Wetlands (2022) 42:122
https://doi.org/10.1007/s13157-022-01632-9

FORESTED WETLANDS

Evaluating At-Risk Black Ash Wetlands as Biodiversity Hotspots in Northern Forests

Alexis R. Grinde[1] · **Melissa B. Youngquist**[2,3] · **Robert A. Slesak**[4] · **Brian J. Palik**[3] · **Anthony W. D'Amato**[5]

Received: 6 December 2021 / Accepted: 3 November 2022

Abstract

Black ash (*Fraxinus nigra*) forests, which cover over 1.2 million hectares in the Great Lakes Region, are threatened by emerald ash borer (EAB; *Agrilus planipennis*), which is eliminating native populations of ash throughout the region. Understanding the contribution of black ash wetlands to local and regional species richness is critical in forming effective conservation policies and informing management plans for these imperiled habitats. We measured breeding bird and anuran communities in black ash wetlands and compared them to nearby non-black ash habitats for each taxa: aspen-dominated upland forest for birds and emergent wetlands for anurans. Our results showed black ash wetlands support unique communities of birds but not of anurans. For birds, black ash wetlands had higher species richness and a greater number of birds that were indicator species compared to upland forests; this is likely due the presence of a water component and more structural diversity in black ash wetlands compared to aspen-dominated aspen forests. In contrast, emergent wetlands had higher richness of breeding anurans and greater number indicator species than black ash wetlands; this reflects a general preference by North American anurans to breed in more open canopy habitats. If EAB invades these systems, expected increases in ponding and canopy openness may be beneficial for some anuran species during the breeding season, but loss of the forest canopy could result in significant changes in bird community composition**.** Our results indicate that implementing management strategies that focus on emulating structural complexity of black ash wetlands will be beneficial for conserving wildlife diversity.

Keywords Anurans · Birds · Black ash · Community ecology · Forested wetlands

Introduction

Loss of forested wetlands have been significant and widespread (Dahl 1990; Zedler and Kercher 2005), and these wetlands continue to face a variety of threats from changes in land use, climate, and forest pests (Mitsch and Hernandez 2013; Lovett et al. 2016; Dahl and Zoltai 2018). Notably, in much of eastern North America the invasive emerald ash borer (EAB; *Agrilus planipennis*) is altering wetlands where ash is a key component of the tree community. For most ash species, EAB causes over 90% mortality of trees over 2.5 cm diameter (at breast height) within a few years following infestation (Klooster et al. 2014). In the western Great Lakes region of North America, black ash (*Fraxinus nigra*) often comprises a majority of overstory trees in northern forested wetlands (D'Amato et al. 2018; Klooster et al. 2018; Hoven et al. 2020; Palik et al. 2021). In these wetlands, black ash is considered a foundation species because of its role modulating wetland structure and function through influences on hydrology, litter quality, and resource availability (Youngquist et al. 2017). Furthermore, given the hydric environment, black ash is unlikely to be replaced by other tree species after EAB mortality occurs (Palik et al. 2021). Therefore, these wetlands are at risk of degrading to emergent wetlands or shrub-swamp communities (Diamond et al.

✉ Alexis R. Grinde
agrinde@d.umn.edu

[1] Natural Resources Research Institute, University of Minnesota Duluth, 5013 Miller Trunk Highway, Duluth, MN 55811, USA

[2] Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, 1200 S Lake Shore Drive, Chicago, IL, USA

[3] USDA Forest Service, Northern Research Station, 1831 Hwy. 169 E., Grand Rapids, MN 55744, USA

[4] USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512, USA

[5] Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA

2018; Bowen and Stevens 2018; Palik et al. 2021). Changes in ecosystem function, including carbon cycles, hydrology, habitats, and food webs, due to loss of black ash have been reported (Gandhi and Herms 2010; Youngquist et al. 2017; Slesak et al. 2014; Grinde et al. 2022).

In addition to their importance in ecosystem function (e.g. Zedler and Kercher 2005; Evenson et al 2018), wetlands contribute significantly to regional biodiversity (e.g., Zedler and Kercher 2005; Dertien et al 2020). In general, wildlife habitats that provide a combination of terrestrial (e.g., canopy structure) and aquatic characteristics are identified as having higher conservation priorities because they support diverse flora and fauna (Bartels et al. 2012; Schindler and Smits 2017; Lafage et al. 2019). For example, riparian ecotones often support higher species richness, diversity, and abundance than adjacent uplands and are therefore often afforded additional protection (e.g., buffers) in forest management guidelines (Sanders and Edge 1998; Macdonald et al. 2006; Morissette et al. 2018). Forested wetlands also provide a combination of terrestrial and aquatic characteristics that may support unique wildlife assemblages compared to upland habitats and are, therefore, an important contributor to regional diversity (Sabo et al. 2005; Dertien et al. 2020). However, surprisingly little has been published about the habitat characteristics of northern black ash wetlands and the wildlife communities they support (Ehrenfeld 2012, Youngquist et al. 2017, Grinde et al. 2022). It stands to reason that the widespread mortality of black ash due to EAB infestation will impact wildlife—but the overall impacts to species diversity are unclear (Kolka et al. 2018; Grinde et al. 2022). Understanding the contribution of black ash wetlands to local and regional diversity is critical in forming effective conservation policies and informing management plans for these imperiled habitats.

The objective of this study were to 1) determine the extent to which wildlife communities in black ash wetlands are unique when compared to non-black ash habitats, including upland forest or non-forested wetlands, and 2) assess the relative importance of vegetation characteristics, using lidar-derived variables, for predicting community assemblage and diversity in the focal habitats. We conducted the study in northern Minnesota, which is not invaded by EAB to date, allowing us to establish baseline community assemblage information. We conducted two separate surveys focused on avian and anuran taxa because they are generally abundant in wetland habitats and are easily observed during the breeding season. For birds, we were interested in the importance of black ash wetland habitat for local and regional diversity; therefore, we compared forest-bird communities between black ash wetlands and aspen (*Populus* spp.)-dominated upland forests. Because black ash wetlands are known to have high levels of structural diversity (Diamond et al. 2019, Diamond et al. 2020, Palik et al. 2021, Grinde et al. 2022), we predicted that black ash wetlands would have higher avian species richness and more indicator species compared to aspen-dominated upland forest; these differences would result in unique bird communities between habitat types. For anurans, we were interested in breeding communities in black ash and non-black ash wetlands; because nearly all deciduous-forest wetlands are black ash wetlands in northern Minnesota, we compared black ash wetlands and emergent wetlands. We predicted that anuran species richness would be similar among black ash and emergent wetland sites, but that species composition and indicator species would be grouped by forest-associated and non-forest associated species (e.g., Van Buskirk 2005; Liner et al. 2008). Our results will provide information to assess the potential impacts of the loss of black ash on bird and anuran biodiversity and help inform management of these in the wake of EAB invasion.

Methods and Materials

Sites and Study Design

The study area, in northeastern Minnesota, is a glacial moraine landscape dominated by aspen, pine (*Pinus* spp.), maple (*Acer* spp.), and paper birch (*Betula papyrifera*) uplands, with black ash and lowland conifer (*Picea mariana* and *Larix laricina*) wetlands occurring in low lying areas. We identified 27 black ash wetland sites, across three study areas, that represented the range of hydrogeomorphic categories (e.g., depressional, lowland flat, riverine) and hydroperiod durations (from temporary to permanent) found in northern Minnesota (Fig. 1; Grinde et al. 2022). Sites were dominated by mature black ash (> 70% of overstory basal area); co-occurring tree species in the overstory included northern white cedar (*Thuja occidentalis*), American elm (*Tilia Americana*), and quaking aspen (*Populus tremuloides*; Palik et al. 2021). The average area (± SD) of selected black ash wetlands was 6.3 ± 3.5 ha, with no evidence of recent management and no ditches, roads, or trails present. Surveyed black ash sites were an average (± SD) 151 ± 121 m from a road (range 20 – 600 m). More information on study site characteristics and vegetation composition can be found in Diamond et al. (2019) and Palik et al. (2021).

