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Spider Assemblages in the Overstory, Understory, and Ground Layers of Managed Stands in the Western Boreal Mixedwood Forest of Canada

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ABSTRACT Logging is the main human disturbance in the boreal forest; thus, understanding the effects of harvesting practices on biodiversity is essential for a more sustainable forestry. To assess changes in spider composition because of harvesting, samples were collected from three forest layers (overstory, understory, and ground) of deciduous and conifer dominated stands in the northwestern Canadian boreal mixedwood forest. Spider assemblages and feeding guild composition were compared between uncut controls and stands harvested to 20% retention. In total, 143 spider species were collected, 74 from the ground, 60 from the understory, and 71 from the overstory, and species composition of these three pools differed considerably among layers. Distinctive spider assemblages were collected from the canopy of each forest cover type but these were only slightly affected by harvesting. However, logging had a greater impact on the species composition in the understory and ground layers when compared with unharvested controls. Guild structure differed among layers, with wandering and sheet-weaving spiders dominant on the ground while orb-weaving and ambush spiders were better represented in the understory and overstory, respectively. Given the ecological importance of spiders and the expectation of faunal changes with increased harvesting, further efforts toward the understanding of species composition in higher strata of the boreal forest are needed.

KEY WORDS forest management, vertical stratification, variable retention, species composition, EMEND

Forest canopies are key to maintaining essential ecosystem functions and services in woodlands (Lowman and Rinker 2004, Ozanne et al. 2003), in addition to providing habitats that support rich and diverse arthropod assemblages (Basset 2001, Erwin 1988, Stork et al. 1997). Canopy characteristics directly affect forest interior environments (i.e., temperature, humidity, and radiation) (Parker 1995), influencing arthropod assemblages not only within the canopy, but also in lower layers and especially on the ground (Huhta 1971, Niemelä et al. 1996, Ziesche and Roth 2008). However, intensive forest harvesting has direct negative consequences for species richness, abundance, and distribution of canopy arthropods (Dumbrell and Hill 2005). These effects become more evident as harvesting intensity (i.e., logged area) increases (Shure and Phillips 1991) and forested patches become smaller and more isolated, amplifying edge effects and reducing forest specialist populations (Ozanne et al. 2000). Moreover, changes in the overstory because of harvesting also have indirect effects on forest understories (Halpern et al. 2005, Smith et al. 2008) and ground-dwelling arthropod assemblages (Buddle et al. 2006, McIver et al. 1992, Siira-Pietkainen et al. 2003). For these reasons and because more than one quarter of the invertebrate species recorded from forest canopies are thought to be unique to this forest layer (Basset et al. 2003, Sørensen 2003), canopy studies are highly relevant for biodiversity management and conservation.

Spiders are among the most species rich groups of macroarthropods (Coddington and Levi 1991) and are ecologically significant as conspicuous and abundant predators in most terrestrial ecosystems (Turnbull 1973, Wise 1993). Although a number of studies have addressed specific questions about canopy spiders in temperate forests (Jennings and Dimond 1988; Halaj et al. 1996, 2000; Mason 1992; Pettersson 1996), to our knowledge only Larrivée and Buddle (2009) have focused exclusively on canopy spider assemblages in the northern forests of Canada.

The EMEND experiment (Ecological-Based Management Emulating Natural Disturbances) takes a multi-disciplinary approach to determine how management practices may best maintain biotic communities in the boreal mixedwood of north-western Alberta in Canada (Spence et al. 1999). The effects of harvesting on invertebrate assemblages have been studied at EMEND in four natural forest cover-types (Jacobs et al. 2008, Lindo and Visser 2004), and this has included work with spiders (Buddle and Shorthouse 2008, Work et al. 2004); however, these studies have generally focused on ground-dwelling assemblages. In

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the current study we document and compare the spider assemblages using different layers of the forest (overstory, understory, and ground) in aspen and spruce dominated stands, and provide an initial approximation of the species composition in the canopy. Additionally, we characterize spider assemblages and feeding guild structure in each of these forest layers and determine how these features are affected by logging.

Materials and Methods

Study Area. The fieldwork was conducted on the land base of the EMEND project, which is located in the boreal mixedwood in the Lower Foothills Ecoregion (Strong and Leggat 1992) of north-western Alberta, Canada (56°46′ N, 118°22′ W). Climate in this region is characterized by cold winters and warm summers (January: −16.6 ± 5.3°C, July: 16.0 ± 1.2°C) with a total annual precipitation of 402.3 mm (Environment Canada 2009). Forests in the area originated from wildfires and are typical of the western boreal mixedwood, ranging from deciduous-dominated stands (mainly trembling aspen, *Populus tremuloides* Michaux, and balsam poplar, *Populus balsamifera* L.; mean age 93.9 ± 16.30 yr) in early successional stages to conifer-dominated stands (mainly white spruce, *Picea glauca* (Moench) Voss; mean age 127.4 ± 24.82 yr). Stands in this area have never been previously logged. Full details about the experimental design of the EMEND project are described elsewhere (Spence et al. 1999, Work et al. 2010).

Data Collection. Spiders were collected during the summer of 2007 from the overstory (*OS*), understory (*US*), and ground (*GR*) layers of the forest. Samples were obtained from twelve 10 ha compartments in stands of two different cover-types (aspen or spruce dominated), in which the canopy consists >70% of the dominant tree species. Three compartments from each cover-type were harvested during the winter of 1998/1999 to 20% dispersed retention from the original tree basal area (mean stems/ha ± SE: DD = 451.4 ± 73.49, CD = 166.7 ± 24.06; mean diameter at breast height (DBH) in centimeters (DBH) ± SE: DD = 41.4 ± 7.70, CD = 50.4 ± 9.26). Tree retention in each stand was obtained after harvesting 5 m wide machine corridors spaced 20 m apart, leaving a 15 m wide retention strip in between, and then removing randomly three out of every four trees from the retention strip. Unharvested stands were used as controls to establish immediate harvest effects and recovery targets (mean stems/ha ± SE: DD = 666.7 ± 153.56, CD = 909.7 ± 363.71; mean DBH ± SE: DD = 60.4 ± 9.37, CD = 96.2 ± 13.24). Thus, a 2 × 2 factorial design with forest cover-type (aspen vs. spruce) and harvesting treatment (harvested vs. unharvested) was used in this study. Three replicates were obtained for each ‘cover × treatment’ combination from stands that were dispersed on a c. 21 km^2 landscape. Pairs of control and harvested compartments within each replicate were within the same stands and the minimum distance between replicates was 1.7 km. Although a full range of retention treatments are included in the EMEND study (see Work et al. 2010), we chose the 20% retention treatment for this resource-intensive study because it is at the upper end of what is operationally feasible for the industry.

