

Research article

Rapid recovery of boreal rove beetle (Staphylinidae) assemblages 16 years after variable retention harvest

Seung-Il Lee, David W. Langor, John R. Spence, Jaime Pinzon, Gregory R. Pohl, Dustin J. Hartley†, Timothy T. Work and Linhao Wu

S.-I. Lee (<https://orcid.org/0000-0001-9339-0156>) ✉ (seungil.lee@lakeheadu.ca), D. W. Langor, J. Pinzon (<https://orcid.org/0000-0002-5312-9356>), G. R. Pohl, D. J. Hartley and L. Wu, Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada. – J. R. Spence, Dept of Renewable Resources, Univ. of Alberta, Edmonton, Alberta, Canada. – T. T. Work, Dépt des Sciences Biologiques, Univ. du Québec à Montréal, CP 8888, Succursale Centre-ville, Montréal, Quebec, Canada. S-IL also at: Faculty of Natural Resources Management, Lakehead Univ., Thunder Bay, Ontario, Canada.

Ecography

2022: e06347

doi: 10.1111/ecog.06347

Subject Editor:

Mikko Mönkkönen

Editor-in-Chief: Miguel Araújo

Accepted 20 September 2022



Post-harvest recovery of biodiversity is one of important goals in modern forestry. A variable retention (VR) approach has been of particular interest in North America because it promotes rapid faunal recovery, while minimizing negative lasting impacts of logging on the natural fauna. We studied responses of rove beetles (Coleoptera: Staphylinidae) to a broad range of retention harvests (2, 10, 20, 50 and 75% retention) in comparison to uncut controls as part of the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment in the boreal mixedwood forest of western Canada. We sampled beetles using pitfall traps 1, 2, 11 and 16 years post-harvest in replicated ($n = 3$) stands representing four cover types (deciduous-dominated, deciduous with spruce understory, mixed and coniferous-dominated). We collected 74 263 individuals distributed across 99 species (excluding Aleocharinae). Estimated species richness was highest in clear-cuts until year 11, but by year 16 species richness was similar among treatments. Species composition initially varied strongly in relation to intensity of harvest treatments, but overall variation decreased with time, and by year 16, species composition overlapped among most treatment combinations. Assemblages recovered more quickly in early successional (deciduous-dominated) than in late successional (mixed and conifer-dominated) stands. Overall, our results show that rove beetle assemblages in stands harvested to all VR prescriptions converged more rapidly toward those in fire-origin mature stands than did assemblages in clear-cuts over the first 16 years post-harvest. Thus, it demonstrates that even modest levels of forest retention can facilitate the recovery of staphylinid assemblages in managed landscapes.

Keywords: biodiversity conservation, boreal mixedwood, EMEND, retention forestry, sustainable forest management

Introduction

Variable retention (VR) harvest has been widely promoted as an ecologically sensitive alternative to conventional clear-cutting (Franklin et al. 1997, 2018, Lindenmayer and Franklin 2002, Gustafsson et al. 2012). In the VR approach, a portion of standing trees retained in harvested stands maintain forest structure and cover to support biodiversity and ecosystem functions (Lindenmayer et al. 2012). VR also maintains legacy elements, such as deadwood, diverse microhabitats and understory vegetation (Gustafsson et al. 2012, Lee et al. 2018), elements thought to speed up post-harvest recovery of forest structure and associated organisms (Lindenmayer et al. 2012).

An inherent principle of VR is that pattern and amount of retention is set to vary across the landscape rather than conforming to a single harvest prescription. This provides landscape mosaics of multiple prescriptions that together somewhat emulate the variability that follows natural disturbances (Pinzon et al. 2016). Spatial patterns of retention vary between highly aggregated patches to more dispersed retention distributed across stands (Lindenmayer and Franklin 2002). Aggregated retention patches preserve areas of canopy cover and leave understory and forest floor undisturbed within harvest blocks (Franklin et al. 1997, Lee et al. 2015). Dispersed retention, in contrast, leaves single trees spread throughout cut-blocks ensuring continuous supply of seedlings, suckers and deadwood, and preserving connections among belowground microhabitats (Franklin et al. 1997). Aggregated and dispersed retention can be combined strategically to meet conservation goals (Lencinas et al. 2011, Pinzon et al. 2012, Lee et al. 2017).

Over the last two decades, large-scale experiments using VR have been implemented around the world to explore how different patterns of retention maintain biodiversity, forest structure, regeneration and productivity (Gustafsson et al. 2012, Fedrowitz et al. 2014, Lee et al. 2018, Koivula and Vanha-Majamaa 2020). The Ecosystem Management Emulating Natural Disturbance (EMEND) experiment in Canada is among the earliest and largest trials designed to assess effects of VR harvest in the boreal forest. EMEND focuses on how spatial distribution of forest structure (i.e. retention pattern) and amount of retention (i.e. retention level) affect ecosystem integrity and forest regeneration at various stages of stand development typical of upland boreal ecosystems (Spence et al. 1999, Work et al. 2010, Lee et al. 2018). The EMEND project has pursued work with an unusually wide range of biodiversity, including microbes, fungi, bryophytes, plants, vertebrates and invertebrates (see <<https://emend.ualberta.ca/knowledge-exchange/publications/>>).

Considerable research effort has been invested in Coleoptera (Jacobs et al. 2007, Work et al. 2010, Lee et al. 2017, Wu et al. 2020), the most biodiverse of all metazoan orders in terms of described species. Here, we focus on rove beetles (Staphylinidae), which are taxonomically and trophically diverse, and especially through their relationships with fungi (Lipkow and Betz 2005) are important to forest function. They occupy many forest microhabitats, including

litter, humus, fungi, scat, animal nests and deadwood (Thayer 2016, Irmeler et al. 2018). Owing to their diverse feeding habits, including predation, mycophagy, saprophagy and phytophagy, staphylinids fill many ecological niches (Thayer 2016). They are sensitive to environmental changes and are thus useful bioindicators for environmental impact studies (Bohac 1999, Pohl et al. 2008, Klimaszewski et al. 2018).

In the present study, we measured responses of rove beetle assemblages following VR harvest over 16 years in four common boreal cover-types. We framed our overall study in terms of two main hypotheses: 1) rove beetle assemblages would differ across retention levels, with differences becoming less evident over time as forests recover; and 2) rove beetle assemblages would respond differently across forest cover types, recovering more quickly in early than in late successional stands, as earlier seres generally harbour species better adapted to disturbance (Pinzon et al. 2016, Wu et al. 2020). We used the fauna of old fire-origin stands as targets to assess recovery, as such stand-types are being reduced most dramatically by commercial forestry in the western boreal forest (Venier et al. 2014), and it is their loss that is feared to have the most serious consequences for biodiversity (Janssen et al. 2017).

As rove beetle species differ in habitat affinity (i.e. mature forest, open habitat and intermediate disturbance) or have no detectable affinity (i.e. generalists) (Pohl et al. 2008), we tracked how common species had subsequently responded to various retention levels in post-harvest years 11 and 16. In relation to the responses of individual species, we hypothesized that: 1) mature forest species would recover faster in higher retention than in lower retention; 2) catches of open habitat species in low retention would decrease over time with canopy closure; 3) species that showed highest catches in the medium level of retention would show no difference across harvest treatment over time; and 4) catches of habitat generalists would not be affected by VR regardless of time since harvest.

Material and methods

Study area

This study was conducted at the EMEND experimental site (56°46'13"N, 118°22'28"W), located in northwestern Alberta, Canada, in an area with little industrial forestry before 1998. The landscape of the study area comprises boreal mixedwood forest, originating from a mixed severity wildfire regime (Bergeron et al. 2017). The EMEND experiment was implemented in ca 1000 ha of mesic upland stands embedded in this larger mix. The stands include mainly trembling aspen *Populus tremuloides*, balsam poplar *Populus balsamifera* and white spruce *Picea glauca*. Black spruce *Picea mariana*, lodgepole pine *Pinus contorta*, balsam fir *Abies balsamea* and paper birch *Betula papyrifera* are less common canopy elements at EMEND (Work et al. 2010, Pinzon et al. 2016). Based on data collected from 1981 to 2007 at Eureka River, Alberta (ca 40 km SW of EMEND),

average summer (June–August) and winter (December–February) temperatures are 13.8°C and −15.1°C, respectively, and average annual precipitation is 436.2 mm, with 128.8 cm of snowfall and 307.4 mm of rainfall (Government of Canada 2019).

