Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 204 (2005) 249–266
Forest Ecology and Management
www.elsevier.com/locate/foreco

Edge effects and the responses of aerial insect assemblages to structural-retention harvesting in Canadian boreal peatland forests

Aaron M. Deans[a], Jay R. Malcolm[a,*], Sandy M. Smith[a], M. Isabel Bellocq[b]

[a]*Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, Ont., Canada M5S 3B3*
[b]*Departamento de Ecología, Genética y Evolución, FCEN-Universidad de Buenos Aires, Ciudad Universitaria, Pab 2, Buenos Aires 1428, Argentina*

Received 18 February 2004; received in revised form 28 September 2004; accepted 28 September 2004

Abstract

Clear-cut harvesting can alter ecosystem conditions and dynamics drastically compared to natural disturbance regimes, hence alternative harvesting systems are being developed in an attempt to better mimic natural forest structure. A recent approach is to harvest trees at variable intensities and spatial configurations in what is known as variable retention harvesting. Our study examines the responses of aerial insect assemblages to a gradient of forest retention at the landscape scale, and provides an assessment of the conservation benefits of alternative versus traditional harvesting systems in lowland boreal forest. The experimental design consisted of six treatments representing decreasing levels of structural retention at the landscape scale (with four replicates per treatment): (1) unharvested forest interior; (2) unharvested forest edge; (3) high-structural retention (strip retention harvesting areas at the edge of adjacent areas of unharvested forest); (4) medium-structural retention (strip retention harvesting areas in the interior of contiguous retention harvesting areas); (5) low-structural retention (strip retention harvesting areas adjacent to clear-cutted areas); (6) clear-cut harvesting. Response variables were the abundances of selected families and trophic assemblages of aerial insects, which were sampled with Malaise traps at each site. Univariate and multivariate analyses showed that the structural-retention harvesting influenced the abundance of most families and trophic assemblages. Most insect families and assemblages were most abundant in the strip retention harvested areas, especially in the medium retention treatment. These increases in abundance reflected strong edge effects, as evidenced by the fact that significant treatment effects were observed even within the two major habitat types of the study (cleared or forested habitat). Increasing structural retention favoured some assemblages such as Diapriidae, herbivores, and parasitoids whereas other groups such as predators decreased in abundance. Results support the potential use of high-level taxonomic and trophic assemblages of aerial insects in monitoring the ecological sustainability of forest harvesting practices.

Keywords: Variable retention harvesting; Insects; Black spruce; Boreal forest; Clear-cutting

* Corresponding author. Tel.: +1 416 978 0142; fax: +1 416 978 3834.
E-mail address: jay.malcolm@utoronto.ca (J.R. Malcolm).

0378-1127/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2004.09.015

1. Introduction

Although better understood for vertebrates than invertebrates, habitat fragmentation and change can strongly affect insect communities (Didham, 1997). Relative to most vertebrates, insects tend to utilize small areas and require narrow microhabitat conditions. Consequently, studies on changes within insect communities are of particular interest because of the potential influence of changes in microhabitat features, such as downed woody debris and canopy openings (Harris, 1984; Niemelä et al., 1993; Økland, 1994, 1996; Bader et al., 1995; Simard and Fryxell, 2003). In many recent approaches in insect conservation, the spatial arrangement of such microhabitats is a major consideration (Winchester and Ring, 1996; Didham, 1997; Tscharntke et al., 2002; Major et al., 2003; Bunnell and Huggard, 1999).

The effects of habitat alterations on insect communities also are of considerable interest given that insect functional assemblages, such as trophic groups, are involved in many of the critical processes that maintain forest ecosystems. Changes in these assemblages following habitat management may affect ecosystem function (Kruess and Tscharntke, 1994; see also Grime, 1997; Chapin et al., 2000; Loreau and Hector, 2001). An increasing number of studies have suggested that use of functional or/and higher-level taxonomic assemblages can aid in revealing information on the impacts of habitat change on insect taxa and functional groups and in directing future monitoring programs (Williams and Gaston, 1994; Malcolm, 1997; Katzourakis et al., 2001; Tscharntke et al., 2002; Bellocq and Smith, 2003). Although such studies will certainly benefit from research at the species level (Danks and Winchester, 2000), evidence of sensitivity to environmental perturbations at high taxonomic levels can define strategic directions with respect to ecological sustainability and serve as a focus for future assessment and monitoring without the time-consuming process of identifying insects to the species level (Williams and Gaston, 1994; Balmford et al., 1996a, 1996b). Here, we examine the responses of high-level taxa and trophic assemblages to different levels of forest retention in the boreal forests of northern Ontario.

The insect fauna of peatland boreal forests, one of Canada's most extensive forest types, has not yet been studied in detail (Danks and Foottit, 1989) and responses to logging are poorly understood. Most work examining the effects of forestry practices on arthropods in this ecosystem have focused on logging per se (Niemelä, 1997) rather than on comparisons of different harvesting techniques (Bird and Chatarpaul, 1986; Bellocq et al., 2001). Most of the Canadian boreal forest is managed using clear-cut silviculture, which initially results in the complete removal of the canopy over relatively large areas. Studies of the effects of clear-cut harvesting on arthropods have included studies of the soil and litter micro and macrofaunas (Bird and Chatarpaul, 1986; Niemelä et al., 1993; Paquin and Coderre, 1997; Duchesne et al., 1999; Bellocq et al., 2001). As yet, variable retention harvesting, which is an increasingly common harvesting method in the boreal forest (Bergeron and Harvey, 1997; Franklin et al., 1997), has received little attention.

After clear-cut logging at a site, certain microhabitat conditions of the original forest may take many decades or longer to re-appear. Thus, alternative harvesting systems are being developed in an attempt to maintain some of the existing natural structure of forests, especially the within-stand variability of boreal old-growth stands that show multi-cohort age structures (Bergeron and Harvey, 1997). A recent approach is to harvest trees at variable intensities and spatial configurations across the landscape in a technique known as Variable Retention Harvesting (Bergeron and Harvey, 1997; Franklin et al., 1997; Sullivan et al., 2001). For example, the Lake Abitibi Model Forest in northeastern Ontario has developed a variable retention harvesting method called harvesting with advance regeneration protection (HARP) that maintains the young trees (advanced regeneration) present in peatland black spruce forests (MacDonell and Groot, 1997). These operations clear trees in strips approximately 5–7 m wide, and remove trees from the adjacent retention rows (5–9 m wide) using a minimum diameter limit cut. The resulting harvested landscape contains retained strips of black spruce forest separated by cleared strips. Although the retention strips are thinned based on a tree diameter limit, which in some even-aged stands results in the removal of most canopy trees, the understory and substrate remain largely intact in the retention rows because of the lack of vehicular traffic and because

such harvesting occurs mainly during the winter when the substrate and soil is frozen and hence less easily damaged. Thus, the HARP technique retains structural features of the forest while preserving regeneration of the stand for the next harvest (Deans et al., 2003). However, although Deans et al. (2003) found that the HARP system retained old-growth structural features better than traditional clear-cut systems, concerns exist as to whether the fine-grained juxtaposition of late-successional retained strips and early-successional clear-cut strips may alter insect community dynamics in the harvested forest (Deans et al., 2003). In particular, the creation of large amounts of edge habitat during the strip cutting may alter insect communities. Although such edge effects are site and taxon specific (e.g., Ozanne et al., 1997), many studies have reported an increase in insect abundance and richness near forest edges (reviewed in Didham, 1997; see also Jokimäki et al., 1998). Certainly, as new alternative methods of harvesting are developed, there is a need to understand their influence on flora and fauna (Bader et al., 1995; Schowalter, 1995).

Here, we test the hypothesis that the abundance of both high-level taxa and functional assemblages of aerial insects are sensitive to landscape configurations resulting from the removal of structural elements in harvested forests. Using univariate and multivariate analyses, we examine richness and abundance of selected families and functional groups of insects across a gradient of black spruce forest removal, from unharvested forests, through variable retention strip-harvested forests, to clear-cut sites. Additionally, we analyze associations between insect abundances and habitat variables.

2. Materials and methods

2.1. Study area and site selection

The study area was in the Lake Abitibi Model Forest within Rowe's (1972) Northern Clay Forest Section of northeastern Ontario, Canada (49°35′N, 80°35′W). The lowland boreal forest landscape in this area is dominated by homogeneous peatlands of black spruce, with larch (*Larix laricina*) found on boggy sites and balsam fir (*Abies balsamea*) on fresh to moist sites. On upland sites of the clay belt, black spruce also grows with white spruce (*Picea abis*) and balsam fir. Mixed forests of balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyfera*) and jack pine (*Pinus banksiana*) are present on glacial till deposits across the landscape. The climate of the area is continental, modified by the presence of the Great Lakes to the South and Hudson and James Bay to the North. Mean annual temperature is approximately 0 °C, with mean January and July temperatures of −19 and 16 °C, respectively, and annual precipitation of 830 mm (McKenney et al., 2001).

