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Cumulative effects of biomass harvesting and herbicide application on litter-dwelling arthropod communities in jack pine-dominated forests: 7th year postharvest assessment

Timothy T. Work[a], **Dave M. Morris**[b], **S. Loboda**[c], **J. Klimaszewski**[d], **K. Wainio-Keizer**[e], **and Lisa Venier**[e]

[a]Département des Sciences biologiques, Université du Québec à Montréal, QC, Canada; [b]Ontario Ministry of Natural Resources and Forestry, ON, Canada; [c]Institut Maurice-Lamontagne, Pêches et Océans Canada, CP 1000, Mont-Joli, QC, Canada; [d]Laurentian Forestry Centre, Natural Resources Canada, QC, Canada; [e]Great Lakes Forestry Centre, Natural Resources Canada, ON, Canada

Corresponding author: **Lisa Venier** (email: lisa.venier@nrcan-rncan.gc.ca)

Abstract

Forest biomass harvest has the potential to provide feedstocks for energy production to offset fossil fuel consumption. However, concerns have been raised regarding the ecological sustainability of removing additional biomass from forests, in particular the impacts on biodiversity. In this paper, we used a suite of ground-dwelling arthropod taxa (ground beetles, spiders, and rove beetles) to measure community compositional changes along a gradient of biomass removal treatments 7 years postharvest, and compared against reference. Based on multivariate regression trees, changes in species composition reflected the intensity gradient of the biomass removal treatments or stand attributes associated with the level of forest floor disturbance across all arthropod groups. For each arthropod group, changes in composition were defined primarily by reductions or loss of abundant forest associated species and increases in the number and abundance of species associated with more xeric conditions and increased disturbance intensity. There were no differences between full-tree and tree-length treatments. Overall, results indicated a strong arthropod response to the removal of overstory, forest floor disturbance, and reductions in understory cover mostly resulting from the glyphosate applications. Arthropod recovery would benefit from overstory retention, reduction in forest floor disturbance, and judicious use of glyphosate.

Key words: biomass harvesting, glyphosate, Carabidae, spiders, Staphylinidae

1. Introduction

Recovery of residual forest biomass from harvesting operations, including branches, unmerchantable tree-tops, and even stumps, may provide an additional source of renewable energy and reduce reliance on fossil carbon (Paré et al. 2011; Verkerk et al. 2011) but may also pose risks for resident biodiversity (Berch et al. 2011; Bouget et al. 2012; Work et al. 2014, 2016). While removal of residual biomass most often occurs simultaneously or shortly after timber harvest, the initial removal is accompanied by additional interventions that commonly include mechanical site preparation, replanting, and applications of herbicides such as glyphosate to reduce competing vegetation (Wiensczyk et al. 2011; Webster et al. 2016). For resident organisms, impacts from subsequent interventions will thus co-occur with impacts from harvesting (Roberts 2007).

The initial impacts of harvesting residual biomass depend on the volume and type of residual material that is removed. For example, branches and tops are often removed through full-tree harvesting where whole trees are removed from harvested blocks and then stems are delimbed at roadside stations or landings for cut logs (OMNR 2010). More intensive removal of stumps requires additional interventions with specialized harvesting machinery and results in extensive impacts on forest soils (Webster et al. 2016; Andersson et al. 2017; Kaarakka et al. 2018). Litter-dwelling arthropods are excellent taxa to examine the impact of harvesting of residual biomass because these are widely recognized as good bioindicators in boreal forest contexts (Niemelä et al. 1993; Pearce and Venier 2006; Work et al. 2008; Lee et al. 2023), their taxonomies and associate identification keys are well developed, and they can be effectively sampled at the scale of operational experiments (Pearce and Venier 2006).

For resident organisms such as litter-dwelling arthropods, removal of the overstory trees and logging residues, along with related impacts on soils from harvesting and site preparation equipment, can have significant negative impacts (Work et al. 2014; Venier et al. 2017). For example, secondary removal of residual biomass using a modified harvester following timber harvest further suppressed ground beetle and spider species with affinities for closed canopy forests but favoured spider species associated with more xeric conditions (Work et al. 2014). Secondary removal of stumps with an excavator likewise further reduced abundances of multiple ground beetle species that had already declined in harvested plots (Venier et al. 2017).

Following the initial removal of overstory and logging residues, resident organisms must also contend with the additional impacts related to the establishment crop of trees including mechanical site preparation and the use of herbicides. The herbicide glyphosate is a broad-spectrum herbicide used to reduce understory vegetation cover that would otherwise limit growth of newly planted conifer seedlings (Wiensczyk et al. 2011). Following harvest, glyphosate is typically applied operationally within 3 years after planting during late summer months to reduce competing vegetation cover (Doug Reid—Boreal Silviculture Research Scientist (personal communication)). Ultimately, glyphosate tends to concentrate in the soil organic layer, particularly on sites with sandy soils where it is thought to be degraded through microbial action over several weeks (Rolando et al. 2017). Toxicity of glyphosate has been evaluated in terms of both mortality and altered behaviour on a limited number of animals, primarily in agricultural landscapes with little evidence of negative effects. For example, predatory arthropods including some wolf spiders (*Pardosa*) and ground beetles (*Poecilus*) showed no mortality and no effects on predation rates, mating, habitat avoidance, or defensive behaviour in response to exposure to day-old residues of glyphosate (Michalková and Pekár 2009). This suggests that any negative effects of herbicide in forests on groups like predatory arthropods are likely the result of indirect interactions with changes in understory vegetation cover.

Here, we compare community-level responses of three groups of litter-dwelling arthropods: ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae) and spiders (Araneae), across an increasing intensity of biomass harvesting options and silvicultural practices required to reestablish the subsequent crop of trees. We anticipated that 7 years following the removal of the overstory and logging debris, more intensive biomass removal treatments, and particularly those that disrupt or remove the existing organic layer, will invoke the largest differences in community composition. We also anticipated that these differences would be compounded by suppression of understory vegetation cover by applications of glyphosate. Cumulative effects of biomass removal and glyphosate application were compared with a range of reference conditions including a 57-year-old planted stand, a 97-year-old jack pine (*Pinus banksiana*) stand of fire origin, and a more recent 6-year-old burn to evaluate whether arthropod composition after biomass removal is similar to either older managed stands or natural stands (i.e., a sign of postdisturbance recovery) at the initial and final stages of stand development in jack-pine ecosystems.

2. Methods

2.1. Experimental treatments and sampling design at Island Lake Biomass Harvest Experiment

We collected litter arthropods from replicated biomass removal treatments 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). The site was a second growth of jack pine plantation that was originally clearcut 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. Standing dead trees were toppled during the harvest operation (i.e., retained on site). 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, where boles were delimbed, topped at 10 cm diameter and removed, with the logging slash (i.e., tops and limbs) distributed evenly throughout the treatment using an excavator; (2) full-tree biomass harvest, where the bole with branches of all merchantable and unmerchantable trees were removed and delimbed at roadside; (3) stump removal, where bole with branches were removed as per the full-tree biomass harvest, and then stumps with large to medium roots attached were removed using an excavator and placed at least 10 m beyond the experimental plot; and (4) blading, where boles with branches were removed as per full-tree biomass harvest, and then stumps, all coarse woody material (CWM), and the forest floor were removed with an excavator fitted with large metal blade. Historically, corridor blading has been practiced operationally in several jurisdictions, including Ontario, Canada, as an approach to vegetation control and site preparation prior to planting, but, for the most part, is no longer done on upland sites. In our experiment, blading was included to push beyond a tree biomass removal endpoint and represent the full continuum of organic matter removals. Each experimental treatment was replicated five times and each experimental plot was 70 m × 70 m (0.49 ha). Experimental plots were separated by at least 20 m from each other and the surrounding uncut forest. Tree-length harvest, full-tree harvest, and stump removal treatments were all site-prepared in the fall of 2011 using disc trenching with 2.1 m spacing between trench centres. Disc trenching results in “flat” undisturbed linear areas with 15–20 cm deep trenches on either side and linear piles of mixed organic and mineral soil beside the trenches called “spoils”. All treatment plots were planted with overwintered container stock in the spring of 2012 at 1.8 m × 2.1 m spacing (2650 stems ha^{-1}), with a refill planting done in the spring of 2013.

2.2. Glyphosate application for vegetation control

Each of the harvested experimental plots was divided in half with glyphosate application in the western half and no glyphosate in the eastern half. Glyphosate was hand sprayed three times between 2012 and 2018 (i.e., during the last week of August 2011, 2014, and 2018). At an application rate of 4 L of product per ha to control vegetation. These applications do not mimic operational tending (e.g., one aerial application 3–4 years after planting). Multiple applications of glyphosate were used to eliminate the understory vegetation to better isolate its role in ecosystem recovery. Arthropod community composition was compared between the herbicide and no herbicide split plots.

2.3. Reference plots

In addition to the harvested site, litter arthropods were collected from three reference stands including a mid-rotation, 57-year-old planted stand (i.e., uncut portion of the Island Lake plantation "mid-managed"), a mature (92-year-old) stand that had regenerated naturally following wildfire ("old"), and a recent (2011) burn ("burn") of similar age to the biomass harvest plots. All sites used in this study were established on glaciofluvial, coarse-textured, glacial outwash deposits characterized by sandy (medium sand) parent material.

The mid-managed reference stand was an uncut portion of the 57-year-old jack pine plantation located adjacent to harvested plots that reflected the same conditions as the harvested plots prior to cutting. The legacy of the 1959 tree-length clearcut resulted in relatively high volumes of advanced decay deadwood as little fresh deadwood has been deposited over the last 50 years (Venier et al. 2017), although the plantation is advancing through the self-thinning phase of stand development, with approximately 45% of the standing dead trees inventoried in 2014 being added to the downed woody debris (DWD) pool by 2018.

The fire-origin, older mature reference stand was a 92-year-old jack pine stand of wildfire origin located ca. 20 km southeast (47°38′N, 83°15′W) of the Island Lake Biomass Harvest Experimental site and was included to reflect community composition in the absence of disturbance. This site was in the stage of stand breakup and was characterized by moderate levels of standing dead volume (37.9 m^3·ha) and much higher volumes of DWD (76 m^3·ha) compared with the low levels of dead wood in the younger, postharvest reference site at Island Lake (Venier et al. 2017).

The recent burned reference stand was a 6-year-old burn located near Ripple Lake, Ontario (47°56′N, 84°09′W). Before burning, this 20-ha stand was a 30-year-old monoculture jack pine plantation that had originated from clearcutting, site preparation, and planting. In spring of 2012, a crown fire advanced through the plantation resulting in almost full mortality. However, a subsequent rainfall event extinguished the ensuing ground fire resulting in minimal duff consumption and relatively little exposed mineral soil compared with fires of higher intensity and burn duration. The forest floor was thinner at the recently burned site (5.4 cm) compared with the other two sites (9–10 cm) due to partial consumption during the fire. Both stand density and tree volume prior to the stand-replacing wildfire were lower in the fire reference site compared with the other sites as it was a younger stand (30-year-old) at the time of burning. The fire did result in much higher amounts of standing dead trees (107.4 m^3·ha) and moderate levels of DWD (41.6 m^3·ha), measured 3 years after the fire (Venier et al. 2017). At the time of arthropod sampling in 2018, 64% (41%–83% across the five blocks) of the standing dead trees had fallen down. Arthropod responses in this stand reflect the immediate impacts of overstory kill by fire as well as any longer term impacts enduring from the initial clearcut. In each reference stand, there were five sampling plots (70 m × 70 m) spaced ca. 20 m from each other. No glyphosate was applied in any of the reference plots.

