



Bird communities reveal the ecological value of non-native Norway spruce plantations in Massachusetts, USA

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ABSTRACT

The establishment of monoculture plantations of non-native tree species is a common practice for supplementing native timber stocks. Since native wildlife species may lack co-evolved traits needed to successfully exploit non-native tree species, non-native plantations are expected to provide inferior habitat for native biodiversity. However, some studies report that plantations may increase net biodiversity at the landscape scale by introducing novel habitats or supplementing existing natural forests. We used point counts to sample birds in 2016 and 2017 in mature Norway spruce (*Picea abies*) plantations in western Massachusetts, as well as representative native forest types, to evaluate bird use of these plantations relative to native forest types. Our findings showed that overall species richness for spruce plantations was similar to that of native forest habitats, and that several native conifer-dependent species (red-breasted nuthatch (*Sitta canadensis*), golden-crowned kinglet (*Regulus satrapa*), blackburnian warbler (*Setophaga fusca*), and brown creeper (*Certhia americana*)) were significantly more abundant in spruce plantations relative to native deciduous, hemlock, and mixed stands. Bird species reported to associate with eastern hemlock (*Tsuga canadensis*), such as blue-headed vireo (*Vireo solitarius*) 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.

1. Introduction

Total forested area has decreased globally in recent decades (Keenan et al., 2015). Although some losses are mitigated through natural reforestation efforts, additional reforestation is achieved through the implementation of planted forests, which increased at a rate of 1.84 % annually from 1990 to 2015 (Keenan et al., 2015). The loss of natural forest and subsequent replacement with planted forest has implications for wildlife species that depend on forested habitats. Plantations differ from surrounding natural forests (Carnus et al. 2006) and are characterized by simplified vegetation, composition, and age structure (Hanuski et al. 1997). Also, production plantations are subjected to disruptive management regimes such as short rotation harvests and high

density planting (Carnus et al. 2006) that may negatively affect some wildlife species (Demarais et al. 2017). Nevertheless, the impact of plantation forestry on wildlife depends on a number of variables including forest structure and composition (Stephens and Wagner 2007). For example, Humphrey et al. (2002) concluded that non-native 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.

Norway spruce (*Picea abies*), a species native to Europe, is 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 is restricted to higher elevations and considered

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Table 1

Top models of abundance as a function of forest type using N -mixture models. Covariates for “ λ ” affect abundance, those for “ p ” affect detectability. Data are from point count surveys we conducted in Norway spruce plantations and native forest types during 2016 and 2017 in Massachusetts, USA. Scientific names are presented in Appendix 1.

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

[‡] obs = Observer.

[†] λ Mixture: P = Poisson, ZIP = Zero-inflated Poisson.

vulnerable to climate change and other stressors (Massachusetts Climate Adaptation Partnership 2015), Norway spruce plantations may supplement native forest stands by introducing a dense-canopy, short-needle coniferous habitat component. These characteristics are similar to those provided by eastern hemlock (*Tsuga canadensis*), a conifer native to Massachusetts (DeGraaf and Yamasaki 2001). Eastern hemlock populations have declined due to the hemlock woolly adelgid (*Adelges tsugae*), an invasive aphid-like insect (Paradis et al. 2008, Case et al. 2017), resulting in fewer pure hemlock stands on the landscape (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 et al., 1998, Paradis et al. 2008, Orwig et al. 2012, 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).

Given the general uncertainty about the effects of plantation forestry on biodiversity, especially within the Northeastern United States, and the potential for Norway spruce to accommodate species associated with declining eastern hemlock, we compared the breeding avifauna of Norway spruce plantations and native forest types, including eastern hemlock. Our primary objective was to compare bird communities among forest types, with an emphasis on the comparison between Norway spruce plantations and eastern hemlock stands, to determine the extent to which Norway spruce supports native birds, both currently and in the face of continued hemlock decline. We hypothesized that bird species associated with short needle leaf trees would have elevated abundance in spruce stands relative to deciduous stands.

2. Methods

2.1. Study area

This study was conducted during 2016 and 2017 at two separate locations in Massachusetts: Quabbin Reservation (42.38° N, 72.36° W) and Beartown State Forest (42.21 N, 73.23 W). Elevations ranged from

approximately 175–325 m at the Quabbin site, and 400–600 m at Beartown. Both sites were characterized predominantly by hardwood-conifer mixed forests. For the region, average forest age was ~ 75 years (de La Crétaz et al., 2010). Study sites were selected based on the presence of mature spruce plantation patches. The spruce plantation patches ranged from approximately 2 to 55 ha and were ~ 80 years old, which is similar to the average age of surrounding native stands.

Initial selection of point count locations was made based on forest cover GIS layers provided by the Massachusetts Department of Conservation and Recreation. We selected 150 point count locations at the Quabbin stratified across five distinct forest types (30 points per forest type), which were characterized by dominant tree species, according to GIS data. The five forest types were Norway spruce, eastern hemlock, white pine (*Pinus strobus*), deciduous, and conifer-deciduous codominant mix, which was composed primarily of red-oak (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*) birches (*Betula* spp.), as well as white pine and eastern hemlock. 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 (Tingley et al. 2002). White pine was the most widespread native conifer in the study area, and as such, was selected as the species with the greatest potential to support hemlock associated species. Deciduous and mixed stands were also included because they would likely replace Norway spruce stands in the event they were converted through silviculture. These forest types comprised the majority of forest cover within the study region. At the Beartown site 24 points were selected using the same method but were limited to Norway spruce and eastern hemlock (12 each). Pine, deciduous, and mixed stands were not sampled at the Beartown site due to time constraints.

We sampled birds using point count surveys (Ralph et al. 1995). Survey points were spaced ≥ 200 m apart and located ≥ 50 m from the nearest edge or stand boundary. To facilitate access, point selection was

Table 2

N-Mixture model coefficients with standard errors from (species for which forest 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. Data are from point count surveys in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. Scientific names are presented in [Appendix 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 vireo	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 (1.69)	0.78 (0.32)	−0.06 (0.38)	1.15 (0.30)	−0.04 (0.40)

constrained to areas within 100 m of trails or narrow access roads. Trails were narrow with limited management, and in most cases did not interrupt canopy coverage, so their effect on point counts was likely minimal ([Deluca and King 2014](#)). Points were randomly selected using stand maps and field-checked to ensure they represented the assigned forest type. In cases where points were deemed unsuitable (wetland areas, clearings, too difficult to access, etc.) a replacement was chosen based on the same criteria described above.