For habitat comparisons, we considered each study area as a block to control for variations across the geographic range, then selected upland forest sites ($n = 27$) and emergent wetland ($n = 20$) sites for that were within 1 km of a given black ash site to control for landscape composition differences. The west study area had 11 black ash wetland, 11 upland forest, and 9 emergent wetland sites; the central study area had 10 black ash wetland, 10 upland forest, and 7 emergent wetland sites; and the east study area had 6 black

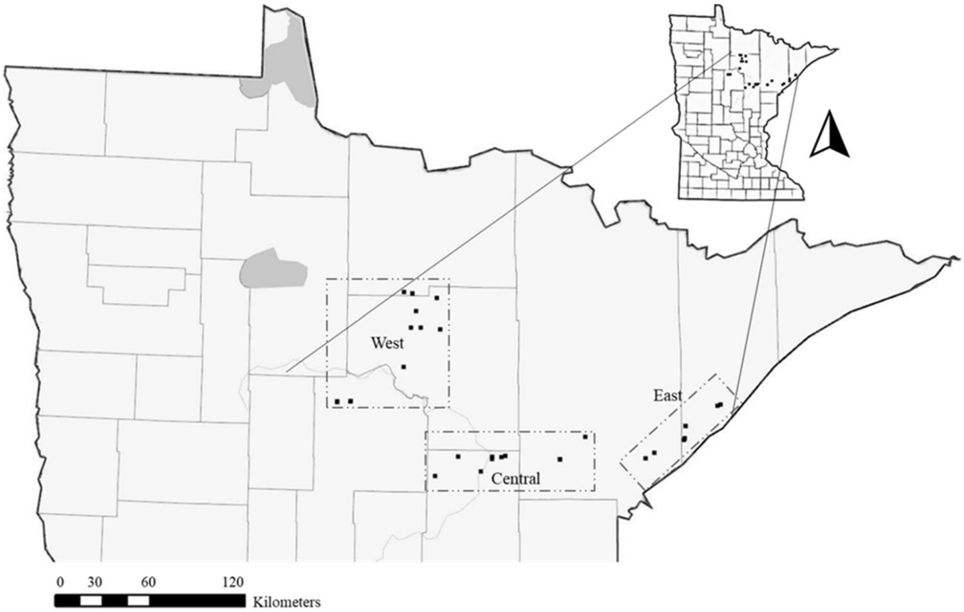

Fig. 1 Wildlife survey locations in northern Minnesota, USA. Points indicate survey locations in black ash wetland, aspen-dominated upland forest, and emergent wetland habitats. Black ash sites ($n = 27$) were selected to represent the range of forested wetland conditions found across three study areas (indicated by dashed lines) in the state. Aspen-dominated upland forest ($n = 27$) and emergent wetland sites ($n = 20$) were located within 1 km of black ash sites and used for habitat comparisons. Dark grey show large lakes; straight gray lines indicate county boarders; light gray meandering line is the Mississippi River

ash wetland, 6 upland forest, and 4 emergent wetland sites (Fig. 1). Non-black ash sites were selected using satellite imagery, National Wetland Inventory Dataset (Kloiber et al. 2019), and on-the-ground observations. Criteria for upland sites were a minimum of 4 ha, and point counts were a minimum 250 m from the edge of the black ash wetlands to avoid double-counting individual birds and 100 m from the road to avoid the influence of edge habitat. The upland forest sites were dominated by quaking aspen, and co-occurring tree species included paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), and balsam fir (*Abies balsamea*). The average area (± SD) of upland forest stands was 7.3 ± 3.3 ha. Emergent wetland sites lacked a tree canopy and were dominated by graminoids and other herbaceous vegetation; they were within 300 m from the nearest road to facilitate roadside call surveys, on average emergent sites were 151 m from the road (range 20 – 600 m). Because many emergent wetlands were riverine floodplains, there was a wide range of sizes: average area (± SD) of emergent wetlands was 4.4 ± 6.9 ha.

Wildlife Surveys

Avian Point Count Surveys We conducted 10-min point count surveys at each black ash wetland ($n = 27$) and paired upland forest sites ($n = 27$) in June 2017 and June 2018, when breeding birds were most active (Niemi et al. 2016). Point count surveys were conducted in the middle of the black ash site and one in center the paired upland aspen stand. Point counts were conducted once per year by two trained observers from approximately 0.5 h before to 4 h after sunrise on days with little wind (< 15 km hr^{-1}) and little or no precipitation. Surveys were conducted by the same people each year All birds heard or seen from the point count locations were recorded, along with their spatial location within the plot and estimated distance (0–25 m, 26–50 m 51- 100 m, > 100 m) from the observer to avoid double counting birds. Analyses was only conducted on birds observed within the 100 m radii to focus on birds detected in the distinct habitats to reduce potential biases related to differential detection issues (Niemi et al. 2016).

Anuran Surveys In 2017 and 2018 we surveyed for calling anurans at 27 of the forested wetland sites and 20 emergent wetland sites. We followed standard call survey protocol for North American anurans (Weir and Mossman 2005). Call surveys were conducted three times each year; surveys took place about every two weeks starting after ice-out (mid-to-late April) and concluded in early June. Surveys were five minutes in duration and took place between 19:00–0:00 on days with little wind and no precipitation. The identity and relative intensity (scale of 0 – 3; where 0 intensity specifies no individuals calling, 1 is a single calling male, 2 indicates overlapping calls but individuals are distinguishable, and 3 specifies a full chorus with all calls continuous and overlapping) of all calling species was recorded. For the black ash sites, we conducted call surveys from the edge of the ponded area within the black ash stand (Grinde et al. 2022). For emergent sites, we conducted surveys from the edge of the wetland or from the road when the wetland was inaccessible. A species was marked as present when we could positively identify calling within the target ponded area (up to 200 m from observer's location in expansive wetlands). Surveys were conducted by the same observers each year.

Environmental Variables

We characterized black ash wetland, upland forest, and emergent wetland sites using eight site-level variables developed from a state-wide lidar dataset that was collected in spring 2011 and 2012 (Table 1; McGaughey 2017). Site boundaries were identified using the Forest Inventory Management and National Wetland Inventory datasets and confirmed using satellite imagery and site visits, boundaries were used to calculate site area of each stand and wetland (ha; MN DNR 2016; Kloiber et al. 2019). For the lidar-derived variables we first created canopy height model rasters with 2 m resolution, then used the model to generate binary canopy products at 20 m resolution using Map Algebra (Spatial Analyst) in ArcGIS (v.10.4.1 ESRI 2019). We developed two datasets to quantify canopy structure: first we used a 9 m height threshold and classified cells as canopy (> 9 m) or gaps (< 9 m), we then used a 2 m threshold to classify cells as sub-canopy (> 2 m) or gaps (< 2 m). The two binary (canopy vs. gap or sub-canopy vs. gap) raster datasets were then used to calculate the proportion of area within each site that consisted of canopy and sub-canopy. The canopy height, canopy cover, and understory indices were summarized for each site by calculating the mean and standard deviation of raster values within the site boundaries (Table 1). The canopy height variables (mean and standard deviation) were calculated using the mean 75th percentile of non-ground return height of all raster pixels within the site boundaries. The canopy cover variables (mean and standard deviation) were calculated as the proportion of site area classified as upper canopy (> 9 m; e.g., a value of 0.54 indicates that 54% of the stand area had a vegetation above the 9 m threshold). The variable understory cover index was calculated as the proportion of returns < 2 m above ground surface; values ranged from 0 (no understory cover) to 1 (very dense cover). The variable all canopy index was calculated as the proportion of the stand classified as canopy using the 2 m threshold.

Data Analysis

Preliminary analyses showed that including year as a covariate did not improve models, therefore biodiversity metrics were calculated by combining data from the two survey years for both taxa. For birds, count data was summed giving total count over two years. For anurans, relative call intensity was converted to presence/absence data so that occurrences could be pooled; a species was marked as “present” if it was observed calling in at least one year. All statistical analyses were run in the R software environment (R Core Team 2021).

Vegetation We used Welch’s two sample t-tests that allowed for unequal variance to compare lidar-derived environmental variables between upland and black ash sites and between black ash and emergent sites. Variables were assessed for normality assumptions and a log-transformation was used to meet assumptions when necessary and were considered significant at $P < 0.10$.

Community Composition Analysis To assess differences in the community composition between habitats, we used model-based unconstrained ordination (Hui 2016); we specifically used the *boral* package (Hui 2016) to implement latent variable models—this approach is also termed joint species distribution modelling. Latent variables represent unmeasured environmental gradients and act as random effects. This method accounts for covariance in and among species responses across sampled sites (Warton et al. 2015). When visualizing results, the latent variables also represent the main axis of the ordination.

