

The Pennsylvania State University

The Graduate School

College of Agricultural Sciences

LONG-TERM AVIAN COMMUNITY RESPONSE TO HEMLOCK DECLINE

A Thesis in

Ecology

by

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Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Science

December 2017

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ABSTRACT

Forest biomes face increasing rates of disturbance from many causes, including climate change, introduced pests, and shifting fire regimes, as well interactions between multiple factors. In particular, the introduction of exotic forest pests is increasing globally, frequently resulting in decline and die-off of affected forest types. The loss of foundational forest species can drastically change the structure and composition of vegetation communities in forests, a phenomenon that holds strong implications for avian communities. However, little research has focused on the long-term effects of forest die-off at a community-wide scale.

To examine the response of bird communities to forest die-off, we studied the community associated with declining eastern hemlock (*Tsuga canadensis*) forests affected by the introduced hemlock woolly adelgid (*Adelges tsugae*). We conducted variable-radius point counts to survey bird communities in both hemlock and hardwood stands in 2000, during 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 where avian surveys occurred. We used multi-species occupancy models to examine species-specific and species group responses to hemlock decline. Results showed that hemlock basal area declined to varying degrees across the hemlock stands, and that hemlock decline was correlated with current vegetation structure, including an increased deciduous understory. Hemlock-associated bird species declined between the two time periods, while all other species groups responded positively, with the strongest responses in species associated with the shrub-layer, forest edge, and mature deciduous habitat. Species composition in hemlock and hardwood stands became more correlated over time, highlighting a trend toward

homogenization of the avian community as the unique species assemblages in hemlock stands give way to the avian community of the surrounding hardwood landscape. Where hemlock-associated species persisted, their presence was correlated with the combined effect of greater hemlock basal area and better hemlock condition. Our results demonstrate that the decline and die-off of foundational forest species can restructure vegetation communities and their associated avian communities over time, with strong implications for forest type specialists.

Due to regional variation in patterns of forest die-off and community composition, understanding impacts on forest-dependent communities requires examining response at broad spatial and temporal scales. To determine how the responses to forest die-off that we observed in the avian community may vary across a large regional scale, we examined bird communities in hemlock stands at four sites across the range of hemlock woolly adelgid in the northeastern/mid-Appalachian regions of the United States. We surveyed the avian community in earlier stages of infestation and again following hemlock decline, and analyzed this data using a multi-species occupancy modeling approach. Despite variability among sites in characteristics of the avian community and of the die-off itself, changes in species richness over time were similar across all sites. Hemlock-associated bird species declined at all sites, with concurrent increases in other species groups, especially those associated with forest edge and shrub-layer habitats. Finer-scale variation in the magnitude of avian response coincided with the varying stages of hemlock decline across sites. Species-specific trends showed that Acadian Flycatcher declined most consistently across this large regional scale. Understanding these patterns is critical to predicting and preparing for changes to not only forested landscapes affected by the loss of hemlock, but also for those that will experience similar die-offs as forest pest introductions increase globally.

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ACKNOWLEDGEMENTS

So many people have helped me on my path toward completion of a thesis in Ecology. I acknowledge some of them here, but the people who have led to my success in this achievement, or any leading up to it, are far too many to thank in detail here.

I thank my advisor David Miller for all of his efforts, guidance, and encouragement over the past two and a half years. From my first visit to Penn State until now, his kindness has made a huge impact on my experience as a graduate student. I thank my co-advisor Matthew Marshall and committee member Margaret Brittingham for all of their guidance and encouragement as well.

This research was funded by the U. S. National Park Service and Penn State University. I would like to thank those who collaborated on this project by contributing data and expertise, including Morgan Tingley, Petra Wood, and Alan Williams. Morgan also helped to re-locate survey locations in Connecticut over a decade after he first surveyed them. Randy Bennett and Carolyn Mahan provided access to raw bird and vegetation data, respectively, collected at Delaware Water Gap National Recreation Area. I also thank the staff at Delaware Water Gap NRA, especially Richard Evans and Jeffrey Shreiner, for providing guidance in project planning and assisting in its implementation. Terry Master also shared his expertise regarding bird research at Delaware Water Gap NRA. The original observer for baseline avian surveys, Robert Ross, was gracious enough to hike through ravines with me to re-locate survey stations fifteen years after his research was completed.

The companionship of fellow graduate students at Penn State has been critical to both academic and social aspects of my graduate experience. I especially thank all of the members of

the Applied Population Ecology Lab. Glenn Stauffer provided great modeling expertise and supplied much of the code for my analysis. My officemate and fellow bird researcher Kim Serno was a constant resource for me to bounce ideas off of, and willingly took the time to answer many questions over the past two years. Eric Teitsworth braved frigid weather to collect basal area data with me, and expanded my tree and herp identification knowledge along the way.

My family deserves immense thanks. My parents and siblings have encouraged me and shown great enthusiasm for my interests and academic pursuits in ecology/wildlife over the years. Most importantly, the seeds of my education and career path were planted in me as a child who was allowed to chase birds through the woods and lie in the grass listening to the nighttime frog chorus. I cannot thank my parents enough for giving me an upbringing in the woods and wetlands, which was critical to the development of an identity and values system that I will carry for life.

Finally, I would like to thank my wonderful Aleix Blasco. Graduate school can be a challenging and potentially isolating experience, and having him by my side for the better part of the process has been critical in getting me through the most difficult parts. His empathy, optimism, and understanding during stressful times are qualities that I both admire and aspire to develop.

Chapter 1

Spatial and temporal relationships between eastern hemlock decline and avian community composition

Abstract

The loss of foundational forest species can drastically change the structure and composition of vegetation communities in forests, a phenomenon that holds strong implications for avian communities. However, little research has focused on the long-term effects of forest die-off at a community-wide scale. To examine the response of bird communities to forest die-off, we studied the community associated with declining eastern hemlock (*Tsuga canadensis*) forests affected by the introduced hemlock woolly adelgid (*Adelges tsugae*). We conducted variable-radius point counts to survey bird communities in both hemlock and hardwood stands in 2000, during 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 where avian surveys occurred. We used multi-species occupancy models to examine species-specific and species group responses to hemlock decline. Results showed that hemlock basal area declined to varying degrees across the hemlock stands, and that hemlock decline was correlated with current vegetation structure, including an increased deciduous understory. Hemlock-associated bird species declined between the two time periods, while all other species groups responded positively, with the strongest responses in species associated with the shrub-layer, forest edge, and mature deciduous habitat. Species composition in hemlock and hardwood stands became more correlated over time, highlighting a trend toward homogenization of the avian community as the unique species assemblages in hemlock stands give way to the avian community of the surrounding hardwood landscape. Where hemlock-associated species persisted, their presence was correlated with the combined effect of greater hemlock basal area and better hemlock condition. Our results demonstrate that the decline and die-off of foundational forest species can restructure vegetation communities and their associated avian communities over time, with strong implications for forest type specialists.

Introduction

Introductions of non-native 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). Examples include the effects of Dutch elm disease on elm (*Ulmus* spp.), chestnut blight on American chestnut (*Castanea dentata*), hemlock woolly adelgid (*Adelges tsugae*) on hemlock (*Tsuga* sp.), gypsy moth (*Lymantria dispar*) on numerous species, and more recently emerald ash borer (*Agrilus planipennis*) on ash (*Fraxinus* sp.; Campbell and Sloan 1977, Anagnostakis 1987, Brasier 1991, Orwig et al. 2002, Herms and McCullough 2014). Losses of these and other species have had profound impacts on the dominant forest types and associated vegetation communities that occur across many of North America's forest ecoregions (Eschtruth et al. 2006, Elliot and Swank 2008). These changes in vegetative communities have strong implications for many other forest taxa, including for avian species that rely on forests as breeding habitats. Previous research has documented the effects of some of these declines on individual species or species groups, such as bark foragers (Drever et al. 2009). However, few studies have focused on the long-term, community-wide temporal changes that 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 case study of the effects of the 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 introduction of hemlock woolly adelgid, an aphid-like insect native to Japan and 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 working their way to the top of the tree. Mortality can occur in as few as four years (McClure 1991), but frequently takes much longer depending upon site characteristics (Orwig et al. 2002). As of 2015, the adelgid had spread to twenty U.S. states, and more than half of the U.S. counties where the 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 mid- 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 show that forest mosaics that include hemlock stands have higher 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 (Table 1-1). These include species that have been considered hemlock obligates in certain regions, including our study area (Benzinger 1994, Ross et al. 2004). One example of a species with an especially strong hemlock association is the Black-throated Green Warbler (*Setophaga virens*), which has been demonstrated to have morphological characteristics specifically adapted to hemlock use (Parrish 1995).

Table 1-1. Bird species significantly associated with hemlock forests in the northeastern United States, as indicated by previously published studies.

Common name	Scientific name	Source
Acadian Flycatcher	<i>Empidonax virescens</i>	a, b, c, d
Blackburnian Warbler	<i>Setophaga fusca</i>	b, c
Black-throated Green Warbler	<i>Setophaga virens</i>	a, b, c
Hermit Thrush	<i>Catharus guttatus</i>	a
Blue-headed Vireo	<i>Vireo solitarius</i>	b

^aTingley et al. 2002

^bRoss et al. 2004

^cBecker et al. 2008

^dAllen et al. 2009

The continued spread of hemlock woolly adelgid and consequent widespread hemlock decline have potentially severe consequences for forest avian communities across the range of hemlock in eastern North America. Previous research has predicted that several of the hemlock-associated species may decline, including the Acadian Flycatcher, Blue-headed Vireo, Black-throated Green Warbler, and Blackburnian Warbler (Ross et al. 2004, Brown and Weinkam 2014). The Acadian Flycatcher frequently ranks as an at-risk species, due to regionally variable population trends and high sensitivity to forest fragmentation (Whitehead et al. 2002). This species has already been shown to have lower breeding densities in hemlock impacted by

adelgid compared to healthy hemlock (Allen et al. 2009). Additionally, all five of these hemlock-associated species are neotropical migrants, another group of high conservation priority (Stotz 1996, Faaborg et al. 2010).

In contrast to the negative effects on hemlock specialists, adelgid invasion may lead to increased abundance in other species due to both short- and long-term increases in habitat availability. Decline and death of hemlocks may benefit non-hemlock-associated species by (1) increasing the number of standing dead trees; (2) enabling dense growth of plants in the understory (Orwig and Foster 1998, Jenkins et al. 1999; Figure 1-1); and (3) accelerating growth of hardwoods in the overstory following release from competing hemlocks (Orwig et al. 2002; Figure 1-2). Each of these structural changes provides new habitat for bird species that may be less abundant in hemlock stands prior to adelgid invasion. In the long term, replacement of hemlock stands by other vegetation communities (Orwig et al. 2002), such as deciduous forest types or communities dominated by invasive plants, may lead to more homogenous bird communities across the regional landscape.



Figure 1-1. Photos taken at the same location within our study area pre-adelgid infestation in 1993 (left, photo courtesy of Richard Evans), and post infestation in 2016 (right, photo by author). Notice the complete absence of understory vegetation prior to hemlock decline compared to the dense, deciduous understory following degradation of hemlock in the canopy.

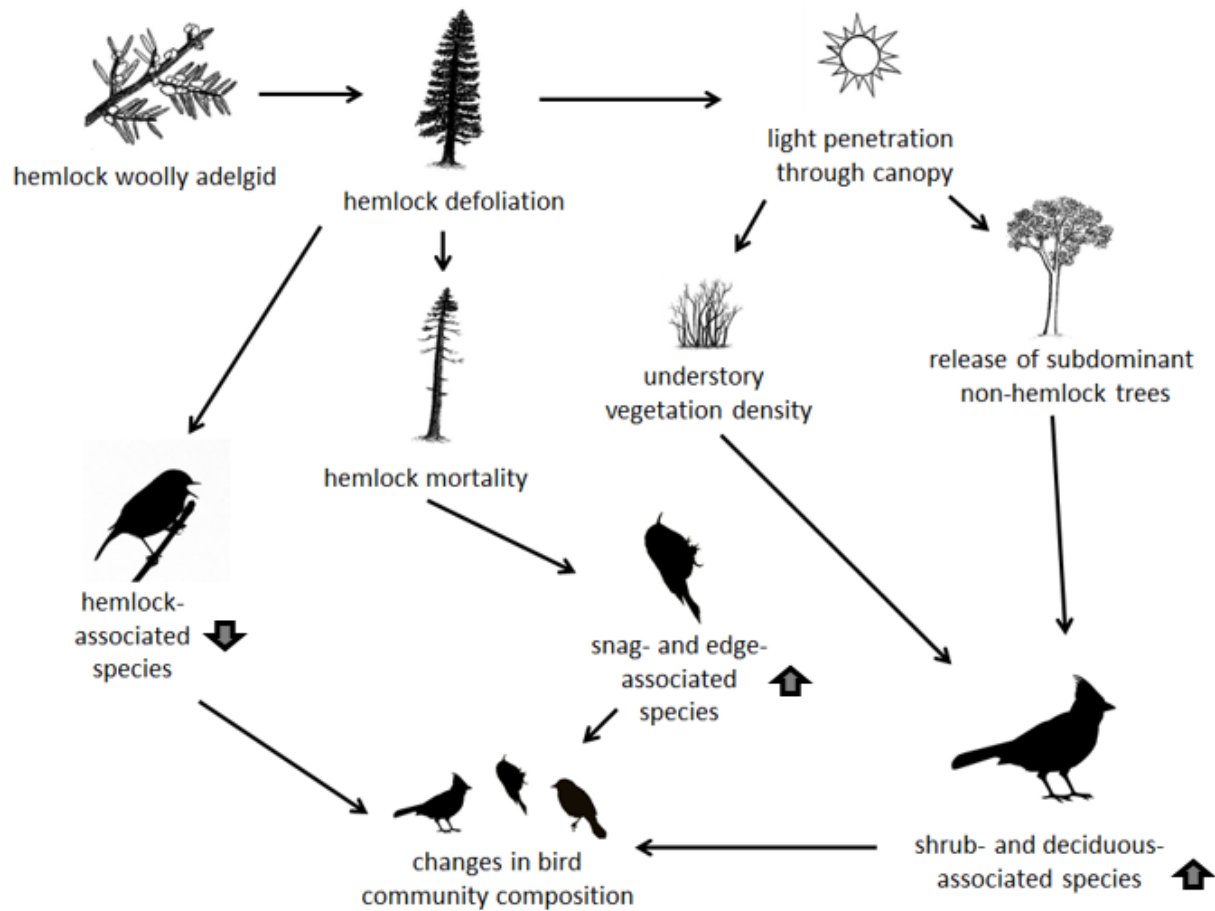


Figure 1-2. Hypothesized causal relationships among hemlock woolly adelgid invasion, consequent changes to vegetation structure, and bird community composition. We hypothesized that adelgid-caused hemlock decline directly and indirectly affects vegetation structure in forests, which in turn leads to different responses among avian species groups.

Previous studies on avian response to hemlock decline have made conclusions based on space-for-time approaches that either (1) compared hemlock bird communities to those in other forest types (Howe and Mossman 1995, Brown and Weinkam 2014), or (2) 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 community by surveying the same hemlock stands both before and after significant hemlock decline. We also investigated the mechanisms by which the avian community changes by examining how specific changes in forest structure associated with hemlock decline relate to current patterns in

the distribution of individual species and the avian community as a whole. This was accomplished by (1) measuring how the condition of hemlock stands has changed since early stages of adelgid infestation at our study site; (2) determining how the distribution of birds across the forest bird community has responded to changes in hemlock stands since early adelgid infestation; and (3) determining how stand and local site level characteristics are related to the current forest bird community. This comprehensive approach allowed us to test the direct pathways that lead to change in the forest community as outlined in Figure 1-2.

