

# High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests

TIMOTHY T. WORK,<sup>1,4</sup> JOSHUA M. JACOBS,<sup>1</sup> JOHN R. SPENCE,<sup>2</sup> AND W. JAN VOLNEY<sup>3</sup>

<sup>1</sup>Departement des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville H3C 3P8 Canada

<sup>2</sup>Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1 Canada

<sup>3</sup>Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta T6H 3S5 Canada

**Abstract.** Recovery of biodiversity and other ecosystem functions to pre-disturbance levels is a central goal of natural disturbance-based approaches to ecosystem management. In boreal mixedwood forests, green-tree retention has been proposed as an alternative approach to traditional clearcutting that may minimize initial displacement of species assemblages and speed recovery of the biota. Here we evaluated the effectiveness of six levels of dispersed green-tree retention for conservation of ground beetle biodiversity in four boreal mixedwood cover types that span a gradient of stand development following wildfire. Each cover type × treatment combination was replicated three times in an operational scale experiment using 10-ha compartments. Ground beetle assemblages (59 species and 45 419 individuals) responded to increasing levels of dispersed, green-tree retention, but even relatively high levels of retention (up to 50% retention) did not retain species assemblages characteristic of uncut forest stands. This latter effect was most pronounced in compartments in later successional stages; i.e., those with developing conifer understories, or mixed and/or conifer-dominated overstories. Beetle assemblages in high levels of retention (50–75%) were statistically similar across all cover types, although we detected modest differences among the 5-year recovery of assemblages, based on initial cover type differences. Thus, recovery to initial conditions likely will be slower in mixed and conifer stands than in deciduous stands. We suggest that recovery of beetle assemblages is strongly linked to stand reinitiation through deciduous “suckering” post-harvest. Increasing levels of harvest appear to homogenize carabid assemblages across the four dominant cover types, and thus higher levels of retention (>50%) will be required to preserve assemblages of later successional stages. Regional renewal of assemblages, however, will require landscape-level planning.

*Key words:* biodiversity; ecosystem management; ecosystem resilience and resistance; green-tree retention; ground beetles; natural disturbance-based management.

## INTRODUCTION

Studies of displacement and subsequent recovery of species assemblages following perturbations contribute both to modern perspectives on biodiversity–stability relationships (Holling 1973, Pimm 1984, Chapin et al. 2000, McCann 2000) and development of disturbance-based approaches to forest ecosystem management (Hunter 1993, Franklin et al. 2002, Drever et al. 2006). Intensive forest harvesting has become a prevalent disturbance factor in boreal forests that is superimposed on natural disturbance regimes (Pratt and Urquhart 1994, Spence 2001). In this context, there has been increased recognition that intensive approaches to forest harvesting such as clearcutting affect native biodiversity differently than natural disturbance factors such as large-scale wildfire (McRae et al. 2001, Gandhi et al. 2004, Buddle et al. 2006, Koivula and Spence 2006,

Cobb et al. 2007). In addition, response of the native biota to forest harvesting may be context dependent and based on initial compositional differences related to forest stand succession (Niemelä et al. 1992, Work et al. 2004). Thus, conservation-oriented managers are employing less intensive methods of harvesting centered on retention harvesting (Harvey et al. 2002, Work et al. 2003) that seek to emulate natural perturbations such as wildfire, insect outbreaks, windthrow, and/or create or maintain stand structures consistent with older-aged forests. Assessing the effectiveness of dispersed retention for maintaining biodiversity and integrating this approach into the larger context of sustainable forest management requires experimental comparisons of species responses to a wide range of retention treatments (Connell and Sousa 1983, Spence 2001).

Although it is unlikely that all organisms will respond similarly to the scale and intensity of stand-level harvesting, insects are increasingly recognized as effective indicators of forest change and the impacts of forest harvesting at the stand level. Notably, carabid beetles have been widely used as bioindicators due in part to

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Corresponding Editor: J. A. Antos.

<sup>4</sup> E-mail: work.timothy@uqam.ca



PLATE 1. An example of the 50% dispersed retention treatment in DDOM (deciduous dominated) stands. Photo credit: Jason Edwards.

their sensitivity to natural disturbances (Holliday 1991, 1992, Gandhi et al. 2001), forest harvesting such as clearcutting (Niemelä et al. 1993, Heliölä et al. 2002, Koivula et al. 2002, Klimaszewski et al. 2005), and, most recently, partial cut harvesting (Martikainen et al. 2006, Work et al. 2008). Previous evaluations of carabid response to forest disturbances have largely concentrated either on responses of communities immediately following a disturbance event (Martikainen et al. 2006, Work et al. 2008) or long-term response of assemblages through chronosequence comparisons of forest stands many years after disturbance events (Buddle et al. 2006).

Here we evaluate the effectiveness of increasing levels of dispersed retention harvest for maintaining biodiversity of carabid beetles relative to uncut control stands across four dominant cover classes in western boreal mixedwood forest. We used replicated, direct manipulations of retention level as applied in the long-term EMEND experiment (Work et al. 2004), located in the boreal forest of northwest Alberta, Canada. Whole stands were initially perturbed by a harvesting in a “pulse” experiment in which evidence of subsequent recovery of carabid assemblages was monitored. We evaluate both the initial response of carabid beetle

assemblages after harvest as well as responses two and five years postharvest. Our hypothesis was that both initial effects of harvesting and recovery times would be linearly related to retention level, with both increasing with proportion of stems removed in the experiment.

