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Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations

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Abstract

Aim This study examines changes in avian community composition associated with the decline and loss of eastern hemlock [*Tsuga canadensis* (L.) Carr.] resulting from chronic hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) infestations.

Location The study was conducted in a 4900-km^2 study region extending from Long Island Sound northward to the southern border of Massachusetts and including the Connecticut River Valley in Connecticut, USA.

Methods Bird surveys were conducted at 40 points in 12 hemlock stands varying in HWA infestation and overstory mortality levels during the avian breeding seasons of 2000 and 2001. Ten-minute, 50-m radius point counts were used to survey all birds seen or heard at each point. Overstory and understory vegetation were sampled at each point. Indicator species analysis and non-metric multidimensional scaling were used to examine relationships between avian community composition and vegetation structure.

Results Overstory hemlock mortality was highly correlated with avian community composition. Abundance of eastern wood-pewee (*Contopus virens*), brown-headed cowbird (*Molothrus ater*), tufted titmouse (*Baeolophus bicolor*), white-breasted nuthatch (*Sitta carolinensis*), red-eyed vireo (*Vireo olivaceus*), hooded warbler (*Wilsonia citrina*), and several woodpecker species was highest at points with >60% mortality. Black-throated green warbler (*Dendroica virens*), Acadian flycatcher (*Empidonax virescens*), blackburnian warbler (*Dendroica fusca*), and hermit thrush (*Catharus guttatus*) were strongly associated with intact hemlock stands that exhibit little or no mortality from HWA.

Conclusions Eastern hemlock has unique structural characteristics that provide important habitat for numerous bird species in the north-eastern US. As a result, removal of hemlock by HWA has profound effects on avian communities. Black-throated green warbler, blackburnian warbler, and Acadian flycatcher are very strongly associated with hemlock forests in southern New England and appear to be particularly sensitive to hemlock removal. The hooded warbler, a species whose status is of regional concern, may actually benefit from the development of a dense hardwood seedling layer associated with high hemlock mortality.

Keywords
Avian communities, hemlock woolly adelgid, bird surveys, point counts, multivariate analysis, black-throated green warbler, hooded warbler, eastern hemlock, exotic pest, Connecticut, New England, forest disturbance.

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INTRODUCTION

Introduced forest insects pose one of the greatest threats to the health of native ecosystems. During the 20th century, an onslaught of non-native pests introduced to temperate North America resulted in altered forest composition, ecosystem structure and function, and plant productivity (Drake *et al*., 1989; Mack *et al*., 2000). Exotic insects can disrupt habitat structure, killing dominant tree species and allowing significant growth in the understory (Bell, 1997). Often, these changes create a mosaic of intact forest and early seral habitat (Thurber, 1992; Bell & Whitmore, 1997; Matsuoka *et al*., 2001). The resulting heterogeneity in vegetation structure often leads to an influx of avian species adapted to disturbed areas (Osborne, 1983, 1985; Thurber, 1992). A pest that provides a food source may further increase bird species richness (Morris *et al*., 1958; Bell, 1997). As forest gaps regenerate, however, the habitat becomes more homogeneous and avian species diversity typically declines (Gale *et al*., 2001). Although several studies suggest that many bird species either benefit or remain unaffected by insect pest outbreaks (Osborne, 1985; Bell, 1997), a few species are known to have declined dramatically following overstory vegetation removal resulting from insect infestations (Rabenold *et al*., 1998; Matsuoka *et al*., 2001).

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), an introduced aphid-like insect from Japan, poses an important and immediate threat to the health of eastern hemlock (*Tsuga canadensis*) in the eastern US. Past studies have documented the impact of HWA and factors associated with hemlock mortality, but the rapid spread of infestation appears to continue unabated (Young *et al*., 2000; Orwig *et al*., 2002). The hemlock's multilayered canopy makes it a structurally unique and critically important species in New England (Orwig & Foster, 1998). Hemlock stands support moderate levels of avian diversity, including several species that are largely restricted to hemlock stands in the region, as well as several species of mammals and amphibians (Benzinger, 1994b; Yamasaki *et al*., 2000; Brooks, 2001). As hemlock disappears it is typically replaced by hardwoods which are dominant across the region; as a result, the forest landscape is expected to become more homogenous (Jenkins *et al*., 2000; Orwig *et al*., 2002), which may eventually lead to a decline in the overall species richness of birds as well as other species.

HWA was first documented in eastern Virginia in the early 1950s (Souto *et al*., 1996). It has spread rapidly to the Northeast and was first reported in Connecticut in 1985 (McClure, 1987). Since that time it has dispersed to every town and caused significant damage throughout large portions of the state (McClure *et al*., 2000). There exists a latitudinal gradient in severity of infestations and damage, with the most heavily damaged stands in southern Connecticut, where HWA has occurred for the longest period of time (Orwig *et al*., 2002).

HWA differs from other exotic pests because of the chronic nature of infestations, which typically last for many years on hemlock, a dominant forest species in the eastern US. While the loss of large stands of eastern hemlock is of great concern, there is a unique opportunity to assess the effects of the loss of a dominant conifer species on avian community composition. This study sought to: (1) document changes in bird species composition resulting from different levels of HWA infestation, and (2) correlate these changes with specific structural components of the habitats that are influenced by the demise and removal of hemlock.

