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Author(s): Matthew J. Toenies, David A. W. Miller, Matthew R. Marshall, and Glenn E. Stauffer
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RESEARCH ARTICLE

Shifts in vegetation and avian community structure following the decline of a foundational forest species, the eastern hemlock

Matthew J. Toenies,[1,2]* David A. W. Miller,[1] Matthew R. Marshall,[3] and Glenn E. Stauffer[1]

[1] Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania, USA
[2] Intercollege Graduate Degree Program in Ecology, Pennsylvania State University, University Park, Pennsylvania, USA
[3] National Park Service, Inventory and Monitoring Division, Eastern Rivers and Mountains Network, University Park, Pennsylvania, USA
* Corresponding author: mkt5213@psu.edu

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ABSTRACT

Eastern hemlock (*Tsuga canadensis*) is undergoing widespread decline throughout the eastern United States due to the introduction of the nonnative hemlock woolly adelgid (*Adelges tsugae*). In light of hemlock's unique significance for avian communities, we examined the long-term response of the breeding bird community to the decline and die-off of this foundational forest species. We conducted variable-radius point counts to survey bird communities in both hemlock and hardwood stands in 2000, during the early stages of adelgid infestation, and again in 2015 and 2016, following significant hemlock decline. We also measured the severity of hemlock decline and associated vegetation variables in the same hemlock stands in which avian surveys were completed. We used multispecies occupancy models to examine species-specific and species group responses to hemlock decline. Results showed that, across hemlock stands, hemlock basal area declined from a mean of 56% of the total basal area to 46%, and that hemlock decline was correlated with current vegetation structure, including an increased deciduous understory. Species richness of hemlock-associated birds declined by an average of ~1 species per survey location. The Black-throated Green Warbler (*Setophaga virens*) was the most strongly affected, declining in occupancy by 30%. All other species groups responded positively, with the strongest responses by species associated with the shrub layer, forest edge, and mature deciduous habitat. The species composition in hemlock and hardwood stands became more similar over time as the unique species assemblages in hemlock stands gave way to the avian community of the surrounding hardwood landscape, highlighting a trend toward homogenization of the avian community. Where hemlock-associated bird species persisted, their presence was correlated with a combined effect of greater hemlock basal area and better hemlock condition. Our results demonstrate that the decline of hemlocks has restructured vegetation communities and their associated avian communities over time, with strong implications for forest-specialist birds.

Keywords: Tsuga canadensis, *Adelges tsugae*, birds, community, occupancy, decline, *Empidonax virescens*, *Setophaga virens*

Cambios en la vegetación y en la estructura de la comunidad de aves luego de la disminución de una especie forestal fundamental, la cicuta oriental

RESUMEN

La cicuta oriental (*Tsuga canadensis*) está experimentando una disminución extendida a través del este de los Estados Unidos, debido a la introducción de la cicuta no nativa *Adelges tsugae*. A la luz de la importancia única de la cicuta para las comunidades de aves, examinamos la respuesta de largo plazo de la comunidad de aves reproductivas a la disminución y la muerte de esta especie forestal fundamental. Realizamos conteos en puntos de radio variable para censar las comunidades de aves en rodales de cicuta oriental y de madera dura en 2000, durante los estadios tempranos de la infestación de *A. tsugae*, y de nuevo en 2015 y 2016, luego de una disminución significativa de *T. canadensis*. También medimos la severidad de la disminución de *T. canadensis* y las variables asociadas de la vegetación en los mismos rodales de *T. canadensis* donde se realizaron los conteos de aves. Usamos modelos de ocupación de múltiples especies para examinar las respuestas específicas de especies y de grupos de especies a la disminución de *T. canadensis*. Los resultados mostraron que, a lo largo de los rodales de *T. canadensis*, su área basal disminuyó desde una media de 56% de área basal total a 46%, y que la disminución de *T. canadensis* estuvo correlacionada con la estructura actual de la vegetación, incluyendo un aumento del sotobosques caducifolio. La riqueza de las especies de aves asociadas a *T. canadensis* disminuyó aproximadamente un promedio de una especie por rodal. *Setophaga virens* fue la especie más fuertemente afectada, disminuyendo en ocupación en un 30%. Todos los otros grupos de especies respondieron positivamente, con las respuestas más fuertes en las especies asociadas con el estrato arbustivo, el borde del bosque y el hábitat maduro deciduo. La composición de especies en los rodales de

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cicuta oriental y de madera dura se volvió más similar a lo largo del tiempo, resaltando una tendencia hacia la homogeneización de la comunidad de aves, a medida que los ensambles únicos de especies de los rodales de *T. canadensis* ceden el paso a la comunidad de aves del paisaje circundante de maderas duras. En los lugares donde persistió la asociación de *T. canadensis* con las especies de aves, su presencia estuvo correlacionada con el efecto combinado de una mayor área basal y una mejor condición de *T. canadensis*. Nuestros resultados demuestran que la disminución de *T. canadensis* ha reestructurado las comunidades vegetales y las comunidades de aves asociadas a lo largo del tiempo, con fuertes implicancias para las aves especialistas de bosque.

Palabras clave: *Adelges tsugae*, aves, comunidad, disminución, *Empidonax virescens*, ocupación, *Setophaga virens*, *Tsuga canadensis*

INTRODUCTION

Introductions of nonnative insects and pathogens have caused repeated large-scale die-offs of dominant tree species in North American landscapes (Liebhold et al. 1995, Herms and McCullough 2014). However, few studies have focused on the long-term, community-wide changes that may result from these die-offs (but see Alsop and Laughlin 1991, Rabenold et al. 1998). The widespread decline of eastern hemlock (*Tsuga canadensis*; hereafter, 'hemlock') provides a useful opportunity for understanding the effects of a decline and loss of a dominant tree species on specialist avian species, as well as the avian community as a whole. Currently, hemlock is undergoing severe and widespread decline throughout the eastern United States. The cause is the hemlock woolly adelgid (*Adelges tsugae*), an aphid-like insect native to Japan that was introduced to Virginia in the early 1950s (Souto et al. 1996). The adelgid defoliates hemlocks by feeding on needles and buds, with defoliation and limb death typically occurring first in lower branches before proceeding to the top of the tree. Hemlock mortality can occur in as few as 4 yr (McClure 1991), but frequently takes much longer depending upon site characteristics (Orwig et al. 2002). As of 2015, the adelgid had spread to 20 U.S. states, and more than half of the U.S. counties where eastern hemlock is native were infested (USDA Forest Service 2016). To date, no large-scale solution for preventing adelgid-induced mortality has been identified. As a result, the hemlock woolly adelgid continues to threaten eastern hemlock in its remaining range.

The loss of hemlock from eastern forests may have disproportionate impacts on avian communities because of its unique structural characteristics. Hemlock generally grows in homogenous, mature stands, and, due to its high shade tolerance, retains live branches lower into the midstory and understory than other tree species (Burns and Honkala 1990). Hemlocks provide dense vertical structure in which birds can forage, nest, and roost, and past studies have shown that forest mosaics that include hemlock stands have greater observed avian diversity (Gates and Giffen 1991, Howe and Mossman 1995). Several bird species are known to be strong hemlock associates in the northeastern United States and elsewhere, including the Acadian Flycatcher (*Empidonax virescens*), Blue-headed Vireo (*Vireo solitaries*), Hermit Thrush (*Catharus guttatus*), Blackburnian Warbler (*Setophaga fusca)*, and Black-throated Green Warbler (*Setophaga virens*; Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008, Allen et al. 2009). Some of these species have been considered hemlock obligates in certain regions, including our study area (Benzinger 1994), and previous research has predicted that they may decline (Ross et al. 2004, Brown and Weinkam 2014). One species that may be especially vulnerable due to its strong hemlock association is the Black-throated Green Warbler, which has been demonstrated to have morphological characteristics specifically adapted to hemlock use (Parrish 1995). The Acadian Flycatcher also frequently ranks as an at-risk species, due to regionally variable population trends and high sensitivity to forest fragmentation (Allen et al. 2017). This species has already been shown to have lower breeding densities in hemlock affected by adelgids compared with healthy hemlock (Allen et al. 2009). Additionally, all 5 of the aforementioned hemlock specialists are Neotropical migrants, another group of high conservation priority (Stotz et al. 1996, Faaborg et al. 2010). In contrast to the negative implications for hemlock specialists, adelgid invasion may lead to increased abundance of other species by causing short- and long-term increases in habitat availability, including (1) more standing dead trees; (2) dense growth of plants in the understory (Orwig and Foster 1998, Jenkins et al. 1999); and (3) accelerated growth of hardwoods in the overstory following release from competing hemlocks (Orwig et al. 2002; Figure 1). In the long term, replacement of hemlock stands by other vegetation communities (Orwig et al. 2002), such as deciduous forests or communities dominated by nonnative plants, may lead to more homogeneous bird communities across the regional landscape.

