count locations was made based on forest cover GIS layers provided by the Massachusetts Department of Conservation and Recreation. At the Quabbin site, I selected 150 point count locations (Fig. 1) stratified across five distinct forest cover types (30 points per cover type), which were characterized by dominant tree species, according to GIS data. The five cover type categories were Norway spruce, eastern hemlock, white pine (*Pinus strobus*), deciduous, and coniferdeciduous codominant mix. The planted Norway spruce stands consisted of discrete habitat patches of nearly pure spruce and represented the focal plantation species within the study. Eastern hemlock was of particular interest due to the potential impact of hemlock woolly adelgid on hemlock stands as well as wildlife species that may depend on the habitat these stands provide. Both Norway spruce and eastern hemlock are short-needled conifers that form dense stands, and these structural similarities suggest the potential for Norway spruce to support bird species commonly associated with eastern hemlock (Tingley et al. 2002), which could have increasingly important implications as hemlock habitat continues to decline. White pine stands represent the

most widespread native conifer habitat in the study area and may also have the potential to support hemlock associated species. Deciduous and mixed stands were also included to contrast Norway spruce with other widespread cover types that would likely replace Norway spruce stands in the event they were converted through silviculture. Any additional cover types within the study area were sparse and fragmented and were therefore not included as a sampled cover type. An additional 24 points were selected at the Beartown site (Fig. 2), split evenly between Norway spruce and eastern hemlock. Pine, deciduous, and mixed stands were not sampled at the Beartown site due to time constraints.

All points were established > 50 m from the "edge" of contiguous cover type patches (according to the GIS cover type data) in order to reduce the chance of sample areas overlapping more than one cover type. All points were spaced > 200 m apart to minimize counting the same birds at multiple locations. Additionally, the first round of point selection was constrained to areas within 100 m of a trail or access road to limit the time spent moving between points. Trails and access roads within the study site were relatively narrow with minimal foot or vehicle traffic, making them unlikely to bias bird abundances or detection probabilities (Deluca and King 2014). If there was not enough suitable habitat within 100 m of a trail to fit the required number of points, the buffer was extended until enough habitat was contained within it. All points were evaluated during the first visit to make sure they were suitable for inclusion. If a point was deemed unsuitable (wetland areas, clearings, too difficult to access, etc.), the point

was eliminated, and a replacement was chosen based on the same process outlined above.

#### 2.3.2 Bird Surveys

Avian point count surveys were conducted over the course of two breeding seasons (May- June 2016 and 2017). Surveys were 50 m fixed-radius point counts with a 10-minute duration (Ralph et al. 1995). All surveys were conducted by trained observers beginning at sunrise and ending no later than 6 hours after sunrise on days with no precipitation or strong sustained winds. During each survey, all birds seen or heard within the 50 m radius sample area were recorded, except for birds only seen flying over without stopping. In order to collect additional information on bird detectability each point was visited three times throughout the breeding season in both years. Whenever possible, repeat visits to survey points were sampled by different observers and at different time-periods (early, mid, and late morning) to minimize biases associated with observer or time of day (Ralph et al. 1995).

#### 2.3.3 Vegetation Surveys

From the center of each point count site, a 10-factor cruising prism was used to select a sample of trees in order to estimate total basal area per tree type for each point. Additionally, I used a point-intercept approach to measure vegetation height in two height classes: herbaceous (0-0.5 m) and understory (0.5 - 3.0 m) (James and Shugart 1980, Martin et al. 1997). Originating from the survey plot center, five measurements were taken in each cardinal direction spaced 3 m apart (twenty measurements total per plot). At each 3m increment, a measuring pole was held

vertically and the height of the highest contact with vegetation in each height class was recorded. An additional 5 m radius sub-plot was established at the survey plot center and all woody vegetation >1.5 m in height were tallied, separated into two size classes (<2.5 cm and 2.5 - 8.0 cm) based on stem diameter. Finally, canopy closure was measured using the average of five densiometer measurements taken from the survey plot center and 15m in each cardinal direction.

#### 2.4 Statistical Analyses

#### 2.4.1 N-Mixture Models

N-mixture models (Royle et al. 2004) were used to analyze the abundance (*A*) of birds as a function of forest cover type while allowing for potential heterogeneity in detectability (*p*) of birds. Detectability was modeled as a function of covariates for observer, date (both linear and quadratic), time, and distance to stream. Distance to stream was included as a proxy variable to account for increased noise caused by streams, potentially reducing the number of birds heard during point counts. Candidate models also included terms for year and site, which were removed if the effects were not significant. In order to increase the likelihood of model convergence, all continuous predictor variables were standardized to have mean equal to 0 and standard deviation equal to 1. Data analysis was conducted using the program R (R Core Team 2017).

Each survey point was combined with the survey year to create a unique pointyear identity, which allowed us to analyze both years of data together similar to a single season model (Fogg et al. 2014). N-mixture models were fit to all species occurring at  $\geq$ 10% of points across both years using the *pcount* function in the *unmarked* R package

(Fiske and Chandler 2011). Species occurring at fewer than 10% of all surveyed points were excluded from this analysis due to increased issues with N-mixture model reliability for smaller sample sizes (Dennis et al. 2015). All potential predictor variables for both abundance and detection probability were first modeled individually. Any variable that produced a model with a lower Akaike's Information Criterion (AIC) value relative to the null model was retained for further selection (Burnham and Anderson 2002). Retained variables were then included in a new global model and a backwards stepwise selection (Hocking 1976) process was used to systematically remove variables until all remaining variables were significant (p < 0.05). From this list of candidate models, the model with the lowest AIC score was selected as the top model. Poisson, negative binomial, and zero-inflated Poisson models were explored for modeling abundance of each species. Model fit was assessed by calculating a chi-squared statistic from the observed data and comparing it to a distribution of expected chi-square statistics derived from a parametric bootstrapping of the data using the global model (Kéry and Royle 2016). For the modeling process, the Norway spruce cover type was set as the intercept in order to assess the differences in mean bird abundances relative to native cover types. The difference in means between spruce and other cover types was considered significant if 95% confidence intervals of the parameter estimates did not overlap zero.

#### 2.4.2 Generalized Linear Models

Abundance for all species observed at ≥5 points was compared among cover types using generalized linear models (GLMs), with Tukey post hoc pairwise comparisons of

group means. For each survey point, the highest observed count value across all withinyear replicate surveys was used as the dependent variable rather than using the mean value, as this metric has been shown to be more closely correlated with true abundance (Toms et al. 2006). The modeling of species abundance using GLMs does not account for imperfect detection and therefore the fitted estimates can only be interpreted as a relative index of true abundance, but given our study objective of comparing relative differences between forest cover types, relative abundance was deemed sufficient for less common species (Johnson 2008). Additionally, using GLM's for the more common species that were also analyzed using N-mixture models allowed us to compare relative patterns between the two methods.

#### 2.4.3 Community Analyses

Non-metric multidimensional scaling (NMDS) was used to visualize dissimilarities between cover types (Shepard 1962, Kruskal 1964). For the NMDS analysis, total counts for each species were calculated within each cover type based off maximum within-year counts across replicate surveys using the R package *vegan* (Jari Oksanen et al. 2019). Analysis of similarity (ANOSIM) was used to test for significant differences in avian communities among cover types (Clarke 1993). Pairwise ANOSIM comparisons were made for each combination of cover types and p-values were adjusted using the Bonferroni method. Similarity percentage (SIMPER) analysis was also conducted to identify particular species that contributed most to among group differences in community using Bray-Curtis dissimilarity matrices (Clarke 1993). For SIMPER analyses, pairwise comparisons among groups were made after converting

species counts to presence-absence data in order to reduce the effect of common species with high average abundances, which can confound results (Warton et al. 2012). To assess overall differences in biodiversity, both Simpson (Simpson 1949) and Shannon-Wiener (Shannon and Weaver 1949) diversity indices were calculated and compared among cover types using Analysis of Variance (ANOVA) and post-hoc comparisons of group means. A model containing an interaction effect between site (Quabbin vs Beartown) and cover type was also evaluated to see if there was a difference in diversity indices between study sites. Additionally, the maximum counts of all species at each site were used to conduct individual based rarefaction in order to estimate the number of expected unique species while compensating for heterogeneity in survey effort and the number of individuals sampled (Gotelli and Colwell 2011).

#### 2.4.4 PIF Ranking

Partners in Flight 2019 regional combined scores (Partners in Flight 2019) for the New England region (Table 1) were used in conjunction with predicted abundance estimates from GLM models. Species scores were multiplied by mean abundance estimates and upper/lower 95% confidence intervals to yield weighted scores. These weighted scores were summed across all species within each cover types and the totals were compared among cover types to assess a relative "value" of each stand type in regard to the combined conservation significance of the species within them (Nuttle et al. 2003).