2.2. Experimental design

Site selection was made based on Forest Resource Inventory maps (Ontario Ministry of Natural Resources, unpubl.) and additional information on harvesting operations. Only lowland, pure black spruce stands were sampled. Harvesting operations occurred in 1995–1997, 2.5–3.5 years prior to the study.

The experimental design consisted of six treatments, with four replications per treatment for a total of 24 sites. Treatments represented decreasing levels of forest retention at the landscape scale: (1) unharvested interior (UI; contiguous unharvested forest more than 150 m from the nearest harvested area); (2) unharvested edge (UE; unharvested forest ca. 150 m from a harvested edge); (3) high-structural retention (HR; strip retention [HARP] areas at the edge of adjacent areas of unharvested forest); (4) medium-structural retention (MR; strip retention areas in the interior of contiguous strip retention harvesting areas); (5) low-structural retention (LR; strip retention areas adjacent to clear-cutted areas); (6) clear-cut harvesting areas (CC; very little to no retention of trees).

A 110 m × 150 m plot was established at each site, with a 10 m × 50 m subplot centered within it. In sites with strip retention harvesting (HR, MR, and LR), subplots were located parallel to the strips and such that 5 m of the subplot extended into the cut strip and 5 m into the retention strip. In HR sites, the plot was positioned such that one 50 m side of the subplot was along the edge of unharvested forest that abutted the strip retention harvest. In LR sites, one 50 m subplot side was at the edge of a clear-cut area. The centers of

the plots were at least 75 m from waterways and forest edges along roads. The average nearest neighbour distance between plot centers was 420 m. Because of the pattern of road access in the area, most of the study sites were grouped into three main research areas (of ca. 3000 ha each). To the extent possible, treatment replicates were randomly interspersed within each area

2.3. Habitat and vegetation variables

Structural features of the forest, understory, and duff were measured at 30 sampling stations systematically placed throughout each plot. These features included: basal area, density, height, DBH, and age of trees; density of advanced regeneration by DBH classes; stump basal area; snag density; percentage ground cover in various substrate classes. Details on sampling procedures and measurement techniques are in Deans et al. (2003). Unfortunately, we did not directly measure the amount of forest edge in each plot; however, we were able to derive an approximate measure by using the presence (=1) or absence (=0) of forest at each of the 30 stations. Specifically, a station was defined as having forest if it had one or more trees $\geq$5 cm DBH; otherwise, it was defined as not having forest. We used the variance of the 30 presence/absence values as an edge index: plots that tended to be either all forested or all cleared had low variances (and low amounts of edge), whereas those that had high amounts of both cover types had higher variances (and higher amounts of edge).

2.4. Insect sampling

Townes-style Malaise traps (Townes, 1972) were used to collect insects. These traps are 2 m long, tent-like structures made of fine mesh fabric netting (mesh width 0.5 mm), with a vertical center panel that blocks the passage of flying insects. The top of each trap is roof-shaped and higher at one end than the other. Insects are funneled upward to the highest point of the trap where they enter into a collecting chamber with a removable container filled with ethylene glycol.

Two Malaise traps were set in each subplot at the 24 sites for a total of 48 traps. The two traps were 5 m apart, with the long axis of the central panel of the traps parallel to a line joining the two traps. In strip retention sites, one trap was placed in the center of the cut strip and the other in the center of the retention strip. The two traps per site were set simultaneously and operated for eight consecutive days in each of June, July, and August 1999. Samples were combined for the three sampling periods to give a total of 24 sampling days for each trap. Insect abundance was standardized as the number of individuals caught per trap per 100 days.

2.5. Insect assemblages

Because of time constraints and the large volume of material, rather than identifying all insect captures to family, we selected 30 families for counting that encompassed a wide spectrum of trophic assemblages, were relatively abundant, and had well-understood trophic ecology. In total, we selected 16 families of Diptera (flies), 10 of Hymenoptera (wasps and sawflies), 3 of Coleoptera (beetles), and 1 of Homoptera (true bugs). Insects were grouped into adult and larval trophic assemblages based on the known biology of each family (Appendix A) and abundances in each trophic assemblage were calculated. Trophic assemblages were assigned based on information in Teskey (1976), McAlpine et al. (1981, 1987), Arnett and Thomas (2001), Arnett et al. (2002) and Triplehorn and Johnson (2005). In cases where more than one trophic assemblage was common in a family (see Appendix A), abundances in the family were added to each of the relevant trophic assemblages. In a subsample of the material (single-month samples from five traps) that was identified exhaustively to family for Diptera, Hymenoptera, and Coleoptera, additional families included Anthomyiidae, Ceratopogonidae, Chaoboridae, Chironomidae, Heleomyzidae, Muscidae, Otitidae, Phoridae, Psychodidae, Scatophagidae, Sciomyzidae, Simuliidae, Tabanidae, Tipulidae (Diptera), Apidae, Encyrtidae, Eumenidae, Formicidae, Perilampidae, Pteromalidae (Hymenoptera), Carabidae, Coccinellidae, Elateridae, and Staphylinidae (Coleoptera).

2.6. Statistical analyses

In all statistical tests, plots were used as the unit of replication. In one set of univariate analyses, we combined captures from the two Malaise traps at each

site and used one-way ANOVAs with Tukey's multiple comparisons to test for differences in the abundances of insect families and trophic assemblages among treatments. In addition, because the insect response might simply reflect the amount of forested and cleared habitat in a treatment, we undertook a second set of analyses in which one-way ANOVAs with Tukey's multiple comparisons were used to test for treatment differences among traps in forest and among those in clearings. Traps in clearings included those in clear-cut sites and in cleared travel corridors, whereas traps in forest included those in undisturbed forest and in retention strips. Finally, in a third set of analyses, we compared abundances between retention and cleared strips for just the HARP treatments. Data were log-transformed in order to meet assumptions of homogeneity of variance and normality and tests were performed using SAS (v. 8.01). In addition to the univariate tests, to identify major patterns of variation in insect communities we conducted principal component analysis (PCA) on the correlation matrix at the trap level.

Variation in insect communities as a function of variation in habitat structure was examined using redundancy analysis (RDA), which was undertaken at the plot level. Rather than including all of the habitat variables to constrain the analysis, we instead focused on the main habitat gradients by just using the scores from the first two axes of a principal components analysis undertaken on the habitat variables. The original habitat variables were then entered "passively" into the analysis in order to allow interpretation of their influence in the triplot (Jongman et al., 1995). Multivariate analyses were performed using CANOCO for Windows (v. 4.0; Lepš and Šmilauer, 2003).

3. Results

3.1. Overall insect abundance

A total of 65,888 individual insects in the selected families of Diptera, Hymenoptera, Coleoptera, and Homoptera were caught during the study. Ichneumonidae was the dominant family (19.0% of the total number of individuals caught in the selected families) followed by Mycetophilidae (10.0%), Tachinidae (9.9%), Dolichopodidae (8.6%), Diapriidae (8.5%), Sciaridae (7.3%), Braconidae (6.0%), and Syrphidae (5.1%). All selected families were present in all treatments, except Anisopodidae, which was absent from the high-retention (HR) harvesting treatment (Table 1).

3.2. Effects of landscape configuration resulting from structural-retention harvesting

3.2.1. Comparisons among treatments

Of the 30 insect families, 19 showed significant differences in abundance among the six treatments (Table 1). Eighteen showed the same pattern in that they were most abundant in one of the three strip retention treatments, which all had relatively large amounts of forest edge (13 families were most abundant in MR, 3 in HR, and 2 in LR). For 10 of these families, abundances were greater in each of the three retention treatments than in any of the other treatments. For all 19 families, Tukey's comparisons showed at least one significant difference between a strip harvested treatment (HR, MR, or LR) and either the clear-cut or unharvested treatments. The exception to the general pattern of greatest abundance in the strip retention treatments was Diapriidae, which showed highest abundance in the UE treatment. Tukey's comparisons revealed that only three families showed differences in abundances between clear-cut and unharvested sites. Mean abundances of Diapriidae and Cicadellidae were greater in unharvested forests than in clear-cut sites whereas the opposite was true for Sarcophagidae (Table 1). Differences between the two unharvested treatments (UI and UE) also were infrequent, occurring only for the Xylophagidae, which were more abundant in interior forests than in unharvested forest closer to edges, and the Diapriidae, which were more common in unharvested forest closer to edges than in interior forests.