2.4. Forest floor characterization

Superimposed over each pitfall sampling location, a 4 m × 4 m subplot was established to describe differences in forest floor characteristics across the gradient of biomass removal treatments and reference conditions. Visual estimates were recorded for % coverage of intact (undisturbed) forest floor, % mineral soil exposure, % coverage of fine woody debris (2–7 cm diameter pieces, based on large-end diameter), % coverage of coarse woody debris (>7 cm, based on small-end diameter), and % cover of understory vegetation (separate categories included moss/lichen, tall/low shrubs, herbs/grasses). The 16 m^2 subplots were divided into four 2 m × 2 m quadrats to improve consistency in the % cover visual estimates, then averaged at the subplot scale for analysis.

2.5. Arthropod collection

Arthropods were collected every two weeks using pitfall traps (diameter 11.5 cm, depth 4.5 cm) between May and August 2018. 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. In tree-length, full-tree and full-tree stumped harvested plots, traps were always placed on the undisturbed flats and not in the trenches or on the spoils. During each collection period, trap contents were emptied into a Whirl-Pak 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, 2010; Paradis and Work 2011; Graham-Sauvé et al. 2013), and biomass removal (Work et al. 2013, 2014; Venier et al. 2017). All mature specimens were identified to species. Carabid species were identified according to Lindroth (1961–1969), following the nomenclature of Bousquet and Larochelle (1993). Spiders were identified to species according to Paquin and Dupérré (2003), Dondale and Redner (1978, 1982, 1990), and references in the World Spider Catalog (2022). Rove beetles were identified primarily according to Ashe (2001), Brunke et al. (2011), and Seevers (1978). Taxonomic identification was conducted by experts that are all co-authors on the paper. Voucher specimens for the three taxonomic groups are stored at the Great Lakes Forestry Centre.

2.6. Statistical analysis

We compared % cover of undisturbed forest floor, coarse and fine woody material (FWM), and shrub and herbaceous plant cover in harvested plots with and without glyphosate and between harvested plots with no glyphosate and reference sites (recent burn, mid-managed, and older mature fire-origin stands) separately. For each comparison, we used beta regression where % cover was transformed according to Smithson and Verkuilen (2006) using the betareg package in R (Cribari-Neto and Zeileis 2010). Beta regression is often used when dependent variables are continuous and constrained between 0 and 1 such as percentage data. In these models, tree-length harvests and no glyphosate were treated as the reference condition.

Abundance of each arthropod species was summed over the season and standardized by the number of trap days. We compared composition of each arthropod group using sum of squares multivariate regression trees (ssMRT) (De'ath 2002) using the mvpart package in R. Multivariate regression trees have been used successfully to group sampling sites based on similarity in species composition similar to other approaches such as ordination. In this approach, sampling sites are constrained on explanatory variables and used to make a tree model whose final size is determined by a v-fold cross-validation procedure. The tree model is particularly useful for exploring complex or nested interactions between explanatory variables, which is commonplace in ecological studies. The explanatory variables used here are the seven harvest and reference treatments as well as % of undisturbed forest floor, % cover of CWM (%CWM), % cover of FWM (%FWM), and shrub and herb cover. We included the treatments as explanatory variables because they result in a suite of environmental changes that co-occur when forests are harvested. Understanding response to treatments is critical for informing policy. However, there is some variation in key environmental variables within treatments, so we also included these variables in the analysis. The ssMRT also provides the variance explained by each species at each split in the tree model. This approach relies on fewer underlying statistical assumptions than other multivariate methods and thus has, in some cases, outperformed other multivariate methods such as redundancy analysis (RDA) or canonical correlation analysis (CCA) (De'ath 2002). For each arthropod group, the size of the final tree model was determined as the tree size with minimum relative error based on 1000 v-fold cross-validation. Prior to analysis, arthropod catch rates were Hellinger transformed.

3. Results

3.1. Ground conditions across treatments

Within harvested plots, increasing the intensity of biomass removal reduced the amount of intact forest floor and the relative cover of deadwood and vegetation (Figs. 1A–1D) (Table 1). As expected, additional application of glyphosate significantly reduced cover (to nearly 0%) of shrubs and herbaceous plants (Fig. 1D) (Table 1). However, within the tree-length biomass removal treatment split plots that received glyphosate, several plots had relatively high cover of CWM and FWM, which contributed to overall greater cover of deadwood found in glyphosate plots compared with the no glyphosate split plots (Figs. 1B and 1C) (Table 1).

When harvested sites with no glyphosate were compared with reference sites, all the reference stands had more intact forest floor (nearly 100%) than any of the biomass removal treatments (Fig. 1E) (Table 2). The recently burned and older fire-origin stands had greater cover of coarse deadwood compared against all of the biomass removal treatments (Fig. 1F) (Table 2). In contrast, the mid-managed reference stand had lower cover of coarse deadwood than the recently burned or old burned stands and was similar to both the tree-length and full-tree biomass removal treatments (Fig. 1F) (Table 2). Relative cover of fine deadwood was similar between mid-managed, burned and tree-length removal treatments but was less in the older reference stand (Fig. 1G). Shrub and herbaceous cover was similar between the older mature fire-origin stand, recently burned, and tree-length removal treatments but was lowest in the mid-managed reference stand compared with all of the biomass removal treatments, except the bladed treatment (Fig. 1H) (Table 2).

3.2. Arthropod responses

Across all arthropod groups, changes in species composition reflected the intensity gradient of the biomass removal treatments or stand attributes associated with the disturbance gradient (Figs. 2–4). For each arthropod group, changes in composition were defined primarily by reductions or loss of abundant forest associated species (i.e., those contributing ≥1% of the variance explained in the final cross-validated tree) and increases in the number and abundance of species associated with more xeric conditions and increased disturbance intensity. For some arthropod groups, we observed a smaller set of species that were most abundant at intermediate levels of the disturbance intensity continuum than at either end of the gradient. Less common species (those contributing between 0.1% and 1% of the variance explained in the final tree) also contributed to differences in species composition but these contributions came through the collective responses of numerous, rarer species. A full species list can be found in Appendix A.

3.2.1. Ground beetles

We collected 7258 ground beetles representing 50 species. The cross-validated tree for ground beetles resulted in six nodes that reflected the disturbance intensity gradient (Fig. 2A; Table 3). This table accounted for 66.5% of the variance and was selected 768/1000 times during the cross-validation. Ground beetle assemblages in mid-managed, and older, mature fire-origin reference stands collectively formed a single node and were distinct from the recently burned reference stand. Tree-length and full-tree treatments with

Fig. 1. Relative cover (95% CI) of undisturbed forest floor, coarse woody material, fine woody material, and shrubs and herbaceous plants in harvested plots with and without application of glyphosate (A–D), and between harvested plots without glyphosate and recent burn, mid-rotation managed and older mature fire-origin reference stands (E–H). Results in panels A–D correspond to regression models including only sites at the Island Lake experimental site. Results in panels E–H correspond to a separate regression model that included reference sites (recent burn, mid-rotation managed and older mature fire-origin stands) and Island Lake sites that did not receive glyphosate.

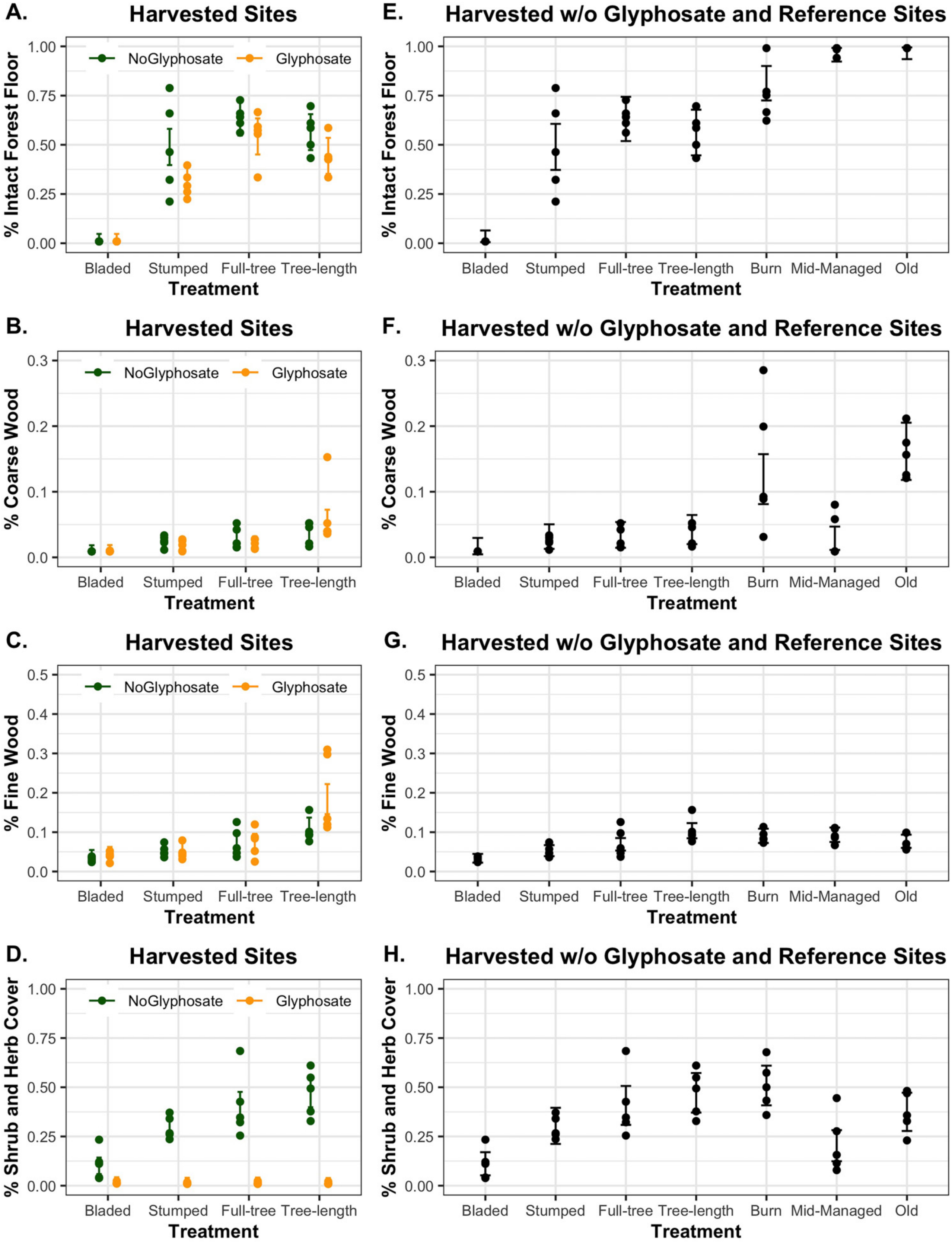


Table 1. Parameter estimates from beta regressions comparing % cover of undisturbed forest floor, coarse and fine woody material, and shrub and herb cover between biomass removal treatments with and without glyphosate application. The reference condition used for comparing significance of model terms is tree-length harvest without glyphosate ($^{+}p < 0.1$; $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$).