#### 2.4.5 Vegetation Variables

Variables derived from vegetation surveys were not normally distributed according to Shapiro-Wilk test (Shapiro and Wilk 1965), and therefore were analyzed using non-parametric methods. Differences in habitat variables among cover types was assessed using Kruskal–Wallis tests (Kruskal and Wallis 1953) with post-hoc pairwise comparison of group means.

#### 2.5 Results

#### 2.5.1 N-mixture models

Over the course of two field seasons, there were 82 unique species observed during 970 point count surveys. Of these 82 species, 27 were observed in  $\geq$  10 % of all surveys and were included in our initial analysis using N-mixture models (Table 1). A Poisson mixture was favored for the error distribution of the abundance portion of the model for 25 species with a zero-inflated Poisson mixture being preferred for the remaining 2 species (Table 2). Model convergence was achieved for all species with cover type included as a predictor of abundance in the top models for 22 of the species. Goodness of fit tests indicated no significant lack of fit due to overdispersion (p < .05). However, 10 species showed a significant level of underdispersion (p > 0.95). Goldencrowned kinglet, red-breasted nuthatch, and Blackburnian warbler were all more abundant in spruce than in any of the native cover types (Table 3). Magnolia warbler and blue jay were more abundant in spruce when compared to hemlock, deciduous, and mixed stands but were similar to abundance estimates within pine stands. Spruce plantations showed higher abundances of blue-headed vireo when compared to pine

stands, and higher abundances of gray catbird compared to mixed stands. Chipping sparrow were less abundant in deciduous and hemlock stands than in spruce but were more abundant in pine when compared to spruce. Relative to spruce, black-and-white warbler were more abundant in mixed stands, black-capped chickadee were more abundant in pine, and yellow-bellied sapsucker were more abundant in both deciduous and mixed stands. With the exception of pine, eastern wood peewee were more abundant in native stands than in spruce. Least flycatcher were less abundant in spruce than in deciduous, mixed, and pine stands.

#### 2.5.2 Generalized Linear Models

In total, there were 47 species that occurred in at least 5 surveys which were modeled using GLMs, including the 27 species that were also analyzed using N-Mixture models (Table 1). Models containing cover type as a significant variable were preferred over the null model for 26 of these species (Table 4). Golden-crowned kinglet and redbreasted nuthatch were more abundant in spruce than in all native cover types with nuthatches also being more abundant in pine stands than deciduous stands. Brown creeper and Blackburnian warbler were more abundant in spruce when compared to hemlock, deciduous, and mixed stands but were similar to abundance estimates within pine stands. Spruce plantations supported more yellow-rumped warblers than either deciduous or hemlock stands. Hemlock stands supported lower numbers of gray catbird than all other forest types, including spruce. Relative to spruce, American robin were more abundant in deciduous, eastern towhee were more abundant in hemlock, eastern wood peewee were more abundant in deciduous and mixed stands, pine warbler were

more abundant in pine, least flycatcher were more abundant in both mixed and pine stands and yellow-bellied sapsucker were more abundant in all native stands except for deciduous. Red-eyed vireo was the only species that was least abundant in spruce compared to all other stand types. Abundance estimates within spruce plantations for all remaining species showed no significant differences when compared to other stand types.

Plots of corrected abundance estimates from N-mixture models and mean abundance estimates from GLMs were visually compared for the species that were analyzed using both methods. Overall, the two methods produced similar patterns in relative abundance among cover types with some exceptions (Fig. 3). N-mixture models identified some small yet significant differences between cover types that were not identified using GLMs, however p-values from GLMs were corrected to adjust for multiple comparisons so this is expected.

#### 2.5.3 Community Analysis

Results from ANOSIM analysis show that cover type has a significant effect on bird communities within the study sites (Table 5). All pairwise comparisons of cover types showed a significant differentiation of bird communities (p < 0.05) with the exception of the comparison between mixed and pine stands. However, the R statistics for these comparisons were low (<0.3) indicating that although the communities were distinct, the effect was weak. Smaller R statistic occur when the differences between sites of the same treatment (cover type) are similar to the differences among sites in

other treatments. This lack of strong community differentiation is further illustrated in NMDS analysis (Fig. 4) where there is substantial species overlap between cover types.

Comparisons of Shannon and Simpson diversity indices showed that spruce, mixed, and pine stands had similar diversity scores (Fig.5). Spruce plantations had significantly higher diversity scores than both deciduous and hemlock stands. There were no significant differences in either diversity index between deciduous, mixed, and pine stands but all three were more diverse than hemlock. Models containing only cover type as the predictor were supported over models containing an interaction effect between site and cover type for both diversity indices.

Individual-based rarefaction curves with 95% confidence intervals (Fig. 6) for all cover types overlap one another across most of the sampling space with the exception of spruce and deciduous. The hemlock cover type had the fewest individual bird detections (n=1145) across the entire study. Using the rarefaction curves to predict species diversity at this sample size across all cover types shows that deciduous stands would contain fewer unique species than spruce stands (Fig. 7).

#### 2.5.4 PIF Ranking

The pooled scores for each cover type all had 95% confidence intervals that overlapped (Fig. 8) suggesting no significant differentiation of conservation value among cover types.

#### 2.5.5 Vegetation Data

With the exception of percent canopy cover, all vegetation related habitat variables showed some level of significant difference between cover types (Table 7).

Hemlock points exhibited the highest percentage of bare ground. Spruce points had more bare ground compared to deciduous points. Understory cover was similar between spruce and hemlock, with the latter being significantly lower than the remaining cover types. Spruce and hemlock stands also had similar shrub densities for both small and large size classes. Spruce plantations had a higher total basal area and percent conifer amongst all cover types.

#### 2.6 Discussion

According to my results, exotic Norway spruce plantations in Massachusetts are capable of supporting diverse avian communities that are not depauperate relative to surrounding native forests. Rarefaction showed that spruce stands, on average, contained more unique species than mixed stands, and species diversity was higher in spruce stands compared to both hemlock and deciduous stands. Norway spruce plantations supported the highest abundances for Blackburnian warbler, goldencrowned kinglet, and red-breasted nuthatch, bird species that are commonly associated with pure coniferous stands (DeGraaf and Yamasaki 2001). Other conifer associated species such as black-throated green warbler, magnolia warbler, blue-headed vireo, and yellow-rumped warbler were all observed utilizing spruce habitat at levels similar to native conifer stands. Spruce stands consistently exhibited the highest percentage of conifer dominance (mean= 93%), with most points being characterized by pure spruce. Conversely, native conifer stands were heavily interspersed with deciduous trees with pine and hemlock stands averaging only 75% and 63% conifer respectively, leading to spruce stands representing the most conifer-pure habitat within the study sites. This

characteristic is likely the reason why conifer associated species utilized spruce habitat at levels similar to less pure native conifer stands, despite plantations being limited to a non-native tree species. Additionally, golden-crowned kinglets and red-breasted nuthatches have a known preference for spruce habitat (DeGraaf and Yamasaki 2001) which explains why these species were only rarely observed in native forest types, given that there was no native spruce within the study area. The characteristics of spruce plantations, such as dense, short-needle canopies for foraging (Andrle 1971), potentially provide supplemental habitat for these species. This pattern is consistent with the findings of Andrle (1971), who also observed golden-crowned kinglets utilizing both Norway and white spruce (*Picea glauca*) plantations in New York, USA, when the species was otherwise uncommon in the area.

Species known to utilize both coniferous and deciduous habitats, such as American redstart, American robin, black-and-white warbler, ovenbird, veery, and various woodpecker species (DeGraaf and Yamasaki 2001) did not show an avoidance of spruce, and abundances were similar among plantations and native cover types. This suggests that the lack of a deciduous component within plantations was not detrimental to the abundance of those species that utilize both coniferous and deciduous habitats. This pattern supports the findings of Christian et al (1998) who noted that relatively common habitat generalists were the species most often observed utilizing plantations consisting of native poplar and cottonwood trees in the American mid-west. My results show that this pattern also holds true for a monoculture of an exotic tree species.

