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Shelterwood and multicohort management have similar initial effects on ground beetle assemblages in boreal forests ☆

Luana Graham-Sauvé [a,b], Timothy T. Work [a,b,*], Daniel Kneeshaw [a,b], Christian Messier [b,c]

[a] *Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Sciences biologiques, Université du Québec à Montréal, CP 8888 Succursale Centre-Ville, Montreal, Québec H3C 3P8, Canada*

[b] *Centre d'étude de la forêt (CEF), CP 8888, Succursale Centre-VilleMontréal, Québec, H3C 3P8 Canada*

[c] *Institut des Sciences de la Forêt Tempérée (ISFORT), Université du Québec en Outaouais, 58 rue principale, Ripon, QC J0V 1V0, Canada*

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ABSTRACT

Partial cutting has been proposed as a means to better conserve biodiversity in managed forest landscapes. However, partial cutting encompasses many forms of silviculture; some with implicit goals of maintaining biodiversity such as multicohort harvesting or others which may specifically focus on regeneration of stands but may still provide some additional benefits for biodiversity such as shelterwood harvesting. Here we compared ground beetle assemblages of clear cuts, shelterwoods, multicohort harvested stands and uncut stands collected using pitfall traps both 2 and 3-years post-harvest. We hypothesized that partial cutting treatments would maintain assemblages that were more similar to uncut stands than to clear cuts. We further hypothesized that among partial cuts the multicohort harvested stands, with relatively high levels of retention (66%), would maintain beetle assemblages that were more similar to uncut stands than would shelterwoods, which had lower levels of retention (50%). We collected 6692 individuals, representing 42 species. Catch rates of beetles were similar among all harvested treatments (shelterwood, multicohort and clear cuts) and lower than uncut stands. Species richness and composition was similar between shelterwood and multicohort stands. Both partial cut treatments fell between clear cuts and uncut stands in terms of species richness and compositional similarity. Compositional differences between uncut stands and partial cut stands were defined primarily by reduced abundances of forest associated species such as *Agonum retractum* (LeConte), *Synuchus impunctatus* (Say) and four *Pterostichus* species within partial cuts. Within partial cuts, beetle assemblages differed between machine corridors with 0% retention and adjacent partial cut strips (50% retention) and uncut vegetation corridors (100%). We conclude that both shelterwoods and multicohort harvesting stands provide at least initially similar benefits for biodiversity compared to clear cutting although neither maintains assemblages consistent with those found in uncut stands. We expect that these similarities will end once trees are removed from shelterwoods. The reductions in abundances within partial cuts may extend the time necessary for individual populations to increase to pre-harvest levels in partial cuts. For land-managers, similar initial responses of beetle assemblages in multicohort and shelterwood harvests may permit some flexibility for conservation planning whereby final removal of seed trees within shelterwoods could be delayed depending on the status of recovering beetle populations.

1. Introduction

Less intensive approaches to forest management, such as partial cutting, are often proposed as a viable form of coarse-filter conservation of biological diversity and thus are key elements commonly included in larger proposed strategies for ecosystem management. A non-trivial finding common in evaluations of partial cutting is that more retention maintains overall species assemblages better than less retention (Craig and Macdonald, 2009; Work et al., 2010; Gustafsson et al., 2011). While the 'more is better' aspects of partial cutting seem intuitive (Lindenmayer et al., 2012), inclusion of partial cutting in larger management plans

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* Corresponding author at: Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Sciences biologiques, Université du Québec à Montréal, CP 8888 Succursale Centre-Ville, Montréal, Québec H3C 3P8, Canada. Tel.: +1514-987-3000 poste 2448.

E-mail addresses: luana_gs@hotmail.ca (L. Graham-Sauvé), work.timothy@uqam.ca (T.T. Work), kneeshaw.daniel@uqam.ca (D. Kneeshaw), ch.messier@gmail.com (C. Messier).

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necessitates empirical estimates as to how much retention should be left following harvest and how best to implement partial cutting over larger landscapes.

In boreal forests, partial cut harvesting has been advocated primarily as a means of creating or maintaining stand structures consistent with specific stages of forest succession (Bergeron and Harvey, 1997; Harvey et al., 2002). In this approach, partial cutting is used to create structures consistent with uneven-aged or older forests which contain multiple cohorts of trees and/or different sizes of trees to maintain diverse stand structure and ensuring a continued albeit partial cover across a site (Messier et al., 2009). Under such a multicohort approach, retention left following partial cutting is meant to serve a primarily ecological role either as habitat for resident biodiversity or as a source of downed wood over several decades or more. Multicohort management is implemented with hopes of maintaining or establishing characteristics consistent with mature or older stands such as multi-layered canopies or a variety of tree diameters (Paradis and Work, 2011, Witté et al., 2013). A lasting implication of this approach, which is sometimes also referred to as continuous cover irregular shelterwood (Raymond et al., 2009), is a substantial portion of the forest canopy is maintained across the stand throughout multiple rotations. Other silvicultural approaches such as shelterwood cuts, where standing trees are left following harvest primarily to establish and promote regeneration, may however provide some *de facto* benefits for biodiversity at least in the short-term. In shelterwood silvicultural systems, standing trees are left for several years to maintain an abundant seed source and ensure successful regeneration following harvest at which point seed trees may then be harvested (Lieffers et al., 2003). As well as potentially leaving trees only temporarily (e.g. 10–20 years), shelterwood systems tend to leave as few trees as possible to ensure both adequate seed and light for regeneration as well as reduced risk of loss to windthrow (Smith et al., 1997; Nyland, 2002). As such, standard shelterwood systems often have lower levels of retention than multi-cohort approaches.