## MATERIALS AND METHODS

### *Study site*

This study was conducted at the Ecosystem Management by Emulating Natural Disturbance (EMEND) research site (Fig. 1). The site is  $\sim 24$  km<sup>2</sup>, located  $\sim 90$  km northwest of Peace River, Alberta ( $56^{\circ}46'13''$  N,  $118^{\circ}22'28''$  W), the elevation ranges from 677 to 880 m above sea level, and soils are fine-textured lacustrine (Work et al. 2004). The forest of the EMEND landscape is characterized as a primeval forest subjected to the first commercial harvest. It comprises four cover classes that are the major successional stages of the boreal mixedwood forest in this area (Liefers et al. 1996) and corresponds to the landbase designations used by the province of Alberta (Liefers et al. 2008). The early succession deciduous-dominated cover class (DDOM) was defined as having  $>70\%$  deciduous trees in the canopy. The major deciduous tree species are *Populus*

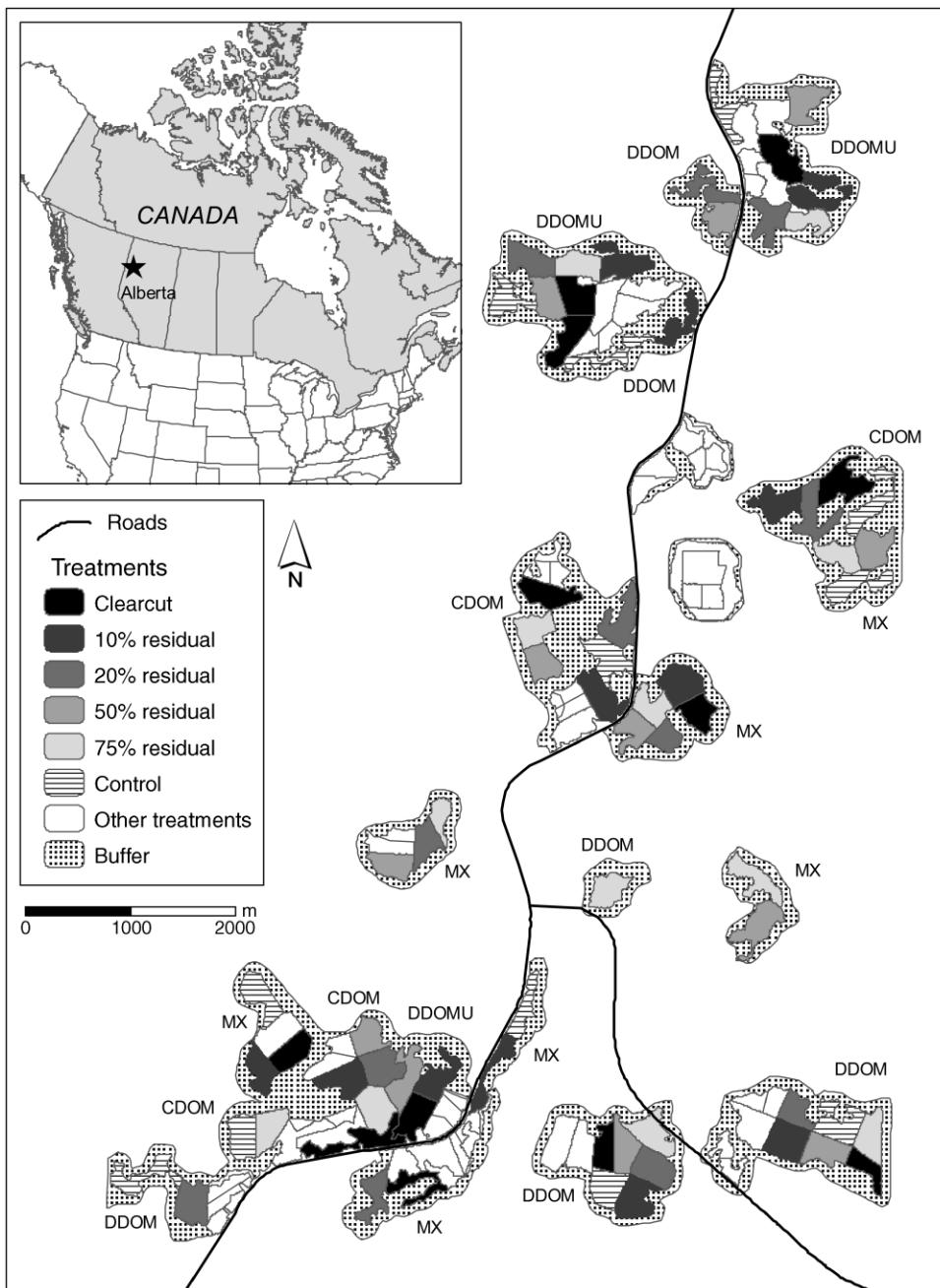


FIG. 1. Map of the EMEND (Ecosystem Management by Emulating Natural Disturbance) experimental site, near Peace River, Alberta, Canada, depicting cover type and harvesting treatments of experimental compartments used in this study. Cover types: DDOM, early-succession deciduous-dominated; DDOMU, deciduous canopy and developing conifer understory; MX, mixed deciduous and coniferous canopy; CDOM, late-successional coniferous-dominated. Projection: NAD 1927 UTM Zone 11 North.