PCA analysis confirmed these patterns: the first axis (30.6% of the total variation) was an abundance axis, with almost all family vectors pointing to the right (positive) side of the axis where the structural retention sites tended to be located (Fig. 1). In contrast, unharvested and clear-cut sites tended to be on the negative side of the axis. The second PCA axis (12.8% of the total variation) was related to the structural-retention gradient, with harvested sites (especially clear-cut sites) in the upper (positive) half

Table 1
Mean abundance (number of individuals per 100 trap days) of 30 insect families (±S.E., $n = 4$) in six treatments of increasing forest retention in peatland black spruce forests in northeastern Ontario

Insect taxon	Treatment[a]												ANOVA (P)
	CC		LR		MR		HR		UE		UI		
Diptera													
Anisopodidae	6.2	±2.0	7.3	±2.7	3.1	±2.3	0.0	±0.0	2.1	±1.0	1.0	±0.7	0.1157
Asilidae	5.7 b	±2.0	24.5 ab	±6.1	39.1 a	±10.7	19.3 ab	±4.1	6.2 b	±1.9	17.0 ab	±4.1	0.0112
Bibionidae	281.9	±155.8	93.2	±30.2	240.1	±80.1	33.8	±9.8	20.8	±5.8	392.2	±212.5	0.0702
Calliphoridae	24.6 b	±5.9	31.2 b	±5.8	45.3 ab	±9.6	76.0 a	±16.3	28.8 b	±5.7	19.4 b	±4.9	0.0026
Culicidae	39.7	±9.3	95.8	±21.7	103.1	±25.5	100.5	±19.2	59.7	±14.7	55.2	±22.6	0.2554
Dolichopodidae	486.3 abc	±53.1	997.9 a	±182.3	803.1 ab	±120.3	433.8 bc	±58.1	126.2 c	±20.6	100.9 c	±17.2	<.0001
Empididae	132.2	±25.1	245.8	±43.2	373.9	±79.0	237.0	±71.8	163.0	±67.4	131.9	±35.5	0.1890
Lonchaeidae	82.0 b	±26.9	194.8 ab	±51.8	295.3 a	±74.5	222.4 a	±57.9	63.5 b	±15.1	110.9 ab	±35.0	0.0376
Mycetophilidae	356.3 b	±54.1	633.3 ab	±120.2	879.2 a	±108.3	595.3 ab	±65.7	575.7 ab	±54.7	555.6 ab	±60.3	0.0023
Pipunculidae	19.8 c	±3.9	87.5 abc	±13.5	121.9 a	±16.8	90.6 ab	±15.4	83.3 abc	±10.4	41.3 bc	±7.3	0.0001
Rhagionidae	5.2	±3.7	9.4	±4.3	13.0	±5.9	2.6	±1.1	1.0	±1.0	4.7	±2.1	0.2927
Sarcophagidae	87.2 a	±16.3	90.1 a	±20.2	90.1 a	±24.8	61.5 a	±19.6	21.5 b	±9.9	23.6 b	±6.7	0.0267
Sciaridae	459.3	±42.8	420.8	±55.0	567.7	±87.8	395.3	±82.0	350.7	±52.7	259.2	±31.3	0.2137
Syrphidae	314.7	±43.4	266.1	±45.6	385.4	±67.8	379.2	±60.1	180.9	±47.6	135.1	±24.6	0.0529
Tachinidae	441.4 b	±36.7	513.0 b	±51.1	897.4 a	±93.8	678.1 ab	±65.5	452.4 b	±44.7	400.7 b	±67.5	0.0002
Xylophagidae	2.1 b	±1.3	5.2 ab	±2.5	8.3 ab	±3.7	2.6 b	±2.1	1.0 b	±1.0	19.8 a	±6.4	0.0058
Hymenoptera													
Braconidae	148.4 b	±19.2	330.2 b	±51.3	629.2 a	±91.6	359.4 ab	±42.5	379.7 ab	±54.7	209.4 b	±29.4	<.0001
Chalcididae	86.8	±15.4	169.3	±43.6	104.7	±30.5	64.6	±30.4	29.0	±7.2	89.9	±25.3	0.1378
Chrysididae	27.5 b	±5.9	77.6 ab	±17.4	101.0 a	±19.4	44.8 ab	±8.3	24.5 b	±4.6	21.3 b	±5.0	0.0003
Cynipidae	22.0 b	±3.4	40.1 ab	±8.0	63.0 a	±10.9	40.1 ab	±8.2	46.5 ab	±6.4	29.2 ab	±4.8	0.0126
Diapriidae	73.0 d	±11.6	277.1 cd	±35.6	499.5 bc	±48.2	307.3 cd	±52.2	1016.7 a	±88.5	705.2 b	±76.5	<.0001
Dryinidae	13.0	±3.8	36.5	±18.2	59.4	±24.1	37.0	±13.4	4.7	±1.8	5.2	±2.0	0.1275
Ichneumonidae	574.8 c	±47.1	1257.8 ab	±115.6	1771.3 a	±168.6	831.2 bc	±101.5	910.6 bc	±79.2	1135.8 abc	±163.7	<.0001
Mymaridae	76.4 ab	±18.1	50.0 bc	±12.0	105.2 ab	±23.9	189.1 a	±58.8	44.3 bc	±7.5	28.5 bc	±5.1	0.0033
Tenthredinidae	105.1 a	±11.6	106.8 a	±13.3	246.3 b	±40.6	121.3 ab	±20.4	222.9 b	±58.3	187.3 ab	±32.5	0.0226
Vespidae	13.4 b	±3.3	28.1 ab	±4.6	59.4 a	±9.4	42.7 ab	±9.1	20.1 b	±5.6	32.8 ab	±8.2	0.0011
Coleoptera													
Buprestidae	2.8 ab	±1.1	8.8 ab	±2.3	14.1 ab	±3.3	17.7 a	±6.4	1.0 b	±0.7	1.0 b	±1.0	0.0052
Cerambycidae	10.4	±3.1	36.5	±13.5	20.3	±5.6	33.3	±7.6	10.9	±3.6	14.1	±3.2	0.2522
Chrysomelidae	14.9 b	±3.9	41.1 a	±20.6	41.7 a	±15.3	17.2 ab	±5.0	4.7 b	±1.7	1.7 b	±0.9	0.1001
Homoptera													
Cicadellidae	19.8 d	±5.7	126.6 a	±24.6	84.4 b	±14.1	74.0 bc	±25.2	59.0 c	±9.2	45.1 c	±9.3	0.0012

[a] CC = clear-cut; LR = low-retention harvesting; MR = medium-retention harvesting; HR = high-retention harvesting; UE = unharvested edge; UI = unharvested interior. Small characters in common indicate a lack of significant difference in Tukey's multiple comparisons ($\alpha = 0.05$).

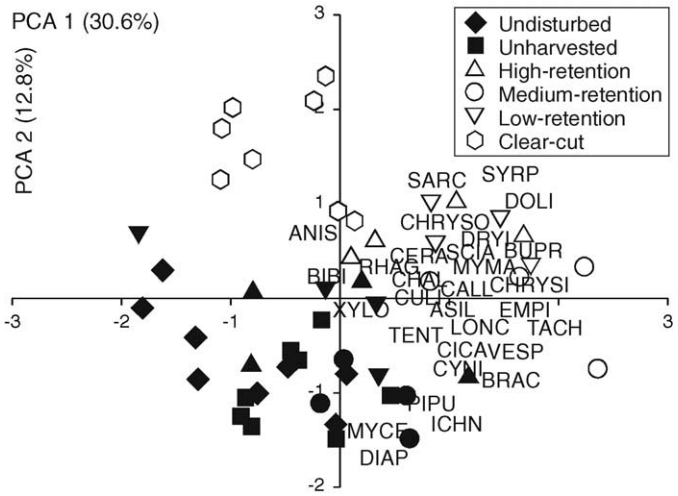

Fig. 1. Principal components analysis of abundances of 30 insect family abundances from 48 Malaise traps in six harvesting treatments in peatland black spruce forests in northeastern Ontario. Solid symbols represent traps set in forested areas; open symbols represent those in open areas. See Appendix A for insect family acronyms.

of the axis, retention harvested sites in the central portion, and unharvested forests in the lower (negative) half. Family vectors that showed highest correlations with this second axis were Diapriidae, Mycetophilidae, and, to a lesser extent, Ichneumonidae and Pipunculidae.

The overall correlation between variation in insect communities along the first PCA axis and the amount of edge at a site was confirmed when scores from the first axis were plotted against an index of the amount of edge (Fig. 2). Structural retention sites had higher amounts of edge on average than either clear-cut or unharvested sites; similarly, they had higher scores on average along the first PCA axis than either clear-cut or unharvested sites (especially for traps in the cleared strips; Fig. 2B).

Harvesting also had a significant effect on abundances of the various larval and adult trophic assemblages (Table 2). In every case, abundance was highest in one of the structural retention treatments (10 in MR, 1 in LR, and 1 in HR). One-half of the families showed greater abundances in each of the retention treatments than in any of the other treatments. As before, for every assemblage that showed a significant difference in the ANOVA, Tukey's comparisons showed at least one significant difference between a strip harvested treatment (HR, MR, or LR) and either the clear-cut or unharvested treatments. Differences between the clear-cut and unharvested treatments also were quite common, with larval parasitoids, adult parasitoids, and adult herbivores showing greater abundances in the unharvested treatments compared to the clear-cut treatment, and adult predators showing greater abundances in the clear-cut treatment compared to unharvested treatments. Abundances were never significantly different between the two unharvested treatments.