Experimental design and staphylinid sampling

Several retention harvesting treatments were applied during the winter of 1998–1999 to randomly selected 10-ha experimental ‘compartments’ within stands of each of four cover-types that span a simplified successional pathway in the western boreal forest (Rowe 1972): deciduous-dominated (DD), deciduous with spruce understory (DU), mixed (MX) and coniferous-dominated (CD) (Spence et al. 1999). The harvest prescriptions were: 2% retention of original stem density (R0; this equates to standard clear-cuts in Alberta), 10% (R10), 20% (R20), 50% (R50) and 75% (R75), plus an unharvested control (CT). Each treated compartment also contained two aggregated retention patches of 0.20 ha and 0.46 ha in addition to the dispersed retention left behind at harvest. The full treatment regime was replicated three times in each forest cover type for a total of 72 experimental units (4 cover types × 6 harvest treatments × 3 replicates).

Pitfall traps (11.2 cm in diameter) following the design of Spence and Niemelä (1994) were used to sample staphylinids from each compartment between May and August (roughly the frost-free season in northern Alberta). Samples were collected in 1999 (year 1; immediately following winter harvest), 2000 (year 2), 2009 (year 11) and 2014 (year 16). Six traps were installed in each compartment, two at either end of three randomly placed permanent sampling plots (40 × 2 m), for a total of 432 traps in each year of sampling (see Pinzon et al. (2016) for further details). Traps contained ca 200 ml of low-toxicity ethylene glycol as a killing agent and preservative. Traps were serviced at ca 3-week intervals to collect the accumulated specimens and replenish the preservative. Each trap was shielded from litter deposition and precipitation by a plastic roof (15 × 15 cm) suspended ~2 cm above the trap (Digweed et al. 1995, Bergeron et al. 2013).

Identification of staphylinids

Whenever possible, specimens were identified to species using relevant taxonomic literature (Newton et al. 2001) and by comparison to authoritatively identified material located in the insect collection at the Northern Forestry Centre (NoFC) in Edmonton, Alberta. Nomenclature follows Bousquet et al. (2013). Genitalia were dissected to identify most males and, when necessary, for females (e.g. *Quedius* spp.). Although about 15% of the taxa could be identified only as either morphospecies or belonging to a suite of cryptic species (Supporting information), we treated these as single entities (i.e. species).

Quedius labradorensis and *Q. molochinoides* were combined as *Quedius labradorensis/molochinoides* because females could not be reliably separated. A few specimens in *Bolitobius*,

Mycetoporus, *Omalius*, *Stenus* and *Tachyporus* could be identified only to genus since reliable taxonomic keys for local species are not available. The subfamily Aleocharinae was excluded from all analyses because reliable species-level identification was impossible. Voucher specimens of all taxa listed in the Supporting information are deposited in the NoFC collection.

Statistical analyses

Prior to analyses, catches were pooled by compartment and standardized to number of individuals per trap-day in each year to account for uneven sampling effort resulting from trap disturbance by wildlife and minor year-to-year differences in total trap-days. All analyses were conducted in R ver. 3.6.0 (<www.r-project.org>) except for permutational multivariate analysis of variance (PERMANOVA) and permutational analysis of homogeneity of multivariate dispersions (PERMDISP), which were conducted using PERMANOVA+ add on package for PRIMER ver. 7 (Anderson et al. 2008, Clarke and Gorley 2015).

Coverage-based rarefaction (Chao and Jost 2012) was used to compare changes in species richness among harvest treatments and cover types in each sampling year. By considering relative abundances of focal species in each community at minimum coverage level (i.e. completeness), coverage-based rarefaction adjusts for both sampling intensity and the species abundance distribution (Chao et al. 2014). Estimated richness values (\pm 95% confidence interval) were obtained using the ‘iNEXT’ package (Hsieh et al. 2016). Estimated means with non-overlapping confidence intervals were considered significantly different (Schenker and Gentleman 2001).

We tested for differences in standardized total catch among years, forest cover types and harvest treatments using a linear mixed-effects model with consideration of temporal correlations implicit in the repeated measures experimental design. In this model we analyzed ‘year × cover type × harvest treatment’ combinations as a fixed effect, and included ‘compartment’ as a random effect. We double square-root-transformed standardized catches and included a power variance structure in the model to satisfy the assumptions of normality and homoscedasticity of residuals. We also analyzed changes in overall abundance of the nine most common species, each representing > 3% of the overall catch, using the same regression approach as for total catch, but without the power variance structure, as the model residuals satisfied the assumption of homoscedasticity. Models were fit using the ‘nlme’ package (Pinheiro et al. 2019). For significant ($p < 0.05$) models we compared estimated marginal means among all factor pairs using the ‘emmeans’ package (Lenth et al. 2020).

Non-metric multidimensional scaling (NMS) was used to visualise staphylinid community structure. NMS is applicable to a broad range of ecological data because it makes relatively few assumptions and places assemblages in a reduced ordination space in relation to their overall similarity (McCune and Grace 2002, Legendre and Legendre 2012). We computed NMS using Bray–Curtis dissimilarity on

square-root-transformed data with 500 random starts, and included a posteriori 95% confidence ellipses around group centroids in the ordination plot to assist visual interpretation of the results. These analyses were done using the 'vegan' package (Oksanen et al. 2019).

We performed PERMANOVA to test differences in species composition of assemblages among years, cover types and harvest treatments. This powerful non-parametric test of multivariate hypotheses compares simultaneous responses of different species by considering relative abundance of each species in a multifactorial ANOVA model (Anderson 2001). We used the Bray–Curtis distance measure on square-root-transformed data and ran 9999 permutations for the main tests with PERMANOVA. Pair-wise comparisons were applied with 999 permutations when the main effects were significant ($p < 0.05$). Components of variation were partitioned using the default 'Type III sums of squares' (Anderson et al. 2008). The assumption of homogeneity of dispersion was checked using PERMDISP when PERMANOVA results were significant (Anderson et al. 2008).

Results

The rove beetle fauna at EMEND

We collected 74 263 rove beetles, representing 99 species in 15 subfamilies. The most species-rich groups were Staphylininae (34 species), Tachyporinae (26 spp.) and Omaliinae (18 spp.). Tachyporinae comprised 64.8% of total catch (48 156 individuals), followed by Staphylininae (20 218; 27.2%) and Omaliinae (1741; 2.3%). The most abundant species were *Lordithon fungicola* Campbell (13 497; 18.1%), *Tachinus fumipennis* (Say) (13 375; 18.0%) and *Tachinus frigidus* Erichson (10 469; 14.1%) (Supporting information). The 47 least common species together represented < 5% of total catch, and singletons and doubletons accounted for 14.1% and 5.1% of the total richness, respectively.

Changes in species richness and catch

Although temporal patterns varied among treatments, estimated species richness (at 98.8% sample coverage) generally increased from immediately post-harvest (year 1) until year 11, but decreased significantly in year 16 (Fig. 1a). Richness tended to be highest in R0 in each year, with the pattern strongest at year 11. Differences in richness between R0 and CT were least evident at year 16. Although this richness pattern was generally similar across cover types, richness tended to be highest in R0 in most years in DD and DU but was highly variable in MX and CD (Supporting information).

We detected highly significant differences in catch across years, cover types and harvest treatments, but the year by treatment interaction was only marginally significant (Table 1). The analysis supports the following three points. Catches from years 11 and 16 were significantly higher than those from

earlier periods (Fig. 1b, Table 1). Catches in early successional stands (DD and DU) were significantly higher than those in late successional stands (MX and CD) (Table 1). Catches were lowest and least variable in R0 in the two earliest years; however, no significant differences among treatments were detected 11 and 16 years post-harvest, consistent with broad recovery of assemblages, even in R0 compartments, toward the target of CT assemblages (Fig. 1b, Table 1).