2.2. Field sampling

Point count surveys were conducted over the course of two breeding seasons from mid-May to early-August 2016–2017. Surveys were 10-min in duration, during which observers recorded all birds heard or seen within 50 m of the survey point that showed signs of territoriality or use of the sampled habitat. Each point was visited three times each year within five hours of dawn during periods of no or light wind and precipitation. Observers and the order in which counts were conducted were rotated to minimize biases associated with observers or time of day ([Ralph et al. 1995](#)).

Vegetative structure and composition were quantified at each point. Tree basal area by species and size class was measured within variable radius plots using a 10-factor wedge prism ([Šálek and Zahradník, 2008](#)). Vegetation height was measured at 5 points 3 m apart in each cardinal direction (20 points per plot) in two height classes: herbaceous (0–0.5 m) and understory (0.5–3.0 m). Stems > 1.5 m in height were counted on a 5-m radius subplot in two size classes, shrubs (<2.5 cm) and saplings (>2.5 – 8 cm dbh). Finally, canopy closure was measured using the average of five densiometer measurements taken 15 m from the survey

Table 3

χ^2 and p-values representing overall effect of forest on type bird abundance using ANOVA. $P < 0.05$ are significant. Data are from point count surveys in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. Scientific names are presented in [Appendix 1](#).

Species	χ^2	p
American crow	353.3	0.063
American goldfinch	323	0.948
American redstart	169.6	0.001
American robin	357	0.007
Baltimore oriole	311	0.037
Black-and-white warbler	201	0.059
Black-billed cuckoo	290	0.038
Bay-breasted warbler	350.8	0.001
Black-capped chickadee	272.3	0.007
Brown-headed cowbird	310	0.697
Blue-headed vireo	230.5	0.094
Blackburnian warbler	220.7	< 0.001
Blue jay	275.6	0.007
Brown creeper	281.1	< 0.001
Black-throated blue warbler	200.8	0.067
Black-throated green warbler	227.9	0.014
Cedar waxwing	397.8	0.385
Chipping sparrow	372.5	< 0.001
Common yellowthroat	242.5	0.236
Chestnut-sided warbler	275.6	0.068
Downey woodpecker	300	0.224
Eastern phoebe	320.2	0.026
Eastern towhee	200.4	0.001
Eastern wood pewee	260.2	< 0.001
Great crested flycatcher	343.8	0.326
Golden-crowned kinglet	265.8	< 0.001
Gray catbird	248.7	< 0.001
Hairy woodpecker	288	0.313
Hermit thrush	344.9	0.295
Least flycatcher	283.9	0.007
Magnolia warbler	282.7	0.03
Mourning dove	301.5	0.204
Northern cardinal	329.7	0.03
Ovenbird	125.4	0.746
Pine warbler	196.7	< 0.001
Pileated woodpecker	299	0.095
Rose-breasted grosbeak	284.9	0.148
Red-breasted nuthatch	312.2	< 0.001
Red-eyed vireo	116.6	< 0.001
Scarlet tanager	216.6	0.9
Tufted titmouse	267.9	0.536
Veery	175.5	0.032
Worm-eating warbler	308	0.196
Wood thrush	317	0.003
Yellow-bellied sapsucker	261	< 0.001
Yellow-rumped warbler	338.7	0.001
Yellow-throated vireo	302	0.507

point in each cardinal direction.

2.3. Statistical analyses

N-mixture models ([Royle et al. 2004](#)) were used to analyze the abundance (λ) of bird species as a function of forest type while allowing for potential heterogeneity in detectability (p) using the *pcount* function in the *unmarked* R package ([Fiske and Chandler 2011](#)). Each survey point was combined with the survey year to create a unique point-year identity, which allowed us to analyze both years of data together similar to a single season model ([Fogg et al. 2014](#)). 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. 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](#)).

Table 4

Mean abundance with standard errors from GLM models. Forest types with differing superscripts represent significant difference among them according to Tukey post hoc pairwise comparisons of group means. Species with no superscripts or common superscripts indicate no significant difference among those forest types. Data are from point count surveys in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. Scientific names are presented in [Appendix 1](#).