We determined which species were significantly correlated and visualized differences in community structure between our habitat types (black ash and upland forest for birds; black ash and emergent wetlands for anurans). We removed rare species that were observed only once (12 bird species; 0 anuran species) and excluded sites with zero species observed

Table 1 Description of environmental variables used for analyses

Variable	Description
Canopy height	Average height (m) of entire stand area calculated using the mean 75th percentile of non-ground return height
	Within-stand variability in stand height (m) calculated using the standard deviation (SD) of 75th percentile of non-ground return height
Canopy cover index	Mean canopy cover value of stands calculated using first returns
	Within-stand variability of canopy cover values calculated using the standard deviation in canopy cover based on first returns
Understory cover index	Mean understory cover index
	Within-stand variability of understory cover index using the standard deviation in canopy cover based on first returns
Upper canopy index	Proportion of stand area classified as canopy using the 9 m threshold
All canopy index	Proportion of stand area classified as canopy using the 2 m threshold
Stand area	Area of stand or wetland

(0 sites for birds; 9 black ash sites for anurans). We set the number of latent variables to ‘two’ and used an ‘exponential’ spatial correlation structure to account for spatial covariance in community composition (sites that were closer together were more likely to have similar species assemblages). For birds we used a negative binomial distribution to model total abundance, and for anurans we used a binomial distribution to model presence/absence. Finally, MANOVA was used to test for differences in community composition (latent variable ordination space) between habitats.

We also tested for effects of stand structure on community composition using multivariate abundance models with the *mvabund* package (Wang et al. 2021). For both taxa, we considered five lidar variables that differed among habitat types (mean canopy height, percent canopy cover, percent understory cover, percent upper canopy cover, and all canopy index) and stand area. We used Pearson’s correlation to test for correlations among variables that were highly correlated ($r = 0.75$). The full model for birds included stand area, mean canopy height, understory cover index, and all canopy index. The full model for the anurans included stand area, mean canopy height, and understory cover index. For birds we used a negative binomial distribution and for anurans we used a binomial distribution. Preliminary analyses showed that mean canopy height was a significant predictor of community structure for both birds and anurans and therefore we included a model with only canopy height. We used ANOVA to compare models, utilizing a log-likelihood ratio test statistic. We used the summary function to assess univariate responses of each species and adjusted *P*-values for multiple-comparisons using a step-down resampling procedure, which is implemented within the R package. We then calculated coefficient estimates and 95% confidence intervals to determine which coefficients were different from zero.

Species Richness and Abundances We calculated species richness (total number of species observed), and total abundance (total number of individuals observed) at all sites for birds and species richness for anurans at all sites. We used these metrics as response variables to determine if there were 1.) Differences between habitat types and 2.) If lidar-derived variables were significant predictors bird and anuran community metrics. We used generalized linear mixed models (GLMM) from the lme4 package (Bates et al. 2015) and included study site and block as a random effects to account for variation among sites and across the geographic regions. Akaike's information criterion (AIC) model selection was used to were ranked and compared models with delta AIC (Anderson and Burnham 2002); models with highest weights were compared the null models (i.e., no fixed effects) to test for model significance (Nickerson 2000; Harrison et al. 2018). Richness and abundance models used a Poisson distribution.

Indicator Species Analysis We used indicator species analysis (ISA) to identify indicator species; species with higher combined frequency of occurrence and abundance in the one of the habitat types, (Dufrêne and Legendre 1997). This technique is useful for evaluating the association between species and a priori site classifications (i.e., habitat types) where species with high indicator values are those found to be almost exclusive to habitat and detected at most sites within that habitat (Dufrêne and Legendre 1997). The indicator values are based on combined within-species abundance and occurrence comparisons and therefore are not affected by the abundance of other species. The maximum indicator value of a species among habitats was tested for statistical significance using Monte Carlo permutations and used $P < 0.10$ as the significance level to identify indicator species (Lehmkuhl et al. 2007). All analyses were conducted using the function indval in the labdsv package (ver. 1.7.8).

Results

Vegetation Results of the Welch’s *t*-t s showed several significant differences between black ash forested wetlands and upland forest sites; mean canopy height ($t = 2.66$, $P = 0.01$), percent canopy cover ($t = 1.90$, $P = 0.06$), and upper canopy index ($t = 2.57$, $P = 0.01$) were higher in upland forest compared to black ash wetlands. However, understory cover index ($t = 1.91$, $P = 0.06$), the variation in canopy cover ($t = 2.22$, $P = 0.03$) and variation in understory cover ($t = 2.71$, $P < 0.01$) was higher in black ash sites. There was not significant differences in the standard deviation of stand height sites ($t = 0.22$, $P = 0.82$) and there was no difference between the site types in the all canopy index ($t = 0.13$, $P = 0.89$) between black ash and upland sites.

The comparisons between black ash forested wetlands and emergent wetlands also showed significant differences. Mean canopy height ($t = 9.75$, $P < 0.01$), percent canopy cover ($t = 15.05$, $P < 0.01$), variation in canopy cover ($t = 1.92$, $P = 0.07$), variation in understory cover ($t = 1.75$, $P = 0.09$), upper canopy index ($t = 12.22$, $P < 0.01$), and all canopy index ($t = 23.60$, $P < 0.01$) were higher in the black ash wetlands. However, the understory cover ($t = 1.35$, $P = 0.18$) and variation in canopy cover ($t = 1.35$, $P = 0.19$) did not differ between habitat types.

Community Composition A total of 51 bird species were documented throughout the duration of the study (Appendix 1 Table 3). There was a significant difference in bird community between black ash and upland sites (Pillia’s Trace $= 0.25$, $df = 1$, $P < 0.01$; Fig. 2). Over half of the bird species exhibited strong correlation, either positive or negative, with at least one other bird species (Appendix 3 Fig. 3). In general, birds that are associated with upland forests (e.g., Ovenbird (*Seiurus aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), and Eastern Wood-Pewee (*Contopus virens*)) tended to be positively associated with each other but negatively associated with bird species that respond favorably to moist conditions (e.g., Northern Waterthrush (*Parkesia noveboracensis*), Alder Flycatcher (*Empidonax alnorum*), and Swamp Sparrow (*Melospiza georgiana*)).

Eight anuran species were documented during the study, and results show that the anuran community composition was also different between black ash and emergent wetlands (Pillia's Trace = 0.49, df = 1, $P < 0.01$ Fig. 2; Appendix 2 Table 4). Emergent wetlands hosted unique species (e.g., Green Frog (*Lithobates clamitans*), Mink Frog (*Lithobates septentrionalis*), Northern Leopard Frog (*Lithobates pipiens*)) that were not observed in black ash wetlands. Furthermore, these three species, which breed later in the year and require longer hydroperiods, appeared to form one cluster that was separate from the early spring breeding species (Chorus Frog (*Pseudacris triseriata*), Spring Peeper (*Pseudacris crucifer*), Wood Frog (*Lithobates sylvaticus*); Fig. 2). When looking at significant correlations among species presence, there were only positive associations among anurans (Appendix 3 Fig. 3).

The canopy height model was the best fit for both birds (Dev = 165.6, $P < 0.01$) and anurans (Dev = 50.6, $P < 0.01$). The results of the bird model showed that after correcting for multiple comparisons, canopy height was a significant predictor for only one species, Ovenbird (LR = 28.4, adj-$P = 0.001$). However, species-specific parameter estimates and 95% confidence intervals indicated that Alder Flycatcher, Black-capped Chickadee, Brown-headed Cowbird, Nashville Warbler, Veery, and White-throated Sparrow had negative coefficients that were different from zero and were most abundant in area with a shorter canopy. Black-throated Green Warbler, Eastern Wood Pewee, Mourning Warbler, Ovenbird, Wood Thrush, and Yellow-bellied Sapsucker had positive coefficients that were different from zero and most abundant in areas with a taller canopy (Appendix 4 Table 5). For anurans, canopy height was a significant predictor for Gray Tree Frog, American Toad, Green Frog, and Leopard Frog, (LR > 10.5, adj-$P < 0.04$). All species had negative estimated coefficients, but only Gray Tree Frog, American Toad, and Green Frog had estimates that were different from zero (Appendix 4 Table 5).

