Canadian Journal of Forest Research
Revue canadienne de recherche forestière

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

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2017-0145.R1
Manuscript Type:	Article
Date Submitted by the Author:	04-Aug-2017
Complete List of Authors:	Venier, Lisa; Natural Resources Canada, Canadian Forest Service Work, Timothy; Département des Sciences Biologiques, Département des Sciences Biologiques Klimaszewski, Jan; Natural Resources Canada, Canadian Forest Service Morris, Dave; Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research Bowden, Joseph; Natural Resources Canada, Canadian Forest Service Kwiaton, Martin; Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research Webster, Kara; Natural Resources Canada, Canadian Forest Service Hazlett, Paul; Natural Resources Canada, Canadian Forest Service
Keyword:	natural disturbance emulation, ecosystem management, carabid beetle, rove beetle, ground spider
Is the invited manuscript for consideration in a Special Issue? :	N/A

SCHOLARONE™
Manuscripts

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

Venier, L. A.^a Work, T.T.^b, Klimaszewski, J.^c, Morris, D.M.^d, Bowden, J.^e, Kwiaton, M.M.^f, Webster, K.^g,
Hazlett, P.^h

^a Corresponding author. Canadian Forest Service, Natural Resources Canada, Great Lakes Forestry
Centre, 1219 Queen St. E. Sault Ste. Marie, Ontario, P6A 2E5, Canada, lisa.venier@canada.ca

^b Département des Sciences Biologiques, Université de Québec à Montréal, C.P. 8888, Succursale
Centre-ville, Montréal, Québec, H3P 3P8, Canada, work.timothy@uqam.ca

^c Canadian Forest Service, Natural Resources Canada, Laurentian Forestry Centre, 1055 Ave du P.E.P.S.,
P.O. Box 10380, Stn. Sainte-Foy, Quebec, Quebec, Canada, G1V 4C7, jan.klimaszewski@canada.ca

^d Centre for Northern Forest Ecosystem Research, 421 James St. South, Thunder Bay, Ontario, P7E 2V6,
Canada, dave.m.morris@ontario.ca

^e Canadian Forest Service, Natural Resources Canada, Atlantic Forestry Centre, Corner Brook Office, P.O.
Box 960, 26 University Drive, Corner Brook, NL, Canada, A2H 6J3, joseph.bowden@canada.ca

^f Centre for Northern Forest Ecosystem Research, 421 James St. South, Thunder Bay, Ontario, P7E 2V6,
Canada, martin.kwiaton@ontario.ca

24

25 ^g Canadian Forest Service, Natural Resources Canada, Great Lakes Forestry Centre, 1219 Queen St. E.

26 Sault Ste. Marie, Ontario, P6A 2E5, Canada, kara.webster@canada.ca

27

28 ^h Canadian Forest Service, Natural Resources Canada, Great Lakes Forestry Centre, 1219 Queen St. E.

29 Sault Ste. Marie, Ontario, P6A 2E5, Canada, paul.hazlett@canada.ca

30

31

Draft

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 northcentral Ontario (47° 42' N, 83° 36' W) in jack pine dominated stands in 2013 using pitfall trapping. Using 222 species (12, 015 individuals), we compared effects of disturbance using recently burned (3 years post-fire) and clearcut sites (3-years post-harvest; tree-length, full-tree, stump removal and blading) as well as older, closed-canopy stands that have regenerated following clearcutting (51 years post-harvest) and fire (92 years post-fire), with multivariate regression trees. Taxa were more similar in the three controls (including recent fire) than to harvested 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 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 epigaeic communities.

Keywords: natural disturbance emulation, ecosystem management, carabid beetle, rove beetle, ground spider.

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 to biodiversity under fire disturbance and in mature forest 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 where overstory mortality and exposure of mineral soil typically increase with fire severity (Weber et al. 1987, Greene et al. 2004) and where deadwood is initially abundant post-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 (ie. branches, tops, stumps) with 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 (OMNR 2013), empirical comparisons of resident biodiversity following both clearcutting and fire in jack pine have been limited to longer-term responses of bryophytes, vascular plants (Reich et al. 2001) and initial responses of moths post-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 post 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, 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 for plants and organisms that rely directly on plants, clearcutting may indeed sufficiently emulate fire in jack pine stands.

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 site 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). Post-harvest 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 post-harvest (Work et al. 2014). However, these impacts of biomass removal have yet to be verified in part due 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 post-harvest) impacts of clearcutting with increasing levels of biomass removal and the longer-term (51 years post-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 that (1) the initial effects of clearcutting on epigaeic assemblages will differ from the initial

impacts of wildfire, (2) that increasing removal of residual biomass will further exacerbate differences in species composition through the compounded effects of loss of coarse wood and increasing soil disturbances, and (3) 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 a) harvested plots in a clearcut (2.5 years post-harvest) and unharvested plots in a 51-year old jack pine stand (Young Control) which was previously clearcut and 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), b) a recent fire (Recent Fire; 3 years post-fire) located near Ripple Lake, Ontario (47° 56' N, 84° 09' W) and c) a 92-year old jack pine stand (Old Control) of pyrogenic origin (47° 38' N, 83° 15' W) (Figure 1). Mean annual temperature and precipitation for the area is 1.7°C and 797 mm (532 mm of rainfall and 277 cm of snowfall), respectively (Environment Canada 2013). These three jack pine-dominated stands (>90% jack pine, based on live tree basal area) all established on glaciofluvial, coarse-textured, glacial outwash deposits characterized by sandy (medium sand) parent material overtopped with a variable depth loess (windblown) cap of finer textured soil (silty fine sand to silt loam) (Table 1). The forest floor was thinner at the recently burned site (5.4 cm) compared to 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 Recent Fire plantation compared to the other sites as it was a younger stand (30-yr-old) at the time of the fire.