Study area

The Delaware Water Gap National Recreation Area (NRA; Figure 1-3) covers an area of 27,742 hectares bordering the Delaware River in northeastern Pennsylvania and northwestern New Jersey, with elevation ranging from 84 to 490 meters (Mahan et al. 2004). The dominant cover type is forest, with 18,575 hectares of hardwood forest, 1,295 hectares of coniferous forest, and 2,015 hectares of mixed evergreen-deciduous forest (Myers and Irish 1981). Prior to the introduction of hemlock woolly adelgid at Delaware Water Gap NRA, hemlock was present in over 1,000 hectares of forest, concentrated in mostly pure stands growing along streams that drain into the Delaware River (Young et al. 2002). Hemlock woolly adelgid was first discovered at Delaware Water Gap NRA in 1989 and was 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, 2015). Research on hemlocks 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 2006). Data from surveys conducted in 2000 therefore provide a reliable baseline of pre-decline conditions.

Surveys were conducted within 22 forest stands—11 hemlock and 11 hardwood -- located along 1st- or 2nd-order streams at Delaware Water Gap NRA (Figure 1-3). Prior to hemlock mortality, digital GIS vegetation maps had been used to designate stands as either hemlock or hardwood, based on the dominance of tree species by canopy area. Stands where hemlock was the first, second, or third most-dominant species were designated as hemlock, 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 53.1% (range 24.8%—77.3%) of basal area in hemlock stands, compared to a mean of 2.7% (range 0%—14.1%) 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 at the park. This effort was motivated by the threat posed by 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 non-vegetative differences between paired hemlock and hardwood stands (Young et al. 2002). In addition to vegetation and bird communities, which are the focus of our resurvey, studies on a wide variety of other taxa occurred in these stands in the late 1990s and early 2000s (see Brotherton et al. 2001, Snyder et al. 2002, Young et al. 2002, Mahan et al. 2004).

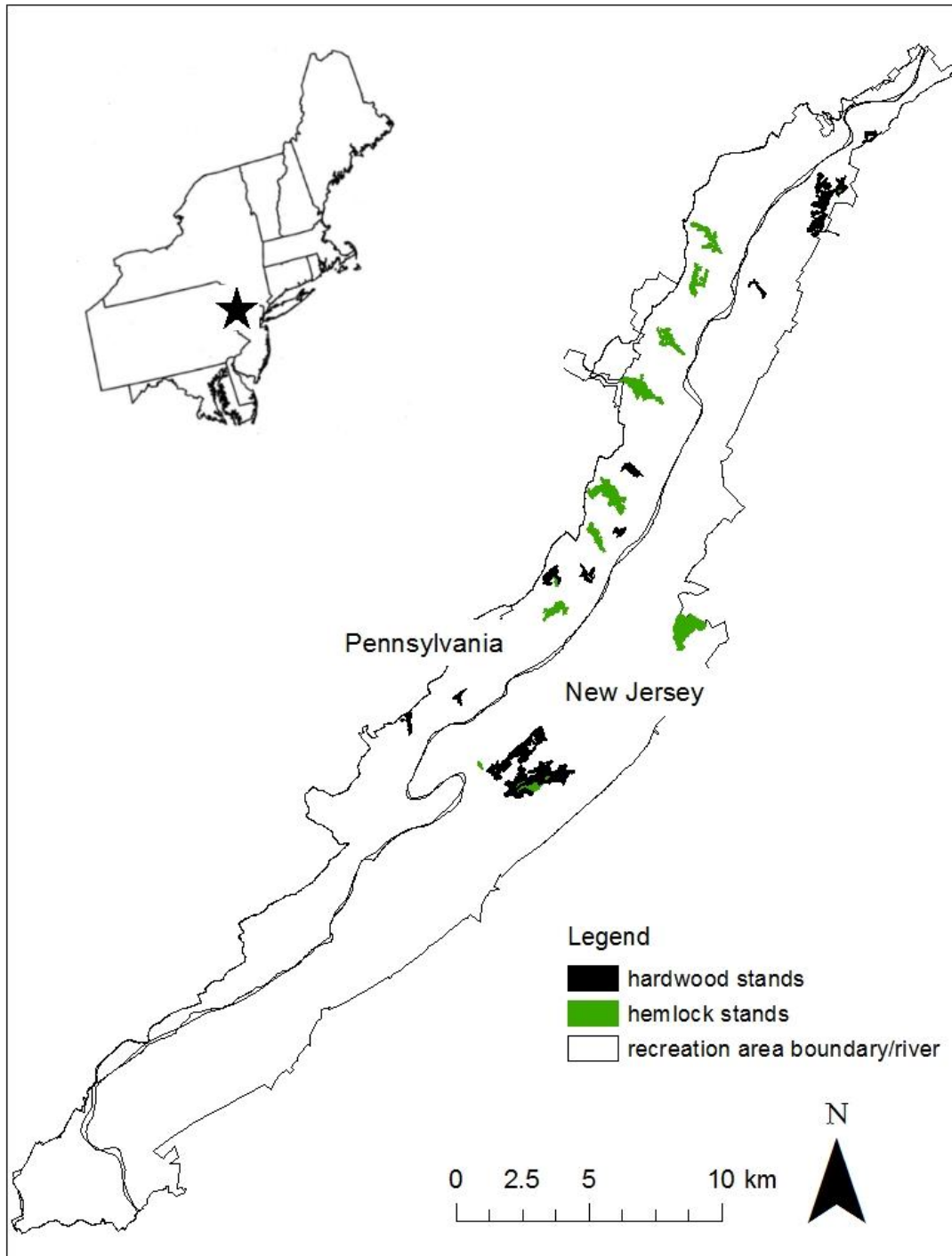


Figure 1-3. Location and outline of study area (Delaware Water Gap National Recreation Area) along the border of Pennsylvania and New Jersey in the northeastern U.S.A. The Delaware River divides the study area longitudinally from northeast to southwest. Dark patches within the study area border represent 22 forest stands where 80 sampling locations were located. Prior to hemlock mortality due to

hemlock woolly adelgid, vegetation maps had been used to designate stands as either hemlock or hardwood.

Methods

Vegetation surveys

We conducted two types of vegetative surveys 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 eleven hemlock stands, we measured percent hemlock basal area in the winter of 2015/2016 (during the leaf-off period) and compared these values with pre-mortality baseline data collected in 1997 along transects at the same locations. These locations did not coincide directly with avian survey locations and instead quantify stand-level change in hemlock through time. The second set of measurements occurred at avian survey locations during 2015, allowing us to examine how contemporary vegetation relates to bird distributions. Unfortunately vegetation was not measured at individual avian survey locations during the 2000 surveys conducted by Ross et al.

Basal area measurements in 2015 followed the same protocol as in 1997 (Mahan et al. 2004). For each stand, we established two transects perpendicular to the stream channel within the forest stand: one transect at either end of a predetermined 80-meter or 160-meter stream length (80 meters for first order streams and 160 meters for second order streams, based on the

original study design). For each transect, we established sampling points 15 meters from the stream edge on either side of the stream, with subsequent points established an additional 30 meters from the stream edge on either side. Using a compass and handheld GPS unit (Garmin GPSmap 60CSx), we established sampling points to a maximum distance of 75 meters from the stream edge for first order streams, and 135 meters 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 ≥ 4 inches 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 non-hemlock.

To examine the relationship between contemporary vegetation and bird communities, we also 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 four quadrats based on the cardinal directions. We then established four sampling points 25 m from the center of the plot--one in each inter-cardinal direction--plus a fifth sampling point in the plot center. We rated the average condition of all hemlocks in a 10-m radius of each of the five 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 $\frac{1}{3}$ of the tree; (3) significant limb die-off and needle loss, but live branches remaining along the top $\frac{1}{3}$ - $\frac{2}{3}$ of the tree; (4) minor limb die-off and needle loss, with live branches remaining along more than the top $\frac{2}{3}$ of the tree; and (5) healthy: no evidence of limb die-off or needle loss. The 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 five points in each plot, using the same methods used at points for the stand-level basal area measurements described previously.

Finally, in 2015 we estimated vegetation coverage from the ground level to the canopy in a 50-m radius plot where avian point count surveys occurred (protocol adapted from Marshall et al. 2016). Plots were divided into four equal quadrats and we estimated vegetation volume in four height categories: 0-0.5 m; 0.5-2 m; 2-5 m; and > 5 m to the upper limit of the forest canopy (hereafter referred to as ground layer, understory, midstory, and canopy). For each level of each quadrat, 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 four vegetation types: (1) hemlock; (2) deciduous species; (3) non-hemlock coniferous species; and (4) rhododendron, mountain laurel, and other broadleaf evergreens. We averaged all vegetation measurements from quadrats and subpoints to generate a single metric for each survey location.

Avian surveys

We compared results of surveys conducted in 2015 and 2016 to baseline surveys conducted in 2000 by Ross et al. (2004) to measure change in avian community composition following hemlock decline. In each of the three study years, we surveyed 80 locations across the 11 pairs of hemlock and hardwood stands in each of the time periods, with 45 locations occurring in hemlock stands and 35 in hardwood stands. Survey locations were a minimum of

250 meters apart and a minimum of 150 meters from the edge of the respective stand type. Due to these distance limitations, the number of survey locations per forest stand varied from one to six. In 2015 and 2016, we returned to the same locations surveyed in 2000 whenever possible. However, for six of the survey locations, records from surveys in 2000 indicated the forest stands, but not the exact locations, where surveys were done. In those cases we used field notes and guidance from Robert Ross (the observer in 2000) to establish these survey locations as close 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 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 two later years we conducted a second set of point counts at each survey location, which occurred from June 15 to July 7 in 2015 and June 16 to June 23 in 2016. Counts occurred in the morning (between 0530 and 1000) and only during suitable weather conditions: no precipitation and wind speed ≤ 12 mph (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 (Gearbest GM1351 Digital Sound Level Meter) aimed in each of the four intercardinal directions (later years only). We disregarded brief noise peaks from sources such as loud bird vocalizations or infrequent traffic noise.

After waiting five minutes to limit the effects of any disturbance on bird activity, observers counted all birds heard or seen over a 10-minute count. Observers recorded whether each bird was detected during the first and second five minutes of the count, as well as the distance at which the bird was first observed (0-50 meters or >50 meters). Observers in both

2000 and 2015/2016 practiced distance estimation prior to avian surveys, in order to accurately place detections into the two distance bands. Because observers were likely to vary in their abilities to detect more distant birds, subsequent analyses only included data for bird detections from < 50 m. This helped to minimize detection differences between observers in 2000 vs. 2015/2016. We conducted counts on dates in 2015 and 2016 to coincide as close as possible to 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 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 one of the eleven hemlock stands, basal area data was excluded from vegetation analyses because survey locations were found to differ between 1997 and 2015. We used function *corr.test* in package *psych* (Revelle 2015) in Program R (v. 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 species, chosen based on shared habitat associations we hypothesized would affect community responses to hemlock decline. The groups included hemlock-associated species (Table 1-1) and species we expected to respond to increases in (1) mature deciduous forest, (2) woodland edge, (3) a dense shrub-layer, (4) snags, and (5) early successional habitat. We assigned species to groups using pre-determined keywords from detailed habitat descriptions for each species in the Birds of North America Online database (Rodewald 2015). We analyzed occurrence probabilities for all species in each group for which the breeding range overlaps our study area, and included only passerine or near-passerine species in the analysis (see Appendix A for full species lists for each group). We excluded wide-ranging corvid species (American Crow [*Corvus brachyrhynchos*] and Common Raven [*Corvus corax*]) and several species that show irruptive breeding patterns in response to resource availability from year to year (e.g. Red-breasted Nuthatch [*Sitta canadensis*] and two cuckoo [*Coccyzus*] species).

Analyses of bird community occurrence patterns included (1) a before-after comparison of bird communities using the pre- and post- hemlock decline bird data, and (2) a comparison of differences in bird communities among survey locations using only the post-decline data. We treated 2015 and 2016 as a single time period in the before-after comparison in order to compare post-hemlock decline survey data to the pre-decline data from 2000 (hereafter, the term *time period* is applied to 2000 and 2015/2016). We performed all analyses using hierarchical multi-species 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 across time. All occupancy analyses were fit using Markov chain Monte Carlo (MCMC) methods and run using JAGS (Plummer 2003) called from program R (v. 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 five-minute intervals within the ten-minute count to estimate the overall probability of detecting each species. For all covariates on 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 subsetting data to include only the first survey visits from 2015/2016 to make results more directly comparable to the single visit in 2000. It is possible that apparent species trends over time could be influenced by observer differences between years and other factors unrelated to hemlock decline (e.g. species trends outside of the breeding range). However, we were able to control for these effects by comparing species-specific responses in hemlock stands to responses in hardwood stands. By comparing changes of each species or group within hemlock stands to 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 results. Thus, our relevant measure of species response was the difference in change over 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 between the composition of avian communities in hemlock and hardwood stands pre- and post- decline using 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 four sampled community types (hemlock and hardwood pre- and post- decline). We used function *vegdist* in package *vegan* (Oksanen et al. 2016) in Program R (v. 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 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 canopy (n=56). For each of our species groups, we estimated the effects of (1) understory deciduous 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 had impacted hemlocks at nearly all survey locations in hemlock stands, although no locations had experienced complete hemlock mortality. The proportion of survey locations with hemlocks in each of the five hemlock condition scores were the following: healthy—6.7%; minor defoliation and limb death—26.7%, significant defoliation and limb death—53.3%; severe defoliation and limb death—13.3%; complete tree mortality—0%. 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 56.1 % of total basal area in 1997, but had declined to 46.1 % by 2015 (Figure 1-4, Table 1-2). Between 1997 and 2015, mortality in hemlock stands also increased, with standing dead trees accounting for a mean of 1.8 % of total standing trees in 1997, compared to 14.8 % in 2015. Greater initial hemlock basal area during pre-mortality surveys in 1997 was correlated with higher 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 1-3). 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.

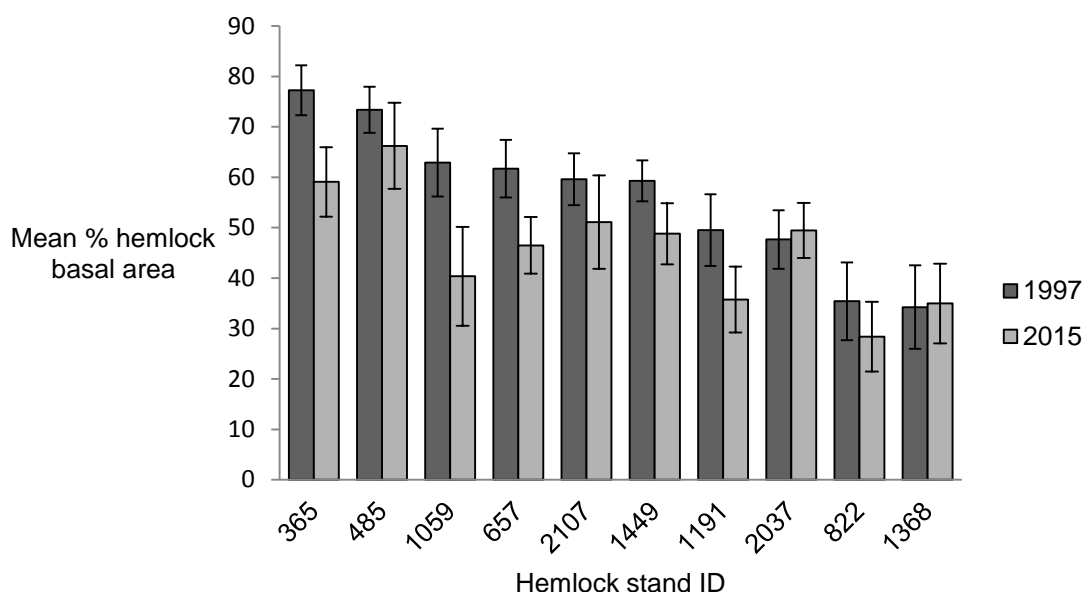


Figure 1-4. Changes in hemlock basal area from 1997 to 2015 across sampled hemlock stands at Delaware Water Gap National Recreation Area. Stands that had more hemlock prior to adelgid infestation proceeded to experience greater decline. For two stands with low initial hemlock basal area, mean % hemlock basal area was slightly higher in 2015.