Changes in rove beetle composition

Results from PERMANOVA showed that assemblage composition differed significantly among years, cover types and harvest treatments, with significant interactions between year \times cover type, and year \times harvest treatment (all p -values = 0.0001; Table 2). However, results from PERMDISP showed that there were significant differences in within-treatment dispersions from year ($p = 0.003$), cover type ($p = 0.020$) and harvest treatment ($p = 0.002$). Multiple comparisons showed that assemblage composition differed among all years and cover types and among most harvest treatments, with the exception that R10 = R20, R20 = R75 and R50 = R75 (Table 2). Differences between cover types in each year were mostly significant, except for two pairs of cover types adjacent in the simplified successional sequence, i.e. MX versus CD in all years and DU versus MX in year 16 (Table 2). Species composition in R0 differed significantly from that in all other harvest treatments in the first two years, but differed from only those in CT and R75 in years 11 and 16 (Supporting information). By year 16, only post-harvest assemblages from R50 differed significantly ($p = 0.04$) from the CT (Supporting information).

NMS ordination revealed temporal shifts in species composition in each cover type. Although species composition largely overlapped between years 1 and 2, 95% confidence ellipses shifted conspicuously in ordination space in subsequent years (Fig. 2). Assemblages from year 16 were more similar to those in years 1 and 2 than to those in year 11 (Fig. 2). The NMS ordination also reflected the gradient of cover types from DD to CD in all years, although assemblages in DU and MX became similar over time as the understorey spruce in DU compartments grew (Fig. 2).

The pattern of assemblage structure depicted in NMS ordination space reflected the gradient of harvest intensity (R0 to CT) in the two initial years, particularly in year 2 (Fig. 3a, b). This effect weakened in year 11 with assemblages showing much overlap from R10 to R50 (Fig. 3c). By year 16, assemblages in all harvest treatments overlapped, suggesting convergence toward a generally common assemblage structure across harvest treatments and controls (Fig. 3d). Assemblages showed similar patterns of change in composition in each cover type (Supporting information) but those in DD stands recovered toward the target faster than those in other cover types. Assemblages from all treatments in DD overlapped in year 11, while those in other cover types remained more distinct (Supporting information).

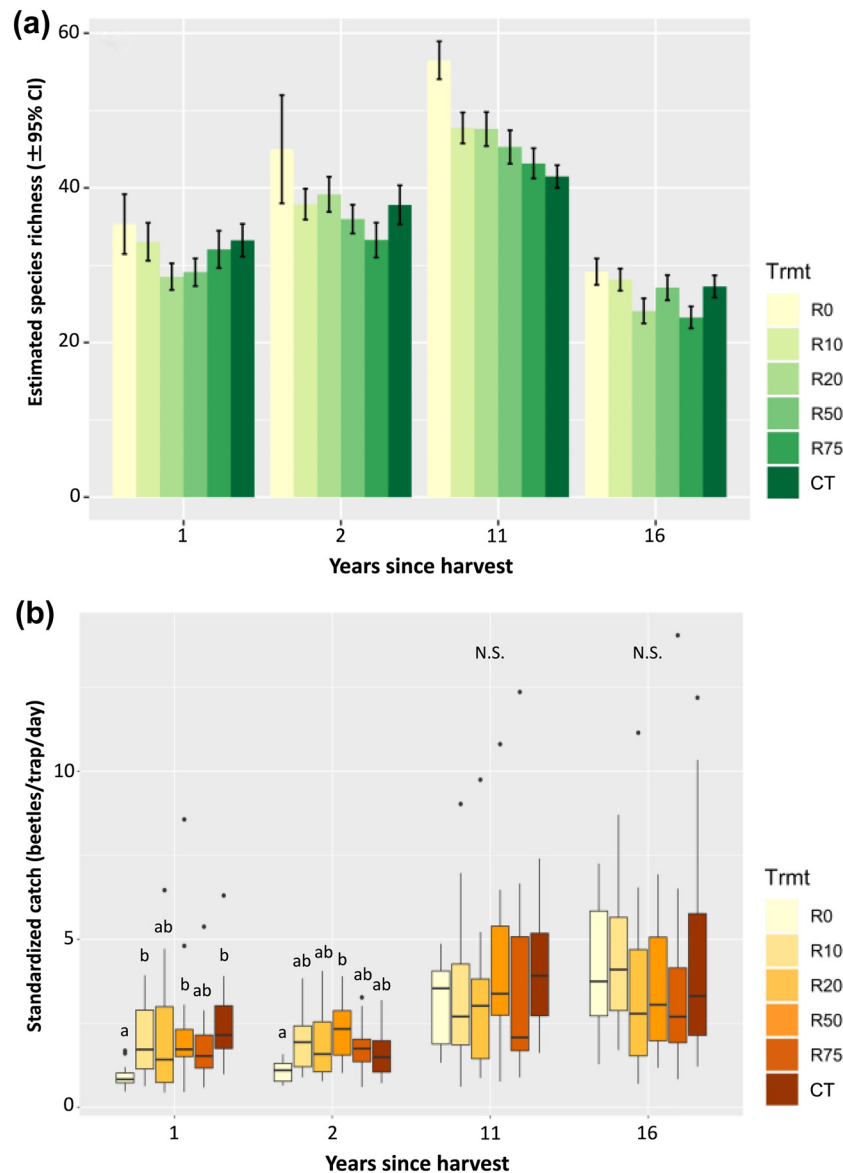


Figure 1. Estimated species richness (a) and standardized catch (b) of rove beetles across harvest treatments in each post-harvest year. Sample completeness in (a) is 98.8%, and non-overlapping confidence intervals are considered significantly different. In (b) the thick horizontal bars in boxplots represent the median, the boxes show interquartile range representing the middle 50% of the data, dots are outliers, upper longitudinal bars are maxima, lower longitudinal bars are minima and different letters indicate significant differences among treatments within each year. CT (unharvested control), N.S. (non-significant), R (% retention level) and Trmt (harvest treatment).

Responses of individual species

We analyzed changes in overall catch rate for nine common rove beetle species. Captures of *T. fumipennis*, *T. frigidus*, *Mycetoporus americanus* and *Quedius rusticus*, all mature forest species, generally increased with increasing retention in the first two years (Fig. 4a–d). However, catch rates did not differ among harvest treatments in year 16 for any of these species even in compartments originally harvested with low retention (Fig. 4a–d). Overall abundances of the first three species were also higher in years 11 and 16 than in years 1 and 2 (Fig. 4a–c). In contrast, catches of *Q. rusticus* were higher in

year 1 than in year 16; also, the catches in years 2 and 11 were significantly higher in CT and high retention compartments than in those cut with low retention prescriptions (Fig. 4d). Catch rates for three mature forest species (*T. fumipennis*, *T. frigidus* and *Q. rusticus*) were higher in compartments dominated by deciduous trees (DD and DU) than in those with high conifer components (MX and CD) (Fig. 4a, b and d). In contrast, catches of *M. americanus* were highest in MX but were not notably reduced in CD relative to the two habitats with canopies dominated by deciduous trees (Fig. 4c).

Catches of the open habitat species, *Q. labradorensis/molochinoides*, generally decreased with

Table 1. Effects of year, forest cover type and harvest treatment on rove beetle catches in boreal mixedwood forest using linear mixed-effects model.

Source ^a	numDF	denDF	F-value	p-value ^b	Multiple comparisons ^c
(Intercept)	1	144	11 617.578	< 0.001	
Year	3	144	43.961	< 0.001	(Y11=Y16) > (Y1=Y2)
Cover	3	48	24.339	< 0.001	DD > DU > (MX=CD)
Trmt	5	48	4.319	< 0.010	N.S.
Year × Cover	9	144	1.345	0.219	
Year × Trmt	15	144	1.888	< 0.050	Y1: (CT=R10=R50) > R0 Y2: R50 > R0
Cover × Trmt	15	48	1.177	0.321	
Year × Cover × Trmt	45	144	0.714	0.904	

^a Year (year since harvest), Cover (forest cover type) and Trmt (harvest treatment).

^b Significant differences ($p < 0.05$) are highlighted in bold, followed by multiple comparisons.

^c CD (coniferous dominated), DD (deciduous dominated), DU (deciduous dominated with spruce understory), MX (mixed), N.S. (not significant), R (% retention level) and Y (years since harvest).

increasing retention in the first two years (Fig. 4e); however, this trend was weak in year 11. The overall catch of *Q. labradorensis/molochinoides* was highest in year 1, and catch did not differ according to cover type (Fig. 4e).