The fire did result in much higher amounts of standing dead trees ($107.4 \text{ m}^3 \text{ ha}^{-1}$) and moderate levels of DWD ($41.6 \text{ m}^3 \text{ ha}^{-1}$), measured three years after the fire. The Old Control (OC) site had moderate levels of standing dead volume ($37.9 \text{ m}^3 \text{ ha}^{-1}$) and much higher volumes of DWD ($76 \text{ m}^3 \text{ ha}^{-1}$) compared to the low levels of dead wood in the Young Control (YC) at Island Lake, as the Old Control 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 dead wood at the Island Lake site, a legacy of the previous tree length harvest done in 1959. In general these stands are very comparable; having 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 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 delimbed, 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 delimbed outside experimental plots; (3) Stump removal (FTS) where bole and branches were removed as per full-tree 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 harvest and stumps, residual coarse woody material and the forest floor were removed with a excavator fitted with large metal blade. The tree-length harvest, full-tree harvest and stump removal treatments were all site prepared post-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 and linear piles of mixed organic and mineral soil beside the trenches (spoils). Each experimental treatment was replicated 5 times and each experimental plot was 70 x 70 m (0.49 ha). Experimental plots were separated by at least 20 m from each other and the surrounding uncut forest. Associated with these experimental plots are 5 sampling plots (70 x 70 m) located directly adjacent to the harvested area in the same stand originated from clearcutting 51 years ago (Young Control = 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 Young Control (YC) to those collected from two locations that had been disturbed by wildfire. The first location was a recent wildfire 55km north-west of the Island Lake Biomass Harvest Experiment (Recent Fire). Prior to burning, this 20 ha stand was a 30 year-old monoculture jack pine stand that originated from clearcutting, seeding and planting. In spring of 2010, an intense crown fire resulted in almost full mortality but resulted in relatively little exposed mineral soil compared to fires of this intensity due to high surface and soil moisture conditions. Within this stand we sampled arthropods from 6 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 (Figure 1). Within the stand we sampled arthropods from 5 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 to control conditions, especially wildfire controls due to limitations

in the availability and accessibility of appropriate controls. There is however, 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 to 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 epigeic 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 (Figure 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). Each collection period, trap contents were emptied into a Whirl Pack bag 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, Work et al. 2010, Paradis and Work 2011, Graham-Sauvé et al. 2013) and biomass removal (Work et al. 2013, Work et al. 2014). All specimens were identified to species. Carabid species were identified

220 according to Lindroth (1961–1969), following the nomenclature of Bousquet and Laroche (1993).
221 Spiders were identified to species according to Paquin and Duperre (2003) and references in the World
222 Spider Catalog (2017). Rove beetles were identified primarily according to Ashe (2001), Brunke et al.
223 (2011) and Seevers (1978).

224

225 2.3 Environmental Variables

226

227 Surface coarse deadwood (DW) was measured using three fixed area sub-plots (rectangular, 15m x 2m)
228 within each of the control (FC, YC, OC) plots. The first sub-plot originated from the treatment plot centre
229 oriented with a random azimuth. The subsequent sub-plots were each offset 120° to form a triangle. The
230 harvest treatment plots (TL, FT, FTS, FTB) were measured using the above technique in pre-harvest plot
231 assessments combined with 12 fixed area sub-plots (circular, 15m x 1m) conducted after the harvest
232 treatments that captured fresh post-harvest slash that contributed to the total DW pool. DW from the
233 pre-harvest assessment in decay classes 1 and 2 was subtracted from the post-harvest assessment to
234 avoid double counting of DW material at the plot level. Each DW piece (>5cm diameter) within the
235 subplots was tallied for species, decay class (DC), length within the sub-plot boundaries, and end
236 diameters. Decaying stumps were also recorded (species, DC, height, diameter). Decay class
237 determinations followed the classification described by Naesset (1999): 1) Recently dead tree, bark
238 intact 2) bark mostly intact, wood of outer layers (sapwood) of the log has started to soften due to rot,
239 3) bark sloughing or absent, soft outer layers of log and are easily removed with a knife, heartwood
240 mostly sound, 4) bark detached, wood soft, no solid core, 5) Fragmented, no structural integrity.
241 Surface deadwood volume was calculated for each piece using the average diameter and length, with
242 the assumption that pieces were cylinders, and converted to m³ ha⁻¹ using the subplot area (10000/30
243 m²). To estimate the amount of buried wood (>90% of log covered by live moss), a narrow trench (15m

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 wood volume for each trench was calculated following the line intersect sampling approach of Marshall et al. (2000)

$$y_i[m^3 ha^{-1}] = \frac{\pi^2}{8 \times L} \times \sum_{j=1}^{m_i} d_{ij}^2 \quad (\text{Eq. 1})$$

Where y_i 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 2 of 5 replicate plots of each harvest treatment and in one location in each of the young control, old control and the recent fire 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 4m x 4m assessment plots around each pitfall trap. Each assessment plot was divided into 4 quadrats. In each quadrat, we estimated the percent cover of mineral soil exposure that resulted from site preparation, from 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 to 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 whose cross validation error fell within one standard deviation of the minimum cross-validated relative error. Response to treatments was interpreted with reference to overstory removal, amount of above ground deadwood, microclimate on and below the soil surface, and mineral soil exposure as a measure of forest floor disturbance. All analyses were done using R version 2.12.2 (R Development Core Team, 2011).

We used mixed effects models (R lme4 package; Bates et al. 2015) and Tukey’s multiple comparisons (R Multcomp package; Hothorn et al. 2008) to examine the differences in coarse woody

debris volumes and mineral soil exposure between treatments. We could not analyse differences in microclimate between treatments as we only had measurements in 2 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 1), 4861 were spiders represented by 118 species (Appendix 2) and 1231 were rove beetles represented by 70 species (Appendix 3). The most common ground beetles were *Pterostichus adstrictus* (34%), *Pterostichus pensylvanicus* (12%), and *Poecilus lucublandus* (12%) representing 58 % of all individuals captured (Appendix 1). The most frequently collected spider species were *Pardosa xerampelina* (17%), *Pardosa moesta* (15%) and *Amaurobius borealis* (11%), representing 43 % of all spiders captured (Appendix 2). The most common rove beetles were *Atheta capsularis* (14%), *Mycetoporus consors* (10%) and *Lordithon fungicola* (8%) representing 32% of all rove beetles captured (Appendix 3). 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%), *Poecilus 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 the harvested treatments i.e., the fire is

313 more similar to the uncut sites than to the harvested sites, the split of the bladed treatment from the
 314 other harvest sites (this extreme treatment seems to negatively impact the carabid community), and the
 315 lack of a split between full-tree and tree-length treatments (the full-tree biomass harvest does not
 316 appear to exceed any threshold for response to biomass removal).

