



# Reductions in downed deadwood from biomass harvesting alter composition of spiders and ground beetle assemblages in jack-pine forests of Western Quebec



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## ABSTRACT

Renewed interest in biomass harvesting has underscored the need for ecologically relevant thresholds and empirical validation of species responses for deadwood retention if biodiversity is to be preserved in managed landscapes. We experimentally reduced volumes of downed deadwood in clear cut jack-pine stands in Western Quebec, Canada and then monitored changes in spider and ground beetle assemblages 1 and 2-years following biomass removal as well as in uncut stands. We reduced volume of downed deadwood by (1) removing residual deadwood placed on machine corridors during the initial harvest of the stand to minimize soil compaction and (2) removing all residual deadwood material throughout the experimental plots. Ground beetle and spider assemblages from deadwood depleted plots were then compared with those in clearcut plots where no additional biomass had been removed and with uncut stands to assess the incremental effect of overstory removal and subsequent biomass removal using multivariate regression trees. We identified 13,822 individual arthropods representing 177 species. We observed differences in species assemblages attributable to the effects of overstory removal (35% of the explained variance) as well as biomass removal, particularly between plots with intensive removal of biomass and those with no additional or moderate removal of biomass (11% of the explained variance). As expected we observed a range of individual species response patterns. Of particular concern were species that experienced incrementally negative effects of overstory and biomass removal and those that were strongly promoted by biomass removal. These species showed responses atypical of those observed following clear cutting and may fall outside both the range of natural variability observed in this region as well as the range of current forest management intensity practiced in North America.

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## 1. Introduction

Renewed interest in the exploitation of forest biomass for bioenergy has been met with concerns related to the negative ecological impacts on biodiversity (Abbas et al., 2011; Berch et al., 2011). Biomass harvesting relies on increased utilization of logging residues such as tree tops, branches and stumps as well as previously non-commercial trees species. The increased use of biomass feedstocks will necessarily reduce availability and diversity of downed deadwood post-harvest (Littlefield and Keeton, 2012; Klockow et al., 2013) and this reduction could possibly create a lasting rup-

ture in the continuity of the deadwood profile for decades (Stokland, 2001). As biomass harvesting often occurs in concert with or soon after harvesting for lumber or pulp it is likely biomass reductions and their initial impacts on biodiversity will play out in the context of overstory removal (Briedis et al., 2011).

Biomass harvesting has been shown to affect a large variety of organisms, both saproxylic and non-saproxylic (Riffell et al., 2011; Bouget et al., 2012). The responses of saproxylic organisms, which require deadwood to complete their life-cycle, have been increasingly well-studied primarily because of the close ecological link with specific deadwood substrates (Hjältén et al., 2012) and the reduced availability and diversity of deadwood substrates following recuperation of biomass. However, for other more generalist organisms, responses to biomass harvesting may reflect a variety of other non-exclusive mechanisms ranging from modification of habitat conditions (Pearce et al., 2003) to more complex changes in detrital based food-webs (Birkhofer et al., 2008).

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Spiders and ground-beetles are abundant, generalist predators which have been widely used to assess the impacts of forest management (Niemelä et al., 1993; Buddle et al., 2000; Martikainen et al., 2006; Halaj et al., 2008; Work et al., 2010; Paradis and Work, 2011; Pinzon et al., 2012). Moreover, compositional changes in both spider (Castro and Wise, 2009, 2010) and ground beetle assemblages (Ulyshen and Hanula, 2009) have both been linked experimentally to changes in the abundance of downed deadwood. Changes in ground beetle composition have been further linked to post-harvest recovery of logging slash (Nittérus et al., 2007) and to whole-tree harvesting (Work et al., 2013). For such speciose groups of animals, multiple mechanisms will likely interact to determine assemblages and perhaps individual species responses to biomass harvesting.

Residual deadwood may serve as a favorable microhabitat for spiders and ground beetles. Increased spider densities (Castro and Wise, 2010) and higher species richness (Varady-Szabo and Buddle, 2006) in close proximity to downed deadwood have been attributed to increased litter layers adjacent to logs and a presumably favorable microclimate. Pearce et al. (2003) suggested that downed deadwood buffers ground beetles from the increased temperature and reduced humidity that accompanies removal of the overstory. Thus deadwood may only become a critical habitat for spiders and ground beetles after overstory removal.

Loss of deadwood following biomass harvesting could also result in a loss of available prey (Komonen et al., 2000). In detrital-based food webs other than forests, reductions in quantities of detrital biomass can increase the incidence of intra-guild predation and alter entire food webs by reducing the abundance of detrital consumers (Polis et al., 1998; Birkhofer et al., 2008). Any interaction among generalist predators related to loss of deadwood following biomass harvesting will likely be intensified by the absence of forest overstory as intensive harvesting often results in massive increases in species that prefer open-habitats such as clearcuts (Paradis and Work, 2011).

The potential risks of biomass harvesting for biodiversity will obviously depend on how much biomass is removed. While recommendations and guidelines for biomass harvesting have been proposed for some regions (Briedis et al., 2011), significant knowledge gaps on the impacts of biomass harvesting have persisted concerning soil properties (Thiffault et al., 2010), stand structure (Littlefield and Keeton, 2012) and biodiversity (Verschuyl et al., 2011). And as such, few studies are available that provide retention targets for biomass harvesting specific for biodiversity (Work and Hibbert, 2011).

Here we have reported the 1- and 2-year responses of spiders and ground beetle assemblages to two increasingly intensive levels of post-harvest biomass removal. To better delineate species responses attributable to silviculture from those specifically attributable to biomass removal, we also compared the response of these assemblages to stem-only harvesting, where the overstory was removed but significant amounts of residual forest biomass were left on site. We hypothesized that increasing intensive levels of biomass removal will cause shifts in spider and beetle assemblages and create assemblages that have yet to be observed following intensive forest harvesting.

## 2. Materials and methods

### 2.1. Study site

This study took place within the Lake Duparquet Research and Teaching Forest (LDRTF), 45 km northwest of Rouyn-Noranda, north-western Quebec, Canada (48°86′–48°32′N, 79°19′–79°30′W). The region is situated in the boreal forest and the climate is continental with a mean annual temperature of 0.8 °C and annual precipitation of 890 mm (Environment Canada; Cana-

dian climatic normals 1971–2000, [www.climate.weatheroffice.ec.gc.ca/climate\\_normals/index\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html)). Located within the Precambrian Shield, the regional topography is generally gentle with short slopes.