In boreal systems, where limited topographic variation permits extensive access by harvesting machinery, dispersed retention targets (i.e. leave trees) within either shelterwood or multicohort management are often achieved through a series of residual vegetation strips, which may be thinned depending on prescription targets, and harvested corridors (David et al., 2000). If retention within residual vegetation strips is held relatively constant, clearly lower overall retention levels within a harvest unit will necessitate either wider or more harvested corridors. Larger harvested corridors may create significant edge effects into residual vegetation strips affecting microclimate (Zheng and Chen, 2000) and may harbor different species assemblages of plants (Craig and Macdonald, 2009), fungi (Lazaruk et al., 2005) and animals (Lindo and Visser, 2004). Conversely, more open habitats, such as machine corridors, may serve as favorable habitats for generalist or disturbance-adapted species (Klimaszewski et al., 2005; Niemelä et al., 2007; Brais et al., 2013).

For organisms that respond to stand-level changes caused by forest management such as ground beetles (Coleoptera: Carabidae), post-harvest retention levels affect both overall abundance and species composition (Koivula, 2002; Martikainen et al., 2006; Halaj et al., 2008; Work et al., 2008). Ground beetles are generalist predators which reside in forest leaf litter and have been widely used to evaluate the impacts of forest management (Niemelä et al., 2007). Recent studies suggest that relatively high levels of retention (>50%) are required to maintain species assemblages, but specific retention thresholds will vary among stand types (Work et al., 2010). Here we compare the efficacy of multi-cohort based management, aimed specifically at maintaining stand structure, and shelterwood silvicultural systems, which may provide some *de facto* benefit for biodiversity, for maintaining ground beetle assemblages. We also compare both of these partial cutting approaches with standard clear cuts to assess any net benefits partial cutting may provide if implemented within a larger strategy of ecosystem management. We hypothesize that the higher levels of retention left following multi-cohort management will be more similar to uncut forests than either shelterwood or clear cuts.

2. Materials and methods

2.1. Study sites

All sample sites were located in the Haute-Mauricie region of Québec, Canada (47°26′16″N, 72°46′35″W) and were dominated primarily by balsam fir (*Abies balsamea* (L.) Miller) and yellow birch (*Betula alleghaniensis* Britton), although numerous other hardwood (including sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx.) and conifer (white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), jack pine (*Pinus banksiana* Lamb.), and white pine (*Pinus strobus* L.)) species were also present. Stand dynamics are controlled predominately by frequent, small fires (<150 ha) and infrequent, large fires (>10,000 ha), windthrow (Côté et al., 2010), as well as outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)).

2.2. Experimental design

We sampled beetles from replicate stands that were clear cut, harvested according to either shelterwood or multicohort silvicultural systems or uncut (Fig. 1). These sites were part of a larger project called TRIADE, which was established to evaluate how partial cutting and other ecosystem management options could be incorporated and implemented over a larger landscape (Côté et al., 2010). Our study stands originated from a wildfire in 1923. Stands were harvested during the winter of 2007–2008 (Witté et al.). Clear cuts, in our study, contained 5% retention isolated within a small aggregate (between 150 and 500 m^2). Retention within the shelterwood treatments consisted of a 5 m band of uncut forest with two adjacent 7 m bands of partial cut forest where retention was 50% of pre-harvest stem density. Each vegetation strip (19 m total width) was separated by 5 m of harvested forest where retention was 0%. In 10–15 years once significant conifer regeneration has established, the 5 m uncut band will be harvested along with larger stems from the adjacent 7 m partial cut strips. Retention within the multicohort treatment consisted of an uncut vegetation strip 19 m wide bordered on each side by a 7 m wide partial cut strip which retains 66% of the original stems. This larger vegetation strip (33 m) is separated from other strips by a 5 m band of harvested forest where retention was 0%. Unlike the shelterwood treatment, where a second pass is anticipated within 10–15 years, multicohort treatments will have interventions 20, 50 and 75 years following the initial harvest. In each of these successive interventions, the 19 m of forest left intact in the prior intervention will be harvested, leaving 5 m of cut forest with 0% retention with adjacent 7 m partial cuts strips where retention is 66% (Fig. 1). We compared the effects of clear cuts (5% retention), shelterwood (50% retention) and multicohort harvests (66% retention) to uncut stands (100% retention) as a control. Each harvesting treatment was replicated 5 times.

2.3. Ground beetle sampling

Beetles were collected using pitfall traps. We placed a total of 9 pitfall traps within each experimental stand. In partial cut stands, we placed 3 traps along the machine corridor with 0% retention, 3 traps within partial cut retention strips (either 50% or 66%

