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Effects of tree retention and woody biomass removal on bird and small mammal communities

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ABSTRACT

Contemporary forest management is increasingly focused on maintaining ecosystem function and services including biodiversity conservation. As a result, harvest guidelines related to retention of live trees and woody biomass (fine and coarse residue arising from harvesting) have been developed to provide benefits for wildlife, but there is much uncertainty on the effectiveness of these guidelines depending on stage of succession, retention levels, and focal taxa. We used an operational-scale, fully replicated factorial experiment to determine the effects of both tree retention (none, dispersed, aggregated) and woody residue harvesting (no removal, 20% retention, all removed) on breeding bird and small mammal communities in aspen forests 7–8 years after harvest. Bird community metric responses showed a clear and consistent positive response to tree retention; both tree retention configurations resulted in higher total abundance, increased diversity, and higher species richness compared to stands with no tree retention. There was no difference in community metrics between the retention configurations and no evidence that early successional species were negatively affected by tree retention. Total abundance of small mammals was lower in clear-cuts compared to tree retention treatments; moreover, clear-cut stands had lower species diversity compared to stands with the aggregated tree retention. There were limited effects of biomass harvest treatments on small mammal communities, likely because actual biomass removal was much lower than experimental targets. Overall, our results provide conclusive evidence on the continued benefits of tree retention on wildlife communities se0ven and eight years post-harvest in regenerating aspen forests.

1. Introduction

Forest management is increasingly focused on conservation of biodiversity and maintenance of ecosystem function and services (Gustafsson et al., 2010; McKinley et al., 2011; Kurth et al., 2014; Puettmann et al., 2015; Ezquerro et al., 2019; Kienast et al., 2019). As a consequence, many agencies and organizations have adopted policies to increase and maintain the ecological and structural complexity of stands during forest management activities with considerable focus on providing benefits for wildlife. Best management practices that promote these features have been developed and incorporated into harvest guidelines that address social, ecological, and economic considerations in forest management (Gulbrandsen, 2005; Auld et al., 2008; Rochelle, 2008; Elbakidze et al., 2011; Gustafsson et al., 2012).

A key component of harvest guidelines is retention of live overstory trees during harvest. Retention as part of forest management was formalized as a concept in North America approximately 30 years ago as a model to better integrate biodiversity conservation with wood production (Franklin, 1989). The retention concept is based on the idea that managed forests should approximate the habitats and structures resulting from natural disturbances, which typically contain live overstory trees (Angelstam and Pettersson, 1997; Lindenmayer et al., 2006). Indeed, "tree retention" has been shown as an effective silvicultural strategy for conserving biodiversity at landscape (Mori et al., 2017; Shea et al., 2017) and stand scales (Fedrowitz et al., 2014; Mori and Kitagawa, 2014; Augustynczik et al., 2018). The retention of clumps, i.e., aggregated retention, of intact forest may act as a refugia for late-successional plant species (Macdonald and Fenniak, 2007; Halpern et al., 2012), provide quality breeding habitat to a large group of forest bird species (Venier et al., 2015), and conserve small mammal communities after harvests (Gitzen et al., 2007; Aubry et al., 2009; Le Blanc et al., 2010). However, there is conflicting evidence of overall

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benefits to wildlife; for example, Otto and Roloff (2012) measured the effects of tree retention levels on forest bird occupancy and found that tree retention guidelines did not increase site occupancy of most mature forest-associated songbirds and may have negative effects on early-successional birds. Despite widespread implementation, there is still uncertainty related to the extent to which tree retention guidelines benefit biodiversity and wildlife depending on stage of succession, retention levels, and focal taxa (Rosenvald and Lõhmus, 2008; Felton et al., 2010; Gustafsson et al., 2010; Gustafsson et al., 2012).

Recent changes in forest markets have led to an increased interest in the utilization of woody biomass for energy to displace fossil fuel-derived carbon, particularly harvest residues including tops, branches, downed wood (Schlamadinger and Marland, 1996; Kurth et al., 2014), which can lead to a reduction of coarse and fine woody material that provides a host of ecological values (Evans et al., 2013). Consequently, harvest guidelines have also been developed for retention of fine and coarse woody material following harvest, to promote structural diversity and ecosystem functions such as improved water quality, soil productivity, and wildlife habitat (Hassinger, 1989; Riffell et al., 2011; Fritts et al., 2016). Removal of fine and coarse woody material during biomass harvesting has been shown to negatively impact diversity of saproxylic organisms (Bouget et al., 2012; Brazee et al., 2012), invertebrate biomass (Horn and Hanula, 2008), and birds during the breeding season (Lohr et al., 2002). However, Fritts et al. (2016) found that there was no impact from biomass harvesting to herpetofauna evenness, diversity, and richness. Similarly, Osbourne and Anderson (2002) found no negative effects of coarse woody material removal on small mammals. Discrepancies in biomass removal impacts to wildlife may be associated with differences in physiographic regions of the studies, level of biomass retention, age since harvest, scale of the studies, and focal taxa (Riffell et al., 2011).

Tree retention and biomass removal may have considerable effects on wildlife but there is conflicting evidence associated with the overall benefits of these practices depending on harvest characteristics and taxa being assessed (Venier et al., 2015; Fritts et al., 2016; Le Blanc et al., 2010; Gray et al., 2019). The goal of this study was to use an operational-scale, replicated experimental design to determine the effects of both tree retention and woody biomass harvesting on breeding bird and small mammal communities in aspen forests in northern Minnesota. Utilizing an experimental design minimizes confounding factors often associated with observational tree retention studies such as variations in age, harvest size, and landscape characteristics. Further, bird and small mammal species respond to different spatial scales and habitat structures, and evaluating the response of multiple taxa allows us to gain a broader understanding of the overall effects of harvest strategies on biodiversity. Our specific research objectives were to 1) determine how the amount and spatial configuration of tree retention affects bird and small mammal community diversity, richness, and total abundance, 2) determine how the amounts of biomass removal affect bird and small mammal community diversity, richness, and total abundance, and 3) examine if bird guilds and small mammal species have differential responses to biomass and tree retention treatments.

