

# Ground-dwelling arthropod response to fire and clearcutting in jack pine: implications for ecosystem management

L.A. Venier, T.T. Work, J. Klimaszewski, D.M. Morris, J.J. Bowden, M.M. Kwiaton, K. Webster, and P. Hazlett

**Abstract:** We tested the response of species composition of three dominant litter-dwelling arthropod taxa (carabid beetles, spiders, and rove beetles) to wildfire and harvest. This study was conducted in north-central Ontario (47°42'N, 83°36'W) in jack pine (*Pinus banksiana* Lamb.) dominated stands in 2013 using pitfall trapping. Using 222 species (12 015 individuals), we compared the effects of disturbance using recently burned (3 years since fire) and clearcut sites (3 years since harvest; tree length, full tree, stump removal, and blading), as well as older, closed-canopy stands that have regenerated following clearcutting (51 years since harvest) and fire (92 years since fire), with multivariate regression trees. Taxa were more similar in the three controls (including recent fire) than between controls and harvest treatments, with increased forest floor disturbance in harvested plots being a likely explanation. In addition, taxa were different in the younger (51 years) harvest-origin plots than in the older (92 years) fire-origin plots, suggesting that communities had not yet recovered from the harvest disturbance possibly due to insufficient coarse woody debris in the younger stand. These results indicate that forest management practices that match natural forest floor disturbance could ameliorate short-term effects, whereas the maintenance of more coarse woody debris could reduce the recovery time of epigeic communities.

**Key words:** natural disturbance emulation, ecosystem management, carabid beetle, rove beetle, ground spider.

**Résumé :** Nous avons étudié l'impact des feux de forêt et de la récolte sur la composition en espèces de trois taxons dominants d'arthropodes qui vivent dans la litière (carabes, araignées et staphylins). Cette étude a été réalisée en 2013 dans le centre-nord de l'Ontario (47°42'N, 83°36'O), dans des peuplements dominés par le pin gris (*Pinus banksiana* Lamb.), au moyen du piégeage dans des trappes. À l'aide de 222 espèces (12 015 individus), nous avons comparé les effets de la perturbation en utilisant des sites récemment brûlés (3 ans après un feu) et des sites coupés à blanc (3 ans après la récolte; bois en longueur, arbre entier, enlèvement des souches et coupe à la cisaille), ainsi que des peuplements plus vieux à couvert fermé qui se sont régénérés après une coupe à blanc (51 ans après la récolte) ou un feu (92 ans après le feu) en utilisant des arbres de régression multivariée. Les taxons étaient plus semblables dans les trois témoins (incluant le feu récent) que entre les témoins et les traitements impliquant une coupe, ce qui s'explique vraisemblablement par la perturbation accrue de la couverture morte dans les parcelles récoltées. De plus, les taxons étaient différents dans les parcelles plus vieilles (92 ans) issues de feux comparativement aux plus jeunes (51 ans) issues d'une coupe, ce qui indique que les communautés n'avaient pas encore récupéré à la suite de la perturbation due à la récolte, probablement à cause du manque de débris ligneux grossiers dans le peuplement plus jeune. Ces résultats indiquent que les pratiques d'aménagement forestier qui correspondent à une perturbation naturelle de la couverture morte pourraient améliorer les effets à court terme tandis que le maintien de plus de débris ligneux grossiers pourrait réduire la période de récupération des communautés épigées. [Traduit par la Rédaction]

**Mots-clés :** imitation des perturbations naturelles, aménagement de l'écosystème, carabe, staphylin, araignée qui vit au sol.

## 1. Introduction

Ecological comparisons of resident biota between managed and naturally disturbed sites are the premise of natural disturbance based approaches to forest management. Natural disturbance based management is founded on the assumption that forestry practices that emulate aspects of natural disturbance will reduce the negative impacts of forest management on biodiversity (Hunter

1993; Bergeron et al. 2002; Long 2009). Forest ecosystem management aims to maintain and enhance the long-term health of our forests including biodiversity (Gauthier et al. 2009), which requires a thorough understanding of the ecological impacts of alternative forest management options and their relationship to both mature and naturally disturbed forests. Assessments of how biodiversity under alternative forest management practices compare with biodiversity under fire disturbance and in mature forest

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conditions provides necessary information to select and adjust practices to best match a natural disturbance regime within an adaptive management framework.

Wildfire and clearcutting are dominant disturbances in jack pine (*Pinus banksiana* Lamb.) forests with differential impacts on residual standing overstory and forest soils that may have lasting effects on resident biodiversity. In the absence of forest management, jack pine forests are subject to frequent and often highly variable severity fires (Bergeron et al. 2001). Variation in fire severity creates a range of conditions for resident biota in which overstory mortality and exposure of mineral soil typically increase with fire severity (Weber et al. 1987, Greene et al. 2004) and deadwood is initially abundant after a fire (Brais et al. 2005). In contrast, overstory removal and soil disturbance following site preparation to improve jack pine regeneration success are comparatively more intense and more uniform following clearcutting (McRae et al. 2001). Forest floor disturbances and reductions in deadwood are intensified when clearcutting is coupled with additional removal of residual forest biomass (i.e., branches, tops, stumps) with the potential to be used as bioenergy feedstocks (Thiffault et al. 2011, 2014). The extent to which forest biota are initially affected by fire and clearcutting and the persistence of impacts dictate whether clearcutting and increasingly intensive variants associated with bioenergy harvest should be viewed as ecologically sustainable in these forests.

Despite the prominence of jack pine in North American boreal forests (Suffling et al. 1982) and continued assertions that clearcutting emulates certain attributes of wildfire (Ontario Ministry of Natural Resources (OMNR) 2013), empirical comparisons of resident biodiversity following both clearcutting and fire in jack pine have been limited to longer term responses of bryophytes and vascular plants (Reich et al. 2001) and initial responses of moths after disturbance (Chaundy-Smart et al. 2012). Vascular plant composition did not differ between stands that had burned or had been logged in regenerated stands (ca. 30–90 years since disturbance) with a standing overstory (Reich et al. 2001). For moths in stands with a shorter disturbance history (ca. 5 years), clearcuts and wildfires maintained a similar suite of dominant species and similar overall diversity of moths and differed only in relative abundance of 12 (of 240) species (Chaundy-Smart et al. 2012). Taken together, these results provide some initial evidence that clearcutting may indeed sufficiently emulate fire in jack pine stands for plants and organisms that rely directly on plants.

However, in boreal stands dominated by tree species other than jack pine, differences in biodiversity between clearcuts and wildfire are more pronounced, particularly in groups such as ground-dwelling arthropods (Niemelä et al. 1993; Buddle et al. 2000, 2006; Pohl et al. 2007; Work et al. 2010), and this research suggests that impacts of clearcutting should be limited and faunal convergence of ground-dwelling arthropods should be observed once the post-disturbance overstory and nutrient cycling have re-established. Clearcutting is, however, a silvicultural prescription that can involve different intensities of site preparation and soil disturbance in addition to overstory removal. For tree species that require exposure of mineral soil to ensure successful regeneration (such as many conifer species), clearcutting prescriptions may include additional measures that create favourable seed beds and plantable microsites (Munson et al. 1993; Munson and Timmer 1995). Following clearcutting of jack pine, soils are often mechanically prepared to create a favourable environment for seed germination or seedling establishment and survival (OMNR 1997; Ryans and Sutherland 2001). In some instances, site preparation such as scarification has caused further reductions in abundance and species richness and compositional changes of litter arthropods beyond those with only overstory removal (Klimaszewski et al. 2005). Thus for litter dwelling arthropods, the effects of clearcut prescriptions in jack pine may be a combination of both overstory

removal and additional impacts related to mechanical site preparation.

With increased interest in climate change mitigation and the development of forest-based bioenergy feedstocks, clearcutting in jack pine may be intensified to include additional removal of logging residuals and stumps. Outside of North America, logging residuals and stumps are increasingly used as bioenergy to reduce dependence on fossil carbon (Hakkila 2004; Björheden 2006). Within North America, declining markets for traditional wood products and the relative abundance of jack pine have led to similar interest in additional recovery of forest biomass following clearcutting (Kwiaton et al. 2014). Postharvest removal of forest biomass in jack pine stands has been shown to cause major compositional shifts in litter-dwelling arthropods initially 1 and 2 years after harvest (Work et al. 2014). However, these impacts of biomass removal have yet to be verified due, in part, to the lack of older stands that have regenerated following biomass removal. It follows that assemblages in sites with additional soil disturbance and reduced deadwood availability are more likely to fall outside the range of natural variability observed in recently burned stands and that these initial differences in composition may contribute to more persistent impacts of clearcutting in jack pine forests.

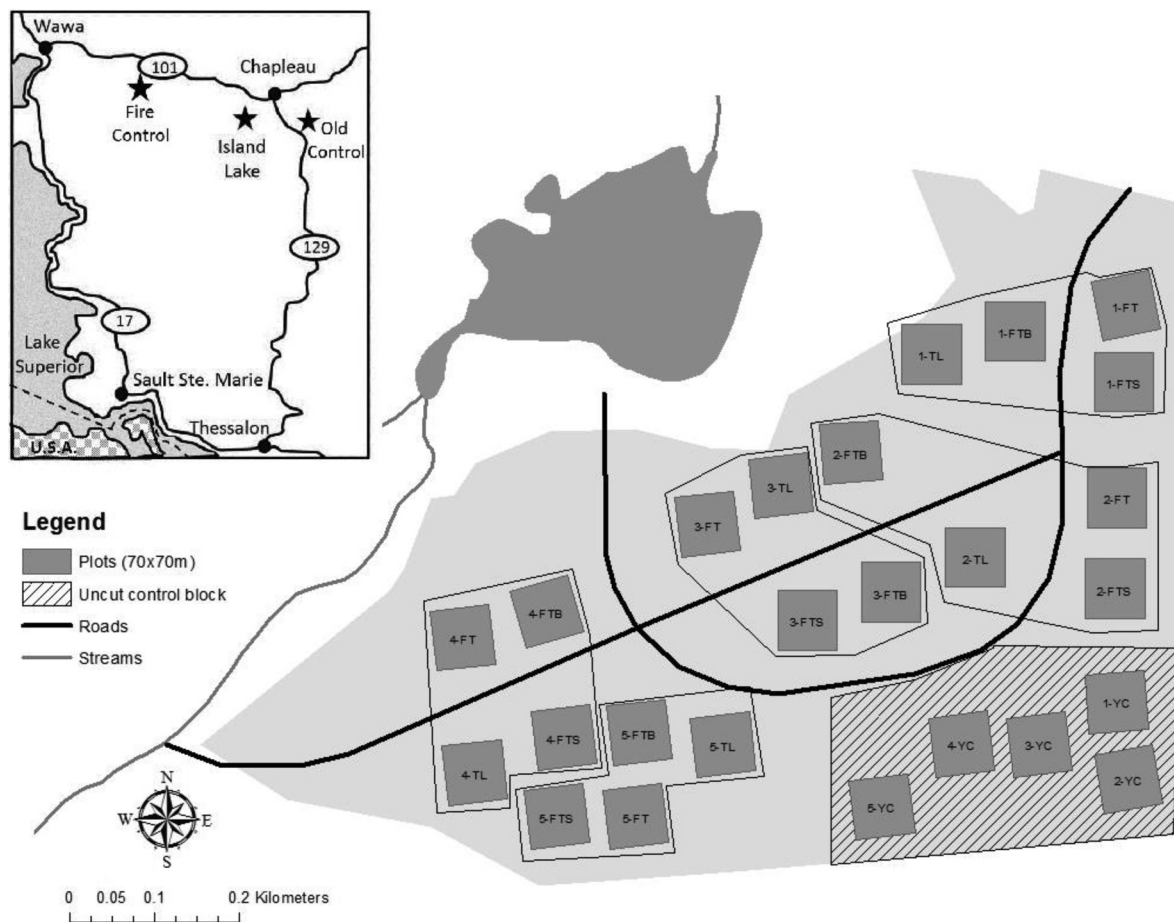
We assessed the short-term (3 years since harvest) impacts of clearcutting with increasing levels of biomass removal and the longer term (51 years since harvest) persistence of the effects of clearcutting in jack pine on three dominant groups of leaf-litter arthropods (ground beetles, spiders, and rove beetles) relative to a recent burn (3 years old) and an 92-year-old stand of pyrogenic origin. We hypothesized (i) that the initial effects of clearcutting on epigeic assemblages will differ from the initial impacts of wildfire, (ii) that increasing removal of residual biomass will further exacerbate differences in species composition through the compounded effects of loss of coarse woody debris (CWD) and increasing soil disturbances, and (iii) that effects of clearcutting will largely be abated once the overstory has re-established and that faunal composition of litter arthropods will be similar in mature stands originating from clearcutting and wildfire.