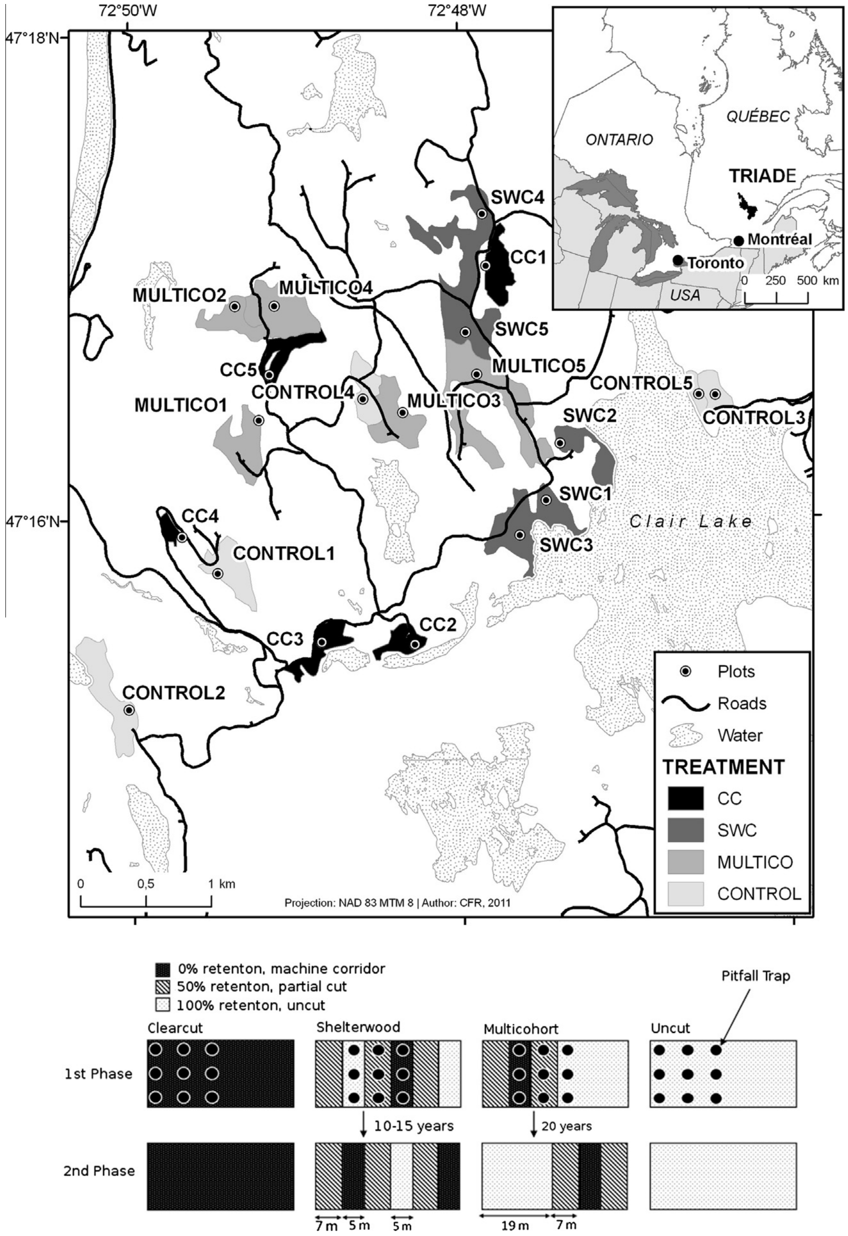

Fig. 1. Map depicting study area and location of experimental stands and schematic diagram depicting harvesting prescriptions for clearcuts, shelterwoods, multicohort and uncut stands as well as pitfall trap placement within individual stands. CC represent clear cuts, SWS represent shelterwood cuts, MULTICO represent multicohort cuts and CONTROL are uncut stands.

retention) and 3 traps with uncut retention strip (100% retention). Within uncut and clearcut stands, we placed the 9 pitfall traps in an identical spatial pattern to that used in partial cut stands. All traps were charged with approximately 200 ml of Prestone® pet-safe antifreeze (propylene-glycol), which served as a preservative and new antifreeze was added as needed. Traps were covered with elevated plastic lids to prevent flooding from rain. Traps were collected approximately every three weeks between 5/23 and 8/17 in 2009 and between 5/25 and 7/25 in 2010. All ground beetle specimens were identified to species using keys developed by Lindroth (1961, 1963, 1966, 1968, 1969).

2.4. Statistical analysis

We pooled the three traps located in each machine corridor, partial cut or uncut retention strip, resulting in 120 samples (3 aggregated samples of three pitfall traps corresponding to within stand heterogeneity × 4 harvesting treatments × 5 replicates × 2 sampling years). We evaluated changes in overall catch rate (beetles/day) using a linear mixed model where harvesting treatment, position within stand (machine corridor, partial cut retention strip or uncut retention strip) and sampling year were fixed, main effects. All two-way and three-way interactions were included in the model and experimental blocks and individual sampling site (subjects) were used as random effects. We compared all fixed effects in the model by using Wald t-tests to compare differences in individual betas (or slopes) for fixed effects with a statistical reference condition. For our comparison, we used uncut control stands and uncut vegetation corridors that were sampled in 2009 as the reference condition for the linear mixed model. We used the nlme package to analyze this mixed model in R.2.12 (R Development Core Team, 2011). Catch rates were transformed using a square-root transformation to meet assumptions of normality in the model.

We used individual-based rarefaction to estimate species richness among specific treatment combinations based on results of the mixed model for catch rate. In this way, we used rarefaction to evaluate how well our sampling characterized overall assemblages among treatment combinations and whether potential interactions with interannual variation or within-stand heterogeneity affect species richness more so than do differences between harvesting treatments. For this analysis we pooled the number of individuals for each combination of harvest treatment× sampling year and harvest treatment× position within the stand. Rarefaction curves for each of these vectors was then derived using the rarefy function in the vegan package in R 2.12 (R Development Core Team, 2011).

We evaluated overall changes in beetle composition using multivariate regression tree analysis (De'ath 2002) using the mvpart package in R 2.12 (R Development Core Team, 2011). We square-root transformed beetle catch rates an aggregated data matrix (120 samples× 42 species) of catch rates (beetles/day) for a sum of squares multivariate regression tree analysis (ssMRT), where harvesting treatment, year, and location within machine corridor, partial cut retention strip or uncut vegetation strip were predictor variables. We selected a final regression tree using cross-validation (based on 1000 iterations).

3. Results

We collected 6692 beetles representing 42 ground beetle species over both years. Overall catch rates were lower in all harvested treatments as compared to uncut stands (Tables 1 and 2). Mean catch rates in clear cuts during 2009 and 2010 were 19% and 23% of those from uncut stands respectively. Mean catch rates in 2009 and 2010 within shelterwoods were 42% and 36% and in multicohort stands 29% and 33% as compared to uncut stands (Table 1 and Fig. 2a). Overall catch rates increased in 2010 as compared to 2009 across all cutting treatments as indicated by Wald *t*-tests (Table 2 and Fig. 2a). Within shelterwoods in 2009, catch rates in machine corridors were higher than in uncut vegetation strips (Fig. 2b and Table 2). We did not observe a similar trend in for multicohort treatments.