Study area

This study was conducted within a 4900-km^2 study region through central Connecticut, extending from Long Island Sound to the Massachusetts border (Fig. 1). The area is

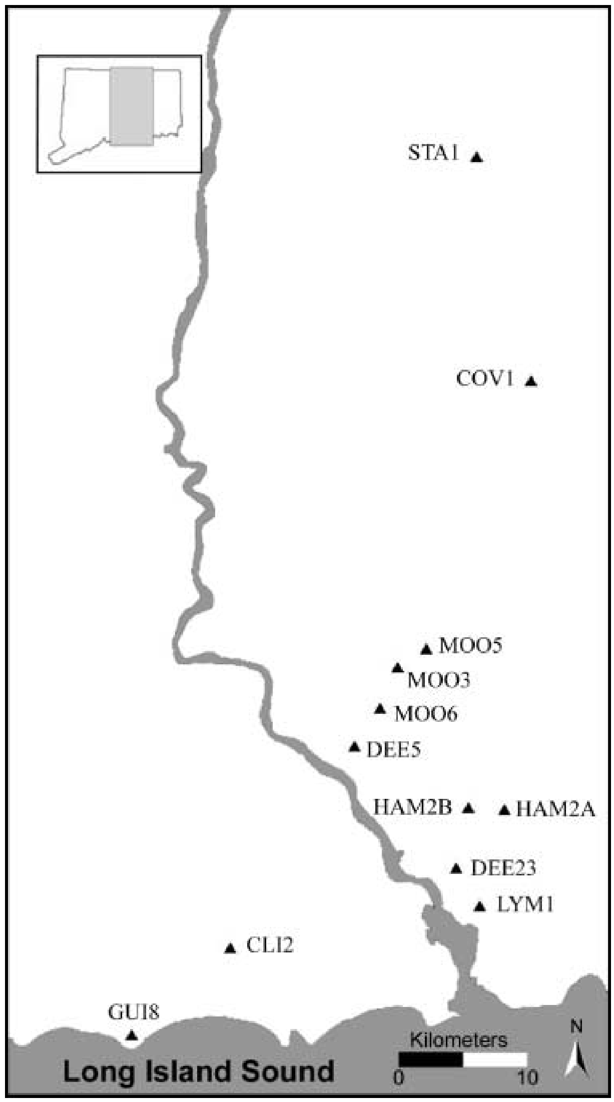

Figure 1 Study area and bird sampling point locations in Connecticut, USA. The Connecticut River is located in the centre of the study region.

variable in topography, vegetation, and land-use history (Orwig *et al.*, 2002). During the summers of 1997 and 1998, 114 stands were sampled to characterize the spatial pattern of HWA damage across southern New England since its arrival in the region in 1985 (Orwig *et al.*, 2002). For the study of avian response to HWA, we selected 12 of those hemlock stands, representing a broad range of forest conditions. In all stands, hemlock represented >60% of stems and HWA-induced mortality ranged from 0% to 100% (Table 1). In order to survey multiple points per stand, only sites >35 ha were selected.

METHODS

Bird surveys

We conducted 112 point counts in 12 stands during the breeding seasons (late May to early July) in 2000 and 2001. The surveys were 10-min, 50-m radius point counts of all birds heard or seen following survey protocols of the BBIRD monitoring system (Martin *et al.*, 1997), with recommendations of Ralph *et al.* (1995). We sampled one series of 32 points in 2000 and expanded the study to include two series of 40 points in 2001. In 2001, all 40 points were sampled completely before beginning the second series. The first survey period in 2001 (5 June–19 June) was earlier in the year than the other two periods (27 June–13 July 2000 and 20 June–4 July 2001), but all were within the time when little or no migration occurs for breeding birds in the region (Martin *et al.*, 1997).

Point counts were conducted a minimum of 200 m apart and at least 100 m from roads or rivers. Points were located off-trail, on lightly travelled trails, or at least 10 m from heavily travelled trails (cf. Martin *et al.*, 1997). Surveys were conducted on days with minimal rain and wind between a half hour after sunrise (*c.* 06:00 h) and 10:00 h. The visitation order of stands and points within a stand varied among repeat samplings. During each 10-min survey, all birds detected inside and outside of the 50-m count radius were noted, along with the bird's sex when verifiable, and method of detection (sight or sound). One observer (M. Tingley) conducted all surveys to reduce potential observer bias and the chance of disturbing birds from unnecessary activity (Ralph *et al.*, 1995). Careful attention was paid during surveys to prevent double-counting of individuals. In addition, although count data were collected with an unlimited-radius, abundance data were analysed only for birds within the 50-m circle (Robinson & Robinson, 1999).

At each site, two to nine point counts were conducted depending on stand size. Points were classified by degree of hemlock mortality and vegetation response. Although levels of HWA infestation and damage varied greatly within stands, individual points were not treated independently as a result of potential problems of pseudoreplication.

Vegetation sampling

Vegetation surveys were conducted at each of the 40 point-count locations during the summer of 2001. Basal area was recorded for all tree species using a 10-factor cruise-all at the centre of each point (Wenger, 1984). Standing hemlock trees were recorded separately as either alive or dead, in order to estimate the original per cent of hemlock in the stand, as well as per cent mortality. The majority of dead hemlock boles in all stands were still standing, so the basal area cruise effectively counted most dead trees.

Live understory vegetation was measured in four rectangular 2 m^2 subplots placed 25 m apart in the four cardinal directions from the centre of each survey point. In each subplot, all tree seedlings and saplings (<5 cm d.b.h.) were counted by species and per cent total shrub and fern cover were visually estimated. Observations on past human activity such as selective hardwood logging and stone walls were recorded. One stand experienced some selective hemlock cutting during the course of this study.

