

Hoverfly (Syrphidae) Communities Respond to Varying Structural Retention After Harvesting in Canadian Peatland Black Spruce Forests

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ABSTRACT Variable retention harvesting (VRH), in which trees are removed at variable intensity and spatial configuration across the landscape, retains greater forest structural heterogeneity than traditional clear-cut harvesting and is being recommended as an alternative for sustainable management of the boreal forest. Little is known about its effects on forest fauna; thus, we studied the influence of one type of VRH (harvesting with advanced regeneration [HARP]) on the Syrphidae (Diptera) community in northern Ontario forests of peatland black spruce (*Picea mariana*). We examined the effects of varying structural retention (from unharvested through partial retention to clear-cut) on syrphid species richness and abundance, and abundance of functional assemblages. Greater species richness and population abundances were found generally in harvested than in unharvested forests. Overall species richness and the abundance of four species (*Platycheirus rosarum*, *Toxomerus marginatus*, *Xylota annulifera*, and *X. tuberculata*) and larval predators were all higher in both clear-cut sites and those with structural retention than in unharvested sites. Similarly, overall species richness and the abundance of nine species were higher in clear-cut than in unharvested sites. Species responses are discussed in an ecological context. Differences among the levels of forest retention harvesting were relatively minor compared with those of the clear-cut and unharvested area, suggesting that local habitat characteristics may play a more important role in determining the syrphid community than the landscape configuration. However, a landscape level effect was evident, suggesting that syrphids may be useful in reflecting changes in stand structure at the landscape scale.

KEY WORDS Syrphidae, species richness, functional assemblages, variable retention harvesting, boreal forest

Clear-cut harvesting is the primary system for extracting wood fiber in the Canadian boreal forest, and in the short term, almost completely changes forest structure over large areas. Both conservation benefits and economic incentives have led to the development of alternative silvicultural methods in which partial clearance retains some of the forest structural heterogeneity and preserves advanced regeneration. A recent approach is to harvest trees at variable intensities and spatial configurations across the landscape to provide structural retention, a technique known as variable retention harvesting (VRH) (Bergeron and Harvey 1997, Franklin et al. 1997). One benefit of this type of harvesting is the greater range of structural heterogeneity within harvested landscapes relative to traditional clear-cut methods. This structural retention has been hypothesized to support a biological community in harvested forests more similar to the un-

harvested condition (Franklin et al. 1997, Humphrey et al. 1999).

As new harvesting methods are developed, there is a need to assess their effects on flora and fauna in comparison to traditional clear-cut systems, as well as to find indicators of sustainable forest management (Dennis et al. 1995, Humphrey et al. 1999). Many insect taxa have shown sensitivity to harvesting in boreal ecosystems, including ground-dwelling or wood-decomposing species in clear-cut areas (Niemelä et al. 1993, Punttila et al. 1994, Okland 1996) and aerial insect families and trophic assemblages in VRH sites (Deans et al. 2005). Dipteran species form a large proportion of the boreal insect fauna (Danks and Footitt 1989) and are of particular interest because of their ubiquity and fine-scale habitat requirements. Changes within this group may have widespread effects on the functioning of boreal ecosystems because some functional groups are represented by few taxa and thus the loss of even a few species could affect ecosystem processes (Pastor et al. 1996). Focusing on functional groups has been advocated because changes in ecosystem function may not be discernable with species analyses alone (Noss 1990, Didham et al. 1996). Observed reductions in pollinators (Aizen and Feinsinger 1994, Didham et al. 1996),

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decomposers (De Souza and Brown 1994, Didham et al. 1996), and the possibility of increased herbivorous insect outbreaks with reduced parasitoid abundances (Kruess and Tscharrtk 1994, Roland and Taylor 1997), all have potential impacts on overall ecosystem processes. Didham et al. (1996) found that particular functional groups such as pollinators and decomposers responded as trophic assemblages to altered habitat conditions.

Species and functional groups within the Syrphidae (hoverflies) family have been identified as potential indicators of forest change (Sommaggio 1999, Humphrey et al. 1999, Sugar 2000). It is one of the most diverse families of Diptera, with ≈ 200 genera and $>5,000$ species (Katzourakis et al. 2001). In addition to their taxonomic diversity, hoverflies are widely collected, in part because of their brightly colored appearance and their natural history is well known compared with many other insect taxa (Katzourakis et al. 2001). As larvae, they present an extensive range of habitat requirements, adaptations, and functional roles (Vockeroth and Thompson 1981, Rotheray 1991, Humphrey et al. 1999), including feeding habits as phytophages, predators, or saprophages (Gilbert 1986, Vockeroth and Thompson 1981, Sommaggio 1999), whereas as adults, they display relatively homogeneous feeding habits but play a key role in pollinating understorey vegetation (Kevan et al. 1993).

Syrphidae have three main characteristics that make them potential candidates for biological indicators (Speight 1986, Sommaggio 1999): (1) they are common and easy to find in almost all terrestrial ecosystems, (2) their identification is not difficult for many genera, and (3) their wide range of larval-feeding habits and habitat requirements allow for a functional approach (Sommaggio 1999, Sugar 2000, Katzourakis et al. 2001). Many aspects of syrphid microhabitat requirements are likely to be modified by forest harvesting, such as standing live or dead trees, stumps, fallen wood, and other features, including living vegetation and decaying organic matter (Gilbert and Owen 1990, Rotheray 1991, Sugar 2000). Many insect taxa, including syrphids, have associations with habitat features that may be dramatically decreased by forest harvesting (Deans et al. 2003, Work et al. 2004). To date, syrphids have been used rarely as indicators of forest change (Kula 1997, Humphrey et al. 1999, Sugar 2000), although they have been considered for studies examining the effects of agricultural pesticides (Daccordi et al. 1988 in Sommaggio 1999) and industrial pollution (Bankowska 1980).