Species	Spruce	Deciduous	Hemlock	Mixed	Pine
American crow	0.13 (0.3)	0.07 (0.5)	0.04 (0.58)	0.02 (1)	0.03 (0.71)
American goldfinch	0.02 (0.71)	0.03 (0.71)	0.01 (1)	0.02 (1)	0.02 (1)
American redstart	0.81 (0.12) ^{ab}	1.16 (0.12) ^b	0.51 (0.17) ^a	0.98 (0.13) ^b	0.9 (0.14) ^{ab}
American robin	0.04 (0.58) ^a	0.21 (0.29) ^b	0.06 (0.5) ^{ab}	0.05 (0.58) ^{ab}	0.15 (0.33) ^{ab}
Baltimore oriole	0.02 (0.71)	0.12 (0.38)	0.01 (1)	0.05 (0.58)	0.1 (0.41)
Black-and-white warbler	0.45 (0.16)	0.43 (0.2)	0.59 (0.15)	0.78 (0.15)	0.66 (0.16)
Black-billed cuckoo	0.14 (0.29)	0.16 (0.33)	0.03 (0.71)	0.1 (0.41)	0.19 (0.3)
Bay-breasted warbler	0.26 (0.21) ^a	0.1 (0.41) ^{ab}	0.27 (0.23) ^a	0.12 (0.38) ^{ab}	0.03 (0.71) ^b
Black-capped chickadee	0.45 (0.16) ^{ab}	0.33 (0.23) ^a	0.49 (0.17) ^{ab}	0.52 (0.18) ^{ab}	0.81 (0.14) ^b
Brown-headed cowbird	0.06 (0.45)	0.09 (0.45)	0.03 (0.71)	0.07 (0.5)	0.07 (0.5)
Blue-headed vireo	0.49 (0.16)	0.52 (0.18)	0.56 (0.16)	0.33 (0.23)	0.31 (0.24)
Blackburnian warbler	0.9 (0.11) ^a	0.22 (0.28) ^b	0.42 (0.18) ^b	0.48 (0.19) ^b	0.51 (0.18) ^{ab}
Blue jay	0.61 (0.14)	0.34 (0.22)	0.34 (0.2)	0.66 (0.16)	0.66 (0.16)
Brown creeper	0.57 (0.14) ^a	0.17 (0.32) ^b	0.15 (0.3) ^b	0.19 (0.3) ^b	0.27 (0.25) ^{ab}
Black-throated blue warbler	0.58 (0.14)	0.97 (0.13)	0.77 (0.13)	0.79 (0.15)	0.59 (0.17)
Black-throated green warbler	1.31 (0.1) ^{ab}	0.88 (0.1) ^a	1.51 (0.1) ^b	1.12 (0.12) ^{ab}	1.08 (0.12) ^{ab}
Cedar waxwing	0.15 (0.28)	0.1 (0.41)	0.06 (0.5)	0.14 (0.35)	0.14 (0.35)
Chipping sparrow	0.31 (0.2) ^{ab}	0.17 (0.32) ^b	0.11 (0.35) ^b	0.34 (0.22) ^{ab}	0.54 (0.18) ^a
Common yellowthroat	0.92 (0.11)	0.69 (0.16)	0.68 (0.14)	0.93 (0.14)	0.92 (0.14)
Chestnut-sided warbler	0.77 (0.12)	0.71 (0.16)	0.48 (0.17)	0.84 (0.14)	0.81 (0.14)
Downy woodpecker	0.05 (0.5)	0.14 (0.35)	0.06 (0.5)	0.14 (0.35)	0.1 (0.41)
Eastern phoebe	0.04 (0.58)	0.05 (0.58)	0.14 (0.32)	0.12 (0.38)	0.02 (1)
Eastern towhee	0.99 (0.11) ^b	0.86 (0.14) ^{ab}	0.49 (0.17) ^a	1.12 (0.12) ^b	0.97 (0.13) ^b
Eastern wood pewee	0.07 (0.41) ^a	0.64 (0.16) ^b	0.21 (0.26) ^{ac}	0.34 (0.22) ^{bc}	0.12 (0.38) ^{ac}
Great crested flycatcher	0.07 (0.41)	0.12 (0.38)	0.03 (0.71)	0.09 (0.45)	0.1 (0.41)
Golden-crowned kinglet	0.68 (0.13) ^a	0.07 (0.5) ^b	0.03 (0.71) ^b	0.05 (0.58) ^b	0.12 (0.38) ^b
Gray catbird	0.32 (0.19) ^b	0.34 (0.22) ^b	0.07 (0.45) ^a	0.34 (0.22) ^b	0.42 (0.2) ^b
Hairy woodpecker	0.13 (0.3)	0.17 (0.32)	0.06 (0.5)	0.16 (0.33)	0.14 (0.35)
Hermit thrush	0.23 (0.23)	0.1 (0.41)	0.14 (0.32)	0.21 (0.29)	0.12 (0.38)
Least flycatcher	0.15 (0.28) ^a	0.38 (0.21) ^{ab}	0.24 (0.24) ^{ab}	0.41 (0.2) ^b	0.42 (0.2) ^b
Magnolia warbler	0.45 (0.16)	0.19 (0.3)	0.25 (0.24)	0.21 (0.29)	0.31 (0.24)
Mourning dove	0.14 (0.29)	0.09 (0.45)	0.06 (0.5)	0.19 (0.3)	0.12 (0.38)
Northern cardinal	0.11 (0.33)	0.03 (0.71)	0.01 (1)	0.02 (1)	0.1 (0.41)
Ovenbird	2.31 (0.07)	2.62 (0.08)	2.32 (0.08)	2.53 (0.08)	2.42 (0.08)

Table 4 (continued)

Species	Spruce	Deciduous	Hemlock	Mixed	Pine
Pine warbler	0.79 (0.12) ^{ab}	0.66 (0.16) ^a	0.56 (0.16) ^a	1.26 (0.12) ^{bc}	1.42 (0.11) ^c
Pileated woodpecker	0.13 (0.3)	0.09 (0.45)	0.08 (0.41)	0.14 (0.35)	0.02 (1)
Rose-breasted grosbeak	0.24 (0.22)	0.17 (0.32)	0.1 (0.38)	0.28 (0.25)	0.19 (0.3)
Red-breasted nuthatch	0.89 (0.12) ^a	0.07 (0.5) ^b	0.08 (0.41) ^{bc}	0.22 (0.28) ^{bc}	0.36 (0.22) ^c
Red-eyed vireo	0.73 (0.13) ^a	1.62 (0.1) ^b	1.34 (0.1) ^b	1.34 (0.11) ^b	1.25 (0.12) ^b
Scarlet tanager	0.43 (0.17)	0.5 (0.19)	0.46 (0.17)	0.5 (0.19)	0.54 (0.18)
Tufted titmouse	0.19 (0.25)	0.24 (0.27)	0.2 (0.27)	0.31 (0.24)	0.29 (0.24)
Veery	1.05 (0.11)	1.47 (0.11)	1.01 (0.12)	1.47 (0.11)	1.32 (0.11)
Worm-eating warbler	0.1 (0.35)	0.09 (0.45)	0.01 (1)	0.05 (0.58)	0.08 (0.45)
Wood thrush	0.35 (0.19) ^{ab}	0.52 (0.18) ^b	0.17 (0.29) ^a	0.45 (0.2) ^b	0.24 (0.27) ^{ab}
Yellow-bellied sapsucker	0.18 (0.26) ^b	0.38 (0.21) ^{ab}	0.17 (0.29) ^b	0.52 (0.18) ^a	0.19 (0.3) ^b
Yellow-rumped warbler	0.42 (0.17) ^a	0.12 (0.38) ^b	0.13 (0.33) ^b	0.16 (0.33) ^{ab}	0.22 (0.28) ^{ab}
Yellow-throated vireo	0.08 (0.38)	0.1 (0.41)	0.13 (0.33)	0.05 (0.58)	0.05 (0.58)

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 intercept-only 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 ($P < 0.05$; [Smetzer et al. 2014](#)). 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 forest type was set as the intercept in order to assess the differences in mean bird abundances relative to native forest types. The difference in means between spruce and other forest types was considered significant if 95 % confidence intervals of the parameter estimates did not overlap zero. 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](#)).