*tremuloides* Michx. and *Populus balsamifera* L., with minor elements of *Betula papyrifera* Marshall. Stands with a deciduous canopy and a developing conifer understory (DDOMU) were taken to represent the early-mid-succession cover class. The understory is dominated by *Picea glauca* (Moench) Voss, with minor elements of *Picea mariana* (P. Mill.) B.S.P., *Abies balsamea* (L.) P. Mill., and *Pinus contorta* Dougl. The

mid-successional cover class had a mixed deciduous and coniferous canopy (MX) with neither making up >70% of the canopy (Table 1). Late-successional coniferous-dominated cover class (CDOM) consisted of stands with >70% coniferous trees in the canopy.

Within each cover class, harvesting treatments were randomly assigned and applied to experimental compartments (~10 ha) in larger forest stands. Cut blocks of

TABLE 1. Comparison of stand basal area and percentage of basal area represented by conifers from pretreatment and posttreatment stands at the EMEND (Ecosystem Management by Emulating Natural Disturbance) experiment, near Peace River, Alberta, Canada.

Treatment period	DDOM				DDOMU			
	Basal area (m <sup>2</sup> /ha)		Conifer basal area (%)		Basal area (m <sup>2</sup> /ha)		Conifer basal area (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pretreatment†								
Clearcut (0–2% residual)	38.67	5.455	5.52	5.522	43.85	1.153	19.17	5.731
10% residual harvest	38.88	2.566	1.67	1.666	51.78	1.931	22.55	6.750
20% residual harvest	43.13	6.248	2.62	2.121	49.74	2.995	17.11	4.851
50% residual harvest	36.60	4.179	0.00	0.000	47.46	2.171	27.56	4.096
75% residual harvest	38.72	3.749	12.65	6.325	47.41	2.526	12.71	6.531
Control (100% retention)	37.75	3.677	2.24	2.243	59.89	3.583	18.12	5.615
Posttreatment								
Clearcut (0–2% residual)	0.55	0.548	0.00	0.000	2.81	0.733	35.59	18.880
10% residual harvest	7.01	2.392	8.39	8.386	12.06	2.258	32.32	12.076
20% residual harvest	11.02	2.093	6.94	4.547	15.11	1.188	24.96	10.337
50% residual harvest	12.10	2.029	0.00	0.000	25.97	5.322	26.70	7.208
75% residual harvest	30.70	2.560	10.65	5.422	35.59	1.611	13.59	6.931
Control (100% retention)	37.65	3.577	2.24	2.243	59.68	3.575	18.18	5.634

Notes: Data are from Jan Volney and John Spence, Forest Mensuration and Health Dataset, EMEND Database (<http://www.emend.rr.ualberta.ca/index.asp?page=data>). Cover type abbreviations: DDOM, early-succession deciduous-dominated cover class; DDOMU, deciduous canopy and developing conifer understory; MX, mixed deciduous and coniferous canopy; CDOM, late-successional coniferous-dominated cover class. Conifer basal area is given as a percentage of total basal area.

† Pretreatment data were based on diameters of residual standing trees as well as stumps (after diameter corrections using Haug [1994]), measured after treatments were applied.

this size are at the low end of the size range operationally employed in Alberta. Harvesting treatments consisted of increasing levels of dispersed retention and included ~2% (clearcut), 10%, 20%, 50% (see Plate 1), and 75%, as well as uncut control stands (100%). Each cover type by treatment combination was replicated three times ( $n = 72$ ). Within each experimental stand, harvesting treatments were applied to consistent prescription in the winter of 1998–1999 using feller-buncher harvesting machines. These machines passed north–south through each treated stand, perpendicularly to the prevailing winds, creating a completely harvested strip 5 m wide and leaving a 15 m wide vegetation corridor. Simply cutting the machine corridors created the 75% retention treatment. Lower retention treatments were applied by removing an additional number of stems (>5.0 cm diameter at breast height), strictly in the order encountered by the machine operators and regardless of species, from the vegetation corridors at the following ratios: (a) 1:2 (cut:left) for 50% retention, (b) 3:1 for 20% retention, and (c) 7:1 for 10% retention.

This cutting approach is effectively whole-tree harvesting as all harvested stems were de-limbed and stacked at log landings at the edge of each stand. The highest intensity treatment was a standard operational clearcut with ~2% residual structure, as has been the previous standard in Alberta. Our retention treatments correspond to strict prescription to percentage of stems present prior to harvesting. Postharvest basal areas or volumes will vary with the distribution of initial stocking density and diameters observed in these stands, and therefore our retention treatments do not translate directly to variation in basal area. Nonetheless, we pro-

vide mean basal area as well as percentage of basal area represented by conifer species, a measure used to reflect cover type differences for all stands prior to harvesting 1998 and postharvest in 1999 (Table 1). Estimates for pretreatment basal area were based on diameters and densities of residual standing trees as well as stumps (diameters adjusted to 1.3 m height with regression [Haug 1994]) measured within 6 months of harvest and as we established the permanent sampling plots within compartments. We consider these pretreatment estimates to closely reflect true basal area.

Volumes of coarse woody material (CWM) in unharvested stands ranged between 52.4 and 76.4 m<sup>3</sup>/ha, with conifer-dominated stands having the largest volumes (D. Langor, *unpublished data*). Volumes of CWM generally increased as a result of harvesting (mean increase of 17.7 ± 9.60 m<sup>3</sup>/ha, mean ± SE) without any clear pattern related to treatment or stand type (D. Langor, *unpublished data*). Thus, carabid populations, which depend to some extent on CWM, were unlikely to be affected differentially across cover types by changes in this variable.