Catches of *Lordithon fungicola* and *Dinothenarus pleuralis* (LeConte) seemed to be highest at medium retention levels in years 1 and 2, but not in years 11 and 16 (Fig. 4f–g). Despite *L. fungicola* being the most frequently trapped species in year 16 (8044 individuals), only 40 specimens were trapped in year 11, all in CT compartments (Fig. 4f).

Catches of *Quedius velox* Smetana and *Tachinus elongatus* Gyllenhal, both forest generalists, were largely unaffected by intensity of VR harvest (Fig. 4h–i). Catches of *Q. velox* were highest in years 1 and 2 but much lower in years 11 and 16 (Fig. 4h). In contrast, catches of *T. elongatus* were much higher in year 11 than in other years (Fig. 4i).

Discussion

Recovery of rove beetle assemblages

Enhancing post-harvest recovery of the fauna is an important goal of VR harvest (Aubry et al. 2009, Gustafsson et al.

2012). VR approaches have been of particular interest in Canada because promoting rapid faunal recovery contributes to minimizing the overall impact of logging on the natural fauna, given that pristine forest contributes a huge proportion of annual harvested volume (Venier et al. 2014). Forest stands in our study area have originated through a mixed severity wildfire regime (Bergeron et al. 2017), and thus, the forest industry seeks to identify management strategies that promote recovery of the fauna toward targets approximating the faunal structure and composition of the original pyrogenic stands. In these fire-prone boreal ecosystems, any species dependent upon old undisturbed forest could be threatened by industrial scale forest harvest that dramatically reduces the amount of old forest habitat developed through natural succession. In 1999, only 10% of the managed boreal forest in Alberta was classified as old forest, a proportion less than was historically present (Venier et al. 2014), and thus there is cause for concern. Although young stands provide habitats for many staphylinid species that thrive in open stands, Buddle et al. (2006) have shown that species composition differs between harvest- and fire-origin stands for at least 30 years post-disturbance (Heikkala et al. 2016). As the original pyrogenic stands are liquidated, management that facilitates rapid faunal recovery that can take advantage of

Table 2. Effects of year, forest cover type and harvest treatment on rove beetle composition in boreal mixedwood forest using three-way PERMANOVA.

Source ^a	df	SS	MS	Pseudo-F	p (perm) ^b	Multiple comparisons ^c
Year	3	1.3883E+05	46276	63.457	0.0001	All pairs of year differed
Cover	3	23 792	7931	10.875	0.0001	All pairs of cover type differed
Trmt	5	17 776	3555	4.875	0.0001	All pairs of harvest treatment differed except for R10=R20; R20=R75; R50=R75
Year × Cover	9	13 109	1457	1.997	0.0001	All pairs of cover type differed except for MX=CD in all years and DU=MX in Year16
Year × Trmt	15	19 728	1315	1.804	0.0001	See Supporting information for details
Cover × Trmt	15	13 432	895	1.228	0.0577	
Year × Cover × Trmt	45	27 099	602	0.826	0.9893	
Residual	192	1.4002E+05	729			
Total	287	3.9378E+05				

^a Year (year since harvest), Cover (forest cover type) and Trmt (harvest treatment).

^b Significant differences ($p < 0.05$) are highlighted in bold, followed by multiple comparisons.

^c CD (coniferous dominated), DU (deciduous dominated with spruce understory), MX (mixed) and R (% retention level).

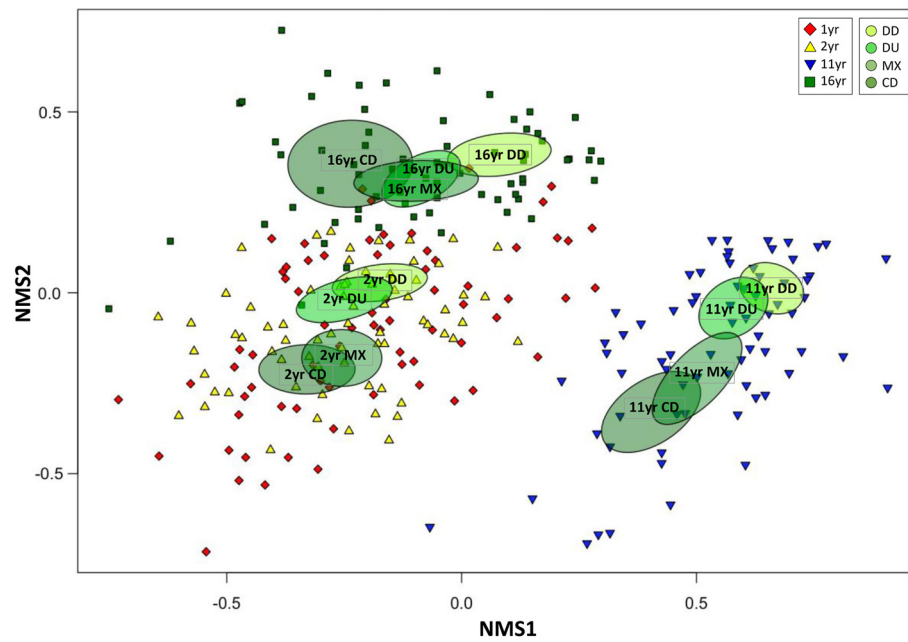


Figure 2. Nonmetric multidimensional scaling (NMS) ordination of rove beetle assemblages in boreal mixedwood stands. Ellipses indicate 95% confidence intervals around group centroids of forest cover types in each year. Ellipses for year 1 are not shown as they largely overlap with those for year 2. Final stress value is 17.9. CD (coniferous dominated), DD (deciduous dominated), DU (deciduous dominated with spruce understory), MX (mixed) and yr (years since harvest).

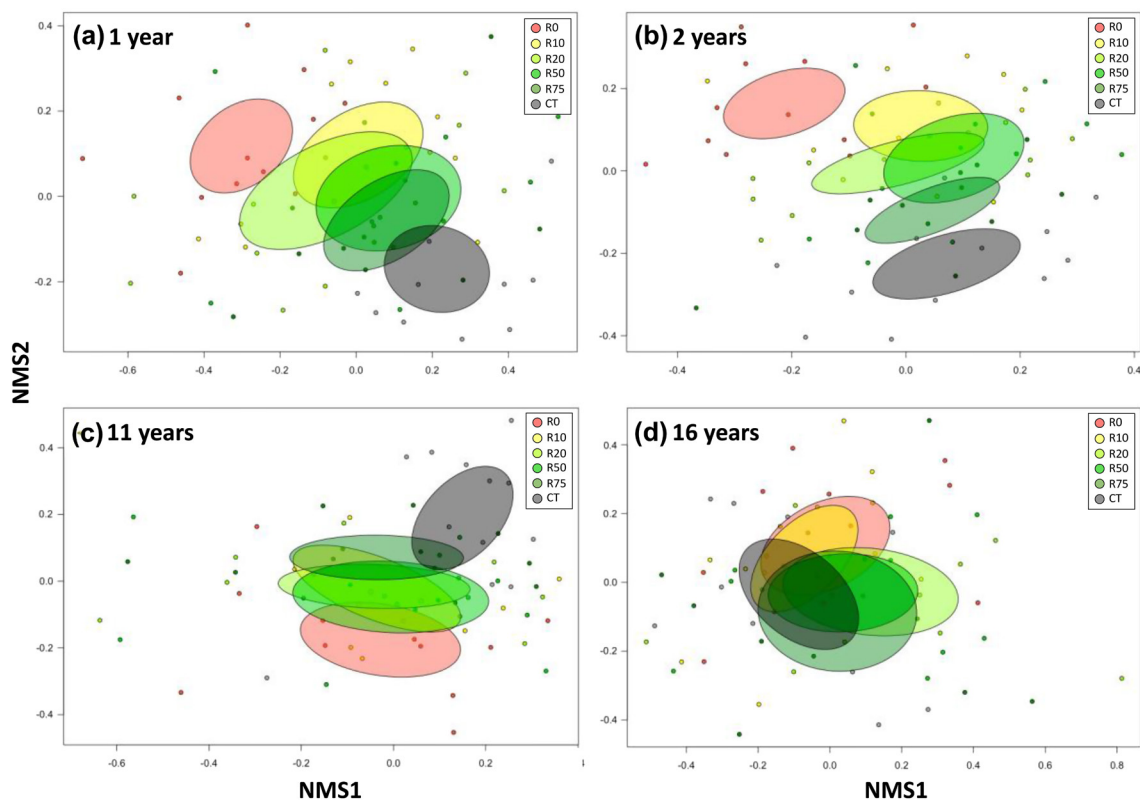


Figure 3. Nonmetric multidimensional scaling (NMS) ordination of rove beetle assemblages in different retention levels (R) in boreal mixedwood stands. Ellipses indicate 95% confidence intervals around group centroids of each harvest treatment. Final stress values are (a) 20.5, (b) 23.3, (c) 20.3 and (d) 18.1. Abbreviation: CT (unharvested control).