For species that were too scarce to analyze using N -mixture models, we compared raw point count data among forest types using generalized linear models (GLMs), with Tukey post hoc pairwise comparisons of group means. This analysis was restricted to species that were observed at least once in each forest type. For each survey point, the highest observed count value across all within-year 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. Given our study objective of comparing relative differences between forest types, relative abundance was deemed sufficient for less common species ([Johnson 2008](#)).

Analysis of similarity (ANOSIM) was used to test for significant differences in avian communities among forest types ([Clarke 1993](#)) using the maximum counts with the R package *vegan* ([Jari Oksanen et al. 2019](#)). Pairwise ANOSIM comparisons were made for each combination

Table 5

Mean values for habitat variables with standard errors. Common superscripts represent lack of significant difference among forest types according to Kruskal–Wallis tests with post-hoc pairwise comparisons of group means. Data are from point count locations in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. BA = Basal Area, DBH = Diameter at Breast Height.

Variable	Spruce	Deciduous	Hemlock	Mixed	Pine	p
% Conifer	0.93 (0.01) ^a	0.13 (0.02) ^d	0.63 (0.02) ^c	0.54 (0.03) ^c	0.75 (0.03) ^b	< 0.001
BA: Spruce	160.2 (7.18) ^a	0 (0) ^b	0.14 (0.14) ^b	0 (0) ^b	0 (0) ^b	< 0.001
BA: Hemlock	0 (0) ^d	3.45 (1.75) ^{cd}	80.85 (5.37) ^a	12.41 (3.45) ^b	9.15 (2.86) ^{bc}	< 0.001
BA: Pine	14.3 (3.49) ^b	11.7 (2.15) ^b	16.9 (2.86) ^b	54.8 (4.5) ^a	84.4 (6.31) ^a	< 0.001
BA: Deciduous	13.1 (2.68) ^d	97.6 (4.89) ^a	53.4 (3.45) ^b	60.3 (4.85) ^b	29.2 (3.14) ^c	< 0.001
Basal Area: Total	187.6 (6.43) ^a	112.7 (5.58) ^c	151.3 (5.86) ^b	127.6 (5.46) ^{bc}	122.7 (6.47) ^c	< 0.001
% Understory Cover	0.34 (0.03) ^b	0.55 (0.03) ^a	0.24 (0.03) ^b	0.48 (0.04) ^a	0.60 (0.03) ^a	< 0.001
% Bare Ground	0.50 (0.03) ^b	0.25 (0.03) ^c	0.68 (0.03) ^a	0.36 (0.04) ^c	0.36 (0.03) ^c	< 0.001
% Canopy Closure	83.8 (2.15) ^b	85.3 (2.55) ^{ab}	90.3 (0.61) ^a	88.1 (1.28) ^{ab}	85.4 (1.25) ^b	< 0.001
Small Shrub Density	0.1 (0.02) ^{bc}	0.17 (0.02) ^a	0.05 (0.01) ^c	0.38 (0.14) ^{ab}	0.28 (0.05) ^a	< 0.001
Large Shrub Density	0.03 (0.01) ^b	0.06 (0.01) ^a	0.03 (0) ^b	0.06 (0.01) ^a	0.08 (0.01) ^a	< 0.001
Snag Count	1.6 (0.2) ^a	0.69 (0.18) ^b	1.22 (0.19) ^{ab}	0.9 (0.19) ^b	0.54 (0.12) ^b	< 0.001
Mean DBH	39.1 (0.9) ^b	39.7 (1.21) ^b	44.2 (0.73) ^a	44.74 (1.09) ^a	42.51 (1.39) ^a	< 0.001

Table 6

Results from pairwise ANOSIM analysis of species communities among forest types with Bonferroni corrected p-values. Data are from point count surveys in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. Scientific names are presented in [Appendix 1](#).

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

of forest 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](#)). The Shannon-Wiener ([Shannon and Weaver, 1949](#)) diversity index was calculated and compared among forest 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 forest 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](#)).

Variables derived from vegetation surveys were not normally distributed and therefore were analyzed using non-parametric methods. Differences in habitat variables among forest types was assessed using Kruskal–Wallis tests ([Kruskal and Wallis 1953](#)) with post-hoc pairwise comparison of group means.

3. Results

We detected 82 bird species of which 27 were observed in $\geq 10\%$ of all surveys and were included in our initial analysis using *N*-mixture models ([Appendix A](#)). 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 1](#)). Model convergence was achieved for all species with forest 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 ($P < 0.05$). However, 10 species showed a significant level of underdispersion ($P > 0.95$).

Golden-crowned kinglet, red-breasted nuthatch, and Blackburnian warbler (scientific names in [Appendix A](#)) were more abundant in Norway spruce than in any of the native forest types ([Table 2](#)). Magnolia warblers and blue jays were more abundant in spruce when compared to hemlock, deciduous, and mixed stands but were similar in abundance as within pine stands. Blue-headed vireos were more abundant in spruce stands than pine stands, and gray catbirds were more abundant in spruce compared to mixed stands. Chipping sparrows were less abundant in deciduous and hemlock stands than in spruce but were more abundant in pine when compared to spruce. Black-and-white warblers were more abundant in mixed stands than spruce stands, black-capped chickadees were more abundant in pine compared to spruce stands, and yellow-bellied sapsuckers were more abundant in both deciduous and mixed stands compared to spruce stands. Eastern wood peewees were more abundant in native stands than in spruce, but numbers were similar in pine and spruce. Least flycatchers were less abundant in spruce than in deciduous, mixed, and pine stands.

There were 47 species that were analyzed using GLMs, including the 27 species that were also analyzed using *N*-Mixture models ([Appendix A](#)). Models containing forest type were supported for 26 of these species ([Table 3](#)) according to ANOVA. Golden-crowned kinglet and red-breasted nuthatch were more abundant in spruce than in all native forest types ([Table 4](#)), 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.

