Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands

Alexis R. Grinde[1] | Melissa B. Youngquist[2] | Robert A. Slesak[3] |
Stephen R. Kolbe[1] | Josh D. Bednar[1] | Brian J. Palik[4] | Anthony W. D'Amato[5]

[1]Natural Resources Research Institute, University of Minnesota Duluth, Duluth, Minnesota, USA

[2]Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, Chicago, Illinois, USA

[3]USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA

[4]USDA Forest Service, Northern Research Station, Grand Rapids, Minnesota, USA

[5]University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, Vermont, USA

Correspondence
Alexis R. Grinde
Email: agrinde@d.umn.edu

Abstract

Black ash wetlands cover approximately 1.2 million ha of wetland forest in the western Great Lakes region, providing critical habitat for wildlife. The future of these wetlands is critically threatened by a variety of factors, including emerald ash borer (*Agrilus planipennis*; emerald ash borer [EAB]), which has been eliminating native populations of otherwise healthy ash throughout the Great Lakes region since it was discovered in 2002. To quantify the potential impacts of tree mortality from EAB on wildlife communities, we measured seasonal bird, mammal, and amphibian diversity in black ash wetlands using a dual approach: (1) documenting bird and amphibian species across 27 mature reference black ash wetlands in northern Minnesota, USA and (2) assessing how bird, mammal, and amphibian communities respond to experimental manipulations of black ash forests that emulate mortality and management strategies related to the potential impact of EAB. In total, 85 wildlife species were recorded for the entire study including 57 bird species, 5 amphibian species, and 23 mammal species. Results from the reference sites show that hydrologic regime, percentage of ash canopy cover, and understory cover were important habitat characteristics for bird and amphibian communities. Results from the experimental sites show there may be short-term increases in species richness for mammal and bird communities associated with changes in forest structure due to ash mortality; however, anticipated changes resulting from EAB-caused mortality, particularly the conversion of these sites to non-forested wetlands, will lead to significant shifts in bird and mammal community composition. Loss of ash may cause declines in forest-dependent species and increases in open-canopy and wetland-associated species. Additionally, whereas increased ponding extent and longer hydroperiods may be beneficial for some amphibian species, the loss of the forest canopy will result in an overall decrease in bird diversity and reduce forest connectivity for all species. Our results indicate the potential for significant large-scale impacts of black ash mortality on forest-associated wildlife. Management strategies that focus on establishing alternative trees species to maintain

long-term forest cover and structural complexity in these wetlands will help to maintain and conserve wildlife diversity.

INTRODUCTION

Native and invasive forest insects are important agents of disturbance and can pose a significant threat to the productivity and diversity of forest ecosystems worldwide (Allen & Humble, 2002; Dale et al., 2001; Flower & Gonzalez-Meler, 2015; Liebhold et al., 1995; Linnakoski & Forbes, 2019). The direct and indirect ecological and economic impacts associated with forest pests, such as hemlock woolly adelgid (*Adelges tsugae* [Annand, 1924]), mountain pine beetle (*Dendroctonus ponderosae* [Hopkins, 1902]), eastern larch beetle (*Dendroctonus simplex* [LeConte, 1868]), and emerald ash borer (EAB; *Agrilus planipennis*, [Fairmaire, 1888]), have received considerable attention due to the extensive tree mortality caused by ongoing outbreaks throughout North America (e.g., Kenis et al., 2009; Kolka et al., 2018; Kreutzweiser et al., 2019; Lovett et al., 2006; Saab et al., 2014; Ward & Aukema, 2019). Research on ecosystems threatened by these insects, among others, suggests that the loss of dominant tree species can affect fundamental ecological function and alter ecosystem services, including nutrient cycling, carbon sequestration, and biodiversity (Ellison et al., 2005; Liebhold et al., 2017; Lovett et al., 2006; Thompson et al., 2011; Youngquist et al., 2020).

In response to these threats, forest managers have developed and applied different techniques, both reactive and adaptive, to slow the spread of pests and sustain forest structure and function. Reactive management strategies that aim to mitigate loss of timber and promote natural regeneration, such as stand thinning and preemptive harvest of host species (i.e., harvesting prior to insect infestation), often accompany the arrival of an invasive pest species to a region (D'Amato et al., 2018; Prober et al., 2019; Six et al., 2014). However, these management actions can sometimes have larger impacts on ecological function than tree mortality caused by an invasive pest (e.g., Foster & Orwig, 2006; Kizlinski et al., 2002); this is likely to be due to the larger spatial scale and faster pace of harvests compared with pest-related mortality. For instance, preemptive logging of eastern hemlock (*Tsuga canadensis* [L.] Carriere) resulted in a greater abundance of shade-intolerant plants and a rapid increase in nitrification following logging compared with forests where

mortality was caused by the hemlock woolly adelgid (Foster & Orwig, 2006). In light of this, forest managers are increasingly turning to adaptive management strategies to proactively mitigate the impacts of pests (Ayres & Lombardero, 2018; D'Amato et al., 2018; Six et al., 2014; Waring & O'Hara, 2005). These adaptive strategies commonly involve diversification of stand composition through understory tree planting or silvicultural systems that promote the natural regeneration of minor co-occurring species (D'Amato et al., 2018). However, the long-term ecological outcomes of reactive and adaptive forest management actions, compared with pest-induced-mortality, are largely unknown (Prober et al., 2019; Six et al., 2014).

One of the main indirect effects of tree mortality, whether caused by pests or forest harvest, is on the abundance and diversity of wildlife communities (Gandhi & Herms, 2010a; Grinde et al., 2020; Tozer et al., 2010). Studies on the effects of different silvicultural regimes on forest-dependent taxa suggest that the amount of canopy trees retained is a key factor influencing community response (e.g., Grinde et al., 2020; Homyack et al., 2005; Semlitsch et al., 2009; Summerville & Crist, 2002; Tozer et al., 2010). For example, Tozer et al. (2010) demonstrated that bird communities were similar in stands harvested with group selection compared with reference stands due to the retention of canopy cover; similarly, Grinde et al. (2020) found the abundance of birds and small mammals to be higher in stands with tree retention after harvest, both aggregated and dispersed, compared with clearcut harvests. Beyond impacts on tree canopy conditions, forest management also affects the structure and composition of the understory layer, litter quality, nutrient availability, and hydrology (e.g., Gandhi & Herms, 2010a). The large body of work examining forest management impacts on wildlife provides important insight into the potential consequences of pest-related tree mortality, and both reactive and adaptive management strategies. However, as the threat of forest pests intensifies in severity and magnitude (Allen et al., 2010; Raffa et al., 2008) and the array of ecosystems that are threatened increases, there is a growing need for research to better understand the consequences of different management approaches to these novel threats on wildlife communities and overall biodiversity in forest ecosystems.

Emerald ash borer is an invasive wood-boring beetle that is native to Asia and was first detected in North America in 2002 (Cappaert et al., 2005). Since its introduction, EAB has killed millions of ash trees (*Fraxinus* spp.) in forest, riparian, and urban settings (Herms & McCullough, 2014). There is little evidence for natural resistance of ash trees to this threat, with the mortality of more than 99% of stems greater than 2.5 cm in diameter reported throughout the invasion zone (Klooster et al., 2014). All North American species of ash that EAB has encountered to date are susceptible to varying degrees, potentially leading to functional extirpation of ash in North America and resulting in devastating cultural, economic, and ecological impacts (Costanza et al., 2017; Herms & McCullough, 2014).

The range of EAB is expanding northward and westward due to warming winters and an absence of predators; the impact EAB will have on black ash (*Fraxinus nigra* [Marshall]) wetlands and associated communities in the western Great Lakes region of North America is of particular concern (Looney et al., 2015; Palik et al., 2021). These wetlands cover more than 1.2 million ha in the region and are often composed almost entirely of black ash, with few co-occurring tree species, making natural regeneration of non-black ash tree species after EAB unlikely (Looney et al., 2015, Palik et al., 2021). Furthermore, because black ash is a foundational species (*sensu* Ellison et al., 2005), loss of ash can lead to changes in natural plant communities and habitat structure, as well as direct and indirect effects on ecosystem processes, such as hydrology and nutrient cycling (Costanza et al., 2017; Kolka et al., 2018; Slesak et al., 2014; Youngquist et al., 2017). Moreover, black ash strongly influences site hydrology (Diamond et al., 2018; Slesak et al., 2014), and preemptive harvest of ash in response to EAB may lead to extended periods of saturated anoxic soil conditions and a shift to non-forested conditions (Diamond et al., 2018; Erdmann et al., 1987). Alternatively, there is the potential for use of adaptive management strategies to proactively mitigate the impacts of EAB in black ash wetlands (D'Amato et al., 2018; Kolka et al., 2018). Use of partial harvesting-based silvicultural systems (e.g., group selection or shelterwoods) can promote natural regeneration while minimizing the risk of water table rise and subsequent conversion to an alternate ecosystem state (Costanza et al., 2017; Diamond et al., 2018).