317 The left hand side of the MRT contain the 3 controls. The first split, separating harvested plots
 318 from uncut plots (including fire) explained 36.7% of the variance (Table 2; Figure 3a). Five carabid
 319 species accounted for most of this variance (*Poecilius lucublandus* (15.2%), *Pterostichus adstrictus*
 320 (11.9%), *Harpalus plenalus* (2.8%), *Harpalus laticeps* (1.8%), and *Sphaeroderus stenostomus* (1.4%)) for a
 321 total of 33.1% variance (Table 2). Of these, the first four were associated with harvested plots whereas
 322 *S. stenostomus* was associated with the uncut stands (Figure 4a). Split 2 separates fire from the uncut
 323 stands and explained 11.3% of the variance with *Pterostichus coracinus* (3.6%), *Sphaeroderus*
 324 *stenostomus* (2.0%), *Myas coracinus* (1.3%) explaining the bulk of the variance (6.9%), all of which were
 325 rarely found in the fire plots (Table 2, Figures 3a, 4a). *Harpalus laticeps* (0.87%) was often associated
 326 with the fire plots (Table 2, Figure 4a). The fourth split contrasts the young plantation control with the
 327 mature fire-origin controls (2.8%) (Table 2, Figure 3a). *Myas coracinus* (1.0%) was associated with the
 328 young plantation control (Table 2, Figure 4a). There do not appear to be any species that were strongly
 329 associated with the mature fire-origin control in comparison to the plantation (Figure 4a).

330 The right hand side of the MRT deals with the harvested treatments. The third split separated
 331 the bladed plots from the other harvested plots (22.8%) (Table 2, Figure 3a). Five species accounted for
 332 greater than 1% of variance each and include *Pterostichus adstrictus* (12.1%), *Pterostichus coracinus*
 333 (1.8%), *Synuchus impunctatus* (1.5%), *Pterostichus pensylvanicus* (1.4%) and *Poecilius lucublandus* (1.2%)
 334 for a total of 18% (Table 2, Figure 4a). All of these species were associated with the harvested but not
 335 bladed plots except for *Poecilius lucublandus* (Figure 4a). In addition, *Bembidion nitidum* (.61%),
 336 *Harpalus affinis* (.65%), *H. fuliginosus* (.19%) , *H. laticeps* (0.87%) and *H. pensylvanicus* (0.47%) were all

more common in bladed plots (Table 2, Figure 4a). The 5th split contrasted the stumped plots with the full-tree biomass and tree-length plots (4.0%) (Table 2; Figure 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 treatment and the young control split into two groups (east plots vs west 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%) (Table 3; Figure 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 (Figure 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, Figure 4b). The second split explained 11.98% of variance, splitting the fire from the young and old controls. Here the most important species were *Trochosa terricola* (2.11%), *Amaurobius borealis* (2.04%), *Sciastes truncatus* (1.72%), which were all associated with old and young controls, and *Pardosa xerampelina* (1.46%) which was associated with fire (Table 3; Figures 3b, 4b). The fourth split separated the old control treatment from the young control treatment (5.76%) (Table 3; Figure 3b). It appeared that *Pardosa hyperborea* was driving this split (3.18%) which was strongly associated with the young control (Table 3; Figure 4b). The fifth split separates the eastern most plots (control plots 1 and 2) of the young control from the western most plots (control plots 3-5). Although all of the control plots are situated

>40m from the harvest edge within a large, contiguous tract of the undisturbed stand, there were notable differences in aboveground DWD volumes (plots 1-2: $23.1 \text{ m}^3 \text{ ha}^{-1}$ versus plots 3-5: $3.4 \text{ m}^3 \text{ ha}^{-1}$) and forest floor depth (plots 1-2: 10.9 cm versus plots 3-5: 6.3 cm) between the eastern versus western plots that may have contributed to this split in the MRT.

The third split (9.16%) separated bladed plots from other harvested plots (Figure 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 non-bladed sites (Figure 4b). This appeared to be true for the vast majority of spider species (Figure 4b). No species showed a clear preference for bladed plots (Figure 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 did not split. The primary difference for rove beetles is that the old control 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; Figures 3c, 4c). In this split the vast majority of species and individuals were associated with the old control, very few individuals were captured in the other 6 treatments (Figure 4c). Of the 1231 individuals captured, 745 were captured in the 5 old control plots whereas only 486 were captured in all plots of the other 6 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 young control treatment separated from the

harvest treatments in a similar fashion to carabid beetles and spiders (Figure 3c). The fourth split separated bladed from the other harvest treatment which was also consistent with the other two taxa (Figure 3c). The old control treatment plots do split into northern (plots 1-3) versus southern (plots 4 and 5) plots. In this case, the southern plots had greater amounts of buried dead wood (plots 4-5: 39.9 $\text{m}^3 \text{ha}^{-1}$ versus plots 1-3: 10.2 $\text{m}^3 \text{ha}^{-1}$) and greater amounts of aboveground DWD in larger (>14 cm) diameter classes (plots 4-5: 34.2 $\text{m}^3 \text{ha}^{-1}$ versus plots 1-3: 10.2 $\text{m}^3 \text{ha}^{-1}$).