	% Undisturbed forest floor	% CWM	% FWM	% Shrub and herb
(Intercept)	0.259 (0.189)	−3.269 (0.178) ***	−2.124 (0.161) ***	−0.116 (0.149)
Bladed	−3.874 (0.464) ***	−1.152 (0.334) ***	−1.132 (0.296) ***	−2.071 (0.278) ***
Stumped	−0.302 (0.267)	−0.356 (0.271)	−0.694 (0.264) **	−0.739 (0.219) ***
Full-tree	0.297 (0.271)	−0.260 (0.265)	−0.426(0.248)$^{+}$	−0.268 (0.212)
Glyphosate	−0.484(0.267)$^{+}$	0.467 (0.229) *	0.634 (0.207) **	−3.664 (0.418) ***
Bladed × glyphosate	0.484 (0.629)	−0.446 (0.458)	−0.471 (0.398)	2.180 (0.595) ***
Stumped × glyphosate	−0.286 (0.384)	−0.767 (0.386) *	−0.716 (0.365) *	0.766 (0.574)
Full-tree × glyphosate	0.099 (0.381)	−0.711(0.374)$^{+}$	−0.654(0.338)$^{+}$	0.339 (0.568)
Phi	21.645 (4.962) ***	166.900 (38.223) ***	76.854 (17.365) ***	35.371 (8.370) ***
Number of observations	40	40	40	40
R2 pseudo	0.956	0.669	0.679	0.940
AIC	−89.1	−232.2	−158.2	−142.3
BIC	−73.9	−217.0	−143.0	−127.1
Log.Like	53.547	125.085	88.122	80.169

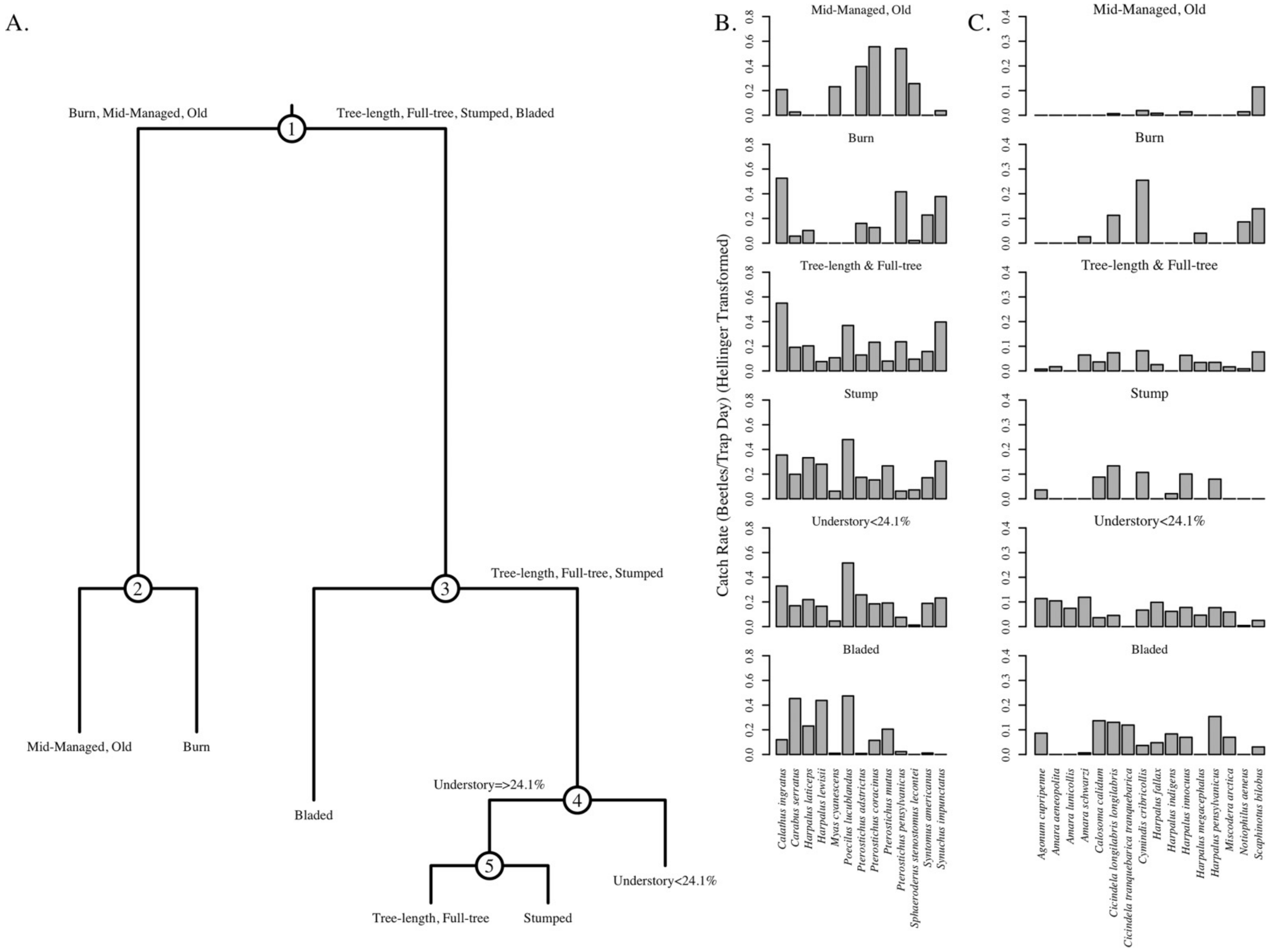
Table 2. Parameter estimates from beta regressions comparing % cover of undisturbed forest floor, coarse and fine woody material, and shrub and herb cover between four biomass removal treatments without glyphosate application and three reference stands. The reference condition used for comparing significance of model terms is tree-length harvest without glyphosate ($^{+}p < 0.1$; $^{*}p \le 0.05$, $^{**}p \le 0.01$, $^{***}p \le 0.001$).

	% Undisturbed forest floor	% CWM	% FWM	% Shrub and herb
(Intercept)	0.250 (0.240)	−3.118 (0.279) ***	−2.156 (0.106) ***	−0.113 (0.206)
Bladed	−3.566 (0.510) ***	−0.930 (0.459) *	−1.200 (0.204) ***	−1.965 (0.366) ***
Stumped	−0.293 (0.339)	−0.302 (0.410)	−0.727 (0.177) ***	−0.716 (0.302) *
Full-tree	0.287 (0.344)	−0.223 (0.405)	−0.444 (0.165) **	−0.261 (0.293)
Burn	1.218 (0.379) **	1.118 (0.333) ***	−0.150 (0.154)	0.148 (0.291)
Mid-managed	2.864 (0.495) ***	−0.388 (0.417)	−0.117 (0.153)	−1.255 (0.323) ***
Old	3.065 (0.507) ***	1.471 (0.322) ***	−0.330 (0.160) *	−0.398 (0.295)
Phi	12.986 (3.301) ***	52.216 (13.037) ***	188.270 (45.151) ***	17.888 (4.197) ***
Number of observations	35	35	35	35
R2 pseudo	0.933	0.719	0.679	0.649
AIC	−87.1	−146.9	−165.5	−46.4
BIC	−74.7	−134.5	−153.1	−34.0
Log.Like	51.550	81.463	90.753	31.198

≥24.1% ground cover collectively formed a single node and were distinct from four stump removal sites with relatively high levels of ground cover. Tree-length, full-tree, and stump removal sites with lower vegetation cover (<24.1%) comprised a single node. With the exception of a single stump removal site with low levels of ground cover, all sites within this node had been treated with glyphosate. Ground beetle assemblages in bladed plots formed a single node, irrespective of glyphosate addition.

Increasing disturbance intensity greatly reduced or eliminated abundant forest-associated species including *Myas cyanescens* Dejean, *Pterostichus adstrictus* Eschscholtz, *Pterostichus coracinus* (Newman), *Pterostichus pensylvanicus* Leconte, and *Sphaeroderus stenostomus lecontei* (Dejean) (Fig. 2B). In contrast, increasing treatment intensity favoured open habitat-associated species such as *Poecilus lucublandus* (Say), *Harpalus laticeps* Leconte, *Harpalus lewisii* LeConte, and *Carabus serratus* (Say) (Fig. 2B). Abundant species falling broadly between the extremes of the gradient included *Calathus ingratus* Dejean, *Syntomus americanus* (Dejean), and *Synuchus impunctatus* (Say), which had higher catch rates than in either young and old stands or the bladed treatments (Fig. 2B). For less common species, increasing disturbance intensity increased the number of species in all bladed plots and tree-length, full-tree, and stumped plots treated with less ground cover including numerous open habitat species within the genus *Harpalus* and *Amara* and two *Cincidela* species (Fig. 2C). In contrast, fewer, less common species were collected from the reference stands (Fig. 2C). These species accounted for 6.74% of the variation explained.

Fig. 2. (A) Sum of squares multivariate regression tree (ssMRT) for ground beetles and Hellinger-transformed mean catch rates for (B) abundant (>1% of total variance) and (C) less common species (0.1%–1% of total variance) comparing differences in ground beetle composition across biomass removal treatments with and without glyphosate and recent burn, mid-rotation managed, and older, mature fire-origin reference stands. The ssMRT explains 66.6% of the variance and was selected 768 times through 1000 v-fold cross validations.



