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Early colonization of white spruce deadwood by saproxylic beetles in aggregated and dispersed retention

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2 **beetles in aggregated and dispersed retention**

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Abstract

Retention harvests may leave retention in aggregations, evenly dispersed, or in various combinations. Although the relative efficacy of aggregated and dispersed retention for biodiversity conservation is widely debated, there has been little study of combinations. We studied this question relative to saproxylic beetles that initially colonize horizontal and upright coarse woody material (CWM) of white spruce in boreal mixedwood stands at the EMEND (Ecosystem Management Emulating Natural Disturbance) in northern Alberta 12-13 years after retention prescription. Neither species richness nor emergence of beetles differed among freshly cut bolts exposed as 'horizontal' or 'upright' in retention patches of two sizes (0.20 ha and 0.46 ha) that were surrounded by different levels of dispersed retention (2%, 20% and 50%). However, species composition in retention patches differed significantly from those in unharvested controls, except in the larger patches surrounded by 50% dispersed retention, although patterns differed among feeding guilds. Both mycetophage and predator assemblages in patches were similar to those in unharvested controls, suggesting that even relatively small patches retain these guilds regardless of the surrounding matrix quality. Because species composition differed between horizontal and upright bolts, an appropriate mix of horizontal and upright CWM may contribute to conservation of saproxylic beetle faunas.

Keywords: retention forestry, aggregated retention, dispersed retention, biodiversity conservation, saproxylic beetles

38 Introduction

39 Balancing timber harvest and biodiversity conservation is a key objective of modern
40 industrial forestry (Gustafsson et al. 2012; Fedrowitz et al. 2014). Retention harvests
41 were first incorporated into forestry practices, mainly as tool to better maintain
42 biodiversity and ecosystem function, nearly 30 years ago. The approach has been
43 deployed largely in North and South America, Australia, and Fennoscandian countries as
44 an alternative to conventional clear-cutting (Franklin 1989; Lindenmayer and Franklin
45 2002; Halaj et al. 2008; Work et al. 2010; Baker and Read 2011; Lencinas et al. 2011;
46 Gustafsson et al. 2012; Koivula et al. 2014).

47 Retention may be aggregated as patches or dispersed as individual trees in harvested
48 blocks (Lindenmayer and Franklin 2002). Aggregated retention may promote multiple
49 tree cohorts in the overstory, stand-level diversity in understory plant assemblages, areas
50 of undisturbed soils, and local conservation of some fauna and flora requiring interior
51 forest habitat (Franklin et al. 1997; Baker 2011; Lee et al. 2018). In contrast, dispersed
52 single trees scattered throughout a harvested area provide a widely distributed short-term
53 deadwood supply, promote conservation of belowground biota, and are aesthetically
54 pleasing to humans (Franklin et al. 1997; Baker and Read 2011).

55 Large-scale experiments have been conducted around the world to understand
56 various effects of these retention harvests (Lee et al. 2018). For example, studies from the
57 Ecosystem Management Emulating Natural Disturbance (EMEND) in western Canada
58 have shown that ground-dwelling spiders responded to the dispersed retention gradient,
59 so that similarity of spider assemblages to those in unharvested forests increased with
60 increasing retention level (Pinzon et al. 2016). Caners et al. (2010) also found that

diversity of epiphytes at EMEND significantly decreased in levels of dispersed retention $\leq 50\%$. Aggregated retention provided refugia for sensitive bryophytes and late-seral herbs in the Pacific Northwest of the USA, although many generalist species were largely similar between aggregated and dispersed retention (Aubry et al. 2009). Studies in Tasmania, Australia demonstrated that aggregated retention better maintained mature forest species of various groups, such as epigeic beetles, vascular plants, bryophytes, lichens, and ectomycorrhizal fungi, while dispersed retention provided continuous availability of deadwood (Baker and Read 2011). In pine forests of eastern Finland a combination of retention and prescribed burning better emulated natural disturbances and maintained more saproxylic (i.e., deadwood-associated) species (Heikkala et al. 2016).

Despite much work to explore consequences of aggregated and dispersed retention worldwide (Aubry et al. 2009; Work et al. 2010; Baker and Read 2011; Lencinas et al. 2011; Fedrowitz et al. 2014), only a few authors have considered potential interactive effects of these two kinds of retention (e.g., Lencinas et al. 2011; Pinzon et al. 2012; Lee et al. 2017). Nonetheless, some forestry companies in North America have applied the combination of aggregated and dispersed retention in harvest designs, actively implementing inferences from the science that does exist (Baker 2011; Gustafsson et al. 2012).

The EMEND experiment is one of the early attempts to explore how stand cover type (deciduous, coniferous, and mixed forest), disturbance type (clear-cut harvest, retention harvest, and burning), and volume of retained trees (retention level) affect biodiversity, ecosystem function, economic viability and public perception (Spence et al. 1999; Work et al. 2004; Lee et al. 2018). The experimental design of EMEND includes two sizes of

aggregated retention (0.20 ha and 0.46 ha) embedded in replicated 10 ha compartments, harvested to several dispersed retention prescriptions (Pinzon et al. 2012; Lee et al. 2017). Thus, the design can support study of conservation potential of aggregated retention for forest organisms in interaction with different levels of dispersed retention in the matrix.

Saproxyllic organisms are threatened by industrial forestry due to their close association with various microhabitats provided by deadwood (Siitonen 2001; Langor et al. 2008; Stokland et al. 2012). We chose saproxyllic beetles (order Coleoptera) for study over other saproxyllic groups because they are abundant and diverse both taxonomically and ecologically, and their taxonomy and natural history are relatively well-known, facilitating species level analyses (Langor et al. 2008). Although community structure of these beetles seems to differ with the position of deadwood (Franc 2007; Ulyshen and Hanula 2009; Bouget et al. 2012), there is no clear pattern of their diversity in relation to whether deadwood is standing or downed (Lee et al. 2018). Thus, species-level conservation efforts should be informed by understanding of beetle responses to different orientation of deadwood in a retention harvest setting.

Previous studies about effects of retention harvest on saproxyllic beetles have focused largely on initial post-harvest responses. For example, Halaj et al. (2009) tested effects of aggregated and dispersed retention on bark-dwelling invertebrates using crawl traps 5–6 years post-harvest in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. They found that retention level affected beetle activity-density but retention pattern did not. Low levels of retention ($\leq 17\%$) better maintained saproxyllic beetle assemblages compared to clear-cuts 10 years post-harvest in Scots pine, *Pinus sylvestris* L. stands (Heikkala et al. 2016). However, the assemblages in these small retention patches

differed from those in unharvested controls. They also demonstrated that retention harvests could not emulate wild fires on saproxylic beetle assemblages (Heikkala et al. 2016). Window-trapped wood- and bark-borers and predators were not strongly affected by harvesting intensity 1–2 years after dispersed retention treatments in white spruce (*Picea glauca* (Moench) Voss) stands, but fungivores were sensitive to levels of dispersed retention $\leq 20\%$ (Jacobs et al. 2007). More recently, Lee et al. (2017) found that aggregated retention in white spruce stands surrounded by $\geq 20\%$ dispersed retention maintained saproxylic beetle assemblages similar to those in unharvested controls 10–11 years after harvest. In this paper we extend that work to explore the effects of retention combinations on this fauna in mixed stands of *Picea* and *Populus*.

The objectives of the study are to identify saproxylic beetle species that initially colonize horizontal and upright white spruce CWM in different sized retention patches surrounded by different levels of dispersed retention in mixed stands, and to evaluate the combined influence of aggregated and dispersed retention on early colonization of CWM by beetles. Based on previous work, we expected that saproxylic beetle assemblages would differ between horizontal and upright CWM (Franc 2007; Bouget et al. 2012; Wood 2012). Also, we expected that the assemblage structure in aggregated retention would be increasingly similar to that in unharvested controls as the level of dispersed retention increased, but based on the results of a previous study (Lee et al. 2017), that there would be no patch size effect on the assemblages. This study extends and compliments that of Lee et al. (2017) in that it focuses on a different stand type and employs a different sampling approach. Both studies have focused on spruce-associated saproxylic beetles, but in the current study we reared beetles directly from pieces of dead

wood sampled from mixedwood stands, whereas Lee et al. (2017) sampled spruce-dominated stands using flight intercept and emergence traps attached to snags.