The ordination of abundances in adult trophic assemblages showed a similar pattern to that based on family abundances (Fig. 3). The first axis (49.7% of the variation) was positively correlated with abundances in the trophic assemblages, with structural retention sites usually on the right (positive) side and undisturbed and clear-cut sites on the left side. The second principal component (23.2% of the variance) corresponded to the retention gradient, with harvested stands in the lower half of the ordination axis and retention forests in the upper half. Trophic assemblages that tended to be more abundant in cleared forest areas, such as pollinators and predators, were seen in the lower right quadrant, whereas assemblages that tended to be more common in the forested areas such as mycophages, parasitoids, and herbivores were located in the upper half of the ordination. The ordination on larval trophic groups was similar to that on adult trophic groups and is not shown.

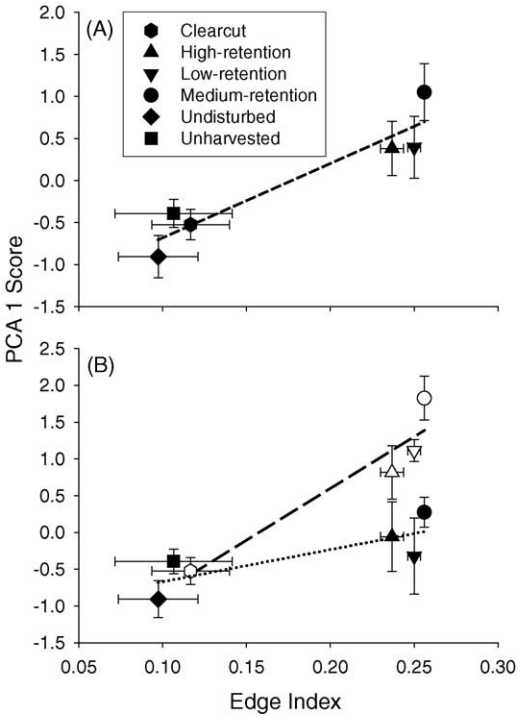

Fig. 2. Mean scores (±S.E.) from the first principal component axis (PCA1) in Fig. 1 plotted against mean values (±S.E.) of an index of edge effects for plots in peatland black spruce forests in northeastern Ontario. The index was defined as the variance in station-level forest presence/absence for 30 sampling stations in each sampling plot (see text for additional details). (A) Means are for all traps; (B) solid symbols represent traps set in forested areas whereas open symbols represent those in open areas. Lines are linear regressions through the means.

3.2.2. Comparisons among traps in cleared areas and forested areas

ANOVAs comparing family abundances among cut strips of HARP treatments and clear-cut sites revealed significant differences for 14 families (Table 3). In each case, family abundance was higher in the cut strips than in clear-cuts. In most cases, abundance was highest in the MR treatment (10 families compared to two in the LR treatment and two in the HR treatment). Larval and adult trophic assemblages showed the same pattern, with all groups with significant differences being more abundant in cut strips of all three HARP treatments than in clear-cuts, and in all cases showing greatest abundance in the MR treatment (Table 4).

Only six insect families showed significant differences among the retention strips and unharvested sites (Table 5). For five families, abundances were greater in the harvested strips than in undisturbed forest. The exception was Diapriidae, which was more abundant in unharvested sites than in retention strips. Significant differences also were relatively infrequent for trophic assemblages, with only three groups showing significant differences among the treatments (Table 6). In every case, abundances were higher in the HARP treatments than in undisturbed forest.

3.2.3. Effects of structural-retention in HARP sites

The abundance of 13 families differed significantly between cut and retention strips, 12 of which were more abundant in cut strips than in adjacent residual strips of thinned forests (Asilidae, Dolichopodidae, Sciaridae, Syrphidae, Tachinidae, Braconidae, Chalcididae, Chrysididae, Tenthredinidae, Buprestidae, Cerambycidae and Chrysomelidae). Mycetophilidae was more common in retention than in cut strips.

3.3. Insect-habitat associations

The ordination constrained by the PCA-based habitat variables showed a pattern very similar to that in the unconstrained ordination (Fig. 4). RDA axes one and two explained 13.5 and 10.5% of the canonical variance, respectively. Most habitat variables reflected the structural gradient of the second axis, with variables such as seedling abundance and dead moss being associated with clear-cut sites, high tree basal area and abundant regeneration from layering being associated with undisturbed sites, and HARP treatments being intermediate. Some variables, such as coarse and fine woody debris, distinguished clear-cut and HARP sites from undisturbed forest, whereas others such as lichen abundance distinguished undisturbed and HARP sites from clear-cuts. In combination, these patterns served to distinguished HARP sites from either clear-cut or undisturbed sites (axis one). Most families were most abundant on the right-hand side of axis one in association with HARP sites. Diapriidae showed a strong correlation with the second axis and its abundance was correlated with features of unharvested forests such as abundant and large-sized trees.

The RDA on adult trophic categories showed a very similar pattern (Fig. 5). RDA axes one and two explained 39.1% and axis two 19.0% of the canonical

Table 2
Mean abundances (number of individuals per 10 trap days) of insect trophic assemblages (±S.E., $n = 4$) in six treatments of increasing forest retention in peatland black spruce forests in northeastern Ontario

Trophic groups	Treatment[a]												ANOVA (P)
	CC		LR		MR		HR		UE		UI		
Insect larvae													
Phytophage	25.5 b	±4.6	48.3 ab	±10.2	68.0 a	±11.0	45.6 ab	±9.9	38.6 ab	±7.1	34.5 ab	±6.8	0.0160
Mycophage	76.7 b	±9.5	97.9 ab	±12.6	145.8 a	±17.7	97.4 ab	±15.0	95.9 ab	±9.7	81.5 b	±8.4	0.0028
Saprophage	24.1	±5.2	29.1	±7.7	45.2	±13.7	25.5	±5.4	10.8	±2.0	46.8	±21.8	0.2126
Predaceous	107.9 b	±12.1	162.7 a	±29.9	174.8 a	±33.4	121.7 ab	±21.6	68.0 bc	±6.7	48.0 bc	±9.9	0.0003
Parasitoids	152.3 c	±13.0	280.5 bc	±35.5	433.6 a	±47.1	265.7 bc	±27.5	312.6 ab	±30.6	266.7 bc	±37.1	<.0001
Adult insects													
Herbivore	15.3 c	±1.6	28.8 ab	±6.4	38.3 a	±6.7	18.4 ab	±3.3	30.5 ab	±6.7	23.4 ab	±4.6	0.0272
Nectar/flower	71.1 b	±8.4	81.2 b	±10.8	136.1 a	±18.4	90.9 ab	±10.4	60.4 b	±6.1	89.8 b	±23.4	<.0001
Mycophage	76.7 b	±9.5	97.9 ab	±12.6	145.8 a	±17.6	97.4 ab	±14.6	95.9 ab	±9.7	81.5 b	±8.4	0.0028
Saprophage	14.3	±4.1	26.3	±7.3	36.6	±9.4	38.4	±9.2	12.9	±3.0	14.4	±4.3	0.0703
Predator	67.9 ab	±8.0	127.8 a	±25.3	127.2 a	±23.4	73.5 ab	±14.0	38.8 c	±10.5	28.3 c	±6.8	<.0001
Parasitoid	105.9 c	±9.6	230.1 b	±30.4	344.4 a	±39.0	199.1 b	±29.9	264.8 ab	±29.0	226.6 b	±32.6	<.0001
Pollinator	35.4	±5.6	26.4	±6.0	39.0	±9.0	38.2	±8.2	22.7	±6.8	13.5	±3.1	0.0529

[a] CC = clear-cut; LR = low-retention harvesting; MR = medium-retention harvesting; HR = high-retention harvesting; UE = unharvested edge; UI = unharvested interior. Small characters in common indicate a lack of significant difference in Tukey's multiple comparisons ($\alpha = 0.05$).

variance, respectively. Predators and pollinators tended to be associated with clear-cut and HARP sites, whereas parasitoids and mycophages tended to be associated with undisturbed and HARP sites. In all cases, vectors of the various trophic assemblages were on the right-hand (HARP) side of axis one.

4. Discussion

Our data suggest that boreal insect assemblages are sensitive to the spatial configuration of habitats, even under the fine-scale forest fragmentation that occurred during the partial retention strip harvesting. Other

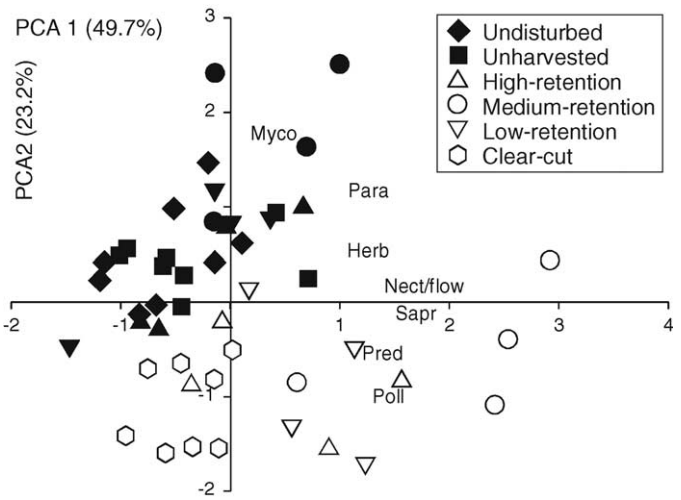

Fig. 3. Principal components analysis of insect abundances in adult trophic groups in six harvesting treatments in peatland black spruce forests in northeastern Ontario. Solid symbols represent traps set in forested areas; open symbols represent those in open areas. See Appendix A for family trophic assemblages.