Interestingly, the data also showed that some unlikely species inhabited spruce plantations within the study area. Chipping sparrows, which are known to prefer open, grassy areas and forest edges (DeGraaf and Yamasaki 2001), were observed in higher abundances within spruce compared to deciduous and hemlock stands. A possible explanation for this pattern involves the unique layout of some of the spruce points. Within the Quabbin study site, one of the three Norway spruce plantations was relatively narrow and laid out in a patchwork arrangement with low scrubby vegetation filling in the gaps. Although each point count location was > 50 m from any edge of contiguous spruce habitat, 8 of the points had a scrubby clearing within 20 m of the survey area periphery that may have attracted chipping sparrows to the area, as well as other species associated with gaps such as Rose-breasted grosbeak and black-capped chickadee. Additionally, Reynolds and Knapton (1984) noted that white spruce was the most common tree species found near chipping sparrow nests in Canada implying that the species selects nest sites with a heavy spruce component. This juncture of low clearings bordering dense spruce trees was unique to the study site and is a potential an example of how the distribution of plantations within a landscape may have differing effects on the native fauna. As plantation patches get smaller, the amount of edge habitat relative to interior habitat increases and attracts more edge-associated species to the plantation (Christian et al. 1998). This is also the likely explanation for the high abundance of bluejays, another edge associated species, observed in spruce plantations despite the species' tendency to avoid pure conifer woodlands (DeGraaf and Yamasaki 2001).

Two types of bird species that were most averse to spruce plantations were those that associate with deciduous dominant stands and those that prefer dense, heterogeneous understory and herbaceous vegetation. Yellow-bellied sapsucker showed a preference for mixed forests over spruce, which is not surprising given the species' affinity for mature deciduous trees for creating nest cavities in (Tozer et al. 2011), a feature entirely absent from spruce plantations. Another species, eastern wood pewee, saw lowest abundance estimates in conifer dominated stands. Wood pewee abundance has been shown to decrease as the amount of living hemlock increases within a stand, but conversely, will increase in abundance during hemlock dieoff. This phenomenon is a response to a marked increase in understory structure that occurs in the wake of hemlock die-off as deciduous and herbaceous plants fill in the gaps (Becker et al. 2008, Toenies et al. 2018). Sitka spruce (*Picea sitchensis*) plantations in Ireland exhibited a negative relationship between canopy cover and bird diversity due to decreased understory structure (Smith et al. 2008). Norway spruce plantations and hemlock stands were similar in terms of their dense canopy and lack of complex herbaceous and understory layers, which many bird species, including least flycatchers and eastern wood pewee, rely on for food, nesting, and cover (Macarthur and Macarthur 1961). Therefore, it is plausible that these species would also begin to utilize plantations as mature trees naturally die off and are encroached by deciduous trees and sub-canopy vegetation. Plantations left in place without management would see their avian communities shift over time to include more species that rely on deciduous trees and complex understories as the mature spruce trees die off.

The only species that exhibited the lowest abundance estimates in spruce was red-eyed vireo, which is often associated with deciduous habitats, but also known to utilize coniferous forest on occasion (Bent 1950). One explanation for this species aversion to spruce plantations is their known preference for deciduous leaves while foraging for insects (Gabbe et al. 2002). So, although red-eyed vireo did nest within the plantations, the lack of prime foraging appears to have made plantations less appealing than the ample deciduous-rich habitats nearby.

Both Shannon and Simpson-Wiener diversity indices suggested a similar pattern, in which hemlock stands had the lowest bird diversity of all the cover types. Blackthroated green warbler, Blackburnian warbler, and red-breasted nuthatch, which are all species that are known to have strong associations with eastern hemlock (Yamasaki et al. 1999), were not more abundant in hemlock stands compared to spruce plantations. All hemlock stands at the Quabbin site had at least some hemlock woolly adelgid infestation, with varying degrees of hemlock dieback as a result. The diminished habitat quality of infested hemlock stands is a likely explanation for lower diversity scores and the relatively low abundances of hemlock associated species (Brown and Todd 2014a, Buchanan et al. 2016). As woolly adelgid kills off hemlock, deciduous trees replace them and begin shifting avian communities more towards habitat generalists and deciduous associated species (Toenies et al. 2018). Although I was not able to directly link hemlock quality or adelgid prevalence to bird abundance or diversity, previous studies have noted such shifts within the region (Tingley et al. 2002, Becker et al. 2008) with reduced needle density in infested stands being a possible mechanism driving this pattern, which

in turn reduces foraging opportunities for birds. Another possible explanation for the lower abundance estimates of these species and others in hemlock is decreased detectability of birds due to ambient noise. Eastern hemlock favors moist ridges and ravines (Foster et al. 2014), leading to a majority of hemlock points in our study being located near running streams that made aural bird detections more difficult. We attempted to correct for this variation in detectability by including distance to stream as a covariate in the detection portion of our N-mixture models. Given the covariates' inclusion in the top model for seven species, it is clear that it did have an effect on overall detectability. However, it is still possible that it did not fully compensate for all missed birds. However, after correcting for unequal sample size using rarefaction curves, hemlock stands were shown to have a similar amount of expected unique species compared to other cover types.

Significant differences in bird communities among all pairwise comparisons of stand types were of note given the high level of overlap among cover types made apparent by NMDS plots. R statistics derived from ANOSIM analysis were low for all comparisons, indicating that although the communities significantly differed among stands types, the overall effects were weak (Clarke and Warwick 2001). Closer examination of NMDS plots highlight that a majority of bird species were mutually common among stand types, with only a few species showing strong preference for one or a subset of stand types. Further investigation using SIMPER analysis supports this notion, and show that red-breasted nuthatch, golden crowned kinglet, and Blackburnian warbler were consistently the most important species in regard to differentiating the

bird community of spruce from those of other cover types. Without these highly selective species, spruce plantations would consist mainly of generalist species and likely would not differ greatly from native conifer stands in terms of bird communities.

The difference in overall species communities between spruce and hemlock stands is of particular interest given the potential loss of significant hemlock habitat in the future due to hemlock woolly adelgid infestation. The fact that a number of hemlock associated species such as black-throated green warbler, Blackburnian warbler, magnolia warbler, red-breasted nuthatch, and blue headed vireo (Yamasaki et al. 1999) were observed utilizing spruce habitat lends further support to the idea that spruce plantations could offer suitable replacement habitat in areas where hemlock stands continue to deteriorate are become absent all together (Evans 2008). Black-throated green warblers in particular were shown to be negatively affected by hemlock decline (Brown and Todd 2014b), and could find refuge in Norway spruce plantations. In the case of Blackburnian warblers and red-breasted nuthatches, abundances were higher in spruce than hemlock. Although both of these species commonly associate with native spruce habitat, it is interesting that a monoculture of non-native spruce was attracting more birds than nearby native hemlock stands. With spruce plantations consisting almost entirely of uninterrupted conifer, it is possible that plantations will become increasingly attractive to species that prefer conifer-rich habitat as hemlock stands decline. However, further research is required to determine which specific characteristics are driving these bird abundances at a scale finer than categorical cover type. Although our vegetation surveys were intended to examine such relationships, we

were not able to capture a specific variable that predicted abundance better than cover type. It should be noted that the plantations within our study were all mature plantations that had not been managed for at least ten years prior to the study. As a result, some natural tree loss has occurred leading to canopy gaps that may have contributed to higher bird diversity and abundances compared to managed plantations.

Of all the species analyzed for this study, there were none that were recognized as being of priority conservation concern according to Partners in Flight scores. Scarlet tanager and wood thrush. However, were regionally important with the two highest PIF scores (17), but scarlet tanagers occurred equally across all cover types and wood thrush differed only slightly between hemlock and mixed stands. Additionally, all species remaining analyzed also occurred across all cover types to some degree. As a result of these distributions and lack of critically important species, there was no differentiation in conservation value among cover types when abundance estimates were pooled and weighted using PIF scores. This lack of differentiation shows that Norway spruce plantations can support native birds, and they are able to maintain biodiversity at levels similar to that found within native forests.

The use of N-mixture models to derive corrected abundance estimates by accounting for imperfect detection has been used widely in recent years despite some criticisms (Barker et al. 2017, Link et al. 2018). Simulations conducted by Coutirier et al. (2013) suggest that biased abundance estimates become more likely as the probability of detecting an animal falls below 0.5. In our study, most species exhibited estimated detection probabilities << 0.5. Although corrected abundance estimates from our N-

mixture models showed signs of significant differences among cover types, the relatively low detection probabilities led to high standard errors and inflated abundance estimates. Even after removing species with lowest detection probabilities, N-mixture models still produced corrected abundance estimates that were several times higher than the actual maximum observed count at a given point. This is cause for concern given the ecological implausibility of such high estimates. As a result, I concede that for many of our species with low detection probabilities, N-mixture model estimates should not be interpreted as true abundance estimates. Rather, these estimates more closely approximate an index of relative abundance similar to those obtained using more traditional GLM regression methods. However, in the case of N-mixture models, uncertainty arising from the detection process has been greatly reduced by accounting for variables that affect heterogeneity in detection across surveys. Given the lack of evidence that accounting for imperfect detection changed the relative abundance predictions combined with the more parsimonious GLM models, I deemed it sufficient to prefer the GLM model predictions over the N-mixture model predictions, which have been shown to become decreasingly reliable as detection probability becomes low (Barker et al. 2017) or when there is unmodeled heterogeneity (Duarte et al. 2018).