3.5 Environmental Variables

The four harvest treatments showed a gradient of CWD from about 40 $\text{m}^3 \text{ha}^{-1}$ in the tree length treatment to no CWD in the bladed treatment. The old control treatment had by far the most CWD at about 70 $\text{m}^3 \text{ha}^{-1}$, whereas the young control treatment had very little CWD ($\sim 5 \text{m}^3 \text{ha}^{-1}$), which was less than in the full-tree harvest treatments. In contrast, the recent fire had similar CWD as the tree-length treatment (Figure 5; Appendix 1). 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 old control (OC) and other treatments although the recent fire (RF) also showed some differences with the more intense harvest disturbances (Appendix 2).

Percent mineral soil exposure was measured as an indicator of forest floor disturbance (Figure 6; Appendix 1). Mineral soil exposure showed a strong gradient from little or no disturbance in the old and young controls, some minimal disturbance in the recent fire and increasing mineral soil exposure from tree-length ($\sim 15\%$ exposure) to the bladed treatment plots (90% exposure) (Mixed Effects Model: Df = 6, F=162.93, $P<0.0001$, Figure 6). Tukey's multiple comparisons found significant differences between all treatments except the controls (OC, YC, RF), and between full-tree and tree-length harvest (FT-SO) (Appendix 2).

We examined the daily mean temperatures at the organic soil –mineral soil interface, at 10 cm below the soil surface and the moisture at 10 cm below the soil surface (Figures 7a,b,c), as well as the air temperature at 15cm and the daily range in soil temperature at 10 cm below soil surface . For mineral soil temperature it was clear that the old and young controls 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 3 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 degrees warmer. By the end of the sampling period (Julian day 231), the difference was closer to 2 degrees (Figure 7b). The air temperatures were highly variable over the short term (8 to 10 degree variation over 5 day span) but very similar between 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 degrees over 5 days for bladed plots versus one to two degrees over 5 days for other treatments; Figure 7b). Patterns between treatments for forest floor temperature were similar to 10 cm below soil surface but our data exclude the bladed plots because 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 old and young control and between 1 and 10% lower relative to harvest treatments depending on time of season). Generally the old and young controls 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 response 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 to harvested treatments with increased forest floor disturbance in harvested plots being a possible explanation. Lack of similarity of arthropod communities between the recent fire 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 epigaeic 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 did not appear to have additional effects to tree-length. In addition, all three taxa had different communities in the older (92 years) fire origin plots than 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 coarse woody debris in the younger harvest origin stand. This was contrary to our third hypothesis that suggested that once the overstory returned (younger harvest origin treatment) the faunal composition would recover. The uniqueness of older fire origin stands was most pronounced in the rove beetle communities where the majority of individuals were found in the older fire origin stands.

4.2 Clearcutting and fire effects on epigaeic assemblages

The primary split for both ground beetles and spiders in the MRT between the mature (92 years old), young (51 years old) and immediate post-fire treatments as compared to the 4 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 epigaeic 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 thirty-five percent of the variance was explained by overstory removal with large increases in open-habitat species (Work et al. 2014). Plots in the post-fire treatment here had limited overstory (live, functioning green canopy) as did harvested plots, whereas mature and young control plots had a closed canopy. Post-fire plots did have 1467 standing dead stems/ha which may have offered some protection, however an examination of the microclimate which is expected to be influenced primarily by overstory, indicates that post-fire 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 epigaeic 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 old control treatment, young control treatment and the recent fire treatment all had the least amount of mineral soil exposure relative to the 4 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; old control, young control, recent fire, tree-length, full –tree biomass, stumped and bladed. In our recent fire 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 post-fire sites. The evidence from this first split (second split for staphylinidae) is that none of the harvest options that we conducted are a good emulation for our post-fire 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 since it is an important factor in epigaeic 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 biodiversity 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 post-fire sites being more similar to the reference conditions than post-harvest 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 coarse woody debris as influencing community patterns. There is some evidence in the literature of species composition change due to effects of coarse woody debris 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. An examination of the pattern of downed coarse wood in the different treatments, however suggests that this factor is not driving the first split since down coarse woody debris is most abundant in the oldest control, the post-fire treatment and the tree-length treatment, and notably very low in the young control, 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 (Figure 3-54). 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 epigaeic 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 epigaeic 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 per ha. 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 maybe 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

550 young and old controls show significant differences in community composition. It is significant and
551 contrary to our third hypothesis that all three assemblages of taxa differ between the old and young
552 controls since it is expected that communities in young forest stands will eventually converge with
553 communities in old forest stands. This convergence has not yet happened in our 51 year old controls
554 and an understanding of when and if this will happen is key to predicting long-term impacts of harvest
555 on biodiversity and sustainability (Venier et al. 2014). The split between old and young controls in all
556 groups may be influenced by deadwood volumes which are much higher in the old control than the
557 young control. None of the other measured environmental factors (overstory, microclimate, and forest
558 floor disturbance) strongly differ between these two treatments. It is possible that community
559 convergence in successional forest stands may therefore be predicted based on accumulated
560 deadwood, an idea that could be tested in a chronosequence experiment. The pattern that rove
561 beetles exhibited using MRT analysis is largely similar to both the spiders and ground beetles in terms of
562 the conclusions we have drawn about our hypotheses, however, most of the rove beetle species were
563 associated with the old control treatment and resulted in an initial split of the old control from all other
564 treatments. The remaining MRT is similar in that the fire and young control communities differ from the
565 harvest stands, the bladed harvest community differs from the other harvest treatment communities,
566 and the stumped, tree-length, and full-tree communities do not split. These results have three
567 implications. First, this suggests that rove beetle communities support the broad conclusions of the
568 other groups. Second, this group could be a very useful indicator of old forest condition, since several
569 species are strongly associated with the old forest control. This is consistent with results from Buddle et
570 al. (2006) which show that rove beetles recover more slowly after harvest disturbance than the other
571 groups. Third, this species group is probably a less useful indicator of alternative harvest or other
572 disturbance treatments than carabid beetles and spiders (Pearce and Venier 2006) due to lower species
573 abundances and fewer species in disturbed plots. Response to loss of old forest and coarse woody

debris may be due to the fungivorous nature of many rove beetles and the associated lower levels of wood decay fungi at lower deadwood levels (Stephani et al. 2016). An alternative explanation for the lack of convergence in the young control plots is the potential isolation of the young controls from older forests that could provide immigration of older-forest specialists. Mature jack pine forests are not common in a 50km radius of the young controls 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 kilometers 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 old and young controls over the recent fire. Only a few species showed an affinity for the old control over the young control (*Harpalus fuliginosus*, *Sphaeroderus stenostomus*, *Synuchus impunctatus*), but these species were still often found in the young control. Differences between young and old controls 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 young and old

controls) 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 old control. No spider species showed a strong affinity for old controls over young controls; 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 indicates that there are many old forest specialists such as *Atheta capsularis*, *A. stigosula*, and *Oxypoda grandipennis* that are found in only very small numbers or not at all in harvested, fire disturbed, or young controls.