### 2.2. Biomass removal experiment

The experiment was established within a ca. 85 year old jack pine (*Pinus banksiana* Lamb) forest originating from a 1923 wildfire (Dansereau and Bergeron, 1993) and growing on coarse-textured thin till deposits. The experiment included two overstory treatments, clear cut and uncut, and three levels of biomass removal nested within clear cut treatments. These four treatments were randomly allocated within experimental blocks. Each experimental block was replicated three times resulting in 12 experimental units. The design allowed us to delineate the relative importance of overstory removal vs the cumulative impacts of overstory removal plus biomass removal.

In the winter of 2008–2009 overstory was removed via stem only harvesting in accordance with careful logging guidelines creating an alternating pattern of protection strips, where no traffic is allowed, and trails to which movement of multifunctional short-wood harvesters and transporters were restricted. Trees were delimited directly on site and unmerchantable portions of the trees such as tops and branches were left in machine trails in front of the harvester, providing a concentrated row of residual green wood intended to minimize soil disturbance.

In the fall of 2009, three levels of biomass removal were applied to 0.25 ha plots nested within clear cut plots using a modified harvester with a retractable arm: (1) residual deadwood including branches and unmerchantable pieces of the trees were left on site (clear cut), (2) residual deadwood along trails and within reach of retractable arm was removed but the harvester was not allowed to leave trails (path), (3) residual deadwood was removed along and between trails and the harvester systematically passed throughout the entire experimental block (intensive) (Fig. 1). Deadwood recovered with the retractable arm was then deposited in an attached transport container as the harvester moved through experimental units. Recovery of forest biomass with this type of harvester is novel in North America.

### 2.3. Deadwood sampling

In May 2010, in each of 12 experimental units, deadwood volume was estimated using the line intercept method (Van Wagner, 1968). Accordingly, along each side (30 m) of an equilateral triangle, the frequency of pieces of wood was recorded by diameter and decomposition classes. Decomposition classes were based on visual criteria such as the presence of branches, bark and mosses and on the relative softness of the wood (Szewczyk and Szewczyk, 1996). Wood pieces intercepting the sampling transect were classed into 1 of 7 diameter classes including 0–0.5, 0.51–1, 1.01–3, 3.01–5, 5.01–7, 7.01–17.5 and >17.5 cm. The length of each transect used to tally wood pieces depended on diameter class; that is, smaller diameter classes were tallied along shorter sections and larger diameter classes were tallied along the entire 30 m length. Thus within first 5 m, all diameter classes were counted; over the first 10 m, all diameter classes except the 0–0.5 cm class were counted and so on. This strategy was applied to subsequent diameter classes such that only pieces greater than 7 cm were sampled over the entire length of each 30 m transect. The total number of pieces were then summed over the 3 transects and the Van Wagner formula was applied using the corresponding sampling distance for a given diameter class to estimate volumes of deadwood (Van Wagner, 1968).



**Fig. 1.** Map of experimental units located in an 85 year old jack pine forest originating from a 1923 wildfire in the Lake Duparquet Research and Teaching Forest in north western Quebec.

#### 2.4. Arthropod sampling

Spiders and ground beetles were collected using pitfall traps every 2–3 weeks between 5/13 and 8/24 in 2010 and 5/18–8/23 in 2011. Six pitfall traps were deployed in triangular arrays within each treatment that corresponded with transects used for downed deadwood inventories. Each trap was charged with ca. 50 ml of propylene glycol as a killing agent and preservative and covered with an elevated lid made of Choroplast to prevent flooding of traps during sampling. Traps were recharged with additional preservative as needed. Traps were separated by at least 15 m along each transect (Digweed et al., 1995). All specimens were then hand-sorted and identified to species using relevant sources (Lindroth, 1961, 1963, 1966, 1968, 1969; Paquin and Duperré, 2003). We identified only adult carabid beetles and mature spiders as few carabid larvae were collected and identification of immature spiders and beetle larvae is difficult. For mature spiders, species identifications were confirmed by genitalic dissection for both male and females. Ground beetle nomenclature followed Bousquet and Laroche (1993) and spider nomenclature followed the World Spider Catalog v13.5 (Platnick, 2013).

#### 2.5. Statistical analysis

We compared differences in overall deadwood volumes among harvesting treatments using a linear mixed model where experimental block was treated as a random effect. This analysis was done using the lme function provided in the nlme package in R. We compared spider and carabid assemblages using sum-of-squares multivariate regression trees (ssMRT) where changes in assemblages were expressed as a function of harvesting treatment and year (De'ath, 2002). For this analysis, all six pitfall traps in a given treatment were pooled and standardized to the total number of trap days for a given year. Catch rates were then square-root transformed to facilitate comparisons between common and rarer species. The ssMRT was pruned based on 1000 fold cross-validation.