2. Methods

2.1. Sites and study design

The study area is located in northern Minnesota USA, which has a continental climate with mean growing season temperature of 15 °C and annual precipitation of ~ 700 mm. Four experimental study blocks were located in St. Louis County, Minnesota, USA near the towns of Independence (47° 0′ N, −92° 24′ W); Melrude (47° 15′ N, −92° 19′ W); south of Orr (48° 1′ N, −92° 59′ W); and north of Orr (48° 9′ N, −92° 59′ W; Fig. 1A). Sites were similar in stand composition, elevation (395–428 m), and topography (0–8% slopes; Klockow et al., 2013), with some variation in soil properties among them (Slesak, 2013).

The study focused on aspen-dominated ecosystems due to the regional extent and economic importance of this cover type (Haynes et al., 2017). The study blocks were located in mesic hardwood forests dominated by quaking aspen (*P. tremuloides*) that originated from clearcutting and ranged in age from 55 to 68 years at time of study establishment. Other common hardwood species in the study blocks included paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), and black ash (*Fraxinus nigra*); softwood species included balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white spruce (*Picea glauca*), with occasional northern white cedar (*Thuja occidentalis*) and eastern white pine (*Pinus strobus*). The site index for the four sites, which is a measure of potential site productivity, ranged from 22 to 24 m height at 50 years for quaking aspen.

The experimental design was a 3X3 randomized complete block factorial design with an untreated control (Fig. 1B), with each site serving as a block. Each study block was comprised of nine experimental treatment stands and one control that were 4.1 ha in size. Treatments were designed to examine the effects of two factors, woody biomass removal and tree retention, which each had three levels. Here we use the term woody biomass in reference to non-merchantable tops and limbs that are not typically removed from a site following harvest (variously referred to as logging debris, slash, harvest residue, organic matter removal). Target biomass retention treatment levels were 0%, 20%, and 100% retention, while tree retention treatment levels were no retention (i.e., clearcut), dispersed tree retention at a density of 30 trees ha^{-1} (~3.5% of pre-harvest trees) and a spacing of 21 m between trees, and aggregated tree retention in two clumps approximately 0.1 ha in size, a total of 5% of the site area. The treatments were designed to reflect operational practices, where woody biomass was backhauled onto the site after processing at the landing. Because of this approach, combined with high levels of incidental breakage during felling, actual levels of biomass retention were much higher than target levels (Klockow et al., 2013). Dispersed and aggregate green-tree retention and 20% biomass retention were based on recommendations within the Minnesota Forest Management Guidelines (Minnesota Forest Resources Council, 2014). Selection of individual retention trees in dispersed treatments and locations of aggregates also followed operational practices with retention trees selected to represent non-merchantable or underrepresented canopy species and aggregates located on unique ecological features (e.g., vernal pools, snags), where possible. Harvest treatments were implemented in February 2010 with mechanized equipment under frozen ground conditions.

2.2. Wildlife surveys

2.2.1. Avian point count surveys

Four, five-minute point count surveys were conducted in each treatment stand for complete coverage of the stand, point count locations were placed approximately 100 m apart (Fig. 1). Point counts were conducted by 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. All birds heard or seen from the point count locations were recorded, their spatial location within the stand recorded, and distance from observer was estimated (Howe et al., 1997; Niemi et al., 2016). We limited observations to birds detected within 50 m point count radius for our analyses to focus on birds observed in the treatment areas.

2.2.2. Small mammal trap surveys

Small mammals were trapped from late September through early October in 2017 and 2018. We used Sherman folding traps (3 × 3.5 × 9 " model LFATDG) baited with peanut butter dipped in oats, with a chunk of potato to serve as a water source and cotton balls for bedding. Two transects with five traps each were deployed in each treatment stand, with each array of five traps oriented in a north–south direction. Traps were placed 15 m apart, with the center of the western

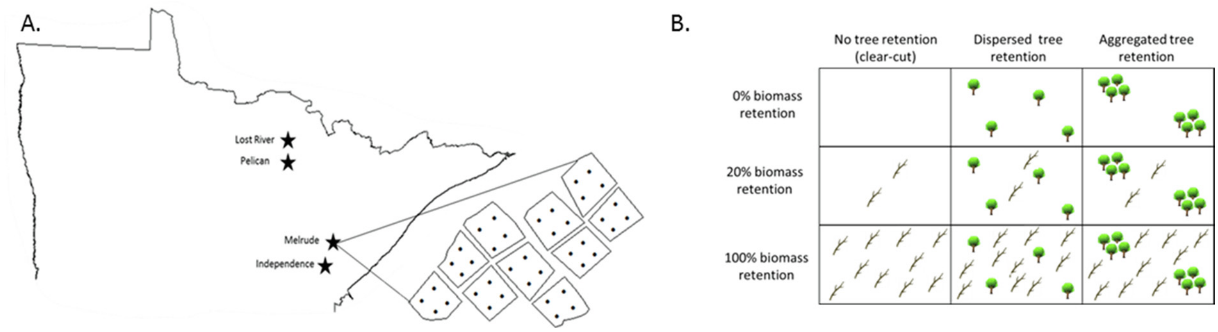

Fig. 1. A.) Four experimental study areas located in St. Louis County, Minnesota, USA. Each experimental study area is composed of 10, 4.1 ha treatment stands. Black dots represent the four bird survey locations in each treatment stand. B.) Experimental design for tree retention and biomass retention treatments implemented at the four study areas. Modified from Kurth et al. (2014).