Material and methods

Study area

This work was conducted at site of the EMEND experiment, located in northwestern Alberta, Canada (56°46'N, 118°22'W) at elevations ranging from 677 m to 880 m above sea level. The forest at EMEND originated from a mosaic of wildfires mainly from 1837, 1877 and 1895 (Bergeron et al. 2017), and had not been subject to commercial harvest before 1999. Merchantable stands there are dominated by two deciduous species, trembling aspen (*Populus tremuloides* Michaux (Salicaceae)) and balsam poplar (*Populus balsamifera* L.), and one coniferous species, white spruce, but also include less-abundant lodgepole pine (*Pinus contorta* Dougl. ex Loud. (Pinaceae)), black spruce (*Picea mariana* (Mill.) B.S.P. (Pinaceae)), balsam fir (*Abies balsamea* (L.) Mill. (Pinaceae)), and paper birch (*Betula papyrifera* Marsh. (Betulaceae)).

During the winter of 1998-1999, variable retention harvest treatments were applied to c. 10-ha compartments in each of four different stand-types (i.e., deciduous-dominated, deciduous with spruce understory, mixed, and conifer-dominated stands) on the EMEND landscape. Treatments included clear-cuts (2% retention), partial retention prescriptions (leaving 10%, 20%, 50%, 75% of basal area in dispersed retention), and unharvested controls. Retention prescriptions also included two sizes of ellipse-shaped aggregated retention patches (0.20 ha and 0.46 ha) in each compartment (see Work et al. (2010), Lee

et al. (2018), and www.emendproject.org for further information about study design). We studied a subset of EMEND compartments in mixedwood stands (canopy cover of both deciduous and coniferous 35%-65%) twelve years after harvest, focusing on aggregated retention patches surrounded by clear-cuts, 20% and 50% dispersed retention. The pre-harvest composition of stands was trembling aspen, balsam poplar, and white spruce (Fig. 1).

Experimental design and beetle sampling

This experiment was established mid-July 2010, in each of three replicate mixedwood stands that included the following six harvest treatments: a small retention patch (S: 0.20 ha) surrounded by 20% and 50% dispersed retention, a large patch (L: 0.46 ha) surrounded by 2% (=clear-cut), 20% and 50% dispersed retention, and an unharvested control compartment (Fig. 1). One mature white spruce tree (> 80 years old) was felled in centre of each retention patch and at least 50 m from the adjacent compartment for the unharvested control compartments. We were unable to sample saproxylic beetles in small patches surrounded by clear-cuts because, after 12 years, there were few live spruce trees left standing in two of the three replicate small patches, and felling a tree for this work was judged to have probable negative impacts on other ongoing studies. Two bolts, each 1.2 m long and 30-40 cm in diameter, were cut from each felled tree, starting c. 2 m from the base; one was placed horizontally on the forest floor as 'horizontal CWM', and the other was propped up against a nearby tree, with one end touching the ground to emulate 'upright CWM'. This pair of bolts was left in the center of each patch or unharvested

control compartment, and beetles were allowed to colonize until mid-June 2011, i.e., one year after cutting.

In mid-June 2011, each bolt was cut in half (i.e., a 60-cm-long section). One half was left in place in the field, while the other half was taken to a forest patch near the EMEND camp, placed in 121-L rearing bins (diameter 60 cm, height 91 cm) to reliably sample resident saproxylic beetles (see Lee et al. 2014). A screw-top canning jar (250 mL), containing ~50 mL of propylene glycol as killing agent and preservative, was attached to the bottom of each rearing bin to collect beetles. Emerged specimens were removed from the jars every three weeks from June to September 2011, and again in mid-June 2012 after winter exposure, and then wood sections were discarded. The remaining sections of bolts that had been exposed to colonization for about two years were then placed in rearing bins in mid-June 2012 and sampled as described above, with the last beetle samples collected in mid-June 2013.

Saproxylic beetle identification and trophic guilds

Both adult and larval saproxylic beetles emerged from the bolts. Only coarse identification was possible for larvae and so these data were not formally analyzed; however, general results and the list of morphospecies of larvae (Appendix B) were provided. Adult beetles were identified, to the species level wherever possible, using the taxonomic literature, the arthropod reference collections at the Northern Forestry Centre and the E. H. Strickland Entomological Museum at the University of Alberta, and with the help of taxonomic experts (see Acknowledgements). Data about specimens of two non-saproxylic families, Chrysomelidae and Coccinellidae, were not included in the

analysis since they were most likely on bolts by chance when they were put into the rearing bins. Individuals belonging to three species of Staphylinidae, *Placusa incompleta* Sjöberg, *P. pseudosuecica* Klimaszewski, and *P. tachyporoides* (Waltl), were pooled as *Placusa* spp. because they could not be reliably separated. Nomenclature followed that of Bousquet et al. (2013).

Each beetle species was assigned to one of five functional trophic guilds, i.e., mycetophages, omnivores, phloeophages, predators, and xylophages, based on published information (e.g., Klimaszewski et al. 2007; Dollin et al. 2008; Wood 2012; Lee et al. 2014). Voucher specimens of all taxa identified were deposited in the arthropod museum collection at the Northern Forestry Centre, Edmonton, and the E. H. Strickland Entomological Museum at the University of Alberta, Edmonton.

Measurements of live trees and coarse woody material

Live trees were enumerated in small and large patches surrounded by 2%, 20% and 50% dispersed retention to clarify the context of the study. We determined volumes of downed CWM and decay classes [DCs; we used the six-class system defined by Lee et al. (2014)] along a 40 m and 60 m line transect (5 mm wide) in each small and large patch, respectively, running E-W crossing through the center of each patch. In unharvested control compartments, CWM volumes were measured using a 60 m E-W line transect through the center of the stump of the tree felled as a source of bolts. We measured diameter and length of every piece of downed CWM (≥ 7 cm in diameter) that intersected the line transect (except for trees felled for the experiment). If sections classified to different DCs existed in one piece of CWM, we calculated separate volumes for each DC.

While this approach does not estimate the amount of CWM per unit of area, it supports a rough comparison of CWM among patches. For analysis, we pooled the data across tree species because we could not confidently identify well-decayed CWM. Furthermore, we combined DCs 1–2, DCs 3–4 and DCs 5–6, and denoted the combinations as ‘early’, ‘intermediate’, and ‘advanced’ decay classes for analyses to reduce the possible effect of high but idiosyncratic variation in volume between adjacent decay classes (Lee et al. 2014).

Data analyses

We used generalized linear models (GLM), to compare species richness and number of individuals for all saproxylic beetles combined and for each of the three most abundant feeding guilds (phloeophages, mycetophages, and predators) among treatments. For this analysis, the initial model included two factors [i.e., ‘bolt orientation’ (horizontal and upright) and ‘harvest treatments’ (2%-L, 20%-S, 20%-L, 50%-S, 50%-L and unharvested control)] as categorical variables. The model also included volumes of DCs 1–2, DCs 3–4, and DCs 5–6 as continuous variables. We selected the best fit among a total of eight models that collectively used all possible combinations of variables, using Akaike's Information Criterion corrected for small sample size (AIC_c). Error distributions were generally modeled as Poisson, or as negative binomial when data were overdispersed. Since no interaction was found in the initial model, we conducted GLM without interaction to improve statistical power. The null model (i.e., bolt orientation + harvest treatments) was selected as the best-fit model for species richness and number of individuals except the abundance of mycetophages (best-fit model: bolt orientation +

harvest treatments + DCs 5–6). Tukey’s honestly-significant-difference tests for *post-hoc* pairwise comparisons were applied when results from a GLM were significant ($p < 0.05$).