Differences in species richness were greater among harvesting treatments than they were among individual sampling years (Fig. 3a). Clear cuts had the highest species richness while uncut stands had the lowest species richness in both sampling years. Shelterwood and multicohort stands had similar species richness and fell between clear cuts and uncut sites. However, differences in sampling position within a harvest treatment were larger than differences between harvest treatments, particularly for shelterwood and multicohort stands, where within stand-heterogeneity was higher than either clear cut or uncut stands (Fig. 3b). In both shelterwood and multicohort treatments, the machine corridor treatments had lower species richness than partial cut strips or uncut vegetation strips and were similar to uncut stands in terms of the estimated number of species present.

Changes in ground beetle assemblages were best characterized using a ssMRT with 7 terminal nodes. This model explained 36.3% of the total variance within the ground beetle assemblage. Individual species responses for species that contributed >0.01% of the total variance of the ssMRT are reported in Table 3, where as rarer species that contributed <0.01% are reported in Appendix A. The principal split in the ssMRT separated harvested sites, including clear cut, shelterwood and multicohort sites, from unharvested sites (Table 3 and Fig. 4). Partially harvested sites were subsequently divided from clear cut sites in the secondary split. Compositional differences in ground beetles between clear cut, partial cut stands (including shelterwood and multicohort) and uncut stands explained 29.7% of the variance (Table 3). Uncut stands were characterized by large abundances of one Cychrine species (*Sphaeroderus canadensis* Chaudoir), two species of Platyines *(Synuchus impunctatus* (Say) and *Agonum retractum* LeConte) and four species of Pterostichines *(Pterostichus pensylvannicus* LeConte, *Pterostichus coracinus* (Newman), *Ptreostichus adstrictus* Eschscholtz, *and Pterostichus tristis* (Dejean)) (Fig. 5). Together these species account for 24.4% of the total variance explained by the difference between uncut and harvested stands (Table 3). For the abundant *Pterostichines*, *P. pensylvanicus* was the most abundant followed by *P. coracinus*, *P. adstrictus* and *P. tristus* (Fig. 5). In contrast, harvested stands were typified by lower overall abundances of species common in uncut stands as well as less variability in catch rate of individual species (Fig. 5). Species common to uncut stands were 2–4 times less abundant in harvested stands (Fig. 5). Cut stands also were typified by the presence of 15 uncommon species; primarily *Harpalus* and *Amara* species. Differences in the relative abundances of *P. pensylvanicus*, *P. coracinus* and *P. adstrictus* were no longer apparent in harvested stands. Ground beetle composition within clear cuts was similar to that of shelterwoods and multicohort stands, although abundances of common species were approximately half of those found in shelterwood and multicohort stands. Three species, *Chlaenius cericius* (Forster), *Sphearoderus stenostomus lecontei* (Dejean) and *Poecilius lucublandus* (Say) were typically more common in clear cuts than in partial cut stands, however these species attributed little to the overall variation explained (1%) (Table 3).

Interannual variation was reflected in the third, fourth and sixth split of the ssMRT and accounted for 4.8% of the variance explained in carabid composition (Fig. 4). In the third split, composition differences in ground beetles within uncut were defined primarily by increased catch rates of dominant species in 2010. Similarly, in the sixth split, beetle composition within retention and uncut vegetation strips within the partial cuts varied by year having greater catch rates in 2010. Clear cut sites however did not show the same overall increased catch rates for individual species in 2010. Rather, the catch-rates of species that distinguished clear cuts from partial

Table 1
ANOVA summary of fixed effects from a linear mixed model used to compare differences in ground beetle catch rate (square root transformed) by harvesting treatment (clear cut, shelterwood, multicohort or uncut), interannual variation and position within stand (machine corridore, retention or uncut vegetation strip).

	Numerator df	Denominator df	*F*-value	*p*-Value
(Intercept)	1	48	649.0866	<0.0001
Harvesting	3	44	44.6232	<0.0001
Position	2	44	1.6227	0.2090
Year	1	48	49.2027	<0.0001
Harvesting × position	6	44	1.4086	0.2329
Harvesting × year	3	48	1.6886	0.1819
Position × year	2	48	2.9405	0.0624
Harvesting × position × year	6	48	0.7731	0.5949

Table 2
Individual slope parameters and Wald *t*-tests for significant fixed effects related to harvesting treatment, sampling year and sampling position from the linear mixed model describing overall catch rate.[a]

	Beta	Standard error	Df	*t*	*p*
Multicohort	−0.3129	0.066	44	−4.7394	<0.0001
Shelterwood	−0.3405	0.066	44	−5.1580	<0.0001
Clear cut	−0.3198	0.066	44	−4.8446	<0.0001
2010	0.1197	0.0389	48	3.0739	0.0035
Shelterwood × machine corridor	0.2188	0.0933	44	2.3439	0.0237

[a] Wald *t*-tests of individual fixed effect betas were compared to uncut vegetation strips within uncut stands collected in 2009 as a statistical reference level.