set of five traps placed at the center of the stand. To maximize capture success, traps were placed opportunistically near the best available microhabitat (e.g., along logs, near stumps). Traps were set in the afternoon on the first day, remained open for two consecutive nights, and were pulled the morning of the third day. Traps were checked twice daily, re-baited, and cotton and potatoes were replaced as needed. Small mammals were identified to species, weighed, and marked either with a single ear tag (Model #1005-1, National Band and Tag Company) or marked with a black marker (shrews, meadow voles). Deer mice (*Peromyscus maniculatus*) are common in the study area; however, white-footed mice (*Peromyscus leucopus*) have also been documented in the region (Jannett et al., 2007). Because these species cannot be reliably distinguished in the field (Tessier et al., 2004), we combined the *Peromyscus* observations and present the results at the genus level. Medium-sized mammals were identified and released without tagging or measurement. 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 Number: 1709-35104A).

2.3. Data analysis

Bird and small mammal communities were summarized using three metrics: total abundance (total number of unique individuals in each treatment stand), Shannon–Wiener index of diversity, and species richness (number of species in each treatment stand). Because the study stands were the same size (4.1 ha) we did not convert abundance estimates to density metrics. Generalized linear mixed-effects models (GLMM) from the lme4 R package (Bates et al., 2015) were used to assess the effect of treatment type on species richness, total abundance, and diversity for breeding bird and small mammal communities. We hypothesized that tree retention treatments would influence bird community responses, whereas biomass removal treatments would have large influence on small mammal community responses. To test these hypotheses, we developed five candidate models to assess the effect of experimental treatments on bird and small mammal communities (Table 1). Study site was used as a random (block) effect in all models to account for variation among sites.

Species diversity was modeled using a gamma distribution; a subset of stands had mammal diversity values of 0 (i.e., species richness was 1) or undefined diversity (i.e., no small mammals were captured). We excluded stands with undefined diversity and transformed species diversity values by adding 1 to diversity values for all stands before fitting gamma GLMMs. Species richness and total abundance were modeled using a Poisson distribution. We compared candidate models using Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson, 2002) to determine best model(s), and the best model(s) were compared to null models (i.e., no fixed effects) to test for model significance (Nickerson, 2000; Harrison et al., 2018). Pairwise comparison with Tukey's post-hoc adjustments using the emmeans R package were applied to the best model to assess differences in response variables between treatments (Yandell, 1997; Zuur et al., 2009).

We used the same modeling approach described above to assess potential differential responses in abundance to treatments between bird guilds. Bird species observed in the study areas were categorized within foraging guilds, nesting guilds, and habitat preference guilds to assess patterns of response to harvest treatments (Appendix A). Information for categorizing species was obtained primarily from Ehrlich et al. (1988), Freemark and Collins (1992), and Niemi et al. (2016). We included only those guilds represented by four or more species in our analysis. Three guilds were used to classify nesting location: subcanopy or shrub (14 species), ground (15 species), and canopy (eight species) nesters. Four guilds were used to classify foraging strategy: aerial insects (four species), foliage insects (23 species), bark insects (five species), and ground insects (nine species). Five guilds were used to classify habitat preference: mixed forest (13 species), deciduous forest (13 species), early-successional (six species), shrub-swamp (five species), and open field (six species). We hypothesized significance of treatments would differ between guilds; for example, we hypothesized biomass removal would significantly affect the ground nesting and ground insect foraging guilds, whereas tree retention treatments would significantly affect canopy nesting and foliage insect

Table 1
Statistical models and associated hypotheses that were used to assess effects of tree and biomass removal on bird and small mammal community metrics, bird habitat and foraging guilds, and individual small mammal species. Five candidate generalized linear mixed models were ranked using an AIC framework.

Model	Hypothesis	Abbreviation
y = tree retention + biomass removal + tree retention:biomass removal + (1 | site)	Tree retention and biomass removal and the interaction of the treatments affect the response variable.	Full model
y = tree retention + biomass removal + (1 | site)	Tree and biomass retention affect response the variable.	Additive model
y = biomass removal + (1 | site)	Biomass removal affects the response variable.	Biomass removal model
y = tree retention + (1 | site)	Tree retention affects the response variable.	Tree retention model
y = 1 + (1 | site)	No tree retention or biomass removal effect.	Null model

foraging guilds.

Due to the lack of diversity in small mammal species captured in this study we were not able to assign meaningful guilds, therefore we fit individual species models to assess effects of treatments on red-backed voles (*Myodes gapperi*) and *Peromyscus*. Red-backed voles are associated with closed-canopy forests and therefore predicted higher abundance in aggregated tree retention treatments, whereas *Peromyscus,* an early-successional species, would be more abundant in clear-cut treatments. The same candidate models and fitting procedure described above were used for guild and small mammal species models.