We studied the influence of VRH on the syrphid community in the peatland black spruce forests of northeastern Ontario, Canada. Specifically, we tested for the effects of different levels of forest retention (from unharvested sites through structural-retention harvesting sites to clear-cut sites) on syrphid species richness, population abundances, and abundance of functional assemblages. Because previous work found syrphids associated with low canopy cover, high understorey cover (Kula 1997, Humphrey et al. 1999, Sugar 2000) and harvested forest areas (Deans et al.

2005), we expected to see a general decrease in species richness and abundance with increasing forest structural retention.

Materials and Methods

Study Area. Research was conducted in the lowland clay belt of northeastern Ontario, Canada (in the Lake Abitibi model Forest; 49°35' N, 80°35' W), where large areas of the boreal forest are dominated by homogeneous peatlands of black spruce [*Picea mariana* (Mill.), Pinaceae], larch [*Larix laricina* (Du Roi) K. Koch, Pinaceae], and balsam fir (*Abies balsamea* L. Mill., Pinaceae). On upland sites, black spruce also grows homogeneously with white spruce [*Picea glauca* (Moench) Voss, Pinaceae] and balsam fir, although mixed forests of balsam poplar (*Populus balsamifera* L., Salicaceae), trembling aspen (*Populus tremuloides* Michx., Salicaceae), white birch (*Betula papyrifera* Marsh, Betulaceae), and jack pine (*Pinus banksiana* Lamb., Pinaceae) are also found in glacial till deposits across the landscape. The climate of the area is continental, with mean annual temperatures of -1.1 – 1.7°C , mean annual precipitation between 66.0 and 76.2 cm, and a frost-free period from June to mid-September. Mean annual snowfall is heavy (280 cm), and mean July temperatures range from 15 to 17°C , with precipitation between 20.3 and 25.4 cm.

Experimental Design. Harvesting with advance regeneration protection (HARP) is one type of VRH used in the Clay Belt area, which varies forest structure by clearing trees in strips ~ 5 – 7 m wide (harvested corridor strips, here called cut strips) and removing additional trees from adjacent retention rows (5–9 m wide) based on a minimum diameter limit cut (the retention strips) (MacDonell and Groot 1997, Deans et al. 2003). We identified six plot types in our study area to obtain a landscape gradient of decreasing structural retention: (1) unharvested interior (UI) = contiguous unharvested forest at least 150 m from a harvested edge; (2) unharvested edge (UE) = unharvested forest within 150 m of an edge; (3) high-structural retention (HR) = HARP adjacent to unharvested forest; (4) medium-structural retention (MR) = HARP in the middle of contiguous retention-harvested (HARP) areas; (5) low-structural retention (LR) = HARP adjacent to clear-cut areas; and (6) clear-cut (CC) = little or no retention of trees. Four plots of each structural retention level were sampled for a total of 24 sites.

In each site, a 110 by 150-m plot was established, and a 10 by 50-m subplot was centered in the plot. In sites with structural-retention harvesting, subplots were located such that 5 m of the subplot extended into the cut strip and 5 m into the retention strip of trees. In high-structural retention sites, the plot was placed such that the subplot was at the edge of unharvested forest. In contrast, the subplot in low-structural retention sites was at the edge of the clear-cut areas. The richness and abundance of species and functional groups of syrphids were estimated in each subplot and

in both cut strips and retention strips of forests in structural-retention harvested plots.

Site Characteristics. Site selection was made based on forest resource inventory maps (Ontario Ministry of Natural Resources), information on harvesting operations and visual assessments of site conditions. Only pure black spruce stands were considered. Harvesting operations in all areas occurred within 1995–1997, 2.5–3.5 yr before the study.

Most habitat characteristics closely followed the harvest intensity gradient that we sampled, from unharvested forests through the three levels of structural retention harvesting to clear-cut sites (Deans et al. 2003). Basal area, density, diameter at breast height (dbh), and mean age of trees increased with increasing structural retention of the forest. The proportion of moss, lichens, and *Ledum* were the highest at the unharvested end of the gradient, whereas the amount of decaying moss, coarse and fine woody debris, exposed soil, and sedge were the highest at the clear-cut end of the gradient. A detailed description of habitat in all of the harvested sites is provided by Deans et al. (2003).

Syrphid Sampling Procedure. To sample flies, two Townes-style malaise traps were set in each subplot in the 24 sites for a total of 48 traps. In structural-retention sites, one trap was placed in the center of the cut strip and the other (5 m away) in the center of the retention strip within the subplot. Orientation of the traps was such that the central vane that intercepted captures was perpendicular to the long axis of the harvest strips. Traps established in clear-cut and unharvested sites had the same configuration and spacing relative to each other as those in the structural retention sites. Although we tried to set traps with similar orientation, cutting patterns in the field (e.g., the direction of the strip cuts) ultimately restricted trap orientation, and this may have led to potential biases in captures caused by differences associated with hours of shade and flyway direction. Traps were set simultaneously and operated for 8 consecutive days in each of June, July, and August 1999. Captures from the three sampling periods were combined for each of the 24 sites. Abundances were estimated as the number of individuals per 100 trap-days.

Syrphid specimens were pinned and dried using a method modified from Vockeroth (1966). First, the insects were placed onto pins and into three consecutive 24-h-long baths of 99% ethyl acetate. The final bath had 12 drops of pure ethylene glycol added to the 500-ml ethyl acetate bath to aid in softening the specimen's exoskeleton. Finally, insects were removed, and wings were air dried under pressure to assure a single wing-vein-plane to ease species identification. Several published keys were referenced during identification, including Shannon (1916, 1939), Curran (1921, 1934, 1941, 1953), Curran and Fluke (1926), Fluke and Hull (1945), Fluke and Weems (1956), Sedman (1966), Telford (1970), Covert and Thompson (1977), Thompson (1981, 1997), Vockeroth and Thompson (1981), and Vockeroth (1992). Reference collections from the Royal Ontario Museum and the

University of Guelph were used to verify taxonomic classifications, and voucher specimens from each species were placed there. Immature stages of these flies were grouped in functional assemblages based on the known biology of each species (Vockeroth and Thompson 1981, Gilbert 1986, Humphrey et al. 1999, Sommaggio 1999). Abundance of functional assemblages was estimated as the number of individuals that belonged to that assemblage per 100 trap-days.