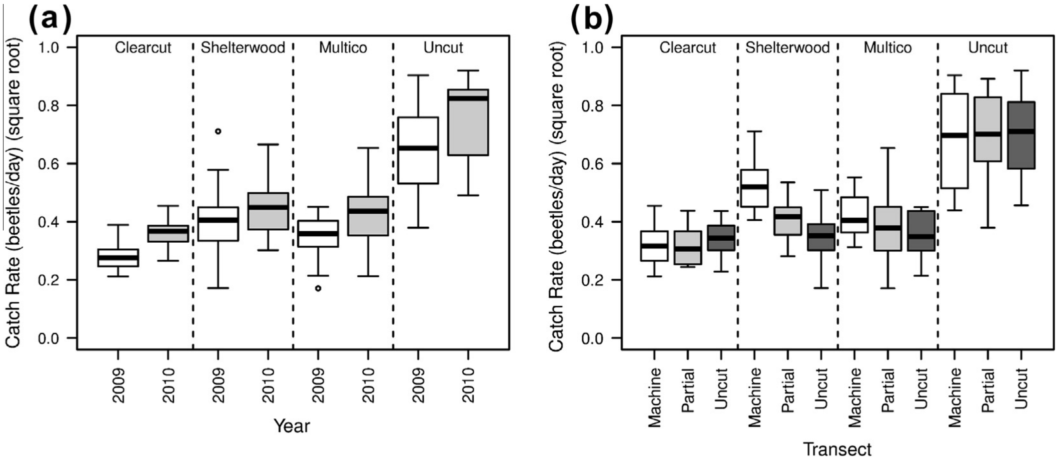

Fig. 2. Box and whisker plots depicting catch rates of ground beetles for (a) harvest × year and (b) harvest × position within stand among clearcut, shelterwood, multicohort and uncut stands. Boxes depict 25% and 75% quantiles, bold lines depict median catch rate, whiskers depict 1.5× the interquantile range.

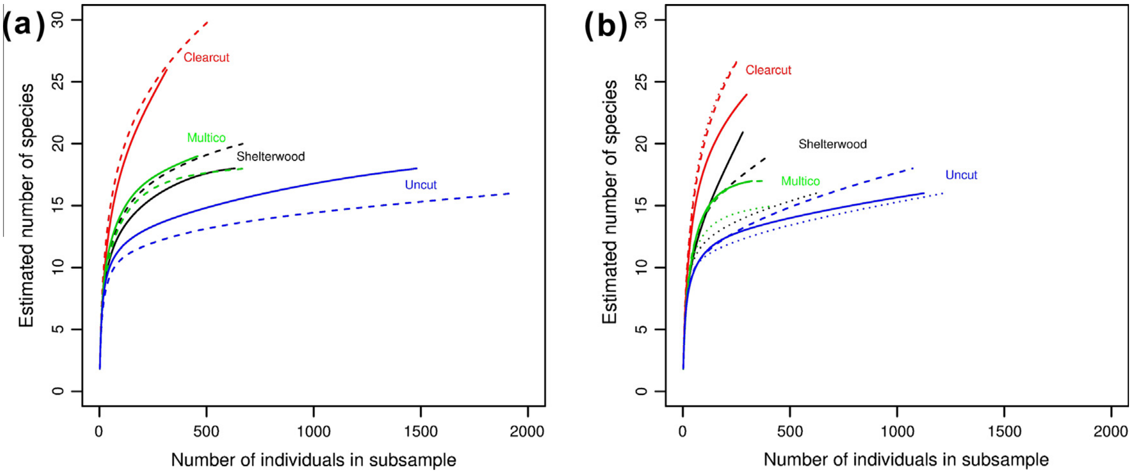

Fig. 3. Individual based rarefaction curves depicting (a) harvest × year and (b) harvest × position within stand among clear cut, shelterwood, multicohort and uncut stands. In panel a, solid lines depict samples collected in 2009 and dashed lines depict samples collected in 2010. In panel b, in shelterwoods and multicohort stands dotted lines depict samples collected from machine corridors, dashed lines depict samples collected from forest adjacent to machine corridors which were partial cut and solid lines depict uncut vegetation strips. In panel b, for clear cuts and uncut stands, dotted and dashed lines correspond to within-stand heterogeneity and similar trap spacing as shelterwood and multicohort stands.

cuts (*C. cericius*, *S. stenostomus* and *P. lucublandus*) were more abundant in 2009.

Within shelterwood and multicohort stands, the effects of within-stand heterogeneity were observed as samples collected from machine corridors formed a terminal node and were separated from samples collected in either the retention strip or uncut vegetation corridors in the fifth split (Fig. 4). Overall catch rates of species commonly associated with uncut forests (*P. adstrictus*, *P. pensylvanicus*, *P. decentis* and *A. retractum*) were greater in machine corridors than in either retention or uncut vegetation strips (Fig. 5).

4. Discussion

While neither shelterwood nor multicohort harvesting maintained overall catch rates similar to those found in uncut stands, partial cutting did maintain some of the compositional characteristics

Table 3
Variation explained by individual species who comprise greater than 0.1% of the total variance and individual splits in the ssMRT model comparing effects of harvesting, interannual variation and position within stand (machine corridor, partial cut retention strip or uncut retention strip).