## 2. Methods

### 2.1. Study area

We collected litter arthropods from (i) harvested plots in a clearcut (2.5 years since harvest) and unharvested plots in a 51-year-old jack pine stand (young control, YC) that was previously clearcut, located at the Island Lake Biomass Harvest Experiment approximately 20 km from Chapleau, Ontario, Canada (47°42'N, 83°36'W; Kwiaton et al. 2014), (ii) a recent fire stand (RF; 3 years since fire) located near Ripple Lake, Ontario (47°56'N, 84°09'W), and (iii) a 92-year-old jack pine stand (old control, OC) of pyrogenic origin (47°38'N, 83°15'W) (Fig. 1). Mean annual temperature for the area is 1.7 °C, and mean annual precipitation is 797 mm (532 mm of rainfall and 277 cm of snowfall; Environment Canada 2013). These three jack pine dominated stands (>90% jack pine, based on live tree basal area) all established on glacioluvial, coarse-textured, glacial outwash deposits characterized by sandy (medium sand) parent material overtopped with a variable-depth loess (wind-blown) cap of finer textured soil (silty fine sand to silt loam) (Table 1). The forest floor was thinner at the RF site (5.4 cm) compared with the other two sites (9–10 cm) due to partial consumption during the wildfire event. Both stand density and tree volume prior to the stand-replacing wildfire were lower in the RF plantation compared with the other sites as it was a younger stand (30-years-old) at the time of the fire. The fire did result in much higher amounts of standing dead trees (107.4 m<sup>3</sup>·ha<sup>-1</sup>) and moderate levels of downed woody debris (DWD) (41.6 m<sup>3</sup>·ha<sup>-1</sup>), measured 3 years after the fire. The OC site had moderate levels of standing dead volume (37.9 m<sup>3</sup>·ha<sup>-1</sup>) and much higher volumes of DWD

**Fig. 1.** Study area layout of main Island Lake Biomass Harvest Experiment and locations of Island Lake, old control (OC), and recent fire (RF) sites. Treatments are labelled by harvest type (TL, tree-length; FT, full-tree biomass; FTS, stumped; FTB, bladed; YC, young control) and block number.



(76 m<sup>3</sup>·ha<sup>-1</sup>) compared with the low levels of deadwood in the YC site at Island Lake, as the OC stand is showing signs of the onset of stand breakup. The proportion of deadwood assigned to the different decay classes also differed slightly between sites. Most notable was the high amount of decay class 5 deadwood at the Island Lake site, a legacy of the previous tree-length harvest done in 1959. In general, these stands are very comparable, with jack pine dominant overstories, comparable tree densities, and very similar soil characteristics (Table 1). Their primary differences are related to the treatment effects.

The Island Lake Biomass Harvest Experiment was a second-growth jack pine stand that was originally clearcut harvested in the fall of 1959. The site was scarified and hand seeded in 1960, but due to poor initial regeneration, it was replanted in 1962. Harvesting and biomass removal treatments were applied in 2011, and standing dead trees were toppled prior to biomass removal (Kwiaton et al. 2014). Four intensities of biomass removal were applied in a randomized complete block design. From least to most severe removal, the treatments were (1) tree-length harvest (TL), where boles were delimited, cut at 10 cm diameter, and removed and residual slash was distributed evenly throughout the treatment using an excavator; (2) full-tree biomass harvest (FT), where the bole with branches of all merchantable and unmerchantable trees were removed and delimited outside the experimental plots; (3) stump removal (FTS), where bole and branches were removed as per full-tree biomass harvest, and stumps with large attached roots were removed using an excavator and placed at least 10 m beyond the experimental plot; and (4) blading (FTB),

where boles and branches were removed as per full-tree biomass harvest, and stumps, residual CWD, and the forest floor were removed with an excavator fitted with large metal blade. The tree-length harvest, full-tree biomass harvest, and stump removal treatments were all site prepared after harvest using disc trenching with 2.1 m spacing between trench centres. Disc trenching results in “flat” undisturbed linear areas with 15 cm deep trenches on either side of the flat area and linear piles of mixed organic and mineral soil beside the trenches (spoils). Each experimental treatment was replicated five times, and each experimental plot was 70 × 70 m (0.49 ha). Experimental plots were separated from each other and from the surrounding uncut forest by at least 20 m. Associated with these experimental plots are five sampling plots (70 × 70 m) located directly adjacent to the harvested area in the same stand originated from clearcutting 51 years ago (YC). These plots were spaced approximately 20 m from one another. This area has the same stand conditions as the experimental plots prior to cutting (Table 1).

We compared litter arthropods collected from the harvested treatments (TL, FT, FTS, FTB) and the YC with those collected from two locations that had been disturbed by wildfire. The first location was a recent wildfire 55 km northwest of the Island Lake Biomass Harvest Experiment (RF). Prior to burning, this 20 ha stand was a 30-year-old monoculture jack pine stand that originated from clearcutting, seeding, and planting. In the spring of 2010, an intense crown fire resulted in almost full mortality but relatively little exposed mineral soil compared with fires of this intensity due to high surface and soil moisture conditions. Within

**Table 1.** Stand characteristics for the three reference condition stands.

	Island Lake	Recent fire	Old control
Stand age at time of epigeaic sampling (years)	51	3 <sup>a</sup>	92
Species composition (%)	Pj <sub>99</sub> Sb <sub>1</sub>	Pj <sub>100</sub>	Pj <sub>90</sub> Sb <sub>10</sub>
Tree density (stems per hectare)	2005	1467 <sup>b</sup>	1870 <sup>c</sup>
Gross total volume (m <sup>3</sup> ·ha <sup>-1</sup> )	189.6	107.4 <sup>b</sup>	289.5
Site index (m @ BHA <sub>50</sub> )	19.3	19.5 <sup>b</sup>	18.8
Standing dead volume (m <sup>3</sup> ·ha <sup>-1</sup> )	9.66	107.41	37.92
DWD, aboveground fine volume (m <sup>3</sup> ·ha <sup>-1</sup> )	1.39	2.81	0.58
DWD, aboveground coarse volume (m <sup>3</sup> ·ha <sup>-1</sup> )	11.03	41.56	75.98
Proportion DWD aboveground coarse volume by decay class (%)			
DC 1	8	4	17
DC 2	23	13	22
DC 3	11	27	19
DC 4	9	36	33
DC 5	48	21	8
DWD, belowground coarse volume (m <sup>3</sup> ·ha <sup>-1</sup> )	13.94	5.21	15.30
Mode of deposition	GF	GF	GF
Profile development	DYB	DYB	DYB
Soil texture	SiS–mS	LmS–mS	SiL–LmS
Coarse fragment (%)	10	0	20
Forest humus form	F	FH	HF
Forest floor depth (cm)	10	5.4	9
Soil moisture regime	Moderately dry	Moderately dry	Moderately dry
Soil drainage	Rapid	Rapid	Rapid

**Note:** “Recent fire” is a recently burned stand and therefore has no standing live volume. Species composition: Pj, jack pine; Sb, black spruce. DWD, downed woody debris. Mode of deposition: GF, glaciofluvial. Profile development: DYB, Dystric Brunisol. Soil texture: LmS, loamy medium sand; mS, medium sand; SiL, silty loam; SiS, silty sand. Forest humus form: F, Fibrimor; FH, Fibri Humimor; HF, Humi Fibrimor. Pretreatment measures that are relevant to justify stand similarity are highlighted in grey. The other measures are different due to treatment effects.

<sup>a</sup>Recent fire was a 30-year-old jack pine plantation when it burned in the spring of 2010.

<sup>b</sup>Data from standing dead inventory measured after the fire.

<sup>c</sup>Pj density is 778 with Sb ingress at 1041 stems per hectare.

this stand, we sampled arthropods from six experimental plots spaced 20 m apart. Arthropods collected from this stand reflect the immediate impacts of overstory kill by fire, as well as any longer term impacts enduring from the initial clearcut. We also collected litter arthropods from a 92-year-old jack pine stand of pyrogenic origin located ca. 20 km southeast of the Island Lake Biomass Harvest Experiment (Fig. 1). Within the stand, we sampled arthropods from five experimental plots spaced 20 m apart. Arthropods collected from this stand reflect community composition in the absence of clearcutting and serve as a benchmark for comparison with harvested sites.

Our forest harvest treatments are set up as a randomized block design, but we acknowledge that our controls represent pseudo replicates. This is a common occurrence in operational-scale studies when comparing harvest treatments with control conditions, especially wildfire controls, due to limitations in the availability and accessibility of appropriate controls. However, there is still value in making comparisons among single stands, especially when the underlying characteristics of stands can be shown to be very similar as is the case here. Assessments of how biodiversity under alternative forest management practices compare with biodiversity under fire disturbance and in mature forest conditions provide valuable information to assess and adjust practices to best match a natural disturbance regime within an adaptive management framework. Hence, the current study provides valuable insight into how epigeaic communities respond to alternative disturbances and time since initiation.

## 2.2. Pitfall trapping

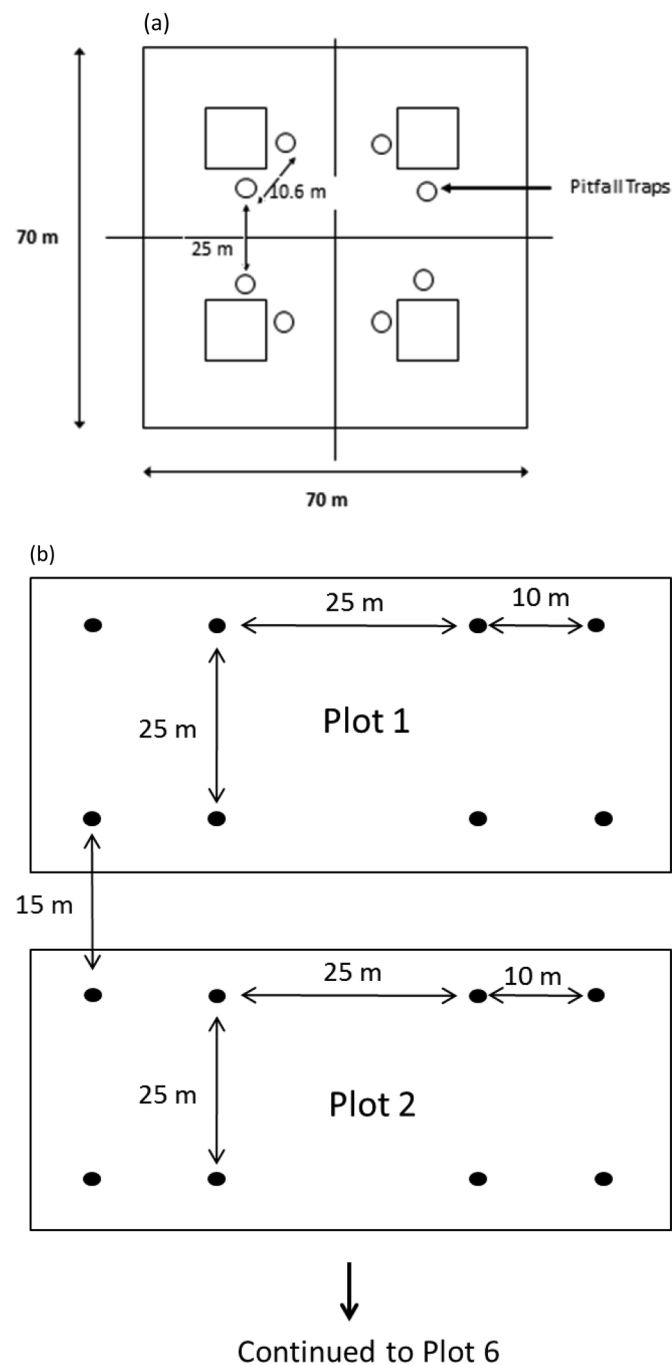
Arthropods were collected every two weeks using pitfall traps (diameter 11.5 cm, depth 4.5 cm) between 15 May and 19 August 2013. Traps were filled with 150 mL of propylene glycol as a preservative, 150 mL of water, and a small amount of detergent to break water surface tension. Traps were covered with suspended white plastic covers to prevent flooding from rain. Eight traps