We used GLM with Gaussian distribution of error to test for effects of bolt orientation and harvest treatments on data about the 11 most common species (total number of individuals > 100). We similarly applied the model selection procedure for these common species, and determined the best-fit model. AIC_c Differences (Δ_i) ≤ 2 were considered as best models (Burnham and Anderson 2002). The results of the model selection are provided in the Appendix C.

We also used a GLM with Gaussian distribution of error to test significance of differences in CWM volumes across harvest treatments. Error distributions were generally modeled as negative binomial for comparisons of number of live trees among harvest treatments. For all GLM analyses, we used R version 3.3.1 (R Development Core Team 2016) using ‘MASS’ (Venables and Ripley 2002), ‘multcomp’ (Hothorn et al. 2008), ‘vegan’ (Oksanen et al. 2015), and ‘MuMIn’ packages (Bartoń 2018).

A two-way permutational multivariate analysis of variance (PERMANOVA) was performed using a crossed design to test the null hypothesis of no difference in species composition among treatments (Anderson et al. 2008). The first and second factor was ‘bolt orientation’ and ‘harvest treatments’, respectively. This non-parametric multivariate analysis uses permutations that require no explicit assumptions, and that can be used to partition variation based on any distance measure (Anderson 2001; Anderson et al. 2008). Bray-Curtis distance calculations were performed on square-root-transformed data with 9999 permutations for the main tests of PERMANOVA, and 999 permutations for *a posteriori* pairwise comparisons when the main tests were significant ($p < 0.05$). We

partitioned variation using the default conservative Type III sums-of-squares because it is satisfactory for both balanced ANOVAs and those unbalanced by missing data (Anderson et al. 2008). These analyses were executed in PERMANOVA+ add on package for PRIMER v7 (Anderson et al. 2008; Clarke and Gorley 2015).

We used non-metric multidimensional scaling (NMS) to visualize community structure of saproxylic beetle assemblages and to further interpret the PERMANOVA results. This ordination technique is widely used in community ecology because it avoids the assumption of linear relationships among variables, decreases the zero-truncation issue by using ranked distances, and supports use of a variety of distance measures to describe the data (McCune and Grace 2002). We generated the 'metaMDS' function using Bray-Curtis distance on square-root-transformed data using 500 random starts, as implemented in the 'vegan' package (Oksanen et al. 2015). The three DC groups were overlaid in the ordination space to visualize relationships between species composition and CWM decay. We also calculated 95% confidence ellipses (CIs) to help assess differences in species composition among harvest treatments.

Indicator species analysis (ISA) (Dufrêne and Legendre 1997) was used to identify significant associations between species and harvest treatments separately for horizontal and upright bolts. Both relative abundance and relative frequency are considered in calculation of indicator values (IV) in ISA. We generated the 'indval' function using 4999 randomizations to calculate IV and probabilities in the 'labdsv' package (Roberts 2013) in R, with significant results determined at ($p < 0.05$).

We did not include the 'year' factor for all analyses. Since samples during the first year varied considerably depending on early colonization success, we decided to combine

data from both years and to focus on the main factors of our interest (i.e., bolt orientation and harvest treatments). This also simplifies the model and increases overall power of the analyses.

Results

The beetle fauna

A total of 20,367 adult saproxylic beetles, representing 24 families and 78 species, were reared from white spruce bolts (Appendix A). Among these, 6,808 (66 spp.) and 13,559 individuals (52 spp.), respectively, emerged from horizontal and upright bolts. The proportion of species shared between bolts from the two orientations was only 51%; 33% and 16% of species were reared only from horizontal and upright CWM, respectively.

The Staphylinidae was the most species-rich family (24 spp.) followed by Curculionidae (13 spp.) and Nitidulidae (5 spp.); however, most individuals were attributed to Curculionidae (mostly Scolytinae), which accounted for 18,668 individuals or 91.7% of total catch, followed by Staphylinidae (1,031; 5.1%) and Monotomidae (236; 1.2%) (Appendix A). The three most-captured species were bark and ambrosia beetles (Curculionidae: Scolytinae): *Dryocoetes affaber* (Mannerheim) (9,631 individuals; 47.3% of total catch); *Trypodendron lineatum* (Olivier) (3,691; 18.1%); and *Polygraphus rufipennis* (Kirby) (2,136; 10.5%).

Overall, 925 (27 morphospecies) and 1,251 (22 morphospecies) beetle larvae emerged from horizontal and upright CWM, respectively (Appendix B), and 44% of

morphospecies were shared between horizontal and upright CWM. Thus, data about both adults and larvae suggest that slight differences in orientation and ground contact of bolts in this experiment alone led to substantially different species composition. As with adults, the most species-rich and abundant family among larvae was Staphylinidae, with 10 morphospecies and 966 individuals (Appendix B).

Species richness and number of individuals

There were only three significant effects of CWM orientation or harvest treatments on total number of individuals of beetles from particular guilds (Table 2). Significantly more mycetophages emerged from upright than from horizontal CWM, and also from bolts taken from control compartments, compared to those from bolts taken from the 2%-L, 20%-S and 20%-L treatments. More predators emerged from bolts from controls than from harvest treatments. There were no significant interactions between CWM orientation and harvest treatments. Species richness was not affected by main effects or their interactions (Table 2).

Assemblage composition

Assemblages differed significantly between horizontal and upright CWM (Two-way PERMANOVA, Pseudo- $F = 3.25$, $p < 0.001$) and among harvest treatments (Pseudo- $F = 1.63$, $p = 0.007$). *Post hoc* pairwise comparisons suggested that species composition in control plots differed significantly from that in all harvest treatments except 50%-L (Table 3).

The PERMANOVA results were supported by an NMS ordination, as 95% CIs indicated that assemblages in controls did not overlap with those in all other harvest treatments except those in 50%-L (Fig. 2). Assemblages in 50%-L were highly variable and thus similar collectively to controls and all harvest treatments. Assemblages associated with horizontal CWM generally did not overlap with those from associated with upright CWM within the same harvest treatment, underscoring the influence of bolt orientation on assemblage structure, and thus on probability of colonization by the local pool of saproxylic species. Assemblages collected from control plots were strongly associated with DCs 5–6, whereas assemblages from 2%-L were associated with either DCs 1–2 or DCs 3–4 (Fig. 2).

PERMANOVAs showed that each of the three most common trophic guilds was affected differently by treatments. The structure of phloeophage assemblages was significantly affected by CWM orientation (Pseudo- $F = 4.95$, $p < 0.001$). As well, phloeophage assemblages varied among harvest treatments (Pseudo- $F = 1.77$, $p = 0.014$), and assemblages from 2%-L, 20%-S and 50%-S differed from those of controls (Table 3). Mycetophage assemblages also varied significantly with CWM orientation (Pseudo- $F = 2.18$, $p = 0.042$), but were not affected by harvest treatments (Table 3). In contrast, predator assemblages were similar across both harvest treatments and CWM orientation (Table 3).

Results of NMS ordinations for each trophic guild supported the PERMANOVA results. For phloeophages, 95% CIs for assemblages from controls and the 50%-L completely overlapped, and there was moderate overlap of controls, 50%-S and 20%-L assemblages (Fig. 3a). Phloeophage assemblages in 2%-L were strongly associated with

DCs 1–4, and those in controls and 50%-L are strongly associated with DCs 5–6 (Fig. 3a). Mycetophaga assemblages were roughly separated by CWM orientation, but confidence ellipses for harvest prescriptions overlapped considerably (Fig. 3b). The 95% CIs for predator assemblages from harvest treatments overlapped considerably (Fig. 3c). Interestingly, assemblages from control samples were the most homogeneous in all ordinations (Figs. 2, 3) suggesting that harvest increased variation in assemblage composition.