Overall, there is a general lack of research related to wildlife use of black ash forests, and significant knowledge gaps exist regarding the assessment of impacts of EAB on habitat quality, resource availability, and overall biodiversity (Flower et al., 2013; Gandhi & Herms, 2010b; Nisbet et al., 2015; Youngquist et al., 2017). However, the expected changes in ecosystem structure and function as related to EAB infestation and tree mortality are likely to impact wildlife. For example, Koeing and Liebhold et al. (2017) found that the short-term availability of EAB as a novel food source in winter months increased local populations of insectivorous birds in infested areas. However, responses to EAB are expected to differ across taxa and over time; Gandhi and Herms (2010b) hypothesized that populations of native insects that are habitat or host tree specialists are most likely to decrease in invaded forests, whereas generalist and opportunistic invertebrate species are generally expected to increase. Still, the magnitude and extent of the effects of EAB-caused mortality, particularly compared with adaptive and reactive management actions across vertebrate wildlife taxa, is unclear. Therefore, an empirical, community-wide assessment is necessary to document baseline conditions of wildlife communities and to fully understand potential implications of EAB-caused mortality and the effects of reactive and adaptive management strategies in black ash wetlands.

Here, we report findings from two related studies designed to broadly assess wildlife communities in black ash wetlands and how those communities will respond to changes in forest structure. The studies were conducted in northern Minnesota USA, which is not widely invaded by EAB but contains expansive black ash wetlands (Palik et al., 2021). For the first study, we used an observational approach across 27 mature reference black ash wetlands to gather baseline data on vertebrate communities across the broad range of black ash wetland types. For the second study, we used a replicated manipulative experiment to assess the effects of stem girdling, as a proxy for large-scale EAB mortality, reactive preemptive harvests (clear-cuts), and adaptive forest management (group selection) on wildlife community composition. We broadly hypothesized that differences in canopy characteristics such as percentage of black ash and overall canopy cover would drive differences between wildlife communities in reference sites and experimental treatments. For the experimental study, we specifically predicted that vertebrate wildlife communities would differ between control and preemptive harvest treatments due to the lack of canopy cover and subsequent changes to the understory, whereas girdled and group selection treatments would have similar wildlife communities due to similar canopy characteristics, but differ from control and preemptive harvest treatments. Our study is a comprehensive assessment of species composition across taxa intended to:

1. Document wildlife species currently using black ash wetland forests.
2. Identify environmental variables (e.g., stand and landscape characteristics) that best predict wildlife communities found in black ash wetlands.
3. Quantify differences in community response between simulated EAB mortality, and adaptive and reactive management approaches.

METHODS

Sites and study design

The study area encompassed the north central and northeastern region of Minnesota, USA. The area lies within a glacial moraine landscape where black ash wetlands occur in lowlands that grade into uplands dominated by aspen (*Populus* spp.) and pine (*Pinus* spp.). The region has a continental climate with mean annual precipitation of 700 mm, of which ~30% occurs as snowfall. The mean growing season temperature is 14.3°C, but extremes can exceed 32°C in summer and −35°C in winter. Plant communities at the sites were classified as either northern wet *Fraxinus* wetland or northern very wet *Fraxinus* wetland, based on Minnesota native plant community classification (MNDNR, 2003).

We investigated the potential impacts of EAB-caused tree mortality on wildlife using two approaches. First, we established 27 reference sites across the range of hydrogeomorphic settings in which black ash grows in northern Minnesota (Figure 1; Palik et al., 2021). These sites were monitored to establish reference conditions for wildlife communities in black ash wetlands. Second, we established wildlife research plots using a fully replicated operational-scale field experiment set in black ash wetlands on the Chippewa National Forest in northern Minnesota, USA (Figure 1; Looney et al., 2015).

Reference sites

Twenty-seven black ash wetland sites were identified across northern Minnesota that encompassed the diversity of black ash wetland types in the region. Sites were selected based on the following criteria: (1) black ash comprised at least 50% of overstory basal area (trees >10 cm diameter at breast height (DBH) [1.4 m], (2) no evidence of recent management or mortality of trees, (3) no ditches, roads, or trails present, and (4) dominated by mature trees (Palik et al., 2021). Hydrogeomorphic settings included depression sites characterized by pool-type geometry and isolated from other water bodies, lowland sites characterized by extensive wetland complexes on gently rolling terrain, and transitional sites characterized as linear transition zones between uplands and peatland bogs (Diamond et al., 2019). Stand sizes ranged from relatively small, isolated depressions (~0.5 ha) to large, flat complexes (~20 ha). Basal area of black ash overstory in these sites had a mean of 28.0 ± 7.7 m^2 ha^{-1}, comprising more than 80% of total basal area across stands. Other minor tree species in the overstory included northern white cedar (*Thuja occidentalis* L.), American elm (*Ulmus americana* L.), and quaking aspen (*Populus tremuloides* Michx.).
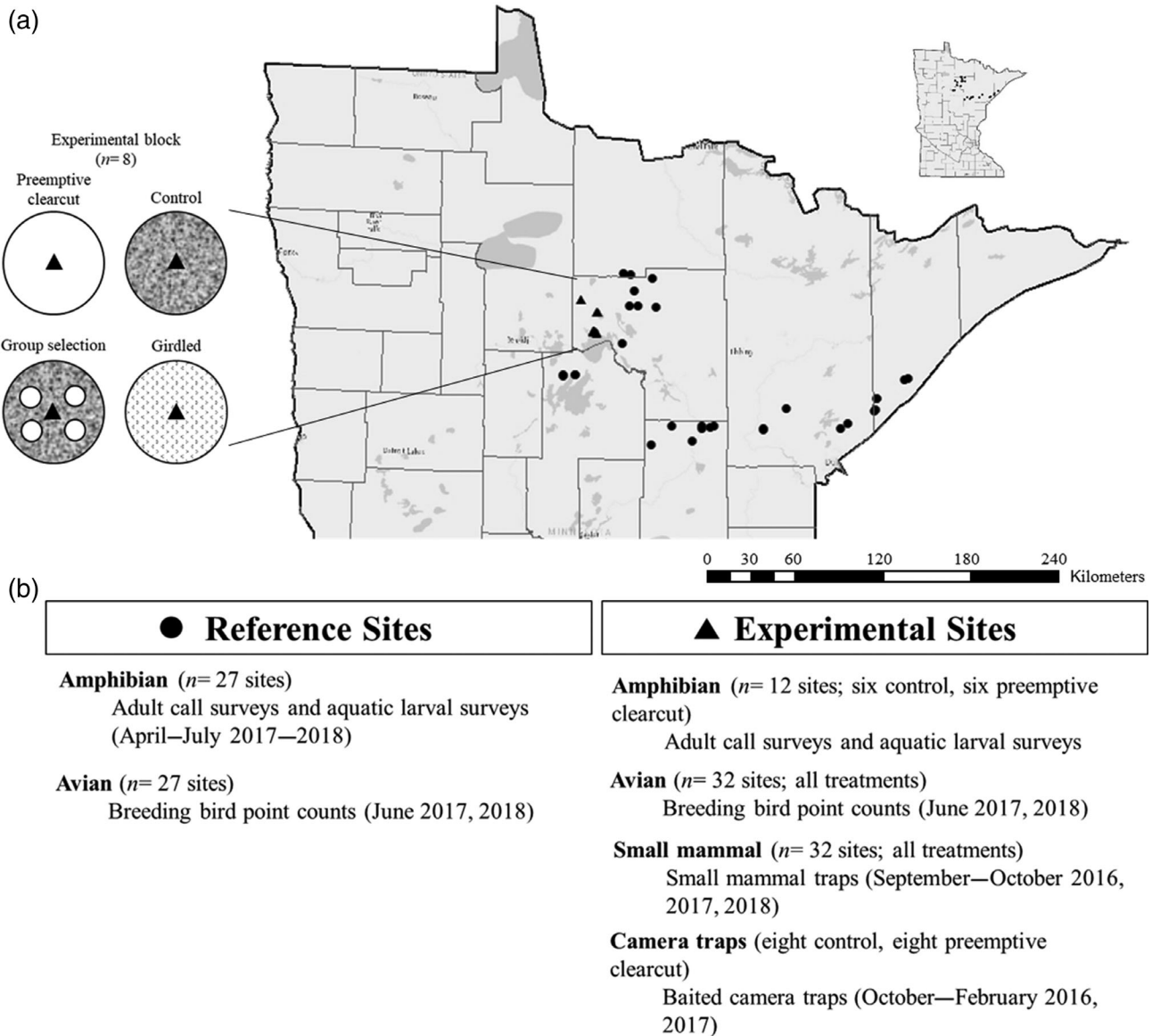
Experimental sites

The experimental study area was divided into eight blocks based on preliminary observations of native plant community (Figure 1; Slesak et al., 2014). Before treatment, basal area for trees >10.0 cm in diameter averaged 28.1 ± 4.3 m^2 ha^{-1}, and mean tree density was 631 ± 19.2 trees ha^{-1}. The predominant overstory species was black ash, which comprised 91% of basal area, with minor components of American basswood (*Tilia americana* L.), balsam fir (*Abies balsamea* L.), quaking aspen (*Populus tremuloides* Michx.), and bur oak (*Quercus macrocarpa* Michx.). Within each block, four 1.62-ha circular plots (radius = 71.8 m) were established, and one of the following treatments was randomly assigned to each one: (1) uncut forest to serve as a control, (2) girdling of all *F. nigra* stems ≥6 cm DBH to emulate EAB-caused mortality, (3) group selection of eight 0.04-ha (400 m^2) circular gaps, occupying ~20% of the area of the stand, and (4) preemptive clear-cutting involving the removal of all trees. The treatments were implemented to assess how alternative management strategies that are currently being used to mitigate the impact of EAB affected the structure and function of these wetlands. The girdled treatment simulated the dynamic processes during active EAB infestation and mortality. Trees were girdled at breast height (~1.3 m) using draw knives first in winter 2012 and again in winter 2013 to ensure complete mortality. Group selection and clear-cut treatments were implemented in late winter 2012 with a mechanized cut-to-length harvest system under frozen ground conditions. The girdle and clear-cut treatments caused a shift from tree-dominated communities to ones dominated by herbaceous and shrub species during the first 4 years following treatment (Looney et al., 2017). More information on the study sites and experimental design can be found in Slesak et al. (2014) and Looney et al. (2015).