OS samples were collected between 1-VI and 24-VI-2007. We aimed to sample two trees of the dominant species from each 10 ha compartment (‘cover × treatment’ combinations; mean tree height ± SE: DD = 22.5m ± 0.61, CD = 22.1 ± 1.25). For reasons beyond our control, only a single tree could be sampled in one replicate of the harvested aspen dominated compartments; thus, samples were provided from a total of 23 trees. The canopy fauna was collected from trees that had been cut and felled onto 15.2 × 9.2 m plastic tarps. All tree branches were removed and beaten on the tarp; spiders were searched thoroughly from the accumulated branch debris and from tree bark. Tree height, crown height (length from the first branch of the tree from the ground to the top of the tree), average crown cover (percentage of foliage covering a circumference in a convex spherical mirror or densiometer, measured under each tree at each cardinal direction) and DBH were measured for each tree. *US* samples were collected between 1-VI and 7-VI-2007 from each ‘cover × treatment’ combination. Spiders were sampled by randomly walking during 45 min within each 10 ha compartment and beating all shrubs on a 1 × 1 m canvas sheet. *GR* samples were collected using six pitfall traps on each ‘cover × treatment’ combination for a total of 72 traps; traps were active between 2-VI and 25-VI-2007. Traps consisted of a plastic container (11 cm diameter) placed at the organic layer level and filled with a small volume of ethylene glycol which was used as preservative; a plastic square roof was suspended over the trap to protect it from rain and debris (for full details about trap design see Spence and Niemelä 1994).

Only adult individuals were identified to the species level using relevant literature and were considered for analyses because juvenile spiders cannot be effectively identified to species. Nomenclature followed the World Spider Catalog (Platnick 2011) and voucher specimens were deposited in the Invertebrate Ecology Laboratory arachnological collection and the E. H. Strickland Entomological Museum at the University of Alberta, Canada (Departments of Renewable Resources and Biological Sciences, respectively).

Data Analyses. Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001) was used to test the null hypothesis of no difference in species composition ($\alpha = 0.05$) across forest layers using a two factor model [‘cover (aspen/spruce) × treatment (20% harvest retention/uncut control)’]. Individual based rarefaction (Colwell et al. 2004, Magurran 2004) was used to compare species richness between ‘cover × treatment’ combinations. Multivariate Regression Tree analysis (MRT) (De’Ath 2002) was used to determine the effect of variables such as forest cover-type, harvesting treatment, tree height, and canopy cover have on the composition of overstory spider assemblages. Analyses were performed in R (R Development Core Team 2010) using the VEGAN (Oksanen et al. 2010) and MVPART (De'Ath 2010) packages (the latter used for MRT). The Bray-Curtis distance measure was used for both PERMANOVA (999 permutations) and MRT (selecting the most consistent tree after 100 runs). Because sampling techniques differed for each forest layer some analyses were carried out separately.

Comparisons of individual characteristics of the sampled trees (crown cover, DBH, tree height, crown height) between harvesting treatments within each forest cover-type and between cover-types within each harvesting treatment were tested using a Kolmogorov-Smirnov test to determine if these variables could be contributing to the results depicted by the analyses mentioned above. Given that multiple comparisons were tested (four for each variable), the rejection of the null hypothesis of no difference was based on an adjusted alpha value of 0.0125).

Abundance of each species within each layer was relativized to the layer total to account for differences because of sampling techniques after removing species with one or two individuals (singletons and doubletons, respectively). These relativized abundances were used to compare assemblages between forest layers. Species composition was evaluated using Non-Metric Multidimensional Scaling ordination (NMS), stepping down in dimensionality (starting with six dimensions) and using predefined stress values as a stopping rule. Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was used to identify species that were strongly associated with particular treatments or treatment combinations.

Species were grouped into functional guilds based on hunting strategies (Uetz et al. 1999) and pooled standardized abundances by guild on each sampling site were used in the NMS ordination obtained above to depict differences in guild structure. Thus, relative abundance for each guild in each sampling site (individual points in the NMS) was used to determine the size of each point in the ordination. ISA was also used to assess the relationship of these guilds to treatment combinations.

Individual-based rarefaction was carried out to compare species richness between layers using non-standardized abundances. In addition, the Marczewski-Steinhaus distance measure (Pielou 1984), also known as complementarity index (C), was used to assess dissimilarity of the three layers in terms of species and guild composition. This measure quantifies biotic distinctness based on the observed richness and the number of unique and shared species between pairs of treatment combinations (Colwell and Coddington 1994, Pielou 1984). The value of C ranges from 0 to one (identical to completely different species assemblages between sites). NMS ordination and ISA were performed in R using the VEGAN (Oksanen et al. 2010) and LABDSV (Roberts 2010) packages, respectively. For NMS, Bray-Curtis distance measure was used and significant indicator species ($\alpha = 0.05$) in ISA were selected after a Monte Carlo test based on 999 permutations.

Results

Overstory Assemblages. A total of 3,054 individual spiders from 14 families and 71 species was collected from the overstory (Supplemental Material available online only), with eight species comprising 72.20% of the total abundance [*Philodromus rufus quartus* Dondale & Redner (Philodromidae), *Dictyna brevitarsa* Emerton (Dictynidae), *Pelegrina flavipes* (Peckham & Peckham) (Salticidae), *Philodromus placidus* Banks (Philodromidae), *Pityohyphantes subarcticus* Chamberlin & Ivie, *Grammonota angusta* Dondale (Linyphiidae), *Araniella displicata* (Hentz) (Araneidae), and *Clubiona canadensis* Emerton (Clubionidae)], were the most abundant species (with >100 individuals each), comprising 72.20% of the total (42 species had <10 individuals). Forty-two species were represented by fewer than 10 individuals, including 18 singletons, and 4 doubletons.