### 2.7 Management Implications

Plantations are an important, and often necessary, component in the production of timber and other ecological services. Although exotic tree plantations are not a preferred substitution for native forest stands in terms of ecological value, they can still contribute towards achieving conservation goals. If maintaining biodiversity is a primary

concern, steps can be taken to establish plantations that help achieve that goal. Spruce plantations incorporated into a landscape of native forests stands (as in our study sites) can provide valuable patches of conifer habitat, especially in areas with limited native conifer stands. It should be noted that plantations benefit different species across their lifespan and may not always align with specific conservation plans. If land managers wish to promote early successional species or specific, non-conifer associated species of special concern, then Norway spruce plantations may not offer as much value. However, this study shows that well-established Norway spruce patches integrated into a mosaic of native forest are relatively benign in terms of negative impacts on biodiversity and can also support species that are not otherwise common in the immediate area. Conclusions on whether to allow existing Norway spruce plantations to persist will depend on site-specific conservation objectives as well as available resources, but given my results, land managers could be justified in allowing some Norway spruce to persist without a negative impact on maintaining healthy avian biodiversity. This conclusion only pertains to existing plantations however, and my research did not explore the effects of plantation age on biodiversity. Therefore, recommendations as to whether establishing new plantations could be justified from a conservation standpoint may differ. However, previous research suggests that the period of time before new Norway spruce plantations reach their full potential in terms of biodiversity is only ~30 years, which lends some support for the idea that new plantations could be an effective method to supplement conifer habitats and support the species that depend on them.

# CHAPTER 3 TABLES

#### Table 1

Common and scientific names for all species included in analyses along with alpha codes, Partners in Flight (PIF) scores and count summaries by cover type.

			# Detections						
Species Name	Alpha Code	PIF Score	NS	DE	EH	мх	WP	Total	Model Type
American crow (Corvus brachyrhynchos)	AMCR	11	10	3	3	1	2	19	GLM
American goldfinch (Spinus tristis)	AMGO	10	2	2	1	1	1	7	GLM
American redstart (Setophaga ruticilla)	AMRE	10	62	45	32	46	43	228	GLM, Nmix
American robin (Turdus migratorius)	AMRO	11	3	10	4	2	9	28	GLM
Baltimore oriole (Icterus galbula)	BAOR	16	2	7	1	3	6	19	GLM
Black-and-white warbler (Mniotilta varia)	BAWW	14	37	25	36	42	31	171	GLM, Nmix
Black-billed cuckoo (Coccyzus erythropthalmus)	BBCU	15	12	9	2	6	11	40	GLM
Bay-breasted warbler (Setophaga castanea)	BBWA	NA	19	6	15	6	2	48	GLM
Black-capped chickadee (Poecile atricapillus)	BCCH	12	33	18	29	25	37	142	GLM, Nmix
Brown-headed cowbird (Molothrus ater)	BHCO	9	5	5	2	4	4	20	GLM
Blue-headed vireo (Vireo solitarius)	BHVI	10	38	26	39	19	16	138	GLM, Nmix
Blackburnian warbler (Setophaga fusca)	BLBW	13	58	12	29	27	28	154	GLM, Nmix
Blue jay (Cyanocitta cristata)	BLJA	14	42	17	24	30	33	146	GLM, Nmix
Brown creeper (Certhia americana)	BRCR	11	46	9	11	9	15	90	GLM, Nmix
Black-throated blue warbler (Setophaga caerulescens)	BTBW	11	44	42	47	35	32	200	, GLM, Nmix
Black-throated green warbler (Setophaga virens)	BTNW	10	63	36	64	43	44	250	, GLM, Nmix
Cedar waxwing (Bombycilla cedrorum)	CEDW	10	13	5	4	5	6	33	GLM
Chipping sparrow (Spizella passerina)	CHSP	10	22	8	7	15	23	75	GLM, Nmix
Common yellowthroat (Geothlypis trichas)	COYE	13	61	32	38	39	41	211	GLM, Nmix
Chestnut-sided warbler (Setophaga pensylvanica)	CSWA	14	51	32	29	33	31	176	GLM, Nmix
Downey woodpecker (Picoides pubescens)	DOWO	11	4	8	4	8	6	30	GLM
Eastern phoebe (Sayornis phoebe)	EAPH	12	3	3	9	7	1	23	GLM
Eastern towhee (Pipilo erythrophthalmus)	EATO	16	64	40	29	46	43	222	GLM, Nmix
Eastern wood pewee (Contopus virens)	EAWP	13	6	34	15	19	7	81	GLM, Nmix
Great crested flycatcher (Myiarchus crinitus)	GCFL	11	6	6	2	4	6	24	GLM
Golden-crowned kinglet ( <i>Regulus satrapa</i> )	GCKI	7	54	4	2	3	7	70	GLM, Nmix
Gray catbird (Dumetella carolinensis)	GRCA	12	26	20	5	20	23	94	GLM, Nmix
Hairy woodpecker (Leuconotopicus villosus)	HAWO	11	11	10	4	9	8	42	GLM
Hermit thrush (Catharus guttatus)	HETH	10	18	5	9	11	6	49	GLM
Least flycatcher (Empidonax minimus)	LEFL	13	13	17	17	22	21	90	GLM, Nmix
Magnolia warbler (Setophaga magnolia)	MAWA	10	33	11	17	12	15	88	GLM, Nmix
Mourning dove (Zenaida macroura)	MODO	9	12	5	4	10	7	38	GLM
Northern cardinal (Cardinalis cardinali)	NOCA	8	8	2	1	1	6	18	GLM
Ovenbird (Seiurus aurocapilla)	OVEN	14	83	58	70	57	57	325	GLM, Nmix
Pine warbler (Setophaga pinus)	PIWA	11	52	34	33	50	53	222	GLM, Nmix
Pileated woodpecker (Dryocopus pileatus)	PIWO	11	11	5	6	8	1	31	GLM
Rose-breasted grosbeak (Pheucticus Iudovicianus)	RBGR	16	20	9	7	15	11	62	GLM
Red-breasted nuthatch (Sitta canadensis)	RBNU	8	61	4	4	13	18	100	GLM, Nmix
Red-eyed vireo (Vireo olivaceus)	REVI	12	53	57	64	55	55	284	GLM, Nmix
Scarlet tanager (Piranga olivacea)	SCTA	17	34	27	30	27	30	148	GLM, Nmix
Tufted titmouse (Baeolophus bicolor)	TUTI	12	15	14	14	17	17	77	GLM, Nmix
Veery (Catharus fuscescens)	VEER	14	62	50	51	55	55	273	GLM, Nmix
Worm-eating warbler (Helmitheros vermivorum)	WEWA	14	8	5	1	3	5	22	GLM, MINX
Woord thrush (Hylocichla mustelina)	WOTH	17	25	25	12	23	10	95	GLM, Nmix
Yellow-bellied sapsucker (Sphyrapicus varius)	YBSA	9	15	23	11	29	10	95 87	GLM, Nmix
Yellow-rumped warbler (Setophaga coronata)	YRWA	3 7	27	6	9	8	12	62	GLM, MILLX
Yellow-throated vireo (Vireo flavifrons)	YTVI	, 13	7	6	9	3	3	28	GLM

\*NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine

Included covariates and output statistics from top N-Mixture models and corresponding goodness-of-fit
tests. Species' scientific names are presented in Table 1.