Table 3
Mean abundance (number of individuals per 100 trap days) of insect families (±S.E., $n = 4$) in the cleared areas of four harvested treatments in peatland black spruce forests in northeastern Ontario

Insect taxon	Treatment[a]								ANOVA (P)
	CC		LR		MR		HR		
Diptera									
Anisopodidae	6.2	±2.0	4.2	±1.9	6.3	±4.6	0.0	±0.0	0.4480
Asilidae	5.7 b	±2.0	36.5 ab	±10.2	57.3 a	±19.3	25.0 ab	±7.5	0.0113
Bibionidae	281.9	±155.8	113.5	±53.0	222.9	±79.5	42.7	±17.1	0.1665
Calliphoridae	24.6 c	±5.9	39.6 bc	±9.4	67.7 ab	±16.0	92.7 a	±23.9	0.0084
Culicidae	39.7	±9.3	130.2	±39.0	144.8	±48.5	129.2	±26.3	0.0764
Dolichopodidae	486.3 b	±53.1	1284.4 a	±307.5	1138.5 a	±205.8	559.4 b	±81.0	0.0205
Empididae	132.2	±25.1	278.1	±70.2	487.5	±144.9	287.5	±129.4	0.1419
Lonchaeidae	82.0	±26.9	179.2	±53.1	371.9	±139.1	192.7	±56.8	0.0986
Mycetophilidae	356.3	±54.1	383.3	±72.1	572.9	±89.4	379.2	±54.2	0.1419
Pipunculidae	19.8 c	±3.9	77.1 ab	±16.8	116.7 a	±23.2	58.3 b	±11.3	0.0010
Rhagionidae	5.2	±3.7	9.4	±5.8	10.4	±5.4	5.2	±2.1	0.9057
Sarcophagidae	87.2	±16.3	119.8	±32.1	122.9	±45.5	67.7	±32.5	0.7381
Sciaridae	459.3	±42.8	570.8	±95.3	710.4	±152.1	562.5	±151.4	0.6412
Syrphidae	314.7	±43.4	390.6	±75.9	622.9	±112.0	467.7	±97.1	0.2545
Tachinidae	441.4 c	±36.7	575.0 b	±71.1	1053.1 a	±144.0	818.7 ab	±99.1	0.0002
Xylophagidae	2.1	±1.3	4.2	±3.3	3.1	±3.1	1.0	±1.0	0.8090
Hymenoptera									
Braconidae	148.4 c	±19.2	401.0 b	±85.1	811.5 a	±155.1	416.7 b	±63.1	0.0001
Chalcididae	86.8	±15.4	250.0	±79.2	141.7	±54.7	116.7	±59.1	0.3086
Chrysididae	27.5 c	±5.9	113.5 ab	±31.0	139.6 a	±28.9	59.4 b	±14.3	0.0013
Cynipidae	22.0 c	±3.4	57.3 ab	±14.6	80.2 a	±18.5	44.8 b	±8.2	0.0077
Diapriidae	73.0 c	±11.6	250.0 b	±40.7	506.2 a	±74.2	263.5 b	±48.9	<.0001
Dryinidae	25.0	±3.8	57.3	±34.9	107.5	±46.0	44.8	±22.9	0.1388
Ichneumonidae	574.8 c	±47.1	1144.8 b	±146.4	1534.4 a	±161.4	816.6 b	±94.9	<.0001
Mymaridae	76.4 c	±18.1	79.2 c	±20.3	186.5 ab	±41.5	217.7 a	±37.8	0.0064
Tenthredinidae	105.1 c	±11.6	130.2 bc	±19.3	361.5 a	±68.0	145.8 b	±26.4	0.0002
Vespidae	13.4 c	±3.3	36.5 b	±7.8	70.8 a	±15.8	46.9 ab	±10.2	0.0003
Coleoptera									
Buprestidae	2.8	±1.1	13.5	±3.7	21.9	±5.9	28.1	±12.0	0.0574
Cerambycidae	10.4	±3.1	60.4	±25.9	29.2	±9.9	47.9	±12.5	0.1767
Chrysomelidae	14.9	±3.9	193.8	±44.2	108.3	±23.8	111.5	±47.5	0.1001
Homoptera									
Cicadellidae	19.8 b	±5.7	69.8 a	±40.6	60.4 a	±28.3	22.9 b	±9.1	0.0002

[a] CC = clear-cut forest; LR = low-retention HARP; MR = medium-retention HARP; HR = high-retention HARP. Small characters in common indicate a lack of significant difference in Tukey's multiple comparisons ($\alpha = 0.05$).

recent studies similarly have shown responses to habitat fragmentation (e.g., Banks, 1998; Golden and Crist, 1999; Steffan-Dewenter and Tscharntke, 2002), with landscape features such as patch size, connectivity, and context all appearing to influence insect assemblages in forested habitats (Dennis, 1997; Didham, 1997; Ozanne et al., 1997; Jokimäki et al., 1998; Tscharntke et al., 2002; Steffan-Dewenter, 2003).

An unexpected result was the higher abundance of nearly all insect families and trophic assemblages in the retention sites (especially in the cleared strips) compared to either the clear-cut or undisturbed sites. Although the insect community also showed evidence of a response to the landscape-level structural retention (along the second axis of the ordinations), the magnitude of this response was less than half as strong as the response to the strip harvesting itself (as

Table 4
Mean abundance (number of individuals per 10 trap days) of insect trophic assemblages (±S.E., $n = 4$) in the cleared areas of four harvested treatments in peatland black spruce forests in northeastern Ontario

Trophic group	Treatment[a]								ANOVA (P)
	CC		LR		MR		HR		
Insect larvae									
Phytophage	25.5 b	±4.6	59.9 ab	±16.2	93.1 a	±18.1	41.0 b	±9.5	0.0004
Predaceous	107.9 b	±12.1	210.3 ab	±49.6	247.8 a	±56.6	149.7 ab	±32.9	0.0186
Parasitoid	152.3 c	±13.0	295.6 b	±53.0	468.1 a	±72.1	285.7 b	±40.5	<.0001
Adult insects									
Herbivore	15.3 c	±1.6	42.0 ab	±11.2	55.9 a	±10.8	21.6 bc	±4.8	0.0001
Nectar/flower	71.1 b	±8.4	95.5 b	±17.0	158.5 a	±23.6	109.3 ab	±14.5	0.0003
Predator	67.9 ab	±8.0	161.0 a	±41.7	175.4 a	±39.9	91.9 ab	±21.2	0.0068
Parasitoid	105.9 c	±9.6	239.4 ab	±46.3	362.8 a	±59.7	203.9 b	±34.7	<.0001

[a] CC = cleared forest; LR = low retention HARP; MR = medium retention HARP; HR = high retention HARP. Small characters in common indicate a lack of significant difference in Tukey's multiple comparisons ($\alpha = 0.05$). Only significant responses are shown.

judged by the percent variance explained by principal component analysis on family and trophic abundances, for example). Surprisingly, the contrast between insect communities in clear-cuts and undisturbed forest was less strong than the contrast between retention treatments and clear-cuts, or the contrast between retention treatments and undisturbed forest. Thus, the gradient in forest retention that dominated our descriptions of forest structure at the sites (Deans et al., 2003) was not the dominant pattern observed for the insect community. The high insect abundance was most marked in the cleared strips of the HARP stands, especially in the interior of retention areas (treatment MR), but also was evident in strips of retained forest. Thus, in the short term at least, and with respect to maintaining insect abundances similar to those observed in unharvested forests, the HARP structural retention technique was not successful in ameliorating the differences between clear-cut and unharvested stands. This conclusion stands in marked contrast to the success of HARP in maintaining forest structure: Deans et al. (2003) found that retention of forest structure in HARP stands was better than might have been expected based on the amount of basal area removed.