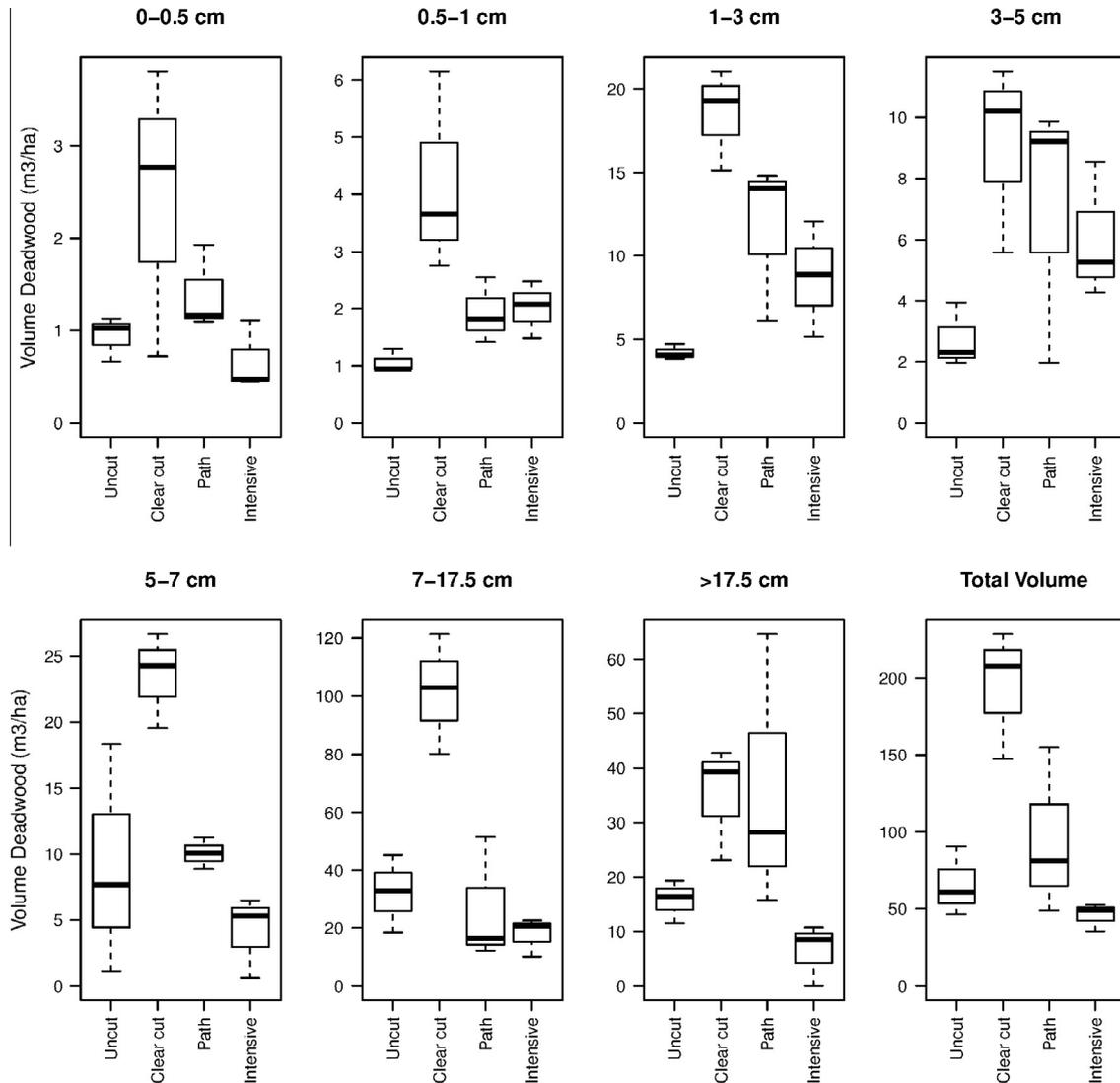
This analysis was done using the mvpart package in R. To better characterize individual species responses among the four treatments, we compared total catch of species that contributed greater than 1% to the explained variance using generalized linear mixed models. We used poisson regression to relate abundance as a function of treatment where total number of trap days was included as an offset and where experimental unit nested within year was treated as a random effect. In the linear mixed models we used clear cut treatments as the reference condition rather than uncut stands to facilitate interpretation of model parameters specifically in the context of recuperation of biomass once the over-story had been removed. This analysis was completed using the lme4 package in R. All analyses were done using R version 2.12.2 (R Development Core Team, 2011).

### 3. Results

#### 3.1. Changes in deadwood with biomass harvesting

Total volume of deadwood was greatest in stem-only clearcuts and decreased with increasing intensity of biomass harvesting (Fig. 2). Mean volumes were 194.2 (SE ± 24.34) m<sup>3</sup>/ha for clearcuts, 95.0 (SE ± 31.35) m<sup>3</sup>/ha for path and 45.8 (SE ± 5.23) m<sup>3</sup>/ha for intensive biomass removal. Mean volume in uncut stands was 66.1 (SE ± 12.94) m<sup>3</sup>/ha. When fixed effects were compared using clearcuts as a reference condition using linear mixed models, differences in overall volumes were highly significant between clearcuts and path biomass removal ( $t$ -value = -4.23,  $p$  = 0.0055), intensive biomass removal ( $t$ -value = -6.33,  $p$  = 0.0007) and uncut stands ( $t$ -value = -5.46,  $p$  = 0.0016).

Fifty-two percent of the residual deadwood in clearcuts with no biomass removal was within the 7–17.5 cm diameter class. Compared to clearcuts, volumes of 7–17.5 cm diameter deadwood were 26.3% and 17.5% in path and intensive biomass treatments respectively. Volumes of larger diameter deadwood (>17.5 cm) in intensive biomass plots were 26–27% of that observed in clearcut and



**Fig. 2.** Box-plots depicting differences in deadwood volumes by diameter class between uncut, clearcuts where residual biomass was left on site (clearcut), clearcuts where biomass had been removed from harvesting trails (path) and clearcuts where biomass was removed throughout the experimental unit (intense).

path treatments. For smaller diameter classes in harvested units, volumes of deadwood generally declined with increasing intensity of biomass harvesting with the exception of small twigs 0.5–1 cm in diameter. For these twigs, both biomass removal treatments had ca. 50% of the volume observed in clearcuts.

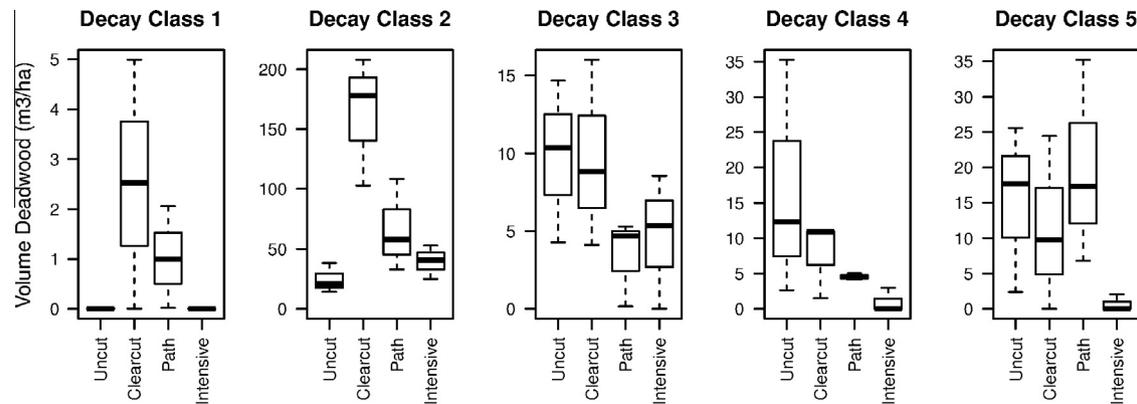
Eighty-three percent of the residual wood left in clearcut sites with no biomass removal was in decay class 2 (Fig. 3). Volumes of this decay class within path and intensive biomass removal treatments were 40.7% and 24.3% of that observed in clearcuts. Within clearcuts, volumes of decay classes 3–5 were similar with means ranging from 7.8 to 11.4 m<sup>3</sup>/ha. These more advanced decay classes accounted for 14% of the total residual wood left following overstory removal. For decay class 3, volumes in path and intensive biomass removal units were 3.3 (SE ± 0.93) and 4.6 (SE ± 1.44) m<sup>3</sup>/ha respectively. These volumes corresponded to 34% and 47% of the volume observed following clearcutting with no additional removal of biomass. For decay classes 4 and 5, volumes of deadwood within intensive biomass removal treatments were lower than path treatments. Volumes of decay class 4 deadwood in path and intensive biomass removal treatments were 58% and 12% of that observed in clearcuts. For the most advanced decay class, volume of deadwood in intensive biomass removal plots were 6% of that