Data analysis

Only observations made within the 50-m count radius were used in the analysis. Because the two counts in 2001 were

Table 1 Average stand characteristics of surveyed hemlock forests in southern New England (cf. Orwig *et al.*, 2002). See 'Methods' for description of mortality classes

Stand	Latitude	Elevation (m)	Average slope (%)	Size (ha)	No. of count stations	Mortality class
CLI2	41.336	61	12.8	133	4	Medium
COV1	41.793	129	7.5	70	2	Low
DEE23	41.404	25	9	118	2	High-A
DEE5	41.498	15	45.3	80	4	Medium
GUI8	41.281	20	7	242	9	High-B
HAM2A	41.459	110	15	136	7	High-B
HAM2B	41.459	80	5	40	2	High-B
LYM1	41.370	15	27.5	51	2	High-A
MOO3	41.576	91	16.4	46	2	Low
MOO5	41.562	76	36.9	36	2	Low
MOO6	41.546	76	19.9	110	2	Low
STA1	41.963	213	17.4	58	2	Low

within one breeding season, we used the highest count for each species during the two visits as an index of abundance for that species at that point (Hagan *et al.*, 1997). The highest count data for each point in 2001 were averaged with count data from 2000 to determine the relative abundance for each species per 50-m radius over two breeding seasons. For the points added in 2001, only the highest count data were used.

Based on original site characteristics, stands were categorized into three levels of hemlock mortality: Low (0–10%), Medium (11–60%), and High (>60%). Initial site reconnaissance suggested that stands with high mortality levels (>60%) differed in vegetation response: high overstory mortality resulted in prolific black birch (*Betula lenta* L.) establishment in some stands but not in others. Thus, data from individual count stations were incorporated into four stand-level hemlock mortality classes (Low, $n = 5$; Medium, $n = 2$; High-A, $n = 2$; High-B, $n = 3$), with High-A representing stands with high hemlock mortality and little birch regeneration, and High-B representing stands with high hemlock mortality and dense birch regeneration.

Avian species composition of individual sampling points were compared among mortality classes with multiresponse permutation procedures (MRPP), a nonparametric multivariate test of differences between groups that compares the points within *a priori* groups with a random allocation of plots (Mielke, 1984). The data for each species were relativized by maximum abundance to equalize the contribution of rare and abundant species to the analyses. Indicator species analysis (Dufendre & Legendre, 1997) was used to evaluate species associations with mortality classes. Indicator species analysis assigns indicator values (IV) to each species based on their relative abundance and frequency within each group. The indicator values range from zero (no group indication) to 100 (perfect group indication). A Monte-Carlo test using 1000 permutations was used to test the statistical significance of the IV for each species.

Non-metric multidimensional scaling (NMS; Kruskal, 1964; Mather, 1976) was used to evaluate the relationship of avian community composition with vegetation structure. The ordinations were rotated to load the vegetation structural variable with the highest correlation onto axis one. All multivariate analyses were conducted with PC-ORD statistical software (McCune & Mefford, 1999).

Species richness, or alpha diversity (cf. Hunter, 2002), was defined as the total number of species detected within the 50-m count circles for all points within a mortality class. Heterogeneity of species, a measure of richness and relative abundance, was measured within classes using the reciprocal of Simpson's Index. The resulting value represents the number of equally abundant species necessary to produce the same heterogeneity as observed in the sample (Peet, 1974). Average bird species abundances and vegetation data were compared among mortality classes and tested for significance using Kruskal–Wallis tests (chi-square approximation) and one-way ANOVAs with least-square means multiple comparison procedure using a Bonferonni adjustment, respectively. All statistical tests were performed using SYSTAT (Wilkinson, 1999).

RESULTS

Vegetation structure

Prior to HWA infestation, the stands surveyed had similar overstory composition and structure (Table 2). Total basal area measurements at survey points ranged from 17 to 55 m^2 ha^{-1}, but average basal area was not significantly different among mortality classes. Likewise, average hemlock basal area ranged from 58% to 77% among classes. High-A and High-B classes had the lowest mean hemlock percentage, but greater percentages of dead, fallen trees in these sites made accurate measurement of pre-HWA hemlock basal area difficult. Consequently, original hemlock basal area in these two classes was probably underestimated. High-B and High-A stations had similar mean hemlock mortality (87% and 85%, respectively) and similar mean per cent dead basal area. The minimum dead basal area was 30% in High-A areas and 50% in High-B areas.

Understory vegetation differed strikingly among the four categories, with High-B areas having significantly ($P < 0.005$) higher black birch seedling densities (>37,000 ha^{-1}) than other mortality classes (Table 3). In addition, High-B areas had significantly taller birch seedlings and higher total seedling densities. There were no statistical differences in seedling characteristics among Low, Medium and High-A survey areas. Average herb cover (primarily hay-scented fern, *Dennstaedtia punctilobula* (Michx.) Moore and wood ferns, *Dryopteris* spp.) was not significantly different among mortality classes. Shrub cover (primarily mountain laurel, *Kalmia latifolia* L.) was significantly higher in High-A stands vs. Low mortality stands (Table 3).

Table 2 Mean overstory characteristics of stands with varying levels of hemlock mortality

	Hemlock mortality class			
	Low ($n = 5$)	Medium ($n = 2$)	High-A ($n = 2$)	High-B ($n = 3$)
Total overstory basal area (m^2 ha^{-1})	34.7 ± 3.9^a	36.2 ± 6.9^a	32.7 ± 0.4^a	37.1 ± 1.4^a
Per cent overstory hemlock basal area	77 ± 3^a	65 ± 6^a	61 ± 9^a	58 ± 2^a
Per cent hemlock mortality	0^a	31 ± 14^b	87 ± 1^c	85 ± 9^c
Per cent dead basal area	0^a	21 ± 10^a	53 ± 7^b	50 ± 3^b

Values in a row followed by the same letter are not significantly different at $P < 0.05$.