Species Richness and Abundances The bird species richness model showed that the habitat type model was significantly different from the null model ($\chi^2 = 5.9$, $P = 0.02$, df = 1) and indicated that average bird species richness (± SE) was significantly higher in black ash sites (richness = 10.2 ± 1.6; $\beta_{ash} = 2.30$ s.e.$_{ash} = 0.06$, $P < 0.01$) compared to paired upland

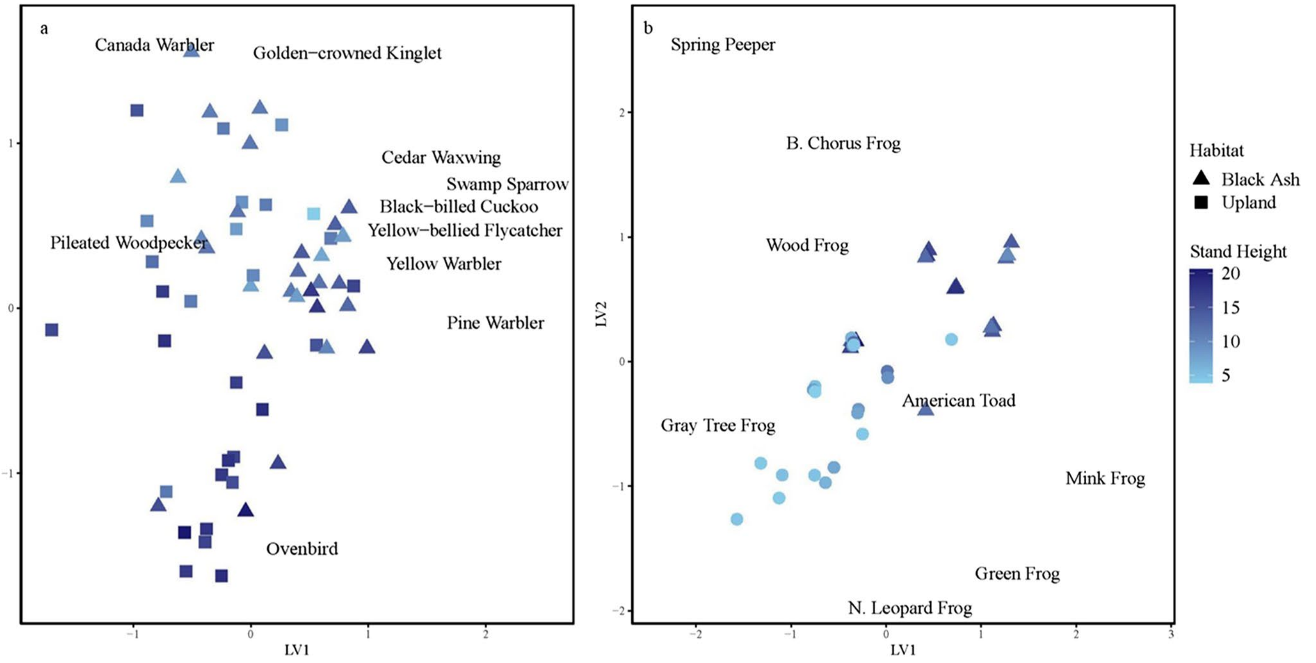

Fig. 2 Results of amphibian and bird Joint Species Distribution Models. Unconstrained ordinations of a.) Bird abundance in black ash wetlands and aspen-dominated upland sites, b.) Anuran presence/absence in black ash wetland and emergent wetland sites. Ordination plots show mean latent variable (LV) 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). Site color indicates mean canopy height for anuran and bird plots

sites (richness = 8.2 ± 1.06; β_{upland} = -0.17 s.e.$_{upland}$ = 0.09, $P = 0.05$; Appendix 5 Table 6). Results showed that the models that included lidar-derived variables were not significantly different from the null model. The bird abundance model also showed that the habitat type model was significant compared to the null model ($\chi^2 = 5.9$, $P = 0.02$, df = 1; Appendix 5 Table 6). However, the results of this model showed that abundance did not differ significantly between habitat types ($\beta = 0.11$ s.e. = 0.07, $P = 0.12$). The bird abundance model that included variation in understory cover index was also significantly different from the null model (($\chi^2 = 4.97$, $P = 0.02$, df = 1). This model indicated that variation in understory index ($\beta = 0.10$, s.e. = 0.04, $P = 0.02$) was positively associated with overall bird abundance.

Top performing models for predicting anuran species richness that were significantly different from the null model included the habitat type ($\chi2 = 27.5$ $P < 0.01$, df = 1) and all canopy index (the proportion of the stand area classified as canopy using the 2 threshold; $\chi2 = 31.2$ $P < 0.01$, df = 1; Appendix 5 Table 6). The habitat type model showed that average anuran species richness (± SE) was significantly higher in emergent wetlands (richness = 3.9 ± 1.1; $\beta_{emg} = 1.12$ s.e.$_{emg}$ = 0.19, $P < 0.01$) compared to black ash wetland habitats (richness = 1.3 ± 1.2; $\beta_{ash} = 0.48$ s.e.$_{ash}$ = 0.16, $P < 0.01$). The canopy index model indicated that richness was negatively associated with canopy above 2 m ($\beta = -0.53$, s.e. = 0.09, $P < 0.01$).

Indicator Species Analysis Black ash sites were characterized by four bird indicator species and upland forests had two indicator species (Table 2). Three of the indicator species of black ash sites, Common Yellowthroat, Northern Waterthrush, and Northern Parula are species that are associated with water components; however, the fourth species, Winter Wren, generally associated with old forests (Appendix 1 Table 3). The results of the anuran ISA showed that six species were significant indicators of emergent wetlands, but no species had significant associations with black ash wetlands (Table 2).

Table 2 Indicator value of bird and anuran indicator species in black ash forest, upland forest, and emergent wetlands based on results of indicator species (ISA) analysis. Values are a function of the frequency of occurrence and abundance at survey locations according to Dufrêne and Legendre (1997). The maximum indicator value of a species among habitats was tested for statistical significance using Monte Carlo permutations and used $P < 0.10$ as the significance level to identify indicator species, bold indicates significant value for the species in the habitat

Birds			
Common Name	Black ash forest	Upland forest	P
Common Yellowthroat	**43.5**	2.3	0.003
Northern Waterthrush	**35.1**	0.1	0.002
Northern Parula	**30.0**	0.7	0.009
Winter Wren	**22.2**	0.0	0.020
Ovenbird	27.4	**63.8**	0.002
Yellow-bellied Sapsucker	1.1	**28.2**	0.018
Anurans			
Common Name	Black ash forest	Emergent wetland	P
Gray Tree Frog	3.0	**79.5**	0.001
Spring Peeper	15.6	**67.5**	0.001
Wood Frog	19.8	**64.3**	0.001
American Toad	0.3	**41.6**	0.003
Northern Leopard Frog	0.0	**30.0**	0.002
Green Frog	0.0	**30.0**	0.006

Discussion

Wetland habitats are generally expected to have higher richness, abundance and/or diversity in many biomes compared to upland habitats (Gopal and Junk 2000; Dertien et al. 2020). Our study provides quantitative evidence to support the hypotheses that black ash wetlands provide important habitat for unique assemblages of breeding birds. Furthermore, these at-risk habitats provide increased regional bird diversity when compared to aspen-dominated upland forests. While black ash wetlands support frogs that depend on temporary ponds, they did not host unique anuran species compared to other wetland types. These results indicate that forested wetlands have high ecological value for birds and provide breeding habitat for some frogs.

Comparisons of vegetation metrics indicate that in general, black ash wetlands have a more complex canopy and understory structure compared to aspen-dominated upland forest. Our results align with findings from Looney et al. (2016), that black ash wetlands in the region have an uneven-age structure with diverse canopy and well-developed understory layer. In contrast to the uneven-aged black ash stands, the upland forests included in this study were younger, even-aged forests that develop following forest harvesting and generally contain lower vertical canopy structure and lower floristic richness. The structural diversity in the canopy and understory of black ash wetlands likely provided unique micro-habitats that are important for supporting diverse bird communities (MacArthur and MacArthur 1961; Roth 1976; Sitters et al. 2016; Fontúrbel et al. 2021).

Bird assemblages in black ash wetlands differed from those in upland forest; black ash wetlands had higher bird species richness and contained more unique species than aspen-dominated upland forests. This pattern matches an analysis of fauna conducted by Dertien et al. (2020) that showed a positive correlation between bird richness and wetland cover across much of the United States, including northern Minnesota. Moreover, Zenzal et al. (2018) found that there was a higher abundance of migratory bird species in areas with water features and suggest that these areas may provide important food resources for birds. Our multivariate analyses of community structure, taken together with the species richness models and ISA suggested that some species respond to canopy structure while other are responding to the wetland environment. The results of the ISA support the prediction that increased structure in the forested wetlands is beneficial for ground nesting and sub-canopy breeding birds by providing increased foraging opportunities and potential nest sites (Sitters et al. 2016; Fontúrbel et al. 2021). For example, Common Yellowthroat are likely responding to areas with dense growth of low vegetation, which is more prevalent in wet areas (Stewart 1953; Guzy and Ritchison 2020). Other indicator species for forested wetlands such as Northern Parula and Northern Waterthrush are likely responding to the combination of variability in the canopy cover, moderate ground and shrub cover, and moist conditions (Collins et al. 1982; Whitaker and Eaton 2020). Winter Wren, however, are likely responding to the structural diversity that is generally more prevalent in of black ash forests. Specifically, this species requires dense undergrowth and downed wood for nesting and foraging during the breeding season (Wolf and Howe 1991); these structures are typically found in older forests (e.g., Hobson and Bayne 2000; Andersson et al. 2018) and are likely more abundant in black ash stands given the uneven-aged conditions of these ecosystems and comparatively low levels of management.