observed in clearcuts. However, we observed greater volumes of decay class 5 in the path treatments than was observed in clearcuts with no biomass removal. Decay class 1, composed mostly of fresh harvest residues, was by far the least abundant decay class observed in our study. Volumes of decay class 1 deadwood declined with increasing intensity of biomass harvesting.

Uncut stands had volumes of deadwood that were generally equal to or lower than the most intensive biomass removal treatment (Fig. 2). However, uncut stands had equal or greater volumes of decay classes 3–5 than harvested units but less volume of early decay classes than harvested units (Fig. 3).

### 3.2. Changes in spiders and ground beetle assemblages with biomass harvesting

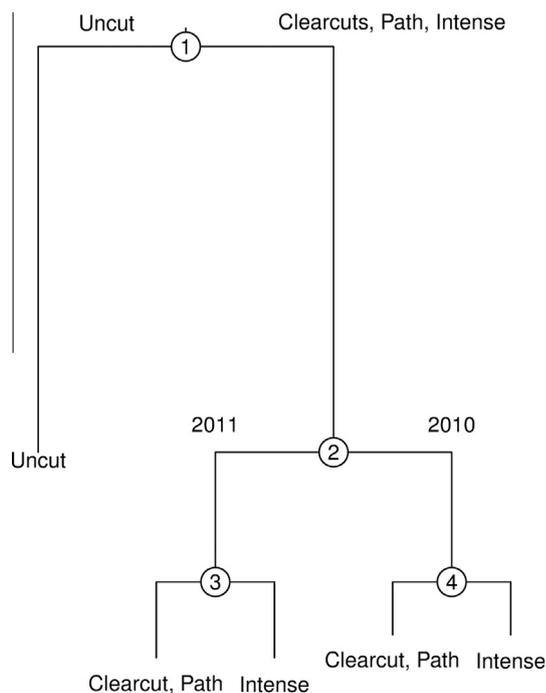
Between 2010 and 2011, we collected 13,822 individual arthropods representing 177 species. Ground beetles (5372 individuals, 46 species) and wolf-spiders (Lycosidae) (5441 individuals, 15 species), dominated the catch, followed by spiders in the family Linyphiidae (806 individuals, 35 species) Erigoninae, 30 species Linyphiinae), Amaurobiidae (790 individuals, 5 species), Gnaphosidae (382 individuals, 15 species) and Thomisidae (320 individuals,



**Fig. 3.** Box-plots depicting differences in deadwood volumes by decomposition stage between uncut, clearcuts where residual biomass was left on site (clearcut), clearcuts where biomass had been removed from harvesting trails (path) and clearcuts where biomass was removed throughout the experimental unit (intensive).

11 species). The remaining 713 individuals were represented by 29 spider species. Of the total catch, 49 species were represented by singletons, 20 species were represented by 2 individuals. Mean catch rates and standard deviations for all species by treatment and year are included as a electronic [Supplemental appendix](#).

Species composition was characterized by a 5 branch ssMRT tree which was derived 561 times following 1000 cross-validations (Fig. 4). The ssMRT explained 56.2% of the total variance in the assemblage. In this tree, differences in assemblages were manifest primarily through changes in the relative abundance of species that occurred throughout most of the experimental units, rather than species that were uniquely associated with a specific harvesting or biomass removal treatment. Sixteen species were responsible for 46.4% of the explained variance (Table 1). The initial split divided uncut stands from harvested stands and accounted for 34% of the total variance explained. This split was characterized

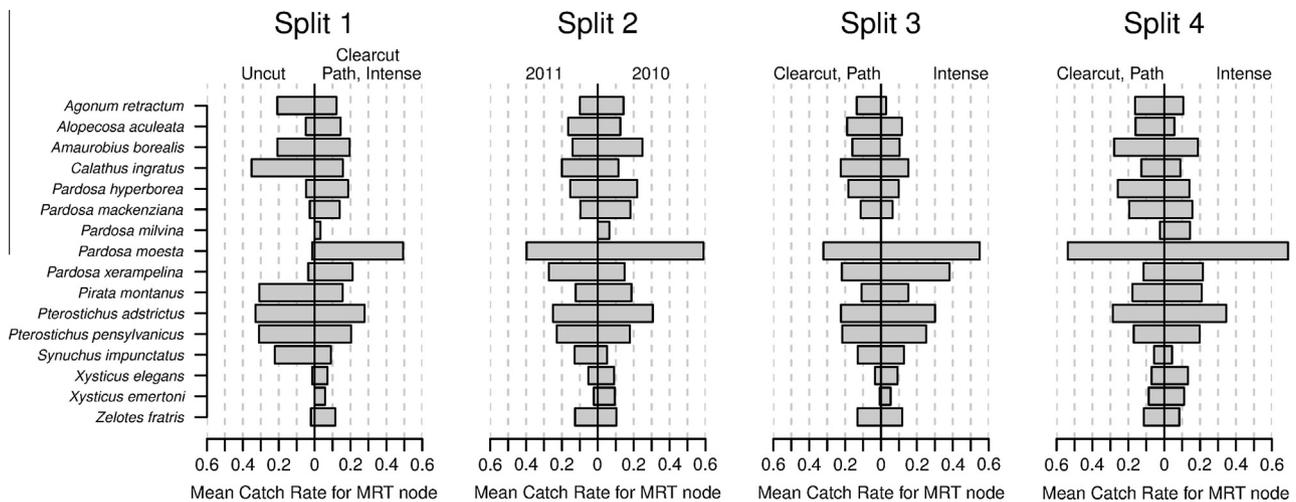


**Fig. 4.** Sum of squares multivariate regression tree (ssMRT) depicting interaction between harvesting and biomass removal treatments as well as interannual variation in sampling. This tree was selected based on 561/1000 cross-validations and accounts explains 56.2% of the total variation.