Table 1-2. Mean hemlock and snag abundance, as a percentage of total basal area, within ten hemlock stands pre- and post- hemlock decline. Since a pre-decline baseline, mean % hemlock basal area declined while % snags increased.

Stand ID	% Hemlock in 1997	% Hemlock in 2015	% Snags in 1997	% Snags in 2015
365	77.25	59.09	3.25	8.03
485	73.41	66.23	0.00	23.99
657	61.68	46.50	0.00	19.24
822	35.40	28.37	0.80	11.11
1059	62.90	40.35	6.20	13.69
1191	49.55	35.75	0.20	16.68
1368	34.25	34.95	3.13	4.89
1449	59.30	48.80	0.90	22.77
2037	47.67	49.46	0.67	17.41
2107	59.63	51.12	2.50	10.22
Mean	56.10	46.06	1.76	14.80

Within the 56 point count locations with hemlock present, we also found strong correlation among our measures. Better hemlock condition was negatively correlated with number of hemlock snags. Healthy hemlock was also negatively correlated with both canopy

hemlock volume and hemlock basal area at individual survey locations, reflecting a similar relationship to the stand-level correlation between initial hemlock basal area and degree of subsequent decline (Table 1-3).

Table 1-3. Correlation matrix between vegetation variables related to hemlock decline. Hemlock decline (the difference between 1997 and 2015 hemlock basal areas) 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 where greater values indicate healthier hemlocks. Superscripts following r-values indicate significance level, and non-significant correlations are represented by hyphens.

	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**

* $p < 0.05$ ** $p < 0.01$

Changes in bird communities over time

Across the three seasons of surveying the 80 point count locations, observers detected a total of 58 species that met the criteria for inclusion in our analyses (see Appendix B for full listing of these species and the number of surveys with species detections). Of the three detection covariates included in our models, one (ambient noise) had a negative mean effect on detection probability, although this effect was nonsignificant at a 95% credible interval ($\beta = -0.18$, 95% CI

-0.38, 0.04). Survey date and time of day did not affect detection probability (see Appendix C for mean and species-specific effects of all detection covariates).

Several species groups showed strong changes in occupancy within hemlock stands over time, relative to any changes within hardwood stands (see Appendix B for occupancy estimates across all species in the two stand types for both 2000 and 2015/2016). Occupancy increased for the species groups associated with the shrub-layer ($\beta = 1.35$, [0.56, 2.21]), forest edge ($\beta = 1.13$, [0.13, 2.17]), and mature deciduous forest ($\beta = 0.998$, [0.276, 1.69]; Figure 1-5a). The snag-nesting species and early successional species both showed positive mean effects ($\beta = 0.712$, [-0.63, 2.01] and $\beta = 1.12$, [-1.64, 3.05], respectively), although the 95% credible intervals overlapped zero for both. Despite fairly strong positive effects for these two groups, especially the early successional species, precision for the mean effects was the lowest of all groups, likely a result of fewer detections for most species in both groups.

The hemlock-associated species showed a strong negative mean effect that clearly contrasted with the positive effects of all other species groups ($\beta = -1.22$, [-2.47, -0.06]; Figure 1-5a). The 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 within the hardwood stands, which acted as the control for comparison. At a species-specific level, responses were similar across the five species in the group, although the effect was slightly stronger and more precise for Acadian Flycatcher (Figure 1-5b).

As the mean effects for the species groups would suggest, the individual species that showed the strongest positive relationships to hemlock decline were mostly species associated with either the shrub-layer (Veery [*Catharus fuscenscens*], Worm-eating Warbler [*Helmitheros*

vermivorum], and Wood Thrush [*Hylocichla mustelina*]); species associated with the forest edge (Blue Jay [*Cyanocitta cristata*], Great Crested Flycatcher [*Myiarchus crinitus*], and Brown-headed Cowbird [*Molothrus ater*]); or species belonging to both groups (Rose-breasted Grosbeak [*Pheucticus ludovicianus*] and Cedar Waxwing [*Bombycilla cedrorum*]; Figure 1-5b). All of the species associated with deciduous forest, snags, and early successional habitat also showed positive responses, although out of all species in the latter two groups, only one species—the Veery—showed an effect with a non-overlapping 95 % credible interval.

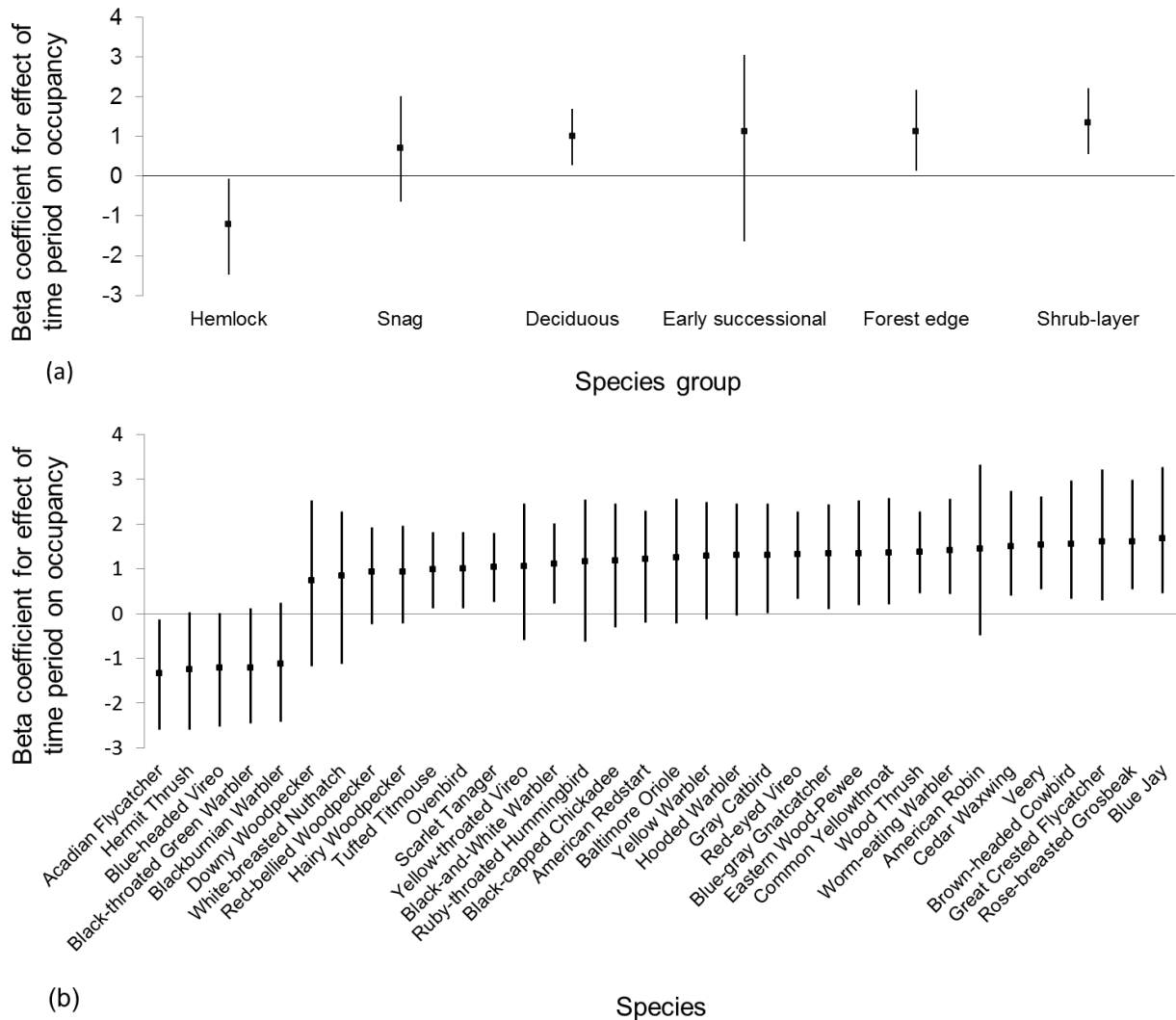


Figure 1-5. Species group responses (a) and individual species responses (b) in hemlock stands, relative to hardwood stands. Error bars represent 95% credible intervals. The effects shown here are the beta slope coefficients on a logit scale for an interaction between time period (2000 vs. 2015/2016) 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.

To illustrate how the effects discussed above translate to changes in species occurrence, we calculated changes in occupancy over time for each species (Figure 1-6b), using back-transformation of the logit-scale slope coefficients. For each species group, we also calculated changes in species richness over time by summing estimated changes in occupancy for all species in the group (Zipkin et al. 2009; Figure 1-6a). Occupancy declined for all hemlock-

associated species, with the greatest decline in Black-throated Green Warbler (mean change in occupancy -0.3, [-0.45, -0.14]). Summed across species, the declines in occupancy for this group indicated that survey locations in hemlock stands lost an average of approximately one hemlock-associated species over time (mean change in species richness -1.03, [-1.52, -0.59]). In contrast to the hemlock specialists, all other species groups showed significant increases in species richness over time (Figure 1-6a). Species richness increased the most for species associated with mature deciduous forest (mean change in richness 1.16, [0.53, 1.76]). While the shrub-layer and edge-associated species groups showed the strongest positive relationships to hemlock decline (Figure 1-5), many of the species in these groups also had very low occupancy estimates (see Appendix B). By contrast, the deciduous associate group included several of the species with the highest occupancy estimates (e.g. Red-eyed Vireo, Ovenbird [*Seiurus aurocapilla*], and Scarlet Tanager [*Piranga olivacea*]). Thus, compared to edge and shrub-layer species, the overall high occupancy of deciduous associates resulted in greater absolute changes in occupancy and species richness for this group (Figure 1-6), despite a slightly weaker positive relationship with hemlock decline (Figure 1-5).

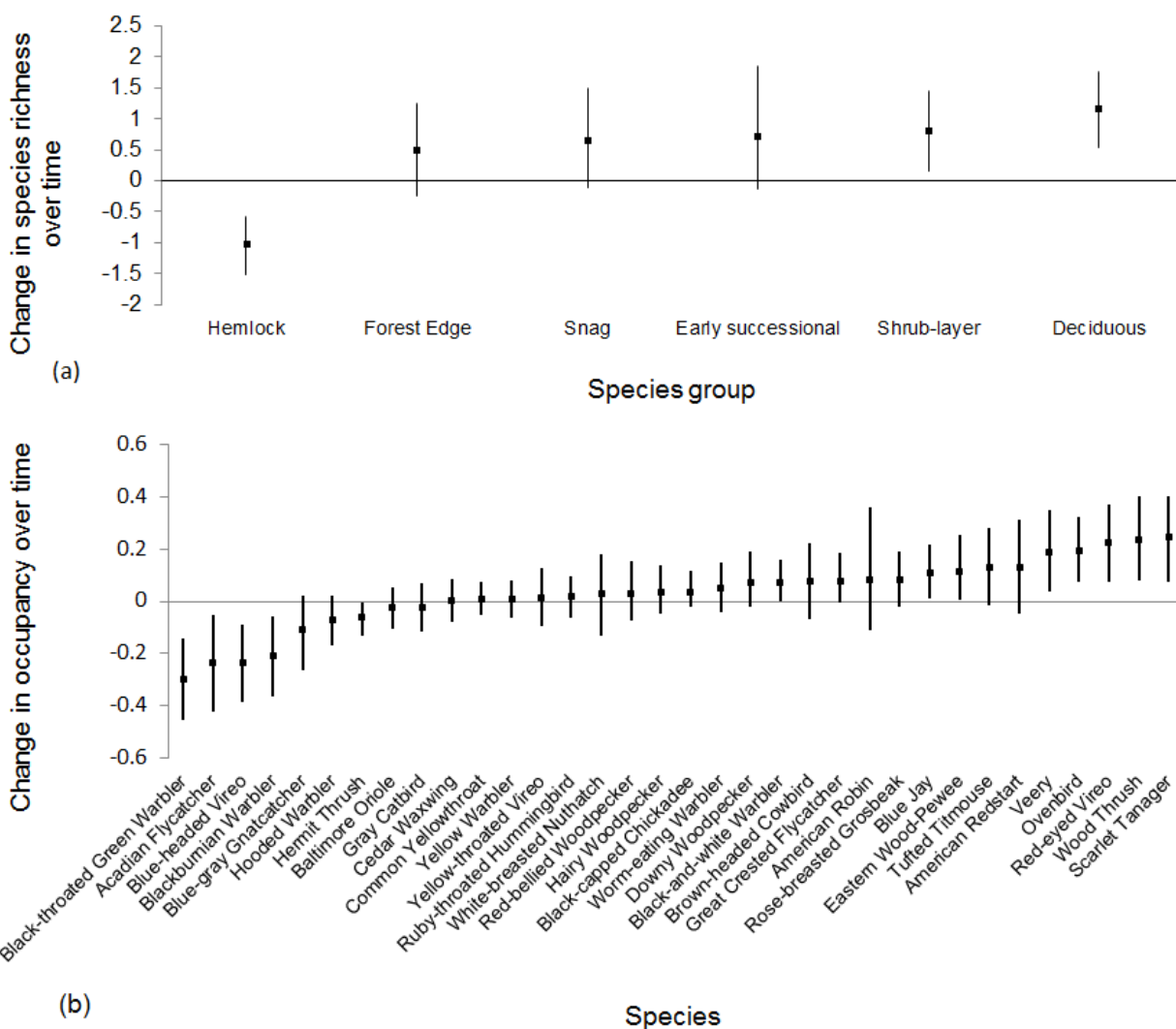


Figure 1-6. Changes over time in (a) avian species richness of species groups and (b) occupancy of bird species in hemlock stands relative to changes in hardwood stands. Error bars represent 95 % credible intervals. Between 2000 and 2015/2016, species richness declined for hemlock-associated species and increased for all other species groups. Species with < 5 total detections are excluded here.

Homogenization of bird community over time

After finding declines in hemlock specialists and increases in other species within hemlock stands, we examined the similarity of bird communities in the two forest types (hemlock vs. hardwood) and during each of the two time periods (pre- and post-decline). Our goal was to test the prediction that the avian community in hemlock stands was becoming more

similar to that in hardwood stands. Bray-Curtis similarity indices showed that communities in hemlock and hardwood stands were indeed more similar post-decline (index = 0.71) than pre-decline (index = 0.60; Table 1-4). Furthermore, following hemlock decline the contemporary avian community of hemlock stands was slightly more similar to that of hardwood stands than that of pre-decline 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.