Species responses

The six most common phloeophagous species were bark beetles, and they responded differently to local forest conditions (Figs. 4a-4f; Appendix C). The most common species, *D. affaber*, was more abundant in upright CWM than in horizontally positioned CWM, and tended to be most abundant in bolts from control plots (Fig. 4a). However, the second-most captured bark beetle, *P. rufipennis*, was most common in the 2%-L treatment (Fig. 4b), a pattern also exhibited by *Orthotomicus caelatus* (Eichhoff) (Fig. 4f). Indicator species analysis also revealed *P. rufipennis* as a significant indicator of upright CWM in the 2%-L (IV = 54.0, $p = 0.007$). *Crypturgus borealis* Swaine (Fig. 4c) and *Scierus annectans* LeConte (Fig. 4e) tended to be more abundant in 20%-L than in other harvest treatments; however, the pattern for *S. annectans* was less clear. *Dryocoetes autographus* (Ratzeburg) emerged more commonly from horizontal CWM than from upright CWM (Fig. 4d). Thus, phloeophages responded in species-specific ways to the treatments, and their responses likely depended much on interactions between their

biological characteristics and environmental variation generated by the harvest prescriptions.

The most common mycetophage, the ambrosia beetle, *T. lineatum*, tended to be most abundant in bolts from controls (Fig. 4g; Appendix C). More of the second-most common mycetophage, *Placusa* spp. (Staphylinidae), tended to increase with the increased amount of dispersed retention and patch size (Fig. 4h; Appendix C).

The three most common predators all have strong associations with bark beetles (Appendix C). *Rhizophagus dimidiatus* Mannerheim (Monotomidae) was more abundant in controls, compared to other harvest treatments (Fig. 4i). Indicator species analysis also showed that *R. dimidiatus* was indicative of both horizontal (IV = 56.1, $p = 0.034$) and upright CWM (IV = 68.0, $p = 0.021$) in control compartments. Together with the bark beetle, *P. rufipennis*, there were only two significant indicators in this study. *Phloeopora* spp. (Staphylinidae) tended to be most abundant in controls (Fig. 4j), whereas *Lasconotus complex* LeConte (Zopheridae) exhibited the opposite pattern (Fig. 4k).

Live trees and coarse woody material in retention patches

There was no significant effect of surrounding dispersed retention level on number of live trees in small patches (Deviance = 10.77, $p = 0.680$) or large patches (Deviance = 11.22, $p = 0.425$). However, there was high variance in number of live trees and total volume of CWM among replicate patches within each dispersed retention treatment (Table 1). The variation was especially remarkable for live trees in patches surrounded by clear-cuts; the three replicates of small patches retained 3, 23 and 150 live trees, and the

three large patches in the same compartments retained 32, 35 and 183 trees. No patches in any other dispersed retention treatments retained fewer than 48 live trees (Table 1).

In comparison to patches in harvested compartments, plots in control stands had lower CWM volume and higher volume of advanced decay classes (i.e., DCs 5–6) relative to earlier decay classes (Table 1). In addition, there was a trend that total volume of CWM decreased with the increasing level of dispersed retention that surrounds patches.

Discussion

Combined effects of aggregated and dispersed retention

Although there were no harvest treatment effects on species richness or total number of individuals of saproxylic beetles in cut bolts of CWM, structure of saproxylic assemblages generally differed between retention patches and unharvested controls, regardless of the amount of dispersed retention surrounding each patch. Only large patches (0.46 ha) surrounded by 50% dispersed retention harboured assemblages similar to those from control stands 12–13 years post-harvest. These results differ from those of a previous study conducted in the same area that focused on saproxylic beetles using spruce snags in spruce-dominated stands. Lee et al. (2017) showed that beetle assemblages from retained spruce snags in retention patches surrounded by 20% or 50% dispersed retention in spruce stands were similar to those of unharvested control sites, and that they differed from those surrounded by clear-cuts. Comparison of results from the two studies suggests that responses of saproxylic beetles vary according to stand cover-type or at least among type of CWM substrates, i.e., in this case, large snags versus 1.2 m cut bolts. In another study of interactions between dispersed and aggregated retention at the EMEND site,

Pinzon et al. (2012) observed that epigaeic spider assemblages in spruce patches surrounded by 75% dispersed retention were similar to those of control stands, but that assemblages in patches surrounded by 2% and 10% dispersed retention differed considerably. Thus, saproxylic beetles and epigaeic spiders both show that the amount of retention in the adjacent matrix can influence the conservation capacity of patches.

Responses of three feeding guilds differed among retention treatments. Phloeophage assemblages (mostly bark beetles) in large patches surrounded by 20% and 50% dispersed retention were similar to those in control plots unless patches were surrounded by clear-cuts. In small patches, however, assemblages differed from those of control plots regardless of the amount of retention surrounding the patches. Therefore, both patch size and the amount of retention in the surrounding harvested matrix act to shape phloeophage assemblages. However, the response of the guild represents a composite of many individual species responses, and species-specific treatment influences varied greatly, providing some insights into possible influences of species-specific habitat affinities. For example, the bark beetles, *P. rufipennis* and *O. caelatus*, showed stronger affinity to patches surrounded by clear-cuts, in contrast to *D. affaber* which showed stronger affinity for less sun-exposed treatments in the matrix and in especially controls. Responses of the latter two species are similar to that observed in the previous study (Lee et al. 2017), suggesting that proposed effects of habitat affinities are real. It is noteworthy that the spruce beetle, *Dendroctonus rufipennis* (Kirby), which is common on mature spruce trees in the study area (D. Langor, unpubl. data), was rarely reared from bolts in patches surrounded by clear-cuts and 20% retention (Appendix A). Earlier work on this species in the same geographic area demonstrated that it does not fare well in sun-exposed habitats

(Wesley 2002). The affinity for particular habitat configurations exhibited by different bark beetle species may minimize interspecific competition for limited and ephemeral phloem resources (Raffa et al. 2015).

Mycetophage and predator assemblages in residual patches were not significantly affected by level of dispersed retention in the matrix, suggesting that retention patches conserve these species regardless of the surrounding matrix quality. Thus, the deadwood environment in patches may meet the needs of many generalist beetles that use early decay classes. Such generalists could be maintained even in relatively small patches as long as there are broadly acceptable deadwood resources and microhabitat conditions. Nonetheless, the two most common mycetophages, *T. lineatum* and *Placusa* spp., tended to be less abundant in patches surrounded by low retention levels. Also, the two most common predators, *R. dimidiatus* and *Phloeopora* spp., both associated with bark beetles (Bousquet 1990; Klimaszewski et al. 2011) were negatively affected by harvest treatments, indicating that relatively small-sized aggregated retention (≤ 0.46 ha) surrounded by dispersed retention did not maintain populations of these sensitive species similarly to control plots. Strong association of *R. dimidiatus* with control plots in the present study supports association of this species with intact forest, as suggested from studies in both eastern Canada (Légaré et al. 2011) and western Canada (Lee et al. 2015).