Results from the Kolmogorov-Smirnov test suggest that neither DBH nor tree height differed significantly among cover type or harvest treatments. In contrast, however, crown cover was significantly lower in harvested as opposed to control trees for both cover-types ($P = 0.0043$ and $P = 0.0022$, respectively), and crown height was shorter in aspen trees for harvested and control trees ($P = 0.0026$ and $P = 0.0042$, respectively).

Highly significant differences in species composition were observed between the canopies of aspen and spruce stands ($F_{[1,19]} = 21.46$, $P = 0.001$), but no differences were evident between harvest treatments ($F_{[1,19]} = 1.81$, $P = 0.108$), nor was the interaction between cover-type and harvest treatment significant ($F_{[1,19]} = 1.87$, $P = 0.104$). Many more individual spiders were collected from spruce (2,876 ind.) compared with aspen canopies (178 ind.). The eight most abundant species were all abundant in spruce, whereas in aspen stands only one of these was reasonably common (see Supplemental Material available online only). Similarly, higher species richness was recorded in spruce (64 spp.) compared with aspen canopies (28 spp.); 21 species were shared between cover-types. A higher number of unique species were observed in spruce canopies (43 spp.), some with high abundances (>200 individuals). In contrast, collections from aspen canopies included only seven unique species, and all but one were singletons. However, individual-based rarefaction suggests few differences in mean species richness between forest cover-harvest treatment combinations when compared at the minimum sample size of 64 individuals (Fig. 1a). Thus, greater spider abundance in spruce canopies accounts for the greater richness of these assemblages.

The MRT analysis resulted in a tree with four terminal branches and three splits, using forest cover-type, crown cover and tree height as the main variables explaining the species composition (Fig. 2). The tree explains a total variance of 84.64% and has pre-

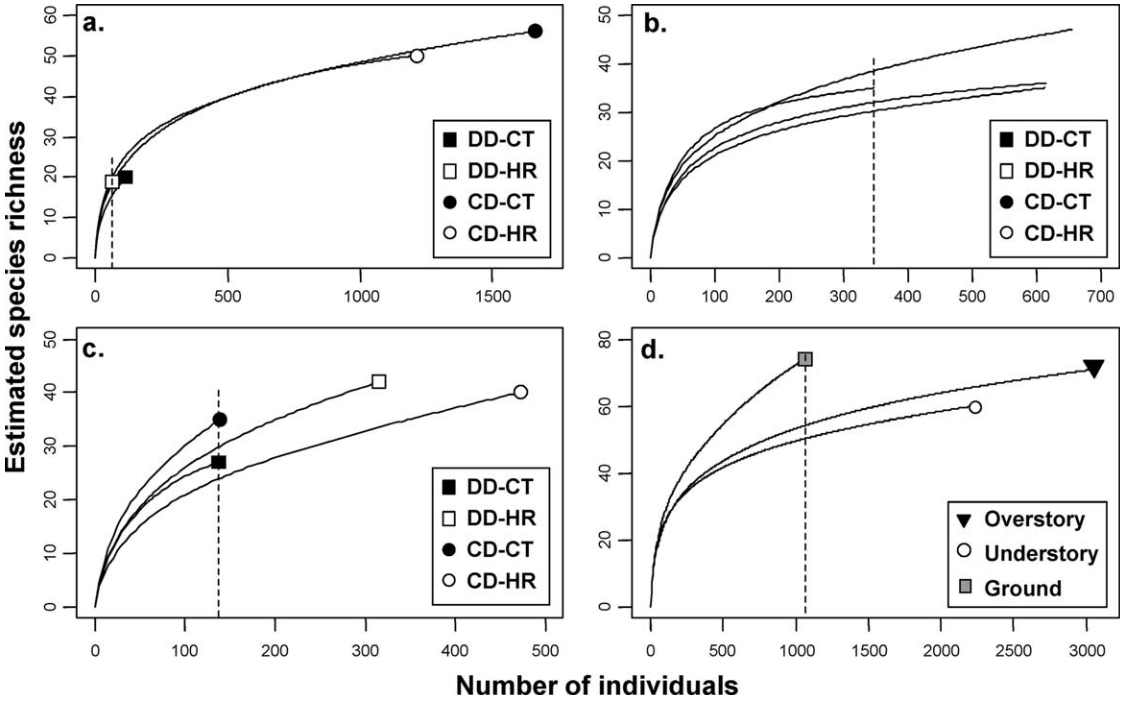

Fig. 1. Individual-based rarefaction for (a) overstory, (b) understory, and (c) ground-dwelling spider assemblages in a boreal mixedwood forest. (d) Overall forest. (Dashed vertical lines represent the minimum sample size for comparison purposes).

diction ability of 73.68%. Most of the variance (80.26%) in the dataset is accounted for by the first split, which is represented by forest cover-type. For spruce sites, crown cover explains the next split in the tree, accounting for 2.34% of variance, with values >80% representing uncut controls and values lower than 80% representing harvested sites. Similarly, for aspen sites, two groups are evident based on tree height, this split explains 2.04% of the variance.

Understory Assemblages. Spider assemblages sampled in the understory included 2,229 individuals grouped in 12 families and 60 species (Supplemental Material available online only). Ten species represented 74.02% of the total, with six of these also among the most abundant in the overstory (*P. subarcticus, P. r. quartus*, *D. brevitarsa*, *P. flavipes*, *C. canadensis*, and *A. displicata*). Singletons and doubletons were represented by 15 and 4 species, respectively. Significant differences in overall spider composition were observed between cover-types ($F_{[1,8]} = 3.69$, $P = 0.001$) and harvest treatments ($F_{[1,8]} = 2.832$, $P = 0.006$), but no statistical interaction was evident between these factors ($F_{[1,8]} = 1.73$, $P = 0.109$).