Table 3 Mean understory vegetation characteristics of stands with varying levels of hemlock mortality

	Hemlock mortality class			
	Low ($n = 5$)	Medium ($n = 2$)	High-A ($n = 2$)	High-B ($n = 3$)
Birch seedling density (ha^{-1})	1875 ± 1281^{a}	2500 ± 2500^{a}	4375 ± 1326^{a}	$37{,}979 \pm 11{,}000^{b}$
Birch height (m)	0.03 ± 0.01^{a}	0.03 ± 0.02^{a}	0.05 ± 0.00^{a}	0.80 ± 0.00^{b}
Total seedling density (ha^{-1})	$14{,}125 \pm 4364^{ab}$	$12{,}656 \pm 6719^{a}$	$11{,}875 \pm 4861^{a}$	$57{,}536 \pm 15{,}958^{b}$
Herb cover (%)	2.1 ± 1.3^{a}	6.8 ± 6.8^{a}	9.5 ± 0.4^{a}	18.4 ± 12.2^{a}
Shrub cover (%)	0.8 ± 0.8^{a}	0.9 ± 0.9^{ab}	23.1 ± 9.9^{b}	3.9 ± 1.9^{ab}

Values in a row followed by the same letter are not significantly different at $P < 0.05$.

Avian species trends

A total of 637 individuals of 49 bird species were recorded within the 50-m circular points and included in the analysis (Table 4). Average number of species per point was not significantly different among mortality classes. Avian community composition differed strongly among hemlock mortality classes (MRPP: $P < 0.0001$, $T = -6.18$, $A = 0.05$), and was broadly distributed in the survey point ordination (Fig. 2). The first two axes of the ordination graph explained 48% of the compositional variation. After rotation, 58% of the variation in avian composition along axis 1 was explained by per cent dead hemlock, which ranged from Low mortality points in the negative portion of the axis to High mortality points in the positive portion. Similarly, 29% of the avian composition variation along axis 1 could be explained by black birch seedling density (Fig. 2). Black-throated green warbler (*Dendroica virens*) and blackburnian warbler (*Dendroica fusca*) had the highest negative correlations with axis 1 ($r = -0.69$ and -0.37, respectively), while hooded warbler (*Wilsonia citrina*), northern cardinal (*Cardinalis cardinalis*), eastern wood-pewee (*Contopus virens*), and tufted titmouse (*Baeolophus bicolor*) had the highest positive correlations with axis 1 (r-values between 0.52 and 0.48).

Survey point distribution along the second axis, which explained 28% of the variation, was not strongly related to any of the vegetation structural variables that we examined. Scarlet tanager (*Piranga olivacea*) and red-eyed vireo (*Vireo olivaceus*) had the highest negative correlations with axis 2 ($r = -0.68$ and -0.45, respectively), while black-capped chickadee (*Parus atricapillus*) and ovenbird (*Seiurus aurocapillus*) had the highest positive correlations with axis 2 ($r = 0.61$ and 0.58, respectively).

Six species were observed exclusively in Low mortality sampling points, although only three, Acadian flycatcher (*Empidonax virescens*), blackburnian warbler, and winter wren (*Troglodytes troglodytes*), were observed repeatedly (Table 4). Nine species were restricted to High mortality points (Table 4). One species, the brown-headed cowbird (*Molothrus ater*), was found exclusively in High-A points while hooded warbler and eastern phoebe (*Sayornis phoebe*) were found only in High-B sampling points (Table 4).

The loss of hemlock and resulting changes in forest composition appeared to negatively affect six species (Fig. 3; Table 4). These species were: black-throated green warbler, ovenbird, hermit thrush (*Catharus guttatus*), blue-headed vireo (*Vireo solitarius*), Acadian flycatcher, and blackburnian warbler. Acadian flycatcher and blackburnian warbler were absent from individual sampling points with any hemlock mortality, and black-throated green warbler and Acadian flycatcher were significant indicator species for the Low mortality class, determined by indicator species analysis ($P < 0.05$; Table 4). Black-throated green warbler exhibited the most substantial decline with hemlock loss, with a 93% decline in abundance from areas of low to high mortality. Hermit thrush also exhibited large (34%) declines in forests with high hemlock mortality (Fig. 3).

Edge or gap-dependent species exhibited higher relative abundances in sites with heavy hemlock mortality (Fig. 3). Five species – brown-headed cowbird, red-eyed vireo, eastern wood-pewee, white-breasted nuthatch (*Sitta carolinensis*), and tufted titmouse showed significant ($P < 0.05$) increases in mean abundance from Low to High mortality sites (Fig. 3). Additional species, including great crested flycatcher (*Myiarchus crinitus*), downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American goldfinch (*Carduelis tristis*), veery (*Catharis fuscescens*), hooded warbler, and scarlet tanager exhibited trends of higher abundances in stands with high levels of hemlock mortality.

Abundance and diversity

Average species abundances for several species differed among High-A and High-B sites. The hooded warbler, found in High-B points at relatively high densities, and eastern wood-pewee were the only significant indicator species for this mortality class (Fig. 3, Table 4). Veery was found in low abundance in Low, Medium, and High-A areas, but was relatively abundant in High-B stands. Conversely, tufted titmouse, which was detected only once in Low mortality points, achieved its highest abundance in High-A stands. The brown-headed cowbird was the only significant indicator species for the High-A mortality class (Table 4). There were no significant indicator species for the medium mortality class.