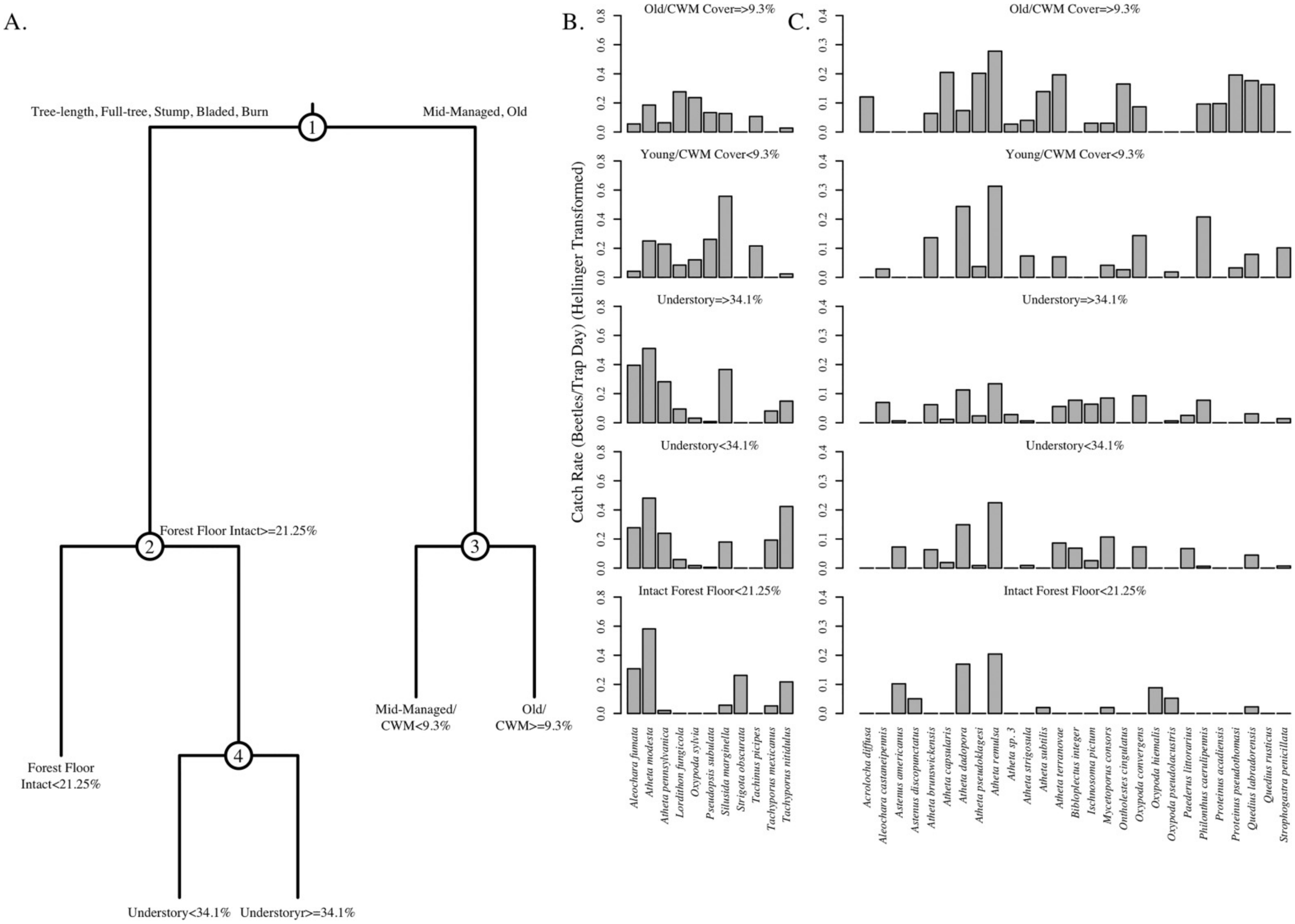
3.2.2. Rove beetles

We collected 3218 rove beetles representing 108 species. The cross-validated tree for rove beetles resulted in five nodes that initially split out the mid-managed and older, mature fire-origin reference conditions (i.e., closed canopy forests) from the younger, regenerating forests (i.e., all biomass removal treatments, along with the recent burn reference). All subsequent nodes were defined by stand attributes related to the amount of intact forest floor, coarse wood cover, or understory vegetation cover (Fig. 3A; Table 4). The ssMRT accounted for 38.0% of the variance and was selected 853/1000 times by the cross-validation.

Rove beetle assemblages in plots with higher levels of CWM (≥9.3%) were distinct from plots with lower levels (<9.3%) of coarse wood cover. This split was, however, synonymous with a separation between older, mature fire-origin and mid-managed reference stands. Harvested (all biomass removal treatments) and the recently burned sites were further split between plots with higher levels of intact forest floor (≥21.25%) from those with less (<21.25%) intact forest floor. Sites with higher levels of intact forest floor were further split based on the amount of understory vegetation cover. In this case, sites with more ground cover (≥34.1%) were distinct from those with less ground cover. Sites with more ground cover included all of the recently burned sites and eight harvested sites that had not received glyphosate. Sites with less ground cover included 15 harvested sites that had been treated with glyphosate and 6 harvested sites that had not received glyphosate. Harvested sites with little intact forest floor (<21.25%) harboured distinct rove beetle assemblages and included all bladed sites and a single stump removal site that had not received glyphosate.

Compared with ground beetles, responses of abundant rove beetle species were generally more broadly distributed across the disturbance gradient. Increasing disturbance intensity reduced or eliminated *Lordithon fungicola* Campbell,

Fig. 3. (A) Sum of squares multivariate regression tree (ssMRT) for rove beetles and Hellinger-transformed mean catch rates for (B) abundant (>1% of total variance) and (C) less common species (0.1%–1% of total variance) comparing differences in rove beetle composition across biomass removal treatments with and without glyphosate and recent burn, mid-rotation managed, and older, mature fire-origin reference stands. The ssMRT explains 38.0% of the variance and was selected 853 times out of 1000 v-fold validations.



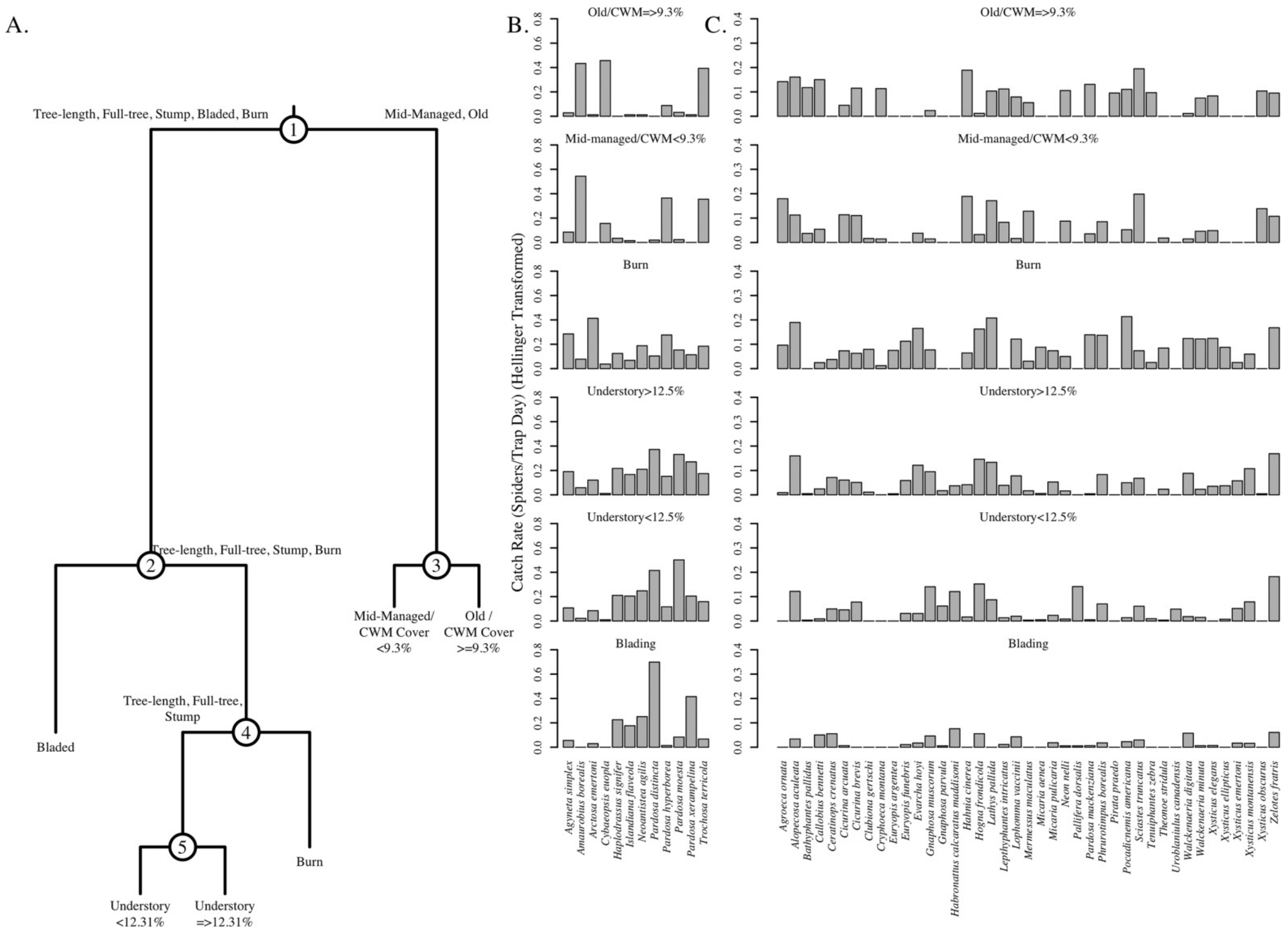
Oxypoda sylvia Casey, *Pseudopsis subulata* Herman, and *Tachinus picipes* Erichson (Fig. 3B). In contrast, increasing disturbance favoured *Atheta modesta* (F.E. Melsheimer), *Strigota obscurata* Klimaszewski and Brunke, *Tachyporus mexicanus* Sharp, and *Tachyporus nitidulus* (Fabricus) (Fig. 3B). *Atheta pensylvanica* Bernhauer and *Silusida marginella* (Casey) were two abundant species falling broadly between the extremes of the gradient. However, the number and abundance of less common rove beetle species declined with increasing disturbance intensity (Fig. 3C). In the most disturbed sites, less common species were primarily a mix of remnant species associated with closed canopy forests (*Atheta dadopora* C.G. Thompson, *Atheta remulsa* Casey, and *Quedius labrodorensis* Stephens) and species that favour disturbed conditions (*Astenus americanus* (Casey), *Astenus discopunctatus* (Say), *Oxypoda hiemalis* Casey, and *Oxypoda pseudolacustis* Casey).

3.2.3. Spiders

We collected 10 854 spiders representing 166 species. The cross-validated tree for spiders resulted in six nodes that largely reflected the disturbance intensity gradient (Fig. 4A;Table 5). Only the final split was based on understory plant cover within the tree-length, full-tree biomass, and stumped grouping. The ssMRT accounted for 63.8% of the variance and was selected 445/1000 times through cross-validation. Spider assemblages in all reference stands were distinct and different from harvested sites. Spider assemblages in recently burned sites, however, were more similar to harvested sites than to older, mature fire-origin, or mid-managed stands. Tree-length, full-tree, and stump removal sites with ≥12.31% ground vegetation cover maintained a distinct spider assemblage from plots with less ground vegetation. This split was, however, synonymous with a separation between sites that did not receive glyphosate and those that did. Spider assemblages in bladed plots formed a single node, irrespective of glyphosate addition.

Increasing disturbance intensity greatly reduced or eliminated abundant forest-associated species including *Amaurobius borealis* Emerton, *Cybaeopsis euopla* (Bishop & Crosby), and *Trochosa terricola* (Thorell) (Fig. 4B). Increasing treatment intensity favoured open habitat-associated species including

Fig. 4. (A) Sum of squares multivariate regression tree (ssMRT) for spiders and Hellinger-transformed mean catch rates for (B) abundant (>1% of total variance) and (C) less common species (0.1%–1% of total variance) comparing differences in spider composition across biomass removal treatments with and without glyphosate and recent burn, mid-rotation managed, and older, mature fire-origin reference stands. The ssMRT accounts for 63.8% of the variance and was selected 445 times out of 1000 v-fold validations.



Haplodrassus signifier (C. L. Koch), *Islandiana flaveola* (Banks), *Neoantistea agilis* (Keyserling), *Pardosa distincta* (Blackwall), and *Pardosa xerampelina* (Keyserling) (Fig. 4B). Abundant species falling broadly between the extremes of the gradient included *Agyneta simplex* (Emerton), *Arctosa emertoni* Gertsch, and *Pardosa hyperborea* (Thorell), which had higher catch rates than in either old stand or the bladed treatment (Fig. 4B). As with rove beetles, the number and abundance of less common spider species declined with increasing disturbance intensity (Fig. 4C).