#### Beetle sampling

Within each experimental compartment, six permanent sampling plots (2 × 40 m) were established to measure tree density, tree mortality, CWM, and understory vegetation. These permanent plots ran perpendicular to the grain of harvest and represented equivalent proportions of vegetation and machine corridors. Three of these permanent sampling plots/experimental compartment were chosen at random to sample ground beetles. Ground beetles were sampled using two, 12 cm diameter pitfall traps, consisting of an

TABLE 1. Extended.

MX				CDOM			
Basal area (m <sup>2</sup> /ha)		Conifer basal area (%)		Basal area (m <sup>2</sup> /ha)		Conifer basal area (%)	
Mean	SE	Mean	SE	Mean	SE	Mean	SE
41.47	2.387	59.81	11.668	49.66	1.310	78.44	3.359
52.79	2.731	36.94	2.136	44.19	7.158	73.58	2.739
50.95	2.168	70.23	5.805	49.86	2.211	83.93	2.731
53.56	4.946	53.62	23.894	54.05	7.559	67.41	7.089
55.45	5.950	68.75	7.681	49.65	5.311	80.95	2.292
51.10	7.486	59.37	14.914	59.13	8.518	81.09	2.207
5.39	3.119	24.33	14.771	0.26	0.263	33.33	33.333
16.54	3.743	25.28	2.997	11.17	1.815	72.99	13.507
19.09	2.236	73.56	8.917	14.75	2.416	75.93	6.057
25.21	6.051	45.15	23.876	35.18	6.609	59.86	11.593
35.29	8.376	61.47	13.559	33.48	4.669	76.12	2.282
50.93	7.395	59.42	14.981	58.87	8.616	81.01	2.156

outer permanent cup (1 L) and a removable inner cup (500 mL; Spence and Niemelä 1994) located, respectively, at each end of a permanent sampling plot. Approximately 200 mL of ethylene glycol was added to each trap as a killing agent and preservative. The traps were serviced approximately every three weeks during the frost free periods (May through August) of 1999, 2000, and 2004 (1, 2, and 5 years postharvest). During trap service, trap contents were strained through cheesecloth, tied into labeled packets and stored in ~70% ethanol. Subsequently, in the laboratory, ground beetles were sorted and identified to species using Lindroth (1961, 1963, 1966, 1968, 1969a, b).

#### Statistical analysis

Interactive effects of cover type, harvesting treatment, and time on carabid assemblages were analyzed using permutational-based multivariate ANOVA (PERMANOVA; Anderson 2001) and multivariate regression trees (MRT; De'ath 2002).

The PERMANOVA used in this study was analogous to the more traditional repeated-measures ANOVA design, where the same degrees of freedom and analogous error terms for estimated error mean square are used to test main effects and interactions, and permutation tests were used to estimate significance of *P* values. In our model, two additional terms, representing "plot nested within the cover × harvest" (*df* = 48) and "time × plot nested within cover × harvest" (*df* = 96), were used to estimate error mean squares in the between- and within-subject factors in the design. We used these terms only in the calculation of error terms and significance tests because these effects are ecologically meaningless. For the analysis, plot-level estimates of catch rate of 59 carabid species were analyzed as Bray-Curtis dissimilarities, and permuted 999 times using the PERMANOVA program (Anderson 2005).

Pairwise a posteriori comparisons were made between all main effects and interaction terms in the model. Pairwise tests were based on Monte-Carlo *P* values generated from 9999 permutations. We interpreted significant differences in pairwise comparisons between harvesting treatments and control stands over time as a measure of resistance and potential resilience of ground-beetle composition to the effects of harvesting.

We used multivariate regression trees (MRT) to successively partition data in order to maximize differences among the splits in the tree (or minimize the "impurity" of a node). We used a distance-based MRT of pooled compartment-level estimates of the catch rate of 59 carabids, for which data were converted to Bray-Curtis dissimilarity. The final number of splits in the tree was determined based on cross-validated error as described in De'ath (2002).

Initially a series of monotonic transformations were applied to the data set. Both square root and log transformations differed little from raw data in terms of their effect on the MRT and the PERMANOVA. Given the relatively minor differences between the monotonic data treatments and the untransformed data, we opted to use untransformed data in the analysis presented here. Catch rate data and the environmental data matrix used in multivariate analysis are available in the Supplement.

#### RESULTS

During 1999–2004, we collected 45419 individual carabids representing 59 species, through a sampling effort comprising >150 000 individual trap days. Median catch rate was similar between 1999 and 2000 but decreased markedly in 2004, particularly in treatments with lower levels (<50%) of retention (Fig. 2). Overall comparisons of rarefaction curves by cover types and by treatments demonstrate that sampling was