Previous studies of avian responses to hemlock decline have made conclusions based on space-for-time approaches that either compared bird communities in hemlock with those in other forest types (Howe and Mossman 1995, Brown and Weinkam 2014), or compared bird communities among hemlock stands with varying degrees of decline (Tingley et al. 2002, Becker et al. 2008). In contrast, we directly measured long-term changes in the bird commu-

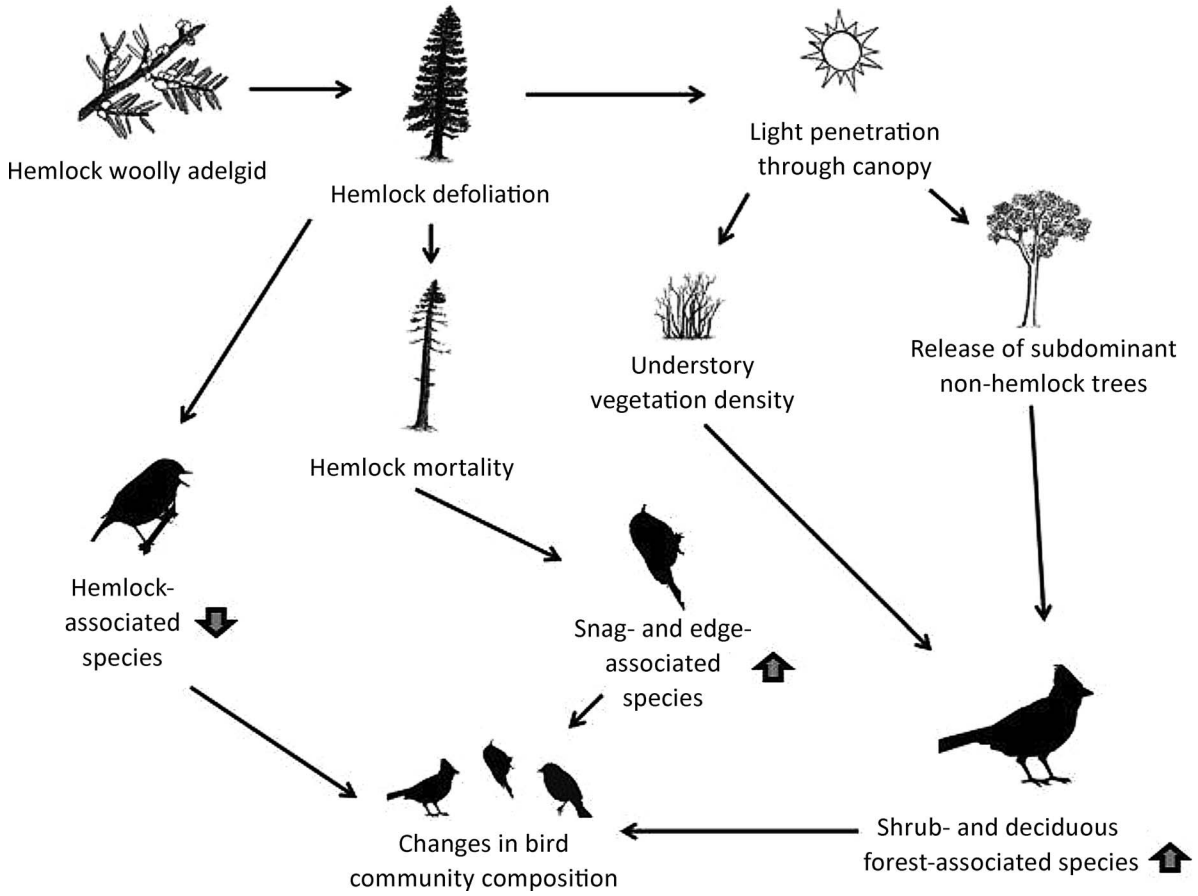

FIGURE 1. Hypothesized causal relationships among hemlock woolly adelgid invasion, consequent changes to vegetation structure, and concomitant changes in bird community composition. We hypothesized that adelgid-caused hemlock decline would directly and indirectly affect vegetation structure in forests, which in turn would lead to different responses among avian species groups.

nity by surveying the same hemlock stands both before and after significant hemlock decline. In addition, we measured changes in hemlock dominance from the early stages of adelgid infestation, and examined the relationship between bird community composition and vegetation characteristics related to hemlock die-off. In doing so, we also provide valuable new baseline data that future surveys may use to monitor ongoing effects of hemlock loss on avian communities.

METHODS

Study Area

The Delaware Water Gap National Recreation Area (NRA; Figure 2) borders the Delaware River in northeastern Pennsylvania and northwestern New Jersey and covers an area of 27,742 ha, with elevations of 84 to 490 m (Mahan et al. 2004). The dominant cover type is forest, with 18,575 ha of hardwood forest, 1,295 ha of coniferous forest, and 2,015 ha of mixed evergreen–deciduous forest (Myers and Irish 1981). Prior to the introduction of the hemlock woolly adelgid at Delaware Water Gap NRA, hemlock was present in >1,000 ha of forest, concentrated in mostly pure stands growing along streams that drain into the Delaware River (Young et al. 2002). Hemlock woolly adelgids were first discovered at Delaware Water Gap NRA in 1989 and were present in more than half of hemlock stands there by 1995 (Evans 2004). However, hemlocks in most stands had not yet experienced significant decline prior to the year 2000, when the baseline avian surveys for our study were conducted (R. Evans and R. Ross personal communication). Research on hemlock in a subset of hemlock stands at Delaware Water Gap NRA showed no change in basal area or relative dominance of hemlock prior to 2003 (Eschtruth et al. 2006). Data from surveys conducted in 2000 therefore provide a reliable baseline of predecline conditions.

Surveys were conducted in 22 forest stands—11 hemlock and 11 hardwood (Figure 2)—located along first- or second-order streams in Delaware Water Gap NRA. Prior to hemlock mortality, digital GIS vegetation maps had been used to designate stands as either hemlock or

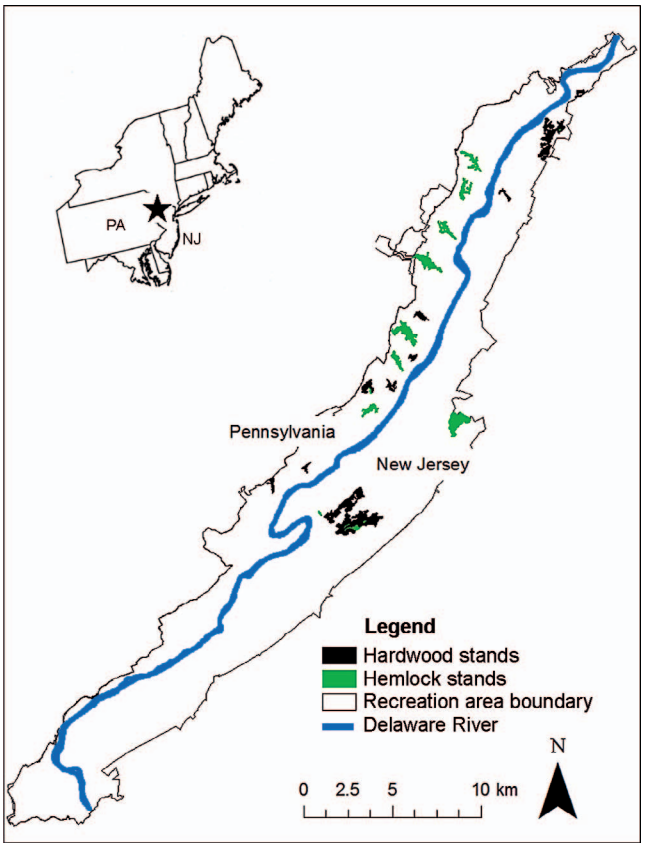

FIGURE 2. Location and outline of study area (Delaware Water Gap National Recreation Area) along the border of Pennsylvania (PA) and New Jersey (NJ) in the northeastern USA, where we studied changes in vegetation structure and avian community composition following the decline of hemlocks due to hemlock woolly adelgid invasion. The Delaware River divides the study area longitudinally from northeast to southwest. Black and green patches within the study area border represent 22 forest stands within which 80 sampling locations were located. Forest stands had previously been designated as either hemlock or hardwood prior to hemlock mortality caused by the hemlock woolly adelgid.

hardwood based on the dominance of tree species by canopy area. Stands in which hemlock was the first, second, or third most dominant species were designated as hemlock stands, with all others classified as hardwood (hereafter, 'hemlock stands' and 'hardwood stands,' respectively; Young et al. 2002). Subsequent basal area measurements in these 22 stands showed that hemlock accounted for a mean of 53% (range: 25%–77%) of the basal area in hemlock stands, compared with a mean of 3% (range: 0%–14%) in hardwood stands (Mahan et al. 2004). Average stand area was 34.5 ha, and ranged from 2.5 ha to 127.5 ha. These stands were selected as part of a wider research effort to inventory the unique communities associated with hemlock stands in the park. This effort was motivated by the threat posed by the hemlock woolly adelgid's recent arrival (Young et al. 2002). Each of the 11 hardwood and hemlock stands were paired based on similar topographic characteristics. This design minimized nonvegetative differences between paired hemlock and hardwood stands (Young et al. 2002).

Vegetation Surveys

We conducted 2 types of vegetation survey to characterize forest structure and composition and how they changed through time. The first set of measurements occurred along transects at standardized locations within hemlock stands that were originally measured in 1997, prior to significant hemlock decline or mortality (Mahan et al. 2004). These measurements allowed us to examine differences between hemlock basal area pre- and post-hemlock mortality. In each of the 11 hemlock stands, we measured percent hemlock basal area in the winter of 2015–2016 (during the leaf-off period) and compared these values with premortality baseline data collected in 1997. These survey locations did not coincide directly with avian survey locations and instead quantified stand-level hemlock decline over time. The second set of measurements occurred at avian survey locations in 2015, allowing us to examine how contemporary vegetation related to bird distributions. Unfortunately, vegetation was not measured at individual avian survey locations during the 2000 surveys conducted by Ross et al. (2004).

Basal area measurements in 2015 followed the same protocol used in 1997 (Mahan et al. 2004). For each stand, we established 2 transects perpendicular to the stream channel within the forest stand: 1 transect at either end of a predetermined 80-m or 160-m stream length (80 m for first-order streams and 160 m for second-order streams, based on the original study design). For each transect, we established sampling points 15 m from the stream edge on either side of the stream, with subsequent points established at 30 m intervals on either side. Using a compass and handheld GPS unit (GPSmap 60CSx; Garmin, Olathe, Kansas, USA), we established sampling points to a maximum distance of 75 m from the stream edge for first-order streams and 135 m for second-order streams. We terminated transects at the maximum distance or at the edge of the stream's watershed (whichever came first). At each waypoint, we used a 10-factor prism to measure basal area for trees $\geq$10 cm in diameter at breast height, following standard point-sample timber cruising methods (Burkhart et al. 1984). Each standing tree was recorded as living or dead and identified as hemlock or not hemlock.

To examine the relationship between contemporary vegetation and bird communities, we measured hemlock condition and associated vegetation variables at each of the 80 avian survey locations during the summer of 2015. We established a 50-m radius plot at each location and divided

the plot into 4 quadrants based on the cardinal directions. We then established 4 sampling points 25 m from the center of the plot, one in each intercardinal direction, plus a fifth sampling point at the plot center. We rated the average condition of all hemlock trees within a 10-m radius of each of the 5 sampling points on a scale of 1 to 5 (in half-unit increments) using the following scale: 1 = complete mortality; 2 = severe limb die-off and needle loss, with live branches remaining along less than the top ⅓ of the tree; 3 = significant limb die-off and needle loss, but live branches remaining along the top ⅓–⅔ of the tree; 4 = minor limb die-off and needle loss, with live branches remaining along more than the top ⅔ of the tree; and 5 = healthy, with no evidence of limb die-off or needle loss. This metric for evaluating hemlock condition is consistent with the pattern of loss of hemlock foliage and branches, which typically follows a systematic bottom-to-top pattern. We also measured hemlock basal area at the 5 points in each plot, using the same method used at points for the stand-level basal area measurements described previously.