Results from ANOSIM analysis show bird communities differed among all forest types ($P < 0.05$), with the exception of mixed and pine stands, which did not differ ([Table 6](#)). The Shannon diversity index did not differ among spruce, mixed, and pine stands, yet diversity was

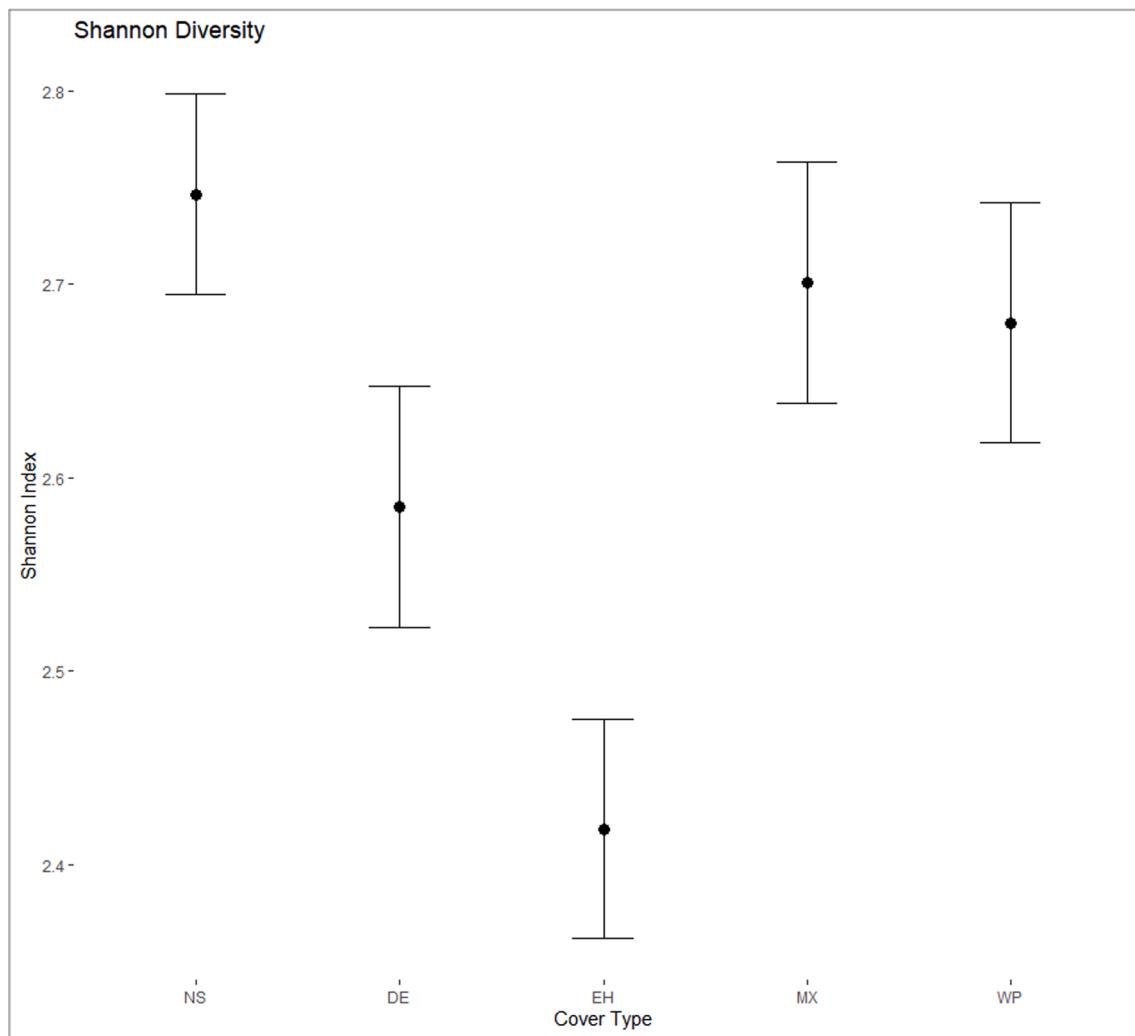


Fig. 1. Mean values for Shannon- Wiener diversity index with 95 % confidence intervals compared among forest types. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine. Data are from point count surveys we conducted in Norway spruce plantations and native forest types during 2016 and 2017 in Massachusetts, USA.

significantly higher in spruce than both deciduous and hemlock stands (Fig. 1). Diversity did not differ between deciduous, mixed, and pine stands, but these three forest types were more diverse than hemlock. Models containing only forest type as the predictor were supported over models containing an interaction effect between site and forest type for diversity index. Confidence intervals of species richness estimates from the individual-based rarefaction indicated species richness was similar across all forest types, with the exception of significantly higher species richness in Norway spruce stands compared to mixed deciduous coniferous stands (Fig. 2).

With the exception of percent canopy cover, all vegetation related habitat variables showed some level of significant difference among forest types (Table 5). 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 forest types. Spruce and hemlock stands also had similar densities of both shrubs and saplings. Spruce plantations had a higher total basal area and percent conifer amongst all forest types. Spruce stands also had a higher mean DBH when compared to other conifer dominant stands.

4. Discussion

Our findings that Norway spruce plantations supported native bird

species that were scarce or absent in native forest cover types, and that bird species diversity, species richness and community composition of Norway spruce plantations were similar to many of the native forest cover types, contrasts with many studies of biodiversity in non-native and monoculture tree plantations that report depauperate fauna (Felton et al. 2011, Castaño-Villa et al. 2014, Iezzi et al. 2018, Harris and Betts 2021). Previous studies reporting lower native biodiversity in exotic tree plantations attribute this pattern to lower plant species and structural diversity in plantations (Repenning and Labisky 1985, Thill and Koerth 2005). The plantations in our study were relatively old (~80 years) and had undergone some self-thinning due to mortality of individual trees. This likely resulted in greater vegetative diversity in these plantations compared to a commercially managed plantation that would have been harvested at an earlier stage (65–70 years; Vattenranta and Miina 1999). Nevertheless, the species identified by the SIMPER analysis (Table 7) as driving the community-level differences between Norway spruce and other cover types (golden-crowned kinglet, red-breasted nuthatch and blackburnian warbler) are all species that are known to be associated with coniferous tree species (Simpson 1976, Adams and Morrison 1993, Young et al. 2005), and thus self-thinning due to the relatively advanced age of the Norway spruce stands seems an unlikely explanation for the higher abundance of these species and distinctive community composition in Norway spruce stands.