	· · ·						
Species	Abundance Covariates	Detection Covariates	AIC	$\lambda$ Mixture <sup>a</sup>	χ <sup>2</sup>	ĉ	р
American redstart	cover	observer + day + stream	1515.1	Р	805.2	0.843	1.000
Black-and-white warbler	cover	observer + day	1143.3	Р	879.4	0.917	0.968
Black-capped chickadee	cover	observer + time + day + day <sup>2</sup>	1053.5	Р	944.4	0.988	0.587
Blue-headed viereo	cover	observer	962.0	Р	898.7	0.936	0.943
Blackburnian warbler	cover	observer	1079.7	Р	935.6	0.979	0.661
Bluejay	cover	time	1118.1	Р	1026.8	1.066	0.083
Brown creeper	cover + year	observer + stream + time	663.1	Р	783.3	0.825	0.953
Black-throated green warbler	cover + site + year	observer + day + day <sup>2</sup>	1370.8	Р	865.0	0.902	0.990
Black-throated blue warbler	cover	observer	1979.5	Ρ	800.3	0.839	0.999
Chipping sparrow	cover + year	observer + day + day <sup>2</sup>	641.4	ZIP	1000.4	1.323	0.052
Common yellowthroat		observer + time	1581.6	Р	916.5	0.953	0.841
Chestnut-sided warbler		observer + stream	1470.4	ZIP	987.9	1.034	0.248
Eastern towhee	cover	observer + stream + time	1611.9	Ρ	806.1	0.843	1.000
Eastern wood-pewee	cover	observer + stream	649.8	Ρ	825.9	0.867	0.942
Golden-crowned kinglet	cover + site	observer + stream	501.0	Р	798.5	0.867	0.767
Grey catbird	cover + site + year	observer	693.0	Р	877.3	0.920	0.892
Least flycatcher	cover + year	observer	667.3	Р	903.4	0.952	0.707
Magnolia warbler	cover		739.4	Р	946.3	0.982	0.619
Ovenbird	site	observer + time	2693.5	Р	458.7	0.479	1.000
Pine warbler	cover + site	observer	1640.8	Ρ	815.4	0.851	1.000
Red-breasted nuthatch	cover + year	observer + stream	765.2	Ρ	823.5	0.863	0.947
Red-eyed vireo	cover	observer	1949.7	Р	641.8	0.672	1.000
Scarlet tanager	site	observer + day + day <sup>2</sup>	1037.2	Р	872.1	0.911	0.984
Tufted titmouse		observer	621.3	Р	909.4	0.941	0.911
Veery	cover + site	observer + day + time	1967.1	Р	772.7	0.810	1.000
Wood thrush	cover	observer + day + day <sup>2</sup> + time	700.1	Р	973.2	1.016	0.368
Yellow-bellied sapsucker	cover	observer	617.8	Р	840.2	0.880	0.934

<sup>*a*</sup> λ Mixture: P = Poisson, ZIP = Zero-inflated Poisson

N-Mixture model coefficients with standard errors from (species for which cover type was not included in top model or did not pass goodness-of-fit tests excluded). Coefficients for deciduous, hemlock, mixed and pine represent differences in relation to spruce (the model contrast). Values in bold signify significant differences. Species' scientific names are presented in Table 1.

Species	Spruce	Deciduous	Hemlock	Mixed	Pine
Black-and-white warbler	1.80 (1.10)	-0.10 (0.25)	0.42 (0.21)	0.53 (0.21)	0.38 (0.22)
Black-capped chickadee	1.78 (1.07)	-0.15 (0.28)	0.26 (0.22)	0.33 (0.24)	0.79 (0.22)
Blue-headed viereo	2.23 (1.75)	-0.08 (0.23)	0.20 (0.2)	-0.51 (0.26)	-0.62 (0.27)
Blackburnian warbler	2.35 (0.95)	-1.68 (0.29)	-0.86 (0.20)	-0.82 (0.20)	-0.80 (0.20)
Bluejay	1.74 (0.76)	-0.72 (0.25)	-0.74 (0.23)	-0.08 (0.2)	-0.04 (0.20)
Brown creeper	0.03 (0.39)	-1.30 (0.35)	-1.21 (0.35)	-1.13 (0.34)	-0.57 (0.29)
Chipping sparrow	2.06 (2.15)	-0.79 (0.38)	-1.23 (0.42)	0.00 (0.30)	0.53 (0.26)
Eastern wood-pewee	-1.96 (0.45)	2.41 (0.44)	1.49 (0.50)	1.80 (0.47)	0.72 (0.57)
Golden-crowned kinglet	1.80 (1.23)	-2.71 (0.52)	-3.30 (0.73)	-2.90 (0.60)	-1.91 (0.40)
Grey catbird	1.01 (1.24)	0.06 (0.29)	-1.52 (0.49)	-0.01 (0.30)	0.25 (0.28)
Least flycatcher	-1.60 (0.51)	1.09 (0.35)	0.48 (0.37)	1.12 (0.34)	1.19 (0.34)
Magnolia warbler	0.58 (0.43)	-1.05 (0.34)	-0.60 (0.28)	-0.93 (0.33)	-0.47 (0.28)
Red-breasted nuthatch	1.98 (0.62)	-2.82 (0.51)	-2.32 (0.43)	-1.60 (0.31)	-1.00 (0.25)
Wood thrush	3.73 (0.95)	0.49 (0.26)	-0.62 (0.33)	0.26 (0.27)	-0.57 (0.33)
Yellow-bellied sapsucker	0.96 <b>(</b> 1.69)	0.78 (0.32)	-0.06 (0.38)	1.15 (0.30)	-0.04 (0.40)

Mean abundance with standard errors from GLM models. Lines in bold represent models in which cover type had a significant effect based on corrected p-values (Bonferroni method). Cover types with common superscripts represent lack of significant difference among them. Species' scientific names are presented in Table 1.

