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Convergence in arthropod assemblages with various restoration approaches for Canadian deciduous forests

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Abstract

Silvicultural practices are traditionally aimed at increasing forest profits; however, recent approaches to forest conservation have broadened to include nature-based silviculture for regenerating forests. In southern Ontario (Canada), originally dominated by deciduous forests, conifer plantations were established on abandoned agricultural sites. Currently, there is an increasing interest to convert these conifer stands to a state that mimics the original deciduous forest. We investigated arthropod abundance, species richness of carabid beetles, and abundance of arthropod assemblages (trophic and prey groups) under five silvicultural treatments conducted to regenerate deciduous forests (the natural forest type) from the old conifer plantations. The treatments included: (1) uniform canopy removal; (2) uniform canopy removal and understory removal; (3) group canopy removal; (4) group canopy removal and understory removal; and (5) untreated control plots (relatively pure red pine). Insects were sampled annually using sweepnets and pitfall traps. Results revealed treatment effects on the abundance of Coleoptera, Heteroptera, herbivores, and small arthropods (<3 mm) caught in sweepnet samples, where plots subjected to group shelterwood removal and understory removal supported higher abundances than the control plots. There was no treatment effect on the abundance of other arthropod groups or on the species richness and abundance of carabid beetles. The silvicultural treatments used to encourage natural regeneration did not seem to affect arthropod food availability for insectivorous vertebrates. Thus, the type of silvicultural strategy used to convert pine plantations to a stage that mimics the natural deciduous forests had little overall impact on arthropods.

Introduction

Studies on how forestry practices affect arthropods have focused on silvicultural techniques for commercial rather than for conservation purposes. In temperate and boreal forests, the effects of forestry practices such as harvesting on arthropod community composition, species richness and/or population abundance of arthropods have been well documented for specific taxa, including carabid beetles (Lenski 1982; Niemelä et al. 1993; Spence et al. 1996), lucanid beetles (Michaels and Bornemissza 1999), ants (Punttila et al. 1994), moths (Holloway et al. 1992), and spiders (Pajunen et al. 1995). Similarly, work has been conducted in several forest types on how site preparation techniques such as prescribed burning or scarification influence arthropod diversity (Huhta et al. 1967; Greenberg and McGrane 1996; Beaudry et al. 1997; Watt et al. 1997; York 1999; Bird et al. 2000; Bellocq et al. 2001). Little is known however about the effects of less drastic techniques such as understory or overstory removal or how specific ecological arthropod guilds respond to different types of vegetative regeneration.

Recent concern about forest conservation in populated areas has led to the need for regenerating natural forests through the use of nature-based silvicultural practices (Bradshaw et al. 1994). During the last 100 years in the Great Lakes basin of southern Ontario (Canada), conifer plantations (primarily pine) were widely established to prevent soil erosion on abandoned agricultural sites. Today, there is an increasing interest to convert these conifer stands to a stage that mimics the original deciduous forests (Elliot 1995). The restoration of these sites, through the encouragement of natural regeneration, is also recognized as a useful technique for maintaining invertebrate diversity (Niemelä 1997). Here we examine the arthropod community following different silvicultural treatments conducted to promote natural regeneration of the deciduous forest under conifer plantations. Light is one of the key factors determining regeneration success in forests (Emborg 1998). Our treatments of the overstory consisted of the removal of the canopy, which allowed an increased amount of full sunlight to reach the understory, thus encouraging the development of natural regeneration (shelterwood system). Brush-saw treatment was also considered because it allows the growth of new shoots at the base of the trees in response to coppicing stress (coppice regrowth), thus encouraging natural regeneration by promoting longer-term tree survival.