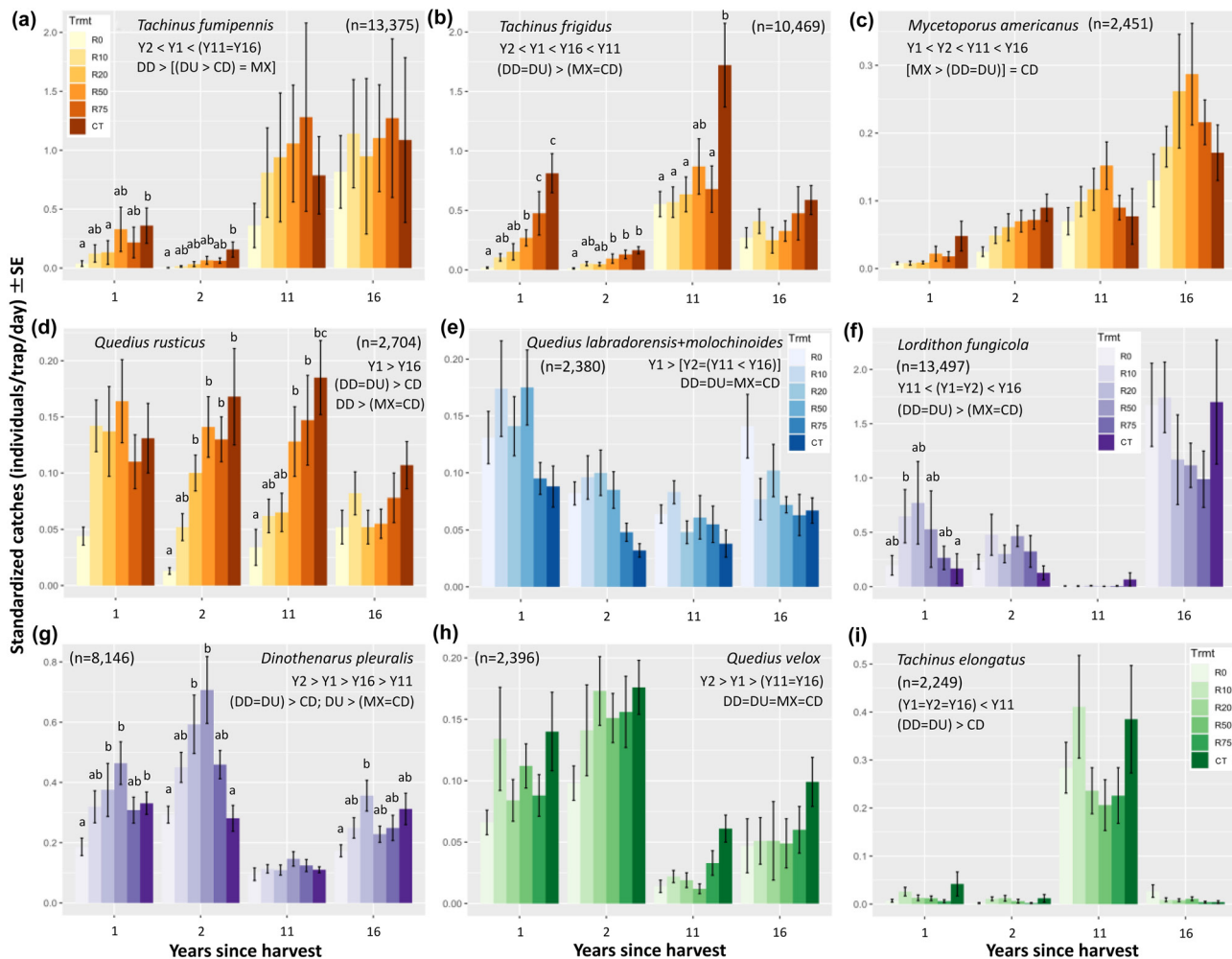


Figure 4. Standardized catches of nine common rove beetles in different harvest treatments 1, 2, 11 and 16 years post-harvest. Species exhibit three general types of habitat affinity: mature forest species (a–d, colored red), open habitat species (e, colored blue), intermediate disturbance species (f–g, colored purple) and generalist species (h–i, colored green). Different case letters above bars indicate significant differences among harvest treatment within each year. CD (coniferous dominated), CT (unharvested control), DD (deciduous dominated), DU (deciduous dominated with spruce understory), MX (mixed), n (beetle catches), R (% retention level), Trmt (harvest treatment) and Y (years since harvest).

source populations in the shrinking inventory of old forest should be preferred.

Our study establishes that rove beetle assemblages show signs of recovery toward pre-harvest conditions, even just 16 years post-harvest in all four cover types and in nearly all retention levels. Contrary to our first overall hypothesis, assemblages at even low levels of retention (10% and 20%) had become generally similar to those of unharvested controls by 16 years post-harvest. Although the NMS and PERMANOVA results suggested a slight difference in staphylinid composition between 16-year-old clear-cuts and unharvested controls, steady convergence of these assemblages over time was evident as indicated by both overlap of the 95% confidence ellipses in year 16 in the NMS (Fig. 3) and the decreasing t-values in PERMANOVA (Supporting information). In contrast, other studies about effects of clear-cut harvesting on biodiversity have

concluded that staphylinid and carabid assemblages had not recovered by 27 years after clear-cut harvest in conifer-dominated Cordilleran forests (Niemelä et al. 1993, Pohl et al. 2007), although carabid assemblages in these same stands had largely recovered by 53 years post-harvest (Belluz et al. 2022). Staphylinid assemblages had not fully recovered 28–29 years after clear-cutting in boreal aspen-dominated forests, although spider and carabid assemblages showed recovery towards their pre-disturbance condition in aspen stands (Buddle et al. 2006). Our results suggest that staphylinids recover faster following application of various retention prescriptions on a mixedwood landscape, compared to those found in pure clear-cut stands with little or no residual.

The rapid recovery of staphylinid assemblages observed in our study may be explained by three factors. Firstly, compartments at EMEND are surrounded by other compartments

harvested with VR and by intact forest buffers. Thus, faunal recovery in harvested compartments has likely been positively influenced by immigration from the surrounding forest matrix (Baker et al. 2013, Lee et al. 2017). Secondly, all treated compartments contain two aggregated retention patches of 0.20 ha and 0.46 ha, and 'life-boating' (Franklin et al. 1997) associated with these patches may accelerate recolonization of the adjacent habitat by forest interior species (Pinzon et al. 2012, Baker et al. 2013, Lee et al. 2017). Thirdly, compartments are relatively small (10 ha) compared to conventional harvest blocks in Alberta (e.g. up to 100 ha; Van Damme et al. 2014) and this may reduce recovery times in our experiment.

Studies at EMEND demonstrate potential benefits of VR for conserving a wide range of biodiversity. For example, breeding songbird assemblages were similar between compartments harvested to $\geq 20\%$ retention and unharvested controls 14–15 years post-harvest (Olsen et al. 2018). Furthermore, composition of epigeic carabid beetle assemblages did not differ between compartments harvested to $\geq 10\%$ retention and unharvested controls at 16 years post-harvest (Wu et al. 2020). Elsewhere, Franklin et al. (2019) reported six species of mammals were detected more often in stands with increasing levels of retention in conifer-dominated stands at 15–18 years post-harvest.