More individuals were collected in spruce stands (aspen: 961; spruce: 1,268 ind.) and in control areas (control: 1,226; harvest: 1,003). The species *P. subarcticus* was equally abundant in aspen and spruce stands (218 vs. 209 ind., respectively) but twice as abundant in spruce controls (aspen: 147; spruce: 280 ind.); the abundance of the other common species varied between cover-types and treatments. Species richness was higher in spruce (53 spp.) than in aspen stands (43 spp.) and higher in harvested sites (54 spp.) in comparison with control sites (44 spp.). A large number of species were shared between cover-types (36 spp.) and harvest treatments (38 spp.). When compared at the minimum sample size of 347 individuals, differences in mean species richness are apparent between harvested areas in both forest-types; however, there were no differences between aspen and spruce controls (Fig. 1b).

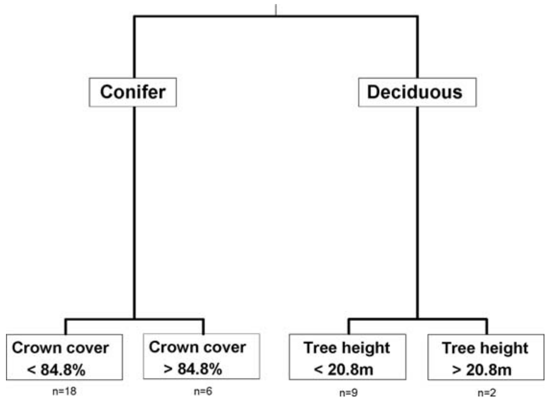

Fig. 2. MRT for overstory spider assemblages in a boreal mixedwood forest (Error: 0.154, coefficient of variation Error: 0.263, SD: 0.03).

Table 1. Complementarity between layer, cover-type, and harvest combinations based on spider species and guild composition in a boreal mixedwood forest

			OS				*US*				*GR*		
			DD		CD		DD		CD		DD		CD
			CT	HR	CT	HR	CT	HR	CT	HR	CT	HR	CT
Species composition													
OS	DD	HR	0.61										
	CD	CT	0.77	0.73									
		HR	0.75	0.75	0.34								
US	DD	CT	0.78	0.80	0.63	0.61							
		HR	0.75	0.77	0.66	0.63	0.35						
	CD	CT	0.78	0.77	0.56	0.56	0.39	0.44					
		HR	0.76	0.78	0.57	0.57	0.46	0.48	0.45				
GR	DD	CT	0.88	**0.90**	**0.91**	**0.93**	**0.98**	**0.97**	**0.98**	**0.96**			
		HR	**0.91**	**0.93**	0.87	**0.90**	**0.95**	**0.96**	**0.95**	**0.93**	0.56		
	CD	CT	**0.90**	**0.92**	0.88	**0.91**	**0.94**	**0.96**	**0.94**	**0.94**	0.65	0.67	
		HR	**0.95**	**0.93**	0.87	**0.90**	**0.96**	**0.97**	**0.96**	**0.95**	0.63	0.51	0.71
Guild composition													
OS	DD	HR	0.13										
	CD	CT	0.13	0									
		HR	0	0.13	0.13								
US	DD	CT	0.25	0.13	0.13	0.25							
		HR	0.14	0.25	0.25	0.14	0.14						
	CD	CT	0.25	0.13	0.13	0.25	0	0.14					
		HR	0	0.13	0.13	0	0.25	0.14	0.25				
GR	DD	CT	0.90	0.50	0.50	0.63	0.63	0.75	0.63	0.63			
		HR	0.25	0.13	0.13	0.25	0.25	0.38	0.25	0.25	0.43		
	CD	CT	0.25	0.13	0.13	0.25	0.25	0.38	0.25	0.25	0.43	0.25	
		HR	0.50	0.38	0.38	0.50	0.50	0.63	0.50	0.50	0.20	0.29	0.29

Values in bold represent highly complementary sites (i.e., more different in species composition).

OS: Overstory, *US:* Understory, *GR:* Ground, DD: Deciduous dominated stands, CD: Conifer dominated stands, CT: Unharvested (control), HR: Harvested (20% retention).

Ground Assemblages. In total, 1,063 individuals in 11 families and 74 species were collected from the ground (Supplemental Material available online only). Twelve species accounted for 74.60% of the total abundance, and most of these were rarely collected from other forest layers [*Pardosa moesta* Banks, *Pardosa xerampelina* (Keyserling), *Pardosa mackenziana* Banks (Lycosidae), *Cybaeopsis euopla* (Bishop & Crosby) (Amaurobiidae), *Pardosa moesta* Banks, and *Pardosa uintana* Gertsch, all with >40 individuals each]. A large number of species were singletons (29 spp.) and doubletons (12 spp.). Significant differences in spider composition were observed between cover-types ($F_{[1,67]} = 5.49$, $P = 0.001$), harvest treatments ($F_{[1,8]} = 12.87$, $P = 0.001$), and the interaction of these two factors ($F_{[1,8]} = 3.43$, $P = 0.002$).

A larger number of individuals were collected from harvested areas in both cover-types (aspen: 315; spruce: 473) compared with control areas (aspen: 137; spruce: 138). Species richness was higher in harvested areas (aspen: 42; spruce: 40) than in controls (aspen: 27; spruce: 35). Nonetheless, individual-based rarefaction shows the highest mean richness in spruce controls and the lowest in spruce harvested sites when compared at the minimum sample size of 137 individuals (Fig. 1c).

Vertical Stratification. Pooling across all three layers, 143 species were recorded, 40 as singletons and 14 as doubletons. Five species accounted for much of the standardized abundance; however, the importance of these species varied among layers. Even though fewer individuals were collected from the ground, individual-based rarefaction shows that this layer maintains the highest mean species richness averaged across cover-type and harvest treatment (Fig. 1d) in comparison to the other two layers, which support lower and approximately equal richness. A large number of species were unique to each forest layer, especially to the ground layer (*OS:* 19; *US:* 20; *GR:* 52) and only 10 species were shared among the three layers. As a result, species composition in each forest layer is highly complementary, each layer maintaining a relatively distinctive spider assemblage.