primarily by differences in the relative catch rates of abundant carabid species associated with uncut stands and abundant Lycosids and thomisids associated with harvested sites (Fig. 5). In uncut stands, we observed increased catch rates of *Agonum retractum* LeConte, *Calathus ingratus* Dejean, *Pterostichus pennsylvanicus* LeConte, *Synuchus impunctatus* (Say) and to a lesser extent *Pterostichus adstrictus* Eschscholtz than in harvested stands (Table 1, Fig. 5). Catch rates of one lycosid, *Pirata montanus* Emerton, were greater in uncut stands than in harvested stands. In contrast, harvested stands were dominated by: (1) lycosids including *Alopecosa aculeata* (Clerck), *Pardosa hyperborea* (Thorell), *Pardosa mackenziana* (Keyserling), *Pardosa moesta* Banks, and *Pardosa xerampelina* (Keyserling), (2) thomisids including *Xysticus elegans* Keyserling and *Xysticus emertoni* Keyserling, and (3) a single gnaphosid, *Zelotes fratris* Chamberlin. The second split reflected inter-annual variation among the harvesting treatments and divided assemblages collected in 2010 from those collected in 2011 and accounted for 10.9% of the total explained variance. Catch rates for all *Pardosa* species decreased in 2011, with the exception of *P. xerampelina*. Likewise, catch rates of *X. elegans* and *X. emertoni* species and one amaurobiid, *Amaurobius borealis* Emerton decreased in 2011 as compared to 2010. Of the carabids collected in harvested blocks, we observed modest decreases in catch rates of *A. retractum* and *P. adstrictus* in 2011. However catch rates of *C. ingratus*, *P. pennsylvanicus* and *S. impunctatus* increased in 2011 within harvested units. The final two splits of the ssMRT reflected the differences in assemblages between intensive biomass removal and less intensive or no biomass removal and accounted for 10.9% of the total variance explained. For species that were collected in both years, individual species responses to intensive biomass removal were consistent across both years. Intensive removal of biomass favored a subset of lycosids, *P. moesta*, *P. xerampelina*, *Pardosa milvina* (Hentz), and both abundant thomisid species, *X. elegans* and *X. emertoni*. Other lycosid species, including *A. aculeata*, *P. mackenziana* and *P. hyperborea* as well as *A. borealis* were more abundant in sites where residual biomass had not been removed or was removed only from harvesting paths. *Z. fratris* abundance did not differ between intensive biomass plots and sites where residual biomass was left or was removed only from harvesting paths. For species that were more positively associated with uncut forests, response to additional removal of biomass varied. *P. adstrictus*, *P. pennsylvanicus* and *S. impunctatus* had similar or even increased abundances in experimental units with intensive biomass removal. For other species such as *A. retractum*, *C. ingratus* and *P. montana*, mean catch rate was lower in sites with intensive biomass removal than sites where residual biomass had not been removed or was removed

**Table 1**  
Variance explained by individual species in 5-node ssMRT describing changes in spider and ground beetle assemblages in response to overstorey removal and increasing intensities of biomass removal.

Species	Split 1	Split 2	Split 3	Split 4	Tree total	Species total
<i>Agonum retractum</i>	0.5485	0.1418	0.3777	0.1024	1.1703	3.2233
<i>Alopecosa aculeata</i>	0.6737	0.1109	0.1751	0.3489	1.3086	1.7524
<i>Amaurobius borealis</i>	0.0121	0.8510	0.1034	0.2692	1.2358	1.7684
<i>Calathus ingratus</i>	2.7534	0.5341	0.1688	0.0460	3.5023	6.3008
<i>Pardosa hyperborea</i>	1.4278	0.3119	0.2271	0.4505	2.4173	3.4214
<i>Pardosa mackenziana</i>	0.9242	0.5330	0.0800	0.0479	1.5852	1.8247
<i>Pardosa milvina</i>	0.0753	0.3011	0.0000	0.4604	0.8368	1.0415
<i>Pardosa moesta</i>	16.8636	2.6871	1.7134	0.7607	22.0247	24.9004
<i>Pardosa xerampelina</i>	2.2661	1.1235	0.8643	0.3274	4.5813	5.8815
<i>Pirata montanus</i>	1.7228	0.3045	0.0613	0.0342	2.1229	3.2214
<i>Pterostichus adstrictus</i>	0.1953	0.2402	0.1982	0.1122	0.7458	2.6564
<i>Pterostichus pensylvanicus</i>	0.8343	0.1780	0.0405	0.0254	1.0782	3.9196
<i>Synuchus impunctatus</i>	1.2631	0.4413	0.0001	0.0054	1.7099	3.5837
<i>Xysticus elegans</i>	0.2491	0.1096	0.1126	0.1249	0.5963	1.1849
<i>Xysticus emertoni</i>	0.2526	0.3844	0.0705	0.0186	0.7260	0.8398
<i>Zelotes fratris</i>	0.6591	0.0383	0.0057	0.0281	0.7312	0.9958
Remaining 162 species	3.6249	2.6944	2.2143	1.3074	9.841	33.484
Total	34.3459	10.9851	6.4129	4.4697	56.2136	100.00



**Fig. 5.** Species means around ssMRT nodes indicating relative contribution to individual regression tree splits. Left and right bars correspond to left and right splits of the ssMRT.

only from harvesting paths, suggesting additive impacts of removal of overstorey and reduction or residual biomass.