Swift et al. (1984) suggested that the effects of hydrologic patterns (e.g., surface water extent and configuration) might be greater than the influence on vegetation structure on breeding birds in forested wetlands. Odum (1950) hypothesized that the higher water content of forested wetlands could be both directly beneficial to birds by providing more available water and moderating temperature changes and indirectly beneficial by influencing understory plant communities. Importantly, several studies have noted that forested wetlands may have greater abundance of invertebrates than mesic forests (e.g., Austin et al. 1996; Smith et al. 1998) that are available as a food resource throughout the breeding season (Riffell et al. 2006). We did not quantify difference in hydrological regimes across black ash wetlands in this study, however it is possible that surface water in forested wetlands increases the availability of high quality food (e.g., seeds, invertebrates) for breeding birds. This should be a focus of future research in order to assess habitat quality and conservation value of forested wetlands.

Results of this study also indicated that anuran community composition between black ash and emergent wetlands were significantly different in terms of richness and community composition. However, in contrast to the results of breeding birds, we found that emergent wetlands hosted more diverse anuran communities and that a higher proportion of emergent wetlands sites were occupied by breeding anurans compared to black ash wetlands. All anuran species observed in this study were indicators of emergent wetlands and were positively correlated with each other, indicating that breeding anurans in the study region prefer open canopy habitats. Grinde et al. (2022) also found increased anuran occupancy of black ash sites where ash had been experimentally harvested and had degraded to emergent wetland. This preference for open canopies is common among anurans, even forest associated species (e.g., Hocking and Semlitsch 2007; Semlitsch et al. 2009). In fact, forest species may preferentially select open canopy wetland on the edges of forested habitat to breed (Hocking and Semlitsch 2007). The emergent wetlands in this study were imbedded in a forested matrix (i.e., adjacent to forest habitat) and may be particularly appealing for forest-associated frogs as well as species that are generally associated with open canopies (e.g., Northern Leopard Frogs and American Toads).

In addition to canopy cover differences between wetland types, the increased anuran species richness observed in emergent wetlands compared to black ash wetlands may also be attributed to differences in hydrologic regime between the surveyed habitats. The vast majority of black ash wetlands in this study had short hydroperiods (drying in early summer) which restricts breeding anurans to those species that lay eggs early in the year and whose tadpoles transform quickly (e.g., Wood frogs, Spring Peepers, and Boreal Chorus Frogs). Many black ash wetlands did not offer suitable ponded habitat for breeding frogs – as evidenced by the absence of calling anurans from 1/3 of black ash wetlands. Grinde et al. (2022) found that anuran larvae only occurred in 60% of black ash wetlands where calling was observed; overall sites with breeding activity had large ponded areas, relative to stand size, and had longer hydroperiods. In contrast, emergent wetlands in this study included a larger proportion of permanent wetlands, including riverine and lake floodplains. These habitats are suitable for species that breed later in the year and/or have longer larval periods including Northern Leopard Frogs, Mink Frogs, and Green Frogs. Indeed, Mink Frogs and Green Frogs often have overwintering tadpoles (Lannoo 2005) and therefore, breeding populations are excluded from many black ash wetlands.

While anuran breeding activity may preferentially occur in emergent wetlands, many species in this study are forest-associated and depend on intact forest for their non-breeding habitat (e.g., Wood Frogs, Gray Tree Frogs; Lannoo 2005). Thus, the long-term consequences of black ash loss on anuran communities is unclear when considering the full anuran life cycle. Other studies have demonstrated that forest harvest and loss can have a net negative effect on adult and juvenile growth and survival, despite potential benefits on the larval stage (Semlitsch et al. 2009). We speculate that most amphibian species could gain short-term breeding benefit as black ash is lost from the landscape and open canopy wetlands become more abundant. However, some species may suffer long-term declines if EAB-caused tree mortality leads to habitat fragmentation and less forest cover in the landscape. Additional data on habitat use by post-breeding adults and juveniles is needed to assess potential long-term impacts of habitat fragmentation and loss of terrestrial habitat from EAB-caused tree mortality.

Prior to European settlement, forested wetlands may have comprised up to 70% of the total wetland area in the northern United States and southern Canada; from the 1780s to the 1980s, it is estimated that the Great Lakes region has lost 59 percent of its wetlands (Dahl 1990). The ecological consequences of these changes cannot be fully quantified, but negative effects on wildlife populations certainly occurred. Now, in the face of EAB, black ash wetlands, which are structurally complex and the predominant hardwood wetland type in the Great Lakes region, face further threats as ash is lost from the landscape and forested wetlands transition to emergent and shrub wetlands. The loss of black ash will result in turnover of wildlife communities from forest-dependent species to open-canopy associated species (e.g., Grinde et al. 2022). Although net changes in wildlife biodiversity may be minimal or potentially increase for some taxa (amphibians), the long-term, large-scale impacts of EAB on forest-associated wildlife will likely be significant. Management strategies that focus on emulating structural complexity of black ash wetlands while establishing non-host alternative native trees species that will maintain long-term forest cover are necessary to conserve critical habitat that supports wildlife diversity.

Appendix 1

Table 3 List of bird species detected within 100 m radius during point counts. Common name, scientific name, nest location, primary diet, and primary breeding habitat along with observed abundance in black ash wetlands and upland forests are provided. Nest, diet, and habitat assignments were sourced from Niemi et al. (2016) and Billerman et al. (2020)

Common name	Scientific name	Abbreviation code	Nest location	Primary diet	Primary habitat	Abundance	
						Black ash wetland	Upland forest
Alder Flycatcher	*Empidonax alnorum*	ALFL	Shrub	Foliage insects	Shrub swamp	1	0
American Redstart	*Setophaga ruticilla*	AMRE	Shrub	Flycatchers	Early-successional	10	6
American Robin	*Turdus migratorius*	AMRO	Shrub	Ground insects and fruit	Fields and meadows	3	5
Black-and-white Warbler	*Mniotilta varia*	BAWW	Ground	Bark insects	Mixed forest	19	19
Blackburnian Warbler	*Dendroica fusca*	BLBW	Canopy	Foliage insects	Coniferous forest	6	3
Black-capped Chickadee	*Poecile atricapillus*	BCCH	Cavity	Foliage insects	Deciduous forest	15	2
Black-throated Green Warbler	*Dendroica virens*	BTNW	Shrub	Foliage insects	Mixed forest	16	14
Blue Jay	*Cyanocitta cristata*	BLJA	Canopy	Omnivores	Deciduous forest	3	5
Broad-winged Hawk	*Buteo platypterus*	BWHA	Canopy	Vertebrates	Mixed forest	2	1
Brown Creeper	*Certhia americana*	BRCR	Cavity	Bark insects	Deciduous forest	12	5
Brown-headed Cowbird	*Molothrus ater*	BHCO	Canopy	Ground insects and fruit	Fields and meadows	1	2
Canada Warbler	*Wilsonia canadensis*	CAWA	Ground	Foliage insects	Mixed forest	3	3
Cedar Waxwing	*Bombycilla cedrorum*	CEDW	Shrub	Foliage insects	Deciduous forest	3	0
Chestnut-sided Warbler	*Dendroica pensylvanica*	CSWA	Shrub	Foliage insects	Early-successional	17	18
Chipping Sparrow	*Spizella passerina*	CHSP	Canopy	Ground insects and fruit	Coniferous forest	0	1
Common Grackle	*Quiscalus quiscula*	COGR	Shrub	Omnivores	Fields and meadows	0	1
Common Yellowthroat	*Geothlypis trichas*	COYE	Shrub	Foliage insects	Shrub swamp	21	4
Downy Woodpecker	*Picoides pubescens*	DOWO	Cavity	Bark insects	Deciduous forest	1	3
Eastern Wood-Pewee	*Contopus virens*	EAWP	Canopy	Flycatchers	Mixed forest	4	2
Golden-crowned Kinglet	*Regulus satrapa*	GCKI	Canopy	Foliage insects	Coniferous forest	0	2
Golden-winged Warbler	*Vermivora chrysoptera*	GWWA	Ground	Foliage insects	Early-successional	1	1
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL	Cavity	Flycatchers	Deciduous forest	7	1
Hairy Woodpecker	*Picoides villosus*	HAWO	Cavity	Bark insects	Deciduous forest	1	5
Hermit Thrush	*Catharus guttatus*	HETH	Ground	Ground insects and fruit	Mixed forest	3	3
Least Flycatcher	*Empidonax minimus*	LEFL	Shrub	Flycatchers	Deciduous forest	28	32