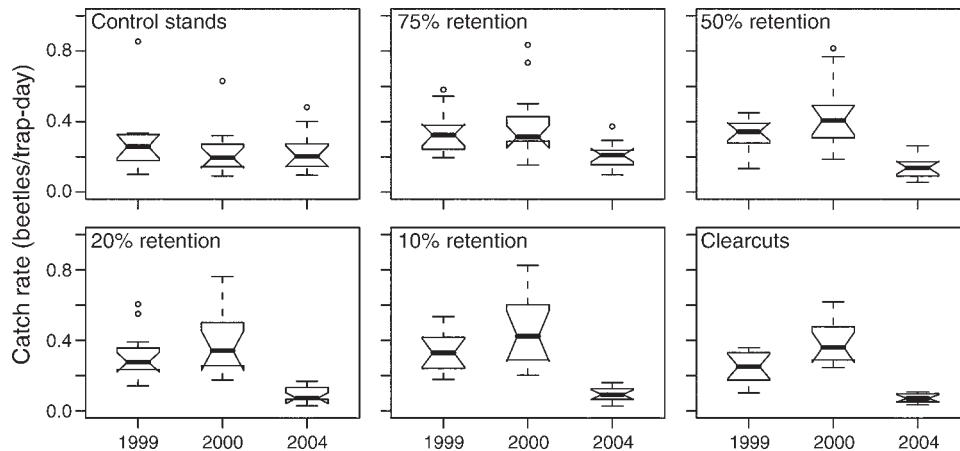


FIG. 2. Box-and-whisker plots depicting beetle catch rate within decreasing levels of dispersed green-tree retention, 1, 2, and 5 years postharvest. Ground beetle (Carabidae) assemblages (59 species) were sampled at the EMEND site near Peace River, Alberta, Canada. The thick line at the box notch is the median; box ends indicate first and third quartiles; whiskers correspond to the range (without outliers); and open circles correspond to outliers.

adequate to characterize the carabid fauna (Fig. 3). For even the steepest rarefaction curves (DDOM and 0–2% retention), fewer than three additional species were collected per 1000 individuals sampled after the initial 3000 individuals.

Main effects of cover type, harvesting, and time since harvest, as well as all two-way interactions with year from the PERMANOVA were significant (Table 2). Pairwise comparisons of cover types demonstrated that in all years, carabid assemblages in both deciduous-dominated stand types (DDOM and DDOMU) compartments differed consistently from each other ( $t = 2.3663$ ,  $P = 0.0010$ ) as well as from those from MX ( $t = 4.28$ ,  $P = 0.001$  and  $t = 2.72$ ,  $P = 0.0010$ , respectively) and CDOM compartments ( $t = 3.55$ ,  $P = 0.0010$  and  $t = 1.99$ ,  $P = 0.0020$ , respectively). In contrast, compartments with higher conifer component (MX and CDOM) did not differ significantly ( $t = 1.0211$ ,  $P = 0.3790$ ).

No initial differences between harvested and control compartments were observed one year postharvest. Two years following harvest, however, there were significant differences in community dissimilarity between control treatments and 0–2% ( $t = 2.15$ ,  $P = 0.0110$ ) and 10% retention treatments ( $t = 1.95$ ,  $P = 0.0370$ ) (Fig. 4A). Five years postharvest, differences between control treatments and 0–2% ( $t = 2.2654$ ,  $P = 0.0110$ ) and 10% ( $t = 2.0372$ ,  $P = 0.0230$ ) were still apparent and differences between controls and 20% ( $t = 2.1343$ ,  $P = 0.0070$ ) retention treatments also became significant. Additionally, carabid assemblages from 75% retention treatments differed significantly from those in the three lower retention treatments five years postharvest (0–2%,  $t = 2.19$ ,  $P = 0.0160$ ; 10%,  $t = 2.09$ ,  $P = 0.0250$ ; and 20%,  $t = 1.89$ ,  $P = 0.0350$ ; Fig. 4A). Within-group variation, measured as average dissimilarity among compartments for a given treatment, was consistently highest in control

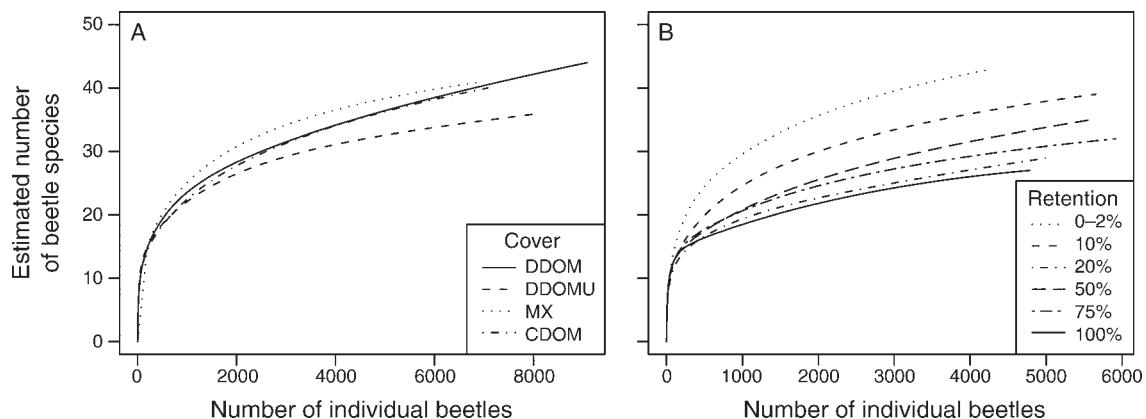


FIG. 3. Rarefaction curves depicting estimated number of ground beetle species per number of individuals sampled grouped among (A) four successional cover types and (B) six levels of dispersed green-tree retention. Rarefaction curves were based on beetle abundance pooled from samples collected 1, 2, and 5 years postharvest. Similar trends were observed when the data were analyzed separately by year.

TABLE 2. Permutational multivariate ANOVA of the effects of cover type (four levels), harvesting intensity (six levels), and time (1999, 2000, and 2004) on ground beetle composition (59 species).