Arthropods fulfil a wide variety of ecological roles, and some assemblages are good indicators of the impact of forestry practices (Kremen et al. 1993). From the taxonomical perspective, carabid beetles are widely recognized as indicators of forest health. They are frequently used to study the influence of forestry practices on insects because they are diverse, well known taxonomically and sensitive to habitat change (Refseth 1980; Niemelä et al. 1988; Butterfield et al. 1995; Eyre and Luff 2002). Thus, we selected the carabid beetles to examine differences in species richness among silvicultural treatments. In addition, we also took a functional approach to study the response of the insect assemblages to varying forest management practices (Kremen et al. 1993; Didham et al. 1996). Insect functional assemblages may change following habitat management and such shifts can affect ecosystem processes (Kruess and Tscharntke 1994). Insect functional assemblages, such as trophic groups (decomposers, herbivores, parasitoids) or prey groups (food types available for wildlife), perform ecological roles or are involved in critical processes that maintain forest ecosystems. Few studies have considered the effects of forestry practices on arthropods as potential food for wildlife (Greenberg and McGrane 1996), which is critical in restoration processes. Many vertebrates feed on insects and often are local top insectivores. Amphibians are primarily insectivores as well as many birds, shrews and other small mammals.

Our underlying question was whether different silvicultural treatments for stand conversion resulted in differences among insect assemblages in the short-term. We investigated arthropod abundance, species richness of carabid beetles, and abundance of various arthropod functional groups (trophic and prey groups) in plots subjected to five treatments of overstory and understory removal conducted to promote natural regeneration of deciduous forests under conifer plantations.

Materials and methods

Study area

The work was conducted in the Durham Regional Forest (44° 03′ N, 79° 06′ W), Ontario, Canada. The area was originally characterized by a mixed deciduous forest dominated by maple (*Acer* sp.) and red oak (*Quercus rubra*). Over the past two centuries, the landscape has been transformed by afforestation followed by farming and agroforestry, resulting in deciduous forest fragments and conifer plantations (primarily red pine, *Pinus resinosa*) within a matrix of cultivated fields.

The study site was within 380 ha of public forests surrounded by planted red pine to the north, planted Scots pine (*Pinus sylvestris*) and jack pine (*Pinus banksiana*) to the west, and mixed deciduous forest to the south and east (Elliot 1995). The site was planted with red and white pine (*Pinus strobus*) at 1.8×1.8 m^2 spacing in alternate rows during 1929. Commercial thinning was done in 1961 and 1984, and non-commercial thinning was prescribed to remove the unhealthy white pine (suppressed by the red pine) in 1971. Prior to the experiment in 1994, mean dbh was 32 cm and mean stand height was 28 m. The understory (natural regeneration) was comprised by red maple (*Acer rubrum*, 31% of the total number of stems per ha), white ash (*Fraxinus americana*, 17%), black cherry (*Prunus serotina*, 14%), hard maple (*Acer saccharum*, 7%), white pine (5%), and red oak (5%) (Elliott 1995).

Experimental design

Experimental plots were set up by the Ontario Ministry of Natural Resources to test the use of silvicultural techniques to encourage natural regeneration of the deciduous forest under an overstory of planted red pine (Elliott 1995). The experiment was design in randomized blocks, with four blocks of five plots (40×43 m^2) each established in 1994. Treatment plots were established next to each other within each block, but insect traps were set at least 8 m apart from the edge of the plots to reduce edge effect. We assumed that treatment plots were large enough to detect differences in the selected variables of the selected arthropod assemblages (those living in the litter layer and on the understory vegetation). Silvicultural treatments were randomly assigned to plots within blocks, and they included the removal of the overstory, the removal of the understory, and the combination of both.

Treatment of the overstory consisted of two types of canopy removal (shelterwood cuts), which resulted in different spatial distribution of the dominant tree species (red pine) and amount of full sunlight reaching the understory. The shelterwood cut is used to establish a new stand by gradually removing the existing stand so that new seedlings become established under the protection of the older trees. The uniform shelterwood removal consisted of the removal of individually selected red pines, creating uniform spacing and allowing for approximately 40% full sunlight in the plot. The group shelterwood removal consisted of the removal of all the red and white pine overstory in a circular 24 m diameter opening within the center of the plot, creating a canopy gap that provided close to 100% full sunlight to the understory in the center of the plot. Treatment of the understory consisted of vegetation removal by cutting to ground level.