Table 1-4. Bray-Curtis similarity indices for species composition (occupancy estimates for all species) of four avian communities at our study area: communities in (1) hemlock stands before hemlock decline, (2) hemlock stands after decline, (3) hardwood stands before hemlock decline, and (4) hardwood stands after hemlock decline. Note that between the two time periods, avian community composition in hemlock stands became more similar to that in hardwood stands (bold highlighted values), demonstrating the homogenization of the avian community over time.

	Hemlock post-decline	Hardwood pre-decline	Hardwood post-decline
Hemlock pre-decline	0.80	0.60	0.57
Hemlock post-decline		0.67	0.71
Hardwood pre-decline			0.85

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 post-decline related to characteristics of vegetation structure that were affected by the adelgid invasion, including canopy hemlock volume, deciduous volume

in the understory, and hemlock health. Canopy hemlock volume was positively related to occupancy probability for the hemlock-associated species group ($\beta = 1.02$, [0.19, 1.97]; Table 1-5). Canopy hemlock volume had very weak effects for most of the other species groups, although the effect for the early successional species group was much higher than that of the others ($\beta = 0.57$, [-0.34, 1.9]); this effect was significant for the Veery ($\beta = 0.65$, [0.03, 1.36]).

Compared to canopy hemlock volume, percent deciduous volume in the understory (0.5-2 m height category) had larger effects for more of the species groups, although credible intervals overlapped zero for all groups (Table 1-5). The hemlock-associated group showed a negative mean effect ($\beta = -0.4$, [-0.86, 0.04]), while all other species groups besides the snag-nesters showed at least weak positive effects for this covariate, with the strongest effect shown in the shrub-layer associated species ($\beta = 0.24$, [-0.06, 0.56]).

As the results of our vegetation analysis showed, there was a strong negative correlation between the amount of hemlock and hemlock health. This could lead to potential confounding in measuring responses to the variables and therefore we modeled the interaction between the number of hemlocks and hemlock health. The interaction was significant for the hemlock-associated species (Table 1-5) but not for the other groups. We found that hemlock associates were positively associated with the number of hemlocks. Once the number of hemlocks was controlled for, we also found a positive relationship between the occurrence of hemlock associates and hemlock health (Figure 1-7).

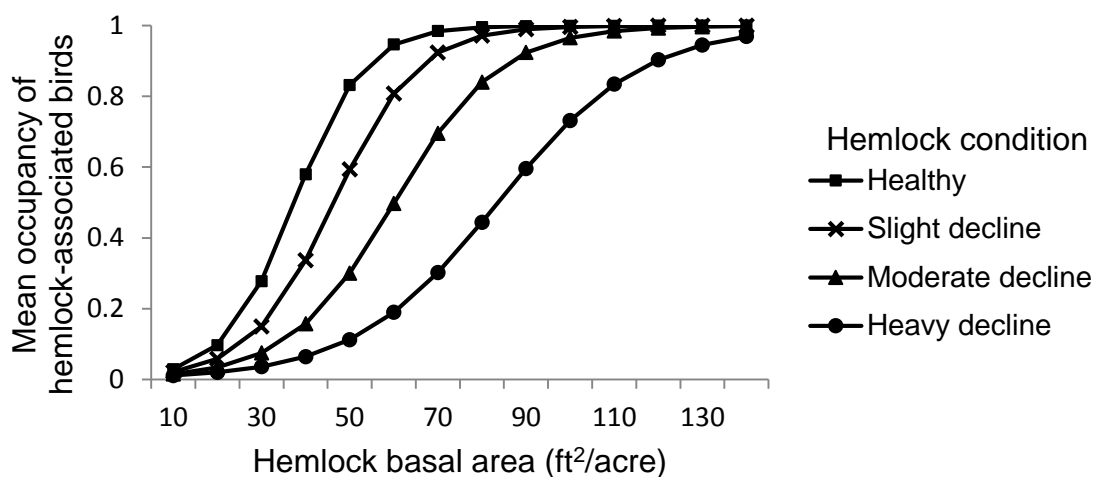


Figure 1-7. Mean occupancy of hemlock-associated bird species in relation to the interaction between hemlock health and hemlock basal area. At points with healthy hemlock, occupancy probability increases abruptly as the number of hemlocks increases, while occupancy increases more gradually in heavily-degraded hemlock.

Table 1-5. Beta coefficients from models examining the effect on occupancy probability of hemlock volume in the canopy (> 5 m height category), an interaction between hemlock abundance (basal area) and hemlock health, and deciduous volume in the understory (0.5-2 m height category). Asterisks indicate 95 % credible intervals not overlapping zero.

Species group	Canopy hemlock volume		Abundance/Health		Understory volume	
	Mean effect	SD	Mean effect	SD	Mean effect	SD
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

Discussion

By examining the same hemlock stands both before and after degradation by the hemlock woolly adelgid, we demonstrate that hemlock decline was associated with changes in vegetation structure and bird communities that matched our predictions (Figure 1-2). Hemlock basal area declined significantly in hemlock stands since 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 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 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 neighboring hardwood stands. This is consistent with a trend of long-term homogenization of the bird community in regions affected by hemlock decline, as the unique species assemblages associated with hemlock forests decline.

Changes in vegetation structure

The results of our vegetation analyses supported our predictions (Figure 1-2), and demonstrate effects of hemlock decline that are consistent with other research on vegetation in dying hemlock forests. For example, Orwig and Foster (1998) also found that hemlock mortality

in Connecticut resulted in a rapid increase in understory growth, including that of deciduous seedlings. As these other vegetation communities eventually replace hemlock stands not only at 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 higher hemlock mortality in stands with greater hemlock basal area, and the corresponding inverse relationship between hemlock basal area and hemlock health at survey locations, holds implications in light of the continued spread of hemlock woolly adelgid. While other tree species 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 adelgid, although Orwig and Foster (1998) found a weak relationship between hemlock stand size and hemlock mortality. This pattern has implications as the adelgid continues to invade new hemlock stands, indicating that where the density of hemlock trees is lower, hemlocks and their associated communities may persist longer.

Changes in avian community composition over time

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. We observed trends that followed our predictions (Figure 1-2) for all bird species groups: hemlock-associated species declined over time while all other groups showed positive responses. We organized species into these groups to determine which habitat variables within dying forests are driving the re-structuring of bird communities over time. Because we observed the strongest responses in groups associated with the shrub-

layer, woodland edge, and the declining forest type, these changing features in dying forests may be most influential in shaping bird communities as die-offs progress. Additionally, these changes are leading to a long-term pattern of homogenization of the avian community, as unique species assemblages in hemlock stands give way to the community composition of the surrounding landscape. This pattern is further evidence of a much broader phenomenon in which non-native species introductions are contributing to biotic homogenization on a global scale (Olden et al. 2004).

Declines in forest type specialists

The declines we observed in hemlock specialists have implications for these species across portions of their ranges where hemlock is either preferred or obligatory breeding habitat. Previous studies of bird communities in dying hemlock have predicted that these species were at risk of decline (Tingley et al. 2002), but have also hinted that some hemlock specialists may persist by shifting their habitat use, and called for long-term studies like ours to examine this possibility (Becker et al. 2008). The regional presence of these species in non-hemlock forest types may also serve as additional support for the idea of habitat plasticity in hemlock-specialized birds. However, the long-term declines in occupancy that we observed in these species indicate that, as a group, species richness of hemlock specialists has already declined within hemlock stands at our study area. If this pattern is consistent across the region we expect these species to experience range contractions at a larger scale as hemlock continues to decline.

While all of the species in this group showed negative responses over time, hemlock specialists will likely be negatively impacted to varying degrees as hemlock continues to decline.

One reason this may occur is that hemlock specialists vary in their usage of microhabitats within hemlock stands. For example, Blackburnian Warbler generally forages and nests high in the treetops (Douglass 2004). In contrast, Hermit Thrush utilizes ground or near-ground microhabitats for both foraging and nesting (Dellinger et al. 2012), and Acadian Flycatcher, Black-throated Green Warbler, and Blue-headed Vireo use intermediate portions of the forest column. Patterns of hemlock decline (such as defoliation that progresses from lower to upper branches), and the complexity of resulting changes in habitat structure, may lead to varying impacts to species with differing microhabitat preferences, at least prior to complete loss and replacement of hemlock stands.

Long-term datasets like the North American Breeding Bird Survey (BBS) provide larger-scale context for the trends we observed in hemlock-associated birds. Across their surveyed ranges, most of the five species in this group have shown either no trend or weak positive trends over the 2005-2015 survey period of the BBS, a period that generally coincides with our study's timeframe. The exception is Acadian Flycatcher, which showed a near-significant negative trend over the ten years (Sauer et al. 2017). Region-specific trends over this same time period vary within and across species as well, including in regions affected by hemlock decline. However, Blackburnian Warbler stands out as having significant regional declines only in the survey regions of Pennsylvania, Virginia, and the Appalachian Mountains (Sauer et al. 2017), all of which have experienced hemlock decline due to the adelgid.

Our approach to studying community change over time—using habitat-based species groups—lends support to our hypothesis that changes in habitat structure/composition are the large-scale mechanism by which hemlock woolly adelgid invasion alters avian community

composition. Further research could deepen our understanding of this process by delving into finer-scale mechanisms: how do gains or losses in habitat lead to the responses we observed in species dependent upon those habitat features? This question may be especially important in examining species-specific vulnerability of hemlock specialists. At least one study has examined mechanisms limiting population viability of hemlock specialists in dying hemlock stands. Allen et al. (2009) found that, at sites with long-term adelgid infestation, hemlock defoliation was related to lower breeding density of Acadian Flycatcher, but was unrelated to nest success. The authors suggest loss of nesting sites as a mechanism for this species' lower breeding density in dying hemlock stands. Other mechanisms that may connect changing habitat to avian population viability are numerous, but include competition, vulnerability to predation/parasitism, and availability of food and microhabitat resources (Marzluff et al. 2000). Management focused on maintaining populations of hemlock-associated birds would benefit from future research into which of these factors limit population viability of hemlock specialists in dying hemlock stands.

Implications of trends in successional and edge species

Based on the trends we observed in the early successional group, continued hemlock decline may provide only limited benefits to these high conservation priority species. Given the increases in early successional habitat and bird communities following many forms of forest disturbance, we expected that hemlock die-off would initially cause a uniform increase in the group. However, while the mean response for the group was indeed positive, this effect was driven almost solely by a strong increase in the Veery and to a lesser extent the American Robin, with no detections occurring in hemlock stands for most of the other species. It may be that the

patterns of vegetation succession in this die-off do not reflect those that typically follow the historical forest disturbances that provided habitat for early successional communities. Specifically, the sudden loss of canopy cover due to fire, windthrow, and other historical disturbances often produces relatively large, uniform patches of open-canopy successional environments. In contrast, following the gradual canopy thinning typical of hemlock decline (Eschtruth et al. 2006), our study area has seen the relatively slow development of small patches of species-poor vegetation communities, with some canopy cover still intact. If this successional pattern is typical of dying hemlock stands across a much larger scale, early successional bird species are unlikely to show a uniform positive response, with increases seen in only a couple of species whose habitat preferences align with these specific successional conditions (e.g., the Veery).

The long-term increases we observed in shrub- and edge-associated bird species align with the findings of other research on bird communities found in dying hemlock. Many of the species that have been observed in higher abundance in dying hemlock are shrub-layer and/or edge-associated birds that also increased 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, increased presence of edge species has unique implications for bird communities in dying forests, especially for interior forest obligate species. The responses of woodland edge species like the Blue Jay and Brown-headed Cowbird ranked among the strongest of all of the species we detected, and both of these species can limit nest success of many passerines, the jay as a nest predator and the cowbird as a brood parasite. As forest die-offs initially lead to the opening of formerly-intact canopies, increases in these edge species will likely add to the threats already

faced by declining populations of many forest interior species. Because higher presence of avian nest predators and brood parasites near edges is a typical pattern across forested landscapes (Brittingham and Temple 1983, Chalfoun et al. 2002), these impacts to bird communities may be similar in other forest types experiencing die-off. Additionally, the initial development of an edge-associated bird community may indicate a more fundamental pattern of “edge effects” occurring in dying forests, which could have ecosystem-wide consequences similar to these well-documented edge effects within fragmented landscapes (Fahrig 2003).

Communities across a gradient of die-off severity

The hemlock specialists were the only group for which vegetation variables measured across survey locations explained patterns of current avian communities with high precision (Table 1-5). This lack of precision in most species groups in the across-survey location analysis may be partly attributed to the limited sample size dictated by our replication of a study design with only 45 survey locations located in hemlock stands. Also, the complexity of changes in habitat suitability following hemlock decline, as well as conflicts between certain habitat variables, may present trade-offs to individual species not strongly associated with hemlock. For example, we expected higher occupancy of both edge- and shrub-associated species in unhealthy hemlock because of the opened canopy and dense shrub-layer that follow hemlock decline. However, this response may have been diluted because many of these species were also more associated with deciduous-dominated habitats, and because hemlock was healthier in these habitats (see occupancy by forest type in Appendix B and correlations from Table 1-3).

Compared to the other species groups, the closer relationship between hemlock specialists and the vegetation variables we modeled may explain the higher precision we observed in 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 trade-off to hemlock specialists. Hemlock associates still persist at reduced but relatively high probabilities in sites with low hemlock basal area but healthy trees or high basal area of unhealthy trees (Figure 1-7). The persistence of live hemlock, despite greater declines in dense hemlock stands (Figure 1-4), means that a large proportion of stands still fall into one of these two groups at our study area. However, continued infestation is likely to reduce hemlock health further in low basal area stands and reduce basal area in dense and currently unhealthy stands. This suggests a potential tipping point, where the rate of decline of hemlock associates accelerates in the future. Still, the relationships we observed may have implications for current management of hemlock woolly adelgid. For example, if management practices are able to maintain (a) sufficient basal area of even highly-degraded hemlock, or (b) relatively healthy hemlock even at a fairly low basal area (~ 70 ft²/acre), then presence of hemlock specialists may be maintained (Figure 1-7).

The general patterns of community changes that we observed, such as declines in forest type specialists with concurrent increases in edge and shrub-layer guilds, likely hold true not only for other regions experiencing hemlock decline but also for other forest types undergoing die-off. However, the changes in vegetation structure associated with dying forest types, especially one as geographically widespread as hemlock, will vary considerably depending on the rate of die-off, species composition of replacement communities (including the potential for

invasion by non-native plants), variation in disturbance regimes, and numerous other factors. The response of communities to this variability in vegetation changes will undoubtedly be variable as well. Further research at larger scales could better explain how the general patterns we have observed will vary with respect to this variability in vegetation restructuring following forest die-off.

Acknowledgements

This project was funded by the National Park Service's Eastern Rivers and Mountains Network and Pennsylvania State University. We would like to thank the staff at Delaware Water Gap National Recreation Area, especially Richard Evans and Jeffrey Shreiner, for their guidance in planning the project and assistance in its implementation. We thank Terry Master at East Stroudsburg University for his input in the project planning stages, and Robert Ross, who conducted point counts in 2000, for helping relocate survey locations. Basal area data from 1997 surveys was supplied by Carolyn Mahan, and Randy Bennett provided access to point count data from 2000. We also thank the Applied Population Ecology Lab at Pennsylvania State University, especially Eric Teitsworth, who collected most basal area data.