The distinctive bird fauna of Norway spruce plantations may have

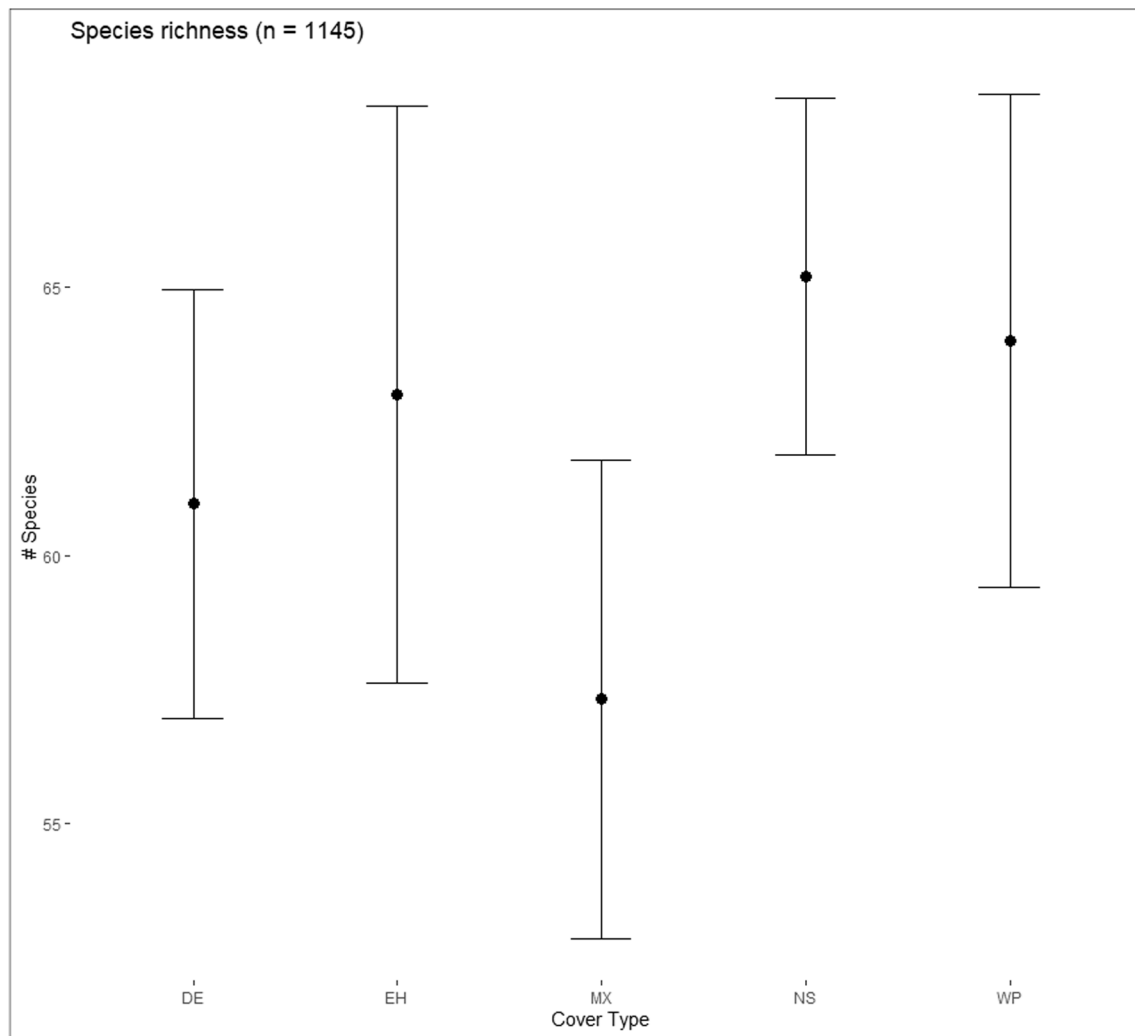


Fig. 2. Number of expected unique species with 95 % confidence intervals when 1145 individuals have been sampled. Values derived from individual based rarefaction. NS = Norway Spruce, DE = Deciduous, EH = Eastern Hemlock, MX = Mixed, WP = White Pine. Data are from point count surveys we conducted in Norway spruce plantations and native forest types during 2016 and 2017 in Massachusetts, USA.

been due in part to the greater dominance of conifer cover and greater overall basal area in Norway spruce stands compared to other forest types. For example, brown creepers, red-breasted nuthatches, golden-crowned kinglets, and blackburnian warblers are all species that are strongly associated with conifers (Simpson 1976, Adams and Morrison 1993, Young et al. 2005), and brown creepers are reported to be associated with large trees (Poulin et al. 2008). The other coniferous forest types in our study had a higher proportion of deciduous trees and lower basal area, raising the possibility that the association of these bird species with Norway spruce were due to higher levels of structural and compositional characteristics not necessarily unique to this forest type. The abundance of these bird species may have been more similar to Norway spruce if, for example, the pine or hemlock stands we studied had a similar proportion of coniferous trees and similar basal areas as Norway spruce. Nevertheless, other studies of the species we found to be spruce-associated suggest the distinctive avifauna of Norway spruce plantations may be due to distinctive characteristics of Norway spruce itself. For example, golden-crowned kinglets and red-breasted nuthatches were reported to be more abundant in spruce stands compared to pine and hemlock (Andrle 1971, Sabo and Holmes 1983), and golden-crowned kinglets at least are reported to use both Norway and native (white spruce *Picea glauca*) plantations in New York, USA, and to use other forest types sparingly (Andrle 1971). Brown creepers are known to be associated with flaking furrowed bark, which supports more

invertebrates and provides nesting sites relative to trees without these features. Although we didn't quantify these features, it is possible they were more pronounced in Norway spruce stands, though creepers are reported to nest readily in deciduous tree species as well (Poulin et al. 2008).

Only the red-eyed vireos were significantly less abundant in Norway spruce compared to native forest types. This species is known to forage preferentially on deciduous foliage (Robinson and Holmes 1984) and also typically nests in horizontal forks of deciduous trees (Lawrence 1953). These features are missing in Norway spruce stands. Presumably the native conifer forest types we studied had enough deciduous trees within them to support red-eyed vireo nesting and foraging. The absence of this bird species from Norway spruce stands demonstrates how non-native plantations could negatively affect native biodiversity if plantations displace large areas of native forest, and conversely, how native biodiversity can potentially be accommodated in plantations by supplementing with native tree species as well (Christian et al. 1998, Zurita et al. 2006, Lindbladh et al. 2017).