As expected, overstory and understory layers were less complementary (C = 0.56; 40 shared species) than these two layers were with the ground layer; however, it is worth noting that *GR* was more complementary with *US* than with *OS* (C = 0.92; 10 shared species versus C = 0.82; 22 shared species, respectively). Contrasting 'cover × treatment' combinations between layers gives similar results (Table 1); pair wise comparisons between *OS* and *US* samples resulted in lower complementarity values than comparisons between these two and *GR*. From the foraging guild structure perspective (Table 1), similar patterns are observed between layers, with *OS* and *US* the least complementary (C = 0.14) followed by *OS* versus *GR* (C = 0.63) and by *US* versus *GR* (C = 0.75), as observed for 'cover × treatment' combinations.

NMS ordination (stress value of 9.06 in a two-dimensional result) depicts the response of spider assemblages to differences in forest cover and harvesting across the three layers (Fig. 3). Differences between the upper layers of the forest (both *OS* and

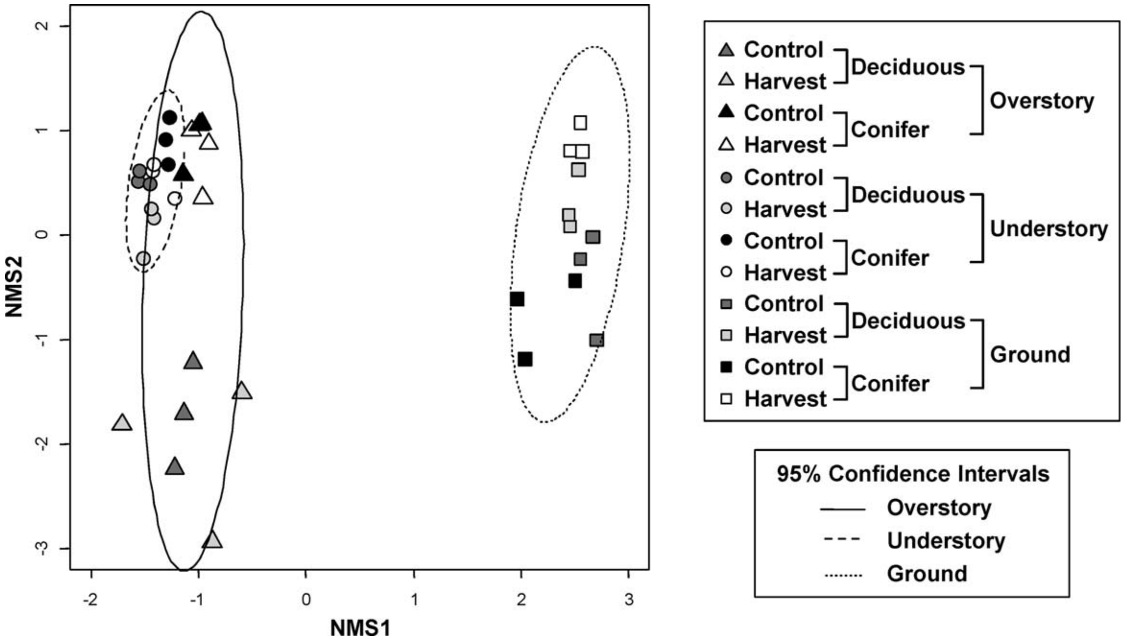

Fig. 3. NMS Ordination of spider assemblages in the overstory (triangles), understory (circles), and ground (squares) layers of unharvested and harvested aspen and spruce dominated stands in a boreal mixedwood forest (Stress: 9.06, Bray-Curtis distance measure).

US) and the ground layer are evident, whereas few differences in species composition are observed between the understory and the overstory. As consistent with the complementarity values above, the ordination shows the similarity between samples from the overstory and ground layers. However, canopy and ground spider assemblages are affected differently; the former are mainly affected by forest cover-type whereas the latter are more affected by harvesting.

Indicator species analysis using forest layer, cover-type, and harvest treatment combinations as grouping variables revealed a total of 47 significant indicators (Table 2), including 16, 11, and 20 species, respectively, as indicators of the overstory, understory, and ground layers. Most of these species, however, were indicators for only spruce forests. Few of these species were strong indicators (*IndVal* > 70.0). Thus, as shown in Table 2, four species were strong indicators for spruce canopies and five species for the ground layer in spruce harvested areas. Only one species strongly indicated aspen sites, and then only harvested sites. No species were strong indicators for the understory.

Overall, guild structure was dominated by Sheet/Tangle weavers and Ground runners, with these comprising a large proportion of the standardized abundance (24.14% and 20.02%, respectively). However, Ambushers and Orb weavers were also numerous, accounting for 17.81% and 12.38% of the total. Marked differences were observed according to forest layer; thus, Ambushers were proportionally dominant in the overstory, followed by Sheet/Tangle and Space web weavers (Fig. 4a, 4f, and 4 g). In contrast, the understory was dominated by Sheet/Tangle weavers followed by Orb weavers and Ambushers (Figs. 4f, 4e, and 4a), while Ground runners (Fig. 4d), Sheet/Tangle and Funnel/Sheet weavers (Figs. 4d, 4f, and 4c) were more important on the ground.

Guild composition was also influenced by cover-type and harvesting treatments. Thus, Sheet/Tangle weavers were proportionally more abundant in the spruce overstory and aspen understory controls, in contrast to Ground runners which dominated the harvested ground layers. Ambushers and Orb weavers were predominant in both harvested and unharvested spruce canopies; however, the latter guild was also important in the understory. Space-web weavers and Stalkers were proportionally more abundant in the overstory of spruce controls and still important in the canopy of harvested sites. Even though Funnel/Sheet weavers were not highly represented in this study (3.82% of the total), it is worth noting that this guild was relatively more important in the harvested aspen ground layers. These results corroborate the indicator species analysis using guilds instead of species. Foliage runners (*IndVal:* 26.9), Stalkers (*IndVal:* 41.7), and Space-web weavers (*IndVal:* 35.8) were significant indicators for spruce unharvested canopies, whereas Ambushers (*IndVal:* 28.4) and Ground runners (*IndVal:* 57.3) were indicators for the overstory and ground layers harvested spruce sites, respectively.