4. Discussion

4.1. Reference benchmarks (recent burn, mid-managed, and older, mature fire-origin stands)

Natural disturbance-based management relies on comparisons of managed stands to a range of ecological benchmarks that capture biotic responses after disturbances, across successional seres and into late-development or old growth phases of stand development (Mitchell et al. 2002; Bergeron et al. 2007; Long 2009). In jack pine ecosystems of eastern North America, ecological benchmarks for ground arthropods are not fully developed. In our study, we provide a partial set of ecological benchmarks demonstrating the endpoints (recent burn and older, mature fire-origin forest) of succession in eastern jack pine ecosystems as well as a 57-year old, mid-rotation, managed stand as reference points to compare the effects of biomass removal and glyphosate application.

In our study, ground beetle and spider communities in recent burns were distinct from those collected from older, mature fire-origin stands reflecting major differences in canopy closure. Ground beetles did not however differentiate between mature fire-origin stands and the mid-managed stand suggesting canopy closure is a major ecological milestone that defines ground beetle assemblages (Work et al. 2010, 2014). In contrast, spider assemblages were distinct between mature fire-origin stands and the mid-managed stand. This difference was defined primarily by greater numbers of

Table 3. Variance explained at successive splits in sum-of-squares multivariate regression tree of 75 ground beetle species (Fig. 2A).

	Split-1	Split-2	Split-3	Split-4	Split-5	Tree total	Species total
Calathus ingratus	0.020	1.452	2.657	0.876	0.468	5.474	7.673
Carabus serratus	2.118	0.013	2.408	0.020	0.001	4.560	5.852
Harpalus laticeps	1.793	0.151	0.000	0.015	0.206	2.165	3.642
Harpalus lewisii	2.329	0.000	2.668	0.030	0.514	5.541	7.292
Myas cyanescens	0.477	0.770	0.112	0.077	0.025	1.462	2.275
Poecilus lucublandus	10.182	0.000	0.005	0.430	0.153	10.770	11.981
Pterostichus adstrictus	1.236	0.799	1.236	0.431	0.025	3.727	4.942
Pterostichus coracinus	2.631	2.644	0.217	0.021	0.078	5.590	6.755
Pterostichus mutus	1.433	0.000	0.054	0.110	0.431	2.028	4.606
Pterostichus pensylvanicus	7.424	0.220	0.349	0.400	0.373	8.767	10.063
Sphaeroderus stenostomus lecontei	0.948	0.795	0.075	0.186	0.007	2.011	2.436
Syntomus americanus	0.162	0.744	0.871	0.024	0.002	1.803	3.326
Synuchus impunctatus	0.242	1.664	2.846	0.620	0.103	5.474	6.879
16 less common species	2.199	1.079	1.737	1.473	0.296	6.784	19.145
21 rare species	0.195	0.079	0.123	0.050	0.023	0.471	3.134
Total variance explained	33.388	10.409	15.359	4.764	2.706	66.626	100.000

Table 4. Variance explained at successive splits in sum-of-squares multivariate regression tree of 108 rove beetle species (Fig. 3A).

	Split-1	Split-2	Split-3	Split-4	Tree total	Species total
Aleochara fumata	2.560	0.046	0.002	1.053	3.661	6.122
Atheta modesta	2.950	0.163	0.044	0.094	3.250	5.501
Atheta pennsylvanica	0.099	1.669	0.283	0.410	2.461	7.801
Lordithon fungicola	0.521	0.170	0.383	0.035	1.109	2.435
Oxypoda sylvia	0.873	0.018	0.138	0.000	1.030	1.555
Pseudopsis subulata	1.260	0.001	0.169	0.001	1.432	2.018
Silusida marginella	0.625	1.101	1.920	0.461	4.108	7.284
Strigota obscurata	0.134	2.694	0.000	0.000	2.828	3.771
Tachinus picipes	0.888	0.000	0.123	0.000	1.012	1.552
Tachyporus mexicanus	0.529	0.486	0.000	0.428	1.444	3.534
Tachyporus nitidulus	2.422	0.351	0.000	1.020	3.793	8.967
27 less common species	4.114	1.781	2.857	1.473	10.224	34.088
70 less common species	0.712	0.298	0.434	0.246	1.690	15.371
Total variance explained	17.688	8.778	6.354	5.220	38.041	100.000

Cybeaopsis eupola in older stands and *Pardosa hyperborea* in mid-managed stands. *Cybeaopsis eupola* has been previously reported to be associated with closed canopy deciduous forests in Western Canada (Pinzon et al. 2016) as well as older black spruce stands with greater levels of retention in eastern Canada (Paradis and Work 2011). In contrast, abundance of *Pardosa hyperborea* is promoted by removal of the overstory (Paradis and Work 2011; Pinzon et al. 2016), which, according to our study, continues to persist for nearly six decades postharvest.

Rove beetle assemblages were distinctive between mature fire-origin stands and the mid-managed stand that was synonymous with differences in cover of CWM. In older stands with greater CWM cover, we collected greater abundances of species defined as forest specialists including *Atheta pseudomoesta*, *Ontholestes cingulatus*, *Quedius labrodorensis*, and *Quedius rusticus* (Klimaszewski et al. 2008). Rove beetle assemblages did not collectively group as recently burned sites, rather were grouped based on the level of soil disturbance and understory vegetation. The results for rove beetles suggest that forest floor condition and vegetative cover should be included in stand-scale examinations of natural disturbance emulation (Venier et al. 2017). The ecological equivalence of recent harvest to recent wildfire for rove beetles does, however, need to be interpreted with caution, since this particular fire left more forest floor intact (>50%) than would normally be expected in medium to intense, stand-replacing wildfires in jack pine systems (de Groot et al. 2009). Interpreting soil impacts caused by wildfire is complicated by the fact that forest floor disturbance is often reported in terms of total fuel consumption rather than mineral soil exposure. There is also ample evidence of high uncertainty and vari-

Table 5. Variance explained at successive splits in sum-of-squares multivariate regression tree of 166 spider species (Fig. 4A).

	Split-1	Split-2	Split-3	Split-4	Split-5	Tree total	Species total
Agyneta simplex	0.256	0.409	0.033	0.327	0.214	1.239	1.977
Amaurobius borealis	6.950	0.066	0.126	0.025	0.042	7.210	7.645
Arctosa emertoni	0.445	0.445	0.002	1.714	0.040	2.646	3.184
Cybaeopsis euopla	2.950	0.007	0.937	0.013	0.000	3.906	4.186
Haplodrassus signifer	1.215	0.019	0.012	0.140	0.001	1.388	2.102
Islandiana flaveola	0.836	0.002	0.000	0.246	0.046	1.129	1.798
Neoantistea agilis	1.686	0.026	0.002	0.029	0.046	1.788	2.780
Pardosa distincta	5.963	3.860	0.004	1.490	0.057	11.374	14.102
Pardosa hyperborea	0.358	0.639	0.790	0.358	0.039	2.183	3.291
Pardosa moesta	2.769	2.814	0.001	1.232	0.892	7.708	10.198
Pardosa xerampelina	2.240	1.226	0.002	0.270	0.135	3.874	5.285
Trochosa terricola	1.756	0.336	0.015	0.005	0.007	2.120	2.616
41 less common species	6.231	3.029	0.964	3.021	1.980	15.225	28.965
113 rare species	0.885	0.355	0.385	0.217	0.209	2.051	11.871
Total variance explained	34.540	13.234	3.271	9.088	3.708	63.840	100.000

ability in forest floor consumption by wildfire (French et al. 2004) which, in turn, suggests that arthropod community response should be examined in the context of more variable wildfire outcomes and provides support for more research on the characterization of the natural range of variability in forest floor disturbance after wildfire.

A caveat to our conclusions in relation to the reference conditions is that, although we have demonstrated strong similarity in the tree species composition and soil characteristics of the three sites (Venier et al. 2017), the reference sites still exist as single locations separated by 10s of kilometers and so the potential exists for a geographic bias. The most parsimonious explanations for differences between sites are the large treatment effects related to stand origin and time since disturbance, but we cannot statistically remove the potential spatial effects.

4.2. Harvest treatments

Following overstory removal, all three taxonomic groups responded to the gradient of increased harvest intensity from the least intense harvest practices (tree-length and full-tree) to the most intense (blading). The range of arthropod responses highlights the interaction of habitat features associated with the forest floor including the surface organic layer and herb and shrub cover. We suggest that treatments that greatly disturb the upper soil surface remove habitat for forest species and are a primary agent of mortality but the presence of herb and shrub cover may buffer the impacts of sun exposure for forest species when the soil surface is left intact.

4.3. Blading

Blading, regardless of herbicide application, consistently reduced abundances of forest-associated species and favoured a much smaller suite of species associated with xeric or disturbed habitats. Reduction or elimination of organic matter on the soil surface is likely a major source of mortality for larvae of both ground beetles and rove beetles, which are highly sensitive to desiccation (Lövei and Sunderland 1996; Bohac 1999; Lundgren et al. 2005). For adult beetles, a thicker organic layer in the soil permits individuals to burrow deeper into the soil surface when surface temperatures are elevated or when surface layers become drier. Experimental leaf litter additions resulted in increases of individual ground beetle species (Koivula et al. 1999; Magura et al. 2004). In contrast, increased disturbance of soil organic layer through scarification greatly reduced the abundance of both ground beetles (Klimaszewski et al. 2005) and rove beetles (Klimaszewski et al. 2008).

In our study, blading increased the abundance of disturbance-adapted ground beetles including *Poecilus lucublandis* and several *Harpalus* and *Cicindela* species. For some groups such as *Cicindela* larvae, exposure of mineral soils likely increases area available for the construction of burrows for ambushing prey. However, greater abundance of disturbance adapted species is likely a reflection of recent congregation of open habitats from neighboring stands rather than survival and increases in populations after blading. For spiders, a similar use of open habitats and a simplified, uniform forest floor manifested as increased capture of xerophilic species, such as *Pardosa distincta* and *Pardosa xerampelina*, which is consistent with other biomass removal studies (Work et al. 2014).

Notably, several species often characterized as open habitat or disturbance-adapted species were absent or largely reduced from the bladed plots. In our study, abundance of *Amara aeneopolita*, *A. lunicollis*, and *A. schwarzi*, often associated with open habitats, was absent from bladed plots. Many *Amara* species feed on seeds of weedy plants as adults and some also as larvae (Saska and Jarosik 2001). While it is tempting to interpret the reduced abundance of these *Amara* to a reduction in seed source, the presence of other seed-feeding carabids such as *Harpalus pensylvanicus*, *Harpalus laticeps*, and *Harpalus lewisii* in bladed plots suggests that changes in *Amara* species may be more linked to changes in habitat conditions rather than availability of food resources such as seeds.

4.4. Stump removal

While removal of residual stumps can pose risks for saproxylic insects that feed on wood tissues and fungi in stumps (Jonsell and Schroeder 2014; Work et al. 2016), impacts were most prevalent in ground beetles and fell between bladed and full-tree and tree-length removal treatments. Similar to bladed plots, less common *Amara* species were further reduced in or absent from stumped sites suggesting that soil disturbance from stump removal is driving these changes. However, in contrast to bladed plots, common ground beetles that are adapted to disturbance conditions, including *Calathus ingratus* and *Synuchus impunctatus*, were present suggesting an ecological lower limit to soil disturbance from biomass harvesting for ground beetles.