Overall bird species richness was similar in the Low, High-A, and High-B mortality classes and lowest in Medium mortality areas (Fig. 4). Heterogeneity, a measure of abundance and richness, showed a positive trend with increasing

Table 4 Relative abundance of all bird species observed in 40 hemlock sampling points of four mortality classes during the breeding seasons of 2000 and 2001 in central Connecticut

		Low	Med	High-A	High-B
Species	Scientific name	Relative abundance†	Relative abundance	Relative abundance	Relative abundance
Black-throated green warbler	*Dendroica virens*	1.54**	0.50	0.30	0.10
Blue-headed vireo	*Vireo solitarius*	0.38	0.125	0.10	0.15
Acadian flycatcher	*Empidonax virescens*	0.17*	0.000	0.00	0.00
Blackburnian warbler	*Dendroica fusca*	0.17	0.000	0.00	0.00
Brown creeper	*Certhia americana*	0.13	0.063	0.05	0.05
Hermit thrush	*Catharus guttatus*	0.29	0.313	0.05	0.20
Red-breasted nuthatch	*Sitta canadensis*	0.08	0.063	0.15	0.00
Black-capped chickadee	*Parus atricapillus*	1.08	0.625	1.05	0.75
Blue jay	*Cyanocitta cristata*	0.46	0.250	0.50	0.15
Canada warbler	*Wilsonia canadensis*	0.00	0.000	0.05	0.10
Golden-crowned kinglet	*Regulus satrapa*	0.13	0.000	0.10	0.00
Pileated woodpecker	*Dryocopus pileatus*	0.13	0.063	0.00	0.20
Black-and-white warbler	*Mniotilta varia*	0.04	0.000	0.15	0.20
Ovenbird	*Seiurus aurocapillus*	0.54	0.563	0.30	0.30
Red-shouldered hawk	*Buteo lineatus*	0.00	0.000	0.15	0.10
Scarlet tanager	*Piranga olivacea*	0.42	0.250	0.70	0.60
Winter wren	*Troglodytes troglodytes*	0.13	0.000	0.00	0.00
Wood thrush	*Hylocichlia mustelina*	0.21	0.063	0.20	0.10
American crow	*Corvus brachyrhynchos*	0.13	0.063	0.10	0.00
American goldfinch	*Carduelis tristis*	0.04	0.125	0.50	0.35
American robin	*Turdus migratorius*	0.17	0.063	0.00	0.00
Brown-headed cowbird	*Molothrus ater*	0.00	0.000	0.35**	0.00
Cedar waxwing	*Bombycilla cedrorum*	0.08	0.250	0.05	0.20
Common grackle	*Quiscalus quiscula*	0.00	0.000	0.10	0.00
Downy woodpecker	*Picoides pubescens*	0.13	0.063	0.20	0.25
Eastern kingbird	*Tyrannus tyrannus*	0.21	0.063	0.00	0.00
Eastern towhee	*Pipilo erythrophthalmus*	0.00	0.000	0.00	0.05
Eastern wood pewee	*Contopus virens*	0.00	0.125	0.10	0.65**
Gray catbird	*Dumetella carolinensis*	0.00	0.188	0.05	0.15
Great-crested flycatcher	*Myiarchus crinitus*	0.08	0.188	0.30	0.45
Hairy woodpecker	*Picoides villosus*	0.08	0.125	0.20	0.45
Mourning dove	*Zenaida macroura*	0.04	0.063	0.10	0.25
Northern cardinal	*Cardinalis cardinalis*	0.00	0.250	0.15	0.20
Northern flicker	*Colaptes auratus*	0.00	0.000	0.20	0.05
Pine warbler	*Dendroica pinus*	0.04	0.000	0.15	0.05
Red-eyed vireo	*Vireo olivaceus*	0.13	0.313	0.40	0.50
Red-tailed hawk	*Buteo jamaicensis*	0.04	0.000	0.10	0.00
Rose-breasted grosbeak	*Pheucticus ludovicianus*	0.04	0.000	0.00	0.00
Ruby-throated hummingbird	*Archilochus colubris*	0.04	0.000	0.00	0.00
Tufted titmouse	*Baeolophus bicolor*	0.04	0.875	1.25	1.10
Veery	*Catharus fuscescens*	0.13	0.125	0.05	0.50
White-breasted nuthatch	*Sitta carolinensis*	0.00	0.063	0.50	0.40
Wild turkey	*Meleagris gallopavo*	0.00	0.063	0.10	0.00
Worm-eating warbler	*Helmitheros vermivorus*	0.00	0.063	0.05	0.10
Yellow-throated vireo	*Vireo flavifrons*	0.00	0.000	0.10	0.10
Dark-eyed junco	*Junco hyemalis*	0.00	0.000	0.00	0.10
Eastern phoebe	*Sayornis phoebe*	0.00	0.000	0.00	0.15
Hooded warbler	*Wilsonia citrina*	0.00	0.000	0.00	0.45**
Ring-necked pheasant	*Phasianus colchicus*	0.04	0.000	0.00	0.00

*Significant indicator species within a mortality class determined from Indicator Species Analysis ($P < 0.05$), ** ($P < 0.01$).
†Relative abundance calculated as the mean number of individuals per 50-m radius point-count for each mortality class.

hemlock mortality. High-B count stations, which had the most diverse habitat including large gaps, intact broadleaf trees, fern cover and dense areas of regeneration, had the greatest diversity of bird species. Low mortality stations were dominated by black-throated green warbler and black-capped chickadee, and had the lowest diversity.