Finally, in 2015, we estimated vegetation coverage from ground level to the canopy in the 50-m radius plots in which avian point count surveys were conducted (protocol adapted from Marshall et al. 2016). Plots were divided into 4 equal quadrants and we estimated vegetation volume in 4 height categories: 0.0–0.5 m; 0.5–2.0 m; 2.0–5.0 m; and >5.0 m to the upper limit of the forest canopy (hereafter referred to as the ground layer, understory, midstory, and canopy). For each level of each quadrant, we estimated the volume of space filled by vegetation, recorded as a percentage to the nearest 10% (essentially a percent cover estimate in a 3-dimensional space). We subdivided these percentage estimates to the nearest 5% based on 4 vegetation types: (1) hemlock; (2) deciduous species; (3) coniferous species other than hemlock; and (4) rhododendron (*Rhododendron* spp.), laurel (*Kalmia* spp.), and other broadleaf evergreens. We averaged all vegetation measurements from quadrants and subpoints to generate a single metric for each survey location.

Avian Surveys

We compared the results of surveys conducted in 2015 and 2016 with baseline surveys conducted in 2000 by Ross et al. (2004) to measure changes in avian community composition following hemlock decline. In each of the 3 study years, we surveyed 80 locations across the 11 pairs of hemlock and hardwood stands, with 45 locations in hemlock stands and 35 in hardwood stands. Survey locations were a minimum of 250 m apart and a minimum of 150 m from the edge of the respective stand type. Due to these distance limitations, the number of survey locations per forest stand varied from 1 to 6. In 2015 and 2016, we returned to the same locations surveyed in 2000 whenever possible. However, for 6 of the survey locations, records from surveys in 2000 indicated the forest stand, but not the exact location, where the survey was done. In these cases, we used field notes and guidance from Robert Ross (the observer in 2000) to establish the survey locations as closely as possible to where the original surveys were done.

All counts in 2000 were conducted by a single observer (R. Ross), as were all counts in 2015 and 2016 (M. Toenies), and survey methodology in 2015–2016 followed the methodology of surveys in 2000. Observers conducted early season point counts (following the recommendations of Ralph et al. 1995) from May 31 to June 14 in 2000, from May 30 to June 14 in 2015, and from June 1 to June 10 in 2016. In the 2 later years, we also conducted a second set of point counts at each survey location, which occurred from June 15 to July 7 in 2015 and from June 16 to June 23 in 2016. Counts occurred in the morning (between 0530 and 1000 hours) and only during suitable weather conditions: no precipitation and wind speed $\leq$19 km hr^{-1} (3 or less on the Beaufort scale). At each point, we measured ambient noise to the nearest tenth of a decibel using a sound meter (GM1351 Digital Sound Level Meter, Shenzhen Jumaoyuan Science and Technology, Shenzhen city, Guangdong province, China) aimed in each of the 4 intercardinal directions (later years only). We disregarded brief noise peaks from sources such as loud bird vocalizations or infrequent traffic noise.

After waiting 5 min to limit the effects of any disturbance on bird activity, observers counted all birds heard or seen in a 10-min period. Observers recorded whether each bird was detected during the first or second 5 min of the count, as well as the distance at which the bird was first observed (0–50 m or >50 m). Observers in both 2000 and 2015–2016 practiced distance estimation prior to avian surveys in order to accurately place detections into the 2 distance bands. Because observers were likely to vary in their abilities to detect more distant birds, subsequent analyses included data for bird detections from <50 m only. This helped to minimize detection differences between observers in 2000 vs. 2015–2016. We conducted counts on dates in 2015 and 2016 that coincided as closely as possible with the same calendar date and time of day as the original count for that point in 2000.

Analyses

Vegetation. We first examined the relationship between hemlock decline and current vegetation communities. We tested for correlations between the change in hemlock basal area over time (measured at the forest stand level) and variables measured at individual point count locations: hemlock basal area, hemlock health, number of standing dead trees, canopy hemlock volume, and deciduous understory volume. For 1 of the 11 hemlock stands, basal area data were excluded from vegetation analyses because survey locations were found to differ between 1997 and

2015. We used function corr.test in package psych (Revelle 2014) in R 3.1.2 (R Core Team 2015) to estimate correlations and their significance levels for vegetation variables.

Estimating bird occurrence. We examined group average and species-specific responses for 6 groups of avian species, chosen based on shared habitat associations that we hypothesized would affect community responses to hemlock decline. The groups included (1) hemlock-associated species, and species that we expected to respond to increases in (2) mature deciduous forest, (3) forest edge, (4) a dense shrub layer, (5) snags, and (6) early successional habitat. We assigned species to groups using predetermined keywords from detailed habitat descriptions for each species in the Birds of North America Online database (Rodewald 2015). For the hemlock-associated group, we included only species that previous studies have shown to have a significant association with hemlock specifically within the northeastern or mid-Appalachian regions of the United States. We analyzed occurrence probabilities for all species in each group for which the breeding range overlapped our study area, and included only passerine or near-passerine species in the analysis (see Appendix Table 3 for species and species groups). We excluded the following species due to wide-ranging or irruptive breeding habits: Yellow-billed Cuckoo (*Coccyzus americanus*), Black-billed Cuckoo (*Coccyzus erythropthalmus*), American Crow (*Corvus brachyrhynchos*), Common Raven (*Corvus corax*), and Red-breasted Nuthatch (*Sitta canadensis*).

Analyses of bird community occurrence patterns included (1) a before–after comparison of bird communities using bird survey data pre- and post-hemlock decline, and (2) a comparison of differences in bird communities among survey locations using only the postdecline data. We treated 2015 and 2016 as a single time period in the before–after comparison in order to compare postdecline survey data with the predecline data from 2000 (hereafter, the term 'time period' is applied to 2000 and 2015–2016). We performed all analyses using hierarchical multispecies occupancy models, which are used to estimate the probability of a species occupying a local site while accounting for imperfect species detection (Mackenzie et al. 2002, Zipkin et al. 2009). This approach allowed us to estimate group and species-specific changes in the proportion of survey locations occupied through time. All occupancy analyses were fit using Markov chain Monte Carlo (MCMC) methods and run using JAGS (Plummer 2003) called from R 3.1.2 (R Core Team 2015) using package runjags (Denwood 2016). We ran separate models for each species group. Our models used species detections in the two 5-min intervals within the 10-min count to estimate the overall probability of detecting each species. For all covariates for detection probability and occupancy, we estimated the group mean response as well as species-specific responses as random effects. For detection, our models included covariates for year (observers varied between 2000 and 2015–2016, so this also accounted for observer differences), time of day, survey date, and ambient noise level.

For the before–after analysis, we subdivided the data to include only the first survey visits from 2015–2016 to make results more directly comparable with the single visit in 2000. It is possible that apparent species trends over time could have been influenced by observer differences between years and other factors unrelated to hemlock decline (e.g., species trends outside the breeding range). However, we were able to control for these effects by comparing species-specific responses in hemlock stands with responses in hardwood stands. By comparing changes in each species or group within hemlock stands with a baseline of that species' or group's trend in hardwood stands, we ensured that observer effects or regional declines unrelated to hemlock change could not explain our results. Thus, our relevant measure of species response was the difference in change through time between hardwood and hemlock stands, measured as the interaction between time period (2000 vs. 2015–2016) and forest type (hardwood vs. hemlock). These responses are represented as the beta slope coefficients (on a logit scale) for the effect of this time*forest type covariate on occupancy probability for each species. In addition, we back-transformed these slope coefficients to show estimated changes in species occupancy over time. As our measure of response at the species group level, we summed changes in occupancy over time across all species in the group to derive estimates of change in species richness for that group (Zipkin et al. 2009). We predicted that this before–after analysis would show a decline in hemlock-associated species and increases in all other species groups. We also examined the similarity in the composition of avian communities between hemlock and hardwood stands pre- and post-decline using a Bray–Curtis similarity analysis (Bray and Curtis 1957), a widely used method for comparing ecological communities (Beals 1984). We derived similarity indices by comparing occupancy estimates across all species for the 4 sampled community types (hemlock and hardwood pre- and post-decline). We used function vegdist in package vegan (Oksanen et al. 2016) in R 3.1.2 (R Core Team 2015) to determine similarity indices.

The second part of our analysis focused on understanding survey location–specific characteristics affecting bird community composition by examining how bird occurrence was related to current vegetation characteristics using the 2015 and 2016 point counts. Because our focus was on the effects of hemlock decline, we only included survey locations with at least one hemlock present in the

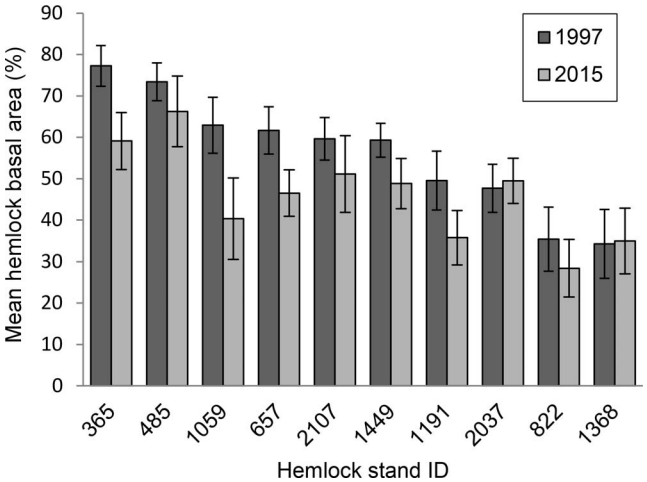

FIGURE 3. Mean hemlock basal area (with standard error bars) in 1997 and 2015 across sampled hemlock stands in the Delaware Water Gap National Recreation Area, northeastern USA. In general, stands that had more hemlock prior to hemlock woolly adelgid infestation experienced greater decline following infestation. For 2 stands with low initial hemlock basal area, the mean percentage of hemlock basal area was slightly greater in 2015.

canopy ($n = 56$). For each of our species groups, we estimated the effects of (1) deciduous understory volume, (2) canopy hemlock volume, and (3) an interaction between hemlock health and hemlock basal area. These relationships are presented as the beta slope coefficients (on a logit scale; hereafter represented by the symbol β) for the effect of each covariate on occupancy probability.

