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Retention forestry influences understory diversity and functional identity

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Abstract. In recent decades, a paradigm shift in forest management and associated policies has led to greater emphasis on harvest practices that retain mature, overstory trees in forest stands that would otherwise be clear-cut. While it is often assumed that the maintenance of compositional and structural complexity, such as that achieved through retention forestry approaches, will also mitigate negative impacts to functional diversity, empirical evidence of this relationship is sparse. We examined the effects of an aggregated retention system on taxonomic and functional diversity in a regenerating aspen-dominated forest. Sampling was conducted along transects arranged to capture the transition from harvested (regenerating) forest to mature, unharvested forest (both intact forest stands and 0.1 ha retention aggregates). We then assessed the magnitude and distance of edge effects on multiple indices of taxonomic and functional diversity as well as functional identity. Twelve years after harvest, the distance and magnitude of edge effects on functional and taxonomic diversity did not differ between the two unharvested patch sizes (intact vs. aggregate); however, intact forest exhibited greater resistance to edge effects and greater depth of edge influence into harvested areas for some traits compared to aggregates. Analyses relying on functional traits were generally applicable across sites within a highly variable forest type, and our results demonstrate the promise of using functional traits to assess management impacts on plant diversity across a landscape. Aggregates maintained some functional attributes associated with interior forest and influenced adjacent regeneration. However, trends in some traits (i.e., shade tolerance and seed mass), particularly in the seedling layer, suggest aggregates of this size provide primarily edge habitat.

Key words: aggregate retention; edge effects; forest influence; functional diversity; functional identity; Populus tremuloides; *quaking aspen; retention forestry.*

INTRODUCTION

As uncertainty associated with the consequences of global environmental change mounts, it becomes increasingly important to understand and maintain the resilience and function of managed forests (Dale et al. 2001, Bonan 2008, Lutz et al. 2013, Mina et al. 2017). Following natural disturbance, surviving trees and other plants constitute a biological legacy that provides continuity between forest generations (Franklin et al. 1997, 2007), influences the regenerating forest (Keenan and Kimmins 1993, Baker et al. 2013), and helps maintain forest resilience and function (Fahey et al. 2018). Anthropogenic disturbances, such as those associated with conventional timber harvest approaches like clearcutting, often differ from natural disturbance in their impact on forest ecosystems (Lindenmayer and Franklin 2002) by removing these legacies and simplifying forest structure (Bergeron et al. 1999, Puettmann et al. 2009). This loss of complexity often negatively impacts biodiversity and may reduce resilience to future stress and disturbance (Bergeron et al. 1999, Elmqvist et al. 2003) and decrease provisioning of ecosystem services (Franklin et al. 1997, Isbell et al. 2011, Lindenmayer et al. 2012). Accordingly, forestry practices have been developed and implemented worldwide to address these potential impacts (Gustafsson et al. 2012, Halpern et al. 2012, Baker et al. 2013, Fedrowitz et al. 2014). These include a greater emphasis on two-aged and

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uneven-aged management systems in hardwood dominated forests of the central and eastern United States (e.g., Knapp et al. 2014, Morrissey et al. 2015), continuous cover forestry and irregular shelterwoods in hardwood and mixed wood forests of Europe and Canada (Pommerening and Murphy 2004, Raymond et al. 2009, Kuuluvainen et al. 2012, Raymond and Bédard 2017), and variable retention harvesting and the adaptation of more traditional silvicultural systems to include biological legacies through overstory retention (referred to collectively as "retention forestry" hereafter; c.f. Lindenmayer et al. [2012], Baker et al. [2016]) applied to a variety of forest types globally (Aubry et al. 2009, Craig and Macdonald 2009, Fedrowitz et al. 2014, Franklin et al. 2018).

Retention forestry involves the long-term reservation of mature, overstory trees to satisfy ecological objectives, including maintaining or increasing structural diversity, maintaining connectivity in an otherwise clear-cut stand, and ameliorating microclimatic conditions for various species (Heithecker and Halpern 2007, Lindenmayer et al. 2012, Fedrowitz et al. 2014, Baker et al. 2016b) in balance with productivity objectives (Franklin 1988, Gustafsson et al. 2012). Overstory trees can be reserved in aggregated and/or dispersed spatial patterns, each providing different benefits and requiring different operational considerations (Halpern et al. 2012, Fedrowitz et al. 2014). Small forest patches retained in harvest units ("aggregates"), comparable to remnants that persist following natural, stand-replacing disturbance, can provide temporary refugia for interior species while the surrounding forest regenerates and develops into suitable habitat (Franklin et al. 1997). Although aggregates do not necessarily provide habitat comparable to interior forest (Rosenvald and Lõhmus 2008, Gustafsson et al. 2010, 2012), multiple studies report higher values of species richness (in vascular plants and arthropods) in stands with retention aggregates compared to mature across temperate and boreal biomes worldwide (Mori and Kitagawa 2014, Fedrowitz et al. 2014). Successful "life-boating" of other taxa, such as birds, bryophytes, and lichens, varies among forest types globally (Moen and Jonsson 2003, Mori and Kitagawa 2014).

Evidence suggests that aggregated retention increases structural diversity at the scale of forest stands and provides habitat otherwise absent from clear-cuts, but less is known about the effect aggregates have on species re-establishment or persistence and biodiversity in surrounding harvests ("forest influence"; Keenan and Kimmins 1993, Baker et al. 2013). Forests have long been managed with the knowledge that uncut forest affects the composition, abundance, and growth of adjacent, regenerating clear-cuts by providing seed and influencing light environments and the associated microclimate (Bradshaw 1992, Cadenasso et al. 1997, Heithecker and Halpern 2007). It is often assumed the influence extends up to one tree height (e.g., Mitchell and Beese 2002), but the magnitude and actual extent of forest influence is expected to vary with region and forest type, in part because of varying tree heights and solar altitude (Baker et al. 2016b). Forest influence on the microenvironment in the surrounding harvested areas varies with age of the regenerating stand and can persist up to 45 yr following harvest (Baker et al. 2014), which has implications for community composition and biodiversity in the understory. Plant traits, including those species characteristics that affect the distance and magnitude of forest influence on plant species re-establishment and community composition (i.e., seed dispersal distance and shade tolerance), may also ultimately impact forest function and disturbance response (Díaz and Cabido 2001, Diaz et al. 2004, Garnier et al. 2004, Funk et al. 2017).