3. Results

3.1. Bird community models

A total of 43 bird species and 1,019 individual birds were detected on the treatment stands during the 2017 and 2018 breeding seasons. The most abundant bird species identified in our study sites were chestnut-sided warbler (*Setophaga pensylvanica*), veery (*Catharus fuscescens*), golden-winged warbler (*Vermivora chrysoptera*), red-eyed vireo (*Vireo olivaceus*), and white-throated sparrow (*Zonotrichia albicollis*). The tree retention treatment model was the best model for all bird community response variables (Appendix B). Based on AICc values of the candidate models, biomass removal was not an important factor for predicting breeding bird community metrics, so results are not presented. Results of the model comparison showed that the tree retention models were significant compared to the null model for total bird abundance ($P < 0.01$), species diversity ($P = 0.02$), and species richness ($P = 0.02$; Appendix B). Pairwise comparisons between tree retention treatments show species diversity, species richness, and total abundance was significantly greater in aggregate compared to clear-cut treatments ($P_{div} = 0.04$; $P_{rich} = 0.03$; $P_{abund} < 0.01$; Fig. 2) and significantly greater in dispersed compared to clear-cut treatments ($P_{div} = 0.02$; $P_{rich} = 0.04$; $P_{abund} < 0.01$; Fig. 2). There was no difference between the dispersed and aggregate treatments ($P_{div} = 0.97$; $P_{rich} = 0.98$; $P_{abund} = 0.82$; Fig. 2).

3.2. Small mammal community models

A total of 257 individuals representing at least 9 species were caught during a sample effort of 1,440 trap nights and 720 trap days (2,160 combined trap period). Red-backed vole accounted for 65% of the total captures, followed by *Peromyscus* (19%), northern short-tailed shrew (*Blarina brevicauda*; 9%), and eastern chipmunk (*Tamias striatus*; 3%). Five additional species represented 4% of the total captures: red squirrel (*Tamiasciurus hudsonicus*), flying squirrel (*Glaucomys sabrinus*), short-tailed weasel (*Mustela ermine*), and meadow vole (*Microtus pennsylvanicus*). Tree retention models were significantly better at predicting small mammal species diversity ($P = 0.01$) and total abundance of small mammals ($P < 0.01$) compared to null models based on model comparison. We were not able to model small mammal species richness due to issues with convergence. Pairwise comparisons between tree retention treatments show small mammal species diversity and total abundance was significantly greater in aggregate compared to clear-cut treatments ($P_{div} = 0.01$; $P_{abund} < 0.01$; Fig. 2), however there were not significant differences between dispersed and clear-cut treatments ($P_{div} = 0.27$; $P_{abund} = 0.06$; Fig. 2) or between dispersed and aggregate treatments ($P_{div} = 0.31$; $P_{abund} = 0.15$; Fig. 2). As for birds, based on AICc values, biomass removal model was not an important factor for predicting small mammal community metrics.

3.3. Breeding bird guild models

Nesting guilds

We had adequate data to assess guild response to tree and biomass retention for canopy, ground, and shrub nesting bird species. Results

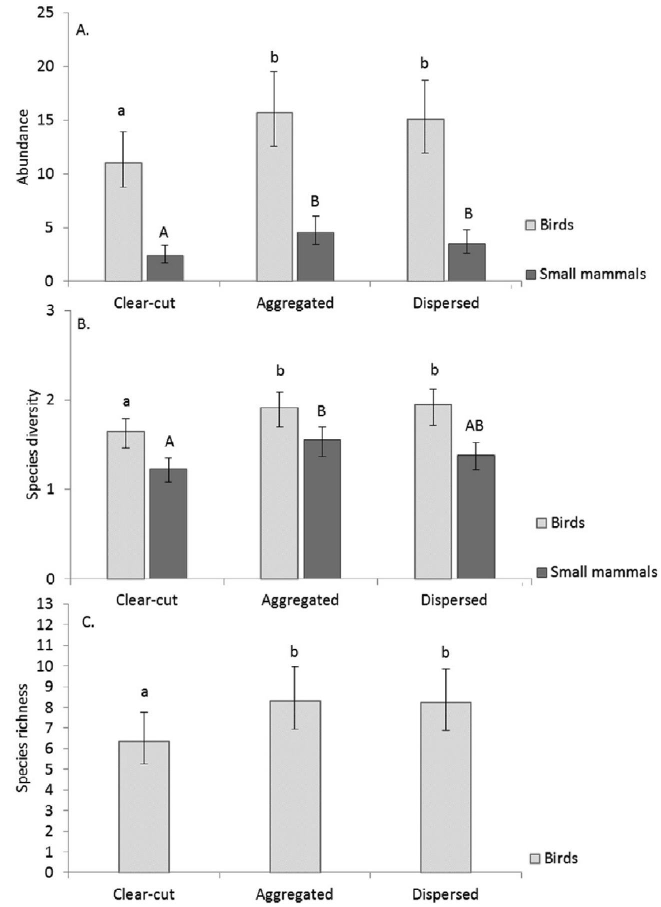

Fig. 2. Effects of tree retention treatments on breeding bird and small mammal community metrics A.) Total abundance, B.) Shannon–Wiener index of diversity, and C.) species richness based on results of generalized linear mixed-effects models with Tukey's post-hoc adjustments. Significant pairwise comparisons ($P < 0.05$) are indicated by different lowercase letters for birds and different uppercase letters for small mammals. Means were back-transformed based on the link function; error bars represent the 95% confidence intervals.

indicate that tree retention models were the best models for predicting total abundance for both canopy ($P < 0.01$) and ground ($P < 0.01$) nesting species. Tree retention was also the best model for shrub nesting species; however, model comparison indicated it was not significantly different from the null model ($P = 0.08$; Appendix B). We were not able to fit models for cavity nesting species due to low sample sizes. Tukey's pairwise comparisons for canopy and ground nesting guilds showed that abundance in dispersed ($P_{canopy} = 0.05$; $P_{ground} = 0.02$; Fig. 3a) and aggregate ($P_{canopy} = 0.05$; $P_{ground} = 0.01$; Fig. 3a) treatments were significantly higher than clear-cuts, but there was no significant difference between aggregated and dispersed treatments ($P_{canopy} = 0.99$; $P_{ground} = 0.86$; Fig. 3a). Based on AICc values, models that included biomass removal was not an important factor for predicting abundance in nesting guilds (Appendix B).Foraging guilds