RESULTS

Vegetation

Hemlock condition measured at avian survey locations indicated that hemlock woolly adelgid infestation had affected hemlocks at nearly all survey locations in hemlock stands, although no locations had experienced complete hemlock mortality. The proportion of 2015–2016 survey locations with hemlocks in each of the 5 hemlock condition scores were: 7% healthy; 27% minor defoliation and limb death; 53% significant defoliation and limb death; 13% severe defoliation and limb death; and 0% complete tree mortality. Between pre-adelgid (1997) and post-adelgid (2015) basal area measurements, hemlock declined to varying degrees across the sampled stands, with the severity of decline correlated with current vegetation characteristics. Across hemlock stands, hemlock accounted for a mean of 56% of the total basal area in 1997, but had declined to 46% by 2015 (Figure 3, Appendix Table 4). Between 1997 and 2015, mortality in hemlock stands also increased, with standing dead trees accounting for a mean of 2% of the total basal area in 1997, compared with 15% in 2015 (Appendix Table 4). Greater initial hemlock basal area in the premortality surveys in 1997 was correlated with greater subsequent loss of hemlock basal area ($r = 0.51$, 95% confidence interval = 0.24–0.71). In addition, the degree of decline from one hemlock stand to another was correlated with several vegetation variables measured at individual survey locations (Table 1). Greater decline at the stand level was correlated with poorer hemlock condition, more standing dead hemlocks, and greater deciduous vegetation volume in the understory at survey locations.

At the 56 point count locations with hemlock present, we also found strong correlations between our measures of vegetation variables. Better hemlock condition was negatively correlated with the number of hemlock snags. Hemlock health was also negatively correlated with both canopy hemlock volume and hemlock basal area at individual survey locations (Table 1), as hemlocks tended to be healthy only where they were sparse. This reflects a similar relationship to the stand-level correlation between initial hemlock basal area and degree of subsequent decline.

Changes in Bird Communities through Time

Across the 3 seasons of surveys of the 80 point count locations, observers detected a total of 58 species that met the criteria for inclusion in our analyses (see Appendix Table 3 for a full listing of these species and the number of surveys during which each species was detected). Of the 3 detection covariates included in our models, 1 (ambient noise) had a mean negative effect on detection probability,

TABLE 1. Correlation matrix between vegetation variables related to hemlock decline. Hemlock decline (the difference in hemlock basal area between 1997 and 2015) was measured at the forest stand level, while all other variables were measured at individual survey locations. The hemlock health variable is based on a scale on which greater values indicate healthier hemlocks. Asterisks following r values indicate significance level (* $P < 0.05$, ** $P < 0.01$), and nonsignificant correlations are represented by dashes.

	Hemlock snags	Deciduous understory	Stand-level hemlock decline	Hemlock basal area	Canopy hemlock
Hemlock health	−0.62**	—	−0.46**	−0.75**	−0.74**
Hemlock snags		0.34**	0.34*	0.49**	0.35**
Deciduous understory			0.31*	—	0.39**
Stand-level hemlock decline				0.34*	—
Hemlock basal area					0.81**

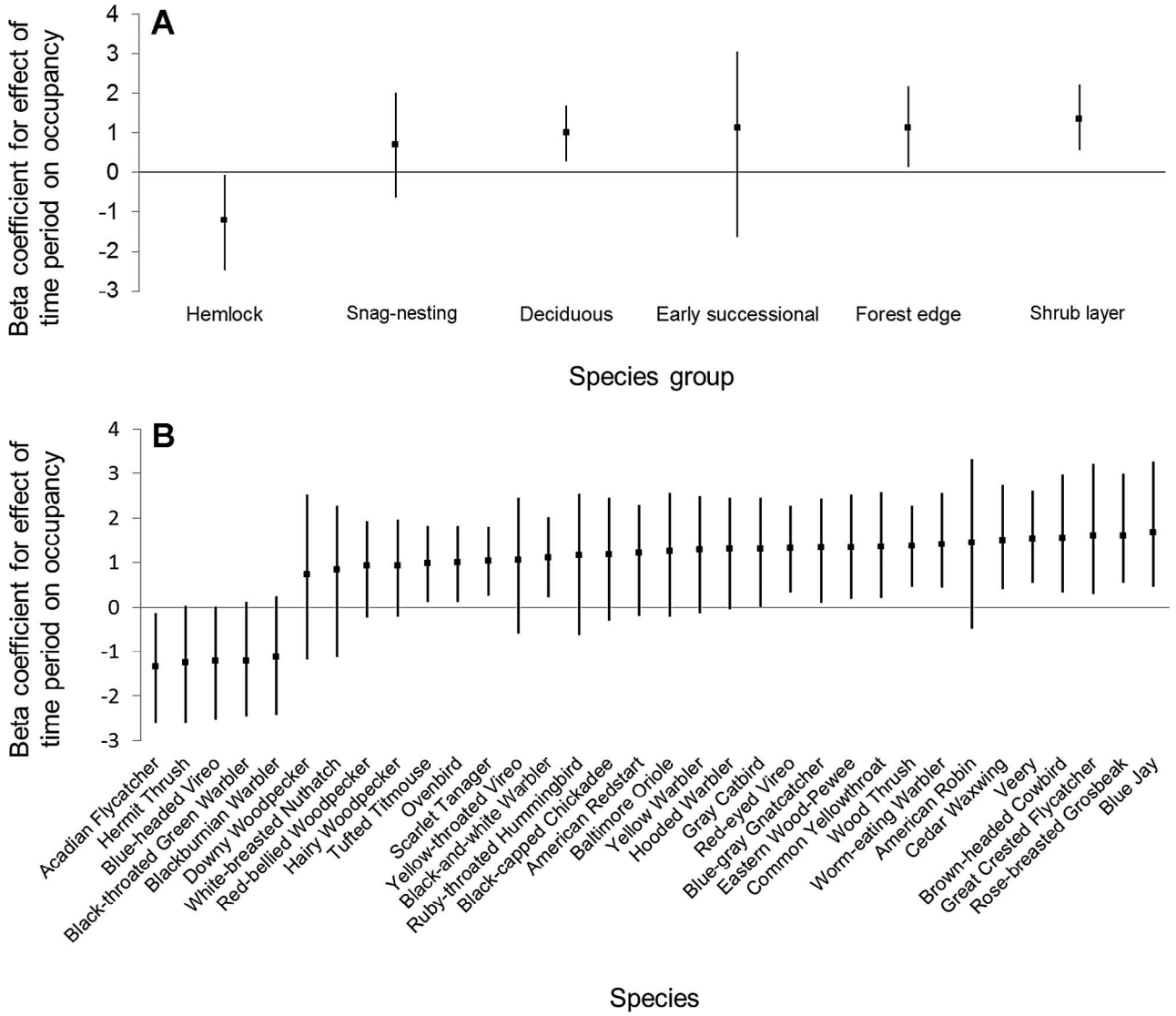

FIGURE 4. (**A**) Avian species group responses and (**B**) individual avian species responses to hemlock decline and die-off in hemlock-dominated stands relative to hardwood-dominated stands in the Delaware Water Gap National Recreation Area, northeastern USA. Error bars represent 95% credible intervals. The effects shown here are the beta slope coefficients on a logit scale for an interaction between time period (2000 vs. 2015–2016) and forest type (hemlock vs. hardwood). Thus, these coefficients represent the effect of time period on occupancy in hemlock stands after controlling for observed effects occurring in hardwood stands. Species with <5 total detections are excluded here.

although this effect was nonsignificant based on a 95% credible interval ($\beta = -0.18$, 95% credible interval [CI]: –0.38 to 0.04). Survey date and time of day did not affect detection probability (see Appendix Table 5 for mean and species-specific effects of all detection covariates).

Several species groups showed strong changes in occupancy in hemlock stands over time, relative to changes in hardwood stands (see Appendix Table 3 for occupancy estimates for all species in the 2 stand types in both time periods). Occupancy increased for the species groups associated with the shrub layer ($\beta = 1.35$, 95% CI: 0.56–2.21), forest edge ($\beta = 1.13$, 95% CI: 0.13–2.17), and mature deciduous forest ($\beta = 1.00$, 95% CI: 0.28–1.69; Figure 4A). The snag-nesting species and early successional species groups also both showed positive mean effects to hemlock decline ($\beta = 0.712$, 95% CI: –0.63 to 2.01, and $\beta = 1.12$, 95% CI: –1.64 to 3.05, respectively), although the 95% credible intervals overlapped zero for both. Despite fairly strong positive effects for these 2 groups, especially the early successional species, precision for these mean effects was the lowest of all groups, likely a result of fewer detections for most species in both groups.