Maintenance of ecosystem function is a fundamental goal of retention forestry. Early objectives for retaining biological legacies, the foundation of retention forestry, highlighted the need to conserve diversity that is "functional" in the sense that it provides specific ecosystem functions such as nitrogen fixation (Franklin 1988), carbon storage (Harmon et al. 1990, Bradford et al. 2009), amelioration of the microclimate (Heithecker and Halpern 2007, Baker et al. 2014), maintenance of source populations for regenerating plant species (Bradshaw 1992, Baker et al. 2013), and maintenance of soil communities, which indirectly impact resource availability (Luoma et al. 2006, Siira-Pietikäinen and Haimi 2009). In the time since retention forestry was first proposed, the importance of diversity in functional attributes ("functional diversity") has become more apparent (i.e., Mouillot et al. 2013). While environmental filtering, a process through which conditions lead to more functionally similar communities, is more frequently associated with gradients at regional scales (Mouchet et al. 2010, Venn et al. 2011, Laliberté et al. 2013), disturbances such as forest harvest can also act as an environmental filter that effectively selects more species because of similar traits (Mouillot et al. 2013). It is often assumed that functional diversity is sustained through maintenance of compositional and structural diversity (Ferris and Humphrey 1999, Hunter and Gibbs 2006), and methods for assessing it in comprehensive and relevant ways continue to be developed (Díaz et al. 2007,Mouillot et al. 2013). Thus, the direct impact of retention on functional diversity has not been extensively tested (but see Lachance et al. 2013).

Quantifying and assessing the responses of functional diversity (the distribution and abundance of species in trait space) and functional identity (mean community values for individual traits (Mouillot et al. 2013) are important for at least two reasons. First, these metrics may have particular importance at broader scales, such as across landscapes or regions. Variability in species composition and abundance increases with increasing spatial extent (Weaver 1995, Reich et al. 1997, Lavorel and Garnier 2002, Garnier et al. 2004, Lavorel et al. 2007), so taxon-independent measures, such as functional identity or functional diversity indices, may enable generalized assessments of community structure and function (e.g., Westoby and Wright 2006). For example, studies reporting increased species richness and species diversity with increasing harvest severity in the Midwestern United States (e.g., Zenner et al. 2006, Kern et al. 2014) have also provided more detailed, treatment-specific information relevant to management by including assessments of functional group response and functional identity. It is possible that inconsistent observations of biodiversity response to retention approaches worldwide may partly result from community compositional differences (Rosenvald and Lõhmus 2008). Second, functional diversity may relate more directly to the mechanisms controlling ecosystem productivity and response to disturbance and stress (Garnier et al. 2004, Hooper et al. 2005). Evidence also suggests that relationships between traits and function may not be static through time, but that a diversity of traits is necessary to maintain ecosystem function as conditions (climatic and otherwise) fluctuate (Isbell et al. 2011).

Our study assesses the influence of retention forestry practices on the biodiversity of regenerating mesic northern hardwood forest near the southern boreal transition zone by testing three hypotheses. First, given the natural heterogeneity that characterizes this forest type (demonstrated by a concurrent study [Baker et al. 2016]), we predicted that functional diversity and identity would be more likely to exhibit consistent responses to the gradient in conditions we tested across sites than more conventional approaches based on taxonomic diversity. Second, we hypothesized that adjacent, intact, and mature forest would influence functional diversity and identity in harvested areas, as would aggregates, albeit to a lesser extent. Last, we expected taxonomic diversity, functional diversity, and functional identity in adjacent intact forest to be more resistant to edge effects than in aggregates. We examined these hypotheses 12 years after a retention harvest with two sample populations of forest plants: (1) saplings and large shrubs (woody stems >1 m height and <10 cm diameter at breast height [DBH]) and (2) seedlings and small shrubs (woody stems <1 m height). This research was accomplished using a data set that includes replicates from multiple sites dominated by *Populus tremuloides* Michx. (quaking aspen), the widest ranging tree species in North America and of particular ecological and economic importance in the Upper Great Lakes region of the United States and Canada.

Methods

Study area

This study examines mesic northern hardwood forests located in northern Minnesota, USA. The mature canopy of the study area is dominated by *P. tremuloides*, *Acer rubrum* L. (red maple), and *A. saccharum* Marshall (sugar maple) with lesser components of *Tilia americana* L. (American basswood), *Quercus macrocarpa* Michx. (bur oak), and *Betula papyrifera* Marshall (paper birch; Appendix S1: Table S1). Prior to harvest, these forests were second-growth, even-aged stands that regenerated following an extensive harvesting period that characterized the region during the period 1930–1940. Parent materials were deposited by glaciation during the Wisconsonian age and are characterized as gently rolling moraines with thick glacial till. Over the last 50 years, total annual precipitation has averaged 63 cm, including an average of 99 cm snowfall (National Climate Data Center, data *available online*).[7] Precipitation is distributed relatively evenly throughout the year but with higher values often recorded in June and July (Palik and Kastendick 2010).

Three sites were selected based on criteria for inclusion in a broader, associated study (Baker et al. 2016a): Ashebun Lake (AL), Soo Line (SL), and Dog Lake (DL). In December 2000 or January 2001 when soils were frozen and snow-covered, merchantable trees (DBH > 11.4 cm) were harvested throughout each site, except for retention patches ("aggregates") of mature, overstory trees. The operational-scale harvests removed all overstory trees, and while some small trees likely persisted, the vast majority of woody vegetation regenerated or recruited post-harvest. The aggregates varied in shape but had a minimum radius of 20 m from harvest edge to center (0.12–0.18 ha in area). Two types of transects, those intersecting the harvested edges of "aggregates" and of "intact forest" immediately adjacent to the harvest unit, were replicated twice at each site (Fig. 1) at least 60 m apart resulting in a total of six replicates for both conditions. Intact forest transects were placed in unharvested forest stands at least 200 m wide and deep, and aggregates with transects had to be located at least 100 m from unharvested forest (Baker et al. 2016a). We used the only three sites of comparable harvest year that met our selection criteria.

Field methods

Sampling occurred during summer 2012, the 12th growing season following harvests. The analysis presented here includes data collected in plots placed every 10 m along both types of transect from −45 m within mature unharvested forest (14 plots/transect, Fig. 1A) and −15 m within aggregates out to 45 m from mature overstory into open, harvested areas (10 plots/transect Fig. 1B). Additionally, plots located 95 m within intact forest were sampled to represent "interior forest" conditions. These transects were replicated twice at each of the three sites with two exceptions. Two +5 m plots at Ashebun Lake were excluded because of a skid trail. This design resulted in a total of 102 plots.