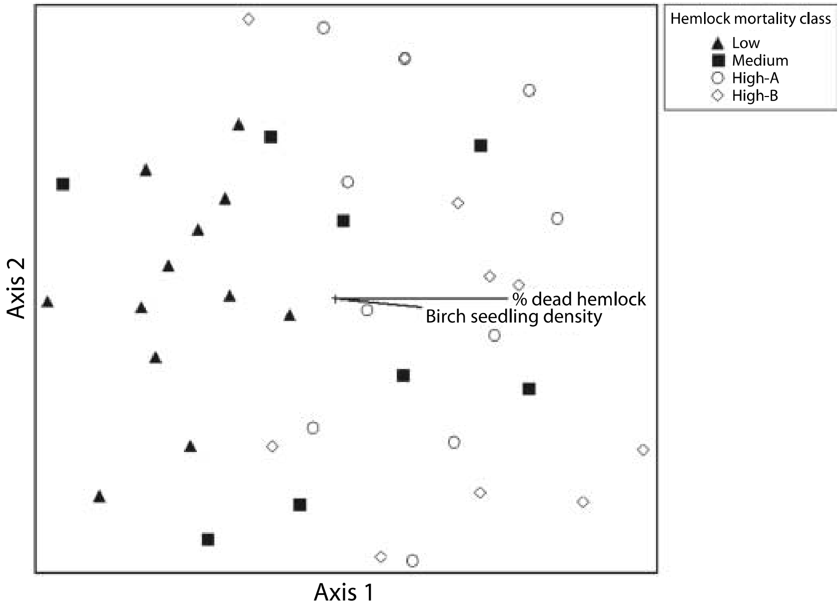

Figure 2 Non-metric multidimensional scaling ordination of bird abundance data from 40 count stations in hemlock stands of southern New England. Bi-plot contains structural vegetation vectors that are significantly correlated ($P < 0.05$) with axes. Symbols indicate hemlock mortality classes.

DISCUSSION

In the 17 years that HWA has infested portions of Connecticut, there have been dramatic changes in forest structure with important implications for associated breeding birds. Because of hemlock's unique structural characteristics, including dense, multi-layered evergreen canopies, the loss of hemlock stands from much of the Northeast is likely to have substantial impacts on numerous wildlife species (Benzinger, 1994a; Orwig & Foster, 1998). Although sparse, data from past range-wide declines of forest overstory dominants such as chestnut [*Castanea dentata* (Marshall) Borkh.] suggest that few long-term impacts on bird communities resulted (Smith & Stephen, 2003), although elm (*Ulmus* spp.) decline led to more significant changes in avifauna composition (Kendeigh, 1982; Osborne, 1985). Canopy openings of up to 25% in elm forests led to increases in edge and open habitat bird species (Kendeigh, 1982). As HWA often leads to substantially greater canopy openings, the impact of hemlock decline on bird species composition may be more dramatic

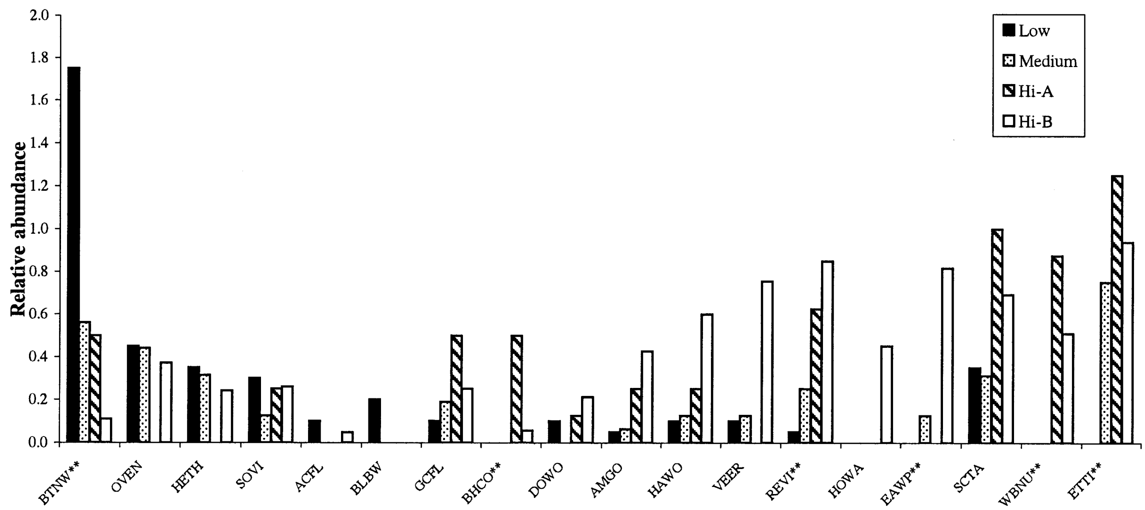

Figure 3 Average relative abundance for common avian species in stands of different hemlock mortality classes. Bird codes are: BTNW, Black-throated Green Warbler; OVEN, Ovenbird; HETH, Hermit Thrush; SOVI, Blue-headed Vireo; ACFL, Acadian Flycatcher; BLBW, Blackburnian Warbler; GCFL, Great-crested Flycatcher; BHCO, Brown-headed Cowbird; DOWO, Downy Woodpecker; AMGO, American Goldfinch; HAWO, Hairy Woodpecker; VEER, Veery; REVI, Red-eyed Vireo; HOWA, Hooded Warbler; EAWP, Eastern Wood Pewee; SCTA, Scarlet Tanager; WBNU, White-breasted Nuthatch; and ETTI, Eastern Tufted Titmouse. **Significant difference among mortality classes at $P < 0.05$.