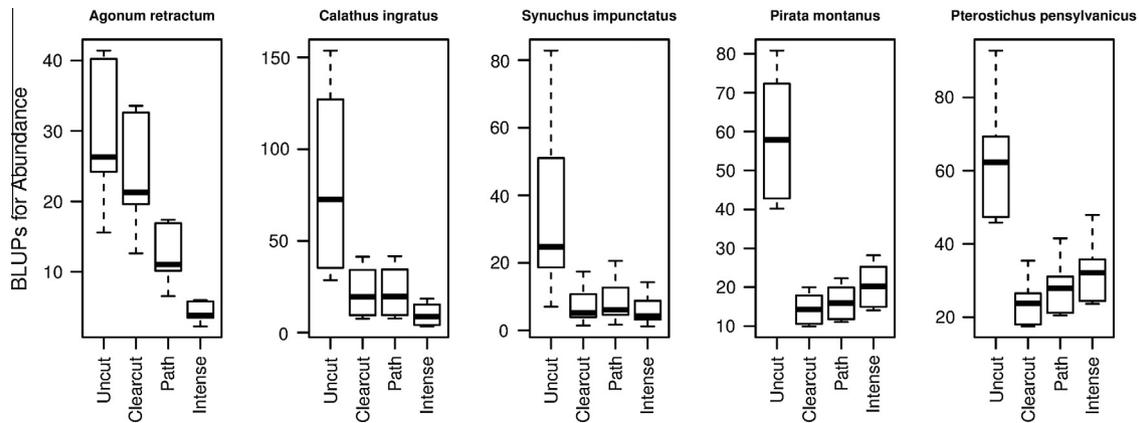
### 3.3. Individual species responses to overstorey and biomass removal

Using generalized linear mixed models, we characterized individual species responses across harvesting treatments for those species that contributed >0.5% of the total variance explained in the ssMRT. Two species, *P. milvina* and *X. emertoni*, which were comparatively rare and restricted only to harvested sites were poorly characterized by regression models and were excluded from statistical analysis.

Captures of four carabids, *A. retractum*, *C. ingratus*, *P. pensylvanicus* and *S. impunctatus*, and one spider, *P. montanus* were reduced in clearcuts as compared to uncut stands (Fig. 6, Table 2). Captures of *A. retractum* were reduced in both biomass removal treatments whereas captures of *C. ingratus* were reduced only in plots with intensive biomass removal. *S. impunctatus* did not differ between clearcuts and either biomass removal treatment. Captures of *P. montanus* and *P. pensylvanicus* were greater in the intense biomass removal, relative to clearcuts, but did not differ in plots where biomass was removed from harvest paths only. Increased captures of

*P. montana* and *P. pensylvanicus* in plots with intensive biomass removal were, however, modest and corresponded to an increase of 9% over clearcuts. The response of *P. adstrictus* in biomass removal plots was inconsistent with all other species that favored uncut forests. Relative to clearcuts, captures of *P. adstrictus* were fewer in plots where biomass was removed only from harvest paths but greater in intensive biomass removal plots.

Captures of eight species, all spiders, increased following harvesting. Of these species, captures of four were reduced in at least one of the biomass removal treatments (Fig. 7, Table 2). *A. aculeata*, *A. borealis* and *P. mackenziana* were less abundant in intensive biomass removal when compared to clearcuts but were not different in plots where biomass was removed from harvest paths. Captures of *P. hyperborea* were lower in both biomass removal treatments as compared to clearcuts. Captures of *Z. fratris* did not differ between clearcuts and either biomass removal treatment. In contrast, captures of *P. moesta* and *X. elegans* increased in intensive biomass removal plots but did not differ in plots where biomass was only removed from harvesting paths (Fig. 8, Table 2). Captures of *P. xerampelina* increased in both biomass removal treatments (Fig. 8, Table 2). Two other species *P. milvina* and *X. emertoni* were favored in intensive biomass treatments (Fig. 8) although these



**Fig. 6.** Best linear unbiased predictors (BLUPs) derived from generalized linear mixed models for the abundance of 5 species that responded negatively to removal of the overstory but showed little response to additional biomass removal. BLUPs, model predictions that have been adjusted by all random factors, are plotted as boxplots.

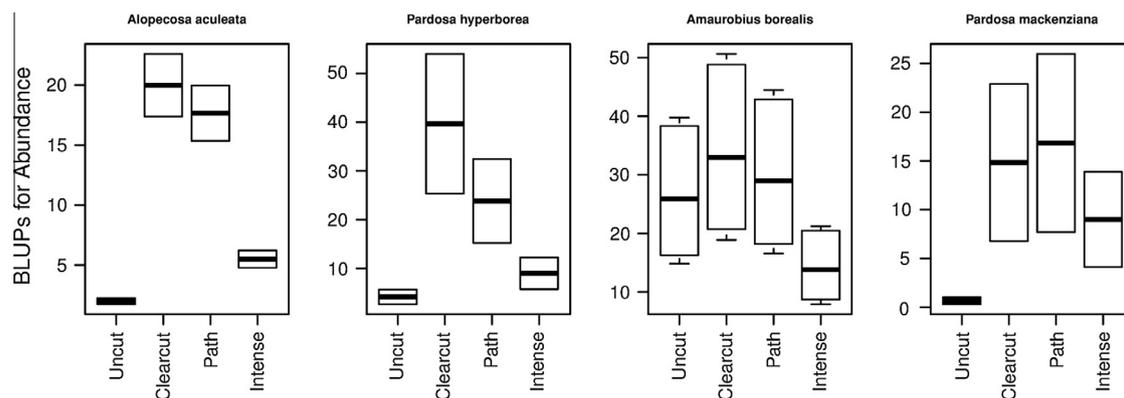
**Table 2**

Fixed effects parameters and the variance associated with random effects derived from generalized linear mixed models predicting change in captures in response to overstory removal and increasing intensities of biomass removal.

Species	Fixed effects <sup>a</sup>			Variance of random effects			Response <sup>b</sup>	
	Intercept	Uncut	Path	Intense	Block	Year	Overstory	Biomass
<i>Agonum retractum</i>	-3.2864	0.2103	<b>-0.6583</b>	<b>-1.7299</b>	0.0793	0.0479	-	--
<i>Alopecosa aculeata</i>	-3.4020	<b>-2.3026</b>	-0.1241	<b>-1.2910</b>	0	0.0358	+	-
<i>Amaurobius borealis</i>	-2.9480	<b>-0.2416</b>	-0.1301	<b>-0.8687</b>	0.0073	0.1566	+	-
<i>Calathus ingratus</i>	-3.5030	1.3116	0.0075	<b>-0.8053</b>	0.0434	0.4797	-	-
<i>Pardosa hyperborea</i>	-2.7780	<b>-2.2534</b>	<b>-0.5094</b>	<b>-1.4833</b>	0	0.1198	+	--
<i>Pardosa mackenziana</i>	-3.8692	<b>-3.1023</b>	0.1265	<b>-0.4997</b>	0	0.3365	+	-
<i>Pardosa moesta</i>	-1.5759	<b>-6.0149</b>	<b>-0.1816</b>	0.5538	0.1017	0.1359	+	+
<i>Pardosa xerampelina</i>	-4.1976	<b>-1.8245</b>	1.1199	1.6959	0.0851	0.3054	+	++
<i>Pirata montanus</i>	-3.7511	1.3977	0.1088	0.3463	0.0103	0.0552	-	(+)
<i>Pterostichus adstrictus</i>	-2.5639	0.3443	<b>-0.2696</b>	0.2713	0.0948	0.0407	-	-+
<i>Pterostichus pensylvanicus</i>	-3.2323	0.9634	0.1591	0.3014	0.0473	0.0455	-	(+)
<i>Synuchus impunctatus</i>	-4.6875	1.5581	0.1670	-0.2007	0.4705	0.3882	-	0
<i>Xysticus elegans</i>	-5.4842	<b>-2.1401</b>	-0.4354	1.2777	0.2228	0.0779	+	+
<i>Zelotes fratis</i>	-4.2934	<b>-2.2824</b>	0.2513	-0.2542	0	0.0229	-	0