Statistical Analyses. One-way analysis of variance (ANOVA) with Tukey's multiple comparisons was performed (version 8.01; SAS 1999) on square-root transformed data to compare syrphid species richness, abundance of common species, and functional assemblages among the different structural-retention plots. Where appropriate, data from harvested interior (UI) and unharvested edge (UE) plots were combined for further analysis. Principal components analyses (PCAs) were conducted (using CANOCO for Windows version 4.0; Lepš and Šmilauer 2003) to examine underlying gradients in community structure relative to habitat structure.

Results

Overall Syrphid Species Richness, Composition, and Abundance. Malaise trap samples yielded 3,209 individual syrphids in 39 genera and 105 species (*Appendix 1*). Of these, 392 females (*Eupeodes*, *Parasyrphus*, *Platycheirus*, and *Sphaerophoria*) could only be identified to genus and thus were excluded from all analyses except those on habitat and feeding guilds. As expected, a few species were very common in the samples, whereas most were rare. The eight most abundant species accounted for 50% of all individuals identified to species. *Toxomerus marginatus* was the most common species, representing 21% of the total individuals caught, followed by *Cheilosia tristis* (150 individuals), *Platycheirus rosarum* (138), *Xylota annulifera* (110), *X. flavifrons* (108), *Sericomyia militaris* (106), *X. quadrimaculata* (103), and *X. hinei* (101 individuals).

We found 2 new records for Ontario (*Platycheirus holarcticus* and *Xylota ouelletti*) and 10 for Northern Ontario (*Heringia calcarata*, *Lejops distinctus*, *Microdon cothurnatus*, *Microdon ocellaris*, *Microdon tristis*, *Orthonевра pictipennis*, *Pipiza femoralis*, *Sphaerophoria brevopilosa*, *Sphaerophoria longipilosa*, and *Trichopsomyia recedens*).

Structural Retention Effects on Species Richness. Species richness of syrphids differed among the varying levels of structural retention (Fig. 1). Comparison of species richness between the unharvested (interior and edge), HARP-harvested (low, medium, and high retention) and clear-cut sites, and between the retention and cut strips within the HARP sites showed consistently greater richness in the cut strips than in either the retention strips or in the unharvested sites ($F = 42.02$; $P < 0.0001$). The average number of species caught in clear-cut sites was similar to that in cut strips in the HARP treatments but was significantly greater than the number of syrphid species caught in

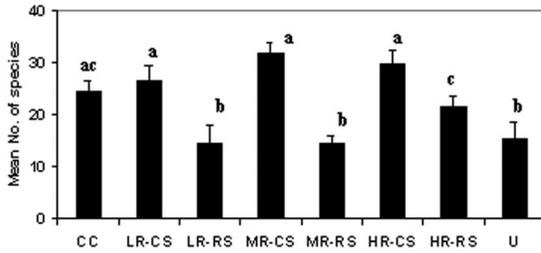


Fig. 1. Species richness of hoverflies (Syrphidae) collected by malaise traps in peatland black spruce forests with varying levels of structural retention harvesting (HARP) from northeastern Ontario, Canada, during 1999 (CC, clear-cut; LR, low-structural retention; MR, medium-structural retention; HR, high-structural retention; Cut, cut strips; RS, retention strips; U, mean for interior [UI] and edge [UE] of unharvested sites). Same letters means no significant difference between treatments at $\alpha = 0.05$ (Tukey's multiple comparisons).

unharvested forests and most retention strips. A comparison between retention strips of HARP-harvested and -unharvested forest areas revealed no significant difference in the mean number of syrphid species caught per trap.

Although more syrphid species were caught in cut strips and clear-cut sites than in retention strips and unharvested sites, the number of individuals caught explained a very high proportion of the variation in the number of species ($R^2 = 0.948, F = 109.35, P < 0.0001$). Because many species were rare, capturing more individuals led to greater species richness. Given this strong relationship between richness and abundance, stand configurations influencing the number of individual syrphids also affected the number of syrphid species.

In the PCA analysis, most of the species vectors were on the right side of the origin of the first axis (8.3%), indicating greater richness and abundance in forest openings of clear-cut and HARP sites on the right side of the ordination (Fig. 2). Conversely, unharvested sites dominated the left side of the ordination with fewer syrphids. Although unharvested forest areas had the lowest syrphid species richness, several common species were found in greater abundance in these forests, including *Toxomerus geminatus*, *Temnostoma vespiforme*, *Helophilus lapponicus*, and *Sericomyia militaris*. Harvested areas, seen predominantly on the right half of the ordination, had the greatest abundance of many common species including *Eupeodes lapponicus*, *Platycheirus rosarum*, and *T. marginatus*. Clear-cut sites tended to be closer to the center of the ordination and the cut strips in forests with retention harvesting (HARP) further to the right, with medium retention strips being furthest to the right. In contrast, little differentiation was shown among retained strips in the HARP stands and the two unharvested treatments. The second axis, which explained 7.1% of the variation, was not readily interpretable with respect to variation among the plots.

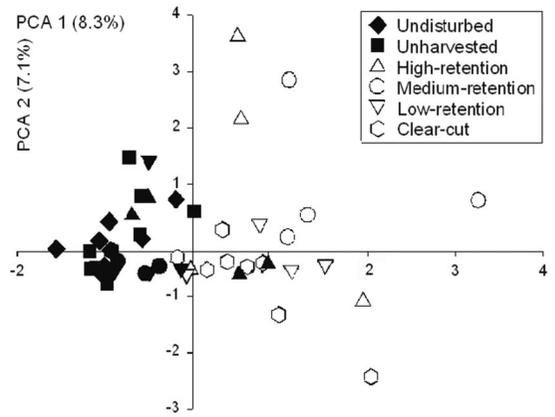


Fig. 2. PCA of syrphid species richness from malaise traps placed in six types of structural-retention harvesting sites of peatland black spruce forests from northeastern Ontario, Canada, during 1999. Solid symbols represent unharvested areas and open symbols cut areas (see Table 1 for definitions of retention).