Patterns in species richness and catch

We suggest that staphylinid species richness tended to be highest in EMEND clear-cuts because they provide new environments that attract open-habitat species, while maintaining populations of habitat generalists and some mature forest species. The higher species richness in regenerating areas compared to mature stands matches observations at other sites in Cordilleran and boreal forests (Spence et al. 1997, Buddle et al. 2006, Pohl et al. 2007). Carabids from the same trap samples as for staphylinids at EMEND exhibited similar patterns in species richness (Wu et al. 2020); however, spider richness tended to be lowest in clear-cuts (Pinzon et al. 2016).

Staphylinid catches in clear-cuts were generally lowest in the initial two years but had increased by 11 and 16 years post-harvest to levels characteristic of unharvested controls. In contrast, staphylinid catches eight years (Spence et al. 1997) and 17 years (Pohl et al. 2007) following clear-cutting elsewhere in Alberta were quite dissimilar to catches in intact forests. As above, the rapid increase in staphylinid catch with time since harvest at EMEND may reflect influence from the surrounding forest matrix or, possibly, lack of additional disturbances after harvest. Scarification, for example, reduces catch of staphylinids (but not carabids) compared to unscarified sites in eastern boreal forests (Klimaszewski et al. 2008). The observation that treatments with $\geq 10\%$ retention at EMEND maintained staphylinid catches similar to those in unharvested controls suggests even low post-harvest retention helps maintain staphylinid populations.

Effects of forest cover type

Retaining a mixture of forest cover types on harvested landscapes is likely critical for maintaining a wide range of species adapted to specific forest successional stages (Pinzon et al. 2016, Bartels et al. 2018). In the present study, staphylinid assemblages differed conspicuously between DD and CD stands, supporting our second overall hypothesis. This reflects the complex boreal stand development trajectory from early to late successional stands, a pattern consistent among other taxa at EMEND, including mesostigmatan mites (Díaz-Aguilar et al. 2013), spiders (Pinzon et al. 2016) and carabid beetles (Wu et al. 2020). Our study also revealed that staphylinid assemblage structure in DU and MX stands had strongly converged by 16 years post-harvest, likely reflecting the increasing conifer contribution to the canopy of DU stands as the spruce understory has grown in the last 16 years to create a canopy more similar to that of MX stands (Bartels et al. 2018).

Our data further support our second hypothesis in showing that staphylinid assemblages would recover faster in early successional DD stands than in harvested compartments of late successional MX and CD stands, a pattern also evident for carabid assemblages at EMEND (Wu et al. 2020). This also supports the previous study that carabid assemblages in boreal aspen-dominated stands recovered more quickly than in Cordilleran conifer stands because of rapid post-disturbance growth of aspen that led to faster recovery of interior forest environments typical of DD stands (Spence et al. 1996). As post-disturbance development of a closed canopy is a critical step in the recovery of epigeic assemblages characteristic of mature stands (Belluz et al. 2022), cover types dominated by fast-growing tree species such as aspen can generally be expected to support faster recovery of ground-dwelling arthropod assemblages than forests dominated by slow-growing conifers.

Responses of individual species

Responses of rove beetle assemblages to disturbance, and the rate, degree and trajectory of their recoveries after harvest, are a composite of response patterns exhibited by individual species constituting the assemblage. While studies of assemblages reveal broad patterns of response, understanding of underlying processes governing those responses requires consideration of individual species. In a simplistic model, species can respond to an environmental disturbance positively, negatively or remain relatively unaffected, and degree of response can vary.

As suggested by our first hypothesis about responses of particular species, relative catches of *T. fumipennis*, *T. frigidus*, *M. americanus* and *Q. rusticus*, species with affinity for mature forests, decreased immediately following harvest and increased most rapidly in compartments with higher retention. Thus, mature forest species can serve as sound indicators of post-disturbance recovery, especially if they show similar habitat affinity across a variety of forest types and

localities (i.e. spatial robustness; Langor and Spence 2006). The four common mature forest specialists identified in our study have also shown strong affinity for intact mature forests in other studies (Pohl et al. 2007, Klimaszewski et al. 2008, Bergeron et al. 2013, Hammond et al. 2018); however, these species recovered more slowly in other studies than at EMEND. We suggest that these differences result because most logged sites at EMEND contained residual canopy left in the wake of VR harvests, whereas other studies started with clear-cuts. Thus, our results suggest that leaving even ca 10% post-harvest residual reduces immediate impact and are associated with better recovery of mature forest species than are traditional clear-cuts.

Too little is known about the biology of these forest species to completely explain post-disturbance responses. Nonetheless, Klimaszewski et al. (2013) found many fungal spores in the guts of *T. fumipennis* and *T. frigidus*, suggesting that they are fungivores or omnivores. The rapid recovery of these two species in our study in comparison to other studies suggests that recovery may be influenced by availability of fungi important in their diet. In contrast, while *Q. rusticus* exhibited affinity for mature forests at EMEND and in the eastern boreal forest (Klimaszewski et al. 2008), the species was most prevalent in clear-cut Cordilleran conifer stands in Alberta (Pohl et al. 2007). Variation in habitat affinity across studies suggests that a species may be locally habitat-specific but that ecological traits like habitat use may vary across the species range.

Open habitat species are positively affected by environmental disturbances and their catches declined with increasing retention as stands mature. Although *Q. labradorensis/molochinoides* showed some responses expected of open habitat species, catches did not decrease in low retention treatments 11 and 16 years post-harvest. This finding does not support our hypothesis about expected responses of open-habitat species. Although these species express affinity for open habitats, they also fared very well in controls and 16-year-old stands. *Quedius labradorensis* exhibited affinity for open habitats in Cordilleran conifer stands in western Alberta (Pohl et al. 2007), but data from a gap harvesting experiment in boreal yellow birch forests in Quebec revealed a strong affinity for mature forests (Klimaszewski et al. 2008). These contrasting results suggest that *Q. labradorensis/molochinoides* cannot be used as an indicator because we do not have sufficient understanding of its habitat associations.

Species that appeared to thrive under intermediate disturbance regimes showed no differences in catches across retention treatments 11 years post-harvest. This supports our third hypothesis about responses of individual species, i.e. abundance of such species will not be favoured by medium retention levels over time. Furthermore, as we hypothesized finally for forest generalist species, eurytopic species were not affected by harvest intensity. Thus, such species are not helpful for discerning treatment effects. Clearly, there is much to learn about the biology of rove beetles and improved knowledge is likely to help with interpretation of patterns of response to disturbances. For example, *Lordithon fungicola*

adults are associated with many polypore fungi (Campbell 1982) where they feed on fly larvae (Klimaszewski et al. 2007). In our study, perhaps 2009 was not conducive to mushroom growth, adversely affecting species like *L. fungicola*. Hammond et al. (2021) reported that populations of many species of carabid and staphylinid beetles varied greatly in catch, even in successive years at the same sites. Thus, there is merit in sampling designs that include multiple years to minimize the effects of poorly understood annual variation. Development of data sets that include multiple years with environmental data should improve understanding of what drives such variation.

Conclusions

Sixteen years following variable retention harvest, rove beetle assemblages in stands with $\geq 10\%$ retention recovered to generally resemble those in uncut forests. Even assemblages in clear-cuts recovered to a considerable extent. Thus, even if there are significant differences between assemblages developing after variable retention harvest and those in intact fire-origin stands, such differences will likely not last long. However, our observations about recovery of rove beetle assemblages in clear-cuts have important caveats. The EMEND experiment does not include true clear-cuts, as compartments harvested to this prescription included two aggregated retention patches. These patches as well as the forest matrix surrounding these small (10 ha) treatment compartments may facilitate faster recovery than would be seen in large clear-cuts with little standing residual. Further research about effects of harvest block size and retention patches embedded in different sizes of harvest blocks on biodiversity will provide better understanding of biodiversity recovery rate.

To our knowledge, no previous studies in the boreal region have demonstrated such rapid biodiversity recovery patterns (Niemelä et al. 1993, Buddle et al. 2006, Pohl et al. 2007, Heikkala et al. 2016), including studies of other taxa conducted at EMEND (Pinzon et al. 2016, Wu et al. 2020). For species with excellent powers of dispersal, such as most rove beetles (Irmeler and Lipkow 2018, Guseva and Koval 2020), landscape composition will exert considerable influence on faunal recolonization and recovery patterns. Thus, the short-term recovery of rove beetles reported here should not be taken as support for widespread implementation of low levels of retention across boreal landscapes. Nonetheless, our results about rove beetles demonstrate the potential utility of VR harvests as a conservation tool that can improve faunal recovery in comparison with clear-cutting. Results from EMEND underscore the value of continuing long-term experimental studies to support understanding of variable retention as a management tool for overall biodiversity conservation in the boreal forest.