Sheet/Tangle weavers (Linyphiidae) deserve special consideration. This family is one of the richest groups of spiders in temperate forests and in Canada (Bennett 1999, Paquin et al. 2010), and as a consequence, generalizations regarding this group are dif-

Table 2. Significant indicator species in three layers of harvested (HR) and unharvested (CT) deciduous (DD) and conifer (CD) dominated stands in a boreal mixedwood forest (*IndVal:* Indicator Value)

Family	Species	DD	CD	*IndVal*
Overstory				
Araneidae	*Araneus saevus* (Koch)		CT	68.0**
	Araniella displicata (Hentz)		HR	35.2*
Clubionidae	*Clubiona canadensis* Emerton		CT	31.1*
	Clubiona moesta Banks	CT		53.1**
Dictynidae	*Dictyna brevitarsa* Emerton		CT	42.2**
Gnaphosidae	*Sergiolus montanus* (Emerton)		HR	76.7**
Linyphiidae	*Grammonota angusta* Dondale		HR	55.2**
	Phlattothrata flagellata Emerton		CT	76.0**
Philodromidae	*Philodromus pernix* Blackwall		HR	75.5**
	Philodromus placidus Banks		CT	45.4*
	Philodromus praelustris Keyserling	CT		43.7*
	Philodromus rufus quartus Dondale & Redner		HR	30.8**
	Thanatus formicinus (Clerck)		HR	43.2*
	Tibellus maritimus (Menge)		HR	58.2*
Salticidae	*Pelegrina flavipes* Peckham & Peckham		CT	45.9**
Theridiidae	*Dipoena* cf. *nigra* Emerton		CT	100**
Understory				
Araneidae	*Araneus marmoreus* Clerk	CT		33.7*
	Araneus trifolium Hentz		HR	56.5**
	Cyclosa conica (Pallas)		CT	49.7**
Clubionidae	*Clubiona kulczynskii* Lessert		CT	44.4*
Dictynidae	*Emblyna phylax* (Gertsch & Ivie)	CT		55.9**
Linyphiidae	*Estrandia grandaeva* (Keyserling)	CT		37.6*
	Helophora insignis (Blackwall)	CT		53.1*
	Neriene radiata (Walckenaer)		HR	32.6*
	Pityohyphantes subarcticus Chamberlin & Ivie	CT		30.4**
Philodromidae	*Philodromus cespitum* (Walckenaer)		HR	40.1**
Thomisidae	*Misumena vatia* (Clerck)		HR	42.2**
Ground				
Amaurobiidae	*Amaurobius borealis* Emerton	HR		36.4*
Gnaphosidae	*Gnaphosa borea* Kulczyn'ski		HR	65.0*
	Gnaphosa microps Holm		HR	55.6*
	Gnaphosa parvula Banks		HR	78.9**
Linyphiidae	*Diplocentria bidentata* Emerton		CT	47.6*
	Hybauchenidium gibbosum Sϕrensen	HR		74.9**
	Improphantes complicatus Emerton		CT	69.0**
	Lepthyphantes alpinus Emerton		CT	61.5*
	Sciastes truncatus (Emerton)	HR		48.1*
	Zornella armata Banks		CT	42.9*
Liocranidae	*Agroeca ornata* Banks		CT	46.1**
Lycosidae	*Arctosa alpigena* (Doleschall)		HR	100**
	Pardosa fuscula (Thorell)		HR	78.6**
	Pardosa hyperborea (Keyserling)		HR	89.5**
	Pardosa mackenziana Banks	HR		38.1*
	Pardosa moesta Banks		HR	68.8**
	Pardosa uintana Gertsch		HR	34.9*
	Pardosa xerampelina (Keyserling)		HR	70.8**
Thomisidae	*Xysticus emertoni* Keyserling		HR	41.3*
	Xysticus obscurus Collett	HR		29.1*

*, $P < 0.05$; **, $P < 0.01$.

ficult. Even though this guild is well represented in all three layers (overall richness: 53 spp.), species composition differs dramatically across layers. Ground-dwelling assemblages have more species (33 spp.) of Sheet/Tangle weavers but these exist at lower relative abundance (17.87% of the sample). In contrast, understory and overstory assemblages have fewer species than the ground layer, and these two layers include similar number of species (*OS:* 17; *US:* 16). These species, however, are relatively more abundant, especially in the understory (*OS:* 19.45%; *US:* 35.08%). In addition, this group shows the highest value of unique species in the ground (33 spp.) in comparison to the understory (8 spp.) and the overstory (5 spp.). Only a few species are shared between layers, with the highest number of species shared (8 spp.) between the overstory and understory.

Discussion

Perhaps the greatest challenges in studies like this, where different layers of the forest are considered, is that collection techniques applied at each layer are often necessarily quite specific. As a consequence, comparisons of species composition across forest layers may be somewhat biased because of differences in collection effort. In this study the fauna of the ground layer was assessed by a passive method (i.e., pitfall traps), whereas the understory and canopy layers were sampled using active methods (i.e., beating and