Results for the four foraging guilds indicated that the tree retention treatment models were the best models for the bark insect ($P = 0.02$) and foliage insect ($P < 0.01$) guilds; however, the null model was the best model for aerial insect and ground insect guilds (Appendix B). Biomass removal was not an important factor for foraging guild abundance (Appendix B). Tukey's pairwise comparisons for the bark insects guild show that abundance in aggregated treatments was higher compared to clear-cut treatments ($P_{bark} = 0.04$; Fig. 3b) but not significantly different than the dispersed treatment ($P_{bark} = 0.15$; Fig. 3b), and there was no significant difference in abundance between clear-cut and dispersed treatments ($P_{bark} = 0.72$; Fig. 3b). The pairwise

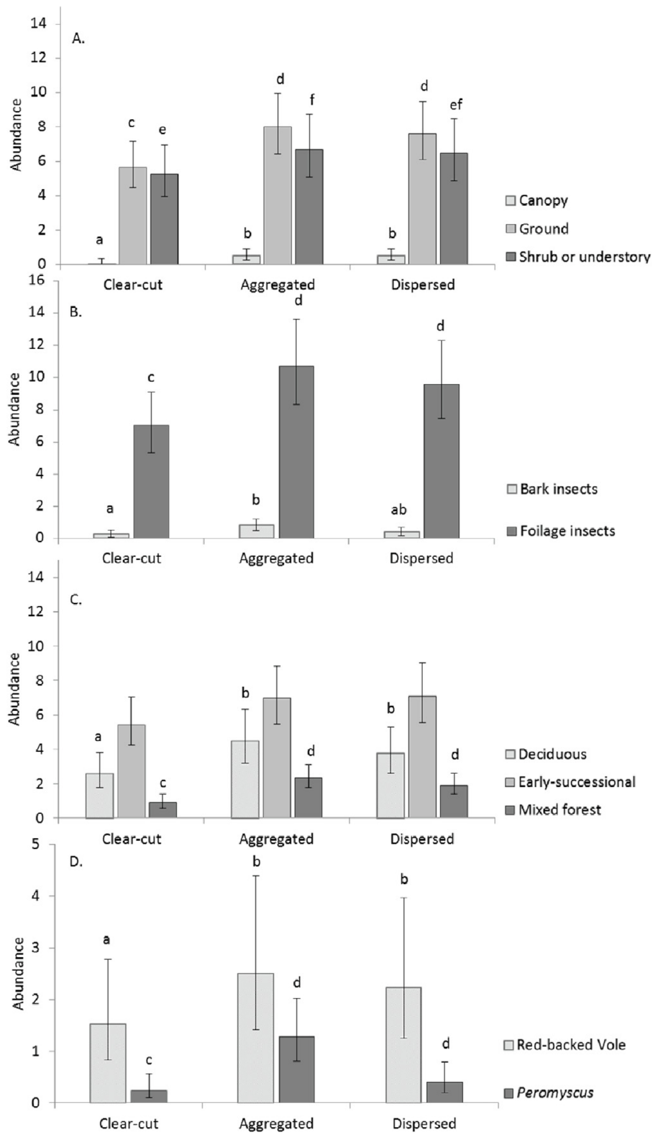

Fig. 3. Effects of tree retention treatments on abundance of A.) breeding bird nesting guilds, B.) breeding bird foraging guilds, C.) breeding bird habitat preference guilds,and D.) small mammal species based on results of generalized linear mixed-effects models with Tukey's post-hoc adjustments. Significant pairwise comparisons within each guild ($P < 0.05$) are indicated by different lower case letters. The means were back-transformed using the link function; error bars represent the 95% confidence intervals. Note that only results of significant models are shown.

comparisons for the foliage insect guild model showed that abundance in clear-cut treatments was significantly lower compared to aggregated ($P_{foil} < 0.01$; Fig. 3b) and dispersed treatments ($P_{foil} < 0.01$; Fig. 3b). There was no difference between the tree retention configurations ($P_{foil} = 0.44$; Fig. 3b).

3.3.1. Habitat preference guilds

The tree retention model was the best model for deciduous forest ($P < 0.01$), early-successional ($P < 0.04$), and mixed forest guilds ($P < 0.01$); however, the null model was the best model for the shrub-swamp and open field habitat guilds (Appendix B). Biomass removal was not an important factor for predicting abundance between habitat guilds (Appendix B). Tukey's pairwise comparisons for deciduous and mixed forest guilds indicated that compared to clear-cut treatments, abundance was significantly higher in aggregated ($P_{dec} < 0.01$; $P_{mixed} < 0.01$; Fig. 3c) and dispersed ($P_{dec} = 0.05$; $P_{mixed} = 0.01$; Fig. 3) treatments, but no difference between aggregated and dispersed treatments ($P_{dec} = 0.42$; $P_{ground} = 0.58$; Fig. 3c). The pairwise comparisons for the early-successional guild showed that there were no significant differences between treatments at the 0.05 level. However, the general trend is similar; the clear-cut treatment had lower abundance of early-successional species compared to the aggregated ($P = 0.09$), and dispersed ($P = 0.06$) treatments and retained tree treatments were similar ($P = 0.98$) in abundance (Fig. 3c).