Each one of the following four treatments was conducted in one plot randomly selected within each block. Treatment A: uniform shelterwood removal; Treatment B: uniform shelterwood removal and understory removal; Treatment C: group shelterwood removal; and Treatment D: group shelterwood removal and understory removal. An additional plot per block was used as a control where no overstory or understory treatment was done in 1994. Homogeneity of variances was not reached even after data transformation; consequently, the Friedman's test for randomized blocks (X^2) was used to test for treatment effects on the various variables describing arthropod groups.

Insect sampling

Arthropods were collected using two sampling techniques in each of the 20 plots during three sampling periods: 23–27 June 1998, 9–13 July 1999 and 6–10 July 2000. Pitfall trapping was used to target insects moving on the litter layer. Pitfall traps consisted of plastic containers, 9 cm depth, 12 cm diameter, 1/3 filled with water (and a few drops of detergent to prevent insects from escaping the trap) and inserted flush with the ground. A grid of 2×3 pitfall traps, 12 m apart, was set centered in each plot. Traps operated for four consecutive days. Captured arthropods were placed into labelled plastic bags and preserved in a solution of 50% alcohol in water for later identification. Sweepnet sampling was conducted to target arthropods associated to low vegetation. Four sweepnet samples were taken in each plot by establishing four parallel transects and making 12 sweeps along each transect. Collected arthropods were placed in plastic bags as described above.

Insect assemblages

All captured insects were sorted, counted and identified to Order, and those collected in sweepnet samples in 1999 were identified to family following Borror et al. (1989). Carabid beetles collected in pitfall traps in 1998 and 1999 were identified to species and the body length of each beetle was measured.

To examine food availability for various vertebrates, insects were grouped by body softness and body size, as these features represent constraints

Table 1. Vegetation variables in experimental plots established in a mature conifer plantation where silvicultural treatments of the over- and understory were conducted to encourage natural regeneration of the deciduous forest. Control: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal

	Treatments				
	Control	A	B	C	D
Vegetation cover (%)					
Herbs	16 ± 3	23 ± 7	31 ± 4	22 ± 6	28 ± 8
Shrubs	34 ± 13	48 ± 2	48 ± 3	49 ± 3	58 ± 14
Saplings	70 ± 10	54 ± 6	53 ± 10	68 ± 8	50 ± 13
Canopy*	68 ± 4	51 ± 6	53 ± 4	25 ± 2	25 ± 4
Vegetation height (cm)					
Herbs	12.5 ± 1.0	14.0 ± 1.2	13.8 ± 0.6	12.5 ± 2.1	9.5 ± 1.0
Shrubs	73.0 ± 8.4	71.8 ± 3.4	70.8 ± 2.2	86.5 ± 5.3	92.3 ± 12.8
Saplings*	497.8 ± 58.3	418.3 ± 61.6	297.3 ± 47.9	419.3 ± 22.4	307.5 ± 37.6
Duff depth (mm)	23.0 ± 3.3	25.5 ± 1.5	19.8 ± 3.7	21.5 ± 2.6	21.8 ± 2.4
Duff composition (%)					
Pine needles	62 ± 7	56 ± 6	63 ± 10	37 ± 5	61 ± 9
Leaves	37 ± 7	43 ± 5	32 ± 12	52 ± 9	33 ± 11
Moss and debris	1 ± 1	1 ± 1	5 ± 1	3 ± 2	6 ± 3

*Significant treatment effect, Friedman's test, $P < 0.05$.

for predators. Some insectivorous vertebrates, such as amphibians, discriminate food by type (Bellocq et al. 2000) or size (Tolf 1985) whereas shrews select arthropod prey based on body rigidity (Bellocq and Smith 1994). Thus, insects collected in 1998 and 1999 were classified based on: (1) body length – small size (<3 mm) and large size (>3 mm); and (2) body softness – soft body (such as immature larvae, Arachnida and Diptera) and hard body (such as adult wasps, bees and ants (Hymenoptera), beetles (Coleoptera) and hard-bodied mites (Acari)). The abundance of other ecologically critical groups of arthropods were also compared among treatments, and included parasitoid wasps (Hymenoptera), herbivores (moth (Lepidoptera) and sawfly (Hymenoptera: Tenthredinidae) larvae) and aphids and leafhoppers (Homoptera)), predators (spiders (Arachnida)), and decomposers (specifically Collembola).