We characterized the understory woody community by sampling two strata: (1) seedlings and small shrubs

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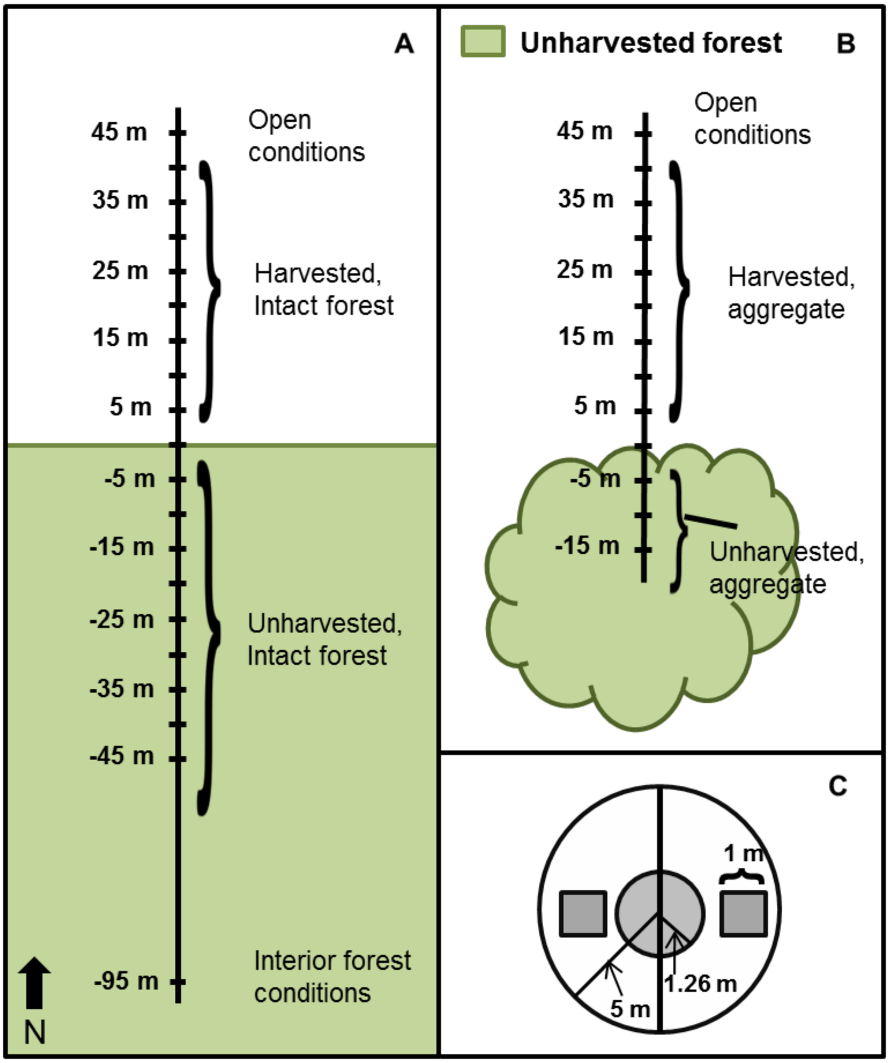

FIG. 1. Transect design. Plots along transects extend from 45 m within unharvested forest (indicated by negative distances) out to 45 m into harvested areas (positive numbers). Similar transects were placed (A) in intact forest and (B) through aggregates, with additional plots placed at −95 m to represent interior forest conditions. (C) Nested, understory, sampling plots of three difference sizes were centered on each 10 m distance mark along transects (A, B).

("seedling layer") and (2) saplings and large shrubs ("sapling layer"). Cover for the seedling layer (all woody stems <1 m in height) was estimated to the nearest 1% (or nearest 0.1% if cover $<1\%$) in paired, 1-m^2 subplots located 2 m perpendicular to and on either side of transects at each 10-m distance and nested within the plot used for quantifying larger vegetation (Fig. 1C). Species abundance in the sapling layer was measured using a combination of two plot sizes (Fig. 1C). Species and DBH (1.37 m) were recorded for larger stems ($2.54 \text{ cm} \geq \text{DBH} \leq 10 \text{ cm}$) in circular 5 m radius plots (78.5 m^2) centered on each 10-m distance mark along transects. Smaller stems with height ≥ 1 m and DBH < 2.54 cm were measured 15 cm above the root collar in circular, 1.26 m radius (5 m^2) plots nested within the larger plots.

Analysis

Species traits, functional identity.—We focused on seven quantitative plant traits relating to function in terms of effects on ecosystem processes and disturbance response (Cornelissen et al. 2003, Lavorel et al. 2007, Suding and Goldstein 2008). Mean trait values for each species were collected from the literature with preference given to studies in the Lake States region (Appendix S2: Table S1). Intraspecific variation occurs in many traits and can be attributed to ontogeny, annual fluctuations in climate, and other factors (Albert et al. 2010, Clough et al. 2017, Burton et al. 2017). This informed our selection of "effect" traits: seed mass, average height at maturity, specific gravity (wood density), and leaf mass per area, which are less plastic than other commonly measured traits and more likely to vary among than within species (Albert et al. 2010, Burton et al. 2017). We also included three traits more directly related to response: drought tolerance, flood tolerance, and shade tolerance. While some traits were significantly correlated for species in this study, correlation coefficients did not exceed |0.7| for pairs of any of the traits included, suggesting minimal risk of collinearity (Dormann et al. 2013).

The functional identity for each site consists of the community-weighted means (CWM) for each of the seven species traits defined as

$$\mathrm{CWM}_{aj} = \sum (S_{ij} \times t_i) \tag{1}$$

where CWM_{aj} is the mean for trait a in plot j, s_{ij} is the relative abundance of species i in plot j, and t_i is the trait value for species i (Lavorel et al. 2008). Relative abundance was defined based on percent cover for woody vegetation shorter than 1 m in height. For the sapling layer, relative abundance was based on standing biomass (Mg/ha) summed for the two size classes sampled. Species-specific allometric equations based on diameter measurements were used for biomass estimation (Perala and Alban 1993).