Table 3 (continued)

Common name	Scientific name	Abbreviation code	Nest location	Primary diet	Primary habitat	Abundance	
						Black ash wetland	Upland forest
Magnolia Warbler	*Dendroica magnolia*	MAWA	Shrub	Foliage insects	Coniferous forest	1	0
Mourning Warbler	*Oporornis philadelphia*	MOWA	Ground	Foliage insects	Early-successional	3	4
Nashville Warbler	*Vermivora ruficapilla*	NAWA	Ground	Foliage insects	Lowland forest	20	15
Northern Flicker (Yellow-shafted)	*Colaptes auratus*	YSFL	Cavity	Ground insects and fruit	Early-successional	1	3
Northern Parula	*Parula americana*	NOPA	Canopy	Foliage insects	Lowland forest	18	2
Northern Waterthrush	*Seiurus noveboracensis*	NOWA	Ground	Foliage insects	Lowland forest	18	1
Ovenbird	*Seiurus aurocapilla*	OVEN	Ground	Foliage insects	Deciduous forest	58	114
Pileated Woodpecker	*Dryocopus pileatus*	PIWO	Cavity	Bark insects	Deciduous forest	0	1
Pine Warbler	*Dendroica pinus*	PIWA	Canopy	Foliage insects	Coniferous forest	2	0
Purple Finch	*Carpodacus purpureus*	PUFI	Canopy	Seeds	Mixed forest	0	2
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	Cavity	Bark insects	Coniferous forest	5	5
Red-eyed Vireo	*Vireo olivaceus*	REVI	Shrub	Foliage insects	Deciduous forest	61	56
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR	Shrub	Foliage insects	Deciduous forest	13	7
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU	Canopy	Nectar and Sap	Deciduous forest	1	2
Ruffed Grouse	*Bonasa umbellus*	RUGR	Ground	Omnivores	Deciduous forest	1	1
Scarlet Tanager	*Piranga olivacea*	SCTA	Canopy	Foliage insects	Deciduous forest	3	4
Song Sparrow	*Melospiza melodia*	SOSP	Ground	Ground insects and fruit	Fields and meadows	2	1
Swamp Sparrow	*Melospiza georgiana*	SWSP	Shrub	Omnivores	Shrub swamp	4	0
Veery	*Catharus fuscescens*	VEER	Ground	Ground insects and fruit	Deciduous forest	35	23
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	Cavity	Bark insects	Deciduous forest	2	0
White-throated Sparrow	*Zonotrichia albicollis*	WTSP	Ground	Ground insects and fruit	Early-successional	15	10
Winter Wren	*Troglodytes troglodytes*	WIWR	Cavity	Foliage insects	Lowland forest	12	0
Wood Thrush	*Hylocichla mustelina*	WOTH	Shrub	Ground insects and fruit	Deciduous forest	0	5
Yellow-bellied Flycatcher	*Empidonax flaviventris*	YSFL	Ground	Flycatchers	Lowland forest	2	0
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA	Cavity	Bark insects	Deciduous forest	2	11
Yellow-throated Vireo	*Vireo flavifrons*	YTVI	Canopy	Foliage insects	Deciduous forest	1	0

Appendix 2

Table 4 List of anuran species detected during surveys. Common name, scientific name, timing of breeding, breeding wetland status, and percent of sites each species was detected in black ash wetlands and emergent wetlands are provided. Breeding ecology classifications were sourced from Lannoo 2005

Common name	Scientific name	Timing of breeding	Breeding wetland status	% of sites present	
				Black ash wetland ($n=27$)	Emergent wetland ($n=20$)
American Toad	*Anaxyrus americanus*	Late spring	Temporary wetland	3.7	45.0
Boreal Chorus Frog	*Pseudacris maculata*	Early spring	Temporary wetland	25.9	55.0
Gray Tree Frog	*Hyla versicolor*	Summer	Temporary wetland	18.5	95.0
Green Frog	*Lithobates clamitans melanota*	Summer	Permanent wetland	0.0	30.0
Mink Frog	*Lithobates septentrionalis*	Summer	Permanent wetland	0.0	10.0
Northern Leopard Frog	*Lithobates pipiens*	Late spring	Temporary wetland	0.0	30.0
Spring Peeper	*Pseudacris crucifer*	Early spring	Temporary wetland	48.1	100.0
Wood Frog	*Lithobates sylvaticus*	Early spring	Temporary wetland	55.6	100.0

Appendix 3

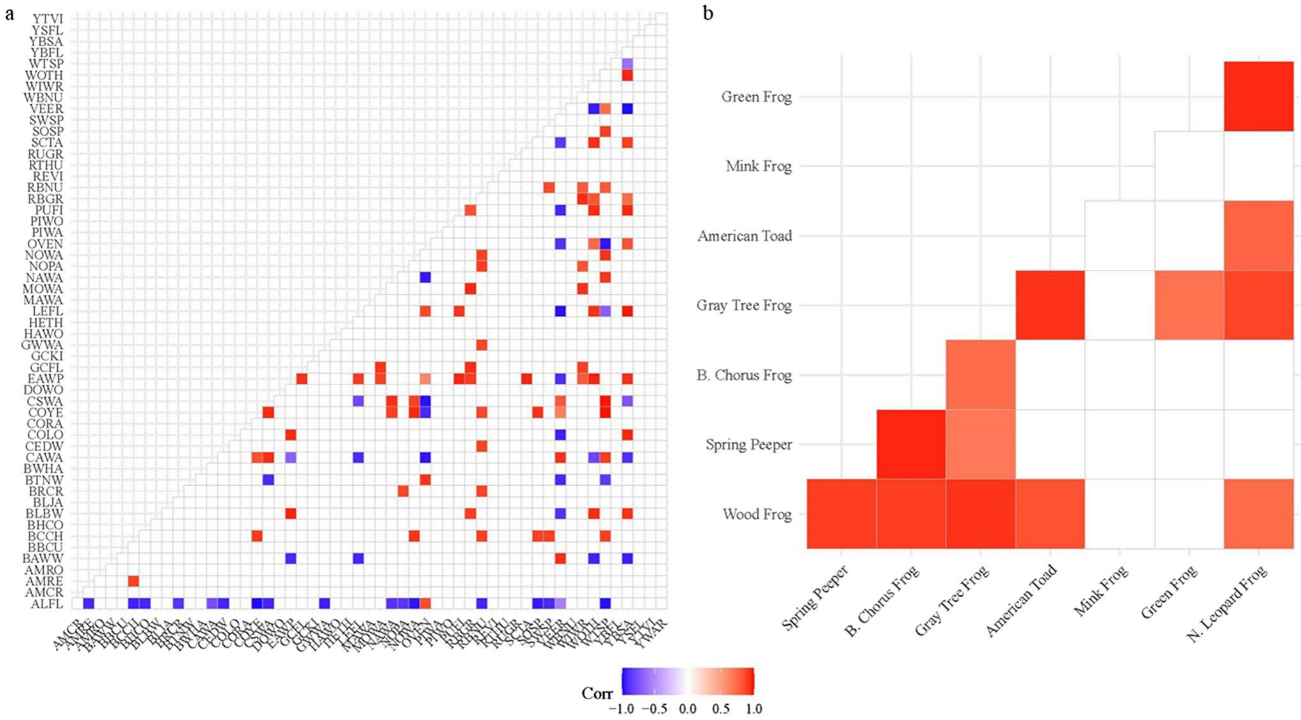

Fig. 3 Species correlation matrices for anuran (A.) and bird (B.) JSDM latent variable models. A.) Anuran species correlations for presence/absence. B.) Breeding bird species correlations; see Appendix 1 Table 3 for bird species abbreviation codes. Red indicates a positive correlation

Appendix 4

Table 5 Mean canopy height coefficient estimates and 95% confidence interval from multivariate community analyses. Bolded species have coefficients different from zero