Species	Spruce	Deciduous	Hemlock	Mixed	Pine	$\chi^2$	р
American crow	0.13 (0.3)	0.07 (0.5	0.04 (0.58)	0.02 (1)	0.03 (0.71)	353.3	0.063
American goldfinch	0.02 (0.71)	0.03 (0.71)	0.01 (1)	0.02 (1)	0.02 (1)	323	0.948
American redstart	0.81 (0.12) <sup>ab</sup>	1.16 (0.12) <sup>b</sup>	0.51 (0.17) <sup>ª</sup>	0.98 (0.13) <sup>b</sup>	0.9 (0.14) <sup>ab</sup>	169.6	0.001
American robin	0.04 (0.58) <sup>a</sup>	0.21 (0.29) <sup>b</sup>	0.06 (0.5) <sup>ab</sup>	0.05 (0.58) <sup>ab</sup>	0.15 (0.33) <sup>ab</sup>	357	0.007
Baltimore oriole	0.02 (0.71) <sup>a</sup>	0.12 (0.38) <sup>a</sup>	0.01 (1) <sup>a</sup>	0.05 (0.58) <sup>a</sup>	0.1 (0.41) <sup>a</sup>	311	0.037
Black-and-white warbler	0.45 (0.16)	0.43 (0.2)	0.59 (0.15)	0.78 (0.15)	0.66 (0.16)	201	0.059
Black-billed cuckoo	0.14 (0.29) <sup>a</sup>	0.16 (0.33) <sup>a</sup>	0.03 (0.71) <sup>a</sup>	0.1 (0.41) <sup>a</sup>	0.19 (0.3) <sup>a</sup>	290	0.038
Bay-breasted warbler	0.26 (0.21) <sup>a</sup>	0.1 (0.41) <sup>ab</sup>	0.27 (0.23) <sup>a</sup>	0.12 (0.38) <sup>ab</sup>	0.03 (0.71) <sup>b</sup>	350.8	0.001
Black-capped chickadee	0.45 (0.16) <sup>ab</sup>	0.33 (0.23) <sup>a</sup>	0.49 (0.17) <sup>ab</sup>	0.52 (0.18) <sup>ab</sup>	0.81 (0.14) <sup>b</sup>	272.3	0.007
Brown-headed cowbird	0.06 (0.45)	0.09 (0.45)	0.03 (0.71)	0.07 (0.5)	0.07 (0.5)	310	0.697
Blue-headed vireo	0.49 (0.16)	0.52 (0.18)	0.56 (0.16)	0.33 (0.23)	0.31 (0.24)	230.5	0.094
Blackburnian warbler	0.9 (0.11) <sup>a</sup>	0.22 (0.28) <sup>b</sup>	0.42 (0.18) <sup>b</sup>	0.48 (0.19) <sup>b</sup>	0.51 (0.18) <sup>ab</sup>	220.7	< 0.001
Blue jay	0.61 (0.14) <sup>a</sup>	0.34 (0.22) <sup>a</sup>	0.34 (0.2) <sup>a</sup>	0.66 (0.16) <sup>a</sup>	0.66 (0.16) <sup>a</sup>	275.6	0.007
Brown creeper	0.57 (0.14) <sup>a</sup>	0.17 (0.32) <sup>b</sup>	0.15 (0.3) <sup>b</sup>	0.19 (0.3) <sup>b</sup>	0.27 (0.25) <sup>ab</sup>	281.1	< 0.001
Black-throated blue warbler	0.58 (0.14)	0.97 (0.13)	0.77 (0.13)	0.79 (0.15)	0.59 (0.17)	200.8	0.067
Black-throated green warbler	1.31 (0.1) <sup>ab</sup>	0.88 (0.14) <sup>a</sup>	1.51 (0.1) <sup>b</sup>	1.12 (0.12) <sup>ab</sup>	1.08 (0.12) <sup>ab</sup>	227.9	0.014
Cedar waxwing	0.15 (0.28)	0.1 (0.41)	0.06 (0.5)	0.14 (0.35)	0.14 (0.35)	397.8	0.385
Chipping sparrow	0.31 (0.2) <sup>ab</sup>	0.17 (0.32) <sup>b</sup>	0.11 (0.35) <sup>b</sup>	0.34 (0.22) <sup>ab</sup>	0.54 (0.18) <sup>a</sup>	372.5	< 0.001
Common yellowthroat	0.92 (0.11)	0.69 (0.16)	0.68 (0.14)	0.93 (0.14)	0.92 (0.14)	242.5	0.236
Chestnut-sided warbler	0.77 (0.12	0.71 (0.16)	0.48 (0.17)	0.84 (0.14)	0.81 (0.14)	275.6	0.068
Downey woodpecker	0.05 (0.5)	0.14 (0.35)	0.06 (0.5)	0.14 (0.35)	0.1 (0.41)	300	0.224
Eastern phoebe	0.04 (0.58) <sup>a</sup>	0.05 (0.58) <sup>a</sup>	0.14 (0.32) <sup>a</sup>	0.12 (0.38) <sup>a</sup>	0.02 (1)a	320.2	0.026
Eastern towhee	0.99 (0.11) <sup>b</sup>	0.86 (0.14) <sup>ab</sup>	0.49 (0.17) <sup>a</sup>	1.12 (0.12) <sup>b</sup>	0.97 (0.13) <sup>b</sup>	200.4	0.001
Eastern wood pewee	0.07 (0.41) <sup>a</sup>	0.64 (0.16) <sup>b</sup>	0.21 (0.26) <sup>ac</sup>	0.34 (0.22) <sup>bc</sup>	0.12 (0.38) <sup>ac</sup>	260.2	< 0.001
Great crested flycatcher	0.07 (0.41)	0.12 (0.38)	0.03 (0.71)	0.09 (0.45)	0.1 (0.41)	343.8	0.326
Golden-crowned kinglet	0.68 (0.13) <sup>a</sup>	0.07 (0.5) <sup>b</sup>	0.03 (0.71) <sup>b</sup>	0.05 (0.58) <sup>b</sup>	0.12 (0.38) <sup>b</sup>	265.8	< 0.001
Gray catbird	0.32 (0.19) <sup>b</sup>	0.34 (0.22) <sup>b</sup>	0.07 (0.45) <sup>a</sup>	0.34 (0.22) <sup>b</sup>	0.42 (0.2) <sup>b</sup>	248.7	< 0.001
Hairy woodpecker	0.13 (0.3)	0.17 (0.32)	0.06 (0.5)	0.16 (0.33)	0.14 (0.35)	288	0.313
Hermit thrush	0.23 (0.23)	0.1 (0.41)	0.14 (0.32)	0.21 (0.29)	0.12 (0.38)	344.9	0.295
Least flycatcher	0.15 (0.28) <sup>a</sup>	0.38 (0.21) <sup>ab</sup>	0.24 (0.24) <sup>ab</sup>	0.41 (0.2) <sup>b</sup>	0.42 (0.2) <sup>b</sup>	283.9	0.007
Magnolia warbler	0.45 (0.16) <sup>a</sup>	0.19 (0.3) <sup>a</sup>	0.25 (0.24) <sup>a</sup>	0.21 (0.29) <sup>a</sup>	0.31 (0.24) <sup>a</sup>	282.7	0.03
Mourning dove	0.14 (0.29)	0.09 (0.45)	0.06 (0.5)	0.19 (0.3)	0.12 (0.38)	301.5	0.204
Northern cardinal	0.11 (0.33) <sup>a</sup>	0.03 (0.71) <sup>a</sup>	0.01 (1)a	0.02 (1)a	0.1 (0.41) <sup>a</sup>	329.7	0.03
Ovenbird	2.31 (0.07)	2.62 (0.08)	2.32 (0.08)	2.53 (0.08)	2.42 (0.08)	125.4	0.746
Pine warbler	0.79 (0.12) <sup>ab</sup>	0.66 (0.16) <sup>a</sup>	0.56 (0.16) <sup>a</sup>	1.26 (0.12) <sup>bc</sup>	1.42 (0.11) <sup>c</sup>	196.7	< 0.001
Pileated woodpecker	0.13 (0.3)	0.09 (0.45)	0.08 (0.41)	0.14 (0.35)	0.02 (1)	299	0.095
Rose-breasted grosbeak	0.24 (0.22)	0.17 (0.32)	0.1 (0.38)	0.28 (0.25)	0.19 (0.3)	284.9	0.148
Red-breasted nuthatch	0.89 (0.12) <sup>a</sup>	0.07 (0.5) <sup>b</sup>	0.08 (0.41) <sup>bc</sup>	0.22 (0.28) <sup>bc</sup>	0.36 (0.22) <sup>c</sup>	312.2	< 0.001
Red-eyed vireo	0.73 (0.13) <sup>a</sup>	1.62 (0.1) <sup>b</sup>	1.34 (0.1) <sup>b</sup>	1.34 (0.11) <sup>b</sup>	1.25 (0.12) <sup>b</sup>	116.6	< 0.001
Scarlet tanager	0.43 (0.17)	0.5 (0.19)	0.46 (0.17)	0.5 (0.19)	0.54 (0.18)	216.6	0.9
Tufted titmouse	0.19 (0.25)	0.24 (0.27)	0.2 (0.27)	0.31 (0.24)	0.29 (0.24)	267.9	0.536
Veery	1.05 (0.11) <sup>a</sup>	1.47 (0.11) <sup>a</sup>	1.01 (0.12) <sup>a</sup>	1.47 (0.11) <sup>a</sup>	1.32 (0.11) <sup>a</sup>	175.5	0.032
Worm-eating warbler	0.1 (0.35)	0.09 (0.45)	0.01 (1)	0.05 (0.58)	0.08 (0.45)	308	0.196
Wood thrush	0.35 (0.19) <sup>ab</sup>	0.52 (0.18) <sup>b</sup>	0.17 (0.29) <sup>a</sup>	0.45 (0.2) <sup>b</sup>	0.24 (0.27) <sup>ab</sup>	317	0.003
Yellow-bellied sapsucker	0.18 (0.26) <sup>b</sup>	0.38 (0.21) <sup>ab</sup>	0.17 (0.29) <sup>b</sup>	0.52 (0.18) <sup>a</sup>	0.19 (0.3) <sup>b</sup>	261	< 0.001
Yellow-rumped warbler	0.42 (0.17) <sup>a</sup>	0.12 (0.38) <sup>b</sup>	0.13 (0.33) <sup>b</sup>	0.16 (0.33) <sup>ab</sup>	0.22 (0.28) <sup>ab</sup>	338.7	0.001
Yellow-throated vireo	0.08 (0.38)	0.1 (0.41)	0.13 (0.33)	0.05 (0.58)	0.05 (0.58)	302	0.507
		-	-		-		

Results from pairwise ANOSIM analysis of species communities between among cover types with
Bonferroni corrected p-values.

Comparison	R	p (corrected)
Spruce-Deciduous	0.304	0.01
Spruce-Hemlock	0.274	0.01
Spruce-Mixed	0.179	0.01
Spruce-Pine	0.146	0.01
Deciduous-Hemlock	0.127	0.01
Deciduous-Mixed	0.076	0.01
Deciduous-Pine	0.153	0.01
Hemlock-Mixed	0.135	0.01
Hemlock-Pine	0.146	0.01
Mixed-Pine	0.022	0.26

## Table 6

Summary of SIMPER results for between-group dissimilarities in species communities. The top six contributing species are listed for each pairwise comparison along with their respective contribution percentages. Species' common and scientific names are presented in Table 1.