Functional diversity indices.—In order to capture multiple aspects of functional diversity at each distance from edge, we calculated functional divergence (FDiv) and functional dispersion (FDis) for both woody strata in each plot using the FD package (Laliberté and Shipley 2011) in R v 3.0.2 (R Core Team 2013). FDiv quantifies the prevalence (based on abundance) of extreme trait values; greater FDiv indicates more extreme values (Mason et al. 2005, Villéger et al. 2008). FDis is more holistic and describes the abundance-weighted mean distance between species in a community and the center of the functional space that a community occupies (Laliberté and Legendre 2010, Mouillot et al. 2013). Both traits are also independent from species richness (Villéger et al. 2008, Laliberté and Legendre 2010) and relatively insensitive to undersampling (van der Plas et al. 2017). We standardized species trait values (mean = 0, standard deviation = 1) across all species observed within the study to meet statistical assumptions and equalize weighting in calculation of indices (Villéger et al. 2008).

Functional diversity and composition across conditions.—Functional diversity and traits in both strata were analyzed using multilevel analysis of variance (ANOVA) to determine whether they differed among treatment conditions as follows: Open conditions (harvested plots [+] 45 m from an edge, n = 12); Harvested, near aggregate (harvested plots [+] 5–35 m from an aggregate edge, n = 22); Harvested, near intact forest (harvested plots [+] 5–35 m from forest edge, n = 24); Unharvested, within aggregate (unharvested plots [−] 5–15 m from aggregate edge, n = 12); Unharvested, intact forest (unharvested plots [−] 5–45 m from forest edge, n = 30); and interior forest (unharvested plots [−] 95 m from forest edge, n = 6). A random effect allowed the intercept to vary by transect, nested within site. For those variables with means that were not the same among groups, Tukey-adjusted post hoc comparisons were used to determine whether differences existed between pairs of conditions as defined above (open conditions, harvested aggregate, etc.). We conducted analyses in SAS 9.4 using the MIXED procedure (SAS Institute, Cary, North Carolina, USA).

Forest influence and edge effects.—For each woody layer, we estimated forest influence and edge effects on three indices of taxonomic diversity (species richness, species evenness, the Shannon index), the four functional diversity indices defined above, and the community-weighted mean for each of seven functional traits using the following equation adapted from methods for assessing magnitude of edge influence (MEI; Harper et al. 2005):

$$\mathrm{MEI} = (e-r)/(e+r) \tag{2}$$

where e represents the mean responses for plots located some distance from edge (pictured in Fig. 1) and r represents the mean of observations from a reference condition. This approach yields values that range between −1 and 1 with a value of 0 indicating no difference from the reference. For our study, we conducted this analysis twice, each with a different reference value and purpose. First, we used observations at 45 m from harvest edges along the same transect to represent harvested, open conditions (Fig. 1A,B). Thus, if MEI equals 0, then the value of a given variable is similar to what might be expected following a conventional clear-cut harvest (Harper et al. 2005). Secondly, we quantified an interior reference by averaging both observations from interior forest (95 m from harvest edge) within each site. A site-wide average was used because it was not possible to have interior forest plots along aggregate transects. In this second approach, if MEI equals 0, then the value of a given variable is similar to expectations for interior forest habitat. Through the use of two reference conditions we were able to assess whether aggregates achieved objectives related to providing refugia for species that require interior forest conditions while also assessing whether aggregates effectively influenced structure and function relative to what might be expected in a clear-cut without retention and, ultimately, the distance (or depth) from edge where these effects occurred. Knowledge of this depth of edge influence (DEI) has potential for informing the most effective size and placement of aggregates within a harvest unit for achieving specific habitat objectives.

After quantifying MEI, we tested the null hypothesis that presence or absence of mature overstory (either intact forest or aggregates) had no influence on regenerating forest habitat (MEI = 0) using the randomized test of edge influence (RTEI) approach (Harper and Macdonald 2011, Dupuch and Fortin 2013, Dodonov et al. 2013). This entailed comparing mean observed MEI to 95% confidence intervals derived from a distribution of randomized MEI values for each response variable at each distance, individually (i.e., Harper et al. 2015, Dupuch and Fortin 2013). The randomized distributions were generated using blocking, with 5,000 permutations per site (block) as described by Harper and Macdonald (2011). If MEI fell within the confidence intervals at all distances, indicating no difference from 0 at any distance, then the DEI was considered nonsignificant (Harper and Macdonald 2011). We define forest influence as occurring at the first of at least two consecutive distances from edge where we observed any evidence of unharvested forest affecting harvested, regenerating forest (Harper et al. 2015). This includes values different from the open, harvested reference. It also includes all harvested plots with values similar to interior forest in those cases where interior forest differed significantly from the open, harvested reference. Likewise, edge effects within unharvested forest were defined as occurring at the nearest of two consecutive (−) distances from edge where a given variable differed from interior forest conditions (e.g., Harper et al. 2015). Edge effects were also interpreted as occurring where values for a given variable were equal to observations in open, harvested conditions if means for open, harvested conditions differed significantly from interior forest.

RESULTS

Twelve years after harvest, means across all harvested plots indicated that *P. tremuloides* dominated the lowest layer of the woody understory (height < 1 m) as well as the sapling layer (height > 1 m and DBH < 10 cm). The presence and abundance of other woody species varied depending on condition. This included whether harvest had occurred, whether unharvested forest was intact or in an aggregate, and distance from the boundary between harvested and unharvested forest. Total species lists for each broad condition (e.g., Figs. 2, 3) are provided in Appendix S1: Table S1.

Functional vs. taxonomic diversity

Generally, the diversity indices that differed among the conditions we compared (within unharvested aggregates, interior forest, etc.) showed consistent responses between taxonomic and functional measures. For example, means for both taxonomic (species evenness and diversity]*H*']) and functional (functional dispersion) measures of diversity in the seedling layer were significantly lower in harvested plots near aggregates relative to unharvested plots (Fig. 2A, B, D). In the sapling layer, taxonomic (species richness) and functional (functional divergence) diversity indices also responded consistently with means lowest in interior forest and increasing in the adjacent harvested area (Fig. 2H, J); however, species evenness in this layer showed an opposite trend with higher values occurring in interior forest compared to open conditions (Fig. 2F).