Wildlife surveys

Bird and amphibian surveys were conducted in reference sites and experimental sites in 2017 and 2018. Small mammal trapping and large mammal surveys were conducted in only the experimental sites in 2016, 2017, and 2018.

Amphibian call and larval surveys

We conducted amphibian surveys at 27 reference sites and the experimental control ($n = 6$) and preemptive harvest plots ($n = 6$). We excluded two of the experimental blocks that did not provide adequate ponding habitat for

(a)

(b)

● **Reference Sites**	▲ **Experimental Sites**
Amphibian (*n*= 27 sites) Adult call surveys and aquatic larval surveys (April–July 2017–2018)	**Amphibian** (*n*= 12 sites; six control, six preemptive clearcut) Adult call surveys and aquatic larval surveys
Avian (*n*= 27 sites) Breeding bird point counts (June 2017, 2018)	**Avian** (*n*= 32 sites; all treatments) Breeding bird point counts (June 2017, 2018)
	Small mammal (*n*= 32 sites; all treatments) Small mammal traps (September—October 2016, 2017, 2018)
	Camera traps (eight control, eight preemptive clearcut) Baited camera traps (October—February 2016, 2017)

FIGURE 1 (a) Wildlife survey locations including reference sites (circles; $n = 27$) and experimental sites (triangles; $n = 32$ sites) located in black ash wetlands in northern Minnesota, USA. Each experimental block ($n = 8$) was composed of four treatments: Control, preemptive clear-cut harvest, girdle to emulate tree mortality from EAB, and group selection to assess the impacts of adaptive forest management. (b) Summary of wildlife surveys conducted at reference and experimental black ash sites

breeding amphibians. We used adult call survey and aquatic larval surveys to ensure the detection of anurans and salamanders, as well as to determine which anurans were actively breeding in the wetlands (Skidds et al., 2007).

Call surveys were conducted following the North American Amphibian Monitoring Program protocol (Weir & Mossman, 2005). We surveyed each site three times each year; surveys took place every 2–3 weeks starting after ice out (mid to late April) and concluded in early June. We conducted surveys between 6:00 PM and 12:00 AM on calm, rain-free nights. At each site, we listened for calling anurans for 5 min and recorded the identity and relative intensity on a scale of 0–3, such that zero indicates no individuals calling and three indicates a full chorus with all calls continuous and overlapping. At the experimental sites, we conducted call surveys in the center of each plot; at the reference sites, we selected the wettest area that seemed suitable for amphibian breeding.

We conducted larval surveys at all sites where we observed calling males and in sites with ponded areas that could serve as amphibian breeding habitat, even if no individuals were heard calling during prior call surveys. Based on breeding observations in other sites, we defined a minimum ponded area as being greater than 20 m^2 and with water depth at the deepest point being greater than 10 cm during the first week of June. Larval

surveys were conducted two times from June to July; however, four sites in 2017 and 2018 were only sampled once because of early dry-down. To obtain quantitative measurements, we used a 29-cm diameter pipe to collect standardized samples. The pipe was submerged at 5-m intervals along the widest portion of the wetland, resulting in a minimum of three samples collected for each survey. For expansive flat wetlands and floodplains, we constrained our sampling effort to 10 samples per wetland (50-m transect). We removed and counted each amphibian larvae using aquarium nets and searched each pipe sample until five consecutive net searches were empty to ensure complete assessment of the samples. Dip-nets were also used to obtain qualitative samples; we standardized the number of sweeps per site by multiplying the number of pipe samples by three (e.g., a site with five pipe samples would have 15 dip-net sweeps). We calculated density (individuals m^{-3}) from core samples and catch-per-unit-effort (CPU) for dip-net sweeps (individuals $dip-net^{-1}$). In some samples, species detection was different between the two methods; often we encountered more species via dip-netting. In these instances, we estimated density using polynomial regression to predict density from CPU based on all instances where both sample methods documented the same species (Density $= 86.7[CPU]^2 + 36.9[CPU] + 27.3$; $r^2 = 0.94$). We calculated average larval density for each species, at each site, by averaging within and then among years.

Avian point count surveys

Ten-minute point count surveys were conducted at the 27 reference sites and all of the experimental sites ($n = 32$) during the peak of the avian breeding season. Each survey consisted of one point count in the middle of the reference site or treatment plot; point counts were conducted by trained observers from ~0.5 h before to 4 h after sunrise on days with little wind (<15 km h^{-1}) and little or no precipitation. All birds heard or seen from the point count locations were recorded, along with their spatial location within the plot and estimated distance from the observer to avoid double counting birds (Niemi et al., 2016). Analyses included only birds observed within a 75-m radius to align with the size of the treatment plots and for consistency between reference and experimental datasets; data were summed over the 2 survey years.

Small mammal trap surveys

Small mammals were live trapped at the experimental plots in all four of the experimental treatments ($n = 32$), from late September through early October, using Sherman folding traps ($3 \times 3.5 \times 9''$ model LFATDG). At each plot, in total 10 traps were deployed 15 m apart in two transects that were oriented in a north–south direction. Traps were baited with peanut butter dipped in oats, a chunk of potato to serve as a water source, and cotton balls for bedding and placed near the best available microhabitat (e.g., along logs, near stumps). Small mammals were trapped in favorable weather conditions (e.g., little to no rain). Small mammal capture and handling protocols met guidelines established by the American Society of Mammalogists (Sikes et al., 2016) and were approved by the University of Minnesota Duluth Animal Care and Use Committee (protocol no. 1608-34042A). Traps were set in the late afternoon of the first day, run for two consecutive nights, and pulled the morning after (Grinde et al., 2020). Small mammals were identified to species, weighed, and marked either with a single ear tag (Model #1005-1, National Band and Tag Company) or with a black marker (shrews, meadow voles). Medium-sized mammals were identified and released without tagging or measurement. *Peromyscus* observations were combined because, whereas deer mice (*Peromyscus maniculatus*) are more common in the study area, white-footed mice (*Peromyscus leucopus*) have also been documented in the region (Jannett et al., 2007); these species cannot be reliably distinguished in the field (Tessier et al., 2004), and we present the results at the genus level (Grinde et al., 2020). Data from the 3 years were summed by plot for analysis.

Large mammal camera-trap surveys

To document the presence of medium and large mammals, 16 camera traps were deployed from December through March in the winters of 2016–2017 and 2017–2018 in the experimental control ($n = 8$) and preemptive harvest ($n = 8$) treatment sites. Similar to the amphibian surveys, we focused on these two treatments because, given limited resources, they represent the end points of the habitat gradients; we were most likely to detect differences in community among these two treatments. Camera-trap stations were baited and set to trigger based on motion detection in bursts of three with a 5-s delay between bursts (Meek et al., 2014). Species were identified by two independent observers, and unknown captures were sent to experts for species identification. Photographs were stored and identified using eMammal; project photographs can be accessed via: https://emammal.si.edu/emerald-ash-borer-infection-impacts-wildlife.

Environmental variables

Because amphibians and forest birds respond to different habitat characteristics at different spatial scales

(Bosch et al., 2004; Grinde et al., 2017), we quantified a total of 55 environmental variables at reference and experimental sites across four spatial scales to determine which variables best accounted for correlations between species and overall community composition (Appendix S1: Table S1). The four spatial scales included (1) within-stand variables, and (2) three spatial scales around the stand, which consisted of a 100-m (3.14 ha) buffer, a 500-m (78.5 ha) buffer, and a 1000-m (314.2 ha) buffer around the stands (Appendix S1: Table S1). Several datasets were used to quantify habitat characteristics of the study sites including National Land Cover Data (Homer et al., 2015), National Wetland Inventory Dataset (Kloiber et al., 2019), Minnesota Roads (MNDNR, 2012), Minnesota statewide lidar data (MnGeo, 2015), and on-the-ground vegetation surveys.

In total, 22 stand-level variables were used, including variables collected from the vegetation surveys and lidar data (Appendix S1: Table S1). We used ArcMap (v.10.4.1 ESRI, 2019) to map the stand boundaries and calculate area (ha). Percentage of canopy cover and average DBH of ash was also collected by wildlife survey crews. We calculated a wetness index (0–12), which was a combination of duration of hydroperiod (permanent, intermittent, seasonal, or saturated) and extent of ponded area within the stand (>80% with continuous ponding, significant area of the stand ponded in non-interconnected puddles, or single small pool). We used lidar data to calculate 10 variables for canopy structure of reference sites.