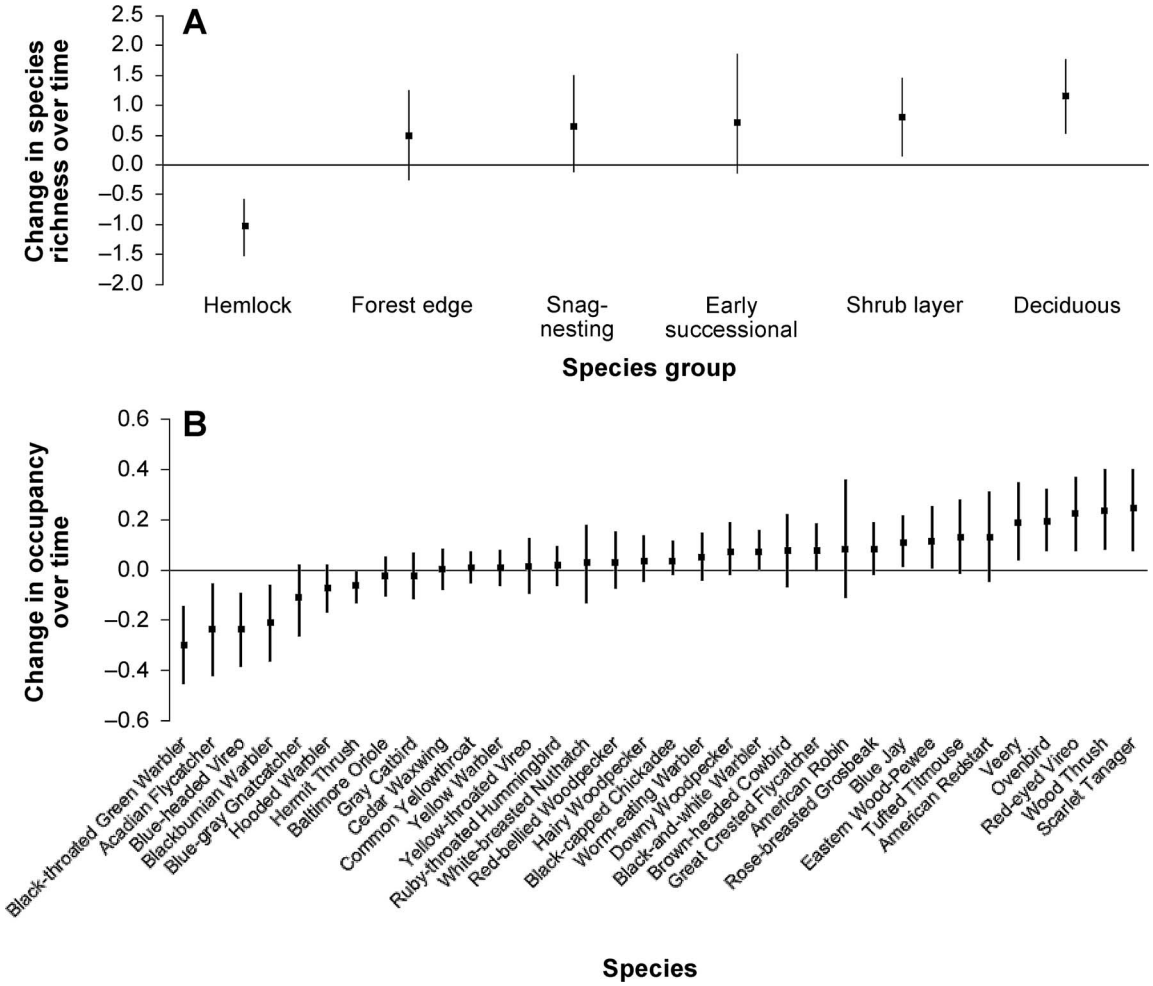

FIGURE 5. Changes through time in (**A**) avian species richness of species groups (see Appendix Table 3 for species groups) and (**B**) occupancy of bird species in hemlock stands relative to changes in hardwood stands in response to hemlock decline and die-off in the Delaware Water Gap National Recreation Area, northeastern USA. Error bars represent 95% credible intervals. Between 2000 and 2015–2016, species richness declined for hemlock-associated species and increased for all other species groups. Species with <5 total detections are excluded here.

The hemlock-associated species showed a strong negative mean effect that clearly contrasted with the positive effect on all other species groups ($\beta = -1.22$, 95% CI: −2.47 to −0.06; Figure 4A). The 95% credible interval for this group was broader than that of most species groups, likely due to low power given the scarcity of hemlock-associated species in the hardwood stands, which acted as the control for comparison. At a species-specific level, responses were similar across the 5 species in the group, although the effect was slightly stronger and more precise for the Acadian Flycatcher (Figure 4B).

As the mean effects for the species groups would suggest, the individual species that showed the strongest positive relationships with hemlock decline were mostly species associated with either the shrub layer (Veery [*Catharus fuscenscens*], Worm-eating Warbler [*Helmitheros vermivorum*], and Wood Thrush [*Hylocichla mustelina*]); the forest edge (Blue Jay [*Cyanocitta cristata*], Great Crested Flycatcher [*Myiarchus crinitus*], and Brown-headed Cowbird [*Molothrus ater*]); or both of these habitats (Rose-breasted Grosbeak [*Pheucticus ludovicianus*] and Cedar Waxwing [*Bombycilla cedrorum*]; Figure 4B). All of the species associated with deciduous forest, snags, and early successional habitat also showed positive responses, although of all species in the latter 2 groups, only 1 species—the Veery—showed an effect with a nonoverlapping 95 % credible interval.

To illustrate how the effects discussed above translated into changes in species occurrence, we calculated changes in occupancy over time for each species (Figure 5B) using back-transformations of the logit-scale slope coefficients. For each species group, we also calculated changes in

TABLE 2. Beta coefficients from models examining the effects of 3 variables on the probability of occupancy of hemlock forest stands by avian species groups: (1) hemlock volume in the canopy (>5 m height category); (2) an interaction between hemlock abundance (basal area) and hemlock health; and (3) deciduous vegetation volume in the understory (0.5–2.0 m height category). Asterisks indicate effects with 95% credible intervals that do not overlap zero. Mean effects are shown, with SD in parentheses. See Appendix Table 3 for species groups.

Avian species group	Canopy hemlock volume	Abundance*Health	Understory volume
Hemlock	1.03* (0.45)	0.72* (0.33)	−0.40 (0.23)
Shrub layer	−0.08 (0.22)	0.10 (0.21)	0.24 (0.16)
Mature deciduous	0.06 (0.22)	0.25 (0.20)	0.14 (0.27)
Forest edge	−0.04 (0.17)	0.26 (0.17)	0.11 (0.14)
Early successional	0.47 (0.54)	0.80 (0.75)	0.03 (0.69)
Snag	0.05 (0.35)	0.21 (0.30)	−0.20 (0.26)

species richness over time by summing estimated changes in occupancy for all species in the group (Zipkin et al. 2009; Figure 5A). Occupancy declined for all hemlock-associated species, with the greatest decline in the Black-throated Green Warbler (mean change in occupancy = –30%, 95% CI: –45% to –14%). Summed across species, the declines in occupancy for this group indicated that survey locations in hemlock stands lost an average of ~1 hemlock-associated species over time (mean change in species richness = –1.03 species per survey location, 95% CI: –1.52 to –0.59). In contrast to the hemlock specialists, all other species groups showed significant increases in species richness over time (Figure 5A). Species richness increased the most for groups associated with mature deciduous forest (mean change in richness = 1.16 species per survey location, 95% CI: 0.53–1.76). While the species groups associated with the shrub layer and forest edge showed the strongest positive relationships with hemlock decline (Figure 4A), many of the species in these groups also had very low occupancy estimates (see Appendix Table 3). By contrast, the deciduous forest–associate group included several of the species with the highest occupancy estimates (e.g., Red-eyed Vireo [*Vireo olivaceus*], Ovenbird [*Seiurus aurocapilla*], and Scarlet Tanager [*Piranga olivacea*]). Thus, compared with species associated with the forest edge and shrub layer, the overall high occupancy of deciduous forest associates resulted in greater absolute changes in occupancy and species richness for this group (Figure 5), despite a slightly weaker positive relationship with hemlock decline (Figure 4).

Homogenization of Bird Community through Time

After finding declines in hemlock specialists and increases in other avian species within hemlock stands, we examined the similarity of bird communities in the 2 forest types (hemlock vs. hardwood) during each of the 2 time periods (pre- and post-decline). Our goal was to test the prediction that, with a decline in hemlock, the avian community in hemlock stands would become more similar to that in hardwood stands. Bray–Curtis similarity indices showed that communities in hemlock and hardwood stands were indeed more similar postdecline (index = 0.71) than predecline (index = 0.60). Furthermore, the contemporary avian community in postdecline hemlock stands was slightly more similar to that in hardwood stands than that in predecline hemlock stands (index = 0.80). This highlights a shift in hemlock stands away from a unique species assemblage and toward the community composition of the surrounding landscape of primarily hardwood forest.

Differences in Occupancy among Hemlock Survey Locations

Vegetation surveys from 2015 and avian surveys from 2015–2016 allowed us to examine how avian community composition following hemlock decline was related to characteristics of vegetation structure that were affected by the hemlock woolly adelgid invasion, including canopy hemlock volume, deciduous understory volume, and hemlock health. Canopy hemlock volume was positively related to the probability of occupancy of the hemlock-associated species group (β = 1.03, 95% CI: 0.19–1.97; Table 2). Canopy hemlock volume had only weak effects on the probability of occupancy of most of the other species groups, although the effect for the early successional species group was much greater than that for the other groups (β = 0.47, 95% CI: –0.34 to 1.90); this effect was significant for the Veery (β = 0.65, 95% CI: 0.03–1.36).

Compared with canopy hemlock volume, the percent deciduous vegetation volume in the understory (0.5–2.0 m height category) had larger effects on the probability of occupancy of more of the species groups, although credible intervals overlapped zero for all groups (Table 2). The hemlock-associated species group showed a negative mean effect of this variable on the probability of occupancy (β = –0.40, 95% CI: –0.86 to 0.04), whereas all other species groups besides snag-nesters showed at least weak positive effects for this covariate, with the strongest positive effect shown by the shrub layer–associated species (β = 0.24, 95% CI: –0.06 to 0.56).