Structural Retention Effects on Population Abundances. Although total syrphid abundance did not differ significantly among the plots of varying structural retention, abundance of the five more common species did (Table 1). In all Tukey's pairwise comparisons but one, species were significantly more common in harvested sites (CC, LR, MR, and HR) than in unharvested sites (UE and UI).

No syrphid species differed in abundance between the unharvested forest edge and interior sites; therefore, data from edge and interior were pooled for further analysis. The mean abundance of 10 syrphid species differed between clear-cut and unharvested sites, all, with the exception of *M. mellinum*, being more common in the cut sites (Table 2).

Within the stands subjected to varying degrees of structural retention, eight syrphid species were more abundant in the cut strips than in the retention strips of the HARP forests (Table 3). Only two species differed significantly in their abundance between the retention strips of the HARP treatments and the combined unharvested forests. *X. subfasciata* had significantly greater abundance in high-retention HARP residual leaves strips (12.5 ± 5.9 individuals/100 trap-days) than elsewhere (1.7 ± 1.2 individuals/100 trap-days; $F = 3.25, P = 0.0416$), whereas *M. mellinum* showed increasing abundance in the retention strips of stands with higher levels of retention; no syrphid was caught in low (LH) and medium (MH) HARP, 3.1 ± 1.0 individuals/100 trap-days were captured in high HARP (HH), 3.6 ± 1.7 were caught in unharvested edge (UE), and 6.8 ± 3.0 were caught in unharvested interior (UI; $F = 3.65; P = 0.0288$). The abundance of all syrphid species was similar between clear-cut sites and the cut strips of the various HARP-harvested sites except for *H. salax*, which was higher in the clear-cut sites (CC; 2.6 ± 1.1 individuals/100 trap-days) and medium HARP cut strips (MR; 3.1 ± 1.0) than the cut strips in either low (LR) or high

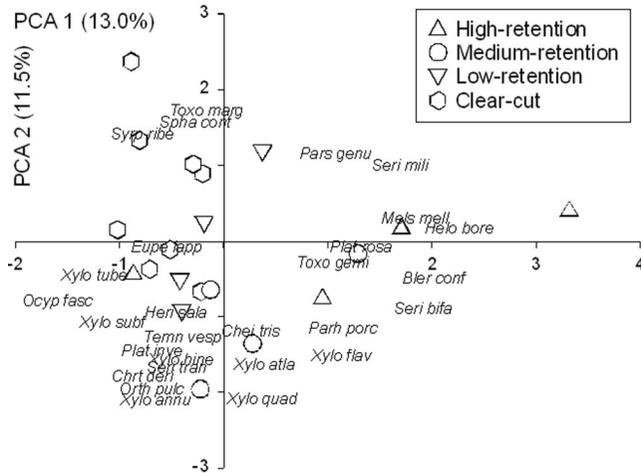


Fig. 3. PCA of common syrphid species captured in malaise traps placed in the cut strips of high, medium, and low structural retention (HARP) sites and clear-cut sites from peatland black spruce forests of northeastern Ontario, Canada, during 1999. See Table 1 for definitions of retention and Appendix 1 for species acronyms.

(HR) HARP sites where no individual was caught ($F = 5.31$; $P = 0.0146$).

A PCA of syrphid abundance in harvested strips and clear-cut sites showed a forest retention gradient along the first axis (13.0% of the variation), with clear-cut areas occupying the left half of the ordination, low and medium-retention HARP cut strips located centrally, and the cut strips of high-retention HARP stands at the far right. The most abundant syrphid species, *T. marginatus*, as well as *S. contigua*, *E. lapponicus*, and *S. ribesii*, were all more abundant in clear-cut areas than in the HARP-treated forests. In contrast, *H. lapponicus*, *S. militaris*, and *M. mellinum* all showed greater abundance in the high-retention areas on the right side of the ordination.

Structural Retention Effects on Functional Assemblages. Changes in structural retention significantly influenced the two functional assemblages of syrphids examined (Table 1). Richness and abundance of pre-deceous syrphids were always greatest in the harvested sites compared with either of the unharvested sites, whereas saprophagous species richness and abundance were greatest at intermediate levels of structural retention (MR and HR), differing significantly from the unharvested sites.

The number of adult syrphid species collected in the traps which could be categorized according to defined larval habitats were 20 wood-dwelling (28%), 17 living in plants (33%), 20 from organic material (13%), 18 living in litter (12%), and 12 tree-dwelling

Table 1. Species richness and abundance of species and functional assemblages of common hoverflies (Syrphidae) collected in malaise traps that show significant differences in mean abundance (no. individuals/100 trap-days \pm SE) among sites of varying harvest levels from peatland black spruce forests of northeastern Ontario, Canada, during 1999