Community-weighted means for individual plant traits (Fig. 3) exhibited pairwise differences between conditions that were not evident in the responses of diversity indices (Figs. 2, 4). Those traits that differed among conditions (drought tolerance, shade tolerance, seed mass, and specific gravity) exhibited trends more clearly suggestive of a gradient in conditions (Figs. 3, 5) as described in greater detail below.

Mature forest influence on harvested areas

While many of the measures we used to characterize biodiversity within the understory woody community responded consistently between harvested areas near aggregates and near intact forest, a few trends for specific indices and plant traits suggest intact forest had greater influence on surrounding regeneration. For example, species evenness (Fig. 2A), *H*' (Fig. 2B), functional dispersion (Fig. 2D), and mean seed mass (Fig. 3F) in the seedling layer regenerating near intact forest were more similar to unharvested forest than those observed in harvested plots near aggregates, although there were nonsignificant trends for higher values of the diversity indices (Fig. 2A,B,D) in open harvested conditions. Also, seed mass in the regenerating sapling layer near intact forest had intermediate values between unharvested areas and open conditions while areas near aggregates were no different from the open (Fig. 3M).

Additionally, some trait responses suggest intact forest has greater depth of influence than aggregates on the seedling layer of adjacent harvested areas (Fig. 5A–D), if not on saplings and large shrubs (Fig. 5I–L). Mean drought tolerance and specific gravity in the seedling layer was comparable to interior forest up to 25 m into harvested areas near intact forest compared to 5 m for aggregates (Fig. 5A,D). Shade tolerance (Fig. 5B) and seed mass (Fig. 5C) showed similar trends, though extending shorter distances (5–15 m), compared to no apparent influence from aggregates. Three traits tested (flood tolerance, maximum height, and leaf mass per area) did not differ between interior forest and open, unharvested conditions for either layer (Fig. 3).

Edge effects in unharvested forest

Edge effects (differences in values relative to interior or open conditions) also indicated varying impacts of intact forest and aggregates on the woody understory. Based on the interior reference, shade tolerance and seed

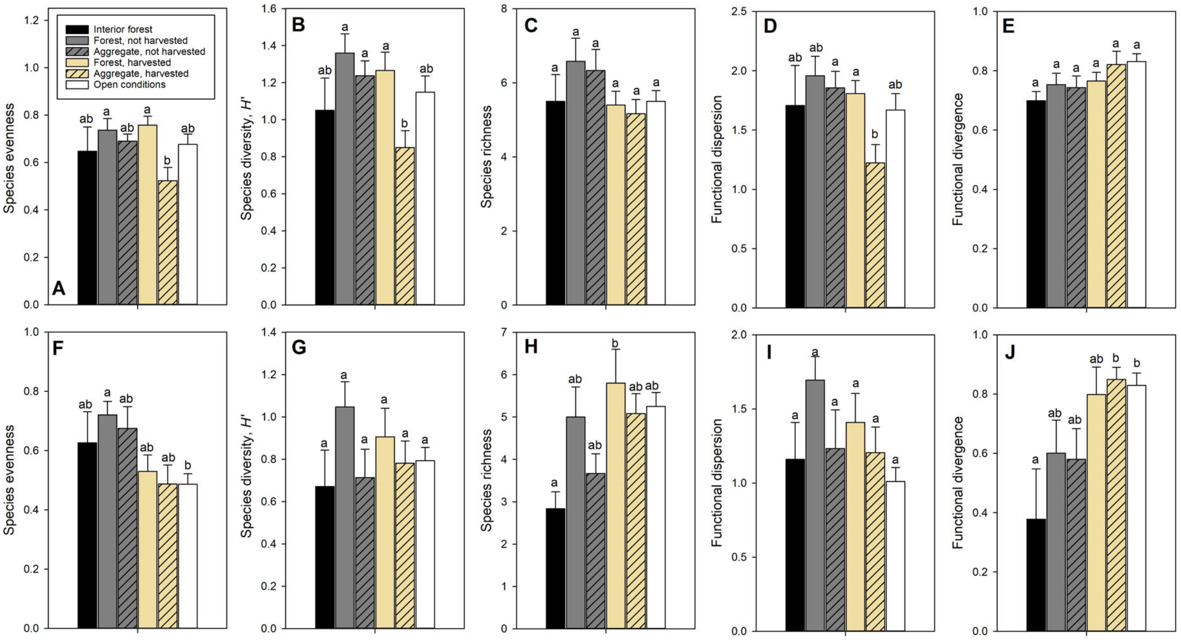

FIG. 2. Mean taxonomic and functional diversity for each treatment condition in (A–E) seedlings and small shrubs (<1 m height) and in (F–J) saplings and large shrubs (>1 m height and <10 cm DBH). Lowercase letters indicate significant differences between treatments based on post hoc Tukey-adjusted pairwise comparisons ($P < 0.05$). Error bars indicate standard errors.