We have focused this study on three taxa of epigaeic 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 a landscape rather than stand scale.

5. Conclusions

Although the inference space is limited, we found that epigaeic communities differed between fire and harvest disturbance immediately post-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 that 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 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 epigaeic groups. This suggests that blading is a practice that is unlikely to be sustainable from an epigaeic 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 difference between communities within full-tree biomass and tree-length 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 epigaeic biodiversity. Lack of a short-term effect however, does not preclude a longer-term impact associated with loss of deadwood availability over time.

The epigaeic communities did differ between old (post-fire) controls (92 years) and young post-harvest controls (51 years), most strongly for rove beetles but also for ground beetles and spiders. The most obvious environmental difference between old and young controls 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.

6. Acknowledgements

Chelene Krezek-Hanes provided references to address variation in fire intensity. Jamie Stewart, Kerrie Wainio-Keizer, Kevin Good, Stephanie Dumas all supported field data collection. Tom Weldon, Mark Primavera, Stephanie Wilson and Gord Brand provided logistic support for field work, data management and figure production. Emilie Rivest identified the ground beetles. Funding was provided through an NSERC Collaborative Research Agreement to Christian Messier and through an EcoEnergy Innovation Initiative Grant, NRCan to Lisa Venier.

7. Literature Cited

- Angelstam, P. 1997. Landscape analysis as a tool for the scientific management of biodiversity. *Ecol. Bull.* 46: 140-170.
- Ashe, J.S. 2001. Key to the tribes and genera of Nearctic Aleocharinae. 8. *In*: American Beetles. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. Edited by R.H. Arnett, Jr, and C.M. Thomas. CRC Press, Boca Raton, London, New York, Washington, D.C. pp. 299-374.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. [doi:10.18637/jss.v067.i01](https://doi.org/10.18637/jss.v067.i01).
- Berch, S.M., Morris, D. and Malcolm, J. 2011. Intensive forest biomass harvesting and biodiversity in Canada: A summary of relevant issues. *For. Chron.* 87 (4): 478-487.
- Bergeron, Y., Gauthier, S., Kafka, V. Lefort, P. and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* 31(3): 384-391. doi: 10.1139/x00-178.
- Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fennica* 36: 81-95.

- 667 Björheden, R. 2006. Drivers behind the development of forest energy in Sweden. *Biomass Bioenergy* 30:
668 289-295.
- 669 Bousquet, A., Larochelle Y. 1993. Catalogue of the Geadephaga (Coleoptera: Trachypachidae,
670 Rhysodidae, Carabidae including Cicindelini) of America north of Mexico. *Mem. Entomol. Soc.*
671 *Can.* 167:397.
- 672 Brais, S., Sadi, F., Bergeron, Y., and Grenier, Y. 2005. Coarse woody debris dynamics in a post-fire jack-
673 pine chronosequence and its relation with site productivity. *For. Ecol. Manage.* 220:216-226.
- 674 Brunke, A., Newton, A., Klimaszewski, J., Majka, C. and Marshall, S. 2011. Staphylinidae of Eastern
675 Canada and Adjacent United States. Key to Subfamilies; Staphylininae: Tribes and Subtribes, and
676 Species of Staphylinina. *Canadian Journal of Arthropod Identification* No. 12, 20 January 2011,
677 Available from http://www.biology.ualberta.ca/bsc/ejournal/bnkmm_12/index.html. doi:
678 10.3752/cjai.2011.12.
- 679 Buddle, C.M., Spence, J.R., and Langor, D.W. 2000. Succession of boreal forest spider assemblages
680 following wildfire and harvesting. *Ecography* 23: 424-436.
- 681 Buddle, C.M., Langor, D.W., Pohl, G.R., and Spence, J.R. 2006. Arthropod responses to harvesting and
682 wildfire: Implications for emulation of natural disturbance in forest management. *Biological*
683 *Conservation* 128: 346-357.
- 684 Castro, A. and Wise, D.H. 2009. Influence of fine woody debris on spider diversity and community
685 structure in forest leaf litter. *Biodiversity and Conservation* 18:3705-3731.
- 686 Castro, A. and Wise, D.H. 2010. Influence of fallen coarse woody debris on the diversity and community
687 structure of forest-floor spiders (Arachnida: Araneae). *For. Ecol. Manage.* 260: 2088-2101.
- 688 Chaundy-Smart, R. F. C., Smith, S.M., Malcolm, J.R. and Bellocq, M.I. 2012. Comparison of moth
689 communities following clear-cutting and wildfire disturbance in the southern boreal forest. *For.*
690 *Ecol. Manage.* 270:273-281.