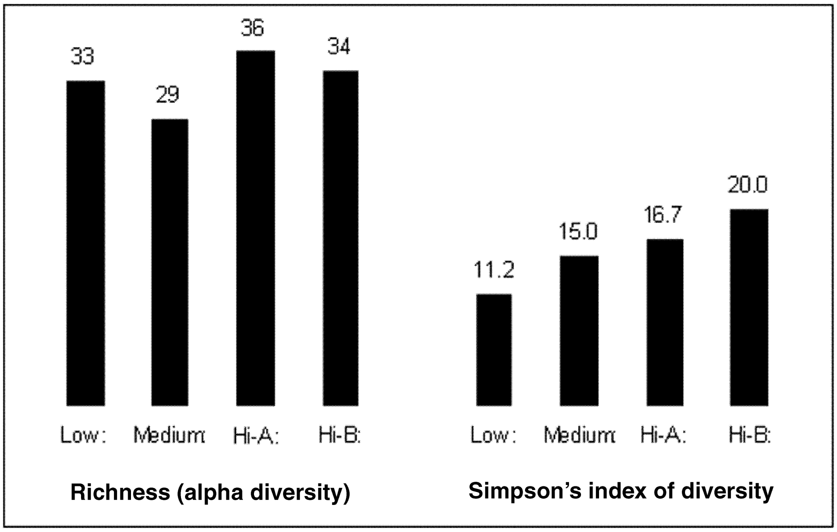

Figure 4 Total avian species richness and diversity (measured by inverse of Simpson's Index) among hemlock mortality classes.

(Benzinger, 1994b). In addition to other significant population stresses on neotropical bird populations in the Northeast such as fragmentation and loss of wintering habitat (Robinson *et al.*, 1995; Maurer & Villard, 1996; Holt, 2000; Boulinier *et al.*, 2001), our results suggest that hemlock loss from HWA causes significant changes in bird population composition and distribution.

Bird species whose populations are most strongly reduced with high hemlock mortality warrant immediate concern. Foremost is the black-throated green warbler, a species that depends on hemlocks for feeding and nesting sites (Kendeigh, 1946; DeGraaf & Rudis, 1986; Haney, 1999; Mitchell, 1999). The black-throated green warbler is considered a hemlock obligate in some eastern forests (Benzinger, 1994b), although it is found in other cover types elsewhere (Collins, 1983; Parrish, 1995; Sauer *et al.*, 2001). For example, in northern New England the black-throated green warbler is commonly associated with spruce (*Picea* spp.) forests where its breeding densities are similar to or greater than populations found in hemlock stands (Collins, 1983; DeGraaf & Rudis, 1986).

Scattered spruce plantations in our region may serve as habitat refugia for black-throated green warblers as hemlock declines; spruce is commonly grown for timber in many parts of the Northeast and is being planted in a few salvaged hemlock stands (B. Spencer, pers. comm.; D. Orwig, pers. obs.). However, this practice may ultimately be unsuccessful for several reasons. Benzinger (1994b) concluded that often black-throated green warblers are not found in spruce plantations because of a lack of structural diversity preferred by the warbler. In addition, they are often out-competed in the upper-canopy by blackburnian warblers (MacArthur, 1958).

In other parts of its range, black-throated green warblers prefer nesting and foraging in deciduous forests (Collins, 1983). Therefore, the possibility exists that birds displaced from hemlocks will shift to deciduous species which dominate much of the region. However, research by Parrish (1995) suggests that habitat preferences by black-throated green warblers in the Northeast are most likely genetic and include significant physiological adaptations. Individuals that are displaced by hemlock decline and mortality, consequently, may be more likely to occupy available spruce forests than surrounding deciduous areas. More research is needed to investigate the role of spruce as suitable replacement habitat for birds preferring hemlock.

The sensitivity of the black-throated green warbler to hemlock mortality exhibited in this study provides troubling implications for its conservation, at least in the Northeast. Because of the unimpeded migration of HWA, the entire range of eastern hemlock is threatened and may be dramatically reduced across large portions of its range (Orwig & Foster, 1998; Foster, 2000; Orwig *et al.*, 2002). As HWA continues to spread to the north and west, we can expect to see species like black-throated green warblers abandoning the infested, declining hemlock stands in lieu of higher quality hemlock stands that have not yet been infested or begun to decline (Canterbury & Blockstein, 1997). Although potential hemlock refugia can not be ruled out, it is unlikely that black-throated green warblers and other species closely associated with hemlock would be able to maintain viable populations within such a limited and fragmented system. On the scale of decades, this may result in regional extinctions. The overall survival of the black-throated green warbler in portions of the north-eastern US may be dependent on its ability to disseminate and adapt to traditionally suboptimal habitat.

Most other species observed in this study that exhibited reduced densities in heavily damaged stands are also known to occur in abundance in other stand types. Thus, the impact of HWA on populations of these birds will probably be less severe. However, the Acadian flycatcher, which expanded its range northward in New England in the last 30 years (Zeranski & Baptist, 1990), nests solely in hemlock ravines in the northern part of its range (Lyons & Livingston, 1997; J. Garrett, unpublished data). With the expected decline of hemlock from most of Connecticut and Massachusetts, the

Acadian flycatcher may once again withdraw from most of New England. Several other species recorded in the current study such as blue-headed vireo, hermit thrush, and ovenbird apparently declined with hemlock mortality, but additional sampling is necessary to confirm these observations and to account for within-stand variation (Fig. 3). Additional species not recorded in this study which may be adversely impacted by the loss of hemlock include the great horned owl (*Bubo virginianus*), long eared owl (*Asia otus*), red-shouldered hawk (*Buteo lineatus*), and northern goshawk (*Accipiter gentiles*) (DeGraaf & Rudis, 1986; DeGraaf *et al*., 1992; Benzinger, 1994b).