Source	df	SS	MS	<i>F</i>	<i>P</i> (perm)	<i>P</i> (MC)	Expected mean squares
Cover	3	116 831.2	38 943.74	8.6817	0.001	0.001	residual + plot(cover × harvesting) + cover
Harvest	5	63 003.52	12 600.7	4.2893	0.001	0.001	residual + (cover × harvesting) + plot(cover × harvesting) + (harvesting × year)
Cover × harvest	15	44 065.29	2937.686	0.6549	0.994	0.999	residual + plot(cover × harvesting) + (cover × harvesting)
Between-subject error	48	215 316	4485.751				residual + plot(cover × harvesting)
Year	2	151 604.6	75 802.32	14.714	0.001	0.001	residual + (plot(cover × harvesting) × year) + (cover × year) + year
Cover × year	6	30 910.24	5151.706	3.0273	0.001	0.001	residual + (plot(cover × harvesting) × year) + (cover × year)
Harvest × year	10	56 688.53	5668.853	3.6516	0.001	0.001	residual + (cover × harvesting × year) + (plot(cover × harvesting) × year) + (harvesting × year)
Cover × harvest × year	30	46 572.32	1552.411	0.9122	0.799	0.796	residual + (plot(cover × harvesting) × year) + (cover × harvesting × year)
Within-subject error	96	163 368.3	1701.754				residual + (plot(cover × harvesting) × year)

compartments, with the exception of the 0–2% retention treatment five years postharvest. Interannual variation in composition within treatment groups, measured as the maximum difference of within-group dissimilarity observed over the course of the experiment, was largest in 0–2% retention treatments, followed, respectively, by controls, and the 10%, 50%, 20%, and 75% retention compartments. Variation in carabid composition within the 20% and 75% retention treatments was relatively consistent over all years (Fig. 4B).

Pruning of the MRT using a cross-validated error procedure resulted in an 11-branched tree explaining 55.4% of the variance (error = 0.466, CV error = 0.595, SE = 0.0448; Fig. 5). This tree was produced 683/1000 times in the cross-validation procedure. The initial split divided the data based on differences observed between 1999 and 2000 and 2004. This split is consistent with the pairwise comparisons of year from the PERMANOVA. In the data from one- and two-year postharvest (1999–2000), a secondary split divided DDOM compartments from those with at least some conifer component in the under- or overstory (DDOMU, MX, and CDOM). The initial effects of cutting within DDOM stands were seen in the subsequent division into stands with ≤20% retention and those with ≥50% retention. For DDOMU, MX, and CDOM compartments, the initial effects of harvesting were more pronounced. All levels of harvesting (0–2% to 75%) were grouped together in a terminal node, regardless of cover type and were separated from uncut control compartments. Cover type differences between DDOMU and compartments with at least some conifer component in the overstory (CDOM and MX) were separated in the subsequent terminal split.

Five years postharvest, overall treatment differences became more important than cover type differences. In 2004, compartments were divided into those with ≤20% retention and those with ≥50% retention. Compartments with ≤20% retention were subsequently divided into

those with 10–20% retention and terminal node of stands with 0–2%. The 10–20% retention treatments were subsequently divided into deciduous-dominated compartments (both DDOM and DDOMU) and those with some conifer overstory (MX and CDOM). In the contrasting node, compartments with ≥50% retention were subsequently divided into DDOM and those with at least some conifer component (DDOMU, MX, and CDOM). DDOM compartments were then subdivided into 50% retention and 75–100% retention.

#### DISCUSSION

The initial response of an ecosystem to perturbation and subsequent return to pre-disturbance condition following disturbance depend both on the intensity and frequency of the disturbance (Connell 1978, Sousa 1979) as well as any successional dynamics initiated following disturbance (Drever et al. 2006). In the boreal mixed-wood forests of western Canada, stand succession, typically initiated by wildfire, progresses from deciduous-dominated stands toward stands dominated by shade-tolerant conifers (Lieffers et al. 1996). While this successional sequence can be influenced by factors such as fire severity, availability of conifer seed sources (Greene et al. 1999), and gap dynamics (Peters et al. 2006), increasing intensity of harvest promotes the reestablishment of deciduous-dominated cover types (Frey et al. 2003). We observed consistent cover type differences in beetle composition among uncut, deciduous-dominated stands (DDOM), deciduous stands with a developing understory of white spruce (DDOMU), and stands with relatively large proportions of conifer in the overstory (MX, CDOM), stressing the importance of stand succession/and or the relative amount of conifer within a stand as a broad-level determinant of carabid assemblages (Work et al. 2004). In many cases, these cover type differences were no longer observable once harvesting treatments were imposed, particularly in