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Chapter 2

Long-term avian community response to regional variability in eastern hemlock die-off

Abstract

Forest biomes face increasing rates of disturbance from multiple causes, including climate change, introduced pests, and shifting fire regimes, as well interactions between multiple factors. In particular, the introduction of exotic forest pests is increasing globally, frequently resulting in decline and die-off of affected forest types. Due to regional variation in patterns of forest die-off, understanding the responses of forest-dependent communities requires examining response at broad spatial and temporal scales. To better understand regional patterns of community response to forest declines, we examined the avian community associated with eastern hemlock (*Tsuga canadensis*), which is declining due to the introduction of hemlock woolly adelgid (*Adelges tsugae*) to eastern North America. We collected or compiled long-term avian survey data from four study areas across the range of hemlock woolly adelgid in northeastern/mid-Appalachian regions of the United States. These study areas represent varying stages of hemlock decline, with avian surveys capturing earlier and later stages of infestation at each area. Despite variability among sites in characteristics of the avian community and of the die-off itself, changes in species richness over time were similar across all sites. Hemlock-associated bird species declined at all sites, with concurrent increases in other species groups, especially those associated with forest edge and shrub-layer habitats. Finer-scale variation in the magnitude and timing of avian response coincided with the varying stages of hemlock decline across sites. Species-specific trends showed that Acadian Flycatcher declined most consistently across this large regional scale. Understanding these patterns is critical to predicting and preparing for changes to not only forested landscapes affected by the loss of hemlock, but also for those that will experience similar die-offs as forest pest introductions increase globally.

Introduction

Forest biomes are facing increased disturbance on a global scale (Schelhaas 2003, Seidl 2011). The causes of forest disturbance are diverse and include changing climatic conditions, introduced forest pests, and changing fire regimes; these factors often interact with one another, frequently leading to compounded effects on forested ecosystems (Dale et al. 2001, Seidl et al. 2011). This phenomenon may be especially significant in light of recent accelerated climate change. For example, climate warming and changing drought regimes can change interactions between forest types and their associated pests, with implications for fire regimes in those forests (Dale et al. 2001, Carroll et al. 2003). Forest disturbance, and the associated changes in vegetation structure that often follow, have strong implications for forest-dependent communities, including the avian community. Increasing patterns of forest disturbance highlight the need to understand and predict how forest-dependent communities will respond to current and future disturbances, and the die-offs that frequently follow.

One cause of disturbance that has increasingly reshaped forests, particularly on the North American landscape, is the introduction of exotic forest herbivores and pathogens. Examples from the past several decades include the decline or loss of American chestnut (*Castanea dentata*), ash (*Fraxinus* spp.), and elm (*Ulmus* spp.; Anagnostakis 1987, Brasier 1991, Herms and McCullough 2014). The loss of these dominant forest species due to exotic pests can cause profound changes in ecosystems, not only by the direct removal of key species but by the restructuring of vegetation communities that often follows (Eschtruth et al. 2006, Elliot and Swank 2008). Despite greater recognition of this threat, the introduction of exotic forest pathogens has been increasing exponentially over the past two centuries (Santini et al. 2013).

The loss of foundational tree species affects a wide variety of forest-associated taxa, including vegetation communities (Orwig and Foster 1998, Anderegg et al. 2012), invertebrates (Opler 1978, Ellison et al. 2005, Ulyshen et al. 2011), mammals (Matsuoka et al. 2001) and birds. In avian communities in particular, changes in species abundance or composition have been documented following the die-offs of several species and forest types, such as elm (Kendeigh 1982), hemlock (Tingley et al. 2002, Chapter 1), boreal spruce-fir forests (Rabenold et al. 1998, Matsuoka et al. 2001), and montane coniferous forests (Hutto 1995).

While previous research has documented the local effects of several forest die-offs on avian communities, it remains unknown whether these responses are consistent across the large regional scales frequently spanned by forest die-off. Patterns of avian community response to forest die-off may vary across spatial and temporal scales due to multiple factors. These include variability in factors related to the die-off, such as the rate and severity of decline, patterns in other disturbance regimes (e.g., fire), and characteristics of vegetation communities that replace the dying forest type. In addition, community responses to die-off may vary due to heterogeneity in the avian community itself, including variability in species composition, the degree to which species are specialized to the forest type, and other factors. While several recent studies have documented spatial heterogeneity in patterns of forest die-offs (Clifford et al. 2013, Eschtruth et al. 2013), research on long-term, community-wide responses to this variability is scarce. However, filling this knowledge gap is critical to making informed predictions and management decisions in light of the increased threat of die-off. If responses of forest-dependent communities are uniform across large regional scales, future effects of forest die-off are more likely to follow predictable patterns, with vulnerable species likely to see consistent declines in the future. In

contrast, if responses are heterogeneous, local context becomes more important in predicting future impacts, and vulnerable species are more likely to respond variably as die-off continues.

The current decline and loss of eastern hemlock (*Tsuga canadensis*; hereafter simply *hemlock*) from landscapes in eastern North America provides a model system for understanding long-term community response to regional variability in forest die-off. This species is currently undergoing widespread decline due to infestation by the hemlock woolly adelgid (*Adelges tsugae*), an aphid-like insect native to Japan and introduced to Virginia in the early 1950s (Souto et al. 1996). The adelgid defoliates hemlocks by feeding on needles and buds, causing tree mortality in as few as four years, depending on site characteristics (McClure 1991, Orwig et al. 2002). As of 2015, the adelgid had spread to twenty U.S. states and more than half of the U.S. counties where the hemlock is native (USDA Forest Service 2016). To date, no management actions have succeeded in stemming adelgid-induced mortality on a large scale, and the hemlock woolly adelgid continues to threaten hemlock in its remaining range.

The decline of hemlock may be especially significant for the avian community because several bird species are strongly associated with eastern hemlock during the breeding season, including the Black-throated Green Warbler (*Setophaga virens*), Acadian Flycatcher (*Empidonax virescens*), and Blackburnian Warbler (*Setophaga fusca*; Tingley et al. 2002, Ross et al. 2004). The unique species assemblages associated with hemlock make the loss of this species especially appropriate for examining community response to forest die-off. In addition, the large geographical extent of hemlock decline lends itself to examining variation in this response as it pertains to heterogeneity in the progression of hemlock decline.

Our study examined variation in long-term community response to hemlock decline across a large geographic scale. This was accomplished by compiling long-term avian survey

data from four study areas that span a regional gradient of forested landscapes affected by hemlock decline. We then used a community occupancy modeling approach to determine species-specific and species group responses to hemlock decline. Our objectives were to (1) measure long-term changes in the bird community to determine which species and species groups are most sensitive to this decline, and (2) examine the relationship of community response to spatial and temporal variability in hemlock decline. Studying these poorly understood relationships is critical to predicting and preparing for future impacts to avian communities as the threat of regional-scale forest die-off increases globally. We sought to fill these knowledge gaps by taking the novel approach of examining multiple stages of forest change across the extent of a single foundational species' die-off, and measuring the response of the whole forest bird community.

Study area and methods

Our study includes long-term data from four study areas that are located across a > 1000 km gradient of forest habitats in the eastern United States. The study areas included central Connecticut, Delaware Water Gap National Recreation Area (NRA) on the border of Pennsylvania and New Jersey, Shenandoah National Park (NP) in Virginia, and New River Gorge National River (NR) and Gauley River NRA in West Virginia (Figure 2-1). We treated New River Gorge NR and Gauley River NRA as a single site (hereafter *New River/Gauley*) for the purposes of this study due to their close proximity. Each site consisted of multiple hemlock stands in which survey locations were established; the numbers of hemlock stands and survey locations varied among the four study areas (Table 2-1). Although data on the relative

dominance of hemlock prior to infestation is not available for all study areas, all forest stands had been previously designated as predominantly hemlock, and had been selected for hemlock-related monitoring projects.

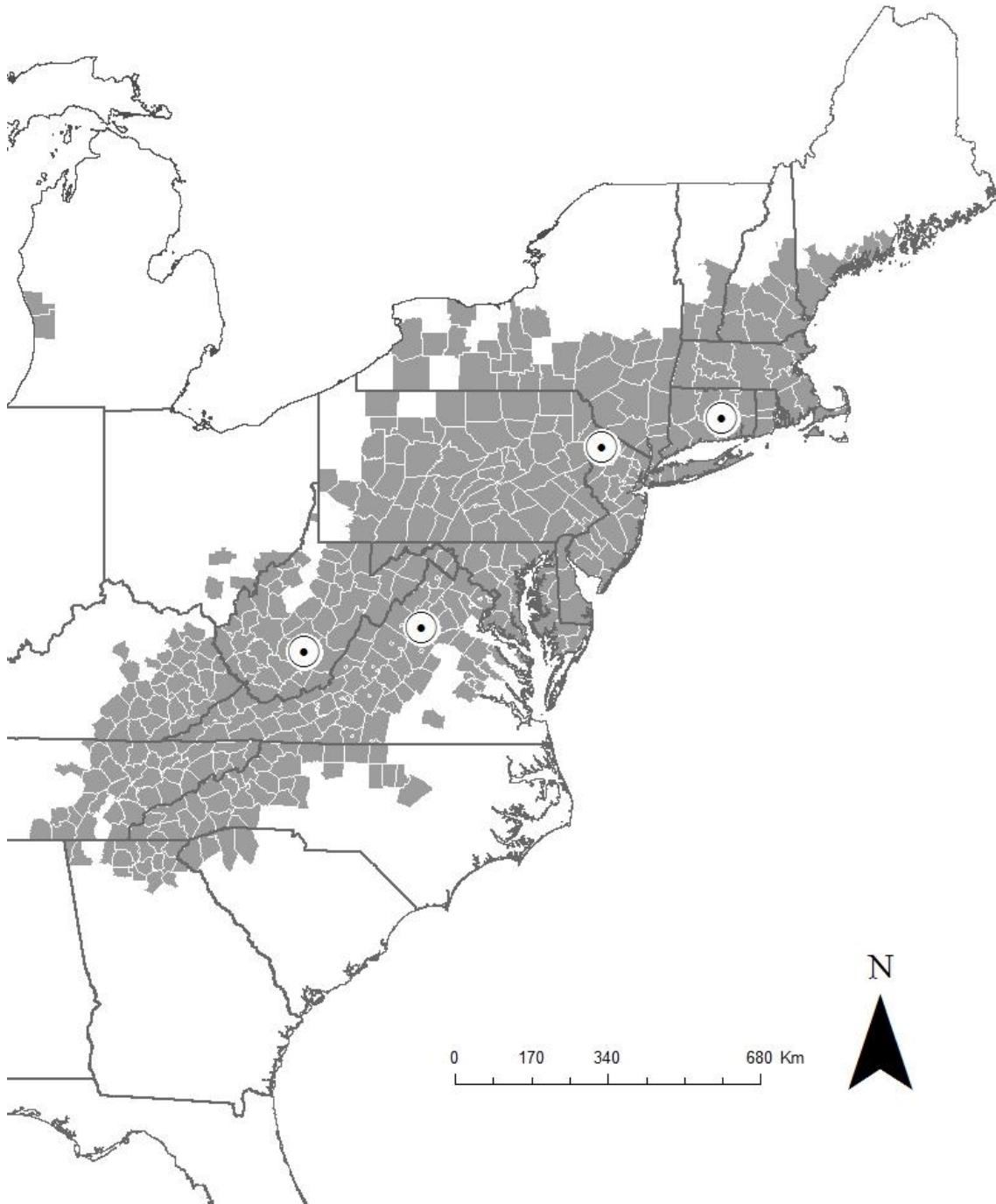


Figure 2-1. Locations of four study areas (marked with circles) in relation to the range of hemlock woolly adelgid infestation in the eastern United States (shaded counties represent adelgid range as of 2015). From northeast to southwest, the study areas are central Connecticut, Delaware Water Gap National Recreation Area, Shenandoah National Park, and New River Gorge National River/Gauley River National Recreation Area. Data on hemlock woolly adelgid infestation is from United States Forest Service (2016).

All four study areas occur within regions affected by hemlock woolly adelgid, with the timing of infestation and the severity of hemlock decline varying among study areas (Table 2-1, Figure 2-2). Both Delaware Water Gap NRA and New River/Gauley have shown relatively slow declines compared to locations with climatic conditions more suitable for hemlock woolly adelgid's life cycle (Fajvan and Wood 2010). However, Delaware Water Gap NRA has been infested far longer than New River/Gauley. Despite hemlock woolly adelgid first reaching Delaware Water Gap NRA by 1989 (Evans 2004), hemlocks in most stands did not show significant signs of decline over a decade later in 2000 (R. Evans, personal communication, 2015), and even as late as 2003 researchers had still found no decline in hemlock basal area in stands sampled at Delaware Water Gap NRA (Eschtruth 2006). By 2016, hemlock basal area had declined across most sampled hemlock stands, but all stands still included a significant, though degraded, hemlock component (Chapter 1). Like Delaware Water Gap NRA, New River/Gauley has experienced a relatively slow rate of decline, but hemlock woolly adelgid arrived approximately fifteen years later at this site, with initial infestation in 2004 (Wood et al. 2009). Since then, monitoring of hemlocks has shown a steady decline in health of hemlock crowns (Wood et al. 2009), although current data on mortality estimates are unavailable.

In contrast to Delaware Water Gap NRA and especially New River/Gauley, hemlock stands at Shenandoah NP and central Connecticut are in a much later stage of decline. Initial infestation at Shenandoah NP in 1988 led to rapid hemlock decline throughout the 1990s, with more than 90 % of sampled hemlocks dead by 2004 (Young and Morton 2002, Bair 2005). Similarly, with the first stands in central Connecticut infested in 1985 (McClure 1987), some stands experienced fairly rapid decline. However, the degree of decline has varied widely given the broad geographical spread of sampled stands in Connecticut (Orwig et al. 2002, Tingley et al.

2002). Mortality ranged from 0—90 % by 2001, at which point some of the most severely impacted stands already had dense growth of deciduous seedlings in the understory (Tingley et al. 2002), a typical successional pattern following hemlock decline (Orwig and Foster 1998). Between 2001 and 2016, mean hemlock basal area for stands with low hemlock mortality declined from 77% to 60% (Tingley et al. 2002, Toenies, unpublished data). In stands originally classified as high-mortality, mean hemlock basal area declined from 58% to 9%.

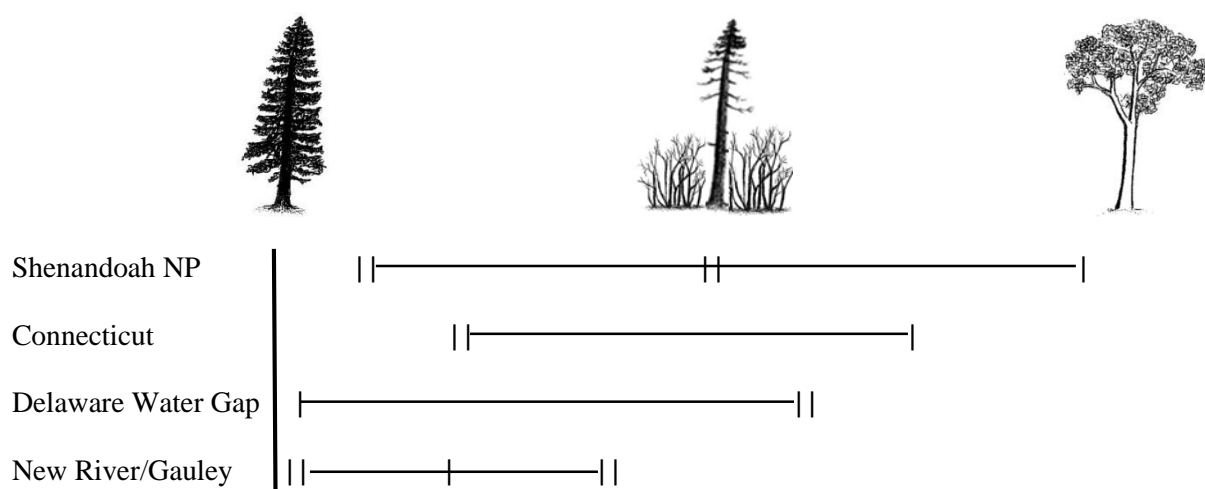


Figure 2-2. Timeline showing the general stage of hemlock decline and associated forest succession captured by avian surveys at four study areas in the eastern United States: Shenandoah National Park, central Connecticut, Delaware Water Gap National Recreation Area, and New River Gorge National River/Gauley River National Recreation Area. Vertical lines indicate years when avian surveys were conducted.