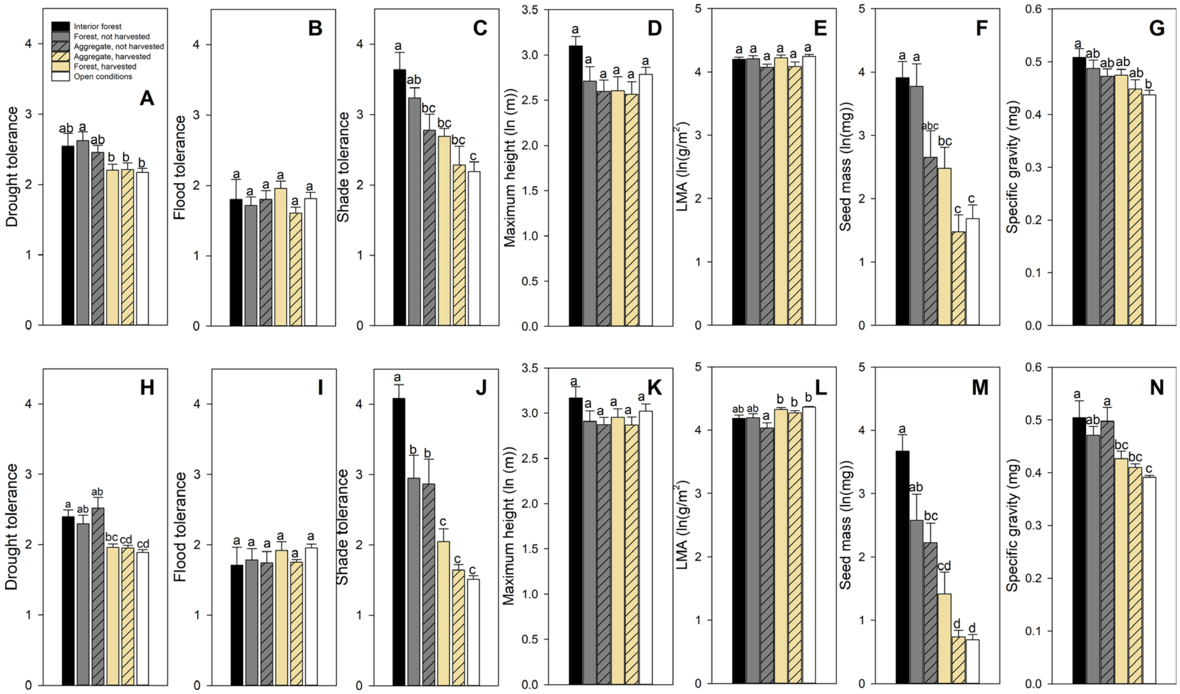

FIG. 3. Mean trait values (CWM) for each treatment condition by layer. Panels A–G show means for the seedlings and small shrubs (<1 m height) with abundance estimated using cover. Panels H–N show community-weighted trait means for large shrubs and saplings (>1 m height and <10 cm DBH) with abundance based on estimated standing biomass. Lowercase letters indicate significant differences ($P < 0.05$) determined with mixed effects ANOVA and post hoc Tukey-adjusted pairwise comparisons. Error bars indicate standard errors. Maximum height was measured in mm, LMA (leaf mass per area) in g/m^2, and seed mass in mg.

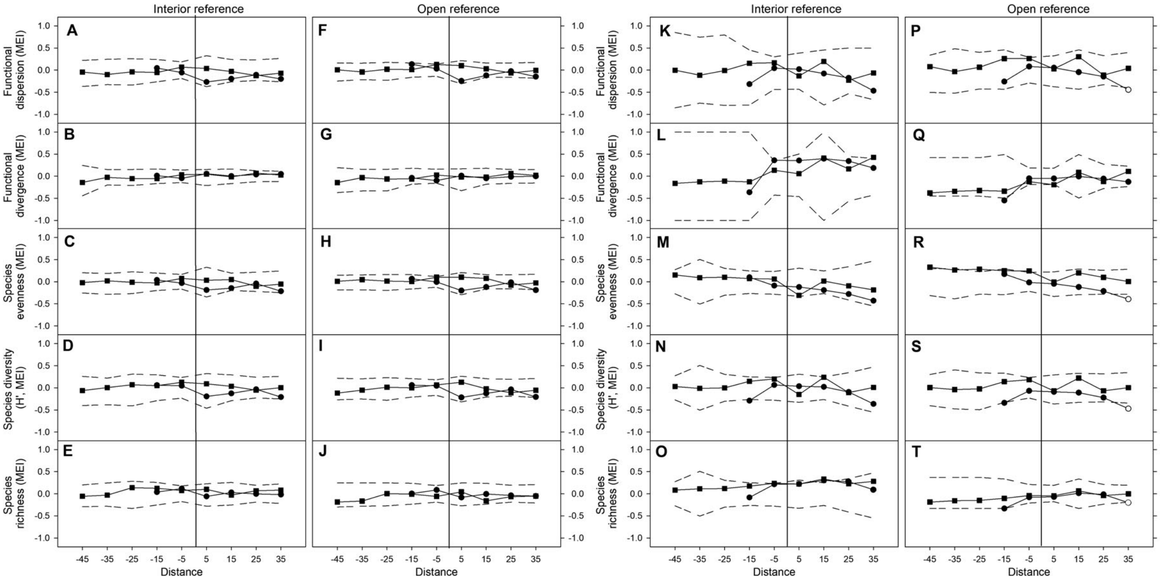

FIG. 4. Magnitude of edge influence (MEI) on taxonomic and functional diversity indices in the sapling layer as it relates to the edge between harvested areas and two types of unharvested forest (aggregate [circles] and intact forest [squares]) in (A–J) the seedling layer (<1 m height) and (K–T) in saplings and large shrubs (>1 m height and <2.54 cm DBH). Observations extend from 45 m within mature canopy (−45 m) up to (+) 35 m from edge into regenerating harvests. Forest influence is interpreted as occurring where MEI for a particular trait differs significantly from 0 ($P < 0.05$) based on references located in interior forest (panels A–E, K–O) or in open, harvested areas (panels F–J, P–T). Dashed lines show 95% confidence intervals. Open symbols indicate the depth of influence or edge effects, defined as occurring at the nearest of at least two consecutive distances where MEI $\neq$ 0. Solid lines at 0 m illustrate the location of the harvest boundary for aggregates and intact forest.