3.4. Small mammal species abundance models

Results indicate that tree retention models were the best models for predicting total abundance for red-backed voles ($P = 0.03$) and *Peromyscus* ($P < 0.01$; Appendix B). Based on AICc values, biomass removal was not an important factor for predicting abundance of either species. Tukey's pairwise comparisons showed abundance was significantly higher in aggregate treatments compared to clear-cuts ($P_{RBVO} = 0.03$; $P_{Pero} < 0.01$; Fig. 3d), and there was not a significant difference between dispersed and clear-cut treatments ($P_{RBVO} = 0.14$; $P_{Pero} = 0.58$; Fig. 3d) for both species. However, models for *Peromyscus* showed that abundance was significantly greater in aggregate compared to dispersed treatments ($P_{Pero} < 0.01$; Fig. 3d), while the abundance of red-backed voles did not differ between aggregate and dispersed treatments ($P_{Pero} = 0.81$; Fig. 3d).

4. Discussion

Forest management guidelines for tree and woody biomass retention are widely implemented across much of the US (Evans et al., 2013; Rossman et al., 2018) and are generally thought to provide benefits to wildlife and conserve biodiversity. However, there are discrepancies amongst studies regarding the overall benefits to wildlife seemingly due to differences in tree retention levels, levels of coarse and fine woody residue removal, harvest size, and time since harvest. Our study used an operational-scale experimental design to assess the effects of tree and biomass retention based on Minnesota's Forest Management Guidelines (MFRC, 2014), allowing for the direct evaluation of management practices on breeding bird and small mammal communities. Bird community metrics responses showed a clear and consistent positive response to tree retention treatments; tree retention treatments resulted in higher total abundance, increased diversity, and higher species richness compared to stands with no tree retention. Similarly, total abundance of small mammals was lower in clear-cuts compared to tree retention treatments. Moreover, clear-cut stands had lower species diversity compared to stands with the aggregated tree retention. The results of our study provide important evidence for the continued benefits tree retention provides for wildlife seven and eight years post-harvest in regenerating aspen forests.

Overall, all bird species that were observed in the clear-cut sites were also observed in tree retention treatment stands, whereas 17 breeding bird species were associated with only one of the tree retention levels; nine species were found only in aggregated treatments and eight were found only in the dispersed treatments (Appendix A). This is an important result because it has been suggested that tree retention negatively effects early-successional and generalist bird species (Otto and Roloff, 2012); however, our results showed that early-successional species were present across retention treatments (Appendix A). The observed differences in species diversity and species richness in the tree retention treatments were associated with the presence of mature forest species such as least flycatcher and scarlet tanager, which were found only in retention treatments (Appendix A). These results suggest that at the successional stage our surveys were conducted, the retained trees provided an important habitat feature birds need for breeding activities such as territorial displays and nesting structures. An important next step is to focus on the effects of these treatments on overall productivity including nest success and juvenile survival.

The composition of observed bird communities differed between the aggregated and dispersed retention treatments (Appendix A); however, the bird community metric models did not indicate significant differences. This apparent null difference may be real but may also be associated with the successional stage at which we conducted our surveys (Leupin et al., 2004; Atwell et al., 2008), the size of the treatment areas, or the size of the aggregated patches (~0.1 ha). Despite the fact that the combination of horizontal and vertical forest structure has long been recognized as important to breeding birds (MacArthur and MacArthur, 1961; Willson, 1974; Whelan, 2001), relatively few studies have examined if and how the spatial configuration of retained trees impacts bird communities. The results of a recent study in red pine forests demonstrated that bird species richness was significantly greater over a 10-year time period in the large gap-aggregated treatment compared to dispersed and small gap-aggregated retention harvests (Shea et al., 2017). Although our results do not indicate a benefit of aggregated over dispersed retention to bird and small mammal communities, there are other benefits of aggregated retention including reduced blowdown risk and increased operational efficiency during harvesting. Ultimately, long-term and spatially-explicit studies are needed to better assess the effects of the spatial configuration of retained trees to maximize benefits for wildlife.

Fine and coarse woody debris affects food availability and microhabitats available for wildlife in forest stands (Riffell et al., 2011; Perry and Herms, 2017; Piętka et al., 2019). Many previous studies noted coarse woody debris as an important habitat feature for small mammals (Sullivan et al., 1999; Moses and Boutin, 2001; Etcheverry et al., 2005; Gitzen, 2006) and bird communities (Riffell et al., 2011). However, biomass retention was not a significant predictor for small mammal or bird community models. This may be associated with the operational treatment application used at study establishment, which resulted in much higher biomass retention than targeted for in each treatment (Klockow et al., 2013). It may also be that biomass removal effects are more important immediately after harvest because coarse woody debris provides structure in an otherwise open area. As the stand regenerates, wildlife communities may begin to respond to forest structure and canopy features, which develop more quickly in aspen forests because of its rapid growth. Overall, fine-scale habitat elements such as coarse woody debris, habitat features such as shrub cover, and tree retention combine to affect the habitat suitability for small mammal communities (Gray et al., 2019).

Reponses to tree retention treatments were relatively consistent across breeding bird guilds. For the nest guild, we predicted only the canopy nesting species to show a significant response to tree retention. Our results showed that abundance was higher for all nesting guilds in treatments with tree retention compared to clear-cut treatments. Our predictions for the effects of tree retention on foraging guilds were correct; the aerial insectivores and the ground insect guilds showed no response to retention treatment, whereas the foliage insect guild and bark insect guild responded positively to tree retention treatments. The tree retention treatments in our study provided a greater range of tree conditions and sizes within the stand compared to the clear-cut treatment, increasing the canopy complexity and foraging opportunities for these guilds (Nakamura et al., 2017; Joelsson et al., 2018). We predicted early-successional bird species to show no response to retention treatments, and birds associated with deciduous and mixed forests to respond favorably to aggregate retention treatments. Indeed, abundance of deciduous and mixed forests guild was higher in stands with retention, but there was no difference between aggregated and dispersed stands. Although the tree retention model for early-successional species was significant compared to the null model, the absence of significant pairwise comparisons at the 0.05 level suggests the effect of tree retention on early-successional species was limited.