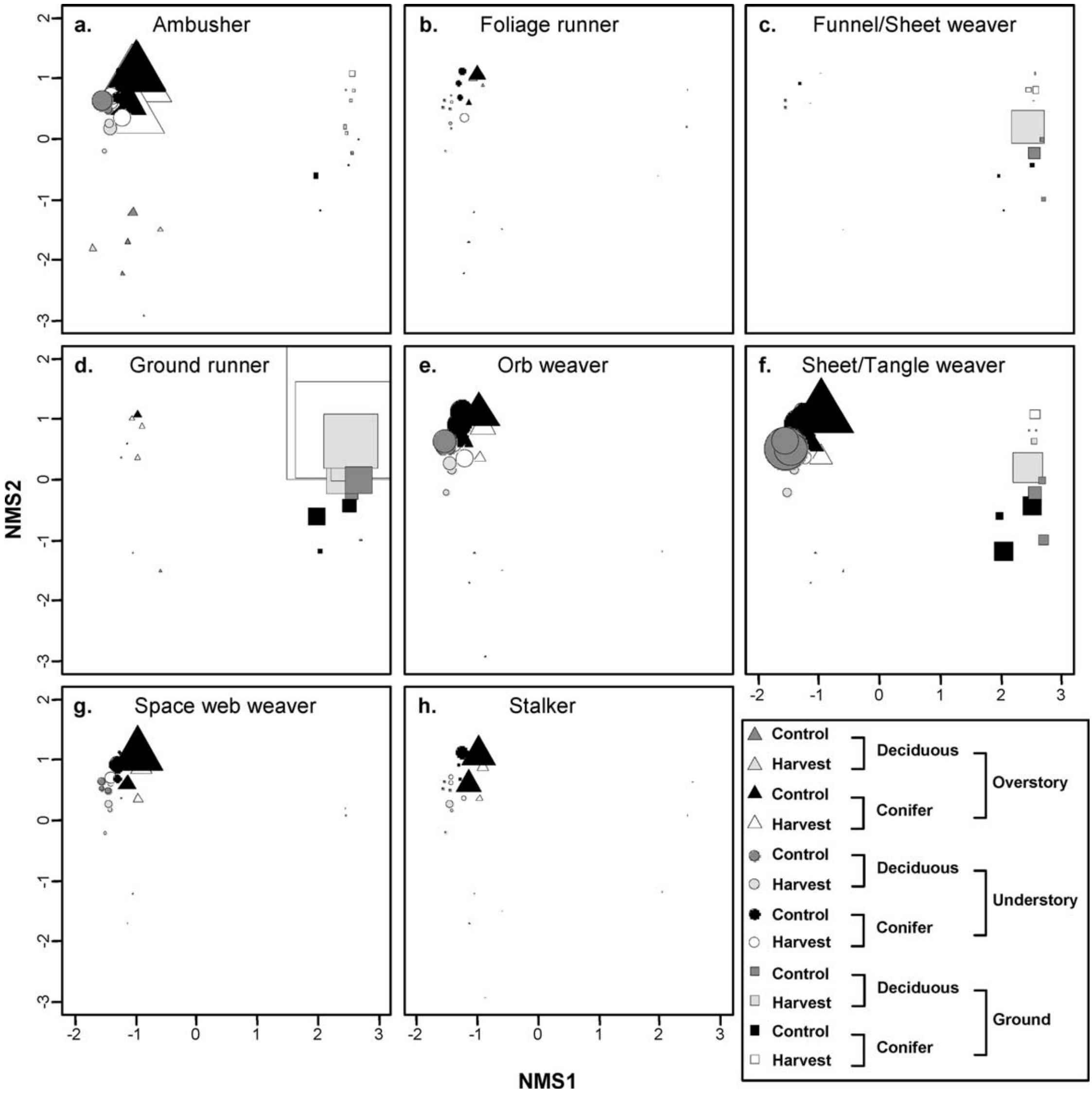

Fig. 4. Spider guild structure in the overstory (triangles), understory (circles), and ground (squares) layers of unharvested and harvested aspen and spruce dominated stands in a boreal mixedwood forest (based on the NMS Ordination in Fig. 3; point size represents the standardized abundance of the guild on each site, higher abundances are represented with larger points; guild classification followed Uetz et al. 1999).

manual searching, which also differ in some respects from each other). These differences in sampling could contribute to differences in species composition. For example, active spiders will be more likely collected in pitfall traps than sedentary spiders, whereas branch or shrub beating likely collects most of the individuals regardless their habits. Given the structural heterogeneity of leaf litter, however, active sampling may result in much more biased samples (e.g., underrepresentation of small or cryptic species that are easily missed in broad scans), rendering comparisons even more problematic. Given the fact that most of the ground-dwelling species are quite specific to this forest layer and that very few species collected on the ground were also observed in higher layers, we are confident that our results reasonably reflect natural differences in species composition among forest layers.

Ground-dwelling arthropod assemblages are relatively well studied in the boreal forest, especially carabid beetles (Koivula et al. 2002, Niemelä et al. 1993, Spence et al. 1996) and spiders (Buddle et al. 2000, Matveinen-Huju and Koivula 2008, Niemelä et al. 1994). However, for a number of reasons, these groups are much more poorly known from higher layers of this forest, even though it has been long known that there are clear faunal differences among forest layers in other forest types. Such differences are particularly well understood for spiders elsewhere (Turnbull 1973 and references therein, Enders 1974). To our knowledge, this is among the first attempts to characterize the spider composition in the overstory of a boreal ecosystem and to consider how it is affected by harvesting practices, in addition to assessing differences in composition across the vertical gradient.

In previous studies of the ground layer, carried out at the same study area, the spider richness ranged between 51 (Work et al. 2004) and 98 (Buddle and Shorthouse 2008) species. Thus, the 143 species reported in the current study suggest that both understory and overstory habitats contribute to maintaining a rich and diverse boreal spider assemblage, with 69 species that were exclusively collected in these upper layers. Even though ground-dwelling assemblages contribute to a large proportion of the spider biodiversity in our study (52 of 74 species exclusively collected in this layer), overstory assemblages must not be ignored, especially when making recommendations about forest management that includes maintaining faunal diversity as a central goal.

It is evident, despite the cautions about differences in sampling techniques, that each forest layer harbors a relatively distinctive species composition. Our results demonstrate marked differences in spider assemblages inhabiting the three forest layers and that forest cover-type and harvesting have significant effects on species composition in all three layers. These observations seemed to be related to differences in structural complexity between stands. For instance, spruce canopies are more complex than those of aspen. Average crown height in spruce trees was significantly greater than in aspen trees in our study; as a consequence, spruce canopies have more branches covered with needles and loose bark, providing more microhabitats for feeding, mating, nesting sites, and refuge. This must contribute to a general explanation for the difference in species richness and abundance of spiders in this layer between cover-types. In addition, crown cover was significantly higher in unharvested sites for both aspen and spruce stands, suggesting an important influence for layers below. Significant differences have also been documented in the understory plant communities of conifer and deciduous stands in the EMEND study area, but with respect to this layer, deciduous stands are more dense and diverse (Macdonald and Fenniak 2007). This, in addition to characteristics of the ground layer such as leaf litter (Uetz 1975, 1979) that differ between forest cover-types, likely explains the distinctiveness of the ground fauna.