Lidar raster layers were created using Fusion software (McGaughey, 2017) from statewide data collected in spring 2011 and 2012. Canopy height model rasters were created at 2-m resolution, whereas other metrics were created at 20-m resolution. The canopy height model was used to create binary canopy products using Map Algebra (Spatial Analyst) in ArcGIS (v.10.4.1; please refer to Appendix S1: Section S1 for lidar methods). We calculated the proportion of cover type classes in the 100-, 500-, and 1000-m buffers, including eight landscape variables from the National Land Cover Data (developed, deciduous forest, evergreen forest, mixed forest, scrub-shrub, woody wetlands, emergent wetlands, and roads) and the percentage of wetlands in each buffer from the National Wetland Inventory Dataset (Appendix S1: Table S1). The percentage of open water, grass, and pasture were calculated at the 500 and 1000 m scales only (Appendix S1: Table S1).

Data analysis

Analysis of reference sites

We analyzed wildlife communities in all black ash sites, combining reference sites and control sites in the experimental study. We excluded two experimental control sites that did not have consistent vegetation data, resulting in a total of 33 sites. For all analyses, we analyzed bird and amphibian communities separately.

Biodiversity metrics

We used generalized linear mixed models (GLMM) from the *lme4* R package (Bates et al., 2015) to assess the characteristics of the black ash wetlands that influenced wildlife biodiversity metrics. Total abundance, Shannon–Wiener diversity index, and species richness were calculated for breeding birds; however, species richness was the only biodiversity metric used for amphibian communities because total abundance data were not collected. Preliminary analyses showed that including year as a covariate did not improve models; therefore, biodiversity metrics were calculated by combining data from the 2 survey years for both taxa. We included stand-level characteristics that could influence breeding bird and amphibian communities in the reference sites. Predictor variables included wetness index, site size (ha), canopy height, canopy cover, percentage of black ash in the canopy (based on crown area), average DBH of ash trees, and percentage of understory cover. We used an information-theoretic approach to assess model performance using AIC_c and combined significant predictors to build final models (Burnham et al., 2011). Shannon–Wiener diversity was modeled using a gamma distribution, and species richness and total abundance were modeled using a Poisson distribution. Study site was used as a random effect in all models to account for variation among sites; the final model(s) were compared with null models (i.e., no fixed effects) to test for model significance (Harrison et al., 2018).

Community composition analysis

We conducted two separate community composition analyses for birds and amphibians. The first examined differences among sites and species correlations; the second tested which environmental factors predicted community composition. For birds, we analyzed total abundance. For amphibians, we analyzed two datasets: presence/absence of our combined survey efforts (call and larval) and tadpole density from larval surveys only. The presence/absence dataset maximized the number of sites we analyzed and included resident and non-resident individuals; the larval surveys show which species were resident breeders. For all datasets, we combined survey years and removed rare species that were observed in fewer than two sites (please refer to Appendix S1: Table S2 for full species list). For amphibians, we also excluded sites with no species present, as these sites were uninformative for community composition analysis. Therefore, we analyzed bird abundance from 33 sites (27 reference, 6 control), amphibian presence/absence from 20 sites (18 reference,

2 control), and amphibian larval density from 12 sites (11 reference, 1 control).

We analyzed differences in species composition among black ash sites as well as interspecies correlations using latent variable joint species distribution modeling (JSDM). In JSDMs, variance and covariance in and among species responses across sampled sites are explicitly modeled and accounted for. Variance and covariance among species can stem from direct biotic interactions (e.g., competition or facilitation) as well as from effects of unmeasured characteristics of the sites (Ovaskainen et al., 2017). Explicit modeling of this variance–covariance addresses potential noise and bias that are introduced by non-independence in species responses (Clark et al., 2014) and handles species-specific extra (residual) variation among sites (overdispersion). We used a latent variable model (LVM) approach, which related observed variables to a set of latent variables and introduced unobserved predictors to account for correlations among taxa. These models are analogous to a model-based ordination and can be interpreted similarly to other ordination analyses (e.g., NMDS; Warton et al., 2015). We used the package *boral* (Hui, 2016; R Development Core Team, 2017) to fit separate LVM for birds and amphibians. For all models, we set the number of latent variables to 'two' and used an 'exponential' spatial correlation structure to account for spatial covariance in community composition. We assumed a priori that sites that were closer together were more likely to have similar species assemblages. For abundance data (birds and larval amphibians) we used a negative binomial distribution, and for presence/absence data we used a binomial distribution. We then created a biplot of means and plotted the significant species correlations to visualize the correlations among species without any specified environmental factors.

Next, we used multivariate generalized linear models (*mvabund* package) to test for effects of environment on community composition and to fit a separate univariate GLM to each species. This approach accounted for the mean–variance relationship of count data and allowed for formal statistical tests of responses to environmental variables at the species-specific and community levels (Wang et al., 2012). Because of the large number of environmental variables ($n = 55$), we performed preliminary data exploration on each response (bird abundance, amphibian presence/absence, amphibian larval density) to select the final candidate variables for our models. For each spatial scale (stand, 100-, 500-, and 1000-m buffer), we first identified and excluded environmental variables that were collinear using Spearman's rank ($r_s > 0.75$). Then, we used model averaging for multivariate models using the *mglmn* package (Katabuchi & Nakamura, 2020) to determine which variables were the most important for predicting community composition based on the sum of AIC$_c$ across all models that included the given variable (Burnham & Anderson, 2002). Finally, we tested again for collinearity among this subset of variables to create a final set of environmental variables. When the same land cover type was a candidate variable across multiple spatial scales, we chose the 500-m scale. Multivariate GLM models were compared with a null model to determine overall model significance using likelihood ratio tests. If the initial multiscale model was not significant, we used backward elimination to drop one variable based on minimizing AIC.

For bird abundance, the final model included 10 environmental variables, amphibian presence/absence included nine variables, and amphibian larval density included eight variables (Appendix S1: Table S1). We used ANOVA to test for global model and variable significance. Likelihood ratio tests (LRT) and p-values, adjusted for multiple comparison using a step-down resampling procedure (implemented within the *mvabund* package), were also calculated for individual species to test for their response to environmental variables.

Analysis of experimental sites

We tested for differences in biodiversity and community composition among all experimental treatments ($n = 32$). We combined data across years and analyzed amphibians, birds, small mammals, and large mammal data separately. Because amphibians were only documented in a few sites and there was high variance in the large mammal data, we were unable to test for differences in community composition between control and preemptive harvest treatments.

Biodiversity metrics

Similar to the analysis of the reference sites, GLMMs were used to assess the effect of treatment type (control, preemptive harvest, girdled, and group selection) on total abundance, Shannon–Wiener diversity index, and species richness for breeding bird and small mammal communities in the experimental sites. Species richness was the only community metric used for amphibian and large mammal data because observations of amphibians were uncommon, and assessing abundance data via camera surveys was not possible. The models included treatment type as a fixed effect to assess differences in biodiversity metrics as related to experimental treatment, and block was used as a random effect in all models to account for variation among treatment blocks. Shannon–Wiener diversity was modeled using a gamma distribution, and species richness and total abundance were modeled using a Poisson distribution. For each biodiversity metric, the treatment effects model was compared with null models (i.e., no fixed effects) to test for model significance (Harrison et al., 2018). For the treatment model being

significant, pairwise comparison with Tukey's post-hoc adjustments using the *emmeans* R package (Lenth et al., 2018) were applied to assess differences between treatments (Yandell, 1997; Zuur et al., 2009).

Community composition analysis

We used the *boral* (Hui, 2016; R Development Core Team, 2017) package, implementing the same methods described above to develop a latent variable JSDM. Total abundance was used as the response variable for bird models, and we used a Poisson distribution. Small mammal data were summarized as presence/absence, and a binomial distribution was used. We used multivariate analysis of variance (MANOVA) to test for differences in community composition among treatments in which our multivariate responses were the latent variable values for each site. We then used Tukey's post-hoc test to assess differences among treatments along each univariate latent variable.

RESULTS

Amphibians

Biodiversity metrics at reference sites

In total, four frog species and one salamander species were detected in the reference sites during the 2017 and 2018 breeding seasons. All frog species identified in our study sites—Wood Frog (*Lithobates sylvaticus* [LeConte, 1825]), Spring Peeper (*Pseudacris crucifer* [Wied-Neuwied, 1838]), Boreal Chorus Frog (*Pseudacris maculata* [Agassiz, 1850]), and Gray Tree Frog (*Dryophytes versicolor* [LeConte, 1825])—were detected during both the call and larval surveys, whereas Blue-spotted Salamander (*Ambystoma laterale* Hallowell 1856) were detected only during larval sampling. Amphibians were detected in 18 reference sites, but larvae were only detected in 11 reference sites. A summary of all species detected is provided in Appendix S1: Table S2. The best performing model for predicting amphibian species richness model showed that richness was positively associated with wetter habitats (coef. est. = 0.49, SE = 0.18), and the model was significantly different from the null model ($\chi^2 = 7.9$, $df = 1$, $p < 0.01$; Appendix S1: Table S3).