<sup>a</sup> Bold parameter values denote significant statistical differences in slopes (beta) ( $p < 0.05$ ) as compared to clearcuts as a reference condition. Italics correspond to parameter values that are marginally different ( $p = 0.06$ ) from clearcuts as a reference condition.

<sup>b</sup> Response of individuals species to removal of the overstory ( $\beta_{\text{Uncut}}$ ) and removal of residual biomass ( $\beta_{\text{Path}}$  and  $\beta_{\text{Intense}}$ ) were characterized using + and - to indicate positive or negative changes in abundance. Single - or + indicate a response to intense biomass removal. Double ++ or -- indicate similar responses between for path and intense treatments. The symbol -+ indicate a negative response to path and a positive response to intense biomass removal. The symbol (+) corresponds to statistically significant but relatively small absolute changes in abundance.

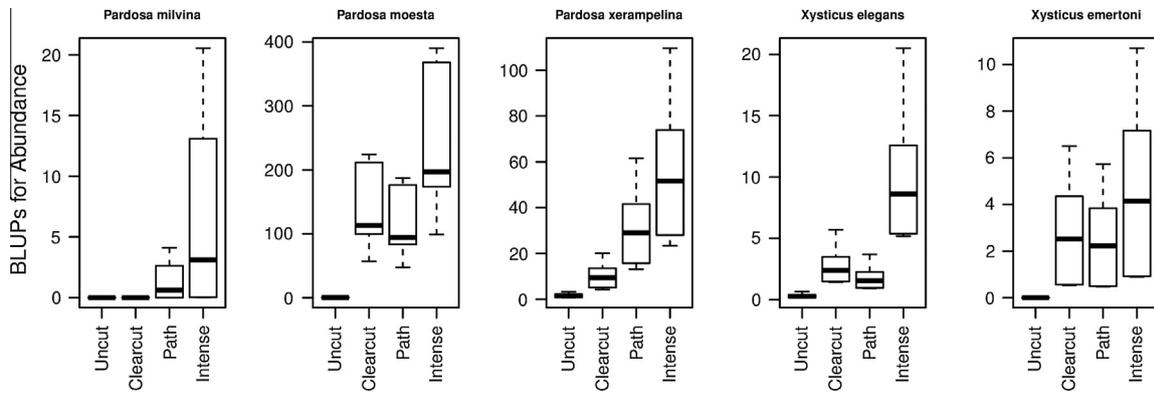


**Fig. 7.** Best linear unbiased predictors (BLUPs) derived from generalized linear mixed models for the abundance of 4 species that responded positively to removal of the overstory but declined following biomass removal. BLUPs, model predictions that have been adjusted by all random factors, are plotted as boxplots.

trends were not significantly significant in part due to low numbers of captures.

Variation attributable to annual differences (captured within random effects of the mixed model) were more pronounced than

the variation among experimental units for the majority of spider species (Table 2). For all spider species, with the exception of *X. elegans*, annual variation was at least 50% greater than variation among experimental units. In contrast, for the majority of carabids,



**Fig. 8.** Best linear unbiased predictors (BLUPs) derived from generalized linear mixed models for the abundance of 5 species that responded positively to removal of the overstory and to additional biomass removal. BLUPs, model predictions that have been adjusted by all random factors, are plotted as boxplots.

variance among experimental units was at least 20% larger than the variance attributable to differences between 2010 and 2011 (Table 2). For one carabid, *P. pennsylvanicus*, the variance attributable to experimental units and inter-annual differences were nearly equal.

#### 4. Discussion

Compared to cut-to-length clearcuts, where branches and tops were left on site, biomass removal reduced overall deadwood volumes by 52% when removals were limited to harvested paths and by 77% when biomass was taken from throughout the experimental block. In comparison, Briedis et al. (2011) estimated that, following whole-tree harvesting where branches and tops are removed at roadside, on average 45% of post-harvest biomass was still left on site. This suggests that post-harvest biomass removal where the biomass harvester was confined to trails may have similar over impacts on overall deadwood volumes as whole-tree harvesting. However intensive recuperation of biomass where the harvester passes throughout the block surpasses whole tree harvesting in its impact on deadwood volume. These reductions came principally from losses of larger diameter fresh deadwood. This is not surprising given that fresh downed wood is a preferable feedstock compared to more advanced decay stages and thus is targeted in post-harvest biomass recuperation. Fresh downed wood is relatively more abundant following harvesting and is likely to be free from rot and thus providing more energy per unit volume. However, we also observed losses of advanced decay classes, particularly in the intensive biomass removal treatments where the biomass harvester systematically passed throughout experimental plots. In on-site (as opposed to roadside), secondary recuperation of biomass, machinery passes throughout the stand at least twice; first for harvesting and forwarding of timber, then for recuperation of residual forest biomass. Consequently, mechanical destruction of advanced decay stages of forest residues is likely compounded and the cause for these losses (Brais et al., 2004). Taken together, recuperation of residual biomass resulted in a smaller homogeneous pool of fresh-deadwood with relatively few advanced decay logs and relatively more soil disturbance caused by the biomass harvester.

For spiders and ground beetles, recuperation of residual biomass further altered assemblages following removal of the overstory. The initial removal of overstory resulted in an assemblage shift where common ground beetles declined and wolf spiders increased. This faunal shift seems to be a generalizable response to removal of the overstory and has been previously documented both for carabid species such as *A. retractum*, *C. ingratus*, certain

*Pterostichus* species and *S. impunctatus* (Work et al., 2010) and for wolf spiders such as *Pardosa* and *Alopecosa* (Buddle et al., 2006; Matveinen-Huju and Koivula, 2008; Paradis and Work, 2011; Pinzon et al., 2012). However following removal of the overstory, additional, intensive recuperation of biomass resulted in assemblages that differed from those observed either in clearcuts where for biomass was left on site or removed from harvester paths. These differences continued to persist 2 years post-harvest.