Differences in habitat heterogeneity between aspen and spruce stands and between harvested and uncut forests are mostly responsible for the observed abundance and richness patterns in this study. Habitat heterogeneity influences structural complexity and consequently has a positive impact on species diversity (Tews et al. 2004); hence, structural habitat complexity strongly affects spider abundances, species richness, and habitat availability (Hatley and Macmahon 1980, Post and Riechert 1977, Robinson 1981, Uetz 1991). It has been shown, for example, that needle density and number of branches have a significant effect on the abundance, richness, and guild structure of spiders in conifer canopies (Gunnarsson 1990; Halaj et al. 1998, 2000; Sundberg and Gunnarsson 1994). Furthermore, ground-dwelling spider assemblages are also affected by variables such as canopy closure, litter type and depth, moss and herb cover, temperature, moisture, and coarse woody debris (Buddle 2001, Bultman and Uetz 1982, Huhta 1971, McIver et al. 1992, Pearce et al. 2004, Ziesche and Roth 2008). Moreover, general environmental features, including tree density, basal area, canopy cover, downed wood, and soil temperature vary conspicuously in both deciduous and conifer stands harvested to 20% retention in the boreal forest (Macdonald and Fenniak 2007). Thus, associated differences in species composition are to be expected between cover types and disturbance regimes.

Effects of environmental features on spiders, such as those of natural forest cover-type and disturbances such as harvesting, appear to depend on what forest layer is considered. This work suggests that assemblages in the overstory, and in lesser degree in the understory, are significantly structured by the dominant tree species in the stand (aspen vs. spruce) as long as canopy habitat remains, but that harvesting more strongly affects ground assemblages. It is worth mentioning that our samples were collected 8 yr postdisturbance and, thus, these results might suggest different degrees of resistance and resilience after disturbance among layers. For example, before harvest, a strong effect of forest cover-type was observed for ground assemblages (Work et al. 2004) but harvesting played a significant role 1 yr postdisturbance (Buddle and Shorthouse 2008). This latter effect is still observed 8 yr postharvest. In contrast, even though some differences were observed in the understory regarding cover-type and harvesting, these differences were not as strongly reflected as they were in the ground and overstory layers. Unfortunately, no data are available from the overstory or understory before or immediately after harvesting at EMEND, although the local unharvested sites provide a stand-level control.

Studies in Sweden and Germany have shown no differences in species richness between the canopy of harvested and unharvested spruce forests (Ammer and Schubert 1999, Pettersson 1996), suggesting that, as in our case, the overstory fauna is relatively resistant or very resilient after harvesting. Some of the environmental features (i.e., temperature, moisture, light) that might influence spider species composition in the forest ground layer are strongly affected by harvest, as shown by the differences in structure between harvested and unharvested stands. In contrast, environmental conditions are more extreme and heterogeneous in the canopy (Nadkarni 1994 and references therein), and thus species inhabiting this layer may be more well adapted to drastic changes than are those of the ground layer and, thus, be more resistant to disturbances because of canopy opening (Schowalter et al. 2005). Thus, as our results suggest, harvesting (at least to 20% retention) seems to have only minor effects on overstory assemblages, as long as some structure and stand connectivity is left after dispersed retention harvesting.

We expected that forest spider assemblages would be stratified following a vertical pattern from the ground to the overstory. Although our results show strong resemblance in assemblages between the overstory and the understory, they also show that spiders of the ground layer are relatively more similar to the overstory than to the understory. This suggests that these two layers are linked supporting some kind of connectivity. This corresponds with other information about spider movement, which suggests that ground species move along tree trunks to access the higher overstory (Pinzón and Spence 2008, 2010). The wolf spider *P. moesta,* which is a clear component of the leaf litter, was also relatively common in overstory samples, especially in spruce stands, but almost absent in the understory (only one individual was collected in this layer). Thus, we observed an interesting gradient in terms of shared species. It seems that this link between the ground and the overstory is relatively stronger in spruce controls, followed respectively by spruce harvested, aspen controls, and aspen harvested. Understanding this pattern poses an interesting question for additional research.

Guilds have been regarded as the basic building blocks of ecosystems (Hawkins and Macmahon 1989), assuming that species have characteristic ecological roles (Simberloff and Dayan 1991). Guilds have been generally defined as "group[s] of species that exploit the same class of environmental resources in a similar way" (Root 1967), and they are held to group "biological communities into functional units . . . not restricted by taxonomic relationships" (Adams 1985). Thus, the guild concept is highly relevant for spiders (Post and Riechert 1977, Uetz 1977, Uetz et al. 1999) in relation to the different ways that species access similar resources through specific hunting strategies. However, exploiting the same class of resources is not the only factor structuring spider guilds. At least for those that spin webs, for example, physical requirements must be met for a spider to place its web effectively (Halaj et al. 1998, Stratton et al. 1978, Turnbull 1973). Thus, the importance of orb-weaving spiders in the overstory and understory reflects not only the availability of flying insects, but also the existing structures for web attachment (Greenstone 1984; McNett and Rypstra 2000; Rypstra 1983, 1986). In fact, this is observed when orb weaver abundance is compared between layers and forest types. In spruce stands the number of individuals is considerably higher in the overstory of both unharvested and harvested sites, whereas in aspen stands this guild is relatively more represented in the understory reflecting the structural heterogeneity in these habitats. Thus, spider guild structure could be considered as a result of groups of potential prey and structure available in each of the forest layers. Consequently, vertical stratification of forest spiders likely reflects the variation in microhabitat characteristics across layers, in addition to variation in prey availability.

In conclusion, our study reveals that spider biodiversity is highly sensitive to changes associated with the successional gradient of forest development. In both the early successional deciduous forest stands and in the later conifer-dominated stands, three somewhat distinct habitat layers contribute to maintenance of overall diversity. Among these, the canopy comes to harbor an especially rich spider fauna dominated by spiders that use silk to capture their prey in the spruce forests constituting the latest sere in the boreal mixedwood. After a 20% retention harvest the canopy fauna was reasonably conserved in both aspen and spruce stands, but the spider fauna of both ground and understory layers changed rather dramatically.

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