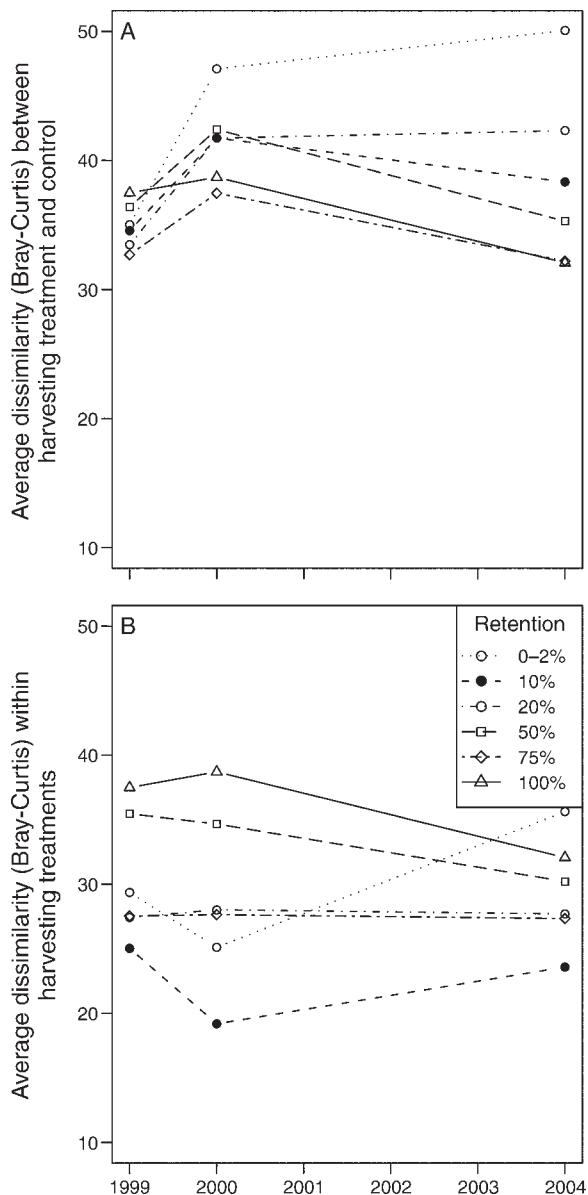


FIG. 4. (A) Average dissimilarity based on Bray-Curtis distance of five intensities of forest harvest in comparison to uncut control stands and (B) average within-treatment dissimilarity among five intensities of forest harvest and uncut control stands 1, 2, and 5 years postharvest.

stands with a relatively higher proportion of conifer basal area (DDOMU, MX, and CDOM) and at retention levels <50%. Reinitiation of a deciduous cohort following harvest among all cover types is one explanation for the initial differences in carabid composition among seral types. Simply put, carabid communities in late seral stages are likely affected by both physical and structural changes within the stand as well as major compositional changes in vegetation that accompany the conversion to more deciduous-dominated stands. Carabid communities in earlier seral stages likely

experience major structural changes but fewer compositional differences in vegetation as the stand reinitiates as the same stand type. These responses may ultimately reflect changes in temperature and humidity related to retention levels as well as any changes in leaf litter related to the reinitiation of the deciduous cohort (Koivula et al. 1999, Jacobs et al. 2008).

Considering Holling's (1973) conception of ecosystem resilience, where periods of revolution or minor changes early in system development have large effects on the final state of the system, these lower retention stands may represent "windows of opportunity" for ecosystem management or critical points of departure from the normal successional trajectory of the mixedwood, depending on one's perspective. The lack of strong cover type differences five years postharvest in later seral stages has several interpretations relevant for forest management and planning. First, harvesting treatments with  $\geq 50\%$  retention could be considered to fall within the range of natural variability observed among the mosaic of cover types found in this region. Second, we could be observing an even larger landscape effect of harvest throughout the EMEND site. At this moment we are unable to distinguish between these two hypotheses. Continued monitoring of the carabid fauna at EMEND will demonstrate whether lower retention sites continue to diverge from uncut controls and whether cover type differences emerge within the cluster of higher retention sites ( $\geq 50\%$ ). Clearly very low levels of retention such as 0–2% are insufficient to maintain cover type differences and these effectively "unmix" the mixedwood. However, intermediate levels of retention (10–20%) may be sufficient to maintain cover type differences in carabid communities between deciduous-dominated stands and stands with some conifer in the overstory (MX and CDOM). Nevertheless, carabid composition at these lower retention levels will not resemble those found at higher retention levels or in uncut stands.

The initial impact and/or recovery of communities must always be considered in light of the experimental design and methods used (Connell and Sousa 1983). "Recovery" in our study has been judged relative to beetle compositions found within uncut stands rather than paired, pretreatment stands in a strict BACI design. A preharvest inventory of epigeic arthropods was conducted in replicated stands of each of the four cover types in 1998 throughout the EMEND site before random assignment of harvesting treatments and is published elsewhere (Work et al. 2004). Comparisons between uncut stands and pretreatment were remarkably consistent. Relative abundance and rank of dominant species that were found pretreatment (Work et al. 2004) were similar to those found in control stands postharvest. All but one species (*Nebria gyllenahli*, a singleton in 1998) were present pretreatment as well as posttreatment in the control stands. This provides compelling evidence that despite the number of replications, the observed