	CC	Retention harvesting (HARP) ^a			Unharvested		F	P
		LR	MR	HR	UE	UI		
No. of species	24.4a ^b \pm 2.1	20.5a \pm 3.1	23.3a \pm 3.5	25.6a \pm 2.2	15.3b \pm 1.2	15.3b \pm 2.5	2.92	0.0237
Syrphid abundance	314.7a \pm 43.4	266.1a \pm 45.6	385.4a \pm 67.8	379.2a \pm 60.1	180.9b \pm 47.6	135.1b \pm 24.6	2.25	0.0529
Species								
<i>O. pulchella</i>	5.2ab \pm 2.5	6.8ab \pm 3.6	10.4a \pm 4.8	3.7b \pm 1.2	0.0c \pm 0.0	1.6bc \pm 1.1	2.88	0.0440
<i>P. rosarum</i>	11.5ab \pm 4.3	13.0ab \pm 6.8	31.8a \pm 16.5	12.0ab \pm 5.1	1.6c \pm 0.8	2.1c \pm 1.1	4.09	0.0118
<i>T. marginatus</i>	99.0a \pm 26.5	53.7ab \pm 22.7	78.7ab \pm 24.8	47.0b \pm 12.0	15.6c \pm 7.5	12.5c \pm 7.4	3.94	0.0137
<i>X. annulifera</i>	10.9ab \pm 2.8	11.5ab \pm 5.1	19.8a \pm 10.4	12.5ab \pm 4.4	1.6c \pm 1.1	1.6c \pm 0.8	3.63	0.0190
<i>X. tuberculata</i>	6.8ab \pm 4.1	13.0a \pm 5.3	8.3ab \pm 3.3	8.9ab \pm 3.6	0.0c \pm 0.0	0.5c \pm 0.5	2.94	0.0411
Trophic groups								
Predators	205.7a \pm 30.9	129.2a \pm 39.1	189.6a \pm 55.6	156.3a \pm 30.6	55.7b \pm 14.6	56.8b \pm 15.8	3.58	0.0086
Saprophage	90.1ab \pm 18.1	90.1ab \pm 24.3	137.5bc \pm 41.6	164.1c \pm 16.3	53.1a \pm 12.4	65.1a \pm 14.1	3.35	0.0124
Habitat groups								
Plant	124.0a \pm 29.0	84.9a \pm 23.7	135.4a \pm 30.2	82.8a \pm 12.5	32.3b \pm 7.8	35.9b \pm 6.3	4.30	0.0030
Litter	40.6a \pm 6.8	27.6a \pm 10.6	45.8a \pm 22.8	33.9a \pm 10.5	7.3b \pm 4.5	3.6b \pm 1.2	2.25	0.0560
Wood	61.5a \pm 11.7	64.6ab \pm 20.5	110.9b \pm 36.0	108.3b \pm 15.2	37.5a \pm 10.4	37.5a \pm 8.1	2.84	0.0267
Organic	28.1a \pm 5.6	22.4a \pm 6.0	25.0a \pm 4.8	63.5b \pm 14.5	19.3a \pm 5.3	31.3a \pm 8.0	4.04	0.0046

^a HARP, a form of variable retention harvesting practiced in lowland boreal forests. LR, MR, and HR retention are HARP sites categorized at a landscape level depending on their adjacency to clear-cut or unharvested sites; UE and UI sites are similarly classified according to the extent of contiguous unharvested area.

^b Numbers followed by the same letter within each row are not significantly different at $\alpha = 0.05$ (Tukey's multiple comparison).

Table 2. Syrphid species showing differences in abundance (mean no. per 100 trap-days, \pm SE) in malaise traps from clear-cut and unharvested (interior and edge combined) peatland black spruce forests of northeastern Ontario, Canada, during 1999

Syrphid species	Forest type		ANOVA	
	CC	UI and UE	$F_{1,11}$	P
<i>Toxomerus marginatus</i>	99 \pm 26.5	15 \pm 4.7	18.51	0.0003
<i>Eupeodes lapponicus</i>	12 \pm 2.3	1 \pm 0.3	43.88	0.0001
<i>Platycybeus rosarum</i>	11 \pm 4.4	2 \pm 0.3	9.59	0.0053
<i>Ocyrtamus fascipennis</i>	11 \pm 3.5	4 \pm 0.9	8.13	0.0093
<i>Xylota annulifera</i>	11 \pm 2.8	2 \pm 0.3	18.78	0.0003
<i>Sphaerophoria contigua</i>	9 \pm 2.4	1 \pm 0.9	11.12	0.0030
<i>Sphaerophoria philanthus</i>	8 \pm 2.6	0	14.09	0.0011
<i>Platycybeus granditarsus</i>	6 \pm 2.1	0	10.48	0.0038
<i>Eristalis dimidiatus</i>	4 \pm 1.3	1 \pm 0	9.96	0.0046
<i>Melanostoma mellinum</i>	2 \pm 0.6	6 \pm 1.4	5.34	0.0306

(6%). Based on this classification, structural-retention harvesting significantly affected the abundance of four larval habitat assemblages (Table 1). The organic habitat group was significantly more abundant in the high-retention HARP stands than in any of the other forest types. The litter and plant assemblages were more abundant in the harvested than in the unharvested stands, whereas the wood guild had the greatest abundance at intermediate levels of structural retention.

The PCA of the abundance of syrphid functional assemblages showed a similar pattern to the PCA on the species matrix, with clear-cut and HARP stands on the right and unharvested sites on the left of the first ordination axis (49.0% of the variance). The second axis (18.5%) showed the unharvested forests generally on the positive side of the origin and the harvested sites mostly negative, but no clear separation was found among functional assemblages.

Discussion

The syrphid community proved to be sensitive to harvesting in the boreal forests of northeastern Ontario, Canada. Overall species richness and the abundance of four species and larval predators were all greater in harvested (both clear-cut and HARP structural-retention sites) than in unharvested sites. In addition, overall species richness and the abundance of nine species were higher in clear-cut sites than in

Table 3. Syrphid species showing differences in abundance (mean no. per 100 trap-days, \pm SE) in Malaise traps from cut and retention strips within variable retention harvested (HARP) stands of peatland black spruce forests from northeastern Ontario, Canada, during 1999

Syrphid species	Strip in harvested stand		ANOVA	
	Cut strip	Retention strip	$F_{1,11}$	P
<i>Cheilosia tristis</i>	29.5 \pm 4.1	10.7 \pm 1.6	7.03	0.0148
<i>Eupeodes lapponicus</i>	7.6 \pm 0.9	2.1 \pm 0.8	8.12	0.0093
<i>Parhelophilus porcus</i>	20.5 \pm 7.2	4.2 \pm 1.7	5.32	0.0309
<i>Platycybeus rosarum</i>	34.7 \pm 7.5	3.1 \pm 1.2	8.60	0.0077
<i>Toxomerus geminatus</i>	11.5 \pm 3.5	5.2 \pm 1.2	4.91	0.0374
<i>T. marginatus</i>	92.0 \pm 13.1	27.4 \pm 3.0	10.83	0.0033
<i>Xylota annulifera</i>	24.0 \pm 3.7	5.2 \pm 1.4	6.88	0.0155
<i>X. tuberculata</i>	13.9 \pm 3.2	6.2 \pm 2.2	4.03	0.0434