Table 2-1. Summary of study area information related to avian surveys and hemlock decline at four study areas in the eastern United States.

Study area	Adelgid 1st detected	Initial avian surveys	Follow-up avian surveys	Number of stands sampled	Number of survey locations	Stage of hemlock decline in 2016
New River/Gauley	2004	2004/2005	2015/2016	8	36	Early
Delaware Water Gap NRA	1989	2000	2015/2016	11	45	Early—Mid
Connecticut	1985	2000/2001	2016	12	40	Mid—Late
Shenandoah NP	1988	1993/1994	2016	2	25	Late

Avian Surveys

In each of the four study areas, observers surveyed the avian community in hemlock stands during both earlier and later stages of hemlock decline. For two study areas (Shenandoah NP and New River/Gauley), observers also conducted surveys during intermediate years (2004/2005 for Shenandoah NP and 2010 for New River/Gauley). Within stands, survey locations were generally at least 200 m apart, with none spaced closer than 100 m apart.

At each survey location, observers conducted variable-radius point counts (following recommendations of Ralph et al. 1995). Survey methodology at Shenandoah NP differed somewhat from that at other study areas. Surveys at the other three areas involved ten-minute variable-radius counts, with bird detections separated into > 50 m and < 50 m distance bands. At Shenandoah NP, observers conducted 5-minute counts, and detections were specified into distance bands only in the later years. Data summaries indicated that the number of detections

were similar across all years when data from the later years was truncated at 100 m, suggesting that observers in the early years may have truncated detections at this distance. Therefore, in subsequent analyses we excluded >100 m detections for the later years, which allowed for a consistent comparison across all years. Furthermore, by using an occupancy modeling approach to analyze data (see *Data Analysis* section), we were able to control for any observer and detection differences among the study areas. This approach enabled us to calculate a single universal metric of species occurrence that was directly comparable across all study areas.

Observers conducted an initial set of counts from May 26 to June 26, and repeated counts from June 11 to July 11, although not every location received a second count in every year. The second count occurred at least 7 days after the first count for each location, with the exception of two locations during one of the years. All counts were conducted during suitable weather conditions (no strong wind or precipitation), and during the morning, starting no earlier than sunrise and no later than noon. Counts had different observers among study areas and years.

Data Analysis

In addition to measuring species-specific responses over time, we also estimated mean responses for species in each of five groups. These species groups were chosen based on shared habitat associations that we hypothesized would affect community responses to hemlock decline. The groups included (1) hemlock-associated species, which we expected to respond negatively to hemlock loss. Other groups included species we expected to respond to increases in availability of certain habitat features following hemlock die-off. These groupings were the following: (2) mature deciduous forest, (3) woodland edge, (4) a dense shrub-layer, and (5)

snags. We assigned species into groups using pre-determined keywords from detailed habitat descriptions for each species in the Birds of North America Online database (Rodewald 2015; see Appendix A for full species lists for each group). We included passerine and “near-passerine” species with > 5 detections per study site. We excluded wide-ranging corvid species (American Crow [*Corvus brachyrhynchos*] and Common Raven [*Corvus corax*]) and several species that show irruptive breeding patterns in response to resource availability from year to year (e.g. Red-breasted Nuthatch [*Sitta canadensis*] and two cuckoo [*Coccyzus*] species).

To minimize observer differences between the early and late time periods, we analyzed data for bird detections from the <50 m distance band for both Connecticut and Delaware Water Gap NRA. Our analysis excluded detections specified as >100 m for Shenandoah NP, and used all detections from New River/Gauley, due to these two study areas having inconsistencies among years in distance band specifications.

We performed all analyses using hierarchical multi-species 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 across time. All occupancy analyses were fit using Markov chain Monte Carlo (MCMC) methods and run using JAGS (Plummer 2003) called from program R (v. 3.1.2, R Core Team 2015) using package *runjags* (Denwood 2016). We ran models individually for each of the four study areas, estimating mean group responses over time, with species-specific responses treated as random effects. We estimated changes in occupancy between time periods as our response variable at the species-specific level. 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). Our models estimated the probability of detecting each species using the two visits at each point count location over the course of the breeding season. For detection probability, we included covariates for both the time of day and day of the year that surveys were conducted.

Results

Across the 146 point count locations within the four study areas, a total of 40 species were detected and met the criteria for inclusion in our analyses (see Appendix A for full listing of species and Appendix C for number of detections by species and study site). Because of the large regional scale of our study area, the number of species and the composition of the avian community varied among the four study areas, including in regards to the hemlock-associated species. The number of species included in the analysis was 30 for central Connecticut, 27 for Shenandoah NP, 29 for New River/Gauley, and 23 for Delaware Water Gap NRA. Of the five hemlock-associated species, three were present at all four study areas: Black-throated Green Warbler, Acadian Flycatcher, and Blue-headed Vireo (*Vireo solitarius*). Blackburnian Warbler did not occur at New River/Gauley, and Hermit Thrush (*Catharus guttatus*) did not occur at either New River/Gauley or Shenandoah NP.

Changes in bird communities over time

Several species groups showed increases or decreases in species richness over the period of hemlock decline (Figure 2-3). The pattern of change was most similar for the three study areas in later stages of hemlock decline (Connecticut, Delaware Water Gap NRA, and Shenandoah

NP). Species richness declined for the hemlock-associated species group across those three study areas, with the change in richness reaching -1.8 species [95 % credible interval -2.9, -0.2] for the site with the greatest decline (Shenandoah NP; Figure 2-3). This indicates that survey locations in this study area lost an average of nearly two species in the hemlock associates group. Because there are relatively few species in this group, these declines in species richness represent the loss of a large proportion of the group's species (nearly half for Shenandoah NP). In contrast to the trend in hemlock-associated species, species richness increased for several other species groups, with the magnitude of this effect varying among study areas (Figure 2-3). The most consistent increases in species richness occurred in species associated with the forest edge and the shrub-layer, with positive trends for both groups across the three study areas. For species associated with snags and mature deciduous forest, species richness showed an increasing trend over time at both Delaware Water Gap NRA and Shenandoah NP, but not in Connecticut.

As the site in the earliest stage of hemlock decline, New River/Gauley showed relatively little change in species richness compared to the other study areas, with none of the species groups increasing between the two time periods (Figure 2-3).

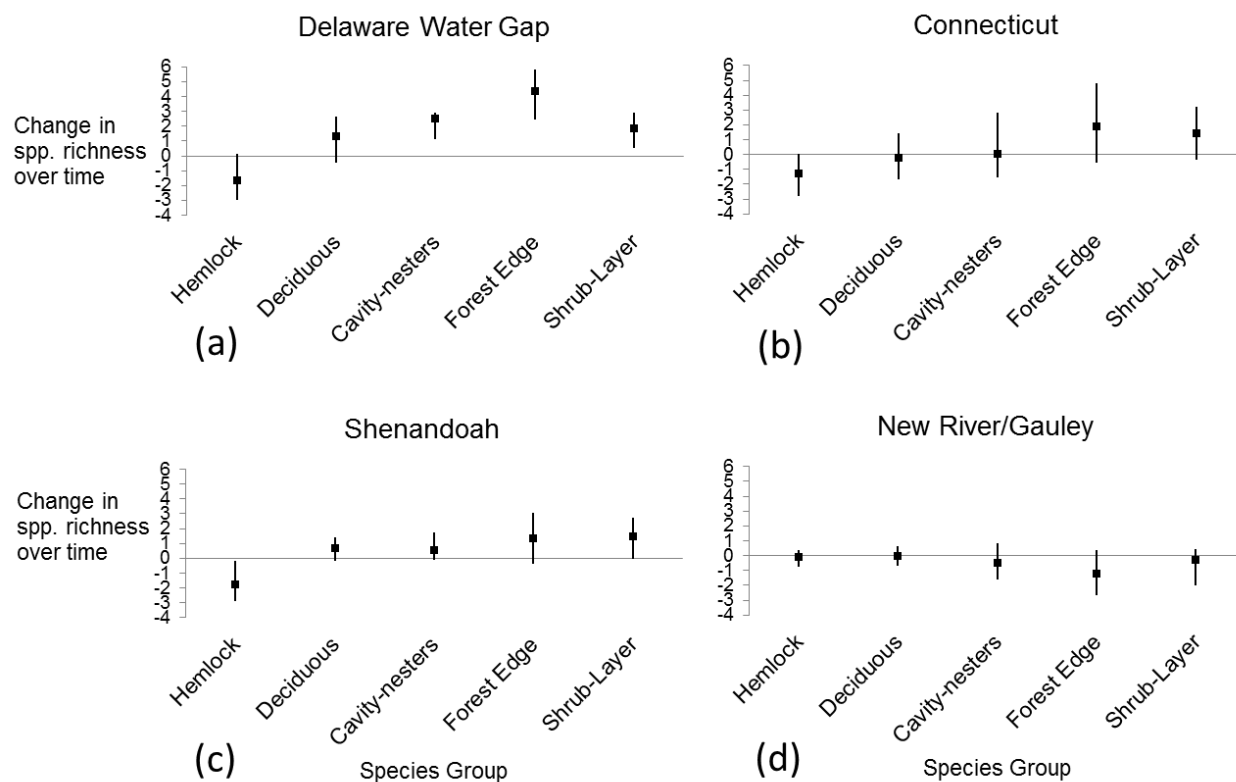


Figure 2-3. Changes in avian species richness at four study areas between earlier and later stages of hemlock woolly adelgid infestation. Error bars represent 95 % credible intervals. Across the three study areas with later stages of adelgid infestation, hemlock-associated species declined over time, while species associated with forest edge and the shrub-layer showed the most consistent increases across the areas. At New River/Gauley, where hemlock is in a much earlier stage of decline, no species groups have increased over time.

For the two study areas that had data from more than two time periods (Shenandoah NP and New River/Gauley), we were able to compare species trends between the early-to-middle and middle-to-late time periods. For both of these study areas, changes in species richness varied between the two time periods (Figure 2-4). At Shenandoah NP, species richness declined for hemlock associates and increased for other groups, especially shrub-layer and forest edge-associated species, during the earlier stages of hemlock decline. However, during the later stage of decline at Shenandoah NP, species richness did not exhibit additional change for any of the species groups. Changes in species richness were much weaker for New River/Gauley, where surveys captured a much narrower window in an earlier stage of hemlock decline. In contrast to

the pattern at Shenandoah NP, it is the later time period where changes in species richness began to follow the patterns observed at other study areas, although these responses are weak for most groups at this point in time. For example, the change in species richness for hemlock associates during the later period was -0.18 $[-0.97, 0.01]$.

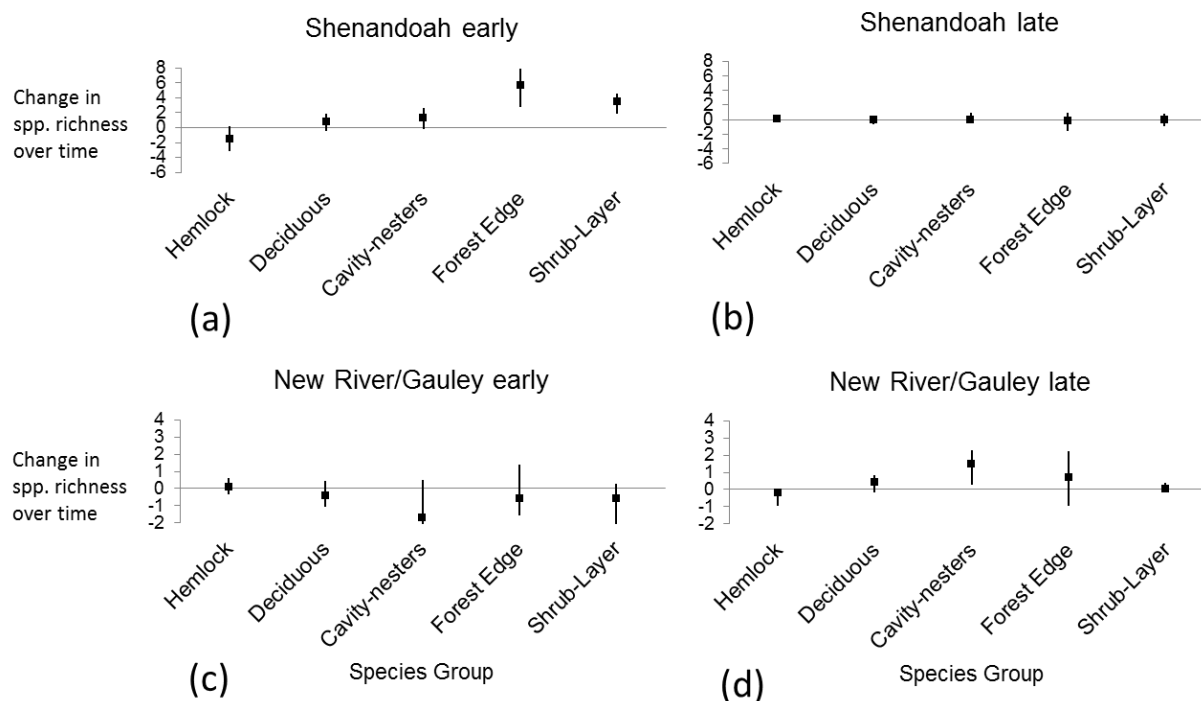


Figure 2-4. Changes in avian species richness at two study areas (Shenandoah NP and New River/Gauley) between early to middle (a and c) and middle to later (b and d) periods of hemlock woolly adelgid infestation. Error bars represent 95 % credible intervals. Avian surveys capture a wide timespan of hemlock decline at Shenandoah NP National Park, whereas the survey period captures a narrow window of early hemlock decline at New River Gorge National River/Gauley River National Recreation Area. At Shenandoah NP, changes in species richness occur only in the early period, with hemlock associates declining and all other groups increasing. At New River/Gauley, changes in species richness are much weaker, and only in the later period do they begin to reflect the patterns observed at other study areas. Axis units differ between study areas.

Since hemlock-specialized bird species were predicted to be uniquely sensitive to hemlock die-off, we also estimated species-specific changes in occupancy over time for this group. The magnitude and precision of decline varied among species and study areas. Acadian Flycatcher showed the most consistent decline across study areas, with negative trends observed

at three of the four study areas (Figure 2-5). For two of the three study areas where it was present, Blackburnian Warbler showed the greatest decline in occupancy out of all of the species.