4.5. Full-tree and tree-length harvesting

A key, policy-relevant result from this study is that in all three taxa, we do not see a different community response in the tree-length and full-tree harvest treatments. Historically, tree-length harvesting (i.e., cut & skid logging operations) was the standard logging method associated with clearcut harvest systems across the boreal. However, there was a rapid shift to highly mechanized full-tree harvesting in the early 1970s to where nearly all clearcut operations were using the full-tree logging method. Early criticism was raised regarding this shift as potentially compromising the sustainability of forest ecosystems due to the removal of important resources (Boyle and Ek 1972; Weetman and Webber 1972), and was the impetus for the North American-wide long-term soil productivity network (Powers 2006) and comparable studies established across Scandinavia (reviewed by Engell 2017). Others have advocated for the precautionary approach to biomass harvesting, and a return to tree-length harvesting systems (Hesselink 2010; Lattimore et al. 2010). Our results, however, would suggest that the full-tree harvest effects cannot be ameliorated by leaving tops and branches on site. Although our results should not be viewed as direct evidence that full-tree harvesting is sustainable, it does suggest that the less intensive option of tree-length harvest would not improve the community composition and it is more likely the overarching effect of clearcut harvest (i.e., complete removal of the overstory removal) that is driving the initial arthropod compositional changes. These specific communities do not appear to respond to the increase in logging debris loadings associated with the tree-length harvest treatments (i.e., neither the amount of coarse woody debris nor fine woody debris resulted in any significant splits in the three ssMRTs with respect to the harvest treatments). This result is consistent with the earlier work on the same plots at 2 years postharvest (Venier et al. 2017), and is also consistent with several other biodiversity-focused studies on biomass harvest experiments (Smenderovac et al. 2017, 2023; Rousseau et al. 2018*a*, 2018*b*, 2019) for other taxonomic groups.

From a policy perspective, one emerging reason why full-tree harvesting will likely remain as the mainstay logging method is that it moves wood residue (i.e., tops and branches) to roadside where they can be easily collected as biomass feedstock for bioenergy (Barrette et al. 2018). Forest logging residue has been identified as an important resource (Paré et al. 2011) that has important greenhouse gas mitigation potential (Laganière et al. 2017). By including the higher (stumping) and extreme (blading) treatments, we did, however, show that they resulted in additional changes in arthropod assemblages beyond those following the tree-length and full-tree harvests. These results, in turn, suggest that threshold levels of biomass retention should be set in forest management guidelines with respect to biomass harvesting systems that will help to conserve biodiversity.

4.6. Vegetation control with glyphosate

In the stumped, full-tree and tree-length treatment plots, differences in composition following biomass removal were further altered by the application of glyphosate. In our study, composition of abundant ground beetles in glyphosate-treated tree-length and full-tree sites was more similar to untreated stumped plots. For less common species, composition in glyphosate-treated tree-length and full-tree sites more closely resembled bladed plots, with an important exception that many *Amara* species, including *A. aeneopolita*, *A. lunicollis*, and *A. schwarzi*, were present. For ground beetles, reduction of vegetation with glyphosate may either intensify the effects or delay recovery of biomass removal treatments. This conclusion is tempered by the fact that a single stumped plot with low vegetation cover that did not receive glyphosate grouped with harvested sites that received glyphosate. This result suggests that the actual driver is the amount of vegetative cover and the associated buffering from direct sun exposure and not a direct toxicity effect of glyphosate per se.

The use of glyphosate appears to delay the recovery of arthropod communities, which, in turn, suggests that glyphosate should be used judiciously, thereby retaining a reasonable level of understory plant cover while still achieving the silvicultural objective of releasing crop trees from heavy competition. Determining what is a “reasonable” level would, however, be complicated across taxa. Even for our arthropod example here, vegetation cover-based splits in the ssMRTs varied across the three taxa, with splits at 34.1%, 24.1%, and 12.3% for ground beetles, rove beetles, and spiders, respectively. The precautionary principle would suggest using the highest value here (34.1%) as a target to support the full range of taxa.

4.7. Management opportunities to improve sustainability

These results highlight key stressors created through current clearcut harvest and renewal practices in jack pine ecosystems that could be modified to improve sustainability. First, the dominant impacts of complete removal of the overstory ground arthropods could be alleviated by maintaining at least some residual retention. Variable retention has been suggested for other, mixed species stands as a harvest alternative where significant overstory is retained in harvested stands (Martikainen et al. 2006; Work et al. 2010; Lee et al. 2023). One form of retention could be through commercial thinning in density-regulated managed jack pine stands. This involves partial canopy retention (i.e., current commercial thinning best management practices suggest a 30%–35% basal area removal at first entry; McKinnon et al. 2006) at 50–60 years and should help to minimize impacts and accelerate recovery to the preharvest conditions. Precommercial thinning promotes growth of the remaining stand and allows for an extension in the rotation age to the final renewal harvest at approximately 100 years.

Second, silvicultural approaches that reduce disturbance of the forest floor layer would benefit a large number of taxa that live in the soil organic layer. Explicit protection of forest soils is not generally considered in the natural disturbance emulation paradigm and requires research on two fronts; characterization of the natural range of variability in forest floor disturbance and a better understanding of how soil disturbance influences soil communities. Aggressive scarification techniques, such as mechanical disc trenching, elicited similar responses of ground beetles and rove beetles (Klimaszewski et al. 2005, 2008) should be more thoroughly examined to better understand their effects relative to the natural range of fire outcomes. Passive site preparation techniques, such as drags or patch scarifiers, that reduce the overall disturbance/disruption to the forest floor should help accelerate recovery while still providing sufficient plantable spots or viable seedbeds for forest renewal efforts.

Third, there is ample evidence to support the need for preservation of CWM in the context of conservation of saproxylic arthropods and fungi (Berg et al. 1994; Stockland et al. 2012). The role of CWM for ground arthropods is less apparent but see Buddle (2001), Grodsky et al. (2018), and Pinzon et al. (2018). This study highlights how many rove beetle species classified as forest specialists (Klimaszewski et al. 2018) were present only in closed canopy stands when cover of CWM was elevated. This and studies from saproxylics suggest that protection of legacy CWM and improvement of the temporal supply of CWM are important refinements in forest management policy to protect biodiversity (Berch et al. 2011).

Finally, understory shrub and herb cover was demonstrated to be important in arthropod community composition and recovery when soil disturbance was reduced. Evidence here suggests that vegetation control that significantly reduces understory vegetation cover, commonly done using broadcast, aerial application of glyphosate, will delay the recovery of arthropod communities. Although this delay is temporary, its effects could be reduced through application only when and where necessary to achieve the silvicultural objective of releasing crop trees experiencing heavy competition.

4.8. Comparison with study 2 years postdisturbance

There are some key differences and similarities in the study conducted in 2013 (2 years postdisturbance; Venier et al. 2017) and the current study (7 years postdisturbance). The current study included a glyphosate treatment in the analysis and found an important interaction between glyphosate and harvest intensity, whereas the original published study did not include a glyphosate treatment. We expect that glyphosate would not have been as important in the earlier study because the understory was not well developed in any of the treatments. As well there is a suggestion of recovery in the ground beetle communities in mid-managed stands that had different communities from the old reference condition in the first study but no difference in the more recent study. In most other respects, however, the results were similar in that the most intense biomass harvest treatments (stumped and bladed) showed significant differences in community composition and tree-length and stem-only treatments did not have different communities. Lastly, both studies demonstrated the continuing importance of overstory removal and forest floor disturbance to the arthropod communities.

5. Conclusions

Our study presents species-level responses of ground arthropods across a very broad gradient in disturbance from an older, mature, fire-origin reference condition to complete organic matter removal by blading. Community change along this gradient was not surprising. Similarities in ground beetle communities between the mid-managed forest and the fire-origin mature forest suggest that canopy closure is a major ecological milestone for these taxa. However, this appears to be less true for spiders and rove beetles that may also be responding to other habitat characteristics (e.g., cover of CWM) offered by the mature fire-origin stand. Within just the biomass harvest gradient, we also observed evidence of community response: in particular, blading always resulted in obvious community shifts, whereas stumping showed some shifts, but these shifts were mostly associated with reduced understory plant cover caused by the glyphosate applications. We interpret these results as an indication of the influence that forest floor disturbance has on arthropod community structure and that the use of glyphosate to reduce understory plant competition sets back the recovery of arthropods. In this case, the disturbance effects in our least intensive harvest treatments (i.e., tree-length and full-tree) were increased with reductions in understory cover. We did not, however, see community differences between the tree-length and full-tree treatments suggesting that the full-tree harvest effects on arthropods cannot be ameliorated by reducing the amount of biomass removed from the site (i.e., retaining the tops and limbs). This result, in turn, provides evidence that supports the continued practice of removing tops and branches to roadside making them available as biomass feedstocks.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Lisa Venier https://orcid.org/0000-0002-7738-1361

Author notes

At the time of manuscript review and acceptance Lisa Venier served as Associate Editor and Timothy Work and Dave Morris as Guest Editors; peer review and editorial decisions regarding this manuscript were handled by Christian MacQuarrie.

Author J. Klimaszewski is retired.

Author contributions

Conceptualization: DMM, LV
Data curation: SL, JK, KW, LV
Formal analysis: TTW
Funding acquisition: LV
Investigation: TTW, DMM, SL, JK, KW
Methodology: TTW, DMM, SL, KW, LV
Project administration: KW, LV
Supervision: KW, LV
Validation: SL, JK
Visualization: TTW
Writing – original draft: TTW, LV
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Competing interests

There are no competing interests for any of the authors.

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Appendix A. Complete species list with abundance

Order	Family	Genus	Species	Abundance
Coleoptera	Carabidae	Agonum	cupripenne	72
Coleoptera	Carabidae	Agonum	retractum	8
Coleoptera	Carabidae	Amara	aeneopolita	49
Coleoptera	Carabidae	Amara	lunicollis	30
Coleoptera	Carabidae	Amara	obesa	3
Coleoptera	Carabidae	Amara	schwarzi	60
Coleoptera	Carabidae	Anisodactylus	harrisii	1
Coleoptera	Carabidae	Anisodactylus	nigerrimus	3
Coleoptera	Carabidae	Anisodactylus	rusticus	1
Coleoptera	Carabidae	Bembidion	mutatum	9
Coleoptera	Carabidae	Calathus	ingratus	872
Coleoptera	Carabidae	Calosoma	calidum	55
Coleoptera	Carabidae	Calosoma	frigidum	4
Coleoptera	Carabidae	Carabus	serratus	392
Coleoptera	Carabidae	Cicindela	limbalis	6
Coleoptera	Carabidae	Cicindela	longilabris longilabris	92
Coleoptera	Carabidae	Cicindela	tranquebarica tranquebarica	28
Coleoptera	Carabidae	Cymindis	cribricollis	65
Coleoptera	Carabidae	Harpalus	affinis	1
Coleoptera	Carabidae	Harpalus	fallax	61
Coleoptera	Carabidae	Harpalus	fulvilabris	7
Coleoptera	Carabidae	Harpalus	herbivagus	2
Coleoptera	Carabidae	Harpalus	indigens	32
Coleoptera	Carabidae	Harpalus	innocuus	57
Coleoptera	Carabidae	Harpalus	laticeps	299
Coleoptera	Carabidae	Harpalus	lewisii	442
Coleoptera	Carabidae	Harpalus	megacephalus	14
Coleoptera	Carabidae	Harpalus	opacipennis	3
Coleoptera	Carabidae	Harpalus	pensylvanicus	85
Coleoptera	Carabidae	Harpalus	plenalis	1
Coleoptera	Carabidae	Harpalus	solitaris	19
Coleoptera	Carabidae	Harpalus	sp.	1
Coleoptera	Carabidae	Miscodera	arctica	34
Coleoptera	Carabidae	Myas	cyanescens	126

(*continued*).