unharvested sites. The association of members of the Syrphidae with forest clearings created by harvesting black spruce trees in this manner is consistent with other work on air pollution-damaged spruce stands in the Czech Republic (Kula 1997) and in structurally altered spruce and pine plantations in the United Kingdom (Humphrey et al. 1999). Greater species richness and abundance were also observed in the cut strips compared with the retention strips in the HARP sites of our study. Differences among the levels of forest-retention harvesting (HARP) were relatively minor compared with those of the clear-cut and unharvested areas, suggesting that local habitat characteristics may play a more important role than the landscape configuration in determining the syrphid community. Similarity in the syrphid community between the retention strips and unharvested forests also suggests that the amount of forest retained is a good indicator of the total amount of available habitat, regardless of the spatial configuration. However, the cut strips showed variation that was correlated with the landscape context, because retention strips in high and medium HARP stands tended toward lower richness than the clear-cut stands or cut strips in the low retention HARP (Fig. 3), a result similar to the edge effect reported by Deans et al. (2005).

Syrphid diversity seems to be lower in these lowland black spruce forests than in other mixedwood boreal stands. Sugar (2000) studied syrphid communities in relatively mature upland mixedwoods of northeastern Ontario and found species richness considerably higher than we did; our study had only 4% greater richness than hers, despite 40% more individuals being captured. Of the 103 species collected from these low-lying peatlands, ~70 were also caught in the mixedwood stands of the study of Sugar (2000). In general, both communities resembled each other in their composition of habitat and feeding assemblages; the plant- and wood-inhabiting guilds and the predators and saprophages represented the greatest proportion of the community in both.

In contrast to our study, the work of Sugar (2000) showed that syrphid species richness and the abundance of several wood-inhabiting species were correlated with late successional characteristics of mixedwood stands. Syrphid specialists in "old-growth" forests were not identified in either study; however, Sugar (2000) found that several taxa increased in abundance with forest age. The organic and wood-inhabiting saprophages, *S. militaris* and *T. vespiforme*, identified as "old-growth" taxa in the mixedwoods, were both found only rarely in our early successional cut areas. One other possible "old-growth" species identified in the mixedwoods, *T. geminatus*, showed only a weak association to our late successional (unharvested) forests, although it is possible that this species was responding to an increase in openness of the older mixedwoods in general rather than to specific old-growth features per se. This species was previously documented as an important pollinator of *Viburnum* spp. (Kevan et al. 1993), but it is likely also an important pollinator of other plants in the forest

understorey (Sugar 2000) and has been observed visiting a wide array of flowering plants (W.J.C., unpublished data).

Toxomerus marginatus, the most abundant species caught in our black spruce forests, was most often found in areas where the canopy was open and flowering plants could provide habitat for larval development (Ferrar 1987). This species is primarily predaceous during the larval stage and, like most species of the subfamily Syrphinae, may feed on aphids (Ferrar 1987, Vockeroth 1992). However, it has also been suggested that *T. marginatus* can survive on plant tissue and sap (Ferrar 1987), suggesting that it may be more of a generalist. This species was consistently higher in number in our early successional forests (low- and medium-retention HARP and clear-cuts) than in our high-retention HARP or unharvested forests, and like numerous other anthophilous species, typifies these types of cleared or open sites. Thus, high abundance of *T. marginatus* may be indicative of postharvested conditions in boreal forests.

The second most abundant species, *Cheilosia tristis*, also requires vegetation as larval habitat, but primarily as a food source rather than for lodging (Ferrar 1987). Most of the literature suggests that this species is associated with plants in general, without specific indication of preferences for understorey plants, shrubs, or saplings (Vockeroth and Thompson 1981, Ferrar 1987). Sugar (2000) found that this species was more abundant in relatively young postlogged stands compared with old postfire stands. In our study, *C. tristis* was more abundant in the cut than in the retention strips of the HARP stands and was consistently associated with open areas in the multivariate biplots.

Platycheirus rosarum was caught rarely in our unharvested lowland black spruce forests. As larvae, this species requires litter in the forest understorey for habitat, whereas it preys on other soil and litter-layer invertebrates (Vockeroth and Thompson 1981, Ferrar 1987). Presumably, the moss-covered forest floor in our northern peat forests reduced the availability of exposed soil and litter and this lowered the suitability of larval habitat. We found *P. rosarum* often in close proximity to *T. marginatus* in the ordinations of the species richness and abundance matrices, suggesting that both prefer open cut forest areas as described above. Accordingly, *P. rosarum* was significantly more abundant in the cut strips of the HARP stands and clear-cut sites than the unharvested areas, and this is also where soil, fine woody, and needle litter were greatest in the understorey (Deans et al. 2003).

Xylota annulifera, *X. flavifrons*, *X. hinei*, and *X. quadrimaculata* all deposit their eggs in decomposing woody material. Stumps, snags, and coarse and fine woody debris all are potential sources of larval habitat for these wood-inhabiting, saprophagous species. Although previous studies have shown the saproxylic (wood-inhabiting) guild to be negatively impacted by logging activities, with an affinity for unlogged forests (Speight 1986, Sugar 2000), this does not seem to be the case in our variable retention HARP stands where all four species were more frequently associated with

the cut strips of the HARP stands. The availability of woody debris in the understorey of these forests, which is often cited as a key issue for sustaining such saproxylic species (Speight 1986, Hansen et al. 1991, Okland 1996), does not seem to be of concern in our HARP stands, at least within the first few years after cutting.

Sericomyia militaris was found in 23 of our 24 peatland forest sites. This genus is often associated with decomposing and sodden peat typical of the lowland conifer bogs (Hartley 1961, Ferrar 1987) and is a saprophagous species that consumes organic matter by filter-feeding in aquatic or semiaquatic habitats (Hartley 1961, Vockeroth and Thompson 1981). Although this species was widely distributed across our study area, it was found twice as often in the unharvested forests and retention strips of the HARP stands than in the clear-cuts or cut strips of the HARP sites.