Species	% Variation explained in ssMRT							Relative % of variation explained
	Split 1	Split 2	Split 3	Split 4	Split 5	Split 6	Total	
Agonum cupripenne (Say)	0.011	0.065	0.000	0.069	0.000	0.001	0.146	0.525
Agonum obsoletum (Say)	0.005	0.000	0.001	0.001	0.015	0.017	0.040	0.496
Agonum retractum LeConte	5.351	0.456	0.094	0.192	0.307	0.079	6.477	12.582
Amara patruelis Dejean	0.001	0.007	0.000	0.001	0.000	0.000	0.010	0.109
Bembidion wingatei Bland	0.003	0.001	0.000	0.001	0.000	0.001	0.006	0.216
Calathus ingratus Dejean	0.982	0.101	0.092	0.021	0.312	0.001	1.509	4.850
Chlaenius sericeus (Forster)	0.006	0.048	0.000	0.073	0.000	0.000	0.127	0.724
Cymindis cribricollis Dejean	0.022	0.001	0.002	0.015	0.014	0.001	0.055	0.708
Harpalus fuliginosus (Duftschmid)	0.003	0.020	0.000	0.011	0.000	0.000	0.034	0.177
Harpalus laticeps LeConte	0.002	0.013	0.000	0.005	0.000	0.000	0.020	0.145
Harpalus pleuriticus Kirby	0.000	0.002	0.000	0.004	0.000	0.000	0.006	0.110
Harpalus sp	0.005	0.024	0.000	0.042	0.000	0.001	0.072	0.286
Lebia moesta LeConte	0.115	0.232	0.000	0.350	0.038	0.114	0.849	1.754
Notiophilus aeneus (Herbst)	0.001	0.033	0.006	0.097	0.013	0.001	0.151	2.729
Platynus decentis (Say)	0.445	0.252	0.003	0.015	0.097	0.025	0.836	5.058
Platynus mannerheimi (Dejean)	0.004	0.049	0.000	0.000	0.003	0.001	0.056	0.956
Poecilius lucublandus (Say)	0.014	0.110	0.000	0.005	0.000	0.000	0.129	0.479
Pterostichus adstrictus Eschscholtz	1.733	0.141	0.284	0.046	1.015	0.408	3.628	13.412
Pterostichus coracinus (Newman)	2.288	0.215	0.709	0.027	0.029	0.023	3.291	8.289
Pterostichus pensylvanicus LeConte	7.461	0.448	0.754	0.006	0.061	0.452	9.182	16.769
Pterostichus punctatissimus (Randall)	0.066	0.113	0.013	0.005	0.331	0.006	0.535	2.176
Pterostichus tristis (Dejean)	1.844	0.000	0.181	0.012	0.011	0.050	2.098	4.918
Sphaeroderus canadensis canadensis (Chaudoir)	1.053	0.035	0.000	0.099	0.020	0.241	1.448	5.555
Sphaeroderus nitidicollis brevoorti LeConte	0.122	0.003	0.000	0.001	0.008	0.000	0.134	0.874
Sphaeroderus stenostomus lecontei Dejean	0.330	0.000	0.011	0.038	0.039	0.000	0.419	2.677
Synuchus impunctatus (Say)	4.727	0.087	0.000	0.075	0.002	0.014	4.905	12.169
Trechus rubens (Fabricius)	0.002	0.001	0.010	0.011	0.008	0.022	0.054	0.599
Total	26.596	2.457	2.160	1.222	2.323	1.458	36.217	99.342

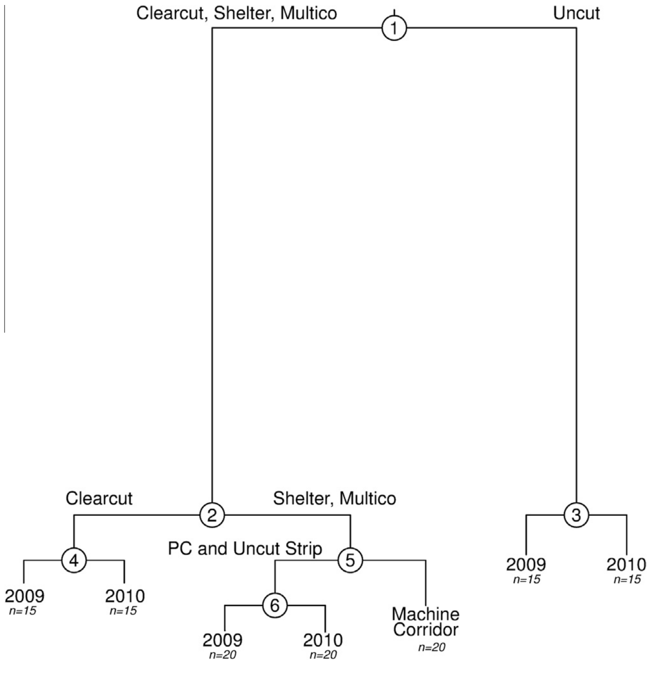

Fig. 4. Sum of squares multivariate regression tree (ssMRT) depicting changes in ground beetle composition based on differences in harvesting, interannual variation and position within stand (machine corridor, partial cut retention strip or uncut retention strip). This analysis explained 36.3% of the total variation based (120 samples and 42 species). The final tree was based on 699/1000 iterations.

of beetle assemblages in uncut stands. The compositional shifts we observed in ground beetles between clear cuts and uncut stands are consistent with the well-documented pattern whereby reductions in standing retention also reduce the abundance of dominant forest species and at the same time promote species associated with more open habitats resulting in increased species richness in harvested stands (Niemelä et al., 1993, 2007; Work et al., 2010). In our study, shelterwood and multicohort cutting had similar impacts on beetle composition and created assemblages that fell between clear cuts and uncut stands in terms of both composition and species richness. This suggests that residual standing retention, at least initially, is providing some benefit over clear cutting for species commonly associated with closed-canopy forests and may also be limiting proliferation of open-habitat species in partial cut stands. It also suggests the shelterwood harvesting initially provides at least some *de facto* benefit for biodiversity. Other studies examining comparatively lower retention levels than tested in our study have also suggested that partial cutting maintains higher abundances of carabids associated with closed canopy forests relative to clear cuts (Martikainen et al., 2006; Halaj et al., 2008; Work et al., 2010). In studies that examined responses of boreal carabid assemblages at retention levels higher than 66%, differences in carabid assemblages were observed even between uncut stand and stands retaining 75% of the pre-harvest basal area at least over the initial 1 and 2 year period sampled post-harvest (Work et al., 2010). These differences were attributable in large part to pre-treatment recruitment by *P. adstrictus*, where individuals were oviposited prior to harvest but emerged post-harvest. Five years post-harvest, these authors were no longer able to distinguish assemblages in conifer dominated stands with 75% retention and uncut stands (Work et al., 2010). In our study, we collected beetles 2 and 3-years post-harvest and did not observe a similar peak in post-treatment recruitment. At present we are unable to make specific conclusions as to how long assemblage differences observed within our study between partial cut and uncut stands will persist. However given that the observed differences in assemblages has already persisted beyond the initial post-harvest changes in beetle assemblages, we expect that assemblage differences in even relatively high levels of retention (up to 66%) should persist at least as long as for stands with even higher levels of retention (75%), which may suggests that these differences could