As the results of our vegetation analysis showed, there was a strong negative correlation between the amount of

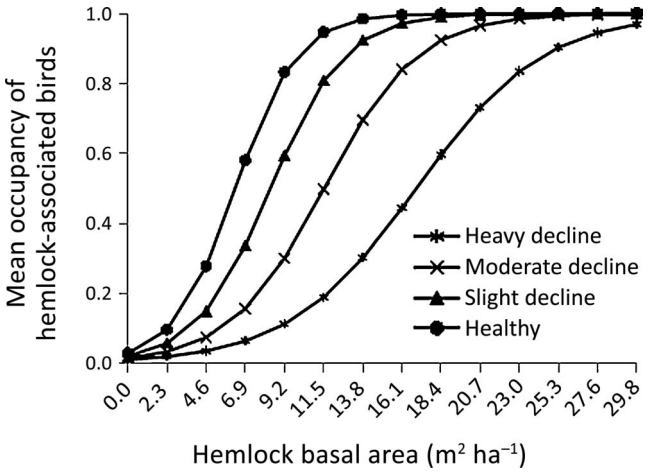

FIGURE 6. Mean occupancy of hemlock-associated bird species in relation to the interaction between hemlock health and hemlock basal area. In areas with healthy hemlock trees, the probability of occupancy of hemlock-associated birds increases abruptly as the basal area of hemlocks increases, while the probability of occupancy increases more gradually in heavily degraded hemlock forest.

hemlock and hemlock health. This could lead to potential confounding of effects when measuring the responses of birds to vegetation characteristics, and therefore we modeled the effects on avian species groups of the interaction between hemlock basal area and hemlock health. The interaction was significant for the hemlock-associated species (Table 2) but not for the other groups. We found that hemlock associates were positively associated with greater hemlock basal area. Once the basal area of hemlocks was controlled for, we also found a positive relationship between the occurrence of hemlock associates and hemlock health (Figure 6).

DISCUSSION

By examining the same hemlock stands both before and after degradation by the hemlock woolly adelgid, we demonstrated that hemlock decline was associated with changes in vegetation structure and bird communities that matched our predictions (Figure 1). Hemlock basal area declined significantly in hemlock stands from the pre-infestation baseline of 1997, with the severity of decline varying across stands. This decline was correlated with changes in vegetation structure, including a denser deciduous understory, decreased live hemlock foliage in the canopy, and a greater number of standing dead hemlocks. Hemlock decline also led to changes in the bird community of hemlock stands, relative to changes in hardwood stands: hemlock specialists declined, but most other species increased, especially those associated with a dense shrub layer, the forest edge, and deciduous forests. Ultimately, the species composition of the avian community in hemlock stands became more similar to that of neighboring hardwood stands. This is consistent with a trend of long-term homogenization of the bird community in regions affected by hemlock woolly adelgid infestation as the unique species assemblages associated with hemlock forests decline. This pattern is yet another example of a much broader phenomenon in which nonnative species introductions are contributing to biotic homogenization on a global scale (Olden et al. 2004).

Changes in Vegetation Structure

The results of our vegetation analyses are consistent with findings from previous research on vegetation in dying hemlock forests. For example, Orwig and Foster (1998) found that hemlock mortality in Connecticut, USA, also resulted in a rapid increase in understory growth, including that of deciduous seedlings. As these other vegetation communities eventually replace hemlock stands, not only in our study area but across the extent of hemlock decline, more homogenized landscapes are likely to develop at a large scale (Orwig et al. 2002). Additionally, the pattern of greater hemlock mortality in stands with greater hemlock basal area, and the corresponding inverse relationship between hemlock basal area and hemlock health at survey locations, hold implications for hemlock forest loss in light of the continued spread of the hemlock woolly adelgid. While other tree species have been known to experience density-dependent effects inflicted by pest species (Bell et al. 2006), this relationship has not previously been well documented in the case of hemlock woolly adelgids and eastern hemlocks, although Orwig and Foster (1998) found a weak relationship between hemlock stand size and hemlock mortality. This pattern indicates that hemlocks and their associated communities may persist longer where the density of hemlock trees is lower.

Changes in Avian Community Composition through Time

Declines in forest type specialists. While previous research has predicted the effects of hemlock loss on certain bird species, to our knowledge this is the first study to have documented long-term changes in bird communities following hemlock decline. Previous studies of bird communities in dying hemlock have predicted that hemlock obligate species are at risk of decline (Tingley et al. 2002), but have also hinted that some hemlock specialists might persist by shifting their habitat use, and have called for long-term studies such as ours to examine this possibility (Becker et al. 2008). The regional presence of these species in other (i.e. not hemlock) forest types may seem to support the idea of habitat plasticity in hemlock-specialized birds. However, the long-term declines in

occupancy that we observed indicate that, as a group, the species richness of hemlock specialists has already declined within hemlock stands in our study area. If this pattern is consistent across a larger scale, we expect these species to experience local extinctions and range contractions in regions where they depend upon hemlock habitat.

Increases in species associated with ephemeral habitat features. The long-term increases that we observed in shrub- and edge-associated bird species align with the findings of other research on bird communities in dying hemlock forests. Many species that have been observed in greater abundance in dying hemlock in other studies are species that also increased in hemlock stands over time in our study, including the Eastern Wood-Pewee (*Contopus virens*), Brown-headed Cowbird, Hooded Warbler (*Setophaga citrina*), Great Crested Flycatcher, and Wood Thrush (Tingley et al. 2002, Becker et al. 2008). In particular, the increased presence of edge-associated species has unique implications for bird communities in dying forests, especially for interior forest obligates. The responses of woodland edge species such as the Blue Jay and Brown-headed Cowbird ranked among the strongest of all of the species that we detected. Both of these species can limit the nest success of other passerines, the jay as a nest predator and the cowbird as a brood parasite. As hemlock die-off initially leads to the opening up of formerly intact canopies, increases in these edge-associated species will likely add to the threats already faced by declining populations of many forest-interior species.

While relatively few previous studies have examined community-wide responses over the long-term progression of a foundational species die-off, several examples support the patterns that we observed. For example, Rabenold et al. (1998) studied bird communities in montane coniferous forests undergoing die-off caused by the invasion of stands of Fraser fir (*Abies fraseri*) by the nonnative balsam woolly adelgid (*Adelges piceae*). In a pattern that parallels our results, this study found that 6 species characteristic of the affected forest type declined over time, while species associated with open and disturbed forest increased. Alsop and Laughlin (1991) also found that several species of edge- and undergrowth-associated birds colonized montane coniferous forests following die-off. In tropical bamboo forests of southeastern Peru, Socolar et al. (2013) observed the loss of 12 bamboo-specialized bird species following die-off, although in this case several specialists persisted.

Communities across a Gradient of Die-off Severity

Compared with the other species groups, the closer relationship between hemlock specialists and the vegetation variables that we modeled may explain the greater precision that we observed in estimates of effects on this group in relation to vegetation metrics at survey locations. The strong positive effect of hemlock abundance on occupancy, combined with a high correlation between abundant hemlock and poor hemlock condition, indicates that areas with high hemlock basal area may currently present a tradeoff to hemlock specialists. These bird species still persist with reduced but relatively high probabilities in locations with sufficiently high basal area or healthy hemlock (Figure 6). However, continued adelgid infestation is likely to reduce hemlock health in low basal area stands and reduce basal area in dense and unhealthy stands. This suggests a potential tipping point, where the rate of decline of hemlock associates will accelerate in the future. Still, the relationships that we observed may have implications for the management of hemlock woolly adelgid infestations. For example, if management practices are able to maintain either (1) sufficient basal area of even highly degraded hemlock, or (2) relatively healthy hemlock even at a fairly low basal area ($\sim$16 m^2 ha^{-1}), then the presence of hemlock specialists may be maintained (Figure 6).

Given the geographically widespread nature of hemlock loss and other forest die-offs, vegetation community responses may vary considerably depending on the rate of die-off, the species composition of replacement communities (including the potential for invasion by nonnative plants), variation in disturbance regimes, and numerous other factors. The responses of bird communities to this variability in vegetation changes will undoubtedly be variable as well. Further research at larger scales could better explain how the avian community response that we observed may vary with respect to this heterogeneity in vegetation restructuring following hemlock die-off.

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LITERATURE CITED

Allen, M. C., M. M. Napoli, J. Sheehan, T. L. Master, P. Pyle, D. R. Whitehead, and T. Taylor (2017). Acadian Flycatcher (*Empidonax virescens*), version 2.0. In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.acafly.02

Allen, M. C., J. Sheehan, Jr., T. L. Master, and R. S. Mulvihill (2009). Responses of Acadian Flycatchers (*Empidonax virescens*) to hemlock woolly adelgid (*Adelges tsugae*) infestation in Appalachian riparian forests. The Auk 126:543–553.

Alsop, F. J., III, and T. F. Laughlin (1991). Changes in the spruce–fir avifauna of Mt. Guyot, Tennessee, 1967–1985. Journal of the Tennessee Academy of Science 66:207–209.

Beals, E. W. (1984). Bray–Curtis ordination: An effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1–55.

Becker, D. A., M. C. Brittingham, and C. B. Goguen (2008). Effects of hemlock woolly adelgid on breeding birds at Fort Indiantown Gap, Pennsylvania. Northeastern Naturalist 15: 227–240.

Bell, T., R. P. Freckleton, and O. T. Lewis (2006). Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology Letters 9:569–574.

Benzinger, J. (1994). Hemlock decline and breeding birds. II. Effects of habitat change. Records of New Jersey Birds 20:34–51.

Bray, J. R., and J. T. Curtis (1957). An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Brown, D. R., and T. Weinkam (2014). Predicting bird community changes to invasion of hemlock woolly adelgid in Kentucky. Southeastern Naturalist 13:104–116.

Burkhart, H. E., J. P. Barrett, and H. G. Lund (1984). Timber inventory. In Forestry Handbook, second edition (K. F. Wenger, Editor). John Wiley & Sons, New York, NY, USA. pp. 361–412.

Burns, R. M., and B. H. Honkala (Technical Coordinators) (1990). Silvics of North America: Volume 1. Conifers. USDA Forest Service Agricultural Handbook 654, Washington, DC, USA.

Denwood, M. J. (2016). runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. Journal of Statistical Software 71:1–25.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey (2006). Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36:1435–1450.

Evans, R. A. (2004). Hemlock woolly adelgid and the disintegration of eastern hemlock ecosystems. Park Science 22:53–56.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Gates, J. E., and N. R. Giffen (1991). Neotropical migrant birds and edge effects at a forest-stream ecotone. The Wilson Bulletin 103:204–217.

Herms, D. A., and D. G. McCullough (2014). Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30.

Howe, R. W., and M. Mossman (1995). The significance of hemlock for breeding birds in the western Great Lakes region. In Hemlock Ecology and Management: Proceedings of a Regional Conference on Ecology and Management of Eastern Hemlock, September 27–28, 1995, Iron Mountain, Michigan (G. Mroz and J. Martin, Editors). Department of Forestry, School of Natural Resources, College of Agricultural and Life Sciences, University of Wisconsin–Madison, Madison, WI, USA. pp. 125–139.