Canopy closure is one of the most important factors that shape species composition of saproxylic invertebrates (Stokland et al. 2012; Bouget et al. 2014), and thus aggregated retention is the only method that is likely to conserve species requiring forest habitats. Traditionally, studies of retention harvests have largely focused on aggregated retention, although there is no consensus about threshold patch size that successfully conserves

biodiversity (Lee et al. 2015; 2018). This is unsurprising because optimal patch size depends on diverse environmental characteristics, such as forest cover-types, qualities of the matrix (e.g., clear-cuts, dispersed retention, agricultural lands, or cities), and time since harvest. Nevertheless, patches less than 1 ha are generally known to be insufficient for conserving forest biodiversity because of edge effects (Matveinen-Huju et al. 2006; Aubry et al. 2009). As previously shown, dispersed retention cannot provide a secure habitat supply for forest saproxylic species; however, there is evidence that it can support faster recovery of the original fauna in harvested stands (Pinzon et al. 2016). For example, studies of dispersed retention alone showed that only high levels of retention could maintain biodiversity similar to that in unharvested forests (Halaj et al. 2008; Work et al. 2010; Pinzon et al. 2012, 2016). In-stand biodiversity conservation is improved by embedding aggregated retention within a dispersed retention matrix, which not only provides windbreaks that protect patches, but also naturally injects CWM of variable qualities into the surrounding matrix as habitat for saproxylic insects during the forest regeneration phase (Lee et al. 2018).

Effect of CWM orientation on saproxylic beetles

Results from the few studies of saproxylic beetles comparing horizontal and upright CWM substrates (i.e., attempts to reflect characteristics of logs and snags) (Hammond et al. 2001; Hjältén et al. 2010; Jonsell and Hansson 2011; Andersson et al. 2015) have given inconsistent results. Species richness of beetles was sometimes reported to be higher in logs than in snags (Franc 2007; Ulyshen and Hanula 2009; Wood 2012); however, both species richness and abundance were higher in snags than in logs of

European oaks (Bouget et al. 2012). In the present study, we found no difference in mean species richness or mean emergence between bolts exposed as either horizontal or upright CWM, in line with results from aspen-dominated forests in northern Alberta, Canada (Hammond et al. 2001) and spruce-dominated forest in Sweden (Hjältén et al. 2010). Nonetheless, more mycetophages emerged from upright than from horizontal CWM in our study, in contrast to findings for oak deadwood (Franc 2007). At present there is no general pattern of species richness or abundance of saproxylic beetles in logs and snags, but rather patterns seem to depend on tree species, geographical regions and life histories of species in particular saproxylic assemblages (Bouget et al. 2012).

Despite lack of consistent pattern, variation in CWM orientation clearly contributes to the structure of saproxylic arthropod assemblages, and thus, effective conservation measures will require such habitat variation maintained on post-harvest landscapes. Despite variation in results about species richness and relative abundance, structure of beetle assemblages appears to consistently differ between horizontal and upright CWM and our study generally supports previous findings (Franc 2007; Ulyshen and Hanula 2009; Hjältén et al. 2010; Jonsell and Hansson 2011; Bouget et al. 2012; Wood 2012; Andersson et al. 2015). Assemblages of predators did not differ between horizontal and upright CWM, perhaps reflecting the more generalized feeding habits of predators in CWM in early decay stages (Bouget et al. 2012).

Windthrow

Long-term structural stability of aggregated retention is essential to the proposed benefits of retention forestry (Beese et al. 2003; Scott and Mitchell 2005). Although

aggregated retention is generally more resistant to wind than dispersed retention (Scott and Mitchell 2005; Aubry et al. 2009), relatively small (≤ 1 ha) retention patches are also highly susceptible to windthrow (Jönsson et al. 2007; Aubry et al. 2009; Urgenson et al. 2013). Both the present study and some previous work at EMEND (Lee et al. 2017) demonstrate that relatively small patches surrounded by clear-cuts collapse as sources of CWM recruitment 10-12 years after harvest. We found remarkable variation in numbers of live trees even in the larger patches (≤ 0.46 ha) of our study throughout all retention levels 12 years after harvest. Most trees had blown down in more than half of the patches surrounded by 2% residual, and if this trend continues these patches will not serve as long-term and continuous sources of CWM recruitment as a forest regenerates. Nonetheless, we note a tendency for even such small patches to maintain more live trees 12 years after harvest if they were surrounded by dispersed retention.

Implications

Saproxylic beetle assemblages in two sizes of most retention patches were generally dissimilar to those in unharvested control plots, regardless of the level of dispersed retention surrounding them. The single exception was in 0.46 ha patches surrounded by 50% dispersed retention, suggesting that conditions of the harvested matrix affects the conservation efficacy of leaving residual forest patches. Most of the dissimilarity that we found was driven by phloeophages, which numerically dominated the assemblage; however, similarity between controls and harvest treatments was higher for mycetophages and predators. Thus, even relatively small-sized retention patches in boreal

mixedwood stands have conservation value for some functional groups of early colonizing saproxylic beetles regardless of the amount of surrounding dispersed retention.

Collectively, results from EMEND suggest that embedding patches within 20% or higher levels of dispersed retention will preserve patch structures better than leaving them in clear-cuts (Lee et al. 2017). For example, we noted in this study that four out of six patches surrounded by clear-cuts were almost eliminated due to windthrow 12 years post-harvest in mixed stands. In short, processes affecting outcome of conservation strategies for saproxylic organisms based on forest retention will likely depend on forest cover type, patch size and matrix quality. Most importantly, such relationships will change over time since harvest, requiring cautious interpretation of data obtained from research about retention harvests.

We suggest that future studies of retention forestry should focus on the following four points to improve forest management: 1) investigating long-term structural persistence of retention patches combined with dispersed retention matrices differing in quality (Lencinas et al. 2011; Lee et al. 2017, 2018); 2) assessing responses of forest organisms associated with later decompositional stages of CWM in retention patches because these organisms are thought to be more susceptible to environmental changes associated with forestry operations (Heikkala et al. 2014; Lee et al. 2014, 2015); 3) exploring interactions between patch size and level of dispersed retention required to promote biodiversity conservation (Lencinas et al. 2011; Lee et al. 2017); and 4) linking retention harvest to a practical distribution of large protected reserves to effectively conserve local biodiversity on a landscape scale (Lindenmayer et al. 2012; Heikkala et al. 2017). Although the EMEND experiment was not solely designed to investigate the

interaction of patch size and surrounding matrix, the uniqueness of its lay-out and long-term plan may provide additional insights to improve strategies for conserving forest biodiversity.

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Appendix supplementary materials

Supplementary data associated with this article can be found, in the online version, at

References

- 581 Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance.
582 *Austral Ecol.* **26**: 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x.
- 583 Anderson, M.J., Gorley, R.N., and Clarke, K.R. 2008. PERMANOVA+ for PRIMER:
584 Guide to Software and Statistical Methods. PRIMER-E, Plymouth, U.K.
- 585 Andersson, J., Hjältén, J., and Dynesius, M. 2015. Wood-inhabiting beetles in low stumps,
586 high stumps and logs on boreal clear-cuts: Implications for dead wood management.
587 *PLoS ONE* **10**(3): e0118896. doi:10.1371/journal.pone.0118896.
- 588 Aubry, K.B., Halpern, C.B., and Peterson, C.E. 2009. Variable-retention harvests in the
589 Pacific Northwest: A review of short-term findings from the DEMO study. *Forest*
590 *Ecol. Manag.* **258**: 398–408. doi:10.1016/j.foreco.2009.03.013.
- 591 Baker, S.C. 2011. Seeking a balance between forestry and biodiversity - the role of
592 variable retention silviculture. Insights from western USA and Canada. *Forest &*
593 *Wood Products Australia*, Melbourne, Australia.
- 594 Baker, S.C., and Read, S.M. 2011. Variable retention silviculture in Tasmania's wet
595 forests: ecological rationale, adaptive management and synthesis of biodiversity
596 benefits. *Austral. For.* **74**: 218–232. doi:10.1080/00049158.2011.10676365.
- 597 Bartoń, K. 2018. MuMIn: multi-model inference. R package Version 1.40.4.
- 598 Beese, W.J., Dunsworth, B.G., Zielke, K., and Bancroft, B. 2003. Maintaining attributes
599 of old-growth forests in coastal B.C. through variable retention. *For. Chron.* **79**: 570–
600 578. doi: 10.5558/tfc79570-3.
- 601 Bergeron, J.A.C., Pinzon, J., Odsen, S., Bartels, S., and Macdonald, S.E. 2017.
602 Ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity
603 after retention harvest. *Oikos* **126**: 1738–1747. doi: 10.1111/oik.04208.