Order	Family	Genus	Species	Abundance
Coleoptera	Carabidae	Notiophilus	aeneus	10
Coleoptera	Carabidae	Notiophilus	semistriatus	7
Coleoptera	Carabidae	Platynus	decentis	2
Coleoptera	Carabidae	Poecilus	lucublandus	1143
Coleoptera	Carabidae	Pterostichus	adstrictus	517
Coleoptera	Carabidae	Pterostichus	commutabilis	2
Coleoptera	Carabidae	Pterostichus	coracinus	732
Coleoptera	Carabidae	Pterostichus	mutus	301
Coleoptera	Carabidae	Pterostichus	pensylvanicus	745
Coleoptera	Carabidae	Pterostichus	punctatissimus	4
Coleoptera	Carabidae	Scaphinotus	bilobus	66
Coleoptera	Carabidae	Sphaeroderus	nitidicollis	24
Coleoptera	Carabidae	Sphaeroderus	stenostomus lecontei	139
Coleoptera	Carabidae	Syntomus	americanus	165
Coleoptera	Carabidae	Synuchus	impunctatus	466
Coleoptera	Carabidae	Tachyta	angulata	1
Coleoptera	Staphylinidae	Acrolocha	diffusa	11
Coleoptera	Staphylinidae	Aleochara	castaneipennis	44
Coleoptera	Staphylinidae	Aleochara	fumata	405
Coleoptera	Staphylinidae	Amischa	analis	1
Coleoptera	Staphylinidae	Astenus	americanus	18
Coleoptera	Staphylinidae	Astenus	brevipennis	2
Coleoptera	Staphylinidae	Astenus	discopunctatus	2
Coleoptera	Staphylinidae	Atheta	brunswickensis	51
Coleoptera	Staphylinidae	Atheta	capsularis	23
Coleoptera	Staphylinidae	Atheta	dadopora	97
Coleoptera	Staphylinidae	Atheta	frosti	25
Coleoptera	Staphylinidae	Atheta	hampshirensis	2
Coleoptera	Staphylinidae	Atheta	klagesi complex	3
Coleoptera	Staphylinidae	Atheta	longiclava	7
Coleoptera	Staphylinidae	Atheta	modesta	628
Coleoptera	Staphylinidae	Atheta	pennsylvanica	307
Coleoptera	Staphylinidae	Atheta	prudhoensis	1
Coleoptera	Staphylinidae	Atheta	pseudoklagesi	18
Coleoptera	Staphylinidae	Atheta	pseudomodesta	1
Coleoptera	Staphylinidae	Atheta	pseudosubtilis	2
Coleoptera	Staphylinidae	Atheta	remulsa	163
Coleoptera	Staphylinidae	Atheta	riparia	1
Coleoptera	Staphylinidae	Atheta	sp.	1
Coleoptera	Staphylinidae	Atheta	sp. 1	2
Coleoptera	Staphylinidae	Atheta	sp. 2	1
Coleoptera	Staphylinidae	Atheta	sp. 3	7
Coleoptera	Staphylinidae	Atheta	strigosula	9
Coleoptera	Staphylinidae	Atheta	subtilis	19
Coleoptera	Staphylinidae	Atheta	terranovae	37
Coleoptera	Staphylinidae	Atheta	ventricosa	10
Coleoptera	Staphylinidae	Atheta (Datomicra)	sp.	1
Coleoptera	Staphylinidae	Atheta (Pseudota)	sp. n.	5
Coleoptera	Staphylinidae	Atrecus	americanus	1
Coleoptera	Staphylinidae	Batrisodes	lineaticollis	2
Coleoptera	Staphylinidae	Bibloplectus	integer	21
Coleoptera	Staphylinidae	Bolitobius	cingulatus	6
Coleoptera	Staphylinidae	Dinothenarus	badipes	2
Coleoptera	Staphylinidae	Dinothenarus	capitatus	3

(*continued*).

Order	Family	Genus	Species	Abundance
Coleoptera	Staphylinidae	Drusilla	canaliculata	1
Coleoptera	Staphylinidae	Euplectus	duryi	1
Coleoptera	Staphylinidae	Eusphalerum	pothos	3
Coleoptera	Staphylinidae	Gabrius	microphtalmus	4
Coleoptera	Staphylinidae	Gabrius	punctatellus punctatellus	1
Coleoptera	Staphylinidae	Gyrophaena	sp.	1
Coleoptera	Staphylinidae	Gyrophaena	uteana	2
Coleoptera	Staphylinidae	Habrocerus	capillaricornis/schwarzi	6
Coleoptera	Staphylinidae	Heterothops	fumigatus	3
Coleoptera	Staphylinidae	Ischnosoma	longicorne	1
Coleoptera	Staphylinidae	Ischnosoma	pictum	26
Coleoptera	Staphylinidae	Lathrobium	sp.	1
Coleoptera	Staphylinidae	Lathrobium	spp.	2
Coleoptera	Staphylinidae	Leptusa	brevicollis	8
Coleoptera	Staphylinidae	Leptusa	opaca	1
Coleoptera	Staphylinidae	Liogluta	terminalis	2
Coleoptera	Staphylinidae	Lordithon	fungicola	61
Coleoptera	Staphylinidae	Lordithon	sp.	2
Coleoptera	Staphylinidae	Lucifotychus	testaceus	1
Coleoptera	Staphylinidae	Medon	sp.	2
Coleoptera	Staphylinidae	Megarthrus	angusticollis	1
Coleoptera	Staphylinidae	Megarthrus	excisus	4
Coleoptera	Staphylinidae	Megarthrus	spp.	1
Coleoptera	Staphylinidae	Mocyta	luteola	8
Coleoptera	Staphylinidae	Mycetoporus	consors	47
Coleoptera	Staphylinidae	Mycetoporus	sp. 1	1
Coleoptera	Staphylinidae	Mycetoporus	sp. 2	1
Coleoptera	Staphylinidae	Mycetoporus	spp.	1
Coleoptera	Staphylinidae	Myllaena	arcana	1
Coleoptera	Staphylinidae	Neohypnus	emmesus	1
Coleoptera	Staphylinidae	Oligota	sp. near parva (Kraatz)	1
Coleoptera	Staphylinidae	Omalium	sp.	1
Coleoptera	Staphylinidae	Omalium	sp. near foraminosum	1
Coleoptera	Staphylinidae	Ontholestes	cingulatus	10
Coleoptera	Staphylinidae	Oxypoda	convergens	45
Coleoptera	Staphylinidae	Oxypoda	hiemalis	3
Coleoptera	Staphylinidae	Oxypoda	lacustris	1
Coleoptera	Staphylinidae	Oxypoda	orbicollis	8
Coleoptera	Staphylinidae	Oxypoda	pseudolacustris	4
Coleoptera	Staphylinidae	Oxypoda	sp.	1
Coleoptera	Staphylinidae	Oxypoda	sp. near nelsoni (Lohse)	3
Coleoptera	Staphylinidae	Oxypoda	sylvia	32
Coleoptera	Staphylinidae	Paederus	littorarius	17
Coleoptera	Staphylinidae	Pelioptera	sp. near americanum (Gusarov)	1
Coleoptera	Staphylinidae	Philonthus	caerulipennis	40
Coleoptera	Staphylinidae	Phloeonomus	laesicollis	4
Coleoptera	Staphylinidae	Proteinus	acadiensis	6
Coleoptera	Staphylinidae	Proteinus	pseudothomasi	15
Coleoptera	Staphylinidae	Pselaphus	bellax	1
Coleoptera	Staphylinidae	Pseudopsis	subulata	45
Coleoptera	Staphylinidae	Quedius	labradorensis	27
Coleoptera	Staphylinidae	Quedius	peregrinus	2
Coleoptera	Staphylinidae	Quedius	plagiatus	1
Coleoptera	Staphylinidae	Quedius	rusticus	11

(*continued*).

Order	Family	Genus	Species	Abundance
Coleoptera	Staphylinidae	Quedius	uteanus	1
Coleoptera	Staphylinidae	Reichenbachia	propinqua	2
Coleoptera	Staphylinidae	Schistoglossa	brunswickensis	1
Coleoptera	Staphylinidae	Silusa	californica	6
Coleoptera	Staphylinidae	Silusida	marginella	389
Coleoptera	Staphylinidae	Staphylinidae	spp.	4
Coleoptera	Staphylinidae	Stenus	sp.	1
Coleoptera	Staphylinidae	Stenus	sp. 1	9
Coleoptera	Staphylinidae	Stenus	sp. 2	3
Coleoptera	Staphylinidae	Stenus	sp. 3	20
Coleoptera	Staphylinidae	Strigota	obscurata	14
Coleoptera	Staphylinidae	Strophogastra	penicillata	9
Coleoptera	Staphylinidae	Tachinus	addendus	5
Coleoptera	Staphylinidae	Tachinus	basalis	2
Coleoptera	Staphylinidae	Tachinus	fumipennis	3
Coleoptera	Staphylinidae	Tachinus	picipes	28
Coleoptera	Staphylinidae	Tachinus	quebecensis	14
Coleoptera	Staphylinidae	Tachyporus	borealis	2
Coleoptera	Staphylinidae	Tachyporus	mexicanus	62
Coleoptera	Staphylinidae	Tachyporus	nitidulus	237
Araneae	Agelenidae	Agelenopsis	utahana	16
Araneae	Amaurobiidae	Amaurobiidae	spp.	2
Araneae	Amaurobiidae	Amaurobius	borealis	500
Araneae	Amaurobiidae	Callobius	bennetti	57
Araneae	Amaurobiidae	Cybaeopsis	euopla	324
Araneae	Araneidae	Araneidae	spp.	1
Araneae	Araneidae	Cercidia	prominens	3
Araneae	Araneidae	Hypsosinga	rubens	8
Araneae	Araneidae	Mangora	placida	1
Araneae	Clubionidae	Clubiona	bishopi	4
Araneae	Clubionidae	Clubiona	canadensis	9
Araneae	Clubionidae	Clubiona	gertschi	15
Araneae	Clubionidae	Clubiona	kastoni	13
Araneae	Clubionidae	Clubiona	kulczynskii	12
Araneae	Clubionidae	Clubionidae	spp.	9
Araneae	Corinnidae	Castianeira	descripta	21
Araneae	Cybaeidae	Cryphoeca	montana	22
Araneae	Dictynidae	Argenna	obesa	1
Araneae	Dictynidae	Dictyna	coloradensis	2
Araneae	Dictynidae	Dictyna	foliacea	1
Araneae	Dictynidae	Dictyna	major	2
Araneae	Dictynidae	Dictynidae	spp.	7
Araneae	Dictynidae	Emblyna	annulipes	2
Araneae	Dictynidae	Emblyna	phylax	1
Araneae	Dictynidae	Emblyna	sp1	5
Araneae	Dictynidae	Lathys	pallida	171
Araneae	Gnaphosidae	Drassodes	neglectus	21
Araneae	Gnaphosidae	Drassyllus	niger	40
Araneae	Gnaphosidae	Gnaphosa	muscorum	126
Araneae	Gnaphosidae	Gnaphosa	parvula	20
Araneae	Gnaphosidae	Gnaphosidae	spp.	171
Araneae	Gnaphosidae	Haplodrassus	eunis	28
Araneae	Gnaphosidae	Haplodrassus	signifer	396
Araneae	Gnaphosidae	Micaria	aenea	14

(*continued*).