were placed in each experimental plot (Fig. 2). In TL, FT, and FTS harvested plots, traps were always placed on the undisturbed flats (i.e., not in the trenches or on the spoils). For each collection period, trap contents were emptied into a Whirl-Pak bag (Nasco, Salida, California) in the field and returned to the laboratory for sorting. Specimens were sorted into three major taxa (carabid beetles (Coleoptera: Carabidae), spiders (Araneae), and rove beetles (Coleoptera: Staphylinidae)) and stored in 70% ethanol. These three groups are among the most abundant macroarthropods on the forest floor and have been used to assess the ecological impacts of a wide variety of natural disturbances and silvicultural interventions, including wildfire and salvage logging (Koivula and Spence 2006; Martikainen et al. 2006), clearcut and partial cut harvesting (Work et al. 2008, 2010; Paradis and Work 2011; Graham-Sauvé et al. 2013), and biomass removal (Work et al. 2013, 2014). All specimens were identified to species. Carabid species were identified according to Lindroth (1961–1969), following the nomenclature of Bousquet and Laroche (1993). Spiders were identified to species according to Paquin and Duperre (2003) and references in the World Spider Catalog (2017). Rove beetles were identified primarily according to Ashe (2001), Brunke et al. (2011), and Seevers (1978).

## 2.3. Environmental variables

Surface coarse deadwood (DW) was measured using three fixed-area subplots (rectangular, 15 m × 2 m) within each of the control (FC, YC, OC) plots. The first subplot originated from the treatment plot centre oriented with a random azimuth. The subsequent subplots were each offset 120° to form a triangle. The harvest treatment plots (TL, FT, FTS, FTB) were measured using the above technique in preharvest plot assessments combined with 12 fixed-area subplots (circular, 15 m × 1 m) conducted after the harvest treatments that captured fresh postharvest slash that contributed to the total DW pool. DW from the preharvest assessment in decay classes 1 and 2 was subtracted from the postharvest assessment to

Fig. 2. Pitfall trap layout in (a) Island Lake and old control (OC) and (b) recent fire (RF).



avoid double counting of DW material at the plot level. Each DW piece (>5 cm diameter) within the subplots was tallied for species, decay class (DC), length within the subplot boundaries, and end diameters. Decaying stumps were also recorded (species, DC, height, diameter). Decay class determinations followed the classification described by Næsset (1999): 1, recently dead tree, bark intact; 2, bark mostly intact, wood of outer layers (sapwood) of the log has started to soften due to rot; 3, bark sloughing or absent, outer layers of log are soft and easily removed with a knife, heartwood mostly sound; 4, bark detached, wood soft, no solid core; and 5, fragmented, no structural integrity. Surface deadwood volume was calculated for each piece using the average diameter and length, with the assumption that pieces were cylinders, and con-

verted to  $\text{m}^3 \cdot \text{ha}^{-1}$  using the subplot area ( $10\,000/30\text{ m}^2$ ). To estimate the amount of buried wood (>90% of log covered by live moss), a narrow trench (15 m in length) that bisected each subplot was dug through the organic layer to expose all buried DW. Each piece of buried DW that was encountered along the trench was tallied for its intersecting diameter. Total buried DW volume for each trench was calculated following the line-intersect sampling approach of Marshall et al. (2000):

$$(1) \quad y_i = \frac{\pi^2}{8 \times L} \times \sum_{j=1}^{m_i} d_{ij}^2$$

where  $y_i$  (in  $\text{m}^3 \cdot \text{ha}^{-1}$ ) is the total volume per hectare based on transect  $i$ ,  $L$  is the length of the trench, and  $d_{ij}$  is the diameter at the point of intersection of individual buried wood pieces  $j$  to  $m$ . Total volume per trench was then averaged for each treatment plot.

Microclimate was measured between 24 May and 6 October 2014 in two of five replicate plots of each harvest treatment and in one location in each of the YC, OC, and the RF sites. The coverage of microclimate data was inconsistent in 2013 (the year of arthropod collection), so we present here the data from 2014 to illustrate the differences in microclimate between treatments. We expect that the relative microclimate between treatments was reasonably constant between 2013 and 2014 but have not included these data in any formal analyses. Temperature was measured using copper constantan thermocouples at 15 cm above the forest floor, at the forest floor (interface between organic and mineral soil; not available for bladed plots), and at 10 cm below the soil surface. Campbell Scientific CS616 Water Content Reflectometers (WCR) measured soil moisture at 10 cm below the soil surface. Soil and air temperatures were read by the datalogger every 2 min and averaged and stored every hour. Mean, minimum, and maximum daily temperatures and moisture content were calculated for each treatment. Mean soil temperature ( $^{\circ}\text{C}$ ) and moisture content (% water by volume) were plotted over time to show seasonal variation in measures. We also plotted the daily temperature range (maximum–minimum) over the season for each treatment.

Mineral soil exposure was measured on  $4\text{ m} \times 4\text{ m}$  assessment plots around each pitfall trap. Each assessment plot was divided into four quadrats. In each quadrat, we estimated the percent cover of mineral soil exposure that resulted from site preparation, the stumping treatment (stump and root removal), complete burning of forest floor, and any other mineral soil exposure (e.g., overturned stumps, etc.).

#### 2.4. Analysis

We standardized trap catches by the total number of trap days for each trapping location. We used multivariate regression trees (MRTs; De'ath 2002) to compare assemblages of each of the three groups with treatment using the mvpart package in R (De'ath 2011). MRTs are hierarchical models that successively split data into more homogeneous groupings based on a set of explanatory variables. This approach makes relatively few underlying assumptions about statistical distributions within the data and, thus, is widely applicable to assemblage data with many species such as the three taxa used herein. We used sum-of-squares multivariate regression trees (ssMRT) to characterize species assemblages as a function of treatment. We selected the final tree size based on cross-validated errors. Following De'ath (2002), we selected the smallest tree with a cross validation error that fell within one standard deviation (SD) of the minimum cross-validated relative error. Response to treatments was interpreted with reference to overstory removal, amount of aboveground deadwood, microclimate on and below the soil surface, and mineral soil exposure as

**Table 2.** Carabid beetle individual species variances by split within the ssMRT, total tree variance, and total variance explained for the multivariate regression tree.

	Split 1	Split 2	Split 3	Split 4	Split 5	Tree total	Species total
<i>Agonum retractum</i>	0.495	0.023	0.017	0.057	0.004	0.595	1.379
<i>Bembidion nitidum</i>	0.120	0.000	0.609	0.000	0.007	0.735	0.791
<i>Calathus ingratus</i>	0.053	0.729	0.911	0.034	0.176	1.903	3.650
<i>Harpalus affinis</i>	0.126	0.000	0.649	0.000	0.007	0.782	0.835
<i>Harpalus fuliginosus</i>	0.301	0.004	0.190	0.021	0.059	0.574	1.072
<i>Harpalus laticeps</i>	1.787	0.872	0.898	0.005	0.170	3.731	4.641
<i>Harpalus pensylvanicus</i>	0.402	0.000	0.471	0.000	0.185	1.057	1.379
<i>Harpalus plenalis</i>	2.835	0.000	0.000	0.005	0.385	3.225	5.583
<i>Myas coracinus</i>	0.052	1.306	0.394	1.047	0.076	2.874	4.159
<i>Poecilium lucublandus</i>	15.186	0.000	1.228	0.000	0.006	16.419	17.760
<i>Pterostichus adstrictus</i>	11.907	0.584	12.102	0.233	1.007	25.832	28.272
<i>Pterostichus coracinus</i>	0.211	3.556	1.792	0.004	0.965	6.527	9.572
<i>Pterostichus pensylvanicus</i>	0.393	1.439	1.437	0.244	0.228	3.740	5.257
<i>Scaphinotus bilobus</i>	0.367	0.618	0.017	0.166	0.004	1.171	1.743
<i>Sphaeroderus stenostomus</i>	1.409	1.973	0.020	0.436	0.041	3.879	4.279
<i>Syntomus americanus</i>	0.216	0.069	0.127	0.005	0.260	0.677	1.219
<i>Synuchus impunctatus</i>	0.307	0.001	1.459	0.367	0.046	2.179	2.989
Less common species (17)	0.551	0.123	0.489	0.159	0.414	1.736	5.420
<b>Total</b>	<b>36.718</b>	<b>11.294</b>	<b>22.808</b>	<b>2.782</b>	<b>4.036</b>	<b>77.638</b>	<b>100.000</b>

a measure of forest floor disturbance. All analyses were done using R version 2.12.2 (R Core Team 2011).

We used mixed-effects models (R lme4 package; Bates et al. 2015) and Tukey multiple comparisons (R Multcomp package; Hothorn et al. 2008) to examine the differences in CWD volumes and mineral soil exposure between treatments. We could not analyze differences in microclimate between treatments as we had measurements in only two replicates of each treatment.

### 3. Results

#### 3.1. Epigaeic abundance

We captured 12 015 individuals in 2013 of which 5923 were ground beetles represented by 34 species (Appendix Table A1), 4861 were spiders represented by 118 species (Appendix Table A2), and 1231 were rove beetles represented by 70 species (Appendix Table A3). The most common ground beetles were *Pterostichus adstrictus* (34%), *Pterostichus pensylvanicus* (12%), and *Poecilium lucublandus* (12%), representing 58% of all individuals captured (Appendix Table A1). The most frequently collected spider species were *Pardosa xerampelina* (17%), *Pardosa moesta* (15%), and *Amaurobius borealis* (11%), representing 43% of all spiders captured (Appendix Table A2). The most common rove beetles were *Atheta capsularis* (14%), *Mycetoporus consors* (10%), and *Lordithon fungicola* (8%), representing 32% of all rove beetles captured (Appendix Table A3). The number of trap days for each plot ranged from 664 to 776 depending on the amount of trap disturbance.

#### 3.2. Carabid beetles

The total variance explained by the carabids MRT was 77.64% (Table 2). The most important species for explaining the variance in the regression trees were *Pterostichus adstrictus* (25.8%), *Poecilium lucublandus* (16.4%), and *Pterostichus coracinus* (6.5%) (Table 2). The most significant results from the ground beetle MRT were the first split of all controls from all harvested treatments, i.e., the fire is more similar to the uncut sites than to the harvested sites, the split of the bladed treatment from the other harvested sites (this extreme treatment seems to negatively impact the carabid community), and the lack of a split between full-tree biomass and tree-length treatments (the full-tree biomass harvest does not appear to exceed any threshold for response to biomass removal).