In contrast, some species of woodpeckers, eastern wood-pewee, white-breasted nuthatch, red-eyed vireo, and tufted titmouse were much more common in areas with high hemlock mortality. The hooded warbler has also apparently benefited from high hemlock mortality; it was only found in High-B areas with dense black birch understories. The hooded warbler is typically associated with early successional deciduous forest habitat resulting from selective hardwood cutting or severe gypsy moth (*Lymantria dispar*) defoliation (Kendeigh, 1946; Robinson & Robinson, 1999; Bell & Whitmore, 2000). Because the warbler is locally uncommon in New England (DeGraaf & Rudis, 1986), it may initially benefit from HWA, but only temporarily. As canopy gaps fill in with deciduous trees, the habitat becomes less desirable to hooded warblers. The presence of hooded warblers in our High-B areas in inland Connecticut may reflect its ability to colonize available early successional habitat that results from hemlock mortality. The northern limit of the hooded warbler's range has historically been coastal Connecticut (Zeranski & Baptist, 1990), and it is not known whether this species will be able to expand substantially into interior forests even with increases in preferred habitat.

The increase in understory vegetation following hemlock mortality parallels responses to other pest-induced conifer declines (Stone & Wolfe, 1996; Matsuoka *et al*., 2001). However, for hemlock stands in the Northeast, the dramatic increase in birch species abundance with hemlock mortality is similar to the response to clear-cutting and selective logging in conifer stands (Schulte & Niemi, 1998; Costello *et al*., 2000). The results of Kizlinksi *et al*. (2002) demonstrated that understory composition is broadly similar whether hemlock stands are cut or deteriorate and die on site because of HWA infestation.

In both logged and HWA-killed sites, one common impact on the avian community is the influx of early successional bird species into interior forest habitat (cf. Wetmore *et al*., 1985; Canterbury & Blockstein, 1997; Costello *et al*., 2000). This change in species composition, and associated increased richness, is a result of ecotonal conditions in early seral habitat (Hagan *et al*., 1997). Without repeated disturbances over time, gap-dependent bird species and bird diversity will decrease as regenerating stands mature (Robinson & Robinson, 1999).

Although logging impacts may provide a useful comparison to consequences of HWA, there are several important differences between the two disturbance types. Logging of hemlock and other natural disturbances, such as wind or fire, do not prevent hemlock regeneration and eventual stand re-establishment (Kendeigh, 1946; Benzinger, 1994a). HWA, by contrast, kills seedlings, saplings, and mature trees, preventing re-growth and depleting the hemlock seed bank (Orwig & Foster, 2000; Orwig, 2002). In addition, understory response and resulting conditions can vary depending on the original abundance of hemlock in the forest. Areas with the highest densities of overstory hemlock typically lead to High-B stands following chronic HWA infestations while stands with more overstory hardwoods, which provide shade following hemlock decline, are more likely to have reduced seedling densities. The continued study of the relationship between HWA-killed stands and logged stands is important because pre-emptive and salvage cutting of hemlock continues to increase, despite its low marketability and undesirable wood characteristics (Howard *et al*., 2000; Ritchie, 2000; Kizlinski *et al*., 2002).

In a similar study, Rabenold *et al*. (1998) examined avian changes in dying Fraser fir [*Abies fraseri* (Pursh) Poiret.] stands following chronic balsam woolly adelgid (*A. piceae*) infestation, and found negative effects for similar species, especially black-throated green warbler and blue-headed vireo. The declines observed in our study support their claim that these are 'consistently sensitive species' and raise concern over the status of these species throughout much of the eastern US.

Reasons for bird demographic changes following disturbances are often species specific (Bourque & Villard, 2001). While black-throated green warblers are sensitive to hemlock deterioration and mortality (Clark *et al*., 1983; in Benzinger, 1994b), ovenbirds may in some cases appear to be negatively impacted by dense birch regeneration (Canterbury & Blockstein, 1997). These factors can limit both species' foraging abilities. In contrast, hairy and downy woodpeckers responded positively to dead and dying trees (Benzinger, 1994b).

CONCLUSIONS

Although a few studies have examined the long–term interactions of bird communities with naturally changing vegetation communities (Holmes & Sherry, 2001), additional work in this area and studies of the adaptability of at-risk bird species to sub-optimal habitats is of critical importance, especially when factors such as exotic pest and pathogen outbreaks may cause shifts in avian species geographical distributions. Our study adds to previous studies (e.g. Rabenold *et al*., 1998) by describing the effects of an introduced, non-native insect on forest habitat and the associated avian community. The ecological changes documented in this study illustrate the importance of limiting and monitoring the invasion of exotic species and highlight the need for parallel studies on the response of other faunal groups and ecosystems (e.g. streams) to HWA.

We have shown that some bird species are highly associated with particular habitats and may also have low adaptability in either the surrounding matrix or in the replacement habitat. In the case of eastern hemlock forests in the north-eastern US, we have examined stands that have been dramatically transformed from nearly monotypic hemlock stands to mixed-hardwood stands dominated by birch seedlings in a matter of a decade or less. Our data suggests that numerous species will be affected positively or negatively by loss of hemlock because of HWA, and a few species are at risk of range retractions or local extinctions. To better estimate the magnitude of these changes, we need additional studies of avian habitat use in hemlock forests across broader geographical regions, as well as long-term studies of bird productivity over the course of HWA infestation and accruing hemlock mortality.

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