Acknowledgements – We thank Jason Edwards, Charlene Hahn, Suzanne Abele, Amy Hayden and numerous undergraduate

students working on EMEND summer crews for trap maintenance, sample collection and sorting. We also thank Bradley Tamm for providing early EMEND data.

Funding – This research was funded by the EMEND partnership, including Mercer Peace River Pulp Ltd, CANFOR, the Government of Alberta, Univ. of Alberta and Natural Resources Canada – Canadian Forest Service, as well as by NSERC Discovery and Strategic Partnership grants to JRS.

Author contributions

Seung-Il Lee: Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead). **David W. Langor:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Supervision (lead); Writing – review and editing (equal). **John R. Spence:** Conceptualization (equal); Data curation (supporting); Funding acquisition (equal); Writing – review and editing (equal). **Jaime Pinzon:** Formal analysis (supporting); Writing – review and editing (equal). **Gregory R. Pohl:** Data curation (equal); Resources (equal); Writing – review and editing (equal). **Dustin J. Hartley:** Data curation (supporting); Investigation (equal). **Timothy T. Work:** Investigation (supporting); Writing – review and editing (equal). **Linhao Wu:** Formal analysis (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.06347>>.

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.0zpc8671p>> (Lee et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. – *Austral Ecol.* 26: 32–46.
- Anderson, M. J., Gorley, R. N. and Clarke, K. R. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. – PRIMER-E.
- Aubry, K. B., Halpern, C. B. and Peterson, C. E. 2009. Variable retention harvests in the Pacific Northwest: a review of short-term findings from the DEMO study. – *For. Ecol. Manage.* 258: 398–408.
- Baker, S. C., Spies, T. A., Wardlaw, T. J., Balmer, J., Franklin, J. F. and Jordan, G. J. 2013. The harvested side of edges: effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. – *For. Ecol. Manage.* 302: 107–121.
- Bartels, S. F., Macdonald, S. E., Johnson, D., Caners, R. T. and Spence, J. R. 2018. Bryophyte abundance, diversity and composition after retention harvest in boreal mixedwood forest. – *J. Appl. Ecol.* 55: 947–957.
- Belluz, V., Langor, D. W., Niemelä, J. K., He, F. and Spence, J. R. 2022. Long-term responses of ground beetles (Coleoptera: Carabidae) to clear-cutting and wildfire in lodgepole pine stands of western Alberta, Canada. – *Can. Entomol.* 154: e41.
- Bergeron, J. A. C., Spence, J. R., Volney, W. J. A., Pinzon, J. and Hartley, D. J. 2013. Effect of habitat type and pitfall trap installation on captures of epigeic arthropod assemblages in the boreal forest. – *Can. Entomol.* 145: 547–565.
- Bergeron, J. A. C., Pinzon, J., Odsen, S., Bartels, S., Macdonald, S. E. and Spence, J. R. 2017. Ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity after retention harvest. – *Oikos* 126: 1738–1747.
- Bohac, J. 1999. Staphylinid beetles as bioindicators. – *Agric. Ecosyst. Environ.* 74: 357–372.
- Bousquet, Y., Bouchard, P., Davies, A. E. and Sikes, D. S. 2013. Checklist of beetles (Coleoptera) of Canada and Alaska, revised 2nd edn. – Pensoft Publishers.
- Buddle, C. M., Langor, D. W., Pohl, G. R. and Spence, J. R. 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. – *Biol. Conserv.* 128: 346–357.
- Campbell, J. M. 1982. A revision of the genus *Lordithon* Thomson of North and Central America (Coleoptera: Staphylinidae). – *Mem. Entomol. Soc. Can.* 114: 5–116.
- Chao, A. and Jost, L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. – *Ecology* 93: 2533–2547.
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K. and Ellison, A. M. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. – *Ecol. Monogr.* 84: 45–67.
- Clarke, K. R. and Gorley, R. N. 2015. PRIMER v7: user manual/tutorial. – PRIMER-E.
- Díaz-Aguilar, I., Quideau, S. A., Proctor, H. C., Kishchuk, B. E. and Spence, J. R. 2013. Influence of stand composition on predatory mite (Mesostigmata) assemblages from the forest floor in western Canadian boreal mixedwood forests. – *For. Ecol. Manage.* 309: 105–114.
- Digweed, S. C., Currie, C. R., Carcamo, H. A. and Spence, J. R. 1995. Digging out the ‘digging-in effect’ of pitfall traps influences of depletion and disturbance on catches of ground beetles. – *Pedobiologia* 39: 561–576.
- Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J. F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. and Gustafsson, L. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. – *J. Appl. Ecol.* 51: 1669–1679.
- Franklin, C. M. A., Macdonald, S. E. and Nielsen, S. E. 2019. Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forest. – *Ecosphere* 10: e02632.
- Franklin, J. F., Berg, D. F., Thornburg, D. and Tappeiner, J. C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. – In: Kohm, K. A. and Franklin, J. F. (eds), *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, pp. 111–139.
- Franklin, J. F., Norman Johnson, K. and Johnson, D. L. 2018. *Ecological forest management*. – Waveland Press.
- Government of Canada 2019. Canadian climate normals 1981–2010 station data. – <www.climate.weather.gc.ca>.