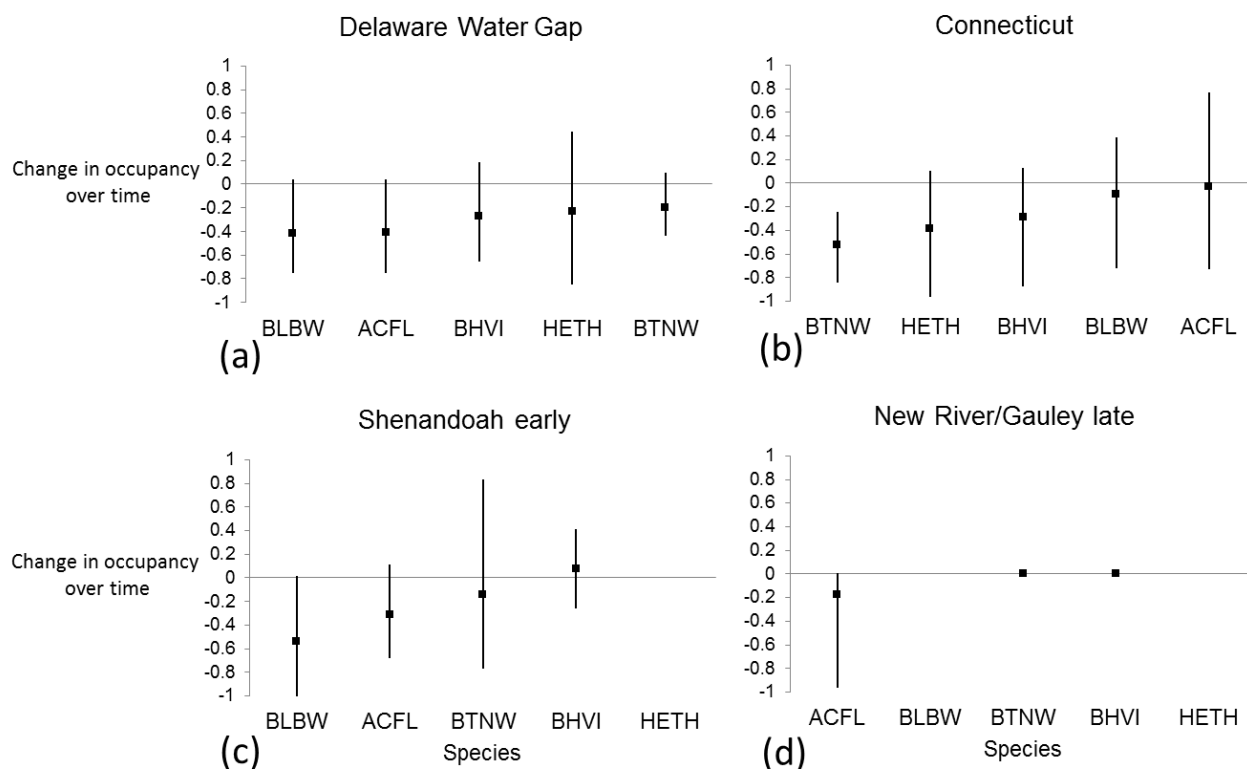


Figure 2-5. Trends for hemlock-associated species between earlier and later stages of adelgid infestation at four study areas. Data points represent the change in occupancy following hemlock decline, and error bars represent 95 % credible intervals. Hermit Thrush and Blackburnian Warbler did not occur at all study areas. Across study areas, the Acadian Flycatcher showed the most consistent negative response to hemlock decline, but precision and magnitude of trends varied among study areas for individual species. (For Shenandoah NP and New River/Gauley, results are shown for the early and later time periods, respectively.)

Given the high variability in the degree of hemlock decline associated with the geographically widespread stands in central Connecticut, we also examined community-wide and species-specific responses at a finer scale for this site, separately analyzing data from survey locations in stands that had been classified as having either low/moderate (<60%, $n = 7$) or high (>60%, $n = 5$) hemlock mortality during the early survey period (Tingley et al. 2002). Patterns of

community change differed between the two stand types (Figure 2-6a and 2-6b). Between the early and late survey periods, survey locations in both types of stands lost hemlock-associated species, but this decline was greater for locations that originally had low/moderate mortality compared to those that had high mortality. Locations in low/moderate stands lost a mean of nearly twice as many species in the hemlock specialist group compared to locations in high mortality stands (mean changes in species richness -2.9 [95 % CI -4.7, -0.7] and -1.7 [95 % CI -3.0, -0.5], respectively). The responses of other species groups also differed between the stand types: stands that originally had low/moderate mortality have seen an increase in cavity-nesters, while species associated with the shrub-layer increased in stands that had high mortality.

At the species-specific level, responses to hemlock decline were fairly consistent between survey locations with low/moderate hemlock mortality and locations with high mortality. For both mortality types, Black-throated Green Warbler showed the strongest decline in occupancy over time, followed by Hermit Thrush and Blue-headed Vireo (Figure 2-6c and 2-6d). At high mortality locations, Blackburnian Warbler was absent during both early and late surveys, and Acadian Flycatcher had too few detections to meet our analysis criteria (< 5 detections across all surveys), so we estimated responses for only three of the five species in the group (Figure 2-6d). The scarcity of these two species in the high mortality stands suggests that they had already been lost by the time of early surveys in 2000/2001. This may also explain the greater loss of species richness from low/moderate mortality stands compared to high mortality stands, since the stands with lower initial mortality still supported the full community of hemlock-associated species during early surveys.

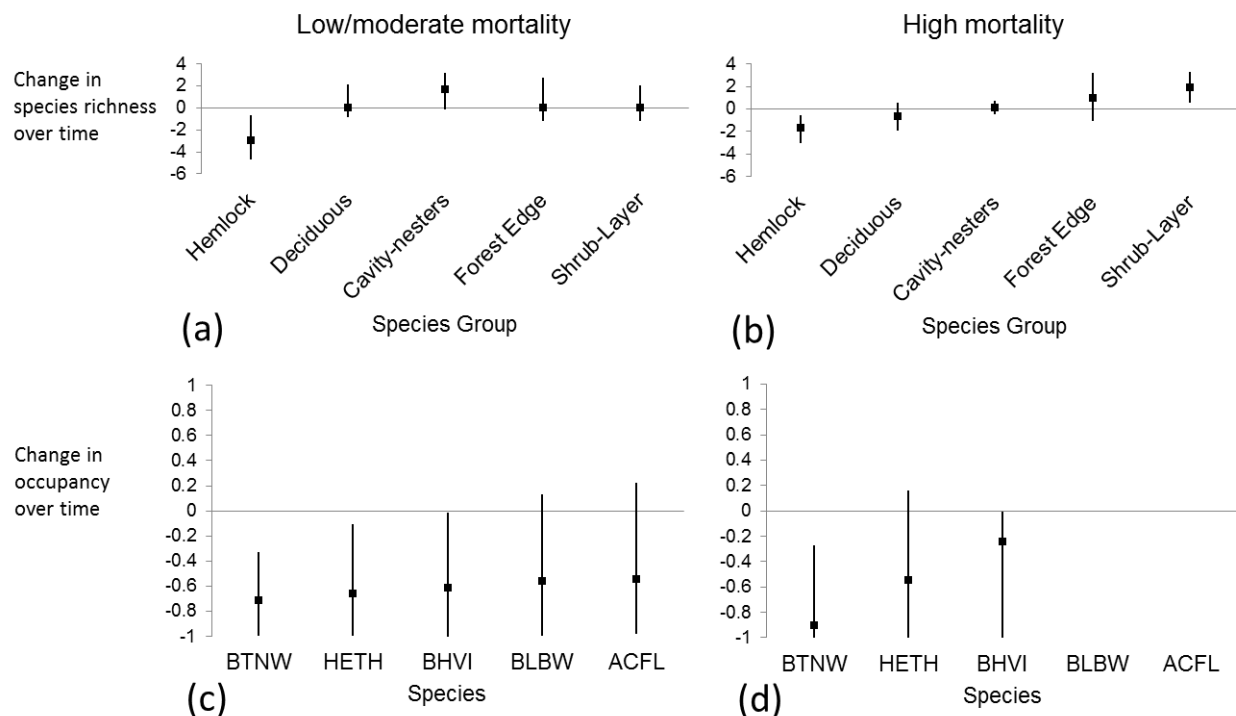


Figure 2-6. Changes in avian species richness (a and b) and occupancy of hemlock-associated bird species (c and d) over time in central Connecticut for hemlock stands classified as having either low/moderate (<60%) or high (>60%) hemlock mortality as of the initial survey period in 2000/2001. Error bars represent 95 % credible intervals. Between 2000/2001 and 2016, both types of stands lost hemlock-associated species, with a stronger decline in the stands that originally had low/moderate mortality. Cavity-nesters increased in the low/moderate mortality stands, while species associated with the shrub-layer increased in the high mortality stands. Among hemlock specialists, Black-throated Green Warbler showed the strongest decline in both stand types, followed by Hermit Thrush and Blue-headed Vireo. Acadian Flycatcher and Blackburnian Warbler had fewer than 5 detections across all surveyed years in high mortality stands.

Discussion

We examined forest bird communities across a large geographic scale to determine long-term community response to regional variability in the die-off of a foundational tree species. Our results show that the long-term responses of avian communities to hemlock decline are consistent at a large regional scale, despite variability in patterns of die-off, community composition, and other factors. Across four study areas in the eastern United States, hemlock-specialized bird species declined in response to hemlock die-off, contrasting with increases in

species associated with successional features such as forest edge, shrubs, and snags. A species-specific analysis of the hemlock specialist group showed varying patterns across study areas, with the most consistent decline observed for the Acadian Flycatcher. These findings are the first to document regional patterns of long-term community response to this die-off. In light of the continuing spread of hemlock woolly adelgid, as well as increased prevalence of other agents of forest die-off on a global scale, our results provide important information on future impacts of forest die-offs on forest-dependent avian communities, including the responses of forest type specialists.

Declines in forest type specialists

The loss of hemlock specialists following hemlock decline holds implications for these species as hemlock woolly adelgid continues to threaten their preferred habitat, and confirms predictions made by other research conducted on a shorter time scale (Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008). Furthermore, the declines in occupancy we observed in hemlock specialists indicate that they are being lost from sites in hemlock stands as trees decline. This demonstrates the utility of a long-term analysis which has revealed that, as a group, these specialists have not been able to persist by showing plasticity in habitat use, which short-term research has suggested could be a response to die-off (Becker 2008). Few other studies have measured the long-term response of forest type specialists to the die-off of a single foundation species, and research on this response across a large geographic scale is even scarcer. However, research that has examined similar responses generally aligns with the patterns we observed. Following the introduction of the exotic balsam woolly adelgid (*Adelges piceae*), Rabenold et al.

(1998) found that six species characteristic of spruce-fir forests declined over a 21-year span of infestation and forest die-off. Socolar et al. (2013) found that 12 avian specialists in tropical bamboo forests were lost following forest die-off, although the large group of specialists associated with this forest type also included several species that persisted.

The species-specific trends of the hemlock specialists provide additional insight into which species are most vulnerable to continuing hemlock decline. The strong declines in Blackburnian Warbler align with larger-scale datasets on species trends in recent years. Specifically, the 2005-2015 survey period of the North American Breeding Bird Survey (BBS) shows that Blackburnian Warbler has declined significantly in three survey regions, all of which have been impacted by hemlock woolly adelgid: Pennsylvania, Virginia, and the Appalachian Mountains (Sauer et al. 2017). Interestingly, Black-throated Green Warbler has not seen significant regional declines over the same time period (Sauer et al. 2017), despite evidence that this species may have an especially close association with hemlock and high vulnerability to degradation caused by the adelgid (Benziner et al. 1994, Tingley et al. 2002). In contrast to Black-throated Green Warbler, prior research indicates that Acadian Flycatcher is not as closely tied to hemlock stands as other hemlock specialists (Ross et al. 2004) and that the species is able to shift to non-hemlock nest substrates in dying hemlock stands, potentially allowing it to persist in hemlock's absence (Becker et al. 2008). Despite these conclusions from short-term studies, the trends we observed indicate that Acadian Flycatcher, like the other hemlock specialists, has declined at geographically widespread study areas, and is vulnerable to the continued loss of hemlock habitat. BBS trend estimates for 2005—2015 show that Acadian Flycatcher has declined significantly in one survey region—West Virginia—and it has seen a near-significant decline across the entirety of its surveyed range. At the survey-wide scale for this time period,

BBS data show that none of the other species in our hemlock specialist group have yet seen significant declines (Sauer et al. 2017).

Increased presence of successional species groups

The increases in avian species associated with ephemeral features provided by forest die-off, especially forest edge habitat and a dense shrub-layer, were consistent across the large geographic scale encompassed by our study area in the eastern United States. These long-term changes in the bird community have been paralleled by results of other multi-year or short-term studies of bird communities in dying forests. For example, bird species associated with open, disturbed forests and early successional habitat increased following die-offs in spruce-fir forests in the southern Appalachian mountains (Alsop and Laughlin 1991, Rabenold et al. 1998). Species that rely on the understory (Matsuoka et al. 2001), and tree cavities (Tingley et al. 2002, Becker et al. 2008) have also been found to be more abundant in locations with greater forest die-off. However, while we observed long-term increases in species associated with several characteristics of forest disturbance (forest edge, shrub-layer, and snags), the decline and loss of hemlock forests in the northeastern United States has led to increases in few successional species (Chapter 1).

For these species groups associated with disturbance-related habitat features, the repeated phenomenon of forest die-off following exotic introductions has important conservation implications. In eastern North America, early successional forests have been a declining component of the landscape due to multiple causes, including fire suppression and changes in forest harvest and agricultural practices (Trani et al. 2001). This has caused conservation concern

for species associated with early successional habitat, many of which have seen regional declines in recent decades (Litvaitis 1993). Because die-offs caused by exotic introductions may mimic historical forest disturbances, their increased prevalence in eastern North American forests could lead to short-term increases in species associated with successional features, in some cases benefiting early successional species of conservation concern. However, despite the increases of many species groups in response to hemlock die-off, species richness at the landscape scale will likely continue to decline in the long term as the communities in hemlock stands become more similar to those of the surrounding deciduous or mixed forest landscape (Chapter 1).

Variability in community response across large scale

The four study areas we sampled varied both in characteristics of their avian communities (e.g., community composition) and in the characteristics of hemlock decline, including the stage and severity of die-off captured by our surveys. Despite this regional variation, we observed generally consistent patterns of avian community response at a large scale. However, finer-scale variation in that response coincides with variability in the timing and severity of hemlock decline within and among study areas. For example, results from study areas with multiple time periods show that strong avian response to die-off does not occur consistently across the timeline of hemlock woolly adelgid infestation and associated die-off. Where hemlock is just beginning to decline (New River/Gauley), the response of the avian community has been relatively weak. In contrast, where hemlock has declined severely (Shenandoah NP), we observed strong avian responses over the first decade captured by surveys, while the following decade saw no additional avian response. The declines of hemlock specialists at high- and lower- mortality

hemlock stands in central Connecticut support this pattern, as the response of this group was much weaker where most hemlocks had already been lost. In light of the scarcity of research on community response to variability in forest die-off, these results establish that communities may vary temporally in their response to a single die-off while still demonstrating consistent patterns of change.

Our findings have direct implications for forest communities across the extent of hemlock die-off. Attributes of hemlock decline and hemlock-associated communities will continue to vary across newly invaded hemlock stands in eastern North America. Despite differences such as these in the current range of die-off, we found consistent patterns of loss of forest type specialists and increases in species adapted to ephemeral habitat features in dying forests. We expect these patterns to continue on a large scale as the hemlock woolly adelgid spreads further into the eastern hemlock's range. Understanding these patterns is critical to predicting and preparing for changes to not only forested landscapes affected by the loss of hemlock, but also for those that will experience similar die-offs as introduced pest species continue to increase in their prevalence globally.