Jenkins, J. C., J. D. Aber, and C. D. Canham (1999). Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29:630–645.

Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro (1995). Invasion by exotic forest pests: A threat to forest ecosystems. Forest Science Monographs 30.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Mahan, C., K. L. Sullivan, B. Black, K. Chung Kim, and R. H. Yahner (2004). Overstory tree composition of eastern hemlock stands threatened by the hemlock woolly adelgid at Delaware Water Gap National Recreation Area. Castanea 69:30–37.

Marshall, M., C. Tzilkowski, and K. Callahan (2016). Streamside Bird Monitoring Protocol for the Eastern Rivers and Mountains Network: Protocol Narrative Version 3.0. Natural Resource Report NPS/ERMN/NRR—2016/1224. National Park Service, Natural Resource Stewardship and Science Office, Fort Collins, CO, USA.

McClure, M. S. (1991). Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomology 20:258–264.

Myers, W. L., and R. R. Irish (1981). Vegetation Survey of Delaware Water Gap National Recreation Area. Final Report. U.S. Department of the Interior, National Park Service, Mid-Atlantic Region, University Park, PA, USA.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner (2016). vegan: Community ecology package. R package version 2.3-5. https://CRAN.R-project.org/package=vegan

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch (2004). Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19:18–24.

Orwig, D. A., and D. R. Foster (1998). Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125: 60–73.

Orwig, D. A., D. R. Foster, and D. L. Mausel (2002). Landscape patterns of hemlock decline in New England due to the

introduced hemlock woolly adelgid. Journal of Biogeography 29:1475–1487.

Parrish, J. D. (1995). Experimental evidence for intrinsic microhabitat preferences in the Black-throated Green Warbler. The Condor 97:935–943.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In DSC 2003: Proceedings of the 3rd International Workshop on Distributed Statistical Computing (K. Hornik, F. Leisch, and A. Zeileis, Editors). Austrian Association for Statistical Computing (AASC) and the R Foundation for Statistical Computing, Vienna, Austria.

Rabenold, K. N., P. T. Fauth, B. W. Goodner, J. A. Sadowski, and P. G. Parker (1998). Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. Conservation Biology 12:177–189.

Ralph, C. J., J. R. Sauer, and S. Droege (Technical Editors) (1995). Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149.

R Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Revelle, W. (2014). psych: Procedures for psychological, psychometric, and personality research. Version 1.5.8. Northwestern University, Evanston, Illinois. http://CRAN.R-project.org/package=psych

Rodewald, P. (Editor) (2015). The Birds of North America. Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna.org/

Ross, R. M., L. A. Redell, R. M. Bennett, and J. A. Young (2004). Mesohabitat use of threatened hemlock forests by breeding birds of the Delaware River basin in northeastern United States. Natural Areas Journal 24:307–315.

Socolar, S. J., S. K. Robinson, and J. Terborgh (2013). Bird diversity and occurrence of bamboo specialists in two bamboo die-offs in southeastern Peru. The Condor 115: 253–262.

Souto, D., T. Luther, and B. Chianese (1996). Past and current status of HWA in eastern and Carolina hemlock stands. In Proceedings of the First Hemlock Woolly Adelgid Review. Charlottesville, Virginia, USA, 12 October 1995 (S. M. Salom, T. C. Tigner, and R. C. Reardon, Editors). Forest Health Technology Enterprise Team, USDA Forest Service, Morgantown, WV, USA. pp. 9–15.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker, III, and D. K. Moskovits (1996). Neotropical Birds: Ecology and Conservation. University of Chicago Press, Chicago, IL, USA.

Tingley, M. W., D. A. Orwig, R. Field, and G. Motzkin (2002). Avian response to removal of a forest dominant: Consequences of hemlock woolly adelgid infestations. Journal of Biogeography 29:1505–1516.

USDA Forest Service (2016). Hemlock Woolly Adelgid Infestation. USDA Forest Service, Northeastern Area State and Private Forestry, Forest Health Protection. https://www.fs.usda.gov/naspf/sites/default/files/naspf/pdf/2015_hwa_infestation_map_20160502.pdf

Young, J. A., D. R. Smith, C. D. Snyder, and D. P. Lemarie (2002). A terrain-based paired-site sampling design to assess biodiversity losses from eastern hemlock decline. Environmental Monitoring and Assessment 76:167–183.

Zipkin, E. F., A. DeWan, and J. A. Royle (2009). Impacts of forest fragmentation on species richness: A hierarchical approach to community modelling. Journal of Applied Ecology 46:815–822.

APPENDIX TABLE 3. Number of surveys with detections, mean occupancy estimates (SD in parentheses), and species group assignments for all bird species in hemlock and hardwood stands in the Delaware Water Gap National Recreation Area, northeastern USA, pre- and post-hemlock decline. Species groups are indicated by one-letter codes: H = hemlock, D = mature deciduous, F = forest edge, S = shrub layer, Sn = snag-nesting, and E = early successional. Dashes indicate that a species was not assigned to any group.

Scientific name	Common name	Surveys with detections	Hemlock predecline	Hemlock postdecline	Hardwood predecline	Hardwood postdecline	Species group(s)
Zenaida macroura	Mourning Dove	5	0.01 (0.01)	0.01 (0.01)	0.05 (0.03)	0.01 (0.01)	—
Archilochus colubris	Ruby-throated Hummingbird	8	0.01 (0.01)	0.01 (0.01)	0.06 (0.03)	0.05 (0.03)	F
Melanerpes carolinus	Red-bellied Woodpecker	9	0.00 (0.01)	0.01 (0.01)	0.08 (0.04)	0.09 (0.04)	D, Sn
Picoides pubescens	Downy Woodpecker	10	0.01 (0.01)	0.01 (0.01)	0.09 (0.04)	0.05 (0.02)	Sn
Picoides villosus	Hairy Woodpecker	10	0.00 (0.01)	0.01 (0.01)	0.07 (0.03)	0.07 (0.03)	D, Sn
Colaptes auratus	Northern Flicker	6	0.03 (0.02)	0.01 (0.01)	0.05 (0.03)	0.01 (0.01)	F, Sn
Dryocopus pileatus	Pileated Woodpecker	5	0.02 (0.02)	0.01 (0.01)	0.04 (0.03)	0.02 (0.01)	Sn
Contopus virens	Eastern Wood-Pewee	48	0.06 (0.03)	0.07 (0.02)	0.22 (0.06)	0.13 (0.04)	F
Empidonax virescens	Acadian Flycatcher	90	0.29 (0.07)	0.24 (0.05)	0.21 (0.06)	0.15 (0.04)	H
Sayornis phoebe	Eastern Phoebe	20	0.04 (0.02)	0.07 (0.03)	0.07 (0.03)	0.07 (0.03)	—
Myiarchus crinitus	Great Crested Flycatcher	17	0.03 (0.02)	0.03 (0.02)	0.09 (0.04)	0.05 (0.02)	F, Sn
Vireo flavifrons	Yellow-throated Vireo	26	0.01 (0.01)	0.02 (0.01)	0.16 (0.05)	0.14 (0.04)	F
Vireo solitarius	Blue-headed Vireo	53	0.36 (0.07)	0.21 (0.05)	0.06 (0.03)	0.02 (0.01)	H
Vireo olivaceus	Red-eyed Vireo	345	0.53 (0.07)	0.73 (0.05)	0.92 (0.03)	0.93 (0.03)	D, S
Cyanocitta cristata	Blue Jay	24	0.08 (0.04)	0.13 (0.04)	0.10 (0.04)	0.07 (0.03)	F
Poecile atricapillus	Black-capped Chickadee	12	0.03 (0.02)	0.05 (0.02)	0.05 (0.03)	0.05 (0.03)	F, Sn
Baeolophus bicolor	Tufted Titmouse	40	0.11 (0.04)	0.09 (0.03)	0.21 (0.06)	0.10 (0.03)	D, Sn
Sitta carolinensis	White-breasted Nuthatch	25	0.01 (0.01)	0.02 (0.02)	0.15 (0.05)	0.16 (0.05)	F, Sn
Certhia americana	Brown Creeper	6	0.02 (0.02)	0.04 (0.02)	0.02 (0.01)	0.01 (0.01)	Sn
Troglodytes hiemalis	Winter Wren	8	0.03 (0.02)	0.03 (0.02)	0.02 (0.01)	0.01 (0.01)	—
Thryothorus ludovicianus	Carolina Wren	1	0.00 (0.00)	0.00 (0.01)	0.02 (0.01)	0.01 (0.01)	Sn
Polioptila caerulea	Blue-gray Gnatcatcher	32	0.01 (0.01)	0.04 (0.02)	0.13 (0.05)	0.26 (0.06)	F, S
Catharus fuscescens	Veery	71	0.10 (0.04)	0.22 (0.04)	0.15 (0.05)	0.16 (0.04)	S, E
Catharus guttatus	Hermit Thrush	13	0.06 (0.03)	0.05 (0.02)	0.04 (0.02)	0.02 (0.01)	H
Hylocichla mustelina	Wood Thrush	96	0.24 (0.06)	0.20 (0.04)	0.37 (0.07)	0.19 (0.04)	D, S
Turdus migratorius	American Robin	16	0.03 (0.02)	0.05 (0.02)	0.06 (0.03)	0.06 (0.03)	E
Dumetella carolinensis	Gray Catbird	20	0.01 (0.01)	0.01 (0.01)	0.08 (0.04)	0.10 (0.04)	F, S
Bombycilla cedrorum	Cedar Waxwing	17	0.02 (0.01)	0.07 (0.03)	0.04 (0.02)	0.09 (0.03)	F, S
Pipilo erythrophthalmus	Eastern Towhee	2	0.00 (0.01)	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	F, S
Spizella passerina	Chipping Sparrow	5	0.01 (0.01)	0.00 (0.01)	0.06 (0.03)	0.03 (0.02)	F, E
Spizella pusilla	Field Sparrow	1	0.00 (0.01)	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	F
Melospiza melodia	Song Sparrow	2	0.00 (0.01)	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	S
Junco hyemalis	Dark-eyed Junco	1	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	—
Icterus galbula	Baltimore Oriole	15	0.01 (0.01)	0.04 (0.02)	0.05 (0.03)	0.09 (0.03)	F
Agelaius phoeniceus	Red-winged Blackbird	2	0.00 (0.00)	0.00 (0.01)	0.02 (0.01)	0.01 (0.01)	—
Molothrus ater	Brown-headed Cowbird	26	0.05 (0.03)	0.15 (0.05)	0.09 (0.04)	0.15 (0.05)	F
Quiscalus quiscula	Common Grackle	3	0.00 (0.00)	0.00 (0.01)	0.02 (0.02)	0.02 (0.02)	F
Seiurus aurocapilla	Ovenbird	391	0.66 (0.07)	0.91 (0.03)	0.83 (0.05)	0.93 (0.03)	D
Helmitheros vermivorum	Worm-eating Warbler	33	0.03 (0.02)	0.06 (0.02)	0.12 (0.04)	0.12 (0.04)	D, S
Parkesia motacilla	Louisiana Waterthrush	45	0.13 (0.04)	0.18 (0.04)	0.13 (0.05)	0.11 (0.04)	—

APPENDIX TABLE 3. Continued.