- Guseva, O. G. and Koval, A. G. 2020. Flight activity of rove beetles (Coleoptera: Staphylinidae) in the agricultural landscape in the Leningrad Region. – *Russ. Entomol. J.* 29: 153–156.
- Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhmus, A., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W. J. A., Wayne, A. and Franklin, J. F. 2012. Retention forestry to maintain multifunctional forests: a world perspective. – *BioScience* 62: 633–645.
- Hammond, H. E. J., Hoffman, P. G. K., Pinno, B. D., Pinzon, J., Klimaszewski, J. and Hartley, D. J. 2018. Response of ground and rove beetles (Coleoptera: Carabidae, Staphylinidae) to operational oil sands mine reclamation in northeastern Alberta, a case study. – *J. Insect Conserv.* 22: 687–706.
- Hammond, H. E. J., García-Tejero, S., Pohl, G. R., Langor, D. W. and Spence, J. R. 2021. Spatial and temporal variation of epigeic beetle assemblages (Coleoptera, Carabidae, Staphylinidae) in aspen-dominated mixedwood forests across north-central Alberta. – *ZooKeys* 1044: 951–991.
- Heikkala, O., Martikainen, P. and Kouki, J. 2016. Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. – *Biol. Conserv.* 194: 39–47.
- Hsieh, T. C., Ma, K. H. and Chao, A. 2016. iNEXT: interpolation and extrapolation for species diversity. – R package ver. 2.0.19, <<http://CRAN.R-project.org/package=iNEXT>>.
- Irmeler, U. and Lipkow, E. 2018. Effect of environmental conditions on distribution patterns of rove beetles. – In: Betz, O., Irmeler, U. and Klimaszewski, J. (eds), *Biology of rove beetles (Staphylinidae): life history, evolution, ecology and distribution*. Springer, pp. 117–144.
- Irmeler, U., Klimaszewski, J. and Betz, O. 2018. Introduction to the biology of rove beetles. – In: Betz, O., Irmeler, U. and Klimaszewski, J. (eds), *Biology of rove beetles (Staphylinidae): life history, evolution, ecology and distribution*. Springer, pp. 1–4.
- Jacobs, J. M., Spence, J. R. and Langor, D. W. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. – *Agric. For. Entomol.* 9: 3–16.
- Janssen, P., Fuhr, M., Cateau, E., Nusillard, B. and Bouget, C. 2017. Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. – *Biol. Conserv.* 205: 1–10.
- Klimaszewski, J., Langor, D., Savard, K., Pelletier, G., Chandler, D. S. and Sweeney, J. 2007. Rove beetles (Coleoptera: Staphylinidae) in yellow birch-dominated stands of southeastern Quebec, Canada: diversity, abundance and description of a new species. – *Can. Entomol.* 139: 793–833.
- Klimaszewski, J., Langor, D. W., Work, T. T., Hammond, J. H. E. and Savard, K. 2008. Smaller and more numerous harvesting gaps emulate natural forest disturbances: a biodiversity test case using rove beetles (Coleoptera, Staphylinidae). – *Divers. Distrib.* 14: 969–982.
- Klimaszewski, J., Morency, M. J., Labrie, P., Séguin, A., Langor, D., Work, T., Bourdon, C., Thiffault, E., Paré, D., Newton, A. F. and Thayer, M. K. 2013. Molecular and microscopic analysis of the gut contents of abundant rove beetle species (Coleoptera, Staphylinidae) in the boreal balsam fir forest of Quebec, Canada. – *ZooKeys* 353: 1–24.
- Klimaszewski, J., Brunke, A. J., Work, T. T. and Venier, L. 2018. Rove beetles (Coleoptera, Staphylinidae) as bioindicators of change in boreal forests and their biological control services in agroecosystems: Canadian case studies. – In: Betz, O., Irmeler, U. and Klimaszewski, J. (eds), *Biology of rove beetles (Staphylinidae): life history, evolution, ecology and distribution*. Springer, pp. 161–181.
- Koivula, M. and Vanha-Majamaa, I. 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning and deadwood manipulation in Fennoscandia. – *Ecol. Process* 9: 11.
- Langor, D. W. and Spence, J. R. 2006. Arthropods as ecological indicators of sustainability in Canadian forests. – *For. Chron.* 82: 344–350.
- Lee, S.-I., Spence, J. R., Langor, D. W. and Pinzon, J. 2015. Retention patch size and conservation of saproxylic beetles in boreal white spruce stands. – *For. Ecol. Manage.* 358: 98–107.
- Lee, S.-I., Spence, J. R. and Langor, D. W. 2017. Combinations of aggregated and dispersed retention improve conservation of saproxylic beetles in boreal white spruce stands. – *For. Ecol. Manage.* 385: 116–126.
- Lee, S.-I., Spence, J. R. and Langor, D. W. 2018. Chapter 19. Conservation of saproxylic insect diversity under variable retention harvesting. – In: Ulyshen, M. (ed.), *Saproxylic insects: diversity, ecology and conservation*. Springer, pp. 639–667.
- Lee, S.-I., Langor, D. W., Spence, J. R., Pinzon, J., Pohl, G. R., Hartley, D. J., Work, T. T. and Wu, L. 2022. Data from: Rapid recovery of boreal rove beetle (Staphylinidae) assemblages 16 years after variable retention harvest. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.0zpc8671p>>.
- Legendre, P. and Legendre, L. 2012. *Numerical ecology*, vol. 24, 3rd English edn. – Elsevier.
- Lencinas, M. V., Pastur, G. M., Gallo, E. and Cellini, J. M. 2011. Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. – *For. Ecol. Manage.* 262: 1236–1250.
- Lenth, R. V., Buerkner, P., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., Singmann, H. 2020. nlme: linear and nonlinear mixed effects models. – R package ver. 1.4.4, <<http://CRAN.R-project.org/package=nlme>>.
- Lindenmayer, D. B. and Franklin, J. F. 2002. *Conserving forest biodiversity: a comprehensive multiscaled approach*. – Island Press.
- Lindenmayer, D. B., Franklin, J. F., Löhmus, A., Baker, S. C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A. and Gustafsson, L. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. – *Conserv. Lett.* 5: 421–431.
- Lipkow, E. and Betz, O. 2005. Staphylinidae and fungi. – *Faunistisch-Ökologische Mitteilungen* 8: 383–411.
- McCune, B. and Grace, J. B. 2002. *Analysis of ecological communities*. – MjM Software Design.
- Newton, A. F., Thayer, M. K., Ashe, J. S. and Chandler, D. S. 2001. 22. Staphylinidae Latreille, 1802. – In: Arnett Jr., R. H. and Thomas, M. C. (eds), *American beetles. Volume 1: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, pp. 272–418.
- Niemelä, J., Langor, D. and Spence, J. R. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. – *Conserv. Biol.* 7: 551–561.
- Olsen, S. G., Pinzón, J., Schmiegelow, F. K. A., Acorn, J. H. and Spence, J. R. 2018. Boreal songbirds and variable retention management: a 15-year perspective on avian conservation and forestry. – *Can. J. For. Res.* 48: 1495–1502.

- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Antoniazzi Evangelista, H. B., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M. O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E. R., Smith, T., Stier, A., Ter Braak, C. J. F. and Weedon, J. 2019. Vegan: community ecology package. – R package ver. 2.5-6, <<https://cran.r-project.org/package=vegan>>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., EISPACk, Heisterkamp, S., Van Willigen, B., Ranke, J. and R Core Team 2019. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-143, <<http://CRAN.R-project.org/package=nlme>>.
- Pinzon, J., Spence, J. R. and Langor, D. W. 2012. Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. – *For. Ecol. Manage.* 266: 42–53.
- Pinzon, J., Spence, J. R., Langor, D. W. and Shorthouse, D. P. 2016. Ten-year responses of ground-dwelling spiders to retention harvest in the boreal forest. – *Ecol. Appl.* 26: 2581–2599.
- Pohl, G. R., Langor, D. W. and Spence, J. R. 2007. Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. – *Biol. Conserv.* 137: 294–307.
- Pohl, G. R., Langor, D., Klimaszewski, J., Work, T. and Paquin, P. 2008. Rove beetles (Coleoptera: Staphylinidae) in northern Nearctic forests. – *Can. Entomol.* 140: 415–436.
- Rowe, J. S. 1972. Forest regions of Canada. – Canadian Forestry Service Publication No. 1300, Publishing Division, Information Canada.
- Schenker, N. and Gentleman, J. F. 2001. On judging the significance of differences by examining the overlap between confidence intervals. – *Am. Stat.* 55: 182–186.
- Spence, J. R. and Niemelä, J. K. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. – *Can. Entomol.* 126: 881–894.
- Spence, J. R., Langor, D. W., Niemelä, J., Cárcamo, H. A. and Currie, C. R. 1996. Northern forestry and carabids: the case for concern about old-growth species. – *Ann. Zool. Fenn.* 33: 173–184.
- Spence, J. R., Langor, D. W., Hammond, H. E. J. and Pohl, G. R. 1997. Beetle abundance and diversity in a boreal mixedwood forest. – In: Watt, A. D. and Stork, N. E. (eds), *Forests and insects: proceedings of the 18th royal entomological society symposium*, 13–15 September 1995. Chapman and Hall, pp. 285–299.
- Spence, J. R., Volney, W. J. A., Lieffers, V. J., Weber, M. G., Luchkow, S. A. and Vinge, T. W. 1999. The Alberta EMEND project: recipe and cook's argument. – In: Veeman, T. S., Smith, D. W., Purdy, B. G., Salkie, F. J. and Larkin, G. A. (eds), *Proceedings of the 1999 sustainable forest management network conference, science and practice: sustaining the boreal forest*. Sustainable Forest Management Network, pp. 583–590.
- Thayer, M. K. 2016. Staphylinidae Latreille, 1802. – In: Beutel, R. G. and Leschen, R. A. B. (eds), *Handbook of zoology. Coleoptera, beetles – volume 1: morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*, 2nd edn. Walter de Gruyter GmbH, pp. 394–442.
- Van Damme, L., Saunders, K., Plante, L. and Burkhardt, R. 2014. Status report on ecosystem-based management (EBM): policy barriers and opportunities for EBM in Canada. – *Canadian Boreal Forest Agreement*.
- Venier, L. A., Thompson, I. D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J. A., Langor, D., Sturrock, R., Patry, C., Outerbridge, R. O., Holmes, S. B., Haeussler, S., De Grandpré, L., Chen, H. Y. H., Bayne, E., Arsenault, A. and Brandt, J. P. 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. – *Environ. Rev.* 22: 457–490.
- Work, T. T., Jacobs, J. M., Spence, J. R. and Jan Volney, W. 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. – *Ecol. Appl.* 20: 741–751.
- Wu, L., He, F. and Spence, J. R. 2020. Recovery of a boreal ground-beetle (Coleoptera: Carabidae) fauna 15 years after variable retention harvest. – *J. Appl. Ecol.* 57: 1717–1729.