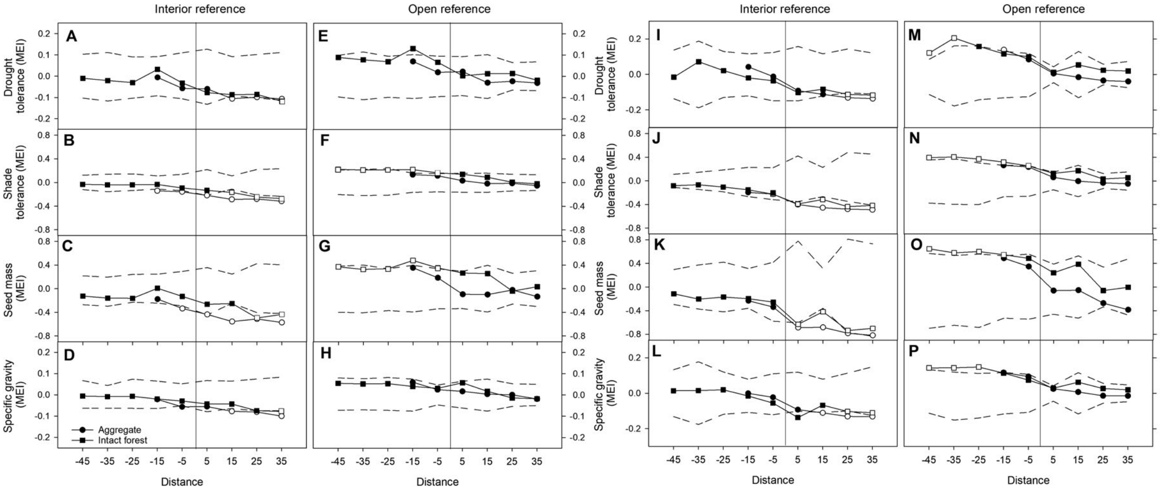

FIG. 5. Magnitude of edge influence (MEI) on community-weighted means of plant traits in (A–H) the seedling layer and (I–P) the sapling layer as it relates to the transition between unharvested and harvested forests along aggregate (circles) and intact forest (squares) transects. Observations extend from 45 m within unharvested forest (−45 m) up to (+) 35 m from edge into harvests. Forest influence is interpreted as occurring where MEI for a particular trait differs significantly from zero ($P < 0.05$) based on references located in interior forest (panels A–D, I–l) or in open, harvested areas (panels E–H, M–P). Dashed lines show 95% confidence intervals. Open symbols indicate the depth of influence or edge effects, defined as occurring at the nearest of at least two consecutive distances where MEI $\neq$ 0. Solid vertical lines at 0 m illustrate the location of the harvest boundary for aggregates and intact forest.

mass in the seedling size class exhibited edge effects up to −15 and −5 m, respectively, within aggregates (and not at all within intact forest; Fig. 5B,C). Comparison with the open reference yielded similar results but with the depth of edge effects for seed mass extending further, up to −15 m, in aggregates (Fig. 5F,G). In the sapling layer, seed mass response also suggests edge effects possibly extend to greater depths in aggregates than intact forest based on the open reference (Fig. 5O), although this was not evident when comparing to interior forest

(Fig. 5K). The depth of edge effects on specific gravity in saplings and large shrubs did not differ between aggregates and intact forest, but were observed up to great enough distances (15 m) that aggregates did not have the capacity for resisting them (Fig. 5P).

Aggregates and intact forest vs. interior forest habitat

Aggregates conserved many measures of diversity and functional identity associated with unharvested forest relative to values observed in open, harvested conditions. While wide variability was observed and may have prevented differences from being detected, none of the seven measures of functional or taxonomic diversity we tested differed significantly between aggregates and interior forests or intact unharvested forest (located within 45 m of the harvest boundary; Fig. 2, Appendix S3: Table S1).

Many individual traits responded similarly and had values in aggregates that were intermediate between (if not significantly different from) conditions in harvested areas and intact mature forest (e.g., drought tolerance, seed mass, and specific gravity in the seedling layer, Fig. 3) or were similar among all conditions (e.g., flood tolerance and maximum height in both strata, Fig. 3). Mean shade tolerance in the seedling layer of aggregates was lower than in interior forests, and there was a non-significant trend for intermediate values between intact forest patches and harvested conditions (Fig. 3C). In the sapling layer, shade tolerance was comparable between aggregates and intact forest patches and, in both cases, was lower than interior forest and higher than harvested areas (Fig. 3J). Negative correlations between sapling and large shrub abundance (biomass, Mg/ha) and shade tolerance, drought tolerance, and seed mass in the seedling layer suggest the larger, taller vegetation does impact some individual trait means of the seedling and small shrub community, if not diversity. At the same time, the sapling and large shrub layer did not impact abundance of seedlings and small shrubs, and all traits quantified in this study were strongly and positively correlated between the two layers suggesting similar composition and overall function (Appendix S3: Table S2).

Discussion

Whereas most studies to date have focused on the impacts of retention forestry practices on individual species, species composition, or taxonomic diversity measures (e.g., Nelson and Halpern 2005, Halpern et al. 2012, Baker et al. 2016a), we assessed functional identity (plant traits) and functional diversity. In doing so, we address a recognized and growing need to understand the impacts of retention forestry on functional diversity in managed forests (Fedrowitz et al. 2014). Our results affirm findings from other operational-scale silvicultural studies across North America including the Demonstration of Ecosystem Management Options study (Nelson and Halpern 2005, Aubry et al. 2009), the Ecosystem Management Emulating Natural Disturbance study (Craig and Macdonald 2009, Bartels et al. 2018), the Missouri Ozark Forest Ecosystem Project (Zenner et al. 2006, Knapp et al. 2014), and the Hardwood Ecosystem Experiment (Morrissey et al. 2015) and others. These long-term experiments as well as other studies conducted in operational harvests (Baker et al. 2015, 2016a) demonstrate that retaining mature, overstory trees and managing with two-aged or uneven-aged systems, depending on what more appropriately emulates natural disturbance dynamics, benefits aspects of biodiversity and/or recovery compared with even-aged management. We also demonstrate the benefit of including trait-based approaches in assessments of disturbance response in temperate forest ecosystems, as multiple individual traits exhibited greater sensitivity to changing conditions than taxonomic diversity indices or patterns in compositional turnover, which were strongly influenced by high β-diversity (Baker et al. 2016a). While this study confirms the conservation value of aggregated retention, it also shows that intact forest patches have greater influence on adjacent regeneration and exhibit greater resistance to edge effects than aggregates, particularly if smaller aggregate sizes, such as those examined in this work, are applied.

It has become increasingly evident that different indices of biodiversity are often complementary and, when interpreted together, allow more thorough evaluations of ecosystem response to stress and disturbance (Díaz et al. 2007, Baraloto et al. 2012). Functional and taxonomic measures of diversity responded similarly to the conditions we assessed, so including both suites of indices in our analyses did not necessarily add to our interpretation, contrary to expectations (Villéger et al. 2010, Baraloto et al. 2012, Maeshiro et al. 2013). However, assessing functional identity for certain traits complemented results based on the diversity indices and provided some advantages over using conventional, taxonomic approaches alone as has been observed elsewhere (Baraloto et al. 2012, Maeshiro et al. 2013, Curzon et al. 2017b). Responses of individual traits also suggest retention forestry practices impact biodiversity and function even when diversity indices do not vary among conditions or treatments. We observed variability in responses across the study (e.g., Figs. 2, 3), and it is possible that greater sampling intensity may have reduced this variability.