This increase in abundance of insects in response to the structural retention may be attributed to various factors. The strip-cut areas provided the highest concentration of transition zones between residual forested areas and cleared habitats (i.e., the greatest amount of edge) and also provided a greater range of forest seral stages than either the clear-cut or undisturbed sites, in that the retention strips maintained some characteristics of late-successional understory and forest structures and adjacent cleared strips had earlier-stage forest characteristics. This close proximity of successional stages may have provided locally diverse microhabitats for insects. Possible responses to this close juxtaposition of early- and late-successional habitats may include increased abundances of habitat generalists, which often dominate boreal faunas (Niemelä et al., 1993; Puntilla et al., 1994; Spence et al., 1996). In addition, these sites may have provided habitat for both open- and closed-forest specializing taxa, with both groups overflowing to some extent into their less-favoured habitat type. The HARP harvesting created edge effects in that the HARP areas had an insect fauna that was characteristic of neither of the two habitats abutting the edge (Angelstam, 1992; Murcia, 1995). This supports the observations of Helle and Muona (1985), who found that several insect taxa had larger numbers at edges than inside adjoining forests and clear-cuts. These edge effects appeared to operate over relatively small spatial scales, presumably 10 s of meters of less, given that the insect communities in unharvested forest close to the harvesting (ca. 150 m) were very similar to those far from any harvesting.

An additional factor may be an influence of the harvesting on the behaviour and flight patterns of insects (Angelstam, 1992; Didham et al., 1996). For example, the cut strips of HARP-harvested forests

Table 5
Mean abundance (number of individuals per 100 trap days) of insect families (±S.E., $n = 4$) in the retention strips of HARP treatments and unharvested sites in peatland black spruce forests in northeastern Ontario

Insect taxon	Treatment[a]										ANOVA (P)
	LR		MR		HR		UE		UI		
Diptera											
Anisopodidae	10.4	±5.0	0.0	±0.0	0.0	±0.0	2.1	±1.0	1.0	±0.7	0.0524
Asilidae	12.5	±6.0	18.8	±7.8	14.6	±3.0	6.2	±1.9	17.0	±4.1	0.4195
Bibionidae	72.9	±29.6	257.3	±138.1	29.2	±11.3	20.8	±5.8	392.2	±212.5	0.2438
Calliphoridae	22.9	±6.7	29.2	±9.7	62.5	±22.0	28.8	±5.7	19.4	±4.9	0.1587
Culicidae	60.4	±17.3	58.3	±12.3	99.0	±36.2	59.7	±14.7	55.2	±22.6	0.8317
Dolichopodidae	701.0 a	±185.5	463.5 ab	±80.9	311.5 ab	±77.0	126.2 c	±20.6	100.9 c	±17.2	0.0003
Empididae	213.5	±51.0	259.4	±57.1	184.4	±64.2	163.0	±67.4	131.9	±35.5	0.7585
Lonchaeidae	210.4	±90.1	221.9	±53.3	349.0	±132.8	63.5	±15.1	110.9	±35.0	0.0778
Mycetophilidae	764.6 ab	±144.3	1206.3 a	±171.7	780.2 ab	±100.8	575.7 b	±54.7	555.6 b	±60.3	0.0038
Pipunculidae	97.9 ab	±21.3	134.4 a	±24.1	126.0 a	±27.3	83.3 ab	±10.4	41.3 b	±7.3	0.0166
Rhagionidae	9.4	±6.5	15.6	±10.4	0.0	±0.0	1.0	±1.0	4.7	±2.1	0.2188
Sarcophagidae	60.4	±23.7	51.0	±17.6	69.8	±25.6	21.5	±9.9	23.6	±6.7	0.2114
Sciaridae	266.7	±36.9	427.1	±79.2	226.0	±46.5	350.7	±52.7	259.2	±31.3	0.2138
Syrphidae	141.7	±37.2	156.3	±36.8	295.8	±69.7	180.9	±47.6	135.1	±24.6	0.3444
Tachinidae	444.8	±73.4	730.2	±112.8	513.5	±75.7	452.4	±44.7	400.7	±67.5	0.2217
Xylophagidae	6.3	±3.8	17.7	±7.4	4.2	±4.2	1.0	±1.0	19.8	±6.4	0.0525
Hymenoptera											
Braconidae	256.3	±55.7	441.7	±84.3	311.5	±54.3	379.7	±54.7	209.4	±29.4	0.1317
Chalcididae	88.5	±30.6	66.7	±25.8	15.6	±7.5	29.0	±7.2	89.9	±25.3	0.0912
Chrysididae	41.7	±12.7	61.5	±23.6	36.5	±9.0	24.5	±4.6	21.4	±5.0	0.2681
Cynipidae	22.9	±4.7	51.0	±11.0	36.5	±14.3	46.5	±6.4	29.2	±4.8	0.1821
Diapriidae	299.0 b	±58.9	495.8 b	±61.1	358.3 b	±91.6	1016.7 a	±88.5	705.2 ab	±76.5	<.0001
Dryinidae	15.6	±9.7	7.3	±3.7	29.2	±14.1	4.7	±1.8	5.2	±2.0	0.0742
Ichneumonidae	1365.6 ab	±180.7	1977.1 a	±288.5	869.8 b	±178.5	910.6 b	±79.2	1135.8 ab	±163.7	0.0213
Mymaridae	20.8	±9.8	25.0	±6.1	160.4	±112.4	44.3	±7.5	28.5	±5.1	0.1301
Tenthredinidae	82.3	±17.2	129.2	±30.6	99.0	±30.6	222.9	±58.3	187.3	±32.5	0.1424
Vespidae	18.8	±4.1	47.9	±9.8	41.7	±15.1	20.1	±5.6	32.8	±8.2	0.3026
Coleoptera											
Buprestidae	4.2 ab	±2.5	6.3 ab	±2.2	9.4 a	±4.2	1.0 b	±0.7	1.1 b	±1.0	0.0229
Cerambycidae	12.5	±4.5	12.5	±4.7	21.9	±8.3	10.9	±3.6	14.1	±3.2	0.7807
Chrysomelidae	15.6	±5.8	18.8	±9.9	2.1	±1.4	4.7	±1.7	1.7	±0.9	0.1120
Homoptera											
Cicadellidae	58.3	±11.7	59.4	±14.0	51.0	±19.8	59.0	±9.2	45.1	±9.3	0.9551

[a] LR = low-retention HARP; MR = medium-retention HARP; HR = high-retention HARP; UE = unharvested edge; UI = unharvested interior. Small characters in common indicate a lack of significant difference in the Tukey's multiple comparisons ($\alpha = 0.05$).

may have acted as 'fly-through' zones that increased airborne insect movements across the landscape. Microhabitat conditions at forest edges are suitable for open-habitat species, which encourages movement between fragments (Spence et al., 1996). In this regard, it would be interesting to test whether differences in the spatial configuration of the cut strips in HARP stands would affect the magnitude of the abundance increases; for example, differences between the linear pattern of HARP harvesting and a more checkerboard pattern of cutting. If the increase in insect abundance in the HARP stands is partly a function of the creation of linear travel corridors, a more checkerboard pattern of cutting might help ameliorate the increase in insect abundances and any associated longer-term effects of the cutting.

The ecological effects of these edge effects are unclear. Super-abundances of insects in the HARP stands presumably could have either positive and negative effects; for example by providing a greater

Table 6
Mean abundance (number of individuals per 10 trap days) of insect trophic assemblages (±S.E., $n = 4$) in retention strips of HARP treatments and unharvested sites in peatland black spruce forests in northeastern Ontario

Trophic group	Treatment[a]										ANOVA (P)
	LR		MR		HR		UE		UI		
Insect larvae											
Mycophage	103.1 b	±20.1	163.3 a	±27.0	100.6 b	±15.2	95.8 b	±9.7	81.4 b	±8.4	0.0048
Adult insects											
Mycophage	103.1 b	±20.1	163.3 a	±27.0	100.6 b	±15.2	95.8 b	±9.7	81.4 b	±8.4	0.0048
Predator	94.5 a	±26.9	78.9 ab	±16.7	55.2 bc	±17.7	38.7 cd	±10.4	28.2 d	±6.8	0.0087

[a] LR = low retention HARP; MR = medium retention HARP; HR = high retention HARP; UE = unharvested edge; UI = unharvested interior. Small characters in common indicate a lack of significant difference in Tukey's multiple comparisons ($\alpha = 0.05$). Only significant responses are shown.

resource prey for insectivores, or by resulting in the local extirpation of resource-specialist insect species through competition with edge-loving generalists. Increased edge habitat may alter normal functioning of ecological processes such as parasitism (Roland and Taylor, 1997). Forest harvesting has been observed to decrease parasitoid species richness and abundance (e.g., Kruess and Tscharntke, 1994; Didham et al., 1996; Roland and Taylor, 1997). Forest fragmentation also has been demonstrated to have an influence on the spatial scale of parasitism rates. Roland and Taylor (1997) found that the incidence of parasitoid species attacking the forest tent caterpillar (*Malacosoma disstria*) was significantly correlated with the proportion of forested to non-forested land in the surrounding area. Larger parasitoid species occupied larger territories and were observed to cause less parasitism in the areas of greatest forest fragmentation. The interaction strength between parasitoids and herbivores, for example, can be disrupted by changes in the relative abundances of each in trophic cascades. We observed some evidence of trophic changes in the retention-harvested stands. For example, in comparison to unharvested forest, HARP stands had increased relative abundances of predators and pollinators and decreased relative abundances of parasitoids and