Acknowledgements

This project was funded by the National Park Service's Eastern Rivers and Mountains Network and Pennsylvania State University. For assistance in project planning and supplying raw survey data and vegetation reports, we would like to thank Richard Evans, Randy Bennett, Robert Ross, and other staff at Delaware Water Gap NRA National Recreation Area,

Shenandoah National Park, and New River Gorge National River/Gauley River National Recreation Area. We also thank the multiple observers who conducted surveys across all study areas and years.

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Appendix A. Species groups

Table 1. Scientific and common names, American Ornithological Union (AOU) alpha codes, and species group assignments used for occupancy analyses examining group mean responses.

AOU Code	Scientific name	Common name	Species Group					
			Hemlock	Mature deciduous	Woodland Edge	Shrub-layer	Snag-nesting	Early successional
RTHU	<i>Archilochus colubris</i>	Ruby-throated Hummingbird			X			
RBWO	<i>Melanerpes carolinus</i>	Red-bellied Woodpecker		X			X	
DOWO	<i>Picoides pubescens</i>	Downy Woodpecker					X	
HAWO	<i>Picoides villosus</i>	Hairy Woodpecker		X			X	
NOFL	<i>Colaptes auratus</i>	Northern Flicker			X		X	
PIWO	<i>Dryocopus pileatus</i>	Pileated Woodpecker					X	
EAWP	<i>Contopus virens</i>	Eastern Wood-Pewee			X			
ACFL	<i>Empidonax virens</i>	Acadian Flycatcher	X					
GCFL	<i>Myiarchus crinitus</i>	Great Crested Flycatcher			X		X	
WEVI	<i>Vireo griseus</i>	White-eyed Vireo				X		
YTVI	<i>Vireo flavifrons</i>	Yellow-throated Vireo			X			
BHVI	<i>Vireo solitarius</i>	Blue-headed Vireo	X					
REVI	<i>Vireo olivaceus</i>	Red-eyed Vireo		X		X		
BLJA	<i>Cyanocitta cristata</i>	Blue Jay			X			
BCCH	<i>Poecile atricapillus</i>	Black-capped Chickadee			X		X	
TUTI	<i>Baeolophus bicolor</i>	Tufted Titmouse		X			X	
WBNU	<i>Sitta carolinensis</i>	White-breasted Nuthatch			X		X	
BRCR	<i>Certhia americana</i>	Brown Creeper					X	

HOWR	<i>Troglodytes aedon</i>	House Wren			X		X	
BGGN	<i>Poliophtila caerulea</i>	Blue-Gray Gnatcatcher			X	X		
VEER	<i>Catharus fuscescens</i>	Veery				X		X
HETH	<i>Catharus guttatus</i>	Hermit Thrush	X					
WOTH	<i>Hylocichla mustelina</i>	Wood Thrush		X		X		
AMRO	<i>Turdus migratorius</i>	American Robin						X
GRCA	<i>Dumetella carolinensis</i>	Gray Catbird			X	X		
BRTH	<i>Toxostoma rufum</i>	Brown Thrasher			X	X		
CEDW	<i>Bombycilla cedrorum</i>	Cedar Waxwing			X	X		
AMGO	<i>Spinus tristis</i>	American Goldfinch						X
OVEN	<i>Seiurus aurocapilla</i>	Ovenbird		X				
WEWA	<i>Helmitheros vermivorum</i>	Worm-eating Warbler		X		X		
GWWA	<i>Vermivora chrysoptera</i>	Golden-winged Warbler				X		X
BWWA	<i>Vermivora cyanoptera</i>	Blue-winged Warbler			X	X		X
BAWW	<i>Mniotilta varia</i>	Black-and-white Warbler		X				
COYE	<i>Geothlypis trichas</i>	Common Yellowthroat					X	
HOWA	<i>Setophaga citrina</i>	Hooded Warbler			X	X		
AMRE	<i>Setophaga ruticilla</i>	American Redstart				X		
BLBW	<i>Setophaga fusca</i>	Blackburnian Warbler	X					
YEWA	<i>Setophaga petechial</i>	Yellow Warbler			X	X		
CSWA	<i>Setophaga pensylvanica</i>	Chestnut-sided Warbler			X	X		X
BTBW	<i>Setophaga caerulescens</i>	Black-throated Blue Warbler				X		
PRAW	<i>Setophaga discolor</i>	Prairie Warbler						X
BTNW	<i>Setophaga virens</i>	Black-throated Green Warbler	X					
CAWA	<i>Cardellina canadensis</i>	Canada Warbler			X	X		X
EATO	<i>Pipilo erythrophthalmus</i>	Eastern Towhee			X	X		
CHSP	<i>Spizella passerina</i>	Chipping Sparrow			X			X
FISP	<i>Spizella pusilla</i>	Field Sparrow			X			
SOSP	<i>Melospiza melodia</i>	Song Sparrow					X	
SCTA	<i>Piranga olivacea</i>	Scarlet Tanager		X				

NOCA	<i>Cardinalis cardinalis</i>	Northern Cardinal	X	X
RBGR	<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	X	X
INBU	<i>Passerine cyanea</i>	Indigo Bunting	X	X
COGR	<i>Quiscalus quiscula</i>	Common Grackle	X	
BHCO	<i>Molothrus ater</i>	Brown-headed Cowbird	X	
BAOR	<i>Icterus galbula</i>	Baltimore Oriole	X	

Appendix B. Occupancy estimates from Chapter 1 analysis

Table 1. Number of surveys with detections, and occupancy estimates for all detected species for hemlock and hardwood stands pre- and post- hemlock decline.

Species	Surveys with detections	Hemlock pre-decline	SD	Hemlock post-decline	SD	Hardwood pre-decline	SD	Hardwood post-decline	SD
Mourning Dove	5	0.01	0.01	0.01	0.01	0.05	0.03	0.01	0.01
Ruby-throated Hummingbird	8	0.01	0.01	0.01	0.01	0.06	0.03	0.05	0.03
Red-bellied Woodpecker	9	0.00	0.01	0.01	0.01	0.08	0.04	0.09	0.04
Downy Woodpecker	10	0.01	0.01	0.01	0.01	0.09	0.04	0.05	0.02
Hairy Woodpecker	10	0.00	0.01	0.01	0.01	0.07	0.03	0.07	0.03
Northern Flicker	6	0.03	0.02	0.01	0.01	0.05	0.03	0.01	0.01
Pileated Woodpecker	5	0.02	0.02	0.01	0.01	0.04	0.03	0.02	0.01
Eastern Wood-Pewee	48	0.06	0.03	0.07	0.02	0.22	0.06	0.13	0.04
Acadian Flycatcher	90	0.29	0.07	0.24	0.05	0.21	0.06	0.15	0.04
Eastern Phoebe	20	0.04	0.02	0.07	0.03	0.07	0.03	0.07	0.03
Great Crested Flycatcher	17	0.03	0.02	0.03	0.02	0.09	0.04	0.05	0.02
Yellow-throated Vireo	26	0.01	0.01	0.02	0.01	0.16	0.05	0.14	0.04
Blue-headed Vireo	53	0.36	0.07	0.21	0.05	0.06	0.03	0.02	0.01
Red-eyed Vireo	345	0.53	0.07	0.73	0.05	0.92	0.03	0.93	0.03
Blue Jay	24	0.08	0.04	0.13	0.04	0.10	0.04	0.07	0.03
Black-capped Chickadee	12	0.03	0.02	0.05	0.02	0.05	0.03	0.05	0.03
Tufted Titmouse	40	0.11	0.04	0.09	0.03	0.21	0.06	0.10	0.03
White-breasted Nuthatch	25	0.01	0.01	0.02	0.02	0.15	0.05	0.16	0.05
Brown Creeper	6	0.02	0.02	0.04	0.02	0.02	0.01	0.01	0.01
Winter Wren	8	0.03	0.02	0.03	0.02	0.02	0.01	0.01	0.01
Carolina Wren	1	0.00	0.00	0.00	0.01	0.02	0.01	0.01	0.01
Blue-gray Gnatcatcher	32	0.01	0.01	0.04	0.02	0.13	0.05	0.26	0.06
Veery	71	0.10	0.04	0.22	0.04	0.15	0.05	0.16	0.04
Hermit Thrush	13	0.06	0.03	0.05	0.02	0.04	0.02	0.02	0.01

Wood Thrush	96	0.24	0.06	0.20	0.04	0.37	0.07	0.19	0.04
American Robin	16	0.03	0.02	0.05	0.02	0.06	0.03	0.06	0.03
Gray Catbird	20	0.01	0.01	0.01	0.01	0.08	0.04	0.10	0.04
Cedar Waxwing	17	0.02	0.01	0.07	0.03	0.04	0.02	0.09	0.03
Ovenbird	391	0.66	0.07	0.91	0.03	0.83	0.05	0.93	0.03
Worm-eating Warbler	33	0.03	0.02	0.06	0.02	0.12	0.04	0.12	0.04
Louisiana Waterthrush	45	0.13	0.04	0.18	0.04	0.13	0.05	0.11	0.04
Blue-winged Warbler	2	0.00	0.00	0.00	0.01	0.02	0.02	0.02	0.02
Black-and-white Warbler	22	0.06	0.03	0.09	0.03	0.08	0.04	0.06	0.03
Common Yellowthroat	12	0.01	0.01	0.01	0.01	0.07	0.03	0.06	0.03
Hooded Warbler	22	0.00	0.00	0.02	0.01	0.06	0.03	0.13	0.04
American Redstart	88	0.03	0.02	0.03	0.01	0.49	0.08	0.39	0.06
Cerulean Warbler	4	0.00	0.01	0.00	0.00	0.03	0.02	0.02	0.01
Northern Parula	17	0.03	0.02	0.07	0.03	0.05	0.03	0.05	0.02
Blackburnian Warbler	64	0.36	0.07	0.24	0.05	0.04	0.02	0.01	0.01
Yellow Warbler	9	0.00	0.01	0.01	0.01	0.07	0.03	0.05	0.03
Chestnut-sided Warbler	5	0.00	0.01	0.00	0.01	0.05	0.03	0.02	0.01
Pine Warbler	10	0.02	0.02	0.06	0.03	0.02	0.01	0.03	0.02
Prairie Warbler	5	0.01	0.01	0.01	0.01	0.05	0.03	0.01	0.01
Black-throated Green Warbler	112	0.59	0.07	0.39	0.05	0.09	0.04	0.03	0.01
Canada Warbler	2	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Eastern Towhee	2	0.00	0.01	0.00	0.00	0.02	0.02	0.01	0.01
Chipping Sparrow	5	0.01	0.01	0.00	0.01	0.06	0.03	0.03	0.02
Field Sparrow	1	0.00	0.01	0.00	0.00	0.02	0.02	0.01	0.01
Song Sparrow	2	0.00	0.01	0.00	0.00	0.02	0.02	0.01	0.01
Dark-eyed Junco	1	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01
Scarlet Tanager	122	0.36	0.07	0.28	0.05	0.52	0.07	0.28	0.05
Northern Cardinal	2	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.01
Rose-breasted Grosbeak	26	0.05	0.03	0.09	0.03	0.10	0.04	0.09	0.03
Indigo Bunting	6	0.01	0.01	0.01	0.01	0.03	0.02	0.03	0.02

Red-winged Blackbird	2	0.00	0.00	0.00	0.01	0.02	0.01	0.01	0.01
Common Grackle	3	0.00	0.00	0.00	0.01	0.02	0.02	0.02	0.02
Brown-headed Cowbird	26	0.05	0.03	0.15	0.05	0.09	0.04	0.15	0.05
Baltimore Oriole	15	0.01	0.01	0.04	0.02	0.05	0.03	0.09	0.03

Appendix C. Detection Covariates in Chapter 1 Analysis

Table 1. Beta coefficients for effects of ambient noise, survey date, and time of day on detection probability of all detected species in Chapter 1 analysis. Asterisks indicate significance with a 95 % credible interval (only Red-eyed Vireo showed a significant effect for a detection covariate).

Species	Ambient noise		Survey date		Time of day	
	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
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
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
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
Red-winged Blackbird	-0.18	0.28	0.01	0.27	0.12	0.30
Common Grackle	-0.22	0.27	0.05	0.27	0.08	0.29
Brown-headed Cowbird	-0.37	0.28	0.04	0.22	0.06	0.21
Baltimore Oriole	-0.23	0.24	0.11	0.26	0.12	0.26
Mean	-0.18	0.11	0.04	0.10	0.04	0.10

Appendix D. Number of detections and estimated changes in occupancy across all species for four study areas from Chapter 2 analysis

Table 1. Number of sites with detections, and estimated changes in occupancy across all species with > 5 detections per study area, for four study areas. Asterisks indicate significance with a 95 % credible interval.

Species	Connecticut			Delaware Water Gap NRA			New River/Gauley (late)			Shenandoah (early)		
	Detections	Mean	SD	Detections	Mean	SD	Detections	Mean	SD	Detections	Mean	SD
Red-bellied Woodpecker	9	0.2	0.36	-	-	-	11	0.9*	0.25	-	-	-
Downy Woodpecker	23	0.05	0.14	-	-	-	-	-	-	23	0.26	0.31
Hairy Woodpecker	18	0.07	0.21	-	-	-	-	-	-	-	-	-
Northern Flicker	-	-	-	-	-	-	7	0.28	0.38	-	-	-
Pileated Woodpecker	-	-	-	-	-	-	25	0.08	0.2	-	-	-
Eastern Wood-Pewee	29	0.16	0.25	17	0.63*	0.31	8	0.07	0.38	23	0.56	0.31
Acadian Flycatcher	7	-0.02	0.36	54	-0.41	0.24	32	-0.3	0.32	112	-0.31	0.19
Great Crested Flycatcher	26	0.1	0.19	7	0.87*	0.22	10	-0.15	0.33	-	-	-
Yellow-throated Vireo	6	0.13	0.37	-	-	-	6	0.21	0.53	-	-	-
Blue-headed Vireo	13	-0.29	0.23	55	-0.28	0.24	84	0.01	0.01	78	0.09	0.18
Red-eyed Vireo	52	0.01	0.25	157	0.29	0.15	138	0.01	0.01	77	0.12	0.16
Blue Jay	37	0.1	0.16	23	0.72*	0.27	57	0.01	0.01	10	0.44	0.39
Black-capped Chickadee	62	0.03	0.08	14	0.78*	0.25	-	-	-	-	-	-
Tufted Titmouse	70	0.03	0.08	16	0.53	0.28	60	-0.01	0.02	9	0.62	0.39
White-breasted Nuthatch	37	0.11	0.21	17	0.83*	0.23	19	0.41	0.44	16	0.53	0.36
Brown Creeper	7	0.05	0.33	12	0.85*	0.27	-	-	-	-	-	-
Carolina Wren	-	-	-	-	-	-	10	0.02	0.09	-	-	-
Blue-gray Gnatcatcher	10	0.48	0.35	9	0.64*	0.33	-	-	-	-	-	-

Appendix E. Mean hemlock and non-hemlock basal area by forest stand

Table 1. Mean hemlock and non-hemlock basal area (in ft²/acre) measured in 2015/2016 along transects in 11 hemlock stands at Delaware Water Gap National Recreation Area.

Stand ID	Mean hemlock basal area	Mean non-hemlock basal area
365	107.50	35.71
485	105.83	31.76
657	71.58	43.33
822	50.00	54.44
1059	64.00	59.38
1191	60.50	46.41
1368	57.50	40.00
1449	71.00	59.23
1509	67.27	66.88
2037	75.56	84.44
2107	87.50	64.44