Community composition at reference sites

The LVM model for amphibian presence/absence suggests a minor separation in community structure between sites with *Pseudacris* species (Boreal Chorus Frog and Spring Peeper) and those without (Figure 2a,b); there was significant residual correlation between Spring Peeper and Boreal Chorus Frog, but not between Spring Peeper and Wood Frog, Gray Tree Frog, or Blue-spotted Salamander (Appendix S1: Figure S1). Similarly, the presence of Wood Frog, Blue-spotted Salamander, and Gray Tree Frog were significantly correlated; Wood frogs and Blue-spotted Salamanders seemed to share the same environmental space and were frequently found in the same sites (Figure 2a,b). When looking at residual correlations among species larval density, there was a strong positive correlation between *Pseudacris* species and, separately, between Wood Frog and Blue-spotted Salamander (Figure 2b, Appendix S1: Figure S1).

The final multivariate model for the entire potential amphibian community (presence/absence) indicated that the percentage of woody wetland at 500 m was significant in the final model; and the final model was significant compared with the null (Dev = 38, $df_{res} = 10$, $p = 0.02$; Appendix S1: Table S4; Figure 2a). For individual amphibian species, the only significant association was percentage of woody wetland at 500 m being negatively correlated with Gray Tree Frog presence (Dev = 9, $p < 0.01$, coef. est. = −0.91).

The final model for predicting amphibian breeding communities (larval density) indicated that the percentage of canopy cover, proportion canopy cover above 2 m, percentage of shrub at 500 m, and percentage of woody wetland at 500 m were all significant variables; the final model was significant when compared with the null (Dev = 198, $df_{res} = 3$, $p = 0.01$; Figure 2b; Appendix S1: Table S4). When looking at individual species, Wood Frog tadpole density was positively associated with proportion canopy cover above 2 m (Dev = 15, $p = 0.02$, coef. est. = 59), percentage of shrub cover (Dev = 22, $p = 0.02$, coef. est. = 0.12), and percentage of woody wetland at 500 m (Dev = 19, $p = 0.02$, coef. est. = 0.05); Spring Peeper tadpole density was positively associated with the proportion canopy cover above 2 m (Dev = 24, $p = 0.01$, coef. est. = 40); Boreal Chorus Frog tadpole density was positively associated with the proportion of canopy cover above 2 m (Dev = 29, $p = 0.01$, coef. est. = 36); and Blue-spotted Salamander larval density was negatively associated with percentage of canopy cover (Dev = 12, $p = 0.03$, coef. est. = −0.06).

Biodiversity metrics at experimental sites

Three frog species (Wood Frog, Spring Peeper, Boreal Chorus Frog) and one salamander species (Blue-spotted Salamander) were detected at the experimental sites during the 2017 and 2018 breeding seasons. At least one species was detected in 6 of 12 sites (4 preemptive harvest, 2 control); however, larval amphibians were only detected in three sites (2 preemptive harvest, 1 control; Table 1). Because of the small sample size, we only report
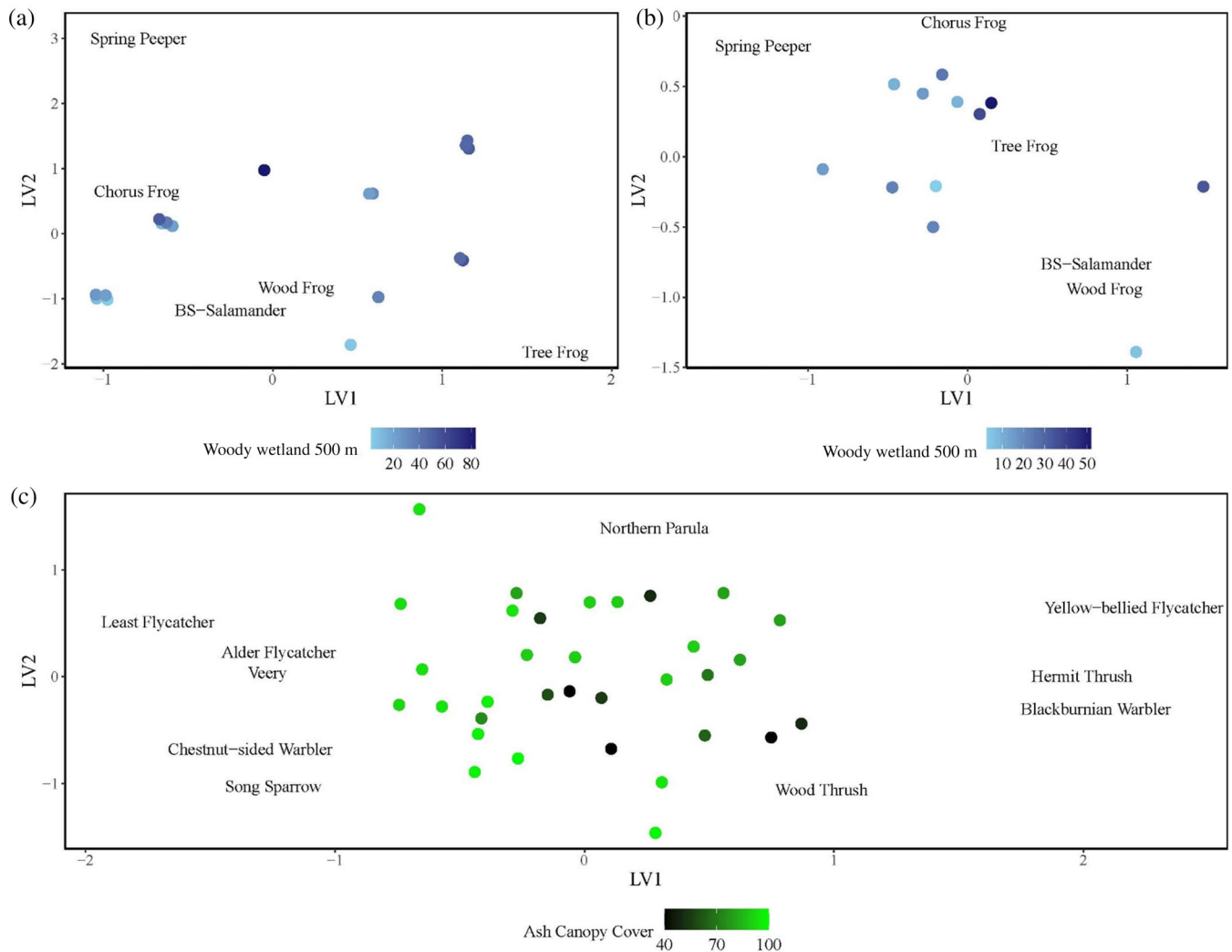
FIGURE 2 Results of amphibian and bird Joint Species Distribution Models for reference and control experimental sites. (a) Amphibian presence/absence unconstrained ordination. (b) Amphibian larval density unconstrained ordination. (c) Bird abundance unconstrained ordination. Ordination plots show the mean latent variable (LV) coefficient for each site (dot) and species (labeled); sites and species that are close together indicate more similar community composition (site) and habitat preferences (species). The top 10 indicator species only are labeled for the bird ordination plot (c). Site color indicates the percentage of woody wetland within a 500-m buffer for amphibian plots (a, b) and the percentage of ash canopy cover within a stand for bird community plot (c)

statistics on species richness based on presence/absence data. A summary of all species detected is provided in Appendix S1: Table S2. Results of the amphibian species richness model from the experimental sites was not significantly different from the null model ($\chi^2 = 0.27$, $df = 1$, $p = 0.60$; Appendix S1: Table S3).

Birds

Biodiversity metrics at reference sites

In total, 46 bird species and 485 individuals were detected at the reference sites in the 2017 and 2018 breeding seasons. The most common bird species were Red-eyed

Vireo (*Vireo olivaceus* [Linnaeus 1766]), Ovenbird (*Seiurus aurocapilla* [Linnaeus, 1766]), and Veery (*Catharus fuscescens* [Stephens, 1817]). A summary of species detections is provided in Appendix S1: Table S2. Results of the bird biodiversity metric analysis in the reference sites showed that the best model for predicting bird abundance was significantly different from the null model ($\chi^2 = 10.2$, $df = 1$, $p < 0.01$) and included understory cover index (proportion of lidar returns <2 m above ground; coef. est. $= 0.13$, SE $= 0.04$), which was positively associated with total bird abundance (Appendix S1: Table S3). Understory cover index was also positively associated with bird species richness (coef. est. $= 0.11$, SE $= 0.53$); the richness model was significant compared with the null model ($\chi^2 = 3.9$, $df = 1$, $p = 0.05$; Appendix S1: Table S3). Bird species

Shannon–Wiener diversity models for the reference sites had convergence issues, therefore model output is not presented.