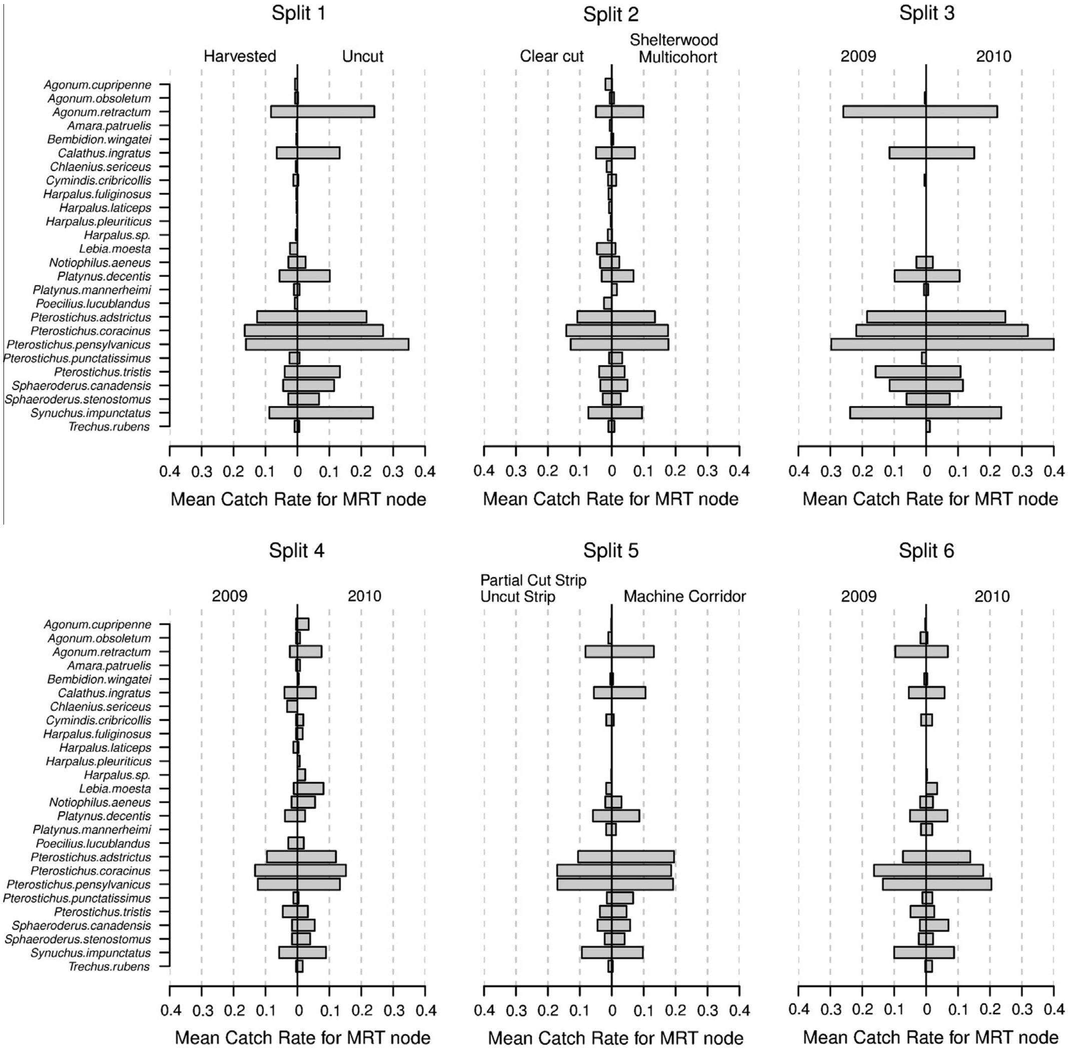

Fig. 5. Mean abundance (square rooted) of dominant ground beetle species (>0.1% of the total species variance) associated with successive splits in the ssMRT model.

persist at least 5 years post-harvest. Recent studies in northern hardwood forests, suggest that changes in the abundance individual carabid species following shelterwood cuts can be very slow (Trager et al., 2013). Trager et al. (2013) compared changes in 10 abundant carabid species including *P. decentis*, *P. tristis*, *S. canadensis* and *S. impunctatus*, along a time-since harvest gradient that spanned 14 years in stands that had been shelterwood harvested leaving 60% retention. In their study, abundance of *S. canadensis* and *S. impunctatus* was not related to time since harvest which suggested little or no recovery by these species in the 14 year study period. Abundance of *P. decentis* and *P. tristis* were positively related to time since harvest suggesting that populations of these species were indeed increasing, however the magnitude of this effect was extremely small (for these two species, Trager et al. (2013) reported Poisson regression coefficients of 0.01) and it is unlikely that populations would increase by more than a few individuals even after the 14 years following the shelterwood cut. Whether beetle assemblages in our study will recover pre-harvest composition prior to the next scheduled removal of residual trees in shelterwood and multicohort stands will depend in part on capacity of individual populations to increase following harvest as well as post-harvest population size.