The left-hand side of the MRT contains the three controls. The first split, separating harvested plots from uncut plots (including

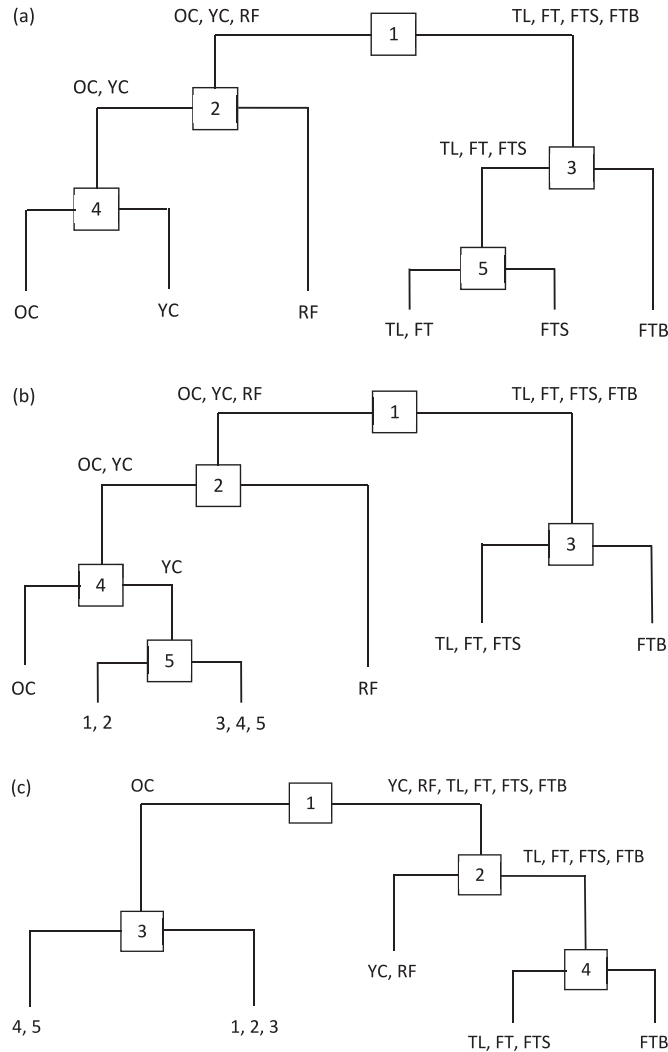
fire), explained 36.7% of the variance (Table 2; Fig. 3a). Five carabid species accounted for most of this variance (*Poecilium lucublandus* (15.2%), *Pterostichus adstrictus* (11.9%), *Harpalus plenalis* (2.8%), *Harpalus laticeps* (1.8%), and *Sphaeroderus stenostomus* (1.4%)) for a total of 33.1% variance (Table 2). Of these, the first four were associated with harvested plots, whereas *S. stenostomus* was associated with the uncut stands (Fig. 4a). The second split separates fire from the uncut stands and explained 11.3% of the variance, with *Pterostichus coracinus* (3.6%), *Sphaeroderus stenostomus* (2.0%), and *Myas coracinus* (1.3%) explaining the bulk of the variance (6.9%), all of which were rarely found in the fire plots (Table 2; Figs. 3a, 4a). *Harpalus laticeps* (0.87%) was often associated with the fire plots (Table 2; Fig. 4a). The fourth split contrasts the young plantation control with the mature fire-origin controls (2.8%) (Table 2; Fig. 3a). *Myas coracinus* (1.0%) was associated with the young plantation control (Table 2; Fig. 4a). There do not appear to be any species that were strongly associated with the mature fire-origin control in comparison with the plantation (Fig. 4a).

The right-hand side of the MRT deals with the harvested treatments. The third split separated the bladed plots from the other harvested plots (22.8%) (Table 2; Fig. 3a). Five species accounted for greater than 1% of variance each and include *Pterostichus adstrictus* (12.1%), *Pterostichus coracinus* (1.8%), *Synuchus impunctatus* (1.5%), *Pterostichus pensylvanicus* (1.4%), and *Poecilium lucublandus* (1.2%) for a total of 18% (Table 2; Fig. 4a). All of these species were associated with the harvested but not bladed plots except for *Poecilium lucublandus* (Fig. 4a). In addition, *Bembidion nitidum* (0.61%), *Harpalus affinis* (0.65%), *H. fuliginosus* (0.19%), *H. laticeps* (0.87%), and *H. pensylvanicus* (0.47%) were all more common in bladed plots (Table 2; Fig. 4a). The fifth split contrasted the stumped plots with the full-tree biomass and tree-length plots (4.0%) (Table 2; Fig. 3a). The full-tree biomass and tree-length treatments did not split in the MRT.

#### 3.3. Spiders

The spider MRT was very similar to the ground beetle MRT except that the stumped treatment did not split from tree-length and full-tree biomass treatments and the YC split into two groups (eastern plots vs. western plots). The total variance explained by the spider MRT is 63.96% (Table 3). The majority of the variance in the tree was explained by *Pardosa moesta* (15.47%), *Pardosa xerampelina* (13.90%), *Amaurobius borealis* (7.63%), *Pardosa hyperborea* (7.11%), *Trochosa terricola* (5.89%), and *Pardosa distincta* (5.01%)

**Fig. 3.** MRT trees for (a) carabid beetles, (b) spiders, and (c) rove beetles. OC, old control; YC, young control; RF, recent fire; TL, tree-length; FT, full-tree biomass; FTS, full-tree stumped; FTB, full-tree bladed.



(Table 3; Figs. 3b, 4b). This split (controls on the left and harvest plots on the right) explained 30.52% of the variance (Table 3). Three species were strongly associated with this split (*Pardosa moesta*, *P. xerampelina*, and *P. distincta*), all three of which were associated with the harvested sites (Fig. 4b). Several species appeared to be more associated with the controls, including *Cybaeopsis euopla* (0.40%), *Pardosa hyperborea* (0.65%), and *Trochosa terricola* (1.73%) (Table 3; Fig. 4b). The second split explained 11.98% of variance, splitting the fire from the YC and OC. Here the most important species were *Trochosa terricola* (2.11%), *Amaurobius borealis* (2.04%), and *Sciastes truncatus* (1.72%), which were all associated with OC and YC, and *Pardosa xerampelina* (1.46%), which was associated with fire (Table 3; Figs. 3b, 4b). The fourth split separated the OC treatment from the YC treatment (5.76%) (Table 3; Fig. 3b). It appeared that *Pardosa hyperborea* was driving this split (3.18%), which was strongly associated with the YC (Table 3; Fig. 4b). The fifth split separates the easternmost plots (control plots 1 and 2) of the YC from the westernmost plots (control plots 3–5). Although all of the control plots are situated >40 m from the harvest edge within a large, contiguous tract of the undisturbed stand, there were notable differences in aboveground DWD volumes (23.1 m<sup>3</sup>·ha<sup>-1</sup> in plots 1–2 vs. 3.4 m<sup>3</sup>·ha<sup>-1</sup> in plots 3–5) and forest floor depth (10.9 cm in

plots 1–2 vs. 6.3 cm in plots 3–5) between the eastern and western plots that may have contributed to this split in the MRT.

The third split (9.16%) separated bladed plots from other harvested plots (Figs. 3b, 4b). Important species in this split include *Amaurobius borealis* (1.55%), *Pardosa moesta* (1.41%), and *P. xerampelina* (1.14%) (Table 3). All three of these species were more strongly associated with nonbladed sites (Fig. 4b). This appeared to be true for the vast majority of spider species (Fig. 4b). No species showed a clear preference for bladed plots (Fig. 4b).

### 3.4. Rove beetles

The rove beetle MRT had some similarities to the other MRTs in that harvest treatments split early from controls, the bladed treatment split from other harvest treatments, and the full-tree biomass and tree-length treatments did not split. The primary difference for rove beetles is that the OC split from all other treatments in the first split. The total variance explained by this regression tree is 71.52% (Table 4). The most important species were *Atheta capsularis* (13.99%), *Atheta strigosula* (8.94%), *Lordithon fungicola* (7.97%), *Oxypoda grandipennis* (6.99%), *Atheta remulsa* (4.53%), and *Aleochara fumata* (3.37%) (Table 4). The first split of the tree explained 57.73% of variance with all of the above species being important except for *Aleochara fumata* (Table 4; Figs. 3c, 4c). In this split, the vast majority of species and individuals were associated with the OC; very few individuals were captured in the other six treatments (Fig. 4c). Of the 1231 individuals captured, 745 were captured in the five OC plots, whereas only 486 were captured in all plots of the other six treatments combined. Only two species were associated with the other treatments, including *Aleochara fumata* (0.32%) and *Mycetoporus consors* (0.70%) (Table 4). In the second split, fire and the YC treatment separated from the harvest treatments in a similar fashion to carabid beetles and spiders (Fig. 3c). The fourth split separated the bladed treatment from the other harvest treatments, which was also consistent with the other two taxa (Fig. 3c). The OC treatment plots do split into northern (plots 1–3) and southern (plots 4 and 5) plots. In this case, the southern plots had greater amounts of buried deadwood (39.9 m<sup>3</sup>·ha<sup>-1</sup> in plots 4–5 vs. 10.2 m<sup>3</sup>·ha<sup>-1</sup> in plots 1–3) and greater amounts of aboveground DWD in larger (>14 cm) diameter classes (34.2 m<sup>3</sup>·ha<sup>-1</sup> in plots 4–5 vs. 10.2 m<sup>3</sup>·ha<sup>-1</sup> in plots 1–3).

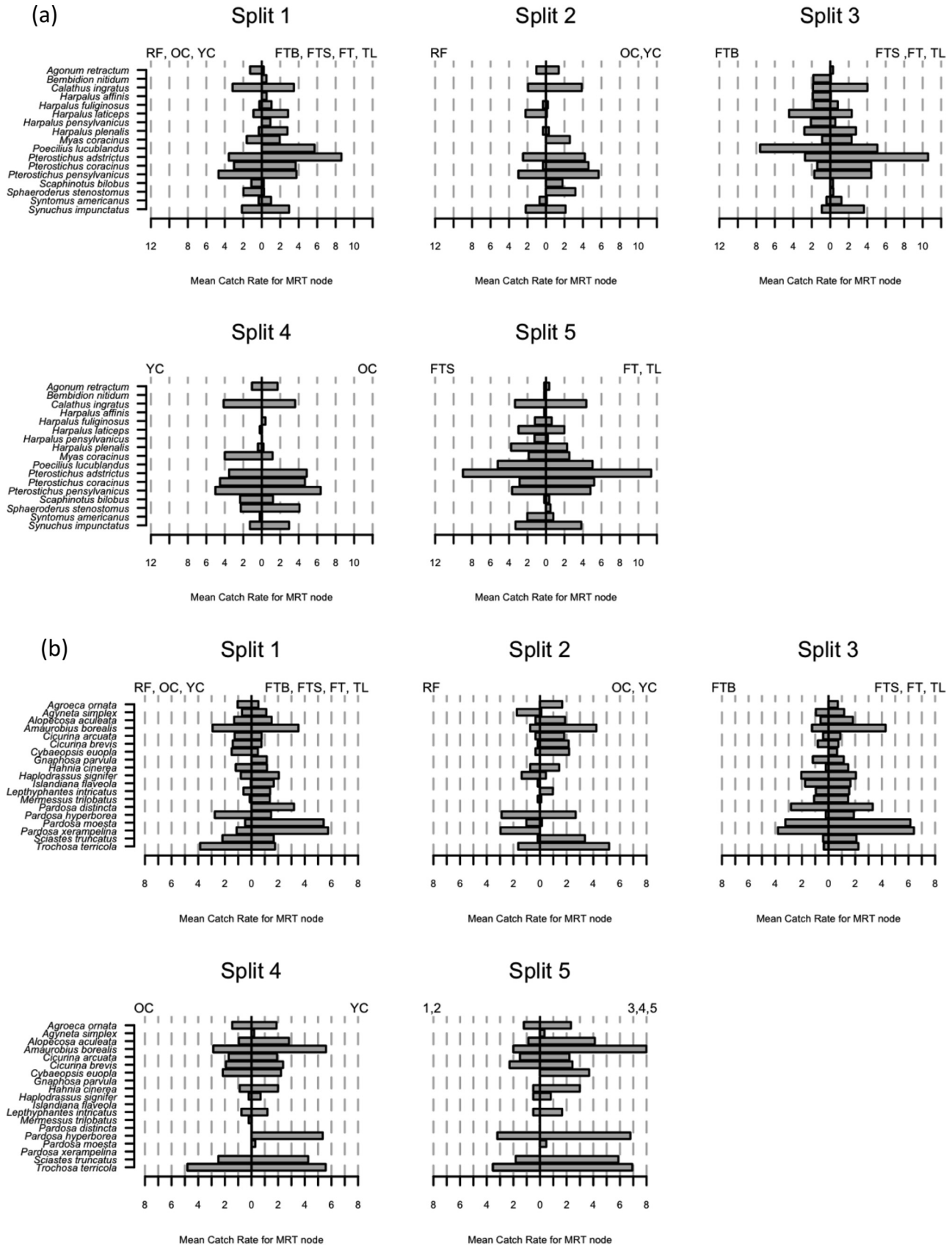
### 3.5. Environmental variables

The four harvest treatments showed a gradient of CWD from about 40 m<sup>3</sup>·ha<sup>-1</sup> in the tree-length treatment to no CWD in the bladed treatment. The OC treatment had by far the most CWD at about 70 m<sup>3</sup>·ha<sup>-1</sup>, whereas the YC treatment had very little CWD (~5 m<sup>3</sup>·ha<sup>-1</sup>), which was less than in the full-tree biomass harvest treatments. In contrast, the RF had similar CWD as the tree-length treatment (Fig. 5; Appendix Table A4). Overall, the mixed-effects model demonstrated significant differences in CWD between treatments (df = 6, F = 10.68, P < 0.0001), but Tukey multiple comparisons indicate that significant differences are primarily between the OC and other treatments, although the RF also showed some differences with the more intense harvest disturbances (Appendix Table A5).