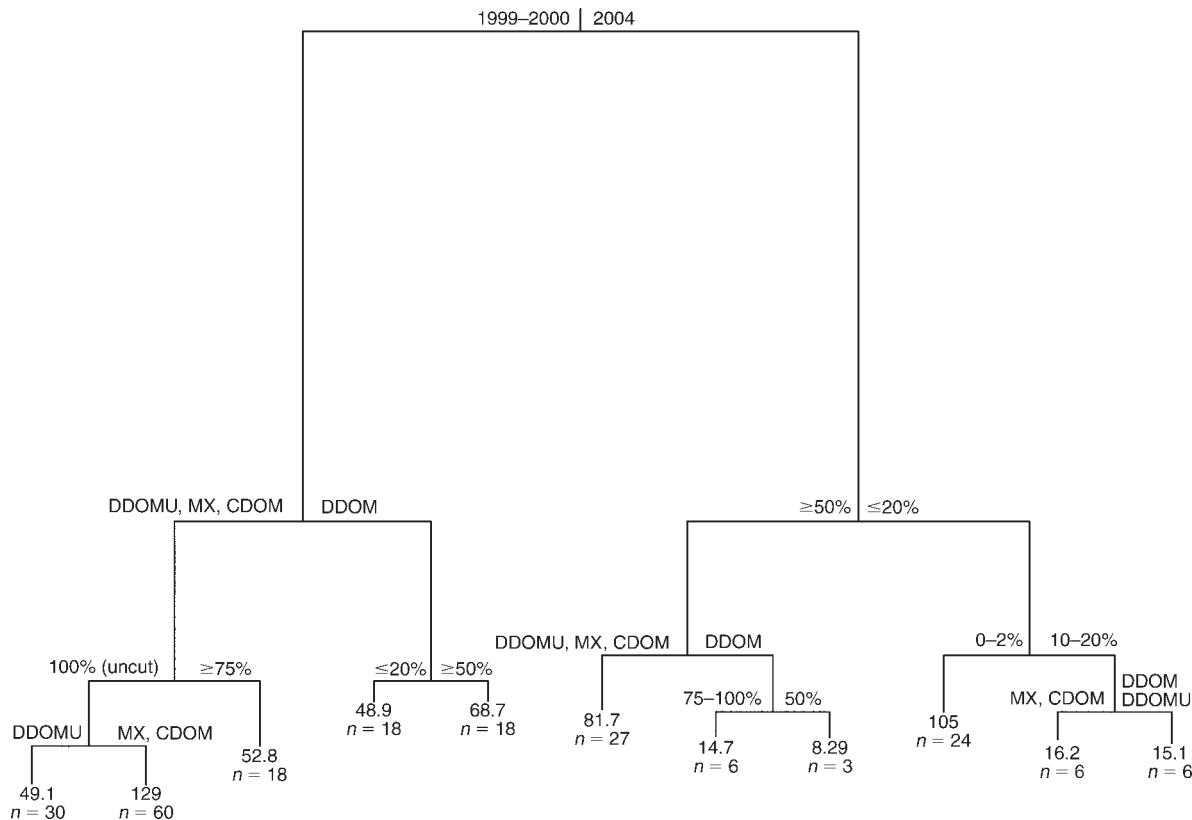


FIG. 5. Distance-based multivariate regression tree (dbMRT) using Bray-Curtis similarity to depict differences in beetle composition among 72 experimentally manipulated stands. See Fig. 1 for cover type abbreviations. Sample size *n* is the number of stands. The percentages refer to retention. Error = 0.446; CV error = 0.595; SE = 0.0448.

differences in assemblages were indeed related to harvesting treatments.

Experimental evaluation should consider changes in community and/or species to relevant perturbations at meaningful spatial scales and over time periods long enough to reflect at least one turnover of all study individuals (Connell and Sousa 1983). Harvesting treatments were clearly sufficient to provoke changes at the community level, even one year after the experiment began. EMEND’s 10-ha harvest blocks reflect a relevant operational scale for forestry management in this area and likely encompass lifetime dispersal abilities of many forest carabids. The duration of the data reported here likely encapsulates at least four complete turnovers of carabid populations at EMEND. We expect to see four complete turnovers as there may have been significant pretreatment recruitment of carabids observed in 1999 (one year postharvest) that existed as larvae in forest soils immediately following harvest. Such pretreatment recruitment may be responsible for diminishing the overall response of carabids in one year after harvest. Any pretreatment recruitment would have been completed before 2000, two years after harvest.

These results contrast in part the findings of other researchers using similar experimental approaches. Martikainen et al. (2006) used a similar approach in

pine-dominated boreal forests in Fennoscandia where retention levels were reduced to 0, 10, and 50 m<sup>3</sup>/ha. Based on initial stand volumes, these harvesting targets correspond roughly to 0%, 3%, and 17% retention (Hyvarinen et al. 2005). These authors did not observe the initial increase in abundance that we observed in lower retention levels (0–20%) in the years immediately following harvest, nor did they observe pronounced differences among retention treatments in the absence of prescribed burning. The peaks in abundance we observed one and two years postharvest from these lower retention levels are largely attributable to increases in *Pterostichus adstrictus* Eschscholtz (Jacobs et al. 2008). This same species dominated the Fennoscandian study and was four to five times more abundant in sites that were prescribed burned following harvest than in sites that were harvested without subsequent burning. Several hypotheses relevant to forest management could be advanced to explain these differences. Fennoscandian forests may be displaying “resistance” as a consequence of a longer land-use history (~100 years longer) than the first rotation forests of western Canada, similar to the hypotheses proposed elsewhere (Niemelä and Mattson 1996). If this hypothesis is true, we will expect to see larger compositional changes across all stands at the EMEND experiment as harvesting throughout this

region continues. Alternatively, Fennoscandian Scots pine stands may have more initial resistance similar to the early successional deciduous stand types used in our experiment if site conditions dictate the reestablishment of Scots pine (Jasinski and Angelstam 2002). In either case, the differences in both overall community patterns and even within individual species between these studies suggest that generalities on the impacts of forest management must be verified from region to region (Work et al. 2008).

Our results have two overarching implications for forest management and for the conservation of biodiversity in managed boreal mixedwoods of Canada. First, compositional differences in the boreal mixedwood are "homogenized" by increasing levels of harvest, and this effect is more pronounced in later seral stages. This implies that higher levels of retention must be left in later successional stages than in earlier deciduous-dominated stands. Second, higher levels of retention ( $\geq 50\%$ ) have similar compositions to uncut stands within five years, whereas lower retention levels do not. This suggests that even higher levels of retention should be implemented than those currently practiced.

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#### SUPPLEMENT

Data matrix of carabid beetle catch rates used in multivariate regression tree analysis (*Ecological Archives* A020-023-S1).