Several species reported to have strong association with eastern hemlock (black-throated green warbler, blackburnian warbler, and red-breasted nuthatch; Yamasaki et al., 1999) were more abundant in spruce plantations in our study and may be due to that fact that all hemlock stands at the Quabbin site had at least some hemlock woolly adelgid infestation, with varying degrees of hemlock mortality.

Table 7

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. Data are from point count surveys in Norway spruce plantations and native forest types, 2016–2017, Massachusetts, USA. Scientific names are presented in [Appendix 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 %)

Interestingly, spruce and hemlock stands had similar levels of standing snags, which were greater than the amount observed in other stand types. The diminished habitat quality of infested hemlock stands is a likely explanation for low numbers of these hemlock associated species, as well as lower species diversity ([Brown and Todd 2014](#), [Buchanan et al. 2016](#)). As woolly adelgid kills off hemlock, deciduous trees replace them shifting avian communities towards habitat generalists and deciduous associated species ([Toenies et al. 2018](#)). Although we were 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 ravines ([Foster et al. 2014](#)), leading to a higher proportion of survey points in hemlock stands near running streams relative to other stand types that may have made aural bird detections more difficult in hemlock stands. 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. Distance to stream was included in the top models of detection for only seven of the 27 species analyzed, however, and for only one of the species (red-breasted nuthatch) that was more abundant in spruce than hemlock. Thus, though stream noise may have affected abundance estimates for some species, it did not alter the overall pattern of greater numbers of putative hemlock associated species in Norway spruce stands. Our finding 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 or become absent all together ([Evans 2008](#)). Black-throated green warblers in particular were shown to be negatively affected by hemlock decline ([Brown and Todd 2014](#)) and could potentially find refuge in Norway spruce plantations.

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 about decreased precision as detection probability becomes low ([Barker et al. 2017](#)) or when there is

unmodeled heterogeneity ([Duarte et al. 2018](#)). Simulations conducted by [Couturier et al. \(2013\)](#) suggested 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 forest types, the relatively low detection probabilities led to high standard errors, so for these species *N*-mixture model estimates should not be interpreted as true abundance estimates. Nevertheless, *N*-mixture model results likely represent relative abundances among cover types ([Barker et al. 2017](#)), which is further suggested by their overall agreement agreed overall with the results of the GLMs.

5. Management implications

Although non-native tree plantations are reported to reduce native biodiversity in many situations, in our study Norway spruce plantations supported a number of bird species that were scarce or absent from native cover types. These included bird species that are reported to be strongly associated with eastern hemlock, which is experiencing widespread decline due to the invasive hemlock woolly adelgid. Thus, we conclude that the Norway spruce stands in our study area augmented native bird diversity, and their importance may increase as hemlock continues to decline. Because some native bird species are less abundant in Norway spruce than native cover types, widespread conversion of native forest to plantations would be deleterious. However, in cases where plantations are already present as a minor component of the overall forest cover, their retention or may contribute to the goal of representing a full complement of native bird species within a landscape, though this could depend on a number of additional factors not examined in this study. It is important to note that Norway spruce showed negligible levels of natural regeneration in our study sites, as the species is not noted for being invasive in the region ([Mottet et al 2021](#)) which limits its ability to displace native stands beyond its initial boundaries.

Although we saw evidence of bird species utilizing plantations at levels similar to native stands, the characteristics of plantations may have a more pronounced impact on other taxa that have reduced potential for dispersal ([Christian et al. 1998](#)). Other studies have observed detrimental effects on mammals, invertebrates, and plants ([Eleck et al 2001](#)) in other regions, necessitating similar studies in in our study area that assess those taxa. Furthermore, Norway spruce trees have been attributed to increases in forest soil acidity ([Binkley and Valentine, 1991](#)), which could be a main driver in altering the associated microbiota communities. For birds, further research would also be advised beyond determining presence and relative abundance, as we were not able to assess population trends, nesting success, or other vital metrics that may be of interest to land managers.

CRedit authorship contribution statement

Calvin Ritter: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **David I. King:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition. **Stephen DeStefano:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition. **Daniel Clark:** Conceptualization, Methodology, Resources, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Data availability

Data will be made available on request.