Taxa	Common name	Coefficient estimate	95% C.I
Birds	**Alder Flycatcher**	**-0.33**	**0.27**
	American Redstart	-0.14	0.15
	American Robin	-0.05	0.12
	Black-and-white Warbler	-0.05	0.07
	Blackburnian Warbler	0.16	0.22
	Black-capped Chickadee	**-0.21**	**0.15**
	Black-throated Green Warbler	**0.09**	**0.07**
	Blue Jay	-0.02	0.09
	Broad-winged Hawk	-0.13	0.30
	Brown Creeper	-0.06	0.11
	Brown-headed Cowbird	**-0.62**	**0.44**
	Canada Warbler	-0.11	0.19
	Cedar Waxwing	-0.02	0.33
	Chestnut-sided Warbler	-0.07	0.09
	Common Yellowthroat	-0.08	0.08
	Downy Woodpecker	0.15	0.25
	Eastern Wood-Pewee	**0.18**	**0.12**
	Golden-crowned Kinglet	-0.89	1.31
	Golden-winged Warbler	-0.05	0.24
	Great Crested Flycatcher	0.05	0.14
	Hairy Woodpecker	0.15	**0.24**
	Hermit Thrush	-0.05	0.16
	Least Flycatcher	0.10	0.10
	Magnolia Warbler	-0.32	0.42
	Mourning Warbler	**0.19**	**0.15**
	Nashville Warbler	**-0.11**	**0.07**
	Northern Flicker (Yellow-shafted)	0.01	0.17
	Northern Parula	-0.13	0.18
	Northern Waterthrush	-0.02	0.15
	Ovenbird	**0.10**	**0.03**
	Pileated Woodpecker	-0.04	0.16
	Pine Warbler	0.58	1.08
	Purple Finch	0.22	0.27
	Red-breasted Nuthatch	-0.06	0.14
	Red-eyed Vireo	0.02	0.03
	Rose-breasted Grosbeak	-0.01	0.10
	Ruby-throated Hummingbird	0.08	0.30
	Ruffed Grouse	-0.27	0.33
	Scarlet Tanager	0.17	0.18
	Song Sparrow	0.01	0.17
	Swamp Sparrow	-0.03	0.30
	Veery	**-0.07**	**0.05**
	White-breasted Nuthatch	0.07	0.30
	White-throated Sparrow	**-0.12**	**0.07**
	Winter Wren	-0.02	0.14
	Wood Thrush	**0.19**	**0.15**
	Yellow-bellied Flycatcher	-0.10	0.30
	Yellow-bellied Sapsucker	**0.15**	**0.10**
	Yellow-throated Vireo	0.27	0.32
Anurans	**American Toad**	**-0.33**	**0.25**
	Boreal Chorus Frog	-0.03	0.11
	Gray Tree Frog	**-0.22**	**0.15**
	Mink Frog	-2.78	4.63
	Green Frog	**-0.44**	**0.41**
	Northern Leopard Frog	-0.64	0.66
	Spring Peeper	-0.13	0.18
	Wood Frog	-0.07	0.21

Appendix 5

Table 6 Results of generalized linear models used to assess relationship between bird species richness and total abundance and anuran species richness and environmental variables. Models that were significantly different from null models are bolded

Candidate models	AIC	Δ AIC	Akaike weights
Bird species richness			
Habitat type	**256.2**	**0.0**	**0.32**
SD Canopy cover index	258.0	1.8	0.13
SD Understory cover index	258.2	2.0	0.12
Mean Canopy height canopy	258.7	2.5	0.09
Mean Understory cover index	259.0	2.8	0.08
SD Canopy height canopy	259.2	3.0	0.07
Mean Canopy cover index	259.3	3.1	0.07
Upper canopy index	259.3	3.1	0.07
All canopy index	259.8	3.6	0.05
Site area	259.9	3.7	0.04
Null	257.9		
Bird total abundance			
SD Understory cover index*	**308.7**	**0.0**	**0.52**
Habitat type	**311.3**	**2.6**	**0.14**
Mean Understory cover index*	313.6	4.9	0.04
SD Canopy height canopy	312.8	4.1	0.07
Mean Canopy height canopy	313.3	4.6	0.05
Site area	313.4	4.7	0.05
SD Canopy cover index	313.6	4.9	0.04
Upper canopy index	313.6	4.9	0.04
All canopy index	313.6	4.9	0.04
Mean Canopy cover index	313.7	5.0	0.04
Null	311.7		
Anuran species richness			
Habitat type	**173.9**	**0.0**	**0.78**
All canopy index	**176.5**	**2.6**	**0.21**
Mean Canopy cover index	182.6	8.7	0.01
Mean Canopy height canopy	188.1	14.2	0.00
Site area	208.6	34.7	0.00
SD Canopy cover index	258.0	84.1	0.00
SD Understory cover index*	258.2	84.3	0.00
Mean Understory cover index*	259.0	85.1	0.00
SD Canopy height canopy	259.2	85.3	0.00
Upper canopy index	259.3	85.4	0.00
Null	206.4		

Acknowledgements Special thanks to Katy Johnson, Josh Bednar, and Steve Kolbe for wildlife data collection. Thanks to Michael Joyce for assistance developing lidar variables. We also thank the USDA Forest Service Chippewa National Forest, county land managers, and Minnesota Department of Natural Resources for providing the sites used in this research. This publication is Natural Resources Research Institute contribution number ###.

Author Contributions All authors contributed to the study conception and design. ARG and MBY designed the wildlife survey methods, conducted the investigation, and analyzed the data. ARG, MBY, RAS, wrote the manuscript, and AWD and BPP provided editorial advice and valuable insight. ARG, RAS, AWD, and BPP were involved with funding acquisition.

Funding Funding for the implementation of the study design and wildlife surveys was provided by the Minnesota Environment and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources (LCCMR). Additional support for this work came from the Upper Midwest and Great Lakes Landscape Conservation Cooperative, Department of Interior Northeast Climate Adaptation Science Center, and USDA Forest Service Northern Research Station.

Data Availability A long-term data sharing and preservation plan will be used to store and make publicly accessible the data beyond the life of the project. The data will be deposited into the Data Repository for the University of Minnesota (DRUM). A persistent link will be added to the manuscript if accepted into the journal.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

References

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. J Wildl Manag pp 912–918

Andersson J, Domingo Gómez E, Michon S, Roberge JM (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scandinavian Journal of Forest Research 33:233–244

Austin MP, Pausas JG, Nicholls AO (1996) Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. Australian Journal of Ecology 21:154–164

Bartels P, Cucherousset J, Steger K, Eklöv P, Tranvik LJ, Hillebrand H (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology 93:1173–1182

Bates D, Kliegl R, Vasishth S, Baayen H (2015) Parsimonious mixed models. arXiv preprint arXiv:1506.04967

Billerman SM, Keeney BK, Rodewald PG, and Schulenberg TS (Eds) (2020) Birds of the world. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home. Accessed 30 Nov 2021

Bowen AK, Stevens MHH (2018) Predicting the effects of emerald ash borer (*Agrilus planipennis*, Buprestidae) on hardwood swamp forest structure and composition in southern Michigan 1, 2. The Journal of the Torrey Botanical Society 145:41–54

Collins SL, James FC, Risser PG (1982) Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. Oikos 39:50–58

D'Amato AW, Palik BJ, Slesak RA, Edge G, Matula C, Bronson DR (2018) Evaluating adaptive management options for black ash forests in the face of emerald ash borer invasion. Forests 9:348

Dahl TE, Zoltai SC (2018) Forested northern wetlands of North America. In: Trettin CC, Jurgensen MF, Grigal DF, Gale MR, Jeglum JK (eds) Northern Forested Wetlands. Routledge, Boca Raton, pp 3–17

Dahl TE (1990) Wetlands losses in the United States, 1780s to 1980s. US Dept of the Interior, Fish and Wildlife Service

Dertien JS, Self S, Ross BE, Barrett K, Baldwin RF (2020) The relationship between biodiversity and wetland cover varies across regions of the conterminous United States. PLoS ONE 15(5):e0232052. https://doi.org/10.1371/journal.pone.0232052

Diamond JS, McLaughlin DL, Slesak RA, D'Amato AW, Palik BJ (2018) Forested versus herbaceous wetlands: can management mitigate ecohydrologic regime shifts from invasive emerald ash borer? Journal of Environmental Management 222:436–446

Diamond JS, McLaughlin DL, Slesak RA, Stovall A (2019) Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences 23:5069–5088

Diamond JS, McLaughlin DL, Slesak RA, Stovall A (2020) Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands. Biogeosciences 17:901–915

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366

Evenson GR, Golden HE, Lane CR, McLaughlin DL, D'Amico E (2018) Depressional wetlands affect watershed hydrological, biogeochemical, and ecological functions. Ecological Applications: A Publication of the Ecological Society of America 28(4):953–966. https://doi.org/10.1002/eap.1701

Fontúrbel FE, Orellana JI, Rodríguez-Gómez GB, Tabilo CA, Castaño-Villa GJ (2021) Habitat disturbance can alter forest understory bird activity patterns: a regional-scale assessment with camera-traps. Forest Ecology and Management 479:118618

Gandhi KJ, Herms DA (2010) North American arthropods at risk due to widespread Fraxinus mortality caused by the alien emerald ash borer. Biological Invasions 12:1839–1846