Percent mineral soil exposure was measured as an indicator of forest floor disturbance (Fig. 6; Appendix Table A4). Mineral soil exposure showed a strong gradient from little or no disturbance in the OC and YC, some minimal disturbance in the RF, and increasing mineral soil exposure from tree-length treatment plots (~15% exposure) to the bladed treatment plots (90% exposure) (mixed-effects model: df = 6, F = 162.93, P < 0.0001; Fig. 6). Tukey multiple comparisons found significant differences between all treatments except the controls (OC, YC, RF) and between full-tree biomass and tree-length (stem-only) harvests (FT–SO) (Appendix Table A5).

We examined the daily mean temperatures at the organic soil–mineral soil interface, at 10 cm below the soil surface, and the

Fig. 4. Relative abundance of individual species for each MRT split for (a) carabid beetles, (b) spiders, and (c) rove beetles. OC, old control; YC, young control; RF, recent fire; TL, tree-length; FT, full-tree biomass; FTS, full-tree stumped; FTB, full-tree bladed.



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Fig. 4 (concluded).

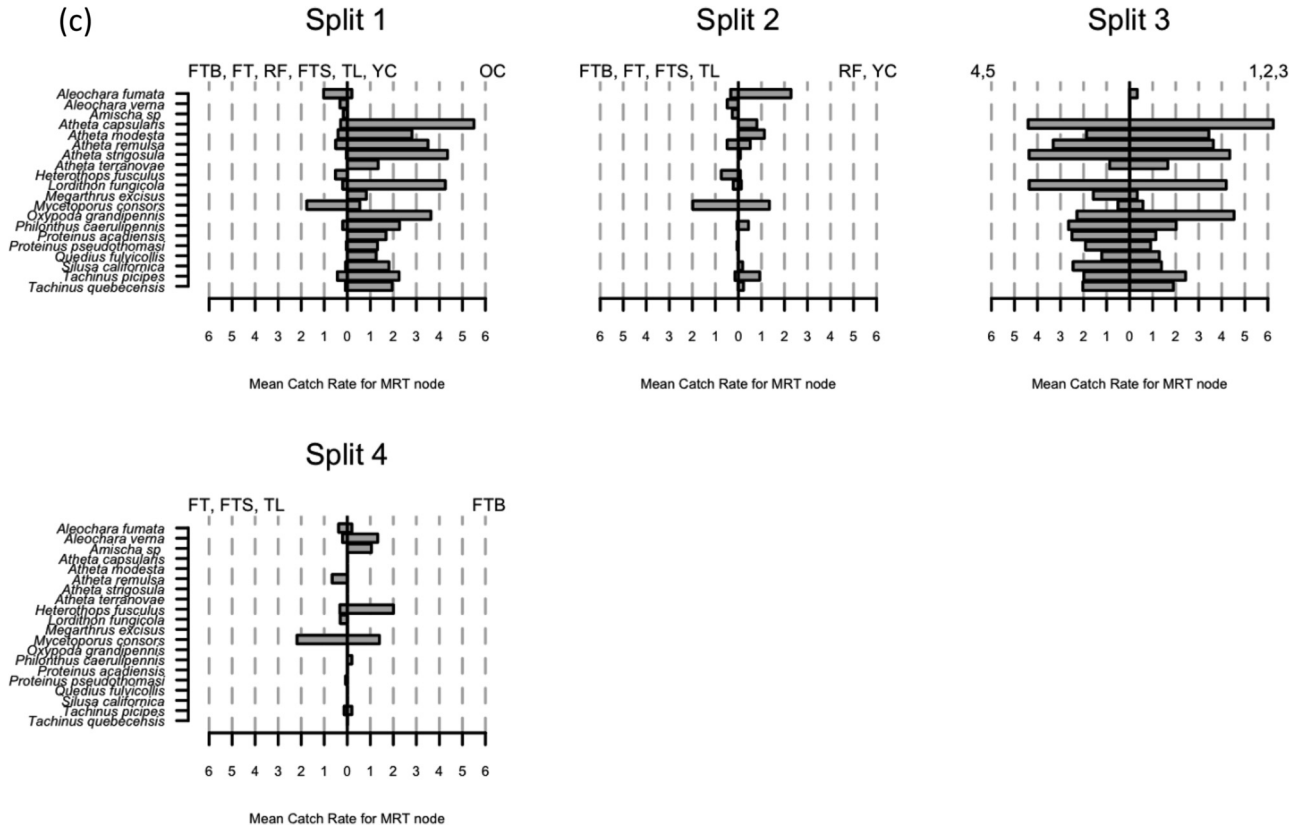


Table 3. Spider individual species variances by split within the ssMRT, total tree variance, and total variance explained for the multivariate regression tree.

Species	Split 1	Split 2	Split 3	Split 4	Split 5	Tree total	Species total
<i>Agroeca ornata</i>	0.107	0.461	0.080	0.020	0.066	0.734	1.144
<i>Agyreta simplex</i>	0.063	0.443	0.008	0.004	0.006	0.525	0.962
<i>Alopecosa aculeata</i>	0.019	0.399	0.251	0.388	0.563	1.621	2.272
<i>Amaurobion borealis</i>	0.143	2.036	1.549	0.826	1.914	6.468	7.632
<i>Cicurina arcuata</i>	0.098	0.366	0.038	0.005	0.027	0.534	0.947
<i>Cicurina brevis</i>	0.170	0.654	0.001	0.023	0.001	0.849	1.469
<i>Cybaeopsis euopla</i>	0.402	0.569	0.068	0.000	0.725	1.765	2.356
<i>Gnaphosa parvula</i>	0.521	0.000	0.000	0.000	0.000	0.521	0.905
<i>Hahnina cinerea</i>	0.000	0.082	0.274	0.137	0.331	0.824	1.732
<i>Haplodrassus signifer</i>	0.627	0.145	0.000	0.026	0.005	0.803	1.511
<i>Islandiana flaveola</i>	1.023	0.005	0.002	0.000	0.000	1.030	1.559
<i>Leptyphantes intricatus</i>	0.247	0.157	0.060	0.022	0.071	0.558	1.273
<i>Mermessus trilobatus</i>	0.619	0.001	0.026	0.004	0.000	0.650	1.101
<i>Pardosa distincta</i>	4.027	0.000	0.043	0.000	0.000	4.070	5.013
<i>Pardosa hyperborea</i>	0.646	0.007	0.481	3.179	0.688	5.001	7.111
<i>Pardosa moesta</i>	9.659	0.130	1.413	0.009	0.012	11.223	15.467
<i>Pardosa xerampelina</i>	8.519	1.464	1.138	0.000	0.000	11.122	13.897
<i>Sciastes truncatus</i>	0.101	1.715	0.475	0.348	0.879	3.518	4.148
<i>Trochosa terricola</i>	1.725	2.109	0.598	0.065	0.614	5.111	5.890
Less common species (99)	1.807	1.239	2.659	0.695	0.629	7.029	23.614
Total	30.523	11.982	9.164	5.755	6.532	63.956	100.000

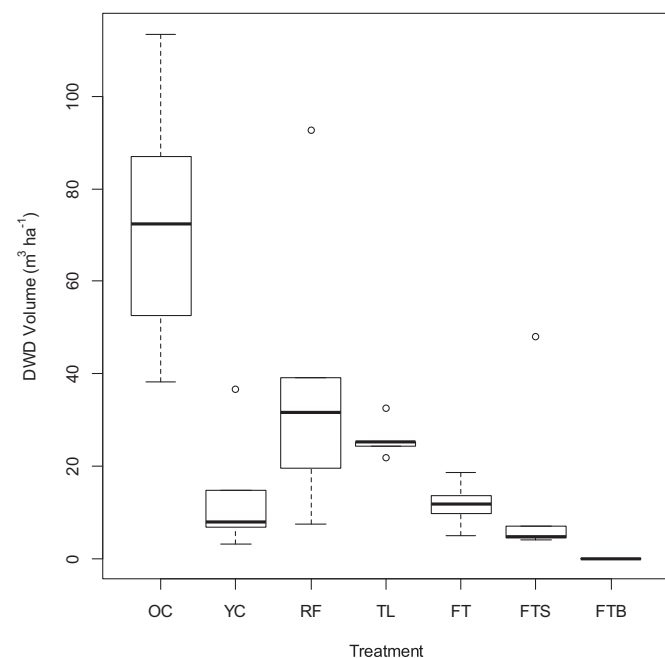
moisture at 10 cm below the soil surface (Figs. 7a–7c), as well as the air temperature at 15 cm and the daily range in soil temperature at 10 cm below soil surface. For mineral soil temperature, it was clear that the OC and YC were generally cooler than the other treatments through most of the frost-free season, particularly during the arthropod collection period. Later in the season, the treatments became more similar. The fire and the three least disturbed

harvest treatments showed a similar pattern to one another. The bladed plot was much warmer than all other treatments throughout the arthropod collection period. Early in the season, the bladed plot was as much as 12 °C warmer. By the end of the sampling period (Julian day 231), the difference was closer to 2 °C (Fig. 7b). The air temperatures were highly variable over the short term (8 to 10 °C variation over 5-day span) but very similar be-

**Table 4.** Rove beetle individual species variances by split within the ssMRT, total tree variance, and total variance explained for the multivariate regression tree.

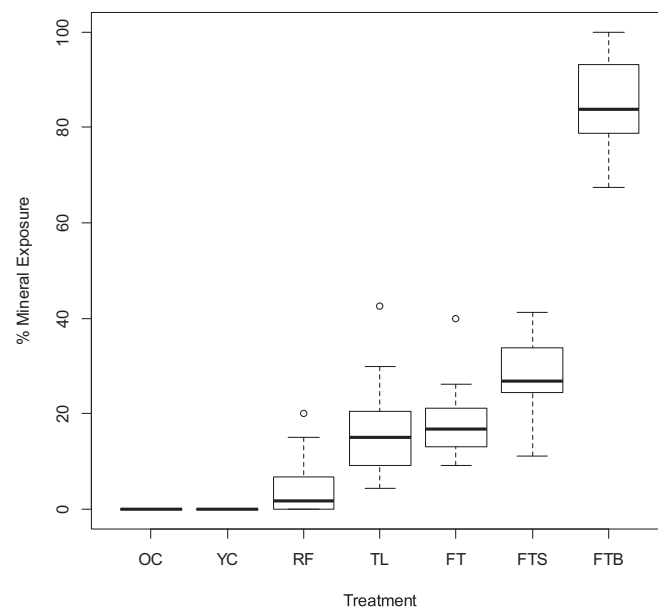
	Split 1	Split 2	Split 3	Split 4	Tree total	Species total
<i>Aleochara fumata</i>	0.324	3.021	0.015	0.012	3.372	5.486
<i>Aleochara verna</i>	0.046	0.182	0.000	0.525	0.754	1.272
<i>Amscha</i> sp.	0.014	0.054	0.000	0.459	0.527	0.694
<i>Atheta capsularis</i>	13.031	0.509	0.451	0.000	13.991	14.720
<i>Atheta modesta</i>	2.779	1.005	0.330	0.000	4.114	4.622
<i>Atheta remulsa</i>	4.339	0.001	0.014	0.175	4.529	6.553
<i>Atheta strigosula</i>	8.934	0.007	0.000	0.000	8.941	9.078
<i>Atheta terranova</i>	0.860	0.000	0.083	0.000	0.943	1.196
<i>Heterothops fusculus</i>	0.124	0.331	0.000	1.193	1.648	2.458
<i>Lordithon fungicola</i>	7.926	0.007	0.003	0.037	7.973	8.843
<i>Megarthus excisus</i>	0.329	0.000	0.205	0.000	0.535	0.614
<i>Mycetoporus consors</i>	0.700	0.323	0.001	0.256	1.280	3.033
<i>Oxyopoda grandipennis</i>	6.316	0.000	0.677	0.000	6.993	7.213
<i>Philonthus caerulipennis</i>	2.077	0.119	0.052	0.017	2.265	2.870
<i>Proteinus acadensis</i>	1.356	0.000	0.248	0.000	1.604	2.117
<i>Proteinus pseudothomasi</i>	0.785	0.002	0.134	0.002	0.923	1.381
<i>Quedius fulvicollis</i>	0.755	0.000	0.001	0.000	0.756	1.102
<i>Silusa californica</i>	1.458	0.026	0.152	0.000	1.636	1.848
<i>Tachinus picipes</i>	1.595	0.476	0.026	0.002	2.100	4.049
<i>Tachinus quebecensis</i>	1.682	0.038	0.002	0.000	1.723	2.100
Less common species (50)	2.297	0.844	0.979	0.797	4.917	18.752
Total	57.725	6.945	3.374	3.475	71.520	100.000