A minimum level of 5–10% overstory retention has been recommended globally (Gustafsson et al. 2012) and locally in Minnesota, USA (MFRC 2013), but assessments of retention forestry practices in Douglas-fir dominated forest of the U.S. Pacific Northwest and aspen mixedwoods in Alberta, Canada indicate that levels should exceed 15–20% in order to achieve ecological objectives (Aubry et al. 2009, Craig and Macdonald 2009). Even though we observed greater influence from intact forest on some traits, the 0.1-ha aggregates in this study did provide some forest influence 12 yr after harvest. Our observations of increasing functional divergence with greater levels of disturbance (from interior forest to open conditions, Fig. 2J) support hypotheses that disturbance acts as an environmental filter and can increase divergence in trait values (Funk et al. 2017). The gradient in functional divergence observed also supports the idea that aggregates mitigate the harsher environmental conditions created in an open, clear-cut harvest similarly to the edge of intact forest. In general, the depth of influence from unharvested forest extended up to distances considerably less than one tree height (the forest managers “rule-of thumb” for forest influence; Keenan and Kimmins 1993, Baker et al. 2013) for the species dominating these forests (20–30 m height, Table S2), regardless of whether plots were adjacent to aggregates or intact forest. This depth of influence also corresponds with observations of varying structure in the regenerating forest (lower understory biomass, lower seedling cover, and lesser sapling diameter diversity) observed up to 5 m from aggregates on these same plots (Curzon et al. 2017a) and is consistent with other observations in forest with a prominent aspen component (e.g., Harper et al. 2015). In other ecosystems, although notably with larger aggregates, research suggests only minor differences in the depth and magnitude of microclimatic influence from intact forest vs. aggregates (Baker et al. 2016b). While the interaction between aggregate structure and air flow may explain lower humidity levels near aggregates (and may have influenced patterns observed in this study), most microclimate effects resulting from forest influence on the microclimate of surrounding harvests are attributed to shade (Baker et al. 2016b). The area of aggregated retention patches significantly influences the likelihood of mortality, with smaller aggregates like those studied here (0.1 ha) losing significantly more overstory trees to windthrow and exposure (Esseen 1994, Jönsson et al. 2007, Xing et al. 2018), which diminish potential shading influence of the aggregate as well as seed dispersal and other effects. While many factors influence overstory mortality, trees such as *P. tremuloides* that are taller, more slender, and have lower crown ratios are more susceptible to mortality related to exposure (Solarik et al. 2012, Xing et al. 2018), so depending on the preharvest structure of aggregates, the average height of the overstory (and thus the depth of influence into surrounding harvest) could decrease over time.

While our results suggest aggregates conserve some aspects of interior forest in these ecosystems (see also Baker et al. 2016b, Curzon et al. 2017a), they also indicate aggregates provide edge-affected habitat for two reasons. First, as has been demonstrated widely in other systems, the edge effects on understory plant communities associated with boundaries between unharvested and regenerating forest can occur further than 15 m into unharvested forest (Palik and Murphy 1990, Fraver 1994, Nelson and Halpern 2005), the greatest depth measured in the 0.1 ha aggregates studied here. Evidence suggests that edge effects on microclimatic conditions (light, air temperature, humidity, soil temperature) extend 10–240 m into forest patches and depend on aspect, forest type, and the variable of interest (Chen et al. 1995, Heithecker and Halpern 2007). Additionally, aggregates in this study exhibited lower resistance to edge effects than intact forest. In other words, edge effects for the same variables (e.g., seed mass and shade tolerance) were observed at greater depths within aggregates. As mentioned above, small aggregates are more susceptible to overstory mortality because of greater exposure (Esseen 1994, Jönsson et al. 2007). A greater loss of overstory trees in aggregates relative to intact forest edges may have contributed to the greater sensitivity to edge effects observed. Larger aggregates would be expected to be less sensitive to edge effects (e.g., Aubry et al. 2009). While not tested here, distributing aggregates in a harvest unit such that lesser distance separates them and/or surrounding the aggregated retention patches with dispersed retention trees may also partially mitigate the conditions that caused aggregates in this study to have deeper edge effects and less influence on surrounding regeneration than intact forest, increasing their capacity for achieving ecological objectives (Franklin et al. 2018).

Populus tremuloides is a particularly dominant species in these ecosystems that responds to disturbance by producing abundant vegetative root sprouts and can influence diversity dynamics (Reich et al. 2012, Curzon et al. 2016). Given the abundance and rapid growth of *P. tremuloides* at these sites, it is likely that forest influence of aggregates and intact forest will continue to change over time (Baker et al. 2015). Competitive exclusion and environmental filtering impact functional diversity in fundamentally different ways (Mouchet et al. 2010, Mouillot et al. 2013), and it is possible that the competitive dominance of aspen in these systems has muted and will ultimately obscure the explicit influence that harvest has on community development and functional diversity. We observed lower functional dispersion in the seedling and small shrub layer adjacent to aggregates compared to regenerating forest adjacent to intact forest and increasing functional divergence from interior forest to open clear-cuts in the sapling and large shrub layer, suggesting a potential filtering effect of the conditions tested. Over the long term, the sapling layer will likely have greater influence over future function because of greater abundance (Grime 1998) and in the case of species such as *P. tremuloides,* faster growth rates that may increase the likelihood of persistence and reproduction (Haddad et al. 2008). Analyzing both layers separately, as we did in this study, provides a more holistic characterization of forest ecosystem response.

Conclusions

With this study, we demonstrate promise for assessing management impacts on plant diversity across highly variable sites. Even though only limited responses were observed in different measures of taxonomic and functional diversity, functional identity (the collection of community-weighted means for plant traits characterizing ecosystem process and disturbance responses), was sensitive to differences occurring along the gradient from interior forest to open harvests. Analyzing functional identity provided a complementary approach to diversity indices, detected trends consistent with our hypotheses, and may prove beneficial for future studies assessing how effectively silvicultural practices achieve ecological objectives related to biodiversity.

Our results also address a key need to increase understanding of how retention forestry impacts functional diversity. By using conditions in harvested areas as a reference, we focused our study on the impacts that retention forestry practices have compared to conventional harvest methods. Retaining mature overstory trees in 0.1-ha aggregates resulted in an understory woody community that was functionally distinct from open, clear-cut areas and intermediate between clear-cuts and interior forest in terms of functional identity. Our results support other findings suggesting that larger aggregates will likely provide greater ecological benefits, particularly in terms of influence on adjacent regeneration, but we also affirm that retaining overstory patches as small as 0.1 ha can benefit function in the understory woody community. Overall, these findings support continued and expanded implementation of retention forestry practices intended to achieve ecological objectives.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2097/full

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z34tmpg8s