Temnostoma vespiforme is another saprophagous species, but is wood-inhabiting (it is one of the only known syrphids that actively bores into relatively firm wood). As a result of logging in Europe, this Holarctic species has been reduced to localized habitats where logging activities have not impacted on its required resources (Sugar 2000). In eastern mixedwoods forests, this species was found to have a positive association with snag density and small-diameter and highly decomposed snags; therefore, it is probable that coarse woody material is required during its development (Sugar 2000). We found that *T. vespiforme* was more abundant in unharvested stands and the retention strips of HARP forests than the cut areas. In the direct gradient analysis, *T. vespiforme* showed an association with retention strips; these strips typically contained snags of varying sizes and densities and greater amounts of larger-diameter trees than the harvested areas.

Other common syrphid species collected in these peatland forests included *Helophilus lapponicus*, *Toxomerus geminatus*, *Blera confusa* and *Melanostoma mellinum*, all of which were more abundant in the high-retention HARP and unharvested forests than in the cut forests. Little is known about these species other than two are saprophagous (*H. lapponicus* and *B. confusa*) requiring wood or organic material for larval habitat, while the other two are predaceous (*T. geminatus* and *M. mellinum*) requiring living plants and litter in the understorey (Vockeroth and Thompson 1981, Ferrar 1987, Vockeroth 1992).

Harvested sites had more predaceous syrphids associated with them than the unharvested stands in our study, and this was similar for the plant and litter habitat guilds, and to a lesser degree, the wood-inhabiting guild. The elevated richness and abundances within these guilds may be attributed to the greater amounts of fresh woody and litter debris in harvested than unharvested sites, as well as an increase in incident light for understorey plant habitats. However, these differences should be taken with caution. Defining guilds based on abundance means that sites with high numbers of individual syrphids will likely have high numbers in the guilds as well (as the case of

predators). Besides, high abundance of a given assemblage may reflect the response of a few common species rather than true assemblage responses. In any case, a more thorough study of the understory plant species (both richness and abundance) in the harvested openings of these stands may elucidate specific relationships between these plant-inhabiting syrphids and their habitats (Owen 1981). Notable exceptions to the above trend were the predators *M. mellinum* and *T.s. geminatus*, which were apparently affiliated with unharvested stands in these peatland black spruce forests.

Tree and wood habitat guilds, as well as saprophagous and phytophagous feeding guilds, had the greatest number of species and individuals in the HARP stands. In contrast, the organic guild, which included species such as *B. confusa*, *H. lapponicus*, *S. militaris*, and *T. vespiforme*, overall was more abundant and speciose in the high-retention HARP and unharvested forests. Presumably, the higher humidity conditions of the relatively intact forest provided better microclimatic conditions and promoted the decomposition of woody debris into nutrient rich organic materials. As both the fine and coarse downed woody debris in the cut areas decays over time (>5 yr after harvest), HARP stands with large volumes of debris may provide a significant source of organic materials for these taxa.

Taylor and Doran (2001) recommended the development of terrestrial invertebrates as indicators of ecological sustainability for forest management under the Montreal Process. We showed that syrphid species and functional assemblages do respond to changes in forest structure resulting from VRH (specifically HARP) in peatland black spruce forests based on their biology and ecology, and this suggests they could be developed as indicators in boreal forest management. Our work further suggests that there is a landscape level effect of VRH on the syrphid community as a whole, and this means that this arthropod group may be particularly useful in reflecting changes in stand structure at a broader scale.

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Appendix 1. Syrphidae species caught in peatland black spruce forests, with their associated larval habitat requirement and trophic category