**Fig. 5.** Aboveground coarse woody debris (CWD) volume by treatment. The line in the boxplot references the median value, the box encompasses the interquartile range from the first to third quartile, and the whiskers account for 1.5 times the interquartile range below and above the first and third quartiles, respectively. Open circles beyond the whiskers are individual data points that are suspected outliers.



tween treatments (data not shown), and soil temperatures in bladed plots were more variable within days (data not shown) and over short time frames (up to 5 °C over 5 days for bladed plots vs. 1–2 °C over 5 days for other treatments; Fig. 7b). Patterns between treatments for forest floor temperature were similar to 10 cm below soil surface but our data exclude the bladed plots because

**Fig. 6.** Mineral exposure by each treatment. The line in the boxplot references the median value, the box encompasses the interquartile range from the first to third quartile, and the whiskers account for 1.5 times the interquartile range below and above the first and third quartiles, respectively. Open circles beyond the whiskers are individual data points that are suspected outliers.



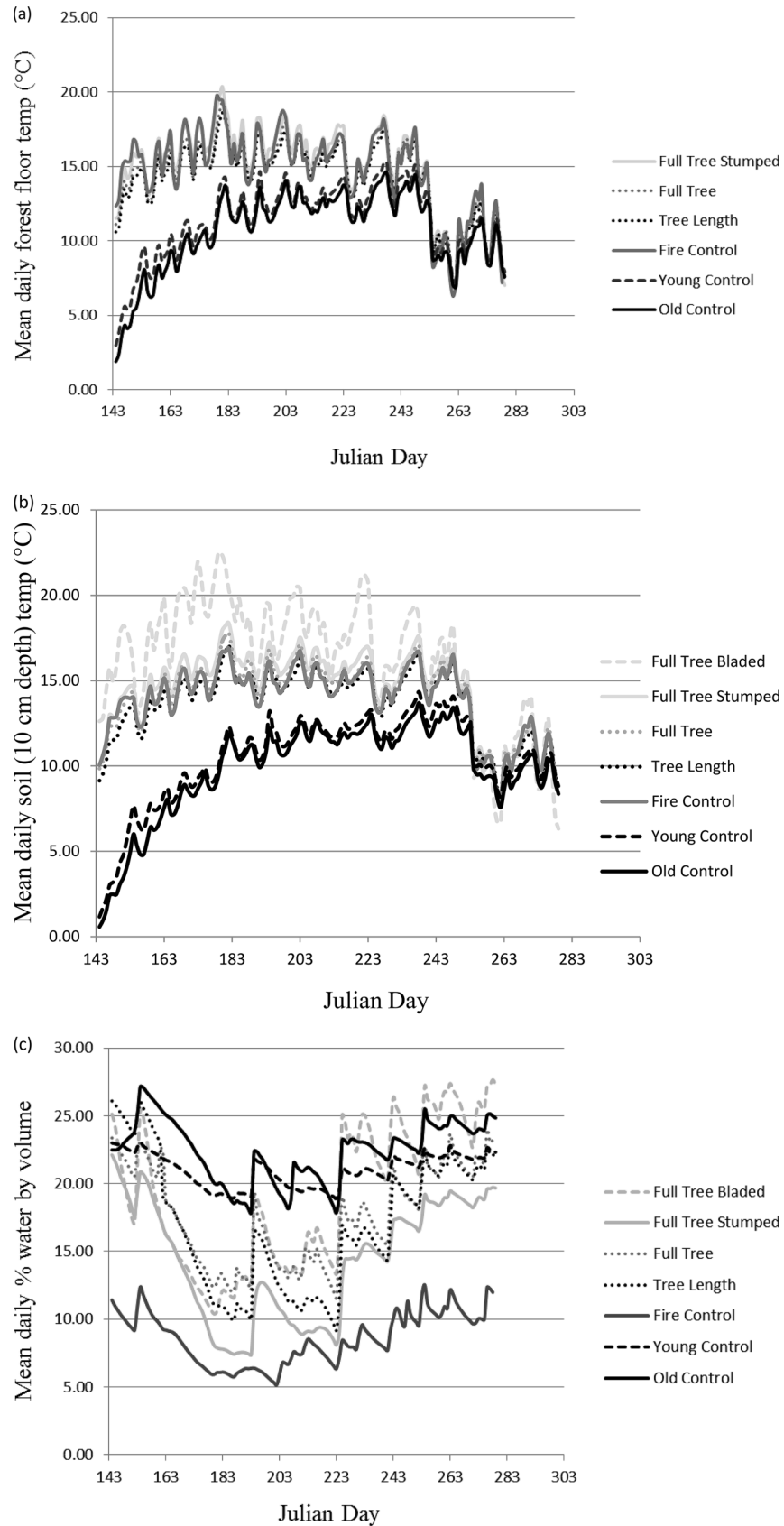
there was no organic–mineral soil interface to place the probe. Soil moisture patterns were quite different from temperature. The fire plot was much drier than all other treatments (up to 15% lower in water by volume relative to OC and YC and between 1% and 10% lower relative to harvest treatments depending on time of season). Generally, the OC and YC remained moister than the harvested plots from the middle of June through to the middle of September (sometimes by as much as 10% or as little as 1%).

## 4. Discussion

### 4.1. General overview

All three taxa investigated in this study showed similarities in their responses to the seven treatments examined here, with some notable exceptions. All three taxa had communities that were more similar in the three controls (including fire) than in the harvested treatments, with increased forest floor disturbance in harvested plots being a possible explanation. Lack of similarity of arthropod communities between the RF and the harvest treatments suggests that natural disturbance emulation could be improved and confirms the first hypothesis that initial effects of harvesting differed from the initial effects of fire for these three taxonomic groups. Within our harvest treatments, tree-length and full-tree biomass harvest communities never differed in any of the three epigeic groups, whereas the most extreme bladed treatment was found to show the greatest differences between communities. This partially confirms the second hypothesis in that the increased level of disturbance associated with blading (all three taxa) and stumping (spiders and rove beetles) did generate significant differences in species composition; however, the full-tree treatment did not appear to have additional effects to the tree-length treatment. In addition, all three taxa had different communities in the older (92 years) fire-origin plots compared with the younger (51 years) harvest-origin plots, suggesting that communities had not yet recovered from the original harvest disturbance possibly due to a lower volume of CWD in the younger harvest-origin stand. This was contrary to our third hypothesis that suggested that once the overstory returned (younger harvest-origin

**Fig. 7.** Microclimate variables plotted from 24 May (Julian day 144) to 6 October 2014 (Julian day 279): (a) mean daily soil temperature at soil surface (no values for bladed plots because the organic soil layer was removed), (b) mean daily soil temperature at 10 cm below soil surface, and (c) mean daily soil moisture at 10 cm below soil surface. Legends are listed in order from highest to lowest level of disturbance.



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treatment), the faunal composition would recover. The uniqueness of older fire-origin stands was most pronounced in the rove beetle communities in which the majority of individuals were found in the older fire-origin stands.

#### 4.2. Clearcutting and fire effects on epigeic assemblages

The primary split for both ground beetles and spiders in the MRT among the mature (92 years old), young (51 years old), and immediate postfire treatments as compared with the four harvested treatments confirms the first hypothesis of expected differences between harvest and fire impacts. This is not entirely consistent with evidence in the literature that points to removal of the overstory as a primary driver of epigeic community response (Buddle et al. 2006; Matveinen-Huju and Koivula 2008; Work et al. 2010, 2014; Paradis and Work 2011; Pinzon et al. 2013). In these studies, up to 35% of the variance was explained by overstory removal with large increases in open-habitat species (Work et al. 2014). Plots in the postfire treatment here had limited overstory (live, functioning green canopy) as did harvested plots, whereas OC and YC plots had a closed canopy. Postfire plots did have 1467 standing dead stems·ha<sup>-1</sup>, which may have offered some protection; however, an examination of the microclimate, which is expected to be influenced primarily by overstory, indicates that postfire plots are more similar to harvested plots with no overstory than to control plots with closed live-tree canopies, suggesting that microclimate (and overstory) does not explain this first split.

One argument that may explain the first split is the forest floor disturbance gradient. Several studies have demonstrated the impact of forest floor disturbance on epigeic community change, but many are confounded with other aspects of forest management (Huhta 1971; Buddle et al. 2000). Siira-Pietikäinen et al. (2003) examined a series of forest management treatments followed in some cases by harrowing (similar to disc trenching). In their study, gap felling followed by harrowing reduced the number of soil macroarthropod predators, whereas gap felling without harrowing had no effects on predators, suggesting that harrowing had an impact on community response. Klimaszewski et al. (2005) also showed some limited evidence for an effect of site preparation (in the form of exposing mineral soil by lightly raking a backhoe bucket across the forest organic layer) on carabid beetle communities, with improved habitat for open-habitat species (Klimaszewski et al. 2005). This form of site preparation is less intense than disc trenching and may therefore have less impact.

In our study, the OC, YC, and RF treatments all had the least amount of mineral soil exposure relative to the four harvested treatments. This is a good fit with the first split of the MRT for carabids and spiders. In fact, the mineral soil exposure provides a good estimate of a general disturbance intensity measure, with treatments ranging from least disturbed to most disturbed: OC, YC, RF, tree-length, full-tree biomass, stumped, and bladed. In our RF treatment, the fire did not expose much of the mineral layer and this would definitely be the low end of the forest floor disturbance gradient for postfire sites. The evidence from this first split (second split for Staphylinidae) is that none of the harvest options that we conducted is a good emulation for our postfire site. Fire intensity can be highly variable with evidence of large variations in soil burn severity measured as soil organic layer consumption, degree of mineral soil exposure, and mean duff layer thickness (Johnstone and Kasischke 2005), so it would be unfair to generalize entirely from our limited sample. There is a need to better understand the variation in fire severity at local, landscape, and regional scales in terms of forest floor disturbance because it is an important factor in epigeic biodiversity (Holliday 1992; Niemela 1999) and critical to emulating natural disturbance (Nguyen-Xuan et al. 2000; Johnstone and Kasischke 2005). Furthermore, natural disturbance emulation needs to consider more than tree species composition and spatial pattern to capture a full range of biodi-

versity responses. Forest fires often expose mineral soil but they do not achieve the kind of soil disturbance associated with mechanical site preparation (disc trenching), stumping, or blading.

Other researchers have come to similar conclusions about the importance of forest floor disturbance but from a different perspective. It has been noted in the literature that ground arthropod succession following wildfires may be delayed relative to harvest due to the generally harsher impact of fire on forest floors than harvest (Holliday 1992; Niemela 1999; Buddle et al. 2006). In our case, the fire was a gentler disturbance than harvest and disc trenching and this resulted in the ground arthropod community in postfire sites being more similar to the reference conditions than to postharvest sites. Either way, the impact of fire on the forest floor should be measured and emulated to achieve sustainability and forest integrity (Angelstam 1997).