Community composition at reference sites

The results of the bird community composition models indicated that Alder Flycatcher (*Empidonax alnorum* Brewster, 1895), Blackburnian Warbler (*Dendroica fusca* [Statius Muller 1776]), Black-capped Chickadee (*Poecile atricapillus* [Linnaeus, 1766]), Blue Jay (*Cyanocitta cristata* [Linnaeus, 1758]), Least Flycatcher (*Empidonax minimus* [W. M Baird & S. F. Baird, 1843]), Veery, Wood Thrush (*Hylocichla mustelina* [Gmelin, 1789]), White-throated Sparrow (*Zonotrichia albicollis* [J. F. Gmelin, 1789]), and Yellow-bellied Sapsuckers (*Sphyracpicus varius* [Linnaeus, 1766]) showed evidence of residual correlations (Appendix S1: Figure S1). In general, the pattern for correlation is related to species that breed in young and/or shrubby forests versus mature forests (Figure 2c).

The final multivariate model for the entire breeding bird community (abundance) included 10 environmental variables; the model was significant when compared with the null (Dev = 720, df_{res} = 22, $p < 0.01$; Appendix S1: Table S4). Significant variables in the final model were average canopy height, percentage of black ash cover, percentage of shrub cover at 100 m, percentage of road at 500 m, and percentage of evergreen forest at 1000 m (Figure 2c; Appendix S1: Table S4). After accounting for multiple comparisons, only four bird species had significant associations with two environmental variables: percentage of cover of black ash and percentage of canopy cover. Northern Waterthrush was positively associated with the percentage of black ash cover (Dev = 16, $p = 0.02$, coef. est. = 1.63), whereas Hermit Thrush was negatively associated with black ash cover (Dev = 15, $p = 0.02$, coef. est. = −0.48). Percentage of canopy cover was also important for two species; Red-breasted

Nuthatch was positively associated with canopy cover (Dev = 13, $p = 0.03$, coef. est. = 0.75), whereas American Robin (Dev = 12, $p = 0.04$, coef. est. = −0.48) was negatively associated.

Biodiversity metrics at experimental sites

In total, 49 bird species and 630 individuals were detected at the experimental sites in the 2017 and 2018 breeding seasons. The most common bird species were Common Yellowthroat (*Geothlypis trichas* [Linnaeus, 1766]), Red-eyed Vireo, and Chestnut-sided Warbler (*Setophaga pensylvanica* [Linnaeus, 1766]). For the bird community, the treatment model was significantly better compared with the null models for predicting total abundance ($\chi^2 = 16.1$, $df = 3$, $p < 0.01$; Appendix S1: Table S3), species diversity ($\chi^2 = 14.1$, $df = 3$, $p < 0.01$; Appendix S1: Table S3), and species richness ($\chi^2 = 13.5$, $df = 3$, $p < 0.01$; Appendix S1: Table S3). Total abundance, diversity, and richness showed similar patterns among treatments, where responses were generally greatest in the girdled treatment followed in descending order by the group, preemptive harvest, and control treatments (Figure 3). Pairwise comparisons of the bird community metrics indicated that the girdled treatment had significantly greater abundance, diversity, and richness compared with the control treatments (Figure 3; Appendix S1: Table S5). Similarly, the girdled treatments had greater abundance and diversity compared with the preemptive harvest treatments (Figure 3; Appendix S1: Table S5). The group selection treatment had significantly greater diversity compared with the control treatment only, and there was no difference in abundance, diversity, or richness between the girdle and group selection treatments (Figure 3; Appendix S1: Table S5). Similarly, there was no difference between the control and preemptive harvest treatments for any of the response variables (Figure 3; Appendix S1: Table S5).

Community composition at experimental sites

Several bird species showed evidence of residual correlations; in general, bird species that breed in upland forest habitats (e.g., Blue Jay) were negatively associated with species that breed in open marsh habitats (e.g., Common Yellowthroat; Appendix S1: Figure S2). We found that treatment had a significant effect on community composition (Pillai's Trace = 0.56, $F = 3.64$, $df = 3$, 56, $p < 0.01$). The first latent variable described variation in community among treatment type. Post-hoc Tukey's test revealed that the bird community in control plots was different from communities in preemptive harvest and girdle treatments (adjusted $p < 0.01$) but not

TABLE 1 Average amphibian larval density (ind. m^{-3}) in three of the experimental plots

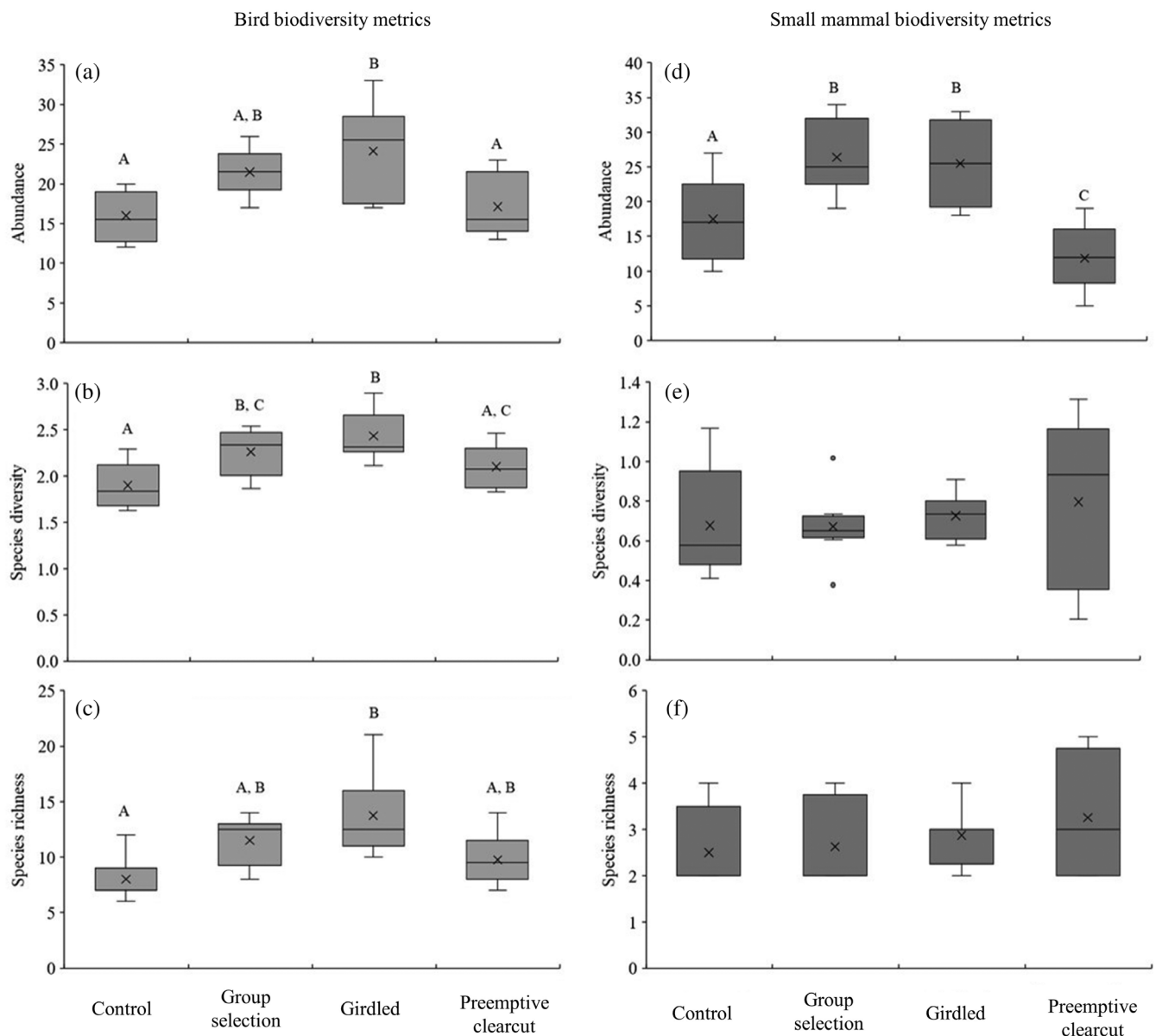| Species	Experimental treatment		
	Preemptive clear cut	Preemptive clear cut	Control
Wood Frog	135.7	29.5	513.6
Spring Peeper	298.1	24.6	240.9
Boreal Chorus Frog	112.5	23.8	34.0
Blue-spotted Salamander	0.0	0.0	80.2

different from the group selection (adjusted $p = 0.06$); group selection, girdle, and preemptive harvest treatments had communities that were similar (adjusted $p = 0.07$; Figure 4a).

Small mammals

Biodiversity metrics at experimental sites

In total, 652 individuals representing 10 species were caught in the experimental treatment areas during a sample effort of 1920 trap nights and 960 trap days (2880 combined trap period). Red-backed vole (*Myodes gapperi* [Vigors, 1830]) accounted for 66% of the total captures, followed by *Peromyscus* spp. (27%), meadow vole (*Microtus pennsylvanicus* [Ord, 1815]; 4%), northern short-tailed shrew (*Blarina brevicauda* [Say, 1823]; 1%), and short-tailed weasel (*Mustela ermine* Linnaeus, 1758; 1%). Four additional species represented 1% of the total captures: masked shrew (*Sorex cinereus* [Kerr 1792]), flying squirrel (*Glaucomys sabrinus* [Shaw 1801]), water shrew (*Sorex palustris* [Richardson 1828]), and meadow jumping mouse (*Zapus hudsonius* [Zimmermann 1780]).