- 691 De'ath, G. 2011 mvpart: Multivariate partitioning. R package version 1.4-0. [http://CRAN.R-](http://CRAN.R-project.org/package=mvpart)
692 [project.org/package=mvpart](http://CRAN.R-project.org/package=mvpart).
- 693 De'ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment
694 relationships. *Ecology* 83:1105-1117.
- 695 Environment Canada. 2013. National Climate Data and Information Archive. Available from
696 http://www.climate.weatheroffice.gc.ca/Welcome_e.htm [accessed 26 June 2013].
- 697 Gauthier, S., Gagnon, J., and Bergeron, Y. 1993. Jack pine (*Pinus banksiana* Lamb.) population age
698 structure: effects of forest age, site types and fire regimes. *Journal of Vegetation Science* 4:783-
699 790.
- 700 Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P.,
701 Bergeron, Y. 2009. *Ecosystem Management in the Boreal Forest*. Presses de l'Université du
702 Québec, Québec.
- 703 Graham-Sauvé, L., Work, T.T., Kneeshaw, D. and Messier, C. 2013. Shelterwood and multicohort
704 management have similar initial effects on ground beetle assemblages in boreal forests. *For.*
705 *Ecol. Manage.* 306:266-274.
- 706 Greene, D. F., Noël, J. Bergeron, Y. Rousseau, M. and Gautier, S. 2004. Recruitment of *Picea mariana*,
707 *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in
708 the southern boreal forest of Quebec. *Can. J. For. Res.* **34**:1845-1857.
- 709 Hakkila, P. 2004. Puuenergian teknologiaohjelma 1999-2003 (Wood energy technology programme
710 1999-2003). Loppuraportti. Teknologiaohjelmaraportti 5/2004, 135 pp. (In Finnish).
- 711 Holliday, N.J. 1992. The carabid fauna (Coleoptera: Carabidae) during post-fire regeneration of boreal
712 forests: properties and dynamics of species assemblages. *Can. J. Zool.* 70: 440-452.
- 713 Hothorn, T., Bretz, F., and Westfall, P. 2008. Simultaneous Inference in General Parametric Models.
714 *Biometrical Journal* 50(3), 346--363.

- 715 Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and
716 prescribed burning. *Ann. Zool. Fenn.* 8:483-542.
- 717 Hunter, M.L. 1993. Natural fires regimes as spatial models for managing boreal forests. *Biological*
718 *Conservation* 65:115-120.
- 719 Johnstone, J.F. and Kasischke, E.S. 2005. Stand-level effects of soil burn severity on postfire regeneration
720 in a recently burned black spruce forest. *Can. J. For. Res.* 35: 2151-2163.
- 721 Klimaszewski, J., Brunke, A., Work, T., **Venier, L.** 2017 in press. Chapter 2.2. Rove beetles (Coleoptera,
722 Staphylinidae) as bioindicators of change in boreal forests and their biological control services in
723 agroecosystems: Canadian case studies. *In* *Biology of Rove Beetles (Staphylinidae) - Life History,*
724 *Evolution, Ecology and Distribution*, Edited by Oliver Betz, Ulrich Irmeler and Jan Klimaszewski.
725 Springer.
- 726 Klimaszewski, J., Langor, D.W., Work, T.T., Pelletier, G., Hammond, H.E.J. and Germaine, C. 2005. The
727 effects of patch harvesting and site preparation on ground beetles (Coleoptera, Carabidae) in
728 yellow birch dominated forests of southeastern Quebec. *Can. J. For. Res.* 35:2616-2628.
- 729 Koivula, M., and Spence, J.R. 2006. Effects of post-fire salvage logging on boreal mixed-wood ground
730 beetle assemblages (Coleoptera, Carabidae). *For. Ecol. Manage.* 236:102-112.
- 731 Kwiaton, M., Hazlett, P., Morris, D., Fleming, R., Webster, K., Venier, I., Aubin, I. 2014. Island Lake
732 Biomass Harvest Research and Demonstration Area: Establishment Report. Natural Resources
733 Canada, Canadian Forest Service, Great Lakes Forestry Centre, Information Report GLC – X – 11.
- 734 Lindroth CH (1961–1969) The ground-beetles (Carabidae, excl Cicindelinae) of Canada and Alaska.
735 (Suppl. 20 (1961), 24 (1963), 29 (1966), 33 (1969), & 35 (1969). *Opuscula Entomologica*, Lund
736 University, Sweden.
- 737 Long, J.N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North
738 American view. *For. Ecol. Manage.* 257: 1868-1873.

- 739 Lovei, G.L. and Sunderland, K.D. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae).
740 *Annu. Rev. Entomol.* 41:231-256. doi: 10.1146/annurev.en.41.010196.001311
- 741 Marshall, P.L., Davis, G., LeMay, V.M. 2000. Using line intersect sampling for coarse woody debris.
742 Technical Report TR-003. Nanaimo (BC): Vancouver Forest Region, British Columbia Ministry of
743 Forests. Available from <http://www.for.gov.bc.ca/rco/research/cwd/tr003.pdf>
- 744 Martikainen, P., Kouki, J. and Heikkala, O. 2006. The effects of green tree retention and subsequent
745 prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests.
746 *Ecography* 29:659-670.
- 747 Matveinen-Huju, K., and Koivula, M. 2008. Effects of alternative harvesting methods on boreal forest
748 spider assemblages. *Can. J. For. Res.* 38: 782-794. doi:10.1139/X07-169.
- 749 McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., and Woodley, S. 2001. Comparisons between
750 wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* 9:223-
751 260.
- 752 Munson, A.D., Margolis, H.A., Brand, D.G., 1993. Intensive silvicultural treatment: Impacts on soil fertility
753 and planted conifer response. *Soil Sci. Soc. Am. J.* 57: 246-255.
- 754 Munson, A.D., Timmer, V.R., 1995. Soil nitrogen dynamics and nutrition of pine following silvicultural
755 treatments in boreal and Great lakes ± St. Lawrence plantations. *For. Ecol. Manage.* 76:169-
756 179.
- 757 Naesset, E. 1999. Relationship between relative wood density of *Picea abies* logs and simple
758 classification systems of decayed coarse woody debris. *Scandinavian Journal of Forest Research*
759 14:454-461.
- 760 Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. *For. Ecol. Manage.*
761 115:127-134.