We also examined the amount of CWD as influencing community patterns. There is some evidence in the literature of species composition change due to effects of CWD on microclimate or as protection from predators (Pearce et al. 2003). Community composition in spiders (Castro and Wise 2009, 2010), carabid beetles (Ulyshen and Hanula 2009; Work et al. 2013, 2014), and Staphylinidae (Work et al. 2013) have been linked experimentally to changes in abundance of deadwood. However, it has also been suggested that deadwood may only become critical habitat for spiders and ground beetles after overstory removal (Work et al. 2014; Pearce et al. 2003) where downed deadwood buffers ground beetles from the increased temperature and reduced humidity that accompanies the removal of the overstory. However, an examination of the pattern of downed coarse wood in the different treatments suggests that this factor is not driving the first split because downed CWD is most abundant in the oldest control, the postfire treatment, and the tree-length treatment and notably very low in the YC, full-tree biomass, stumped, and bladed harvest treatments.

#### 4.3. Increasing levels of removal of residual biomass

To explore the second hypothesis that increasing levels of removal of residual biomass will further exacerbate differences in species composition through the compounded effects of loss of coarse wood and increasing soil disturbances, we examined the harvest side of the MRTs. In support of the second hypothesis, the communities in bladed plots were different from all other harvest treatments. This result could be a function of very high forest floor disturbance associated with bladed plots relative to other harvest plots or a function of no coarse wood on bladed plots. We are not able to separate the effects of these two potential factors with our data. Spiders and rove beetles do differ somewhat from ground beetles in that carabid beetle communities differ between stumped plots and the other harvested plots, whereas spider and rove beetle communities do not. This may be a function of carabid beetles having part of their life cycle under the soil surface (Lövei and Sunderland 1996), which is disturbed by the stumping process. Alternatively, carabid beetles could also just be more sensitive to the additional forest floor disturbance associated with stumping.

None of the communities in the three taxa examined differed between full-tree biomass and tree-length harvesting, suggesting that the intensification of removal associated with biomass harvesting for bioenergy does not cause a significant shift in epigeic communities, at least in the short term. This is an important result because full-tree biomass harvesting practices have been criticized as being too intense for the maintenance of sustainability. It remains to be seen if there are longer term implications of this type of harvesting to epigeic communities. In particular, there is a concern over changes in the long-term availability of deadwood that may be associated with more intense biomass removal (Berch et al. 2011). In response to this concern in Ontario, the most recent forest management guidelines (OMNR 2010) require the retention of 25 wildlife tree stems·ha<sup>-1</sup>. A wildlife tree

can include standing healthy, dead, or dying trees but is most often living. Ten of these stems must be large. In addition, guidelines require that there be 25 ha of residual forest within any 500 ha circle. These requirements were intentionally not met in our experiment but would improve the availability of deadwood over the long term and could help improve the time required for arthropod and other communities to recover from disturbance.

#### 4.4. Recovery of stands after harvest

We examined the third hypothesis by exploring the control side of the MRT, which is very similar for both carabid beetles and spiders. As expected, fire communities split first from the two controls probably due to loss of overstory and changes in associated microclimate (generally warmer and drier) but also perhaps due to altered soil chemistry from the chemical processes of fire (McRae et al. 2001). We are unable to separate out the effects of these factors with our current data. In all three taxa, the YC and OC show significant differences in community composition. It is significant and contrary to our third hypothesis that all three assemblages of taxa differ between the OC and YC because it is expected that communities in young forest stands will eventually converge with communities in old forest stands. This convergence has not yet happened in our YC plots and an understanding of when and if this will happen is key to predicting long-term impacts of harvest on biodiversity and sustainability (Venier et al. 2014). The split between OC and YC in all groups may be influenced by deadwood volumes, which are much higher in the OC than in the YC. None of the other measured environmental factors (overstory, microclimate, and forest floor disturbance) strongly differ between these two treatments. It is possible that community convergence in successional forest stands may therefore be predicted based on accumulated deadwood, an idea that could be tested in a chronosequence experiment. The pattern that rove beetles exhibited using MRT analysis is largely similar to both spiders and ground beetles in terms of the conclusions that we have drawn about our hypotheses; however, most of the rove beetle species were associated with the OC treatment and resulted in an initial split of the OC from all other treatments. The remaining MRT is similar in that the fire and YC communities differ from the harvest stands, the bladed harvest community differs from the other harvest treatment communities, and the stumped, tree-length, and full-tree communities do not split. These results have three implications. First, this suggests that rove beetle communities support the broad conclusions of the other groups. Second, this group could be a very useful indicator of old forest condition as several species are strongly associated with the old forest control. This is consistent with results from Buddle et al. (2006), which show that rove beetles recover more slowly after harvest disturbance than the other groups. Third, this species group is probably a less useful indicator of alternative harvest or other disturbance treatments than carabid beetles and spiders (Pearce and Venier 2006) due to lower species abundances and fewer species in disturbed plots. Response to loss of old forest and CWD may be due to the fungivorous nature of many rove beetles and the associated lower levels of wood decay fungi at lower deadwood levels (Stefani et al. 2016). An alternative explanation for the lack of convergence in the YC plots is the potential isolation of the YC plots from older forests that could provide immigration of older forest specialists. Mature jack pine forests are not common in a 50 km radius of the YCs and so insufficient dispersal of rove beetles may limit their ability to recover.

A caveat to all of our conclusions related to the control sites is that although we have demonstrated strong similarity in the tree species composition and soil characteristics of all of our sites, the control sites still exist as single sites separated by 10s of kilometres and so the potential for a geographic effect is present. We believe that the most parsimonious explanations for differences between controls are related to the large treatment effects related

to stand origin and time since disturbance, but we cannot statistically eliminate geographic effects. This is not an issue for the harvest treatments, which are laid out in a randomized block design.

#### 4.5. Species-specific responses

In terms of species-specific responses, only a few carabid species showed a strong affinity for the control treatments and included *Sphaeroderus stenostomus*, *Scaphinotus bilobus*, and *Agonum retractum*, all species known for their association with closed forest conditions (Buddle et al. 2006). These species showed an affinity for OC and YC over the RF. Only a few species showed an affinity for the OC over the YC (*Harpalus fuliginosus*, *Sphaeroderus stenostomus*, *Synuchus impunctatus*), but these species were still often found in the YC. Differences between YC and OC are an indication of lack of convergence, i.e., it is expected that communities in young forests will converge over time to become more similar to communities in old forests. The lack of complete convergence (the difference between communities in YC and OC) for beetles seems to be as much about species with affinity for young forests (i.e., *Myas coracinus*) as it is about old forest specialists being restricted to the OC. No spider species showed a strong affinity for OC over YC, suggesting that for spiders, there is not much concern over habitat supply for old forest specialists. Rove beetles tell a different story. Individual responses of rove beetles indicate that there are many old forest specialists such as *Atheta capsularis*, *A. stigosula*, and *Oxytropa grandipennis* that are found in only very small numbers or not at all in harvested, fire disturbed, or YC treatments.

We have focused this study on three taxa of epigeic fauna that have been demonstrated to act as good indicators of environmental change (Pearce and Venier 2006; Work et al. 2008; Klimaszewski et al. 2017), but we have not specifically examined saproxylic fauna that are directly dependant on the deadwood resource. Response of saproxylics is expected to be more directly related to quantity of deadwood, and deadwood volumes may provide a good surrogate for saproxylic abundance. Saproxylic sustainability may need to be managed at the landscape rather than stand scale.

## 5. Conclusions

Although the inference space is limited, we found that epigeic communities differed between fire and harvest disturbance immediately after disturbance. An examination of environmental factors suggests that an important driver of this difference could be related to forest floor disturbance or mineral soil exposure but is unlikely to be due to differences in microclimate. In our study, site preparation caused significant forest floor disturbance, unlike our fire treatment, which had low levels of mineral soil exposure. This draws attention to the need to include forest floor disturbance in any consideration of natural disturbance emulation and suggests that we need a good understanding about the range of forest floor disturbance precipitated by fire through the natural range of fire intensity.

Within our harvest treatments, the bladed treatment was found to show the greatest differences between communities of all three taxonomic groups, whereas tree-length and full-tree biomass harvest communities never differed in any of the three epigeic groups. This suggests that blading is a practice that is unlikely to be sustainable from an epigeic community perspective, and although it is not a current practice, it may reflect longer term impacts of repeated deadwood removal. It clearly demonstrates that there is a point at which forest disturbance will undermine biotic communities. The lack of differences between communities within full-tree biomass and tree-length treatments suggests that increased removals associated with full-tree biomass harvest beyond the tree-length alternative that has been promoted as more sustainable do not appear to be compromising the short-term epigeic biodiversity. Lack of a short-term effect, however,

does not preclude a longer term impact associated with loss of deadwood availability over time.

The epigeaic communities did differ between old (postfire) controls (92 years) and young postharvest controls (51 years), most strongly for rove beetles but also for ground beetles and spiders. The most obvious environmental difference between OC and YC sites was the amount of deadwood available and may have accounted for community differences. Mature forest communities of ground beetles and spiders are not composed of many unique old-growth species but do have compositions that are distinguishable from younger closed-canopy forest. Mature forest rove beetle communities are much more unique and contain many species that are very poorly represented in any of the other treatments, suggesting that old forest conditions are a more necessary element in the landscape for rove beetles.

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## Appendix A

**Table A1.** Carabid species list, abundance, and percent representation of all carabids.

Species	Abundance	Representation (%)
<i>Agonum cupripenne</i>	5	0.1
<i>Agonum retractum</i>	43	0.7
<i>Amara erratica</i>	4	0.1
<i>Badister obtustus</i>	1	0.0
<i>Bembidion nitidum</i>	18	0.3
<i>Bembidion quadrimaculata</i>	5	0.1
<i>Calathus ingratus</i>	470	7.9
<i>Calosoma calidum</i>	18	0.3
<i>Calosoma frigidum</i>	4	0.1
<i>Carabus serratus</i>	12	0.2
<i>Cymindis cribricollis</i>	8	0.1
<i>Dromius piceus</i>	1	0.0
<i>Harpalus affinis</i>	19	0.3
<i>Harpalus egregius</i>	2	0.0
<i>Harpalus fuliginosus</i>	38	0.6
<i>Harpalus fulvilabris</i>	28	0.5
<i>Harpalus laticeps</i>	230	3.9
<i>Harpalus megagephalus</i>	20	0.3
<i>Harpalus pensylvanicus</i>	36	0.6
<i>Harpalus plenalus</i>	209	3.5
<i>Harpalus</i> sp.	5	0.1
<i>Myas coracinus</i>	196	3.3
<i>Notiophilus aeneus</i>	4	0.1
<i>Platynus decentis</i>	11	0.2
<i>Poecilus lucublandus</i>	703	11.9
<i>Pterostichus adstrictus</i>	2002	33.8
<i>Pterostichus chalcites</i>	1	0.0
<i>Pterostichus coracinus</i>	592	10.0
<i>Pterostichus pensylvanicus</i>	725	12.2
<i>Pterostichus punctatissimus</i>	6	0.1
<i>Scaphinotus bilobus</i>	47	0.8
<i>Sphaeroderus stenostomus</i>	119	2.0
<i>Syntomus americanus</i>	41	0.7
<i>Synuchus impunctatus</i>	300	5.1

Appendix Tables A2–A5 appear on the following pages.