Gopal B, Junk WJ (2000) Biodiversity in wetlands: an introduction. In Biodiversity in wetlands: assessment, function and conservation. Vol. 1. Backhuys Publishers, pp 1–10

Grinde AR, Youngquist MY, Slesak RA, Kolbe SR, Bednar JD, Palik BJ, D'Amato AW (2022) Potential impacts of emerald ash borer and adaptation strategies on wildlife communities in black ash wetlands. Ecol Appl 32(4). https://doi.org/10.1002/eap.2567

Guzy MJ, Ritchison G (2020) Common Yellowthroat (*Geothlypis trichas*), version 1.0. In: Rodewald PG (ed) Birds of the World. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.comyel.01

Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CE, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6:e4794

Hobson KA, Bayne E (2000) Breeding bird communities in boreal forest of western Canada: consequences of "unmixing" the mixedwoods. The Condor 102:759–769

Hocking DJ, Semlitsch RD (2007) Effects of timber harvest on breeding-site selection by gray treefrogs (Hyla versicolor). Biological Conservation 138:506–513

Hoven BM, Knight KS, Peters VE, Gorchov DL (2020) Release and suppression: forest layer responses to emerald ash borer (*Agrilus planipennis*)-caused ash death. Annals of Forest Science 77:1–27

Hui FK (2016) boral–Bayesian ordination and regression analysis of multivariate abundance data in R. Methods in Ecology and Evolution 7:744–750

Kloiber SM, Norris DJ, Bergman AL (2019) Minnesota Wetland Inventory: User Guide and Summary Statistics [June, 2019]. Minnesota Department of Natural Resources, St. Paul

Klooster WS, Gandhi KJ, Long LC, Perry KI, Rice KB, Herms DA (2018) Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. Forests 9:250

Klooster WS, Herms DA, Knight KS, Herms CP, McCullough DG, Smith A, Gandhi KJ, Cardina J (2014) Ash (Fraxinus spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biological Invasions 16:859–873

Kolka RK, D'Amato AW, Wagenbrenner JW, Slesak RA, Pypker TG, Youngquist MB, Grinde AR, Palik BJ (2018) Review of ecosystem level impacts of emerald ash borer on black ash wetlands: what does the future hold? Forests 9:179

Lafage D, Bergman E, Eckstein RL, Österling EM, Sadler JP, Piccolo JJ (2019) Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a worldwide meta-analysis. Ecosphere 10:e02697

Lannoo M (2005) Amphibian declines. Univeristy of California Press, Berkeley

Lehmkuhl JF, Burger ED, Drew EK, Lindsey JP, Haggard M, Woodruff KZ (2007) Breeding birds in riparian and upland dry forests of the Cascade Range. The Journal of Wildlife Management 71(8):2632–2643

Liner, AE, Smith, LL, Golladay, SW, Castleberry, SB and Gibbons, JW (2008) Amphibian distributions within three types of isolated wetlands in southwest Georgia. The American Midland Naturalist, pp.69–81

Looney CE, D'Amato AW, Fraver S, Palik BJ, Reinikainen MR (2016) Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. Forest Ecology and Management 375:238–248

Lovett GM, Weiss M, Liebhold AM, Holmes TP, Leung B, Lambert KF, Orwig DA, Campbell FT, Rosenthal J, McCullough DG, Wildova R (2016) Nonnative forest insects and pathogens in the United States: Impacts and policy options. Ecological Applications 26:1437–1455

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology 42:594–598

Macdonald SE, Eaton B, Machtans CS, Paszkowski C, Hannon S, Boutin S (2006) Is forest close to lakes ecologically unique?: Analysis of vegetation, small mammals, amphibians, and songbirds. Ecological Applications 223:1–17

McGaughey RJ (2017) FUSION/LDV: Software for LIDAR data analysis and visualization. Ver. 3.6. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Seattle. https://www.fs.usda.gov/pnw/tools/update-fusionldv-lidar-processingand-visualization-software-version-360. Accessed 13 Feb 2020

Mitsch WJ, Hernandez ME (2013) Landscape and climate change threats to wetlands of North and Central America. Aquatic Sciences 75:133–149

MN DNR (2016) MNDNR Forest Stand Inventory. https://gisdata.mn.gov/dataset/biota-dnr-forest-stand-inventory. Accessed 30 July 2021

Morissette JL, Kardynal KJ, Bayne EM, Hobson KA (2018) Are boreal riparian bird communities unique? Contrasting riparian and upland bird assemblages in the Boreal Plain of western Canada. Wetlands 38:1299–1311

Nickerson RS (2000) Null hypothesis significance testing: a review of an old and continuing controversy. Psychological Methods 5:241

Niemi GJ, Howe RW, Sturtevant BR, Parker LR, Grinde AR, Danz NP, Nelson MD et al (2016) Analysis of long-term forest bird monitoring data from national forests of the western Great Lakes region. Gen Tech Rep NRS-159. US Dept of Agriculture, Forest Service, Northern Research Station, Newton Square

Odum EP (1950) Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31:587–605

Palik BJ, D'Amato AW, Slesak RA (2021) Wide-spread vulnerability of black ash (*Fraxinus nigra* Marsh.) wetlands in Minnesota USA to loss of tree dominance from invasive emerald ash borer. Forestry: An International Journal of Forest Research 94:455–463

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 29 Jan 2021

Riffell S, Burton T, Murphy M (2006) Birds in depressional forested wetlands: area and habitat requirements and model uncertainty. Wetlands 2–6:107–118

Roth RR (1976) Spatial heterogeneity and bird species diversity. Ecology 57:773–782

Sabo JL, Sponseller R, Dixon M, Gade K, Harms T, Heffernan J, Jani A, Katz G, Soykan C, Watts J, Welter J (2005) Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62

Sanders TA, Edge WD (1998) Breeding bird community composition in relation to riparian vegetation structure in the western United States. The Journal of Wildlife Management 62:461–473

Schindler DE, Smits AP (2017) Subsidies of aquatic resources in terrestrial ecosystems. Ecosystems 20:78–93

Semlitsch RD, Todd BD, Blomquist SM, Calhoun AJ, Gibbons JW, Gibbs JP, Graeter GJ, Harper EB, Hocking DJ, Hunter ML Jr, Patrick DA (2009) Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. Bioscience 59:853–862

Sitters H, York A, Swan M, Christie F, Di Stefano J (2016) Opposing responses of bird functional diversity to vegetation structural diversity in wet and dry forest. PLoS ONE 11:e0164917

Slesak RA, Lenhart CF, Brooks KN, D'Amato AW, Palik BJ (2014) Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Canadian Journal of Forest Research 44:961–968

Smith R, Hamas M, Dallman M, Ewert D (1998) Spatial variation in foraging of the Black-throated Green Warbler along the shoreline of northern Lake Huron. The Condor 100:474–484

Stewart RE (1953) A life history study of the Yellowthroat. The Wilson Bulletin 65:99–115

Swift BL, Larson JS, DeGraaf RM (1984) Relationship of breeding bird density and diversity to habitat variables in forested wetlands. The Wilson Bulletin 96:48–59

Van Buskirk J (2005) Local and landscape influence on amphibian occurrence and abundance. Ecology 86(7):1936–1947

Wang Y, Naumann U, Eddelbuettel D, Wilshire J, Warton D (2021) mvabund: statistical methods for analysing multivariate abundance data. R package version 4.1.12. https://CRAN.R-project.org/package=mvabund. Accessed 7 March 2021

Warton DI, Guillaume Blanchet F, O'Hara RB, Ovaskainen O, Taskinen S, Walker SC, Hui FKC (2015) So many variables: joint modeling in community ecology. Trends in Ecology & Evolution 30:766–779

Weir, LA and Mossman, MJ (2005) North American Amphibian Monitoring Program (NAAMP), p. 307-313. In Lannoo MJ (ed) Amphibian Declines: Conservation Status of United States Species. Univ. of California Press, Berkeley, 1094 pp

Whitaker DM, Eaton SW (2020) Northern Waterthrush (*Parkesia noveboracensis*), version 1.0. In Poole AF (ed) Birds of the World. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.norwat.01

Wolf AT, Howe RW (1991) The winter wren in Wisconsin. Passenger Pigeon 52:103–112

Youngquist MB, Eggert SL, D'Amato AW, Palik BJ, Slesak RA (2017) Potential effects of foundation species loss on wetland communities: a case study of black ash wetlands threatened by emerald ash borer. Wetlands 37:787–799

Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39–74

Zenzal TJ Jr, Smith RJ, Ewert DN, Diehl RH, Buler JJ (2018) Fine-scale heterogeneity drives forest use by spring migrant landbirds across a broad, contiguous forest matrix. The Condor: Ornithological Applications 120(1):166–184