- 762 Niemelä, J., Langor, D. and Spence, J.R. 1993. Effects of clear-cut harvesting on boreal ground-beetle
763 assemblages (Coleoptera: Carabidae) in Western Canada. *Conservation Biology* 7:551-561.
- 764 Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., Paré, D. 2000. The importance of forest floor
765 disturbance in the early regeneration patterns of the boreal forest of western and central
766 Quebec : a wildfire versus logging comparison. *Can. J. For. Res.* 30: 1353-1364.
- 767 OMNR 1997. Silvicultural guide to managing for black spruce, jack pine, and aspen on boreal forest
768 ecosites in Ontario. Version 1.1. Ontario Ministry of Natural Resources. Queen's Printer for
769 Ontario, Toronto. 3 books. 822pp.
- 770 OMNR 2010. Forest Management Guide for Conserving Biodiversity at the Stand and Site Scales.
771 Toronto: Queen's Printer for Ontario. 211pp.
- 772 OMNR 2013. Emulating natural disturbances : clearcut silviculture in Ontario. State of Resources
773 Reporting. Ontario Ministry of Natural Resources. Available from
774 <https://dr6j45jk9xcmk.cloudfront.net/documents/3123/stdprod-110056.pdf>
- 775 Paquin P and Duperre N. 2003. Guide d'identification des araignees (Araneae) du Quebec. Varieties,
776 Quebec: Association des entomologistes amateurs du Quebec.
- 777 Paradis, S. and Work, T.T. 2011. Partial cutting does not maintain spider assemblages within the
778 observed range of natural variability in Eastern Canadian black spruce forests. *For. Ecol.*
779 *Manage.* 262: 2079-2093.
- 780 Pearce, J.L., Venier, L.A., McKee, J., Pedlar, J., McKenney, D. 2003. Influence of habitat and microhabitat
781 on carabid (Coleoptera: Carabidae) assemblages in four stand types. *The Canadian Entomologist*
782 135: 337-357.
- 783 Pearce, J.L. and Venier, L.A. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders
784 (Araneae) as bioindicators of sustainable forest management: A review. *Ecol. Indic.* 6: 780-793.

- 785 Pinzon, J., Spence, J.R. and Langor, D.W. 2013. Effects of prescribed burning and harvesting on ground
786 dwelling spiders in the Canadian boreal mixedwood forest. *Biodiversity and Conservation*
787 22:1513-1536.
- 788 Pohl, G. R., Langor, D. and Spence, J.R. 2007. Rove beetles and ground beetles (Coleoptera:
789 Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western
790 Canadian foothills forests. *Biological Conservation* 137:294-307.
- 791 R Development Core Team (2011). R: A language and environment for statistical computing. R
792 Foundation for Statistical Computing, Vienna, Austria. Available from [https://www.R-](https://www.R-project.org/)
793 [project.org/](https://www.R-project.org/).
- 794 Reich, P. B., P. Bakken, P. Carlson, D., Frelich, L.E., Friedman, S.K., and Grigal, D.F. 2001. Influence of
795 logging, fire, and forest type on biodiversity and productivity in southern boreal forests. *Ecology*
796 82:2731-2748.
- 797 Ryans, M. and Sutherland, B. 2001. Site preparation-mechanical. In R.G. Wagner and S.J. Colombo, eds.,
798 Regenerating the Canadian Forest: Principles and Practice for Ontario. Ontario Ministry of
799 Natural Resources, Fitzhenry & Whiteside Limited, Markham, Ontario, Canada.
- 800 Seevers, C.H. 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera:
801 Staphylinidae). *Fieldiana Zoology* 71: 289 pp.
- 802 Siira-Pietikainen, A., J. Haimi, and J. Siitonen. 2003. Short-term responses of soil macroarthropod
803 community to clear felling and alternative forest regeneration methods. *For. Ecol. Manage.*
804 172: 339-353.
- 805 Stephani, F.O.P., Klimaszewski, J., Morency, M.-J., Bourdon, C., Labrie, P., Blais, M., Venier, L. and Seguin,
806 A. 2016. Fungal community composition in the gut of rove beetles (Coleoptera: Staphylinidae)
807 from the Canadian boreal forest reveals possible endosymbiotic interactions for dietary needs.
808 *Fungal Ecology* 23: 164-171.

- 809 Suffling, R, Smith, B., Dal Molin, J. 1982. Estimating past forest age distributions and disturbance rates in
810 north-western Ontario: A demographic approach. *Journal of Environmental Management* 14:45-
811 56
- 812 Thiffault, E., Bechard, A., Pare, D., & Allen, D. 2014. Recovery Rate of harvest residues for bioenergy in
813 boreal and temperate forests: A Review. *WIREs Energy and Environment*, 4(5). Retrieved from
814 [http://onlinelibrary.wiley.com/doi/10.1002/wene.157/abstract;jsessionid=844E315A775517D1](http://onlinelibrary.wiley.com/doi/10.1002/wene.157/abstract;jsessionid=844E315A775517D1AA9F125081F03076.f01t04?userIsAuthenticated=false&deniedAccessCustomisedMessage=)
815 [AA9F125081F03076.f01t04?userIsAuthenticated=false&deniedAccessCustomisedMessage=](http://onlinelibrary.wiley.com/doi/10.1002/wene.157/abstract;jsessionid=844E315A775517D1AA9F125081F03076.f01t04?userIsAuthenticated=false&deniedAccessCustomisedMessage=)
- 816 Thiffault, E., Hannam, K. D., Paré, D., Titus, B. D., Hazlett, P. W., Maynard, D. G., & Brais, S. 2011. Effects
817 of forest biomass harvesting on soil productivity in boreal and temperate forests — A review.
818 *Environmental Reviews*, 19, 278-309. Retrieved from
819 <http://www.nrcresearchpress.com/action/showCitFormats?doi=10.1139%2Fa11-009>
- 820 Ulyshen, M.D. and J.L. Hanula. 2009. Responses of arthropods to large-scale manipulations of deadwood
821 in loblolly pine stands in the southeastern United States. *Environmental Entomology* 38: 1005-
822 1012
- 823 Venier, L.A., Thompson, I.D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J.A., Langor, D., Sturrock, R.,
824 Patry, C., Outerbridge, R.O., Holmes, S.B., Haeussler, S., De Grandpré, L., Chen, H.Y.H., Bayne, E.,
825 Arsenault, A. and Brandt, J.P. 2014. Effects of natural resource development on the terrestrial
826 biodiversity of Canadian boreal forests. *Environmental Reviews* 22: 457-490.
827 [Dx.doi.org/10.1139/er-2013-0075](https://doi.org/10.1139/er-2013-0075).
- 828 Weber, M. G., M. Hummel, and C. E. Van Wagner. 1987. Selected parameters of fire behavior and *Pinus*
829 *bankisana* Lamb. regeneration in Eastern Ontario. *Forestry Chronicle* 63:340-346.
- 830 Work, T.T., Brais, S., and Harvey, B.D. 2014. Reductions in downed deadwood from biomass harvesting
831 alter composition of spiders and ground beetle assemblages in jack-pine forests of Western
832 Quebec. *For. Ecol. Manage.* 321:19-28.