Small mammal diversity in our study was low but representative of the small mammal community that occurs in northern Minnesota (Christian et al., 1996; Staus et al., 1999; Rentz, 2014). The community results are largely driven by red-backed vole and *Peromyscus* abundance, eastern chipmunk, and northern short-tailed shrew, which had about the same catch rate across tree retention treatments; however, flying squirrel were caught only in aggregated treatments, and short-tailed weasels were caught exclusively in dispersed treatments. Overall, the results of the small mammal models are consistent with other studies. For example, Gitzen et al. (2007) reported that small mammal capture rates were similar in dispersed and aggregated retention units. Likewise, Aubry et al. (2009) did not find any small mammal species that responded to pattern of retention but did report that the abundance of some small mammal species varied significantly with level of retention. Le Blanc et al. (2010) reported red-backed voles were most abundant in uncut treatments; However, other studies have shown that the species can persist in moderate numbers in harvested stands with > 10% tree retention (Moses and Boutin, 2001; Sullivan and Sullivan, 2001; Sullivan et al., 2001; Gitzen et al., 2007). Our results indicated red-backed voles were significantly lower in abundance in clear-cut areas, but abundance did not differ between aggregated and dispersed treatments. The retained trees along with the successional stage of the study areas likely provided adequate canopy cover, allowing for conditions that favor the growth of hypogeous ectomycorrihizal fungi, an important food source for the species (Gagné et al., 1999). Our results showed higher abundance of *Peromyscus* in treatments with tree retention, which was unexpected because several studies have reported positive response of deer mice to a range of overstory removals; this may be due to differences in cover types and physiographic regions (Sullivan et al., 1999; Moses and Boutin, 2001; Etcheverry et al., 2005; Gitzen, 2006). However, other studies have reported no change or negative effects of forest harvest on abundance (Healy and Brooks, 1988; Kirkland, 1977), which aligns with our findings.

5. Conclusions

Many studies have evaluated the impacts of tree and biomass retention on wildlife communities; however, conflicting results have been reported regarding the benefits of these practices depending on focal taxa, timeline of study, and level of retention. Because early-successional forests are dynamic, it is important to use a controlled experimental design to specifically evaluate treatment effects on wildlife. Overall, our results show that tree retention treatments at the levels implemented in this study do increase biodiversity of small mammal and breeding bird communities at 7–8 years after harvest. At the same time, we found no effect of biomass removal on bird and small mammal communities, either because implemented levels were much higher than planned or because the effect of biomass removal is limited to shortly after harvest. It is likely that responses to tree retention will change over time based on community composition and habitat needs of individual species, and as the stand continues to develop into a functioning forest (Price et al. 2020). In at least the short term, it appears that these retention recommendations will help to maintain biologically diverse forests needed to sustain ecological processes under changing environmental conditions. However, retention levels and configurations needed to sufficiently maintain biodiversity are still unknown, and future experiments should evaluate a wider range of tree retention to identify the level where biodiversity is optimized within the constraints of management.

6. Author statement

RAS, AWD, and BPP conceived and designed the experiment. ARG conducted the investigation and analyzed the data. ARG and RAS wrote the manuscript, and all other authors provided editorial advice. All authors were involved with funding acquisition.

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Appendix A. . List of bird species observed in experimental stands during the breeding season of 2017 and 2018. Guild assignments were based on Ehrlich et al. (1988), Freemark and Collins (1992), Niemi et al. (2016). Observations of species found in tree retention treatments are denoted with an "x"; species observed in only one treatments are bolded.