- 604 Bouget, C., Nusillard, B., Pineau, X., and Ricou, C. 2012. Effect of deadwood position on
605 saproxylic beetles in temperate forests and conservation interest of oak snags. *Insect*
606 *Conserv. Divers.* **5**: 264–278. doi: 10.1111/j.1752-4598.2011.00160.x.
- 607 Bouget, C., Larrieu, L., and Brin, A. 2014. Key features for saproxylic beetle diversity
608 derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* **36**: 656–664.
609 doi:10.1016/j.ecolind.2013.09.031.
- 610 Bousquet, Y. 1990. A review of the North American species of *Rhizophagus* Herbst and a
611 revision of the Nearctic members of the subgenus *Anomophagus* Reitter (Coleoptera:
612 Rhizophagidae). *Can. Entomol.* **122**: 131–171.
- 613 Bousquet, Y., Bouchard, P., Davies, A.E., and Sikes, D.S. 2013. Checklist of beetles
614 (Coleoptera) of Canada and Alaska. Revised 2nd ed. Pensoft, Sofia–Moscow,
615 Bulgaria.
- 616 Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a
617 practical information-theoretic approach. 2nd ed. New York, Springer-Verlag.
- 618 Caners, R.T., Macdonald, S.E., Belland, R.J. 2010. Responses of boreal epiphytic
619 bryophytes to different levels of partial canopy harvest. *Botany* **88**: 315–328.
- 620 Clarke, K.R., and Gorley, R.N. 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E,
621 Plymouth, U.K.
- 622 Dollin, P.E., Majka, C.G., and Duinker, P.N. 2008. Saproxylic beetle (Coleoptera)
623 communities and forest management practices in coniferous stands in southwestern
624 Nova Scotia, Canada. *ZooKeys* **2**: 291–336. doi: 10.3897/zookeys.2.15.

- 625 Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need
626 for a flexible asymmetrical approach. *Ecol. Monographs* **67**: 345–366. doi:
627 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.
- 628 Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R.,
629 Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson,
630 A., and Gustafsson, L. 2014. Can retention forestry help conserve biodiversity? A
631 meta-analysis. *J. Appl. Ecol.* **51**: 1669–1679. doi: 10.1111/1365-2664.12289.
- 632 Franc, N. 2007. Standing or downed dead trees - does it matter for saproxylic beetles in
633 temperate oak-rich forest? *Can. J. Forest Res.* **37**: 2494–2507. doi: 10.1139/X07-096.
- 634 Franklin, J.F. 1989. Towards a new forestry. *Am. Forests* **95**: 37–44.
- 635 Franklin, J.F., Berg, D.R., Thornburgh, D.A., and Tappeiner, J.C. 1997. Alternative
636 silvicultural approaches to timber harvesting: variable retention harvest systems. *In*
637 *Creating a Forestry for the 21st Century: The Science of Ecosystem Management.*
638 *Edited by* K.A. Kohm, and J.F. Franklin. Island Press, Washington, D.C, U.S.A. pp.
639 111–139.
- 640 Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer,
641 D.B., Lohmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-
642 Thygeson, A., Volney, W.J.A., Wayne, A. and Franklin, J.F. 2012. Retention forestry
643 to maintain multifunctional forests: A world perspective. *BioScience* **62**: 633–645.
644 doi: 10.1525/bio.2012.62.7.6.
- 645 Halaj, J., Halpern, C.B. and Yi, H. 2008. Responses of litter-dwelling spiders and carabid
646 beetles to varying levels and patterns of green-tree retention. *Forest Ecol. Manag.*
647 **255**: 887–900. doi: 10.1016/j.foreco.2007.09.083.

- 648 Halaj, J., Halpern, C.B., Yi, H. 2009. Effects of green-tree retention on abundance and
649 guild composition of corticolous arthropods. *Forest Ecol. Manag.* **258**: 850–859.
- 650 Hammond, H.E.J., Langor, D.W., Spence, J.R. 2001. Early colonization of *Populus* wood
651 by saproxylic beetles (Coleoptera). *Can. J. Forest Res.* **31**: 1175–1183. doi:
652 10.1139/x01-057.
- 653 Heikkala, O., Suominen, M., Junninen, K., Hämäläinen, A., Kouki, J. 2014. Effects of
654 retention level and fire on retention tree dynamics in boreal forests. *Forest Ecol.*
655 *Manag.* **328**:193–201. doi: 10.1016/j.foreco.2014.05.022.
- 656 Heikkala, O., Martikainen, P., Kouki, J. 2016. Decadal effects of emulating natural
657 disturbances in forest management on saproxylic beetle assemblages. *Biol. Conserv.*
658 **194**: 39–47.
- 659 Heikkala, O., Kouki, J., Martikainen, P. 2017. Prescribed burning is an effective and
660 quick method to conserve rare pyrophilous forest-dwelling flat bugs. *Insect Conserv.*
661 *Diver.* **10**: 32–41. doi: 10.1111/icad.12195.
- 662 Hjältén, J., Stenbacka, F. and Adnerson, J. 2010. Saproxylic beetle assemblages on low
663 stumps, high stumps and logs: Implications for environmental effects of stump
664 harvesting. *Forest Ecol. Manag.* **260**: 1149–1155. doi: 10.1016/j.foreco.2010.07.003.
- 665 Hothorn, T., Bretz, F., and Westfall, P. 2008. Simultaneous inference in general
666 parametric models. *Biometrical J.* **50**: 346–363. doi: 10.1002/bimj.200810425.
- 667 Jacobs, J.M., Spence, J.R., and Langor, D.W. 2007. Variable retention harvest of white
668 spruce stands and saproxylic beetle assemblages. *Can. J. Forest Res.* **37**: 1631–1642.

- 669 Jonsell, M., and Hansson, J. 2011. Logs and stumps in clearcuts support similar
670 saproxylic beetle diversity: implications for bioenergy harvest. *Silva Fenn.* **45**(5):
671 1053–1064.
- 672 Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M., and Esseen, P.-A.
673 2007. Eighteen years of tree mortality and structural change in an experimentally
674 fragmented Norway spruce forest. *Forest Ecol. Manag.* **242**: 306–313.
675 doi:10.1016/j.foreco.2007.01.048.
- 676 Klimaszewski, J., Langor, D.W., Pelletier, G., Bourdon, C., Perdereau, L. 2011.
677 Aleocharine beetles (Coleoptera, Staphylinidae) of the province of Newfoundland
678 and Labrador, Canada. Pensoft Publishers, Sofia, Bulgaria.
- 679 Klimaszewski, J., Langor, D.W., Savard, K., Pelletier, G., Chandler, D.S., and Sweeney,
680 J. 2007. Rove beetles (Coleoptera: Staphylinidae) in yellow birch-dominated stands
681 of southeastern Quebec, Canada: diversity, abundance, and description of a new
682 species. *Can. Entomol.* **139**: 793–833. doi: <http://dx.doi.org/10.4039/n06-057>.
- 683 Koivula, M., Kuuluvainen, T., Hallman, E., Kouki, J., Siitonen, J., and Valkonen, S. 2014.
684 Forest management inspired by natural disturbance dynamics (DISTDYN) – a long-
685 term research and development project in Finland. *Scand. J. Forest Res.* **29**: 579–592.
686 doi: 10.1080/02827581.2014.938110.
- 687 Langor, D.W., Hammond, H.E.J., Spence, J.R., Jacobs, J., and Cobb, T.P. 2008.
688 Saproxylic insect assemblages in Canadian forests: diversity, ecology, and
689 conservation. *Can. Entomol.* **140**: 453–474. doi: <http://dx.doi.org/10.4039/n07-LS02>.