Species	Habitat	Trophic group
<i>Baacha elongata</i> (Fabricus)	Litter	Predator
<i>Blera armillata</i> (Osten Sacken)	Wood	Saprophagous
<i>Blera umbratilis</i> (Williston)	Wood	Saprophagous
<i>Blera confusa</i> (Johnson)	Wood	Saprophagous
<i>Blera nigra</i> (Williston)	Wood	Saprophagous
<i>Brachyopa ferruginea</i> (Fallen)	Wood	Saprophagous
<i>Chalcosyrphus inarmatus</i> (Hunter)	Wood	Saprophagous
<i>Chalcosyrphus libo</i> (Walker)	Wood	Saprophagous
<i>Cheilosia rita</i> (Curran)	Plant	Phytophagous
<i>Cheilosia tristis</i> (Loew)	Plant	Phytophagous
<i>Chrysogaster antitheus</i> (Walker)	Wood	Saprophagous
<i>Chrysotoxum derivatum</i> (Walker)	Wood	Predator
<i>Chrysotoxum flavifrons</i> (Macquart)	Wood	Predator
<i>Dasysyrphus venustus</i> (Meigen)	Tree	Predator
<i>Epistrophe emarginata</i> (Say)	Plant	Predator
<i>Epistrophe terminalis</i> (Curran)	Plant	Predator
<i>Eriozona laxa</i> (Osten Sacken)	Tree	Predator
<i>Eristalis flavipes</i> (Walker)	Organic	Saprophagous
<i>Eristalis cryptarum</i> (Fabricius)	Organic	Saprophagous
<i>Eristalis dimidiatus</i> (Weidemann)	Organic	Saprophagous
<i>Eristalis arbustorum</i> (Linnaeus)	Organic	Saprophagous
<i>Eristalis obscurus</i> (Loew)	Organic	Saprophagous
<i>Eristalis tenax</i> (Linnaeus)	Organic	Saprophagous
<i>Eupeodes americanus</i> (Weidemann)	Tree	Predator
<i>Eupeodes lapponicus</i> (Zatterstedt)	Tree	Predator
<i>Eupeodes latifasciatus</i> (Macquart)	Tree	Predator
<i>Eupeodes luniger</i> (Macquart)	Tree	Predator
<i>Eupeodes perplexus</i> (Osburn)	Tree	Predator
<i>Eupeodes pomus</i> (Curran)	Tree	Predator
<i>Ferdinandea dives</i> (Osten Sacken)	Wood	Saprophagous
<i>Helophilus lapponicus</i> (Wahlberg)	Organic	Saprophagous
<i>Helophilus fasciatus</i> (Walker)	Organic	Saprophagous
<i>Helophilus groenlandicus</i> (O. Fabricius)	Organic	Saprophagous
<i>Helophilus latifrons</i> (Loew)	Organic	Saprophagous
<i>Helophilus obscurus</i> (Loew)	Organic	Saprophagous
<i>Heringia calcarata</i> (Loew)	Plant	Predator
<i>Heringia salax</i> (Loew)	Plant	Predator
<i>Lejops distinctus</i> (Williston)	Organic	Saprophagous
<i>Lejops lunulatus</i> (Meigen)	Organic	Saprophagous
<i>Lejops chrysostomus</i> (Wiedemann)	Organic	Saprophagous
<i>Lejota cyanea</i> (Cyanea)	Wood	Saprophagous
<i>Melangyna lasiophthalmus</i> (Zetterstedt)	Plant	Predator
<i>Melangyna triangulifera</i> (Zetterstedt)	Plant	Predator
<i>Melangyna umbellatarum</i> (Fabricius)	Plant	Predator
<i>Melanostoma mellinum</i> (Linnaeus)	Litter	Predator
<i>Meliscaeva cinctella</i> (Zetterstedt)	Tree	Predator
<i>Microdon cothurnatus</i> (Bigot)	Nest	Predator
<i>Microdon ocellaris</i> (Curran)	Nest	Predator
<i>Microdon tristis</i> (Loew)	Nest	Predator
<i>Ocyptamus fascipennis</i> (Say)	Unknown	Predator
<i>Orthonевра pictipennis</i> (Loew)	Unknown	Saprophagous
<i>Orthonевра pulchella</i> (Williston)	Unknown	Saprophagous
<i>Paragus haemorrhous</i> (Meigen)	Unknown	Unknown
<i>Parasyrphus genualis</i> (Williston)	Tree	Predator
<i>Parasyrphus semiinterruptus</i> (Fluke)	Tree	Predator
<i>Parhelophilus porcus</i> (Walker)	Unknown	Unknown
<i>Pipiza femoralis</i> (Loew)	Plant	Predator
<i>Platycheirus granditarsus</i> (Forster)	Litter	Predator
<i>Platycheirus holarcticus</i> (Vockeroth)	Litter	Predator
<i>Platycheirus hyperboreus</i> (Staeger)	Litter	Predator
<i>Platycheirus immarginatus</i> (Zetterstedt)	Litter	Predator
<i>Platycheirus inversus</i> (Ide)	Litter	Predator
<i>Platycheirus obscurus</i> (Say)	Litter	Predator
<i>Platycheirus rosarum</i> (Fabricius)	Litter	Predator
<i>Platycheirus scambus</i> (Staeger)	Litter	Predator
<i>Rhingia nasica</i> (Say)	Organic	Saprophagous
<i>Sericomyia bifasciata</i> (Williston)	Organic	Saprophagous
<i>Sericomyia chrysotoxoides</i> (Macquart)	Organic	Saprophagous
<i>Sericomyia lata</i> (Coquillett)	Organic	Saprophagous
<i>Sericomyia militaris</i> (Walker)	Organic	Saprophagous
<i>Sericomyia transversa</i> (Osburn)	Organic	Saprophagous
<i>Sphaerophoria abbreviata</i> (Zetterstedt)	Litter	Predator

(continued)

Appendix 1. Continued.

Species	Habitat	Trophic group
<i>Sphaerophoria asymmetrica</i> (Knutson)	Litter	Predator
<i>Sphaerophoria bifurcata</i> (Knutson)	Litter	Predator
<i>Sphaerophoria brevipilosa</i> (Knutson)	Litter	Predator
<i>Sphaerophoria contigua</i> (Macquart)	Litter	Predator
<i>Sphaerophoria longipilosa</i> (Knutson)	Litter	Predator
<i>Sphaerophoria novaeangliae</i> (Johnson)	Litter	Predator
<i>Sphaerophoria philanthus</i> (Meigen)	Litter	Predator
<i>Sphegina rufiventris</i> (Loew)	Tree	Saprophagous
<i>Syrphus rectus</i> (Osten Sacken)	Plant	Predator
<i>Syrphus ribesii</i> (Linnaeus)	Plant	Predator
<i>Syrphus torvus</i> (Osten Sacken)	Plant	Predator
<i>Syrphus vitripennis</i> (Meigen)	Plant	Predator
<i>Temnostoma alternans</i> (Loew)	Wood	Saprophagous
<i>Temnostoma venustum</i> (Williston)	Wood	Saprophagous
<i>Temnostoma vespiforme</i> (Linnaeus)	Wood	Saprophagous
<i>Toxomerus geminatus</i> (Say)	Plant	Predator
<i>Toxomerus marginatus</i> (Say)	Plant	Predator
<i>Trichopsomyia recedens</i> (Walker)	Plant	Predator
<i>Xylota annulifera</i> (Bigot)	Wood	Saprophagous
<i>Xylota naknek</i> (Shannon)	Wood	Saprophagous
<i>Xylota bicolor</i> (Loew)	Wood	Saprophagous
<i>Xylota bigelowi</i> (Curran)	Wood	Saprophagous
<i>Xylota bigelowi</i> (Shannon)	Wood	Saprophagous
<i>Xylota flavifrons</i> (Walker)	Wood	Saprophagous
<i>Xylota flukei</i> (Curran)	Wood	Saprophagous
<i>Xylota hinei</i> (Curran)	Wood	Saprophagous
<i>Xylota naknek</i> (Shannon)	Wood	Saprophagous
<i>Xylota oueletti</i> (Curran)	Wood	Saprophagous
<i>Xylota quadrimaculata</i> (Loew)	Wood	Saprophagous
<i>Xylota subfasciata</i> (Loew)	Wood	Saprophagous
<i>Xylota tuberculata</i> (Curran)	Wood	Saprophagous