The reduced abundance in both shelterwood and multicohort stands was surprisingly large compared to other studies at similar levels of retention. For example, the shelterwood and multicohort treatments in our study had between 50% and 66% standing retention but only maintained between ∼30% and 40% of the abundance observed in uncut stands. In western boreal mixedwood forests, similar levels of retention (50%) yielded catch rates that were 67% of those observed in uncut stand five years following harvest (Work et al., 2010). In deciduous dominated mixedwood stands in Western Québec, retention levels of 66% maintained catch rates of approximately 70% of those observed in uncut stands (O'Connor *unpublished data*). We are unable to explain why shelterwood and multicohort cuttings in our study would have disproportionately greater effects than in these other studies. In boreal mixedwoods, older successional stages are known to be more severely affected by reduced retention than earlier successional stages (Work et al., 2010). Our study sites were 85 years old and are considered as mature stands for this forest type and thus may be more affected by harvesting than earlier successional stages. Other factors beyond stand age and forest composition such as regional differences in topography and climate likely also interact with silvicultural prescriptions (Work et al., 2008). Regardless of the underlying mechanism, disproportionately lower abundances within shelterwood and multicohort stands will likely lengthen any potential recovery period of beetle assemblages.

Any potential recovery will also depend on when second pass of harvesting takes place. At least initially, both shelterwood and multicohort approaches may result in relatively high albeit different levels of retention. With successive stand interventions aimed at harvesting seed trees, retention levels within shelterwoods will necessarily decrease. For more intensive approaches such as clear-cutting there is evidence of lasting impact of the effects of harvesting whereby composition, species richness and the abundance of forest specialist species were affected as long as ca. 30 years following harvest (Niemelä et al., 1993; Koivula et al., 2002). While partial cut harvesting does not impact beetle assemblages to the extent of clear cutting (Work et al., 2010), recovery time following clear cutting may serve as a worst-case bench mark by which to judge the value of shelterwood and multicohort harvesting. In shelterwood harvests, the removal of standing retention follows the successful establishment of regeneration which may occur 10–20 years following the initial harvest in boreal forests (Smith et al., 1997). In contrast, following the second pass in multicohort stands, young trees regenerating within machine corridors and taller stems left in partially cut strips adjacent to both the past and new machine corridors will be present. Given the relationship between reduced retention and increased impact on abundance and composition, the persistence of canopy cover in multicohort managed stands suggests that multicohort management may be preferable to shelterwood cutting for maintaining ground beetles over the long-term.

Within shelterwood and multicohort stands, we were able to detect differences in ground beetle assemblages between machine corridors and the intact and partially harvested vegetation strips, despite the limited number of traps used in each habitat type. Species commonly associated with uncut forests, including *P. adstrictus*, *P. pensylvanicus*, *P. decentis* and *A. retractum* were greater in machine corridors. This suggests that machine corridors may adequately emulate smaller-scale features such as canopy gaps that are present in uncut forest stands without promoting the abundance of common open-habitat species like *Amara* and *Harpalus* (Koivula, 2002; Klimaszewski et al., 2005; Brais et al., 2013). For shelterwoods, this stand-level heterogeneity will only be present until seed trees and retention is recovered during the subsequent harvest. Thus it is more likely that multicohort management will maintain carabid beetle communities in managed stands longer than will shelterwoods.

5. Conclusions

Partial cutting either through shelterwood or multicohort harvesting had similar initial effects on ground beetle abundance, species richness and composition. Neither partial cutting treatment maintained ground beetle assemblages consistent with uncut stands, but both shelterwood and multicohort harvesting provided at least some initial benefits for carabid assemblages as compared to clear cuts. In the long-term, we expect multicohort stands will maintain ground beetle assemblages closer to those found in uncut stands longer than shelterwoods simply because it will maintain uneven-aged structures longer on the landscape. This implies that shelterwood stands with similar levels of retention may provide similar benefits for ground beetles at least until the final removal cut. For land-managers this may offer some flexibility in achieving biodiversity related objectives in the short-term. For example, final removal cuts in shelterwoods could be delayed in order to allow assemblages more time to recover. However, given the initial differences between either partial cut treatment and uncut stands, the conservation value of shelterwoods or multicohort stands for ground beetle assemblages will depend on whether remnant populations of forest associated species are capable of increasing significantly prior to the next silvicultural entry into the stand.

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Appendix A

Variation explained by individual species that comprise less than 0.1% of the total species variance and individual splits in the ssMRT model comparing effects of harvesting, interannual variation and position within stand (machine corridor, partial cut retention strip or uncut retention strip).

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Species	% Variation explained in ssMRT							Relative % variation explained
	Split-1	Split-2	Split-3	Split-4	Split-5	Split-6	Total	
Amara discors Kirby	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Amara sp	0.000	0.003	0.000	0.005	0.000	0.000	0.009	0.073
Bradycellus lugubris (LeConte)	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Bradycellus nigrinus (Dejean)	0.000	0.000	0.000	0.001	0.000	0.001	0.003	0.073
Calosoma frigidum Kirby	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Elaphrus clairvillei Kirby	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.039
Gastrellarius honestus (Say)	0.001	0.000	0.001	0.000	0.000	0.000	0.002	0.036
Harpalus nigritarsis C.R. Sahlberg	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Harpalus pensylvanicus (DeGeer)	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.036
Notiobia nitidipennis LeConte	0.001	0.000	0.001	0.000	0.000	0.000	0.002	0.038
Pterostichus melanarius (Illiger)	0.001	0.000	0.001	0.000	0.000	0.000	0.002	0.036
Pterostichus mutus (Say)	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Pterostichus sp1	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.037
Stenolophus spretus Dejean	0.000	0.001	0.000	0.001	0.000	0.000	0.002	0.037
Trechus apicalis Motschulsky	0.003	0.000	0.005	0.000	0.000	0.000	0.008	0.069
Total	0.006	0.010	0.008	0.013	0	0.003	0.044	0.659

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