- 690 Lee, S.-I., Spence, J.R., and Langor, D.W. 2014. Succession of saproxylic beetles
691 associated with decomposition of boreal white spruce logs. *Agr. Forest Entomol.* **16**:
692 391–405. doi: 10.1111/afe.12069.
- 693 Lee, S.-I., Spence, J.R., Langor, D.W., and Pinzon, J. 2015. Retention patch size and
694 conservation of saproxylic beetles in boreal white spruce stands. *Forest Ecol. Manag.*
695 **358**: 98–107. doi:10.1016/j.foreco.2015.09.002.
- 696 Lee, S.-I., Spence, J.R., and Langor, D.W. 2017. Combinations of aggregated and
697 dispersed retention improve conservation of saproxylic beetles in boreal white spruce
698 stands. *Forest Ecol. Manag.* **385**: 116–126. doi:10.1016/j.foreco.2016.11.032.
- 699 Lee, S.-I., Spence, J.R., Langor, D.W. 2018. Chapter 19. Conservation of saproxylic
700 insect diversity under variable retention harvesting. *In* *Saproxylic Insects: Diversity,*
701 *Ecology and Conservation. Edited by M. Ulyshen.* Springer, Heidelberg, Germany.
702 pp. 639–667.
- 703 Lencinas, M.V., Martínez Pastur, G., Gallo, E., and Cellini, J.M. 2011. Alternative
704 silvicultural practices with variable retention to improve understory plant diversity
705 conservation in southern Patagonian forests. *Forest Ecol. Manag.* **262**: 1236–1250.
706 doi:10.1016/j.foreco.2011.06.021.
- 707 Légaré, J.-P., Hébert, C., and Ruel, J.-C. 2011. Alternative silvicultural practices in
708 irregular boreal forests: response of beetle assemblages. *Silva Fenn.* **45**: 937–956.
- 709 Lindenmayer, D.B., and Franklin, J.F. 2002. *Conserving forest biodiversity: A*
710 *comprehensive multiscaled approach.* Island Press, Washington, D.C., U.S.A.

- 711 Matveinen-Huju, K., Niemelä, J., Rita, H., O'Hara, R.B., 2006. Retention-tree groups in
712 clear-cuts: do they constitute 'life-boats' for spiders and carabids? *Forest Ecol.*
713 *Manage.* **230**: 119–135. doi:10.1016/j.foreco.2006.04.025.
- 714 McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software
715 Design, Gleneden Beach, Oregon, U.S.A.
- 716 Oksanen J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B., Simpson,
717 G.L., Solymos, P., Stevens, M.H.H., and Wagner, H. 2015. *vegan*: Community
718 Ecology Package. R Package Version 2.1-1.
- 719 Pinzon, J., Spence, J.R., and Langor, D.W. 2012. Responses of ground-dwelling spiders
720 (Araneae) to variable retention harvesting practices in the boreal forest. *Forest Ecol.*
721 *Manag.* **266**: 42–53. doi:10.1016/j.foreco.2011.10.045.
- 722 Pinzon, J., Spence, J.R., Langor, D.W., Shorthouse, D.P. 2016. Ten-year responses of
723 ground-dwelling spiders to retention harvest in the boreal forest. *Ecol. Appl.* **26**:
724 2581–2599.
- 725 R Development Core Team, 2016. R: A Language and Environment for Statistical
726 Computing, Version 3.3.1. R Foundation for Statistical Computing, Austria.
727 Available from <http://www.R-project.org> [accessed 27 June 2018].
- 728 Raffa, K.F., Grégoire, J.-C., Lindgren, B.S. 2015. Chapter 1. Natural History and Ecology
729 of Bark Beetles. *In* *Bark Beetles: Biology and Ecology of Native and Invasive*
730 *Species. Edited by F.E. Vega and R.W. Hofstetter. Academic Press, London, U.K. pp.*
731 *1–28.*
- 732 Roberts, D.W. 2013. *labdsv*: Ordination and Multivariate Analysis for Ecology. R
733 Package Version 1.6–1.

- 734 Scott, R.E., and Mitchell, S.J. 2005. Empirical modelling of windthrow risk in partially
735 harvested stands using tree, neighbourhood, and stand attributes. *Forest Ecol. Manag.*
736 **218**: 193–209. doi:10.1016/j.foreco.2005.07.012.
- 737 Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms:
738 Fennoscandian boreal forests as an example. *Ecol. Bull.* **49**: 11–41.
- 739 Spence, J.R., Volney, W.J.A., Lieffers, V., Weber, M.G., and Vinge, T. 1999. The
740 Alberta EMEND project: recipe and cook's argument. *In* Proceedings of the 1999
741 Sustainable Forest Management Network Conference. Science and Practice:
742 Sustaining the Boreal Forest. 14–17 February 1999. *Edited by* T.S. Veeman, D.W.
743 Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin. Sustainable Forest Management
744 Network, Edmonton, Canada. pp. 583–590.
- 745 Stokland, J.N., Siitonen, J., and Jonsson, B.G. 2012. Biodiversity in Dead Wood.
746 Cambridge University Press, New York, U.S.A.
- 747 Ulyshen, M.D., and Hanula, J.L. 2009. Habitat associations of saproxylic beetles in the
748 southeastern United States: A comparison of forest types, tree species and wood
749 postures. *Forest Ecol. Manag.* **257**: 653–664. doi: 10.1016/j.foreco.2008.09.047.
- 750 Urgenson, L.S., Halpern, C.B., and Anderson, P.D. 2013. Level and pattern of overstory
751 retention influence rates and forms of tree mortality in mature, coniferous forests of
752 the Pacific Northwest, USA. *Forest Ecol. Manag.* **308**: 116–127.
753 doi:10.1016/j.foreco.2013.07.021.
- 754 Venables, W.N., and Ripley, B.D. 2002. Modern Applied Statistics with S. Fourth edition.
755 Springer.

- 756 Wesley, J., 2002. The Impacts of Variable Retention Harvesting on Spruce Beetle
757 (*Dendroctonus rufipennis*) and Canopy Dwelling Lepidopteran Parasitoids in the
758 Boreal Forest. Department of Biological Sciences, University of Alberta, Edmonton,
759 Alberta, Canada.
- 760 Wood, C.M. 2012. Saproxylic beetles (Coleoptera) associated with aspen deadwood in
761 broad-leaved boreal mixedwood stands. MSc thesis. Department of Renewable
762 Resources, University of Alberta, Edmonton, Alberta, Canada.
- 763 Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., and Langor, D.W. 2004.
764 Stand composition and structure of the boreal mixedwood and epigaeic arthropods of
765 the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in
766 northwestern Alberta. *Can. J. Forest Res.* **34**: 417–430. doi: 10.1139/x03-238.
- 767 Work, T.T., Jacobs, J.M., Spence, J.R., and Volney, W.J. 2010. High levels of green-tree
768 retention are required to preserve ground beetle biodiversity in boreal mixedwood
769 forests. *Ecol. Appl.* **20**: 741–751. doi: 10.1890/08-1463.1.

< FIGURE LEGENDS >

Fig. 1. Aerial photos of aggregated retention patches illustrating small (S; 0.20 ha) and large (L; 0.46 ha) patches surrounded by three different retention levels of boreal mixedwood stands on the EMEND landscape: a, b – 2% retention (clearcut); c, d – 20% dispersed; e, f – 50% dispersed retention. The same stands were photographed in 1999 and 2010. Photo credit: EMEND.

Fig. 2. Non-metric multidimensional scaling (NMS) of saproxylic beetle assemblages in white spruce CWM in boreal mixedwood stands. Final stress is 14.4. Ellipses show 95% confidence intervals around treatment centroids (horizontal and upright CWM combined). Abbreviations: CT (unharvested control), DCs (decay classes), L (large aggregated retention) and S (small aggregated retention).