Six species showed clear negative responses to increased recuperation of biomass. For species that responded negatively as well to overstory removal, such as the ground beetles *A. retractum* and *C. ingratus*, recuperation of biomass may further depress populations and thus further denude the already reduced ground beetle assemblage in clearcuts. Successive, additive disturbances have been reported elsewhere with similar results. For example, scarification of soils reduced abundances of *A. retractum* and *C. ingratus* to zero following significant declines after clear cutting (Klimaszewski et al., 2005). For these species, it is difficult to distinguish the effects of soil disruption and deadwood removal as both scarification and intensive biomass removal cause significant changes in both. Cobb and colleagues reported similar findings for *C. ingratus* following post-fire salvaging logging (Cobb et al., 2007). This species was less abundant in sites that had been burned and then harvested as compared to harvesting alone and showed a strong affinity for sites with large amounts of fine woody material (Cobb et al., 2007). Spider species that are commonly promoted by removal of the overstory such as *A. aculeata*, *A. borealis*, *P. hyperborea* and *P. mackenziana* (Buddle et al., 2000; Paradis and Work, 2011; Pinzon et al., 2012) were however reduced by additional recuperation of biomass. These losses were met with further increases of *P. moesta*, *P. xerampelina* and *X. elegans* and to a lesser extent *P. milvina* and *X. emertoni* following biomass harvesting. These species are often characterized as either ambush predators (*Xysticus*) or ground running hunters (*Pardosa*) (Uetz et al., 1999) which feed on litter insects including Collembola, Diptera (Nyffeller and Benz, 1988) as well as other spiders (Buddle, 2002). Both *P. moesta* and *P. milvina* have been strongly implicated in intraguild predation and cannibalism (Buddle, 2002; Buddle et al., 2003). The net result is a relatively simplified predator assemblage which uses relatively fewer foraging strategies and which has higher propensity for complex interactions like intraguild predation and cannibalism as well as novel predator assemblage that appears to exist outside the range of natural variability in disturbed or managed boreal forests in North America.

A strict interpretation of the ssMRT suggests that between 45 and 95 m<sup>3</sup>/ha of residual biomass should be left on site following forest harvest to maintain spiders and ground beetles assemblages

consistent with those observed following the initial impacts of overstory removal. Such a conclusion is derived through comparisons of the final splits of the ssMRT and the corresponding differences in the total volumes of deadwood found under intensive biomass removal (45 m<sup>3</sup>/ha) and the path treatments (95 m<sup>3</sup>/ha). These volumes translate to 23% and 48% of the mean deadwood volume observed in the clear cuts. However several important caveats apply. First, we have only observed the initial responses of assemblages following biomass removal and it may be possible that differences between clearcuts and paths treatments will increase with time just as it is possible that initial differences in intensive biomass removal plots may become increasingly muted. Longer-term responses by litter arthropod assemblages over the coming decades will likely be related to decomposition of the residual biomass and re-establishment of forest canopy cover. While recuperation of biomass necessarily reduced overall volumes of deadwood, the great majority of the residual wood in the clearcut (85%), path (71%) and intensive biomass (86%) removal treatment was in decay class 1 and 2. This simply suggests that in the absence of additional sources of deadwood, which would be expected at least initially under even-aged forest management, future volumes of advanced decay classes will be reduced proportionately with the initial reduction in deadwood volume. Based on decomposition rates proposed by Brais et al. (2006), freshly cut jack pine logs will have a half-life of ca. 35 years which will coincide roughly with canopy closure of replanted stands. Thus under the intensive biomass recovery treatment at canopy closure, we anticipate volumes of deadwood will be approximately 1/8 of the volume that was initially present following status quo clear cutting with no additional recuperation of biomass.

A second caveat to a strict interpretation of ssMRT is that the relatively large range of this proposed target is a function of the limited number of removal intensities used in our experiment. It is likely that similar experiments exploiting a wider range of biomass removal would refine this relatively broad target. Still similar targets have been proposed for other organisms. Work and Hibbert (2011) studied saproxylic diptera in neighboring mixedwood stands and suggested that 40 m<sup>3</sup>/ha of downed deadwood would be required to prevent declines in overall species richness. Preliminary comparisons of stem-only and whole-tree harvesting have shown differences in beetle assemblages, primarily driven by differences in abundant rove beetle species, occurred when downed deadwood volume was reduced to ca. 100 m<sup>3</sup>/ha (Work et al., 2013).

## 5. Conclusions

Unlike some countries in Europe, biomass harvesting in North America is relatively recent (Levin and Eriksson, 2010) and there is pressing need to develop ecologically pertinent guidelines for deadwood retention. We have compared responses of spiders and ground beetles and concluded that intensive biomass removal that left 23% of the deadwood left following clearcutting generated a novel assemblage dominated by *Pardosa* and *Xysticus* species but denuded in ground beetles. For particular species with affinities for closed-canopy forest, intensive removal of biomass compounded the negative impacts of overstory removal. The assemblage that is left following biomass removal differs from those observed after cut-to-length harvesting. We suggest that following cutting in mature jack pine stands, residual deadwood targets should fall within the range of 45–95 m<sup>3</sup>/ha or between ca. ¼ and ½ of the deadwood volume found in clearcuts with no additional recuperation of biomass. This relatively broad target range is an artifact of our study design and future studies aimed at refining this target should include deadwood removal treatments within this range. However

we also caution that longer-term monitoring is warranted as these differences may converge or diverge with time and as such policy makers and land-managers may need to adjust these targets as new information becomes available. It does however serve as an initial benchmark for biomass harvesting operations which is corroborated by other studies examining other organisms. It also represents ca. 50% of the total deadwood available post-harvest suggesting that for this site, approximately 100 m<sup>3</sup>/ha of residual deadwood could be removed for biomass. Biomass retention targets on the order of 50–100 m<sup>3</sup>/ha may seem comparatively high compared to other European boreal regions. However we think that differences in land-use history, disturbance regime and assemblage composition justify the need for site-specific empirical evaluations for a variety of taxa as well as thoughtful consideration species responses over the range of natural variability within an area.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.06.021>.

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