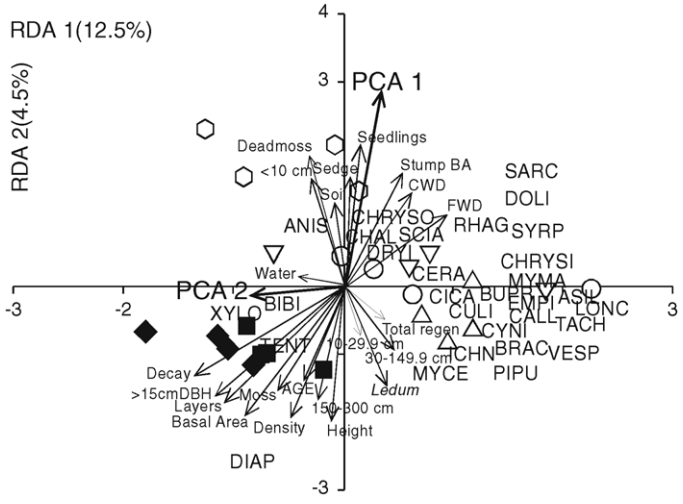

Fig. 4. Redundancy analysis of insect family abundances in six harvesting treatments in peatland black spruce forests in northeastern Ontario (see Fig. 1 for symbol legend). Principal component analysis on the habitat variables was used to derive composite habitat variables (PCA1 and PCA2) that were then used to constrain family abundances. Raw habitat variables (small font) were entered into the analysis passively. Family acronyms are in Appendix A and habitat variable acronyms are in Deans et al. (2003).

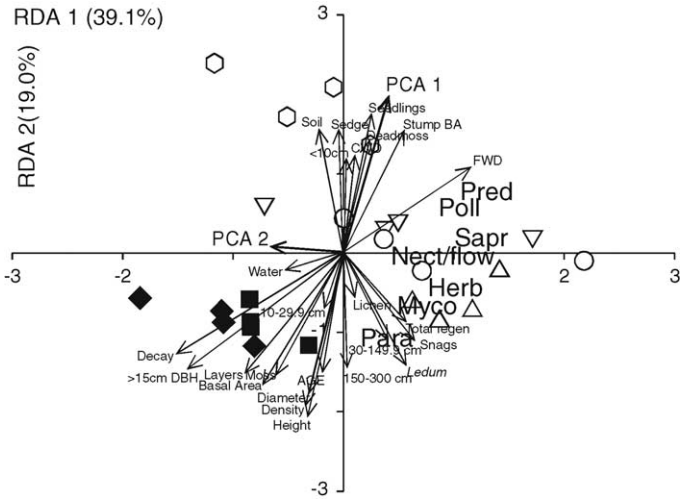

Fig. 5. Redundancy analysis of insect abundances in adult trophic assemblages in six harvesting treatments in peatland black spruce forests in northeastern Ontario (see Fig. 1 for symbol legend). Principal component analysis on the habitat variables was used to derive composite habitat variables (PCA1 and PCA2) that were used to constrain the analysis. Original habitat variables were entered into the analysis passively. Family trophic assemblages are in Appendix A and habitat variable acronyms are in Deans et al. (2003).

mycophages. However, these trophic differences should be taken as indicative rather than conclusive. Assignment to trophic levels at the family level is approximate given that variation in trophic behaviour is sometimes observed within families. In addition, the weighting of trophic representation according to abundances rather than according to the presence or absence of species may confound true trophic responses with responses that are due to peculiarities of the species or group in question. For example, decreased mycophagy may have reflected idiosyncratic responses of Mycetophilids as much as any reduction in possibilities for mycophagy per se. Therefore, these trophic changes need further investigation at the species level.

Our study provided some evidence of positive impacts of the HARP treatments in comparison to clear-cut logging in that some families (notably microparasitic wasps in the Diapriidae) were at higher abundances in the HARP forests. In addition, differences in family abundances between retained strips and unharvested forest were relatively minor compared to those between cleared strips and unharvested forest, and evidence of reduced impacts of HARP harvesting compared to clear-cutting was evident on the second axes of the ordinations. Thus, compared to the cleared strips, the retained strips provided some evidence of ''life-boating'' of the insect community of undisturbed forest (Franklin et al., 1997).

It is important to note that our results provide a snapshot of the insect community shortly after the harvest. It remains to be seen whether the observed changes in insect communities, notably the pervasive edge effects, will persist for a long period of time, perhaps diminishing the benefits of structural retention over the long term, or will exist for only a short time, and have a minor net ecological effect, as trees in the cleared strip grow. Of particular importance in this regard is long-term monitoring of insect communities in the strip harvested areas to see if the HARP harvesting has the desired long-term effect; namely, a more rapid return to conditions typical of the original old-growth forest compared to clear-cuts.

Our results support the possibility that higher-level taxonomic groups, such as insect families, can be used to monitor forest practices in boreal peatland black spruce forests. Several possible candidates for more detailed study are indicated. At the family level, the Diapriidae demonstrated the strongest relationship with unharvested forest areas and increased in abundance with stand density, age, height and diameter of trees. This group could be further assessed to gauge family composition at the species-level and

to gain insight into the composition and abundance of the parasitoid guild. Mycetophilids (fungus gnats), which include a large compliment of species with Diapriid parisitoids, were consistently found less often in the cleared than closed forest areas and abundances were positively correlated with density and diameter of trees as well as density of large-class advance regeneration. Mycetophilids appeared to be dependent on certain forest conditions such as highly decayed wood and an intact forest floor under a relatively intact forest canopy, which supports the previous findings of Økland (1996) in the southern spruce forests of Norway. The predatory family Dolichopodidae (long-legged flies) and Sarcophagidae were positively influenced by open areas, a similar response to that shown by the predator assemblage overall. Correlations indicated an inverse relationship between dolichopodid abundance and forest basal area retention, stand height and tree density. The Dolichopodidae might be used as an ecological indicator of the degree to which the predatory guild is present in the insect community. Parasitoid insects as well as mycophages represented greater proportions of the insect community in high-retention areas of the forest. Four parasitoid families (Braconidae, Diapriidae, Ichneumonidae, and Pipunculidae) and one family of the mycophages (Mycetophilidae) were notably less well represented in the clear-cut than in the HARP-harvested or unharvested forests. Pollinators, predators and, to some degree, saprophages all demonstrated a greater proportion of the insect community in HARP-harvested compared to other areas.

5. Conclusions

In conclusion, our results provide evidence that the boreal insect community is sensitive to the spatial configuration of forest harvesting, and in particular shows strong increases in abundance in strip cut areas. The ecological effects of this increase and associated shifts in trophic guilds, and whether or not they will prove to be long-lived, are unknown. Our study provides evidence of the utility of higher-level taxonomic insect groups in ecological comparisons of alternative harvesting regimes.

Acknowledgements

We are grateful to the employees of Abitibi Consolidated Inc. for providing harvesting information and for assisting in site selection. We would like to thank A. Tatarnic and C. Darling for assistance with identification of insects, T. Carleton for assistance in the field, B. Campbell for assistance with data analyses, and two anonymous reviewers from helpful suggestions. Financial and logistic supported was provided by the Lake Abitibi Model Forest, the Canadian Forest Service, and the Natural Sciences and Engineering Research Council of Canada.

Appendix A. Common names, acronyms, and trophic categorizations of insect families

Order	Family	Family code	Common name	Larval trophic group[a]	Adult trophic group[a]
Diptera	Anisopodidae	ANIS	Wood gnat	2, 8	4
	Asilidae	ASIL	Robber fly	5	5
	Bibionidae	BIBI	March fly	2	2, 4
	Calliphoridae	CALL	Blow fly	9	9
	Culicidae	CULI	Mosquito	5	1, 4
	Dolichopodidae	DOLI	Long-legged fly	5	5
	Empididae	EMPI	Dance fly	5	4, 5
	Lonchaeidae	LONC	Lonchaeid flies	2	2
	Mycetophilidae	MYCE	Fungus gnat	3, 8	3, 8
	Pipunculidae	PIPU	Big-headed fly	6	6
	Rhagionidae	RHAG	Snipe fly	5	1, 4

Appendix A. (*Continued*)

Order	Family	Family code	Common name	Larval trophic group[a]	Adult trophic group[a]
	Sarcophagidae	SARC	Flesh fly	9	4
	Sciaridae	SCIA	Dark-winged fungus gnat	3, 8	3, 8
	Syrphidae	SYRP	Hover fly	2, 5, 8, 9	7
	Tachinidae	TACH	Tachinid fly	6	4
	Xylophagidae	XYLO	Xylophagid fly	5	4, 8
Hymenoptera	Braconidae	BRAC	Braconid wasp	6	6
	Chalcididae	CHAL	Chalcid wasp	6	6
	Chrysididae	CHRYSI	Cuckoo wasp	6	6
	Cynipidae	CYNI	Gall wasp	6	6
	Diapriidae	DIAP	Diapriid wasp	6	6
	Dryinidae	DRYI	Dryinid wasp	6	6
	Ichneumonidae	ICHN	Parasitoid wasp	6	6
	Mymaridae	MYMA	Fairyflies	6	6
	Tenthridinidae	TENT	Sawflies	2	2
	Vespidae	VESP	Yellowjacket wasps and hornets	5	5, 8
Coleoptera	Buprestidae	BUPR	Metallic wood-boring	8	8
	Cerambycidae	CERA	Long-horned beetle	8	8
	Chrysomelidae	CHRYSO	Leaf beetle	2	2
Homoptera	Cicadellidae	CICA	Leaf hopper	2	2

[a] Trophic groups: 1 = blood-feeders; 2 = herbivorous (including saprophagous-decaying organic material); 3 = mycophagous; 4 = nectar/flower feeders; 5 = predators/carnivores; 6 = parasitoids; 7 = pollinators; 8 = wood/sap feeders; 9 = scavenger (carrion).