Common name	Scientific name	Nest guild	Habitat guild	Foraging guild	Clear-cut	Aggregated	Dispersed
Alder Flycatcher	*Empidonax alnorum*	Subcanopy or Shrub	Shrub swamp	Aerial insects	x	x	x
American Goldfinch	*Carduelis tristis*	Subcanopy or Shrub	Fields and meadows	Seeds	x	x	x
American Redstart	*Setophaga ruticilla*	Subcanopy or Shrub	Early-successional mixed	Aerial insects	x	x	x
American Robin	*Turdus migratorius*	Subcanopy or Shrub	Fields and meadows	Ground insects	x	x	x
Black-and-white Warbler	*Mniotilta varia*	Ground	Mixed forest	Bark insects	x	x	x
Black-billed Cuckoo	*Coccyzus erythropthalmus*	Subcanopy or Shrub	Deciduous forest	Foliage insects			**x**
Blackburnian Warbler	*Dendroica fusca*	Canopy	Mixed forest	Foliage insects		**x**	
Black-capped Chickadee	*Poecile atricapillus*	Cavity, Hole, or Bank	Deciduous forest	Foliage insects		x	x
Black-throated Green Warbler	*Dendroica virens*	Subcanopy or Shrub	Mixed forest	Foliage insects		x	x
Blue Jay	*Cyanocitta cristata*	Canopy	Deciduous forest	Omnivores		**x**	
Brown-headed Cowbird	*Molothrus ater*	Nest Parasite	Fields and meadows	Ground insects		x	x
Canada Warbler	*Wilsonia canadensis*	Ground	Mixed forest	Foliage insects		x	x
Cedar Waxwing	*Bombycilla cedrorum*	Subcanopy or Shrub	Deciduous forest	Foliage insects		**x**	
Chestnut-sided Warbler	*Dendroica pensylvanica*	Subcanopy or Shrub	Early-successional mixed	Foliage insects	x	x	x
Common Yellowthroat	*Geothlypis trichas*	Ground	Shrub swamp	Foliage insects	x	x	x
Eastern Wood-Pewee	*Contopus virens*	Canopy	Mixed forest	Aerial insects			**x**
Evening Grosbeak	*Coccothraustes vespertinus*	Canopy	Mixed forest	Foliage insects			**x**
Golden-winged Warbler	*Vermivora chrysoptera*	Ground	Early-successional mixed	Foliage insects	x	x	x
Gray Catbird	*Dumetella carolinensis*	Subcanopy or Shrub	Early-successional mixed	Foliage insects	x	x	x
Hairy Woodpecker	*Picoides villosus*	Cavity, Hole, or Bank	Deciduous forest	Bark insects		x	x
Hermit Thrush	*Catharus guttatus*	Ground	Mixed forest	Ground insects			**x**
Least Flycatcher	*Empidonax minimus*	Subcanopy or Shrub	Deciduous forest	Aerial insects			**x**
Lincoln's Sparrow	*Melospiza lincolnii*	Ground	Shrub swamp	Ground insects		**x**	
Mourning Dove	*Zenaida macroura*	Canopy	Fields and meadows	Seeds			**x**
Mourning Warbler	*Oporornis philadelphia*	Ground	Early-successional mixed	Foliage insects	x	x	x
Nashville Warbler	*Vermivora ruficapilla*	Ground	Mixed forest	Foliage insects	x	x	x
Northern Flicker (Yellow-shafted)	*Colaptes auratus*	Cavity, Hole, or Bank	Fields and meadows	Ground insects		x	x
Northern Parula	*Parula americana*	Canopy	Mixed forest	Foliage insects	x	x	x
Northern Waterthrush	*Seiurus noveboracensis*	Ground	Mixed forest	Foliage insects		**x**	
Ovenbird	*Seiurus aurocapilla*	Ground	Deciduous forest	Foliage insects	x	x	x
Purple Finch	*Carpodacus purpureus*	Canopy	Mixed forest	Seeds			**x**
Red-breasted Nuthatch	*Sitta canadensis*	Cavity, Hole, or Bank	Mixed forest	Bark insects		**x**	
Red-eyed Vireo	*Vireo olivaceus*	Subcanopy or Shrub	Deciduous forest	Foliage insects	x	x	x
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Subcanopy or Shrub	Deciduous forest	Foliage insects	x	x	x
Scarlet Tanager	*Piranga olivacea*	Canopy	Deciduous forest	Foliage insects		**x**	
Song Sparrow	*Melospiza melodia*	Ground	Fields and meadows	Ground insects	x	x	x
Veery	*Catharus fuscescens*	Ground	Deciduous forest	Ground insects	x	x	x
White-throated Sparrow	*Zonotrichia albicollis*	Ground	Early-successional mixed	Ground insects	x	x	x
Wilson's Snipe	*Gallinago delicata*	Ground	Shrub swamp	Aquatic invertebrates		**x**	
Winter Wren	*Troglodytes troglodytes*	Ground	Mixed forest	Foliage insects		**x**	
Wood Thrush	*Hylocichla mustelina*	Subcanopy or Shrub	Deciduous forest	Ground insects	x		x
Yellow Warbler	*Dendroica petechia*	Subcanopy or Shrub	Shrub swamp	Foliage insects	x	x	x
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Cavity, Hole, or Bank	Deciduous forest	Bark insects			**x**

Appendix B. . Results of candidate generalized linear mixed models used to assess effects of tree and biomass removal on bird and small mammal community metrics, bird habitat and foraging guilds, and individual small mammal species. Akaike's Information Criterion adjusted for small sample sizes for candidate are given, models were compared to the null models to assess significance, and significant values are bolded.

	Full model	Additive model	Biomass retention model	Tree retention model	Null model	*P*-value
	y = tree retention + biomass removal + tree retention:biomass removal + (1 | site)	y = tree retention + biomass removal + (1 | site)	y = biomass removal + (1 | site)	y = tree retention + (1 | site)	y = 1 + (1 | site)	

Birds						
Community metrics						
Species diversity	89.1	87	91.2	**84.9**	88.8	**0.02**
Species richness	342.6	337.5	341.5	**334**	338	**0.02**
Total abundance	448.3	445.3	463.9	**441.6**	460.9	< **0.01**
Nesting guild						
Canopy	117	112.3	118.2	**108.5**	114.3	< **0.01**
Shrub or subcanopy	385.9	380.8	381.4	378.6	379.6	0.08
Ground	393.2	391.3	398.2	**387.7**	394.8	< **0.01**
Habitat guild						
Deciduous	345.4	343.8	352.5	**340.3**	349.1	< **0.01**
Mixed forest	255.2	248.6	261.9	**247.3**	259.4	< **0.01**
Early-successional	379.5	374.9	376.4	**373.8**	376.2	**0.04**
Fields and meadows	160.9	154	150.3	152.2	148.7	na
Shrub swamp	235.9	233.3	229.9	229.9	226.4	na
Foraging guild						
Aerial insects	199.6	198.7	199.8	196	197	na
Foliage insects	391.6	385	400.5	381.1	396.9	< **0.01**
Bark insects	139.5	135.4	139.6	133.3	137.1	**0.02**
Ground insects	311.4	307.7	305.9	304.7	303.4	na
Small mammals						
Community metrics						
Species diversity	80	72.8	77.3	**69.1**	73.6	**0.01**
Total abundance	337.1	332.7	345.5	**329**	341.7	< **0.01**
Individual species						
Red-backed vole	292.7	288.4	292	**286.2**	289	**0.03**
Peromyscus	150	156.5	175.7	**152.7**	171.8	< **0.01**

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118090.

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