- 833 Work, T.T., Jacobs, J.M., Spence, J.R. and Volney, W.J. 2010. High levels of green-tree retention are
834 required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological*
835 *Applications* 20: 741-751.
- 836 Work, T.T., Klimaszewski, J., Thiffault, E., Bourdon, C., Pare, D., Bosquet, Y., Venier, L.A., Titus, B.D. 2013.
837 Initial responses of rove and ground beetles (Coleoptera, Staphylinidae, Carabidae) to removal
838 of logging residues following clearcut harvesting in the boreal forest of Quebec, Canada.
839 *Zookeys* 258: 31-52.
- 840 Work, T.T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J., Sweeney, J. and Hebert, C. 2008.
841 Evaluation of carabid beetles as indicators of forest change in Canada. *Can. Entomol* 140: 393-
842 414.
- 843 World Spider Catalog. 2017. World Spider Catalog. Natural History Museum Bern online at
844 <http://wsc.nmbe.ch>, version 18.0

Table 1: Stand characteristics for the three reference condition stands. The Recent Fire is a recently burned stand and therefore has no standing live volume. Pre-treatment measures that are relevant to justify stand similarity are highlighted in grey. The other measures are different due to treatment effects.

	Island Lake	Recent Fire	Old Control
Stand Age at time of epigeaic sampling(yrs)	51	3*	92
Species Composition (%)	Pj ₉₉ Sb ₁	Pj ₁₀₀	Pj ₉₀ Sb ₁₀
Tree Density (stems per hectare)	2005	1467**	1870***
Gross Total Volume (m ³ ha ⁻¹)	189.6	107.4**	289.5
Site Index (m @ BHA ₅₀)	19.3	19.5**	18.8
Standing Dead Volume (m ³ ha ⁻¹)	9.66	107.41	37.92
DWD Aboveground Fine Volume (m ³ ha ⁻¹)	1.39	2.81	0.58
DWD Aboveground Coarse Volume (m ³ ha ⁻¹)	11.03	41.56	75.98
% Proportion DWD Aboveground Coarse Volume by Decay Class			
	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 ³ ha ⁻¹)	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

*Recent Fire was a 30-year-old jack pine plantation when it burned in the spring of 2010

** Data from standing dead inventory measured post-fire

*** Pj density is 778 with Sb ingress at 1041 stems per hectare

Species Composition: Pj = Jack Pine, Sb = Black Spruce

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

Draft

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>Poecilus 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
Total	36.718	11.294	22.808	2.782	4.036	77.638	100.000

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>Agyneta 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>Amaurobius 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>Hahnia 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>Lepthyphantes 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

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>Amischa sp.</i>	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 fuscus</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>Megarthritis 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>Oxypoda grandipennis</i>	6.316	0.000	0.677	0.000	6.993	7.213
<i>Philonthus caeruleipennis</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

(a)

(b)

Figure 3

(a)

Draft

(b)

Draft

(c)

Draft

Figure 4

(a)

(b)

(c)

Figure 5

Figure 6

Figure 7

(a)

(b)

(c)

1 Appendix 1: Carabid species list, abundance and % 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 megacephalus</i>	20	0.3%
<i>Harpalus pensylvanicus</i>	36	0.6%
<i>Harpalus plenalis</i>	209	3.5%
<i>Harpalus sp.</i>	5	0.1%
<i>Myas coracinus</i>	196	3.3%

2

<i>Notiophilus aeneus</i>	4	0.1%
<i>Platynus decentis</i>	11	0.2%
<i>Poecilius 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 pennsylvanicus</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%

2

3

4

5

6

7 Appendix 2: Spider species list with abundance and % 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>Bassaniana utahensis</i>	1	0.0%
<i>Bathypantes 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%

4

<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>Euryopsis 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</i>	1	0.0%
<i>cymbadentatum</i>		
<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>Nerienne 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%
<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 formicum</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 fratrīs</i>	64	1.3%

8

Zelotes puritanus

10

0.2%

8

9

Draft

10 Appendix 3: Staphylinidae species list with total abundance and % representation of all rove beetles.

Species	Abundance	% Representnation
<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 sp.</i>	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 sp.</i>	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 sp.</i>	6	0.5%
<i>Bolitobius cingulatus</i>	2	0.2%
<i>Byroporus rufescens</i>	1	0.1%
<i>Carphacis nepigonensis</i>	3	0.2%

10

<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 sp.</i>	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 sp.</i>	2	0.2%
<i>Nitidulidae sp.</i>	1	0.1%
<i>Omalium sp.</i>	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 acadiensis</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>Quedius fulvicollis</i>	11	0.9%
<i>Quedius labradorensis</i>	15	1.2%
<i>Quedius rusticus</i>	2	0.2%
<i>Silusa californica</i>	20	1.6%
<i>Silusida marginella</i>	6	0.5%
<i>Stenus sp.</i>	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 obliques</i>	1	0.1%

11 Appendix 4: 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 ³ /ha)	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)

12

13

14

15 Appendix 5: Tukey multiple comparisons of treatments for Total Coarse Woody Debris and
16 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

17

18

19