**Table A2.** Spider species list with abundance and percent representation of all spiders.

Species	Abundance	Representation (%)
<i>Agroeca ornata</i>	46	0.9
<i>Agyneta simplex</i>	53	1.1
<i>Alopecosa aculeata</i>	124	2.6
<i>Amaurobius borealis</i>	553	11.4
<i>Aphileta misera</i>	4	0.1
<i>Arctosa emertoni</i>	23	0.5
<i>Bassamiana utahensis</i>	1	0.0
<i>Bathyphanes pallidus</i>	5	0.1
<i>Callobius bennetti</i>	39	0.8
<i>Centromerus furcatus</i>	5	0.1
<i>Ceraticelus fissiceps</i>	2	0.0
<i>Ceraticelus laetabilis</i>	4	0.1
<i>Ceraticelus minutus</i>	6	0.1
<i>Ceraticelus similis</i>	1	0.0
<i>Ceratinella brunnea</i>	1	0.0
<i>Ceratinops crenatus</i>	4	0.1
<i>Cercidia prominens</i>	6	0.1
<i>Cicurina arcuata</i>	56	1.2
<i>Cicurina brevis</i>	72	1.5
<i>Clubiona bishopi</i>	2	0.0
<i>Clubiona canadensis</i>	1	0.0
<i>Clubiona kastoni</i>	7	0.1
<i>Clubiona kulczynskii</i>	6	0.1
<i>Crustulina sticta</i>	6	0.1
<i>Cryphoeca montana</i>	5	0.1
<i>Cybaeopsis euopla</i>	84	1.7
<i>Dictyna coloradensis</i>	3	0.1
<i>Diplocentria bidentata</i>	23	0.5
<i>Diplocentria retinax</i>	12	0.2
<i>Diplocephalus cristatus</i>	1	0.0
<i>Drassodes neglectus</i>	22	0.5
<i>Drassyllus niger</i>	2	0.0
<i>Erigone atra</i>	3	0.1
<i>Euryopis argentea</i>	3	0.1
<i>Evarcha hoyi</i>	8	0.2
<i>Floricomus plumalis</i>	2	0.0
<i>Gnaphosa muscorum</i>	35	0.7
<i>Gnaphosa parvula</i>	35	0.7
<i>Grammonota angusta</i>	1	0.0
<i>Habronattus waughii</i>	1	0.0
<i>Hahnina cinerea</i>	88	1.8
<i>Halorates plumosus</i>	2	0.0
<i>Haplodrassus eunis</i>	2	0.0
<i>Haplodrassus hiemalis</i>	10	0.2
<i>Haplodrassus signifer</i>	114	2.3
<i>Hogna frondicola</i>	17	0.3
<i>Hybauchenidium cymbadentatum</i>	1	0.0
<i>Hypselistes florens</i>	3	0.1
<i>Improphantes complicatus</i>	2	0.0
<i>Islandiana flaveola</i>	68	1.4
<i>Lathys pallida</i>	49	1.0
<i>Lepthyphantes intricatus</i>	68	1.4
<i>Mermessus maculatus</i>	21	0.4
<i>Mermessus trilobatus</i>	49	1.0
<i>Micaria aenea</i>	2	0.0
<i>Micaria pulicaria</i>	10	0.2
<i>Micrargus longitarsus</i>	2	0.0
<i>Neon nellii</i>	10	0.2
<i>Neriene radiata</i>	3	0.1
<i>Ostearius melanopygius</i>	1	0.0
<i>Ozyptila sincera canadensis</i>	8	0.2
<i>Pardosa concinna</i>	3	0.1
<i>Pardosa distincta</i>	226	4.6
<i>Pardosa fuscula</i>	1	0.0
<i>Pardosa hyperborea</i>	310	6.4

**Table A2 (concluded).**

Species	Abundance	Representation (%)
<i>Pardosa mackenziana</i>	31	0.6
<i>Pardosa milvina</i>	7	0.1
<i>Pardosa modica</i>	1	0.0
<i>Pardosa moesta</i>	721	14.8
<i>Pardosa xerampelina</i>	803	16.5
<i>Pelegrina flavipes</i>	3	0.1
<i>Philodromus imbecillus</i>	1	0.0
<i>Philodromus rufus</i>	7	0.1
<i>Phrurotimpus certus</i>	11	0.2
<i>Pirata canadensis</i>	1	0.0
<i>Pirata minutus</i>	5	0.1
<i>Pocadicnemis americana</i>	21	0.4
<i>Porrhomma terrestre</i>	3	0.1
<i>Robertus fuscus</i>	1	0.0
<i>Robertus riparius</i>	25	0.5
<i>Rugathodes aurantius</i>	1	0.0
<i>Sciastes truncatus</i>	222	4.6
<i>Scotinella pugnata</i>	1	0.0
<i>Scotinotylus pallidus</i>	4	0.1
<i>Scyletria inflata</i>	1	0.0
<i>Sibianor aemulus</i>	3	0.1
<i>Sisicottus montanus</i>	1	0.0
<i>Souessa spinifera</i>	2	0.0
<i>Steatoda albomaculata</i>	10	0.2
<i>Styloctetor stativus</i>	2	0.0
<i>Tapinocyba minuta</i>	30	0.6
<i>Tapinocyba simplex</i>	11	0.2
<i>Tennesseellum formicium</i>	7	0.1
<i>Tenuiphantes zebra</i>	5	0.1
<i>Tetragnatha laboriosa</i>	1	0.0
<i>Thanatus formicinus</i>	12	0.2
<i>Thanatus striatus</i>	2	0.0
<i>Theonoe stridula</i>	5	0.1
<i>Trochosa terricola</i>	394	8.1
<i>Tunagyna debilis</i>	7	0.1
<i>Tutelina similis</i>	2	0.0
<i>Walckenaeria castanea</i>	2	0.0
<i>Walckenaeria communis</i>	1	0.0
<i>Walckenaeria digitata</i>	14	0.3
<i>Walckenaeria directa</i>	6	0.1
<i>Walckenaeria exigua</i>	8	0.2
<i>Walckenaeria spiralis</i>	2	0.0
<i>Xysticus canadensis</i>	1	0.0
<i>Xysticus discursans</i>	2	0.0
<i>Xysticus elegans</i>	14	0.3
<i>Xysticus emertoni</i>	4	0.1
<i>Xysticus luctuosus</i>	3	0.1
<i>Xysticus montanensis</i>	10	0.2
<i>Xysticus obscurus</i>	12	0.2
<i>Xysticus punctatus</i>	2	0.0
<i>Xysticus triguttatus</i>	5	0.1
<i>Zelotes fratris</i>	64	1.3
<i>Zelotes puritanus</i>	10	0.2



**Table A3.** Staphylinidae species list with total abundance and percent representation of all rove beetles.

Species	Abundance	Representation (%)
<i>Achenomorphus corticinus</i>	1	0.1
<i>Acidota crenata</i>	3	0.2
<i>Acidota subcarinata</i>	12	1.0
<i>Aleochara fumata</i>	79	6.4
<i>Aleochara verna</i>	14	1.1
<i>Amischa</i> sp.	7	0.6
<i>Atheta brunswickensis</i>	5	0.4
<i>Atheta capsularis</i>	169	13.7
<i>Atheta dadopora</i>	7	0.6
<i>Atheta frosti</i>	7	0.6
<i>Atheta modesta</i>	61	5.0
<i>Atheta pennsylvanica</i>	20	1.6
<i>Atheta pseudosubtilis</i>	11	0.9
<i>Atheta remulsa</i>	89	7.2
<i>Atheta</i> sp.	4	0.3
<i>Atheta strigosula</i>	96	7.8
<i>Atheta terranova</i>	12	1.0
<i>Atheta ventricosa</i>	1	0.1
<i>Athetini</i> sp.	6	0.5
<i>Bolitobius cingulatus</i>	2	0.2
<i>Byroporus rufescens</i>	1	0.1
<i>Carphacis nepigonensis</i>	3	0.2
<i>Dinaraea pacei</i>	1	0.1
<i>Eusphalerum pothos</i>	6	0.5
<i>Gabrius microphthalmus</i>	15	1.2
<i>Heterothops fuscus</i>	29	2.4
<i>Heterothops minor</i>	1	0.1
<i>Heterothops</i> sp.	3	0.2
<i>Ischnosoma fimbriatum</i>	4	0.3
<i>Ischnosoma pictum</i>	7	0.6
<i>Lathrobium washingtoni</i>	3	0.2
<i>Leptusa brevicollis</i>	1	0.1
<i>Liogluta granulosa</i>	2	0.2
<i>Lordithon facilis</i>	3	0.2
<i>Lordithon fungicola</i>	100	8.1
<i>Megarthus excisus</i>	6	0.5
<i>Mycetoporus consors</i>	118	9.6
<i>Mycetoporus</i> sp.	2	0.2
<i>Nitidulidae</i> sp.	1	0.1
<i>Omalium</i> sp.	4	0.3
<i>Ontholestes cingulatus</i>	1	0.1
<i>Oxypoda convergens</i>	2	0.2
<i>Oxypoda grandipennis</i>	74	6.0
<i>Oxypoda orbicollis</i>	1	0.1
<i>Oxypoda pseudolacustris</i>	3	0.2
<i>Oxyporus vittatus</i>	1	0.1
<i>Paederus littorarius</i>	1	0.1
<i>Philonthus caerulipennis</i>	34	2.8
<i>Philonthus couleensis</i>	1	0.1
<i>Proteinus acadensis</i>	21	1.7
<i>Proteinus parvulus</i>	1	0.1
<i>Proteinus pseudothomasi</i>	14	1.1
<i>Pseudopsis subulata</i>	2	0.2
<i>Quedi</i> sp.	11	0.9
<i>Quedi</i> sp.	15	1.2
<i>Quedi</i> sp.	2	0.2
<i>Silusa californica</i>	20	1.6
<i>Silusida marginella</i>	6	0.5
<i>Stenus</i> sp.	3	0.2
<i>Strophogastra penicillata</i>	1	0.1
<i>Tachinus addendus</i>	3	0.2
<i>Tachinus fumipennis</i>	1	0.1
<i>Tachinus luridus</i>	3	0.2
<i>Tachinus memnonius</i>	5	0.4
<i>Tachinus picipes</i>	53	4.3
<i>Tachinus quebecensis</i>	23	1.9
<i>Tachyporus dispar</i>	10	0.8
<i>Tachyporus nitidulus</i>	1	0.1
<i>Tympanophorus puncticollis</i>	1	0.1
<i>Zyras obliquus</i>	1	0.1

**Table A4.** Mean (standard error) values for environmental variables.

Variable	Old control (OC)	Young control (YC)	Recent fire (RF)	Stem-only (SO)	Full-tree (FT)	Full-tree stumped (FTS)	Full-tree bladed (FTB)
Total CWD (m <sup>3</sup> ·ha <sup>-1</sup> )	72.72 (13.13)	9.82 (6.52)	36.16 (14.21)	17.02 (0.72)	9.74 (2.03)	4.46 (1.73)	0.00 (0.00)
Soil exposure (%)	0.00 (0.00)	0.00 (0.00)	5.14 (2.58)	16.30 (3.26)	17.92 (2.01)	27.94 (2.34)	85.74 (3.75)

Note: CWD, coarse woody debris.

**Table A5.** Tukey multiple comparisons of treatments for total coarse woody debris (CWD) and mineral soil exposure.

Treatment comparison	Total CWD		Mineral soil exposure	
	z value	P value	z value	P value
OC–YC	5.712	0.001	0.000	1.000
OC–RF	3.320	0.016	1.547	0.716
OC–SO	5.058	0.001	-4.904	<0.001
OC–FT	5.719	0.001	-5.392	<0.001
OC–FTS	6.199	0.001	-8.407	<0.001
OC–FTB	6.604	0.001	-25.798	<0.001
YC–RF	-2.392	0.202	-1.547	0.716
YC–SO	0.654	0.995	-4.904	<0.001
YC–FT	0.007	1.000	-5.392	<0.001
YC–FTS	0.487	0.999	-8.407	<0.001
YC–FTB	0.892	0.974	-25.798	<0.001
RF–SO	1.738	0.590	-3.358	0.014
RF–FT	2.399	0.199	-3.845	0.002
RF–FTS	2.879	0.061	-6.860	<0.001
RF–FTB	3.284	0.018	-24.251	<0.001
SO–FT	0.661	0.995	-0.487	0.999
SO–FTS	1.141	0.916	-3.502	0.008
SO–FTB	1.546	0.717	-20.893	<0.001
FT–FTS	0.479	0.999	-3.015	0.041
FT–FTB	0.884	0.975	-20.406	<0.001
FTS–FTB	0.405	1.000	-17.391	<0.001

Note: OC, old control; YC, young control; RF, recent fire; SO, stem only; FT, full-tree; FTS, full-tree stumped; FTB, full-tree bladed.