Order	Family	Genus	Species	Abundance
Araneae	Gnaphosidae	Micaria	longispina	1
Araneae	Gnaphosidae	Micaria	pulicaria	28
Araneae	Gnaphosidae	Orodrassus	canadensis	1
Araneae	Gnaphosidae	Zelotes	fratris	269
Araneae	Gnaphosidae	Zelotes	puritanus	23
Araneae	Hahniidae	Antistea	brunnea	2
Araneae	Hahniidae	Cicurina	arcuata	55
Araneae	Hahniidae	Cicurina	brevis	75
Araneae	Hahniidae	Hahnia	cinerea	99
Araneae	Hahniidae	Hahniidae	spp.	2
Araneae	Hahniidae	Neoantistea	agilis	527
Araneae	Hahniidae	Neoantistea	magna	1
Araneae	Linyphiidae	Linyphiidae	spp.	40
Araneae	Linyphiidae (Erigoninae)	Ceraticelus	crassiceps	1
Araneae	Linyphiidae (Erigoninae)	Ceraticelus	fissiceps	4
Araneae	Linyphiidae (Erigoninae)	Ceraticelus	laetabilis	4
Araneae	Linyphiidae (Erigoninae)	Ceraticelus	minutus	11
Araneae	Linyphiidae (Erigoninae)	Ceraticelus	similis	1
Araneae	Linyphiidae (Erigoninae)	Ceratinella	brunnea	11
Araneae	Linyphiidae (Erigoninae)	Ceratinops	crenatus	47
Araneae	Linyphiidae (Erigoninae)	Ceratinopsis	labradorensis	4
Araneae	Linyphiidae (Erigoninae)	Ceratinopsis	nigriceps	1
Araneae	Linyphiidae (Erigoninae)	Diplocentria	bidentata	10
Araneae	Linyphiidae (Erigoninae)	Diplocentria	rectangulata	9
Araneae	Linyphiidae (Erigoninae)	Diplocentria	retinax	5
Araneae	Linyphiidae (Erigoninae)	Diplocephalus	subrostratus	1
Araneae	Linyphiidae (Erigoninae)	Eridantes	erigonoides	1
Araneae	Linyphiidae (Erigoninae)	Floricomus	plumalis	5
Araneae	Linyphiidae (Erigoninae)	Gonatium	crassipalpum	1
Araneae	Linyphiidae (Erigoninae)	Grammonota	angusta	2
Araneae	Linyphiidae (Erigoninae)	Hybauchenidium	cymbadentatum	3
Araneae	Linyphiidae (Erigoninae)	Islandiana	flaveola	270
Araneae	Linyphiidae (Erigoninae)	Lophomma	vaccinii	67
Araneae	Linyphiidae (Erigoninae)	Maso	sundevalli	5
Araneae	Linyphiidae (Erigoninae)	Mermessus	maculatus	24
Araneae	Linyphiidae (Erigoninae)	Mermessus	tridentatus	1
Araneae	Linyphiidae (Erigoninae)	Mermessus	trilobatus	28
Araneae	Linyphiidae (Erigoninae)	Micrargus	longitarsus	6
Araneae	Linyphiidae (Erigoninae)	Phlattothrata	flagellata	1
Araneae	Linyphiidae (Erigoninae)	Pocadicnemis	americana	105
Araneae	Linyphiidae (Erigoninae)	Sciastes	truncatus	127
Araneae	Linyphiidae (Erigoninae)	Scotinotylus	pallidus	3
Araneae	Linyphiidae (Erigoninae)	Scotinotylus	sacer	3
Araneae	Linyphiidae (Erigoninae)	Sisicottus	montanus	5
Araneae	Linyphiidae (Erigoninae)	Sisis	rotundus	1
Araneae	Linyphiidae (Erigoninae)	Styloctetor	compar	1
Araneae	Linyphiidae (Erigoninae)	Tapinocyba	simplex	14
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	atrotibialis	1
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	castanea	2
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	communis	36
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	digitata	59
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	directa	4

(*continued*).

Order	Family	Genus	Species	Abundance
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	minuta	54
Araneae	Linyphiidae (Erigoninae)	Walckenaeria	tibialis	1
Araneae	Linyphiidae (Linyphiinae)	Agyneta	allosubtilis	1
Araneae	Linyphiidae (Linyphiinae)	Agyneta	fabra	4
Araneae	Linyphiidae (Linyphiinae)	Agyneta	olivacea	4
Araneae	Linyphiidae (Linyphiinae)	Agyneta	simplex	269
Araneae	Linyphiidae (Linyphiinae)	Agyneta	sp1	2
Araneae	Linyphiidae (Linyphiinae)	Bathyphantes	eumenis	2
Araneae	Linyphiidae (Linyphiinae)	Bathyphantes	pallidus	24
Araneae	Linyphiidae (Linyphiinae)	Centromerus	furcatus	6
Araneae	Linyphiidae (Linyphiinae)	Centromerus	persolutus	2
Araneae	Linyphiidae (Linyphiinae)	Frontinella	pyramitela	8
Araneae	Linyphiidae (Linyphiinae)	Improphantes	complicatus	2
Araneae	Linyphiidae (Linyphiinae)	Lepthyphantes	intricatus	42
Araneae	Linyphiidae (Linyphiinae)	Lepthyphantes	turbatrix	1
Araneae	Linyphiidae (Linyphiinae)	Neriene	clathrata	2
Araneae	Linyphiidae (Linyphiinae)	Oreonetides	flavescens	12
Araneae	Linyphiidae (Linyphiinae)	Oreonetides	vaginatus	2
Araneae	Linyphiidae (Linyphiinae)	Oreophantes	recurvatus	1
Araneae	Linyphiidae (Linyphiinae)	Porrhomma	terrestre	2
Araneae	Linyphiidae (Linyphiinae)	Sisicus	penifusifer	3
Araneae	Linyphiidae (Linyphiinae)	Tennesseellum	formica	4
Araneae	Linyphiidae (Linyphiinae)	Tenuiphantes	zebra	21
Araneae	Liocranidae	Agroeca	ornata	69
Araneae	Liocranidae	Liocranidae	spp.	3
Araneae	Lycosidae	Alopecosa	aculeata	219
Araneae	Lycosidae	Arctosa	emertoni	336
Araneae	Lycosidae	Arctosa	rubicunda	1
Araneae	Lycosidae	Hogna	frondicola	176
Araneae	Lycosidae	Lycosidae	spp.	582
Araneae	Lycosidae	Pardosa	distincta	2084
Araneae	Lycosidae	Pardosa	hyperborea	357
Araneae	Lycosidae	Pardosa	mackenziana	63
Araneae	Lycosidae	Pardosa	moesta	1300
Araneae	Lycosidae	Pardosa	spp.	4
Araneae	Lycosidae	Pardosa	xerampelina	582
Araneae	Lycosidae	Pirata	montanus	10
Araneae	Lycosidae	Pirata	piraticus	2
Araneae	Lycosidae	Pirata	praedo	17
Araneae	Lycosidae	Piratula	canadensis	1
Araneae	Lycosidae	Piratula	minuta	29
Araneae	Lycosidae	Trochosa	terricola	516
Araneae	Mimetidae	Ero	canionis	2
Araneae	Mimetidae	Mimetidae	spp.	1
Araneae	Mimetidae	Mimetus	sp1	1
Araneae	Parajulidae	Uroblaniulus	canadensis	12
Araneae	Philodromidae	Ebo	iviei	8
Araneae	Philodromidae	Philodromidae	spp.	10
Araneae	Philodromidae	Philodromus	oneida	1
Araneae	Philodromidae	Thanatus	formicinus	17
Araneae	Philodromidae	Tibellus	oblongus	3
Araneae	Philomycidae	Pallifera	dorsalis	80

(*concluded*).

Order	Family	Genus	Species	Abundance
Araneae	Phrurolithidae	Phrurotimpus	borealis	87
Araneae	Phrurolithidae	Scotinella	pugnata	9
Araneae	Pisauridae	Dolomedes	sp1	1
Araneae	Salticidae	Evarcha	hoyi	88
Araneae	Salticidae	Habronattus	calcaratus maddisoni	77
Araneae	Salticidae	Habronattus	viridipes	5
Araneae	Salticidae	Habronattus	waughi	1
Araneae	Salticidae	Neon	nelli	35
Araneae	Salticidae	Pellenes	lapponicus	12
Araneae	Salticidae	Phidippus	borealis	2
Araneae	Salticidae	Phidippus	clarus	1
Araneae	Salticidae	Salticidae	spp.	27
Araneae	Salticidae	Sibianor	aemulus	3
Araneae	Salticidae	Sitticus	finschi	1
Araneae	Salticidae	Synageles	canadensis	1
Araneae	Salticidae	Talavera	minuta	4
Araneae	Salticidae	Tutelina	similis	6
Araneae	Theridiidae	Enoplognatha	marmorata	4
Araneae	Theridiidae	Euryopis	argentea	11
Araneae	Theridiidae	Euryopis	funebris	49
Araneae	Theridiidae	Neottiura	bimaculata	2
Araneae	Theridiidae	Robertus	fuscus	1
Araneae	Theridiidae	Robertus	riparius	32
Araneae	Theridiidae	Rugathodes	aurantius	2
Araneae	Theridiidae	Steatoda	albomaculata	7
Araneae	Theridiidae	Steatoda	mexicana	1
Araneae	Theridiidae	Theonoe	stridula	22
Araneae	Theridiidae	Theridiidae	spp.	5
Araneae	Thomisidae	Ozyptila	sincera canadensis	7
Araneae	Thomisidae	Thomisidae	spp.	19
Araneae	Thomisidae	Xysticus	canadensis	2
Araneae	Thomisidae	Xysticus	discursans	2
Araneae	Thomisidae	Xysticus	durus	1
Araneae	Thomisidae	Xysticus	elegans	43
Araneae	Thomisidae	Xysticus	ellipticus	24
Araneae	Thomisidae	Xysticus	emertoni	33
Araneae	Thomisidae	Xysticus	ferox	2
Araneae	Thomisidae	Xysticus	labradorensis	4
Araneae	Thomisidae	Xysticus	luctuosus	11
Araneae	Thomisidae	Xysticus	montanensis	65
Araneae	Thomisidae	Xysticus	obscurus	33
Araneae	Thomisidae	Xysticus	punctatus	3
Araneae	Thomisidae	Xysticus	triguttatus	5