FIGURE 3 Effects of experimental treatments on bird (a–c) and small mammal biodiversity metrics (d–f). Metrics included total abundance (a, d), Shannon–Wiener index of diversity (b, e), and species richness (c, f) based on the results of generalized linear mixed effects models with Tukey's post-hoc adjustments. Significant pairwise comparisons ($p < 0.05$) are indicated by different letters; means were back-transformed based on the link function; error bars represent 95% confidence intervals

A summary of species detections is provided in Appendix S1: Table S2.

Results of the small mammal biodiversity metric models indicated that treatment was better at predicting total small mammal abundance compared with the null model ($\chi^2 = 28.3$, $df = 3$, $p < 0.01$), but not for species diversity ($\chi^2 = 2.24$, $df = 3$, $p = 0.52$) and species richness ($\chi^2 = 1.01$, $df = 3$, $p = 0.79$; Appendix S1: Table S3; Figure 3). The pairwise comparisons between treatments in the small mammal total abundance model indicated that total abundance in the girdled and group treatments was greater than either the control or preemptive harvest treatments (Figure 3; Appendix S1: Table S5). In addition, the control treatment had significantly greater abundance compared with the preemptive harvest treatment (Figure 3; Appendix S1: Table S5).

Community composition at experimental sites

The only significant residual correlation for small mammals was a positive association between short-tailed weasel and water shrew; both species were largely found in preemptive harvest (open and wet) sites (Appendix S1: Figure S2). Treatment also had a significant effect on community composition (Pillai's Trace = 0.70, $F = 5.02$, $df = 3$, 56, $p < 0.01$; Figure 4b). The first latent variable described variation in community among treatment type, and post-hoc Tukey's test revealed that the preemptive harvest treatment had a community that was significantly different from all other treatments (adjusted $p < 0.01$; Figure 4b); control, group selection, and girdle treatments all had similar small mammal communities (adjusted $p = 0.56$; Figure 4b).

Large mammals

Throughout the survey periods in 2016 and 2017, 737 photographs were taken; of these, 424 had animals, 81 had captures that were not identifiable to species, and 232 had no animals recorded. Seven bird species were captured on the cameras, including Blue Jay, Common Raven (*Corvus corax* [Linnaeus 1758]), Canada Jay
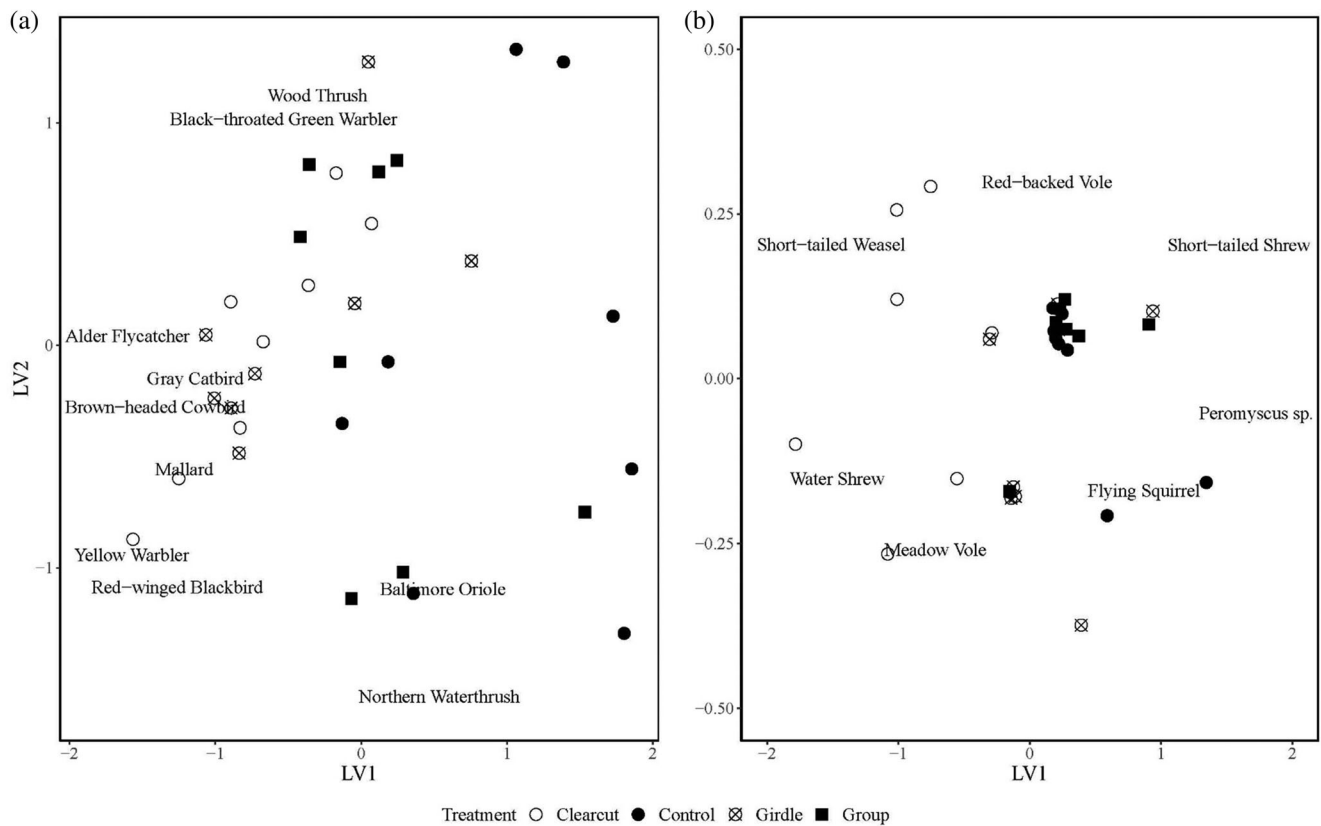
FIGURE 4 Results of bird and small mammal JSDM latent variable models for experimental sites. (a) Bird species abundance unconstrained ordination, and (b) small mammal presence/absence unconstrained ordination. Ordination plots show mean latent variable (LV) coefficient for each site (dot) and species (labeled); sites and species that are close together indicate more similar community composition (site) and habitat preferences (species). Top 10 indicator species only are labeled for bird plot (a). Site shape indicates experimental treatment
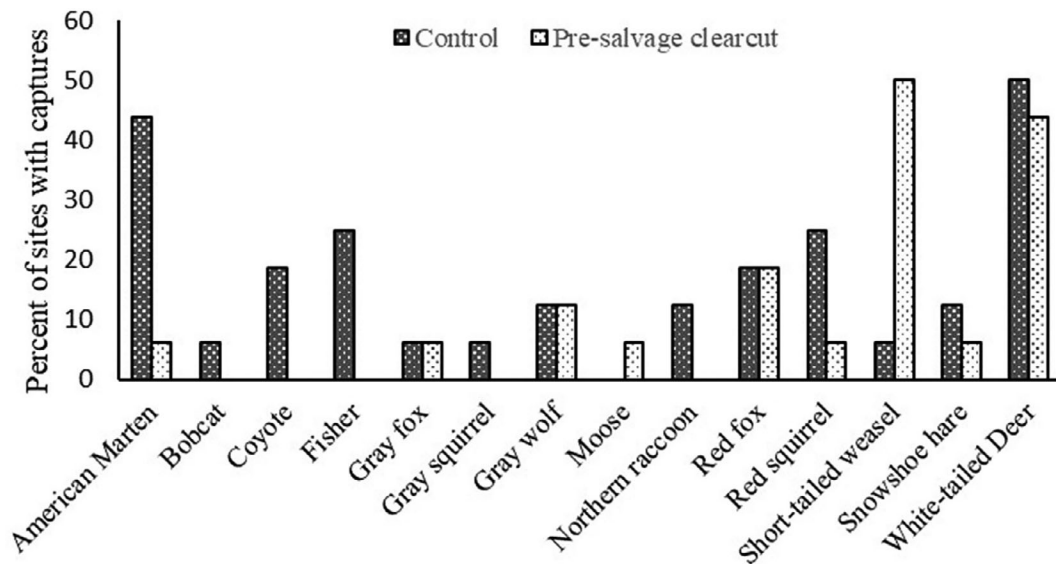
FIGURE 5 Percentage of sites with mammal species detected at camera traps in black ash control and preemptive harvest treatment sites from November to February, 2016–2017 and 2017–2018

(*Perisoreus canadensis* [Linnaeus 1766]), and Ruffed Grouse (*Bonasa umbellus* [Linnaeus 1766]; Appendix S1: Table S2). In total, 14 mammal species were identified on the camera traps; the most commonly identified mammal species were white-tailed deer (*Odocoileus virginianus* [Zimmermann 1780]), American marten (*Martes americana* [Turton 1806]), and short-tailed weasel (Appendix S1: Table S2). Results of the species richness model indicated that there was no significant difference between control and preemptive harvest treatments ($\chi^2 = 3.08$, $df = 1$, $p = 0.08$; Appendix S1: Table S3). However, several forest-dependent species were more likely to be captured in control sites including American marten, red squirrel, coyotes, and fisher (Figure 5).