Comparison	Top Contributing Species							
Hemlock-Spruce	RBNU (2.4%)	GCKI (2.2%)	EATO (1.9%)	BLBW (1.9%)	AMRE (1.8%)	BRCR (1.8%)		
Hemlock-Deciduous	EAWP (2.1%)	EATO (2%)	AMRE (2%)	BHVI (1.9%)	PIWA (1.9%)	CSWA (1.9%)		
Hemlock-Mixed	EATO (2%)	PIWA (1.9%)	AMRE (1.9%)	BHVI (1.8%)	CSWA (1.8%)	BLJA (1.8%)		
Hemlock-Pine	EATO (2%)	PIWA (2%)	AMRE (1.9%)	BCCH (1.9%)	BHVI (1.9%)	BLJA (1.9%)		
Spruce-Deciduous	RBNU (2.2%)	BLBW (2%)	GCKI (2%)	EAWP (1.8%)	BRCR (1.7%)	BLJA (1.6%)		
Spruce-Mixed	RBNU (1.9%)	GCKI (1.9%)	BAWW (1.6%)	BRCR (1.6%)	BLBW (1.5%)	BLJA (1.5%)		
Spruce-Pine	GCKI (1.8%)	RBNU (1.8%)	BCCH (1.6%)	BRCR (1.6%)	BLBW (1.6%)	BAWW (1.5%)		
Deciduous-Mixed	BAWW (1.8%)	EAWP (1.7%)	BLJA (1.6%)	YBSA (1.6%)	CSWA (1.6%)	SCTA (1.6%)		
Deciduous-Pine	EAWP (1.8%)	BCCH (1.8%)	BLJA (1.7%)	BAWW (1.7%)	SCTA (1.7%)	CSWA (1.7%)		
Mixed-Pine	BCCH (1.6%)	SCTA (1.6%)	CSWA (1.6%)	BLJA (1.6%)	BLBW (1.6%)	YBSA (1.5%)		

Mean values for habitat variables with standard errors. Common superscripts represent lack of significant difference among cover types according to Kruskal–Wallis tests with post-hoc pairwise comparisons of group means.

Variable	Spruce	Deciduous	Hemlock	Mixed	Pine	р
% Conifer	0.93 (0.01)ª	0.13 (0.02) <sup>d</sup>	0.63 (0.02) <sup>c</sup>	0.54 (0.03) <sup>c</sup>	0.75 <mark>(</mark> 0.03) <sup>b</sup>	< 0.001
Basal Area: Spruce	160.24 (7.18) <sup>ª</sup>	0 (0) <sup>b</sup>	0.14 (0.14) <sup>b</sup>	0 (0) <sup>b</sup>	0 (0) <sup>b</sup>	< 0.001
Basal Area: Hemlock	0 (0) <sup>d</sup>	3.45 (1.75) <sup>cd</sup>	80.85 (5.37)ª	12.41 (3.45) <sup>b</sup>	9.15 (2.86) <sup>bc</sup>	< 0.001
Basal Area: Pine	14.29 (3.49) <sup>b</sup>	11.72 (2.15) <sup>b</sup>	16.9 (2.86) <sup>b</sup>	54.83 (4.5)ª	84.41 (6.31) <sup>ª</sup>	< 0.001
Basal Area: Deciduous	13.1 (2.68) <sup>d</sup>	97.59 (4.89)ª	53.38 (3.45) <sup>b</sup>	60.34 (4.85)b	29.15 (3.14) <sup>c</sup>	< 0.001
Basal Area: Total	187.62 (6.43)ª	112.76 (5.58) <sup>c</sup>	151.27 (5.86) <sup>b</sup>	127.59 (5.46) <sup>bc</sup>	122.71 (6.47) <sup>c</sup>	< 0.001
% Understory Cover	0.34 (0.03) <sup>b</sup>	0.55 (0.03)ª	0.24 (0.03) <sup>b</sup>	0.48 (0.04) <sup>a</sup>	0.6 (0.03)ª	< 0.001
% Bare Ground	0.5 (0.03) <sup>b</sup>	0.25 (0.03) <sup>c</sup>	0.68 (0.03) <sup>a</sup>	0.36 (0.04) <sup>c</sup>	0.36 (0.03) <sup>c</sup>	< 0.001
% Canopy Closure	83.82 (2.15) <sup>b</sup>	85.28 (2.55) <sup>ab</sup>	90.31 (0.61) <sup>ª</sup>	88.09 (1.28) <sup>ab</sup>	85.38 (1.25) <sup>b</sup>	< 0.001
Small Shrub Density (stems / m <sup>2</sup> )	0.1 (0.02) <sup>bc</sup>	0.17 (0.02)ª	0.05 (0.01) <sup>c</sup>	0.38 (0.14) <sup>ab</sup>	0.28 (0.05)ª	< 0.001
Large Shrub Density (stems / m <sup>2</sup> )	0.03 (0.01) <sup>b</sup>	0.06 (0.01) <sup>a</sup>	0.03 (0) <sup>b</sup>	0.06 (0.01)ª	0.08 (0.01)ª	< 0.001

# CHAPTER 4 FIGURES

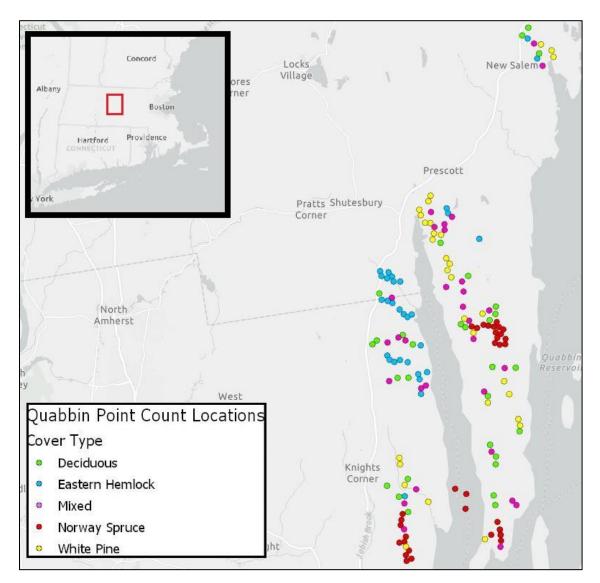


Figure 1. Point count locations for the Quabbin study site, Hampshire and Franklin counties, MA.