References

Angelstam, P., 1992. Conservation of communities—the importance of edges, surroundings, and landscape mosaic structure. In: Hansson, L. (Ed.), Ecological Principles of Nature Conservation. Elsevier Applied Science, New York, pp. 9–70.

Arnett, Jr., R.H., Thomas, M.C. (Eds.), 2001. American Beetles, vol. 1. CRC Press, Boca Raton, FL.

Arnett, Jr., R.H., Thomas, M.C., Skelley, P.E., Frank, J.H. (Eds.), 2002. American Beetles, vol. 2. CRC Press, Boca Raton, FL.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72, 355–362.

Banks, J.E., 1998. The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. Oecologia 117, 236–246.

Balmford, A., Green, M.J.B., Murray, G., 1996a. Using higher-taxon richness as a surrogate for species richness. I. Regional tests. Proc. Roy. Soc. London B 263, 1267–1274.

Balmford, A., Jayasuriya, H.M., Green, M.J.B., 1996b. Using higher-taxon richness as a surrogate for species richness. II. Local applications. Proc. Roy. Soc. London B 263, 1571–1575.

Bellocq, M.I., Smith, S.M., 2003. Convergence in arthropod assemblages with various restoration approaches for Canadian deciduous forests. J. Insect Conserv. 7, 99–109.

Bellocq, M.I., Smith, S.M., Doka, M.E., 2001. Short-term effects of harvest technique and mechanical site preparation on arthropod communities in jack pine plantations. J. Insect Conserv. 5, 187–196.

Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal

mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.

Bird, G.A., Chatarpaul, L., 1986. Effect of whole-tree and conventional forest harvest on soil microarthropods. Can. J. Zool. 64, 1986–1993.

Bunnell, F.L., Huggard, D.J., 1999. Biodiversity across spatial and temporal scales: problems an opportunities. For. Ecol. Manage. 115, 113–126.

Chapin, F.S., et al., 2000. Consequences of changing biodiversity. Nature 405, 234–242.

Danks, H.V., Foottit, R.G., 1989. Insects of the boreal zone of Canada. Can. Entomol. 121, 625–690.

Danks, H.V., Winchester, N.N., 2000. Terrestrial arthropod biodiversity projects—building a factual foundation. Biological Survey of Canada, Document Series 7, 1–38.

Deans, A.M., Malcolm, J.R., Smith, S.M., Carlton, T.J., 2003. A comparison of forest structure among old-growth, variable retention harvested, and clear-cut peatland black spruce (*Picea mariana*) forests in boreal northeastern Ontario. For. Chron. 79, 579–589.

Dennis, P., 1997. Impact of forest and woodland structure on insect abundance and diversity. In: Watt, A.D., Stork, N.E., Hunter, M.D. (Eds.), Forest and Insects. Chapman & Hall, pp. 321–340.

Didham, R.K., 1997. An overview of invertebrate responses to forest fragmentation. In: Watt, A.D., Stork, N.E., Hunter, M.D. (Eds.), Forest and Insects. Chapman & Hall, pp. 302–320.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests: A functional approach. Trends Ecol. Evol. 11, 255–260.

Duchesne, L.C., Lautenschlager, R.A., Bell, F.W., 1999. Effects of clear-cutting and plant competition control methods on carabids (Coleoptera: Carabidae) assemblages in northwestern Ontario. Environ. Monit. Assess. 56, 87–96.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 111–139.

Golden, D.M., Crist, T.O., 1999. Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. Oecologia 118, 371–380.

Grime, J.P., 1997. Biodiversity and ecosystem functioning: the debate deepens. Science 277, 1260–1261.

Harris, L.D., 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago.

Helle, P., Muona, J., 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. Silva. Fennica. 19, 281–294.

Jokimäki, J., Huhta, E., Itämies, J., Rahko, P., 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Can. J. For. Res. 28, 1068–1072.

Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R. (Eds.), 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge.

Katzourakis, A., Purvis, A., Azmeh, S., Rotheray, G., Gilbert, F., 2001. Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. J. Evol. Biol. 14, 219–227.

Kruess, A., Tscharntke, T., 1994. Habitat fragmentation, species loss and biological control. Science 264, 1581–1584.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge.

Loreau, M., Hector, A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

MacDonell, M.R., Groot, A., 1997. Harvesting peatland black spruce: impacts on advance growth and site disturbance. For. Chron. 73, 249–255.

Major, R.E., Christie, F.J., Gowing, G., Cassis, G., Reid, C.A.M., 2003. The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia. Biol. Conserv. 113, 35–48.

Malcolm, J.R., 1997. Insect biomass in Amazonian forest fragments. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), Canopy Arthropods. Chapman & Hall, London, pp. 510–533.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (Coords.), 1981. Manual of Nearctic Diptera, vol. 1. Agriculture Canada Monograph No. 27. Biosystematics Research Institute, Ottawa, Canada.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (Coords.), 1987. Manual of Nearctic Diptera, vol. 2. Agriculture Canada Monograph No. 28. Biosystematics Research Institute, Ottawa, Canada.

McKenney, D.W., Kesteven, J.L., Hutchinson, M.F., Venier, L., 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. Can. J. Plant Sci. 81, 139–143.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62.

Niemelä, J., 1997. Invertebrates and boreal forest management. Conserv. Biol. 11, 601–610.

Niemelä, J., Spence, J.R., Langor, D., Haila, Y., Tukia, H., 1993. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. In: Gaston, K.J., New, T.R., Samways, J. (Eds.), Perspectives on Insect Conservation. Intercept Publications, Andover, pp. 29–50.

Økland, B., 1994. Mycetohilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forest in southern Norway. Biodivers. Conserv. 3, 68–85.

Økland, B., 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biol. Conserv. 76, 297–310.

Ozanne, C.M.P., Hambler, C., Foggo, A., Speight, M.R., 1997. The significance of edge effects in the management of forests for invertebrate diversity. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), Canopy Arthropods. Chapman & Hall, pp. 535–550.

Paquin, P., Coderre, D., 1997. Deforestation and fire impact on edaphic insect larvae and other macroarthropods. Environ. Entomol. 26, 21–30.

Puntilla, P., Haila, Y., Niemelä, J., Pajunen, T., 1994. Ant community in fragments of old-growth taiga and managed surroundings. Ann. Zool. Fennici 31, 131–144.

Roland, J., Taylor, P.D., 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386, 710–713.

Rowe, J.S., 1972. Forest Regions of Canada. Canadian Forest Service, Ottawa.

Schowalter, T.D., 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. For. Ecol. Manage. 78, 115–125.

Simard, J.R., Fryxell, J.M., 2003. Effects of selective logging on terrestrial small mammals and arthropods. Can. J. Zool. 81, 1318–1326.

Spence, J.R., Langor, D.W., Niemelä, J., Carcamo, H.A., Currie, C.R., 1996. Northern forestry and carabids: the case for concern about old-growth species. Ann. Zool. Fennici 33, 173–184.

Steffan-Dewenter, I., 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv. Biol. 17, 1036–1044.

Steffan-Dewenter, I., Tscharntke, T., 2002. Insect communities and biotic interactions on fragmented calcareous grasslands: a mini review. Biol. Conserv. 104, 275–284.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. J. Appl. Ecol. 38, 1221–1233.

Teskey, H.J., 1976. Diptera larvae associated with trees in North America. Mem. Entomol. Soc. Can. 100, 1–53.

Townes, H., 1972. A light-weight Malaise trap. Entomol. News 18, 239–247.

Triplehorn, C.A., Johnson, N.F., 2005. Borror and DeLong's Introduction to the Study of Insects, 7th ed. Thompson Books/Cole, Belmont, CA.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecol. Appl. 12, 354–363.

Williams, P.H., Gaston, K.J., 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biol. Conserv. 67, 211–217.

Winchester, N.N., Ring, R.A., 1996. Centinelan extinctions: extirpation of Northern temperate old-growth rainforest arthropod communities. Selbyana 17, 50–57.