DISCUSSION

EAB has infested and killed ash species (*Fraxinus* L.) in much of eastern North America, but it has yet to reach the vast black ash wetlands in northern Minnesota, USA. In these forested wetlands, black ash is the dominant overstory species and has a foundational role in regulating ecosystem function (Kolka et al., 2018; Youngquist et al., 2017). Previous assessments at our experimental sites indicated that loss of black ash causes a reduction in evapotranspiration and a rise in the water table, which alters the hydrologic regime and promotes prolonged inundated conditions (Diamond et al., 2018; Slesak et al., 2014). These changes in hydrology were associated with shifts in vegetation community composition that favored more graminoid and non-tree wetland obligate

species (Looney et al., 2017). Given these outcomes, adaptation strategies that include active planting to diversify tree composition and maintain a forested condition are needed (Looney et al., 2015; Palik et al., 2021). However, an understanding of the impacts of these approaches, as well as that of EAB, on vertebrate wildlife communities and habitat is critical for making science-based decisions in the face of this novel threat. This study is one of the most comprehensive to date that documents the extent to which black ash wetlands provide a habitat for a diverse assemblage of amphibians, birds, and mammals. Our findings support our hypothesis that canopy cover and structure is an important predictor of vertebrate communities in black ash wetlands. Furthermore, changes in ash canopy that are associated with tree mortality will probably result in a turnover of wildlife communities; however, the degree to which vertebrate communities change can be mitigated by adaptive management.

Amphibian diversity was highest in black ash forests with large ponded areas and longer hydroperiods, greater structure in the understory, and a relatively open canopy. Hydroperiod is known to be a key determinant of amphibian community assemblage (e.g., Batzer & Sharitz, 2014), and open canopies around ponds are often beneficial for larval growth (Ouellet et al., 2009; Semlitsch et al., 2009; Skelly et al., 2014; Werner & Glennemeier, 1999) and support higher species richness (Skelly et al., 2014). Given that most wetlands in our study dried in early summer, amphibian species were confined to those that breed early in the year, have short larval periods, and can tolerant high canopy cover. EAB-related mortality of black ash or small-scale preemptive

harvest will cause reductions in canopy cover and increase ponding duration (Slesak et al., 2014), which could be beneficial for most amphibian species in the short-term by creating better breeding and larval habitat. However, breeding behavior is just one factor affecting population persistence. The species we documented in black ash wetlands—Boreal Chorus Frog, Spring Peeper, Gray Tree Frog, Wood Frog, and Blue-spotted Salamander—depend on intact forest for their non-breeding habitat; the loss of black ash forest could have negative long-term consequences. In their review, Semlitsch et al. (2009) concluded that, although forest harvesting can have a net positive effect on breeding activity (opening of wetland canopy), there is a net negative effect on adult and juvenile growth and survival (clear-cutting creates inhospitable environments).

For avian communities, our study clearly indicated that the amount of black ash and its influence on canopy characteristics and understory cover was the most important predictor for community composition. Black ash forests tend to be unevenly aged and contain trees across all size and age classes, and natural canopy disturbance regimes are dominated by the creation of small gaps associated with wind and flooding events that result in patchy canopy cover and a well developed understory layer (D'Amato et al., 2018; Looney et al., 2016; Palik et al., 2011; Tardif & Bergeron, 1999). The bird community composition documented in the reference sites reflected the characteristic structural diversity in the canopy and understory; bird communities were a unique combination of upland-associated species (e.g., American Redstart, Rose-breasted Grosbeak) and wetland-associated species (e.g., Common Yellowthroat, Northern Parula) along with species associated with mature forest (e.g., Ovenbird, Winter Wren) and young forests (e.g., Veery, Chestnut-sided Warbler). Mature, unevenly aged, and structurally diverse stands often support higher avian richness and abundance compared with managed forests (Niemi & Hanowski, 1984; Zlonis & Niemi, 2014). Compared with managed, evenly aged forests that are more typical across the region, unmanaged black ash wetlands may provide unique microhabitats that are beneficial for breeding birds by providing protection from predators, increased foraging opportunities, potential nest sites, and suitable singing perches that support high species diversity (Fontúrbel et al., 2021; Sitters et al., 2016). Our survey results provide fundamental information for developing management guidelines that will improve and restore habitat conditions for the persistence of avian and amphibian diversity in black ash wetlands after EAB-related mortality of black ash.

Results from our experiment further point to specific forest management actions that will optimize diversity. Similar to other studies on the effects of silviculture on bird and small mammal communities, we showed a shift in community composition between control and preemptive harvest plots from forest-dependent species to species associated with open areas and wetlands (Degrassi, 2018; Grinde et al., 2020; Saab et al., 2014). Although we did not detect a change in species assemblage of amphibians, we documented amphibian breeding activity more often in preemptive harvest plots, as predicted from amphibian preferences for open-canopy wetlands (e.g., Semlitsch et al., 2009). Abundance and diversity of birds and mammals were highest in the group selection and girdled treatment; this aligns with Degrassi (2018), who also showed a similar increase in small mammal diversity in gridled treatment sites used to simulate hemlock woolly adelgid mortality. Our observed pattern of higher diversity is predicted by diversity-disturbance models (e.g., Haber et al., 2020; MacArthur & MacArthur, 1961; Niemi & Hanowski, 1984; Tews et al., 2004) and suggests that there may be short-term benefits to vertebrate species following black ash mortality due to alterations in structure such as standing dead snags (Perry et al., 2018). Importantly, these results showed conclusively that adaptive management techniques can maintain vertebrate communities and offer a viable option of mitigating EAB-related impacts. Encouragingly, other studies in different types of ecosystems have also found limited impacts of group selection on amphibians, birds, and small mammals over the short and long terms (Campbell et al., 2007; Gitzen & West, 2002; Hollie et al., 2020; Kellner et al., 2019; Tozer et al., 2010).

Finally, if large expanses of black ash wetlands transition to more open water marsh-like conditions as has been predicted (e.g., Diamond et al., 2018), vertebrate communities are likely to be affected in ways beyond what is documented in this study, which largely focused on local breeding activity (amphibians and birds). Our camera-trap data points to differences in habitat use and movement by medium and large mammals, even in our relatively small experimental plots. Cameras documented fewer species and fewer detections in the preemptive clear-cut harvest areas compared with control areas; these differences in habitat use were particularly pronounced for forest-dependent species such as American marten and fisher. These results align with other studies that have demonstrated forest-associated vertebrates, across all taxa, actively avoid dispersing through open areas (e.g., Day et al., 2020; Potvin et al., 2000; Todd et al., 2009); therefore EAB infestation has the potential to impact forest connectivity and could exacerbate habitat loss for forest-dependent species.

CONCLUSION

Our results provide strong evidence that changes in black ash canopy cover, hydroperiod, and understory structure

that could occur with the invasion of EAB will fundamentally alter wildlife communities in these forested wetlands and point toward clear management priorities and strategies. First, prioritizing adaptive management to large black ash wetland complexes in regions where the proportion of forest in the landscape matrix (not open or developed) is high will be beneficial for wildlife. Preserving black ash wetlands with long hydroperiods may be particularly important for amphibians. Second, our study demonstrates that group selection is a viable adaptive management solution that maintains bird and small mammal communities that are similar to communities found in mature, undisturbed black ash forests. Group selection may also preserve landscape connectivity over the long term (e.g., Bigelow & Parks, 2010; Kuuluvainen et al., 2021). Based on the findings of this and other studies (e.g., D'Amato et al., 2018), adaptive management strategies that rely on partial harvesting combined with planting replacement tree species to maintain forest cover and promote structural complexity will help to maintain wildlife diversity. Future studies of the landscape-level impacts following the loss of black ash wetlands need to be conducted to guide management and policy designed to address the threat of EAB. More specifically, monitoring or post hoc assessments of the outcomes of reactive and adaptive practices are essential to understanding the short-term and long-term effects of management actions. Given the increasing and largely uncontrolled threat that forest ecosystems face from invasive species, our results for black ash wetlands, and the resultant management and policy guidelines they can generate, can serve as models to guide policy and adaptive management more broadly.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Robert A. Slesak, Anthony W. D'Amato, and Brian J. Palik conceived and established the study design. Alexis R. Grinde and Melissa B. Youngquist designed the wildlife survey methods. Alexis R. Grinde, Melissa B. Youngquist, Josh D. Bednar, and Stephen R. Kolbe conducted the investigation and Alexis R. Grinde and Melissa B. Youngquist analyzed the data. Alexis R. Grinde, Melissa B. Youngquist, Robert A. Slesak, and Stephen R. Kolbe wrote the manuscript, and all other authors provided editorial advice and valuable insight. Alexis R. Grinde, Robert A. Slesak, Anthony W. D'Amato, and Brian J. Palik were involved with funding acquisition.

DATA AVAILABILITY STATEMENT

ORCID

Alexis R. Grinde https://orcid.org/0000-0001-7141-0494
Melissa B. Youngquist https://orcid.org/0000-0003-2721-1871
Robert A. Slesak https://orcid.org/0000-0002-6523-5383
Brian J. Palik https://orcid.org/0000-0003-0300-9644
Anthony W. D'Amato https://orcid.org/0000-0002-2570-4376

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