Scientific name	Common name	Surveys with detections	Hemlock predecline	Hemlock postdecline	Hardwood predecline	Hardwood postdecline	Species group(s)
Vermivora cyanoptera	Blue-winged Warbler	2	0.00 (0.00)	0.00 (0.01)	0.02 (0.02)	0.02 (0.02)	F, S, E
Mniotilta varia	Black-and-white Warbler	22	0.06 (0.03)	0.09 (0.03)	0.08 (0.04)	0.06 (0.03)	F
Geothlypis trichas	Common Yellowthroat	12	0.01 (0.01)	0.01 (0.01)	0.07 (0.03)	0.06 (0.03)	S
Setophaga citrina	Hooded Warbler	22	0.00 (0.00)	0.02 (0.01)	0.06 (0.03)	0.13 (0.04)	F, S
Setophaga ruticilla	American Redstart	88	0.03 (0.02)	0.03 (0.01)	0.49 (0.08)	0.39 (0.06)	S
Setophaga cerulea	Cerulean Warbler	4	0.00 (0.01)	0.00 (0.00)	0.03 (0.02)	0.02 (0.01)	—
Setophaga americana	Northern Parula	17	0.03 (0.02)	0.07 (0.03)	0.05 (0.03)	0.05 (0.02)	—
Setophaga fusca	Blackburnian Warbler	64	0.36 (0.07)	0.24 (0.05)	0.04 (0.02)	0.01 (0.01)	H
Setophaga petechia	Yellow Warbler	9	0.00 (0.01)	0.01 (0.01)	0.07 (0.03)	0.05 (0.03)	F, S
Setophaga pensylvanica	Chestnut-sided Warbler	5	0.00 (0.01)	0.00 (0.01)	0.05 (0.03)	0.02 (0.01)	F, S, E
Setophaga pinus	Pine Warbler	10	0.02 (0.02)	0.06 (0.03)	0.02 (0.01)	0.03 (0.02)	—
Setophaga discolor	Prairie Warbler	5	0.01 (0.01)	0.01 (0.01)	0.05 (0.03)	0.01 (0.01)	E
Setophaga virens	Black-throated Green Warbler	112	0.59 (0.07)	0.39 (0.05)	0.09 (0.04)	0.03 (0.01)	H
Cardellina canadensis	Canada Warbler	2	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	F, S, E
Piranga olivacea	Scarlet Tanager	122	0.36 (0.07)	0.28 (0.05)	0.52 (0.07)	0.28 (0.05)	D
Cardinalis cardinalis	Northern Cardinal	2	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	F, S
Pheucticus ludovicianus	Rose-breasted Grosbeak	26	0.05 (0.03)	0.09 (0.03)	0.10 (0.04)	0.09 (0.03)	F, S
Passerine cyanea	Indigo Bunting	6	0.01 (0.01)	0.01 (0.01)	0.03 (0.02)	0.03 (0.02)	F, S

APPENDIX TABLE 4. Mean hemlock and snag abundance, as a percentage of total basal area, within 10 hemlock stands in the Delaware Water Gap National Recreation Area, northeastern USA, pre- and post-hemlock decline. Since a predecline baseline, mean percent hemlock basal area declined while the percentage of snags increased.

Stand ID	% hemlock in 1997	% hemlock in 2015	% snags in 1997	% snags in 2015
365	77	59	3	8
485	73	66	0	24
657	62	47	0	19
822	35	28	1	11
1059	63	40	6	14
1191	50	36	0	17
1368	34	35	3	5
1449	59	49	1	23
2037	48	49	1	17
2107	60	51	3	10
Mean	56	46	2	15

APPENDIX TABLE 5. Beta coefficients for effects of ambient noise, survey date, and time of day on detection probability of all detected bird species in hemlock and hardwood stands in the Delaware Water Gap National Recreation Area, northeastern USA. Asterisks indicate significance determined by a 95% credible interval (only the Red-eyed Vireo showed a significant effect of a detection covariate).

	Ambient noise		Survey date		Time of day	
Species	Mean	SD	Mean	SD	Mean	SD
Mourning Dove	−0.17	0.28	0.03	0.26	−0.11	0.28
Ruby-throated Hummingbird	−0.13	0.28	0.12	0.27	−0.02	0.27
Red-bellied Woodpecker	−0.19	0.26	−0.02	0.26	0.03	0.23
Downy Woodpecker	−0.16	0.28	−0.06	0.25	0.10	0.29
Hairy Woodpecker	−0.22	0.27	0.06	0.25	0.16	0.27
Northern Flicker	−0.18	0.28	0.03	0.25	0.06	0.28
Pileated Woodpecker	−0.12	0.29	0.05	0.27	0.12	0.28
Eastern Wood-Pewee	−0.17	0.26	0.17	0.27	−0.09	0.23
Acadian Flycatcher	−0.12	0.22	0.01	0.22	−0.03	0.21
Eastern Phoebe	−0.12	0.25	0.20	0.24	−0.12	0.27
Great Crested Flycatcher	−0.21	0.28	0.03	0.26	0.04	0.25
Yellow-throated Vireo	−0.08	0.26	0.03	0.22	0.03	0.22
Blue-headed Vireo	−0.10	0.23	0.18	0.23	−0.06	0.20
Red-eyed Vireo	−0.31*	0.17	−0.05	0.15	−0.02	0.15
Blue Jay	−0.23	0.21	−0.08	0.21	0.19	0.26
Black-capped Chickadee	−0.10	0.27	−0.04	0.26	0.11	0.26
Tufted Titmouse	−0.12	0.23	0.13	0.23	−0.01	0.20
White-breasted Nuthatch	−0.30	0.29	0.03	0.24	0.07	0.23
Brown Creeper	−0.11	0.28	0.07	0.25	0.12	0.28
Winter Wren	−0.23	0.28	0.13	0.29	−0.10	0.30
Carolina Wren	−0.17	0.27	0.03	0.26	0.04	0.29
Blue-gray Gnatcatcher	−0.16	0.19	−0.04	0.22	−0.10	0.25
Veery	−0.12	0.23	−0.05	0.20	−0.23	0.30
Hermit Thrush	−0.26	0.29	−0.04	0.24	0.01	0.25
Wood Thrush	−0.08	0.24	0.06	0.19	0.03	0.18
American Robin	−0.15	0.25	0.05	0.24	−0.03	0.24
Gray Catbird	−0.09	0.27	0.08	0.25	0.18	0.33
Cedar Waxwing	−0.11	0.23	−0.04	0.25	−0.04	0.26
Eastern Towhee	−0.17	0.28	0.06	0.27	0.10	0.29
Chipping Sparrow	−0.22	0.28	0.03	0.25	0.01	0.27
Field Sparrow	−0.18	0.28	0.03	0.27	0.03	0.28
Song Sparrow	−0.17	0.28	−0.02	0.26	0.04	0.29
Dark-eyed Junco	−0.18	0.28	0.04	0.26	0.04	0.27
Baltimore Oriole	−0.23	0.24	0.11	0.26	0.12	0.26
Red-winged Blackbird	−0.18	0.28	0.01	0.27	0.12	0.30
Brown-headed Cowbird	−0.37	0.28	0.04	0.22	0.06	0.21
Common Grackle	−0.22	0.27	0.05	0.27	0.08	0.29
Ovenbird	−0.18	0.17	0.00	0.16	0.08	0.16
Worm-eating Warbler	−0.11	0.26	0.01	0.24	0.09	0.23
Louisiana Waterthrush	−0.17	0.19	−0.09	0.23	0.17	0.22
Blue-winged Warbler	−0.17	0.28	0.03	0.27	0.02	0.26
Black-and-white Warbler	−0.13	0.27	0.04	0.25	−0.05	0.23
Common Yellowthroat	−0.19	0.27	0.16	0.31	0.01	0.25
Hooded Warbler	−0.20	0.26	0.15	0.31	0.00	0.23
American Redstart	−0.14	0.24	0.14	0.25	0.01	0.19
Cerulean Warbler	−0.20	0.28	0.06	0.27	0.00	0.28
Northern Parula	−0.14	0.24	0.02	0.25	0.21	0.30
Blackburnian Warbler	−0.32	0.32	0.11	0.21	−0.07	0.21
Yellow Warbler	−0.18	0.28	0.04	0.24	0.11	0.28
Chestnut-sided Warbler	−0.19	0.28	0.12	0.27	0.13	0.31
Pine Warbler	−0.23	0.26	0.03	0.23	0.13	0.29
Prairie Warbler	−0.17	0.28	0.05	0.26	0.15	0.31
Black-throated Green Warbler	−0.18	0.23	−0.20	0.24	0.14	0.19
Canada Warbler	−0.21	0.27	0.01	0.27	0.06	0.29

APPENDIX TABLE 5. Continued.

	Ambient noise		Survey date		Time of day	
Species	Mean	SD	Mean	SD	Mean	SD
Scarlet Tanager	−0.12	0.19	0.06	0.17	0.01	0.15
Northern Cardinal	−0.20	0.28	0.07	0.27	0.03	0.29
Rose-breasted Grosbeak	−0.20	0.24	−0.05	0.23	−0.15	0.27
Indigo Bunting	−0.22	0.28	0.06	0.27	0.06	0.28
Mean	−0.18	0.11	0.04	0.10	0.04	0.10