Fig. 3. Non-metric multidimensional scaling (NMS) of three trophic guilds of saproxylic beetles in white spruce CWM in boreal mixedwood stands: a – phloeophages (final stress is 12.7); b – mycetophages (10.7); c – predators (17.1). Ellipses show 95% confidence intervals around treatment centroids (horizontal and upright CWM combined). Abbreviations: CT (unharvested control), DCs (decay classes), L (large aggregated retention) and S (small aggregated retention).

Fig. 4. Mean (+SE) number of individuals of common species of phloeophages (a-f), mycetophages (g-h), and predators (i-k) in cut white spruce bolts oriented horizontally and upright in small (S; 0.20 ha) and large (L; 0.46 ha) patches of forest surrounded by

793 three levels of dispersed retention (2%, 20%, 50%) and in unharvested controls (CT) of
794 boreal mixedwood forest on the EMEND landscape. Different letters indicate significant
795 *post-hoc* results (Tukey's honestly significant difference test, $p \leq 0.05$).

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(a) 2%-S & L in 1999

(b) 2%-S & L in 2010

(c) 20%-S & L in 1999

(d) 20%-S & L in 2010

(e) 50%-S & L in 1999

(f) 50%-S & L in 2010

Phloeophages

Mycetophages

Predators

Harvest treatments

< TABLES >

Table 1. Mean ($\pm$ SE) total numbers of live trees and volumes of downed CWM of three decay classes in aggregated retention patches of two sizes surrounded by variable dispersed retention and in unharvested controls in mixed stands of mainly *Picea* and *Populus* spp.

Patch Sizes	Treatments ^a	Numbers of live trees ^b	Proportion of coniferous and deciduous trees	Volumes of downed CWM (m ³)	Volumes of DCs ^c 1–2 (m ³)	Volumes of DCs 3–4 (m ³)	Volumes of DCs 5–6 (m ³)
0.20 ha	2%-S	58.67 $\pm$ 46.03 (3-150)	55:45	8.29 $\pm$ 3.42	1.21 $\pm$ 0.71	6.95 $\pm$ 3.19	0.13 $\pm$ 0.07
	20%-S	103.33 $\pm$ 41.68 (48-185)	70:30	6.41 $\pm$ 2.94	2.73 $\pm$ 1.37	3.67 $\pm$ 2.25	0.02 $\pm$ 0.02
	50%-S	70.67 $\pm$ 8.41 (57-86)	60:40	4.40 $\pm$ 1.75	2.44 $\pm$ 1.94	1.40 $\pm$ 0.29	0.57 $\pm$ 0.44
0.46 ha	2%-L	83.33 $\pm$ 49.84 (32-183)	58:42	14.06 $\pm$ 6.94	6.71 $\pm$ 6.39	6.16 $\pm$ 1.45	1.19 $\pm$ 0.61
	20%-L	158.33 $\pm$ 56.89 (97-272)	58:42	11.28 $\pm$ 5.66	6.49 $\pm$ 2.70	4.09 $\pm$ 2.94	0.69 $\pm$ 0.41
	50%-L	104.33 $\pm$ 40.48 (52-184)	73:27	8.24 $\pm$ 4.02	4.41 $\pm$ 3.21	2.60 $\pm$ 1.26	1.23 $\pm$ 0.47
Control	Control	- ^d	-	2.91 $\pm$ 0.98	0.29 $\pm$ 0.24	1.05 $\pm$ 0.85	1.58 $\pm$ 0.58
		$p = 0.608$	-	$p = 0.361$	$p = 0.502$	$p = 0.173$	$p = 0.058$

^a L (large patch = 0.46 ha), and S (small patch = 0.20 ha); percentages refer to surrounding dispersed retention level.

^b Numbers in parenthesis indicate ranges.

^c DCs (decay classes).

^d Total numbers of live trees were not measured in unharvested control.

Table 2. Generalized Linear Model results testing effects of CWM bolt orientation and harvest treatments in boreal mixedwood stands on species richness and total number of individuals of saproxylic beetles in white spruce.

Trophic guilds ^a	Source ^b	df	Deviance	AIC	<i>p</i> ^c	Pairwise comparisons ^d
<i>Species richness</i>						
All trophic guilds	Orient	1	44.49	222.78	0.128	
(78 spp.)	Trmt	5	51.48	221.77	0.097	
Phloeophages	Orient	1	29.96	158.40	0.392	
(12 spp.)	Trmt	5	34.98	155.41	0.332	
Mycetophages	Orient	1	19.92	133.35	0.326	
(22 spp.)	Trmt	5	23.80	129.22	0.436	
Predators	Orient	1	26.17	154.92	0.231	
(29 spp.)	Trmt	5	29.00	149.74	0.512	
<i>Number of individuals</i>						
All trophic guilds	Orient	1	44.21	531.87	0.064	
(20367 individuals)	Trmt	5	49.29	528.95	0.130	
Phloeophages	Orient	1	44.76	510.77	0.122	
(14968 individuals)	Trmt	5	49.26	507.27	0.230	
Mycetophages	Orient	1	49.86	382.91	0.008	Upright CWM > Horizontal CWM CT > (2%-L, 20%-S, 20%-L) (50%-S, 50%-L) > 20%-S
(4510 individuals)	Trmt	5	68.14	393.19	< 0.001	
Predators	Orient	1	41.48	269.19	0.253	
(670 individuals)	Trmt	5	76.66	296.37	< 0.001	CT > all treatments

^a Numbers in parenthesis indicate either total number of species or individuals.
^b Orient (Orientation) and Trmt (Harvest treatments).
^c Significant differences ($p < 0.05$) are highlighted in bold, followed by *a posteriori* pairwise comparisons.
^d CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha); percentages refer to surrounding dispersed retention level.

Table 3. Two-way PERMANOVA results testing effects of CWM bolt orientation and harvest treatments in boreal mixedwood stands on saproxylic beetle assemblages in white spruce.

Trophic guilds	Source ^a	df	SS	MS	Pseudo- <i>F</i>	<i>p</i> (perm) ^b	Pairwise comparisons ^c
All trophic guilds	Orient	1	6306.8	6306.8	3.25	< 0.001	Horizontal CWM ≠ Upright CWM
	Trmt	5	15814.0	3162.8	1.63	0.007	(CT, 50%-L) ≠ (2%-L, 20%-S, 20%-L, 50%-S)
	Orient × Trmt	5	6387.5	1277.5	0.66	0.978	
	Residual	24	46610.0	1942.1			
	Total	35	75119.0				
Phloeophages	Orient	1	7430.9	7430.9	4.95	< 0.001	Horizontal CWM ≠ Upright CWM
	Trmt	5	13273.0	2654.7	1.77	0.014	CT ≠ (2%-L, 20%-S, 50%-S) 2%-L ≠ (20%-L, 50%-L, CT)
	Orient × Trmt	5	4734.6	946.9	0.63	0.938	
	Residual	23	34552.0	1502.3			
	Total	34	60113.0				
Mycetophages	Orient	1	5788.8	5788.8	2.18	0.042	Horizontal CWM ≠ Upright CWM
	Trmt	5	13621.0	2724.2	1.03	0.418	
	Orient × Trmt	5	11818.0	2363.7	0.89	0.632	
	Residual	23	61050.0	2654.3			
	Total	34	93099.0				
Predators	Orient	1	1860.1	1860.1	0.74	0.624	
	Trmt	5	17497.0	3499.4	1.40	0.090	
	Orient × Trmt	5	4399.0	879.8	0.35	0.999	
	Residual	24	59976.0	2499.0			
	Total	35	83732.0				

^a Orient (Orientation) and Trmt (Harvest treatments).

^b Significant differences ($p < 0.05$) are highlighted in bold, followed by *a posteriori* pairwise comparisons.

^c CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha); percentages refer to surrounding dispersed retention level.