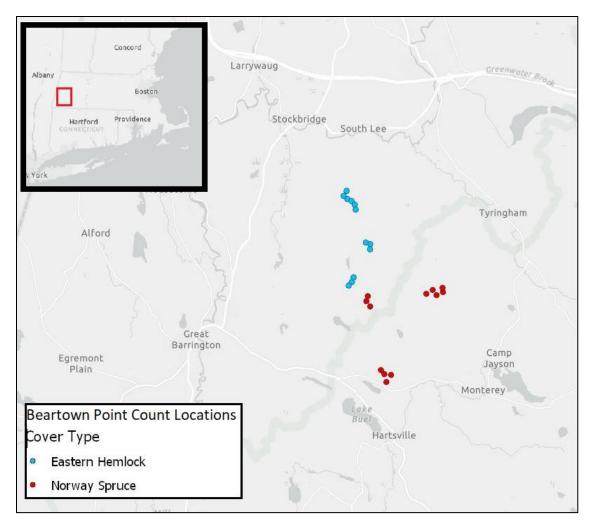
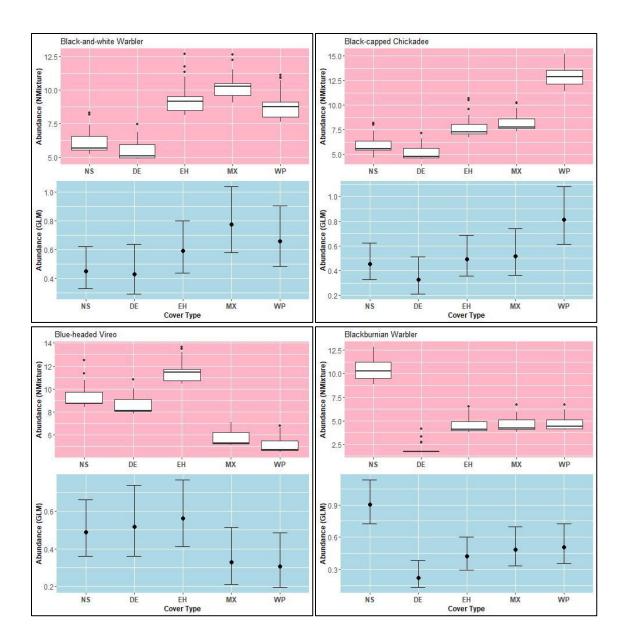
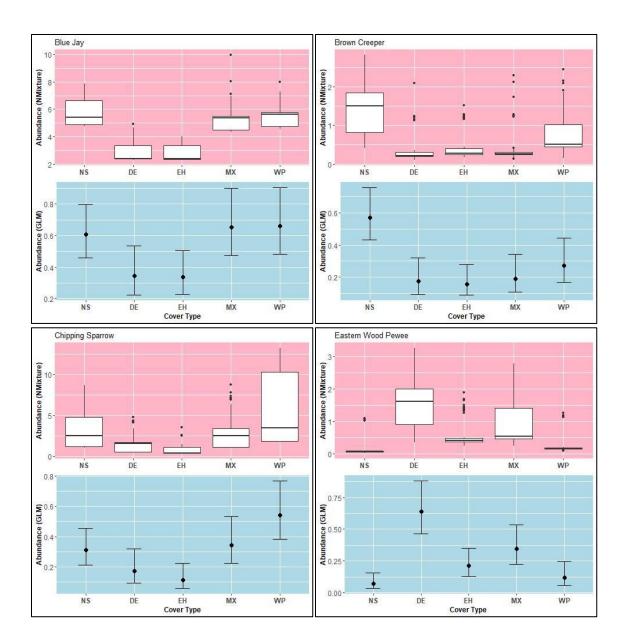
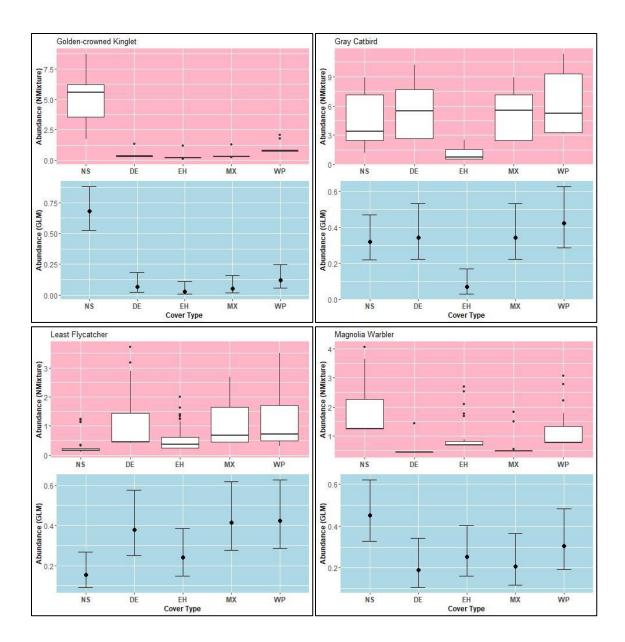
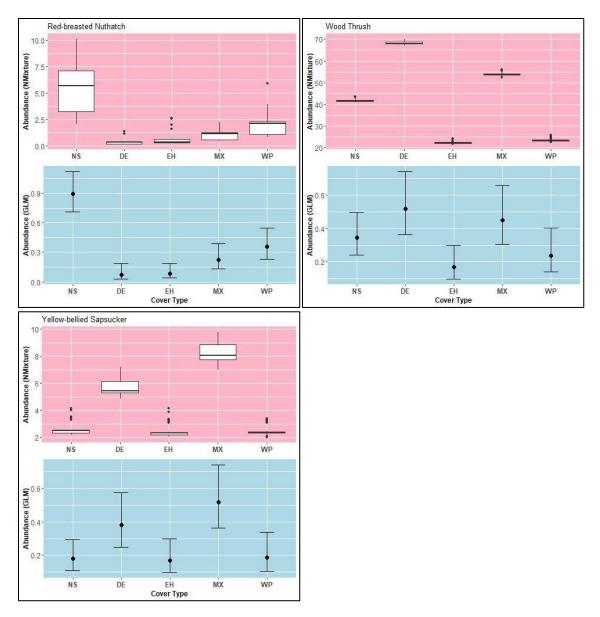


Figure 2. Point count locations for the Beartown study site, Berkshire county, MA.

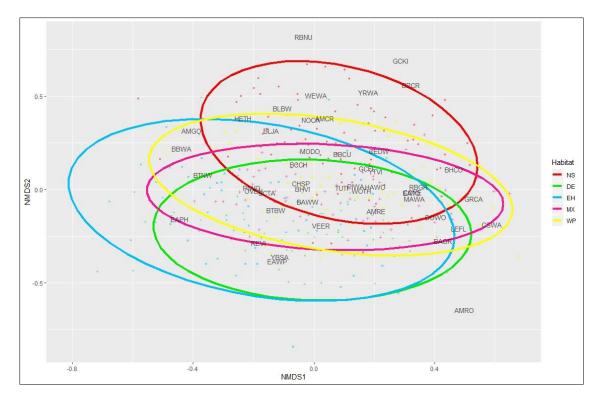




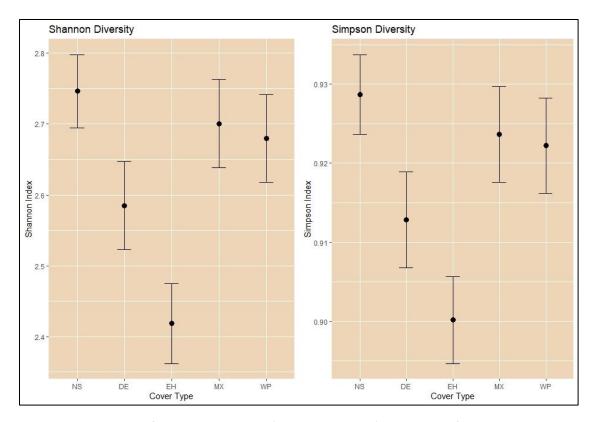




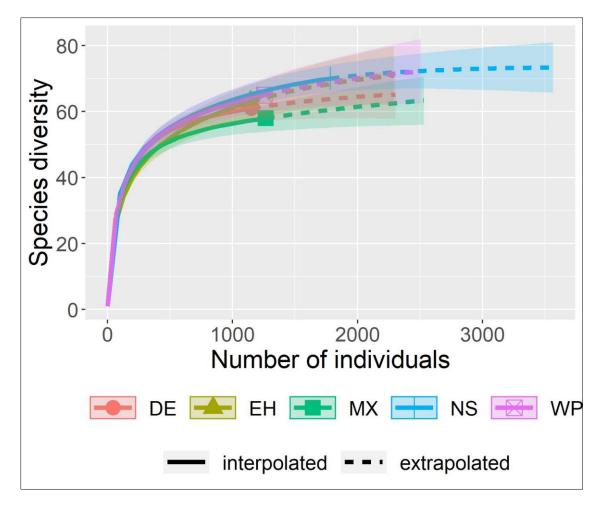
**Figure 3.** Comparison of abundance estimates from N-Mixture models and GLMs (species for which cover type was not included in top N-Mixture models or did not pass goodness-of-fit tests excluded). NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine



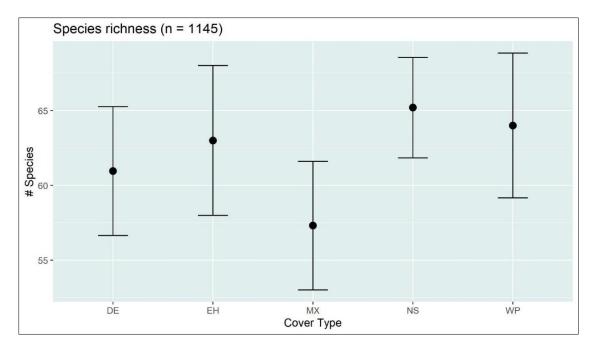
**Figure 4.** Non-metric multidimensional scaling ordination based on cover type for all 47 species observed in at least 5 points. Colored confidence interval ellipses encompass 95% of all points for each respective cover type and species alpha codes are overlain to show the species' associations to each cover type. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine. Species' alpha codes are presented in Table 1.



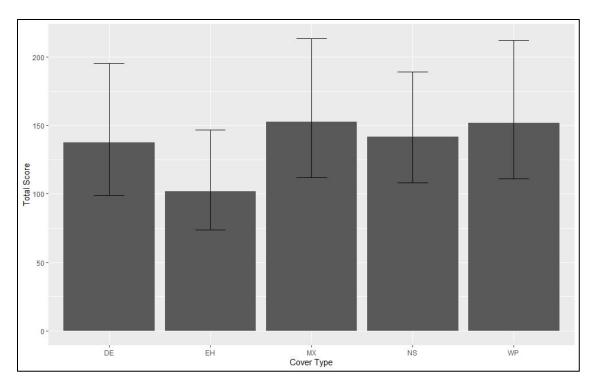
**Figure 5**. Mean values of two diversity indices (Shannon, Simpson) with 95% confidence intervals compared among cover types. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine



**Figure 6.** Sample based rarefaction curves with 95% confidence intervals comparing expected number of unique species as a function of total individuals sampled. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine



**Figure 7.** Number of expected unique species with 95% confidence intervals when 1145 individuals have been sampled. Values derived from individual based rarefaction. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine



**Figure 8.** Pooled PIF scores weighted by abundance with 95% confidence intervals. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine

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