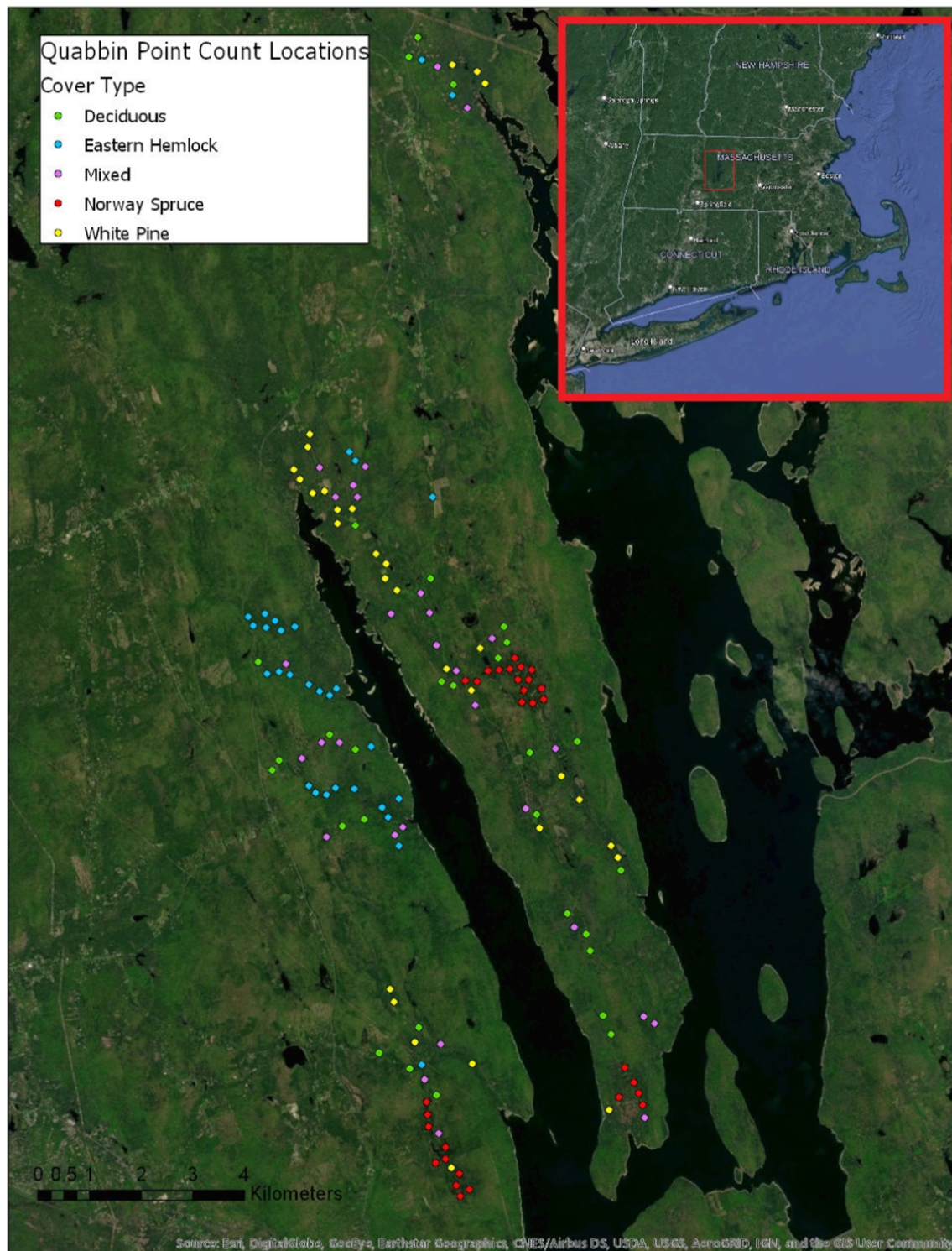
Acknowledgements

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Appendix A. Common and scientific names for all species included in analyses along with alpha codes, total number of detections, and model types used in analyses. Data are from point count surveys we conducted in Norway spruce plantations and native forest types during 2016 and 2017 in Massachusetts, USA.

Species Name	Code	# Detections	Model
American Crow (<i>Corvus brachyrhynchos</i>)	AMCR	19	GLM
American Goldfinch (<i>Spinus tristis</i>)	AMGO	7	GLM
American Redstart (<i>Setophaga ruticilla</i>)	AMRE	228	GLM, Nmix
American Robin (<i>Turdus migratorius</i>)	AMRO	28	GLM
Baltimore Oriole (<i>Icterus galbula</i>)	BAOR	19	GLM
Black-and-white Warbler (<i>Mniotilta varia</i>)	BAWW	171	GLM, Nmix
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	BBCU	40	GLM
Black-capped Chickadee (<i>Parus atricapillus</i>)	BCCH	142	GLM, Nmix
Brown-headed cowbird (<i>Molothrus ater</i>)	BHCO	20	GLM
Blue-headed Vireo (<i>Vireo solitarius</i>)	BHVI	138	GLM, Nmix
Blackburnian Warbler (<i>Setophaga fusca</i>)	BLBW	154	GLM, Nmix
Blue Jay (<i>Cyanocitta cristata</i>)	BLJA	146	GLM, Nmix
Brown Creeper (<i>Certhia americana</i>)	BRCR	90	GLM, Nmix
Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	BTBW	200	GLM, Nmix
Black-throated Green Warbler (<i>Setophaga virens</i>)	BTNW	250	GLM, Nmix
Cedar Waxwing (<i>Bombicilla cedrorum</i>)	CEDW	33	GLM
Chipping Sparrow (<i>Spizella passerina</i>)	CHSP	75	GLM, Nmix
Common Yellowthroat (<i>Geothlypis trichas</i>)	COYE	211	GLM, Nmix
Chestnut-sided Warbler (<i>Setophaga pensylvanica</i>)	CSWA	176	GLM, Nmix
Downy Woodpecker (<i>Picoides pubescens</i>)	DOWO	30	GLM
Eastern Phoebe (<i>Sayornis phoebe</i>)	EAPH	23	GLM
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	EATO	222	GLM, Nmix
Eastern Wood Pewee (<i>Contopus virens</i>)	EAWP	81	GLM, Nmix
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	GCFL	24	GLM
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	GCKI	70	GLM, Nmix
Gray Catbird (<i>Dumetella carolinensis</i>)	GRCA	94	GLM, Nmix
Hairy Woodpecker (<i>Leuconotopicus villosus</i>)	HAWO	42	GLM
Hermit Thrush (<i>Catharus guttatus</i>)	HETH	49	GLM
Least Flycatcher (<i>Empidonax minimus</i>)	LEFL	90	GLM, Nmix
Magnolia Warbler (<i>Setophaga magnolia</i>)	MAWA	88	GLM, Nmix
Mourning Dove (<i>Zenaidura macroura</i>)	MODO	38	GLM
Northern Cardinal (<i>Cardinalis cardinalis</i>)	NOCA	18	GLM
Ovenbird (<i>Seiurus aurocapilla</i>)	OVEN	325	GLM, Nmix
Pine Warbler (<i>Setophaga pinus</i>)	PIWA	222	GLM, Nmix
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	PIWO	31	GLM
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	RBGR	62	GLM
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	RBNU	100	GLM, Nmix
Red-eyed Vireo (<i>Vireo olivaceus</i>)	REVI	284	GLM, Nmix
Scarlet Tanager (<i>Piranga olivacea</i>)	SCTA	148	GLM, Nmix
Tufted Titmouse (<i>Baeolophus bicolor</i>)	TUTI	77	GLM, Nmix
Veery (<i>Catharus fuscescens</i>)	VEER	273	GLM, Nmix
Worm-eating Warbler (<i>Helminthophila vermivora</i>)	WEWA	22	GLM
Wood Thrush (<i>Hylocichla mustelina</i>)	WOTH	95	GLM, Nmix
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	YBSA	87	GLM, Nmix
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	YRWA	62	GLM
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	YTVI	28	GLM

Appendix B. Quabbin Site map



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