Vegetation sampling

Within each plot, vegetation measures were taken at six points (where pitfall traps were set) during 21–23 July 1998. Percentage coverage of herbaceous plants was visually estimated in 1×1 m^2 quadrats, and 5×5 m^2 quadrats were used to estimate percentage cover of shrubs, saplings, and canopy. The same observer made all the estimations of plant cover. Height of the herbaceous plants, shrubs, and saplings was measured using measuring tape. Depth of the duff was measured to the near centimeter, and the percentage of the ground covered by pine needles and leaves of deciduous trees was visually estimated in a 1×1 m^2 quadrat.

Results

Vegetation analysis

Vegetation analysis showed significant differences in canopy cover among treatments ($X^2 = 13.4$, $P < 0.01$) where percentage canopy cover was the highest in control plots, intermediate in plots with uniform shelterwood removal (Treatments A and B) and the lowest in plots with group shelterwood removal (Treatments C and D) (Table 1). Herbaceous cover was the lowest in the control plots, intermediate in plots with no understory removal (Treatments A and C) and highest in plots where understory was removed (Treatments B and D); however, differences were not significant ($X^2 = 4.60$, $P > 0.05$). Saplings were taller in the control plots than in plots where understory was removed (Treatments B and D) ($X^2 = 11.4$,

Table 2. Mean number of arthropods ($\pm$SE, $n = 4$) caught per 12 sweeps and per pitfall trap/4 days over three sampling periods in plots where different combinations of over- and understory removal were used to promote natural regeneration of the deciduous forest under planted conifers in southern Ontario. Control: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal

	Treatments				
Taxa	Control	A	B	C	D
Sweepnet samples					
Araneae	8.1 ± 1.1	9.8 ± 0.9	8.6 ± 1.1	9.4 ± 1.0	9.3 ± 0.8
Opilionida	1.1 ± 0.3	1.1 ± 0.3	1.1 ± 0.3	1.4 ± 0.3	0.9 ± 0.3
Acarina	18.4 ± 4.7	15.5 ± 5.0	14.9 ± 6.9	8.0 ± 2.7	6.7 ± 1.9
Collembola	24.4 ± 12.2	16.2 ± 2.7	20.5 ± 4.1	15.6 ± 4.0	17.5 ± 3.0
Psocoptera	4.6 ± 1.1	3.5 ± 0.6	3.6 ± 0.6	4.4 ± 0.9	2.3 ± 1.1
Homoptera	4.0 ± 1.2	6.6 ± 1.5	5.6 ± 1.5	8.5 ± 3.5	17.2 ± 5.5
Heteroptera*	1.7 ± 0.8	3.5 ± 0.5	3.7 ± 2.1	7.6 ± 5.0	10.3 ± 4.6
Thysanoptera	0.5 ± 0.2	0.6 ± 0.2	0.3 ± 0.04	0.4 ± 0.1	0.5 ± 0.2
Coleoptera*	2.0 ± 0.3	2.9 ± 0.2	2.8 ± 0.4	3.0 ± 0.4	4.5 ± 0.6
Diptera	18.5 ± 3.9	24.9 ± 5.5	19.3 ± 4.4	23.3 ± 4.1	24.2 ± 4.7
Lepidoptera	2.0 ± 0.3	2.9 ± 0.2	2.8 ± 0.4	3.0 ± 0.4	4.5 ± 0.6
Hymenoptera	8.9 ± 1.5	12.6 ± 3.2	11.7 ± 1.6	12.1 ± 1.1	12.6 ± 2.4
Others[a]	0.5 ± 0.2	0.6 ± 0.2	0.5 ± 0.1	0.7 ± 0.2	0.6 ± 0.1
Total	95.0 ± 23.0	99.9 ± 16.0	93.6 ± 14.1	94.6 ± 18.0	107.9 ± 19.3
Pitfall samples					
Araneae	2.2 ± 0.3	2.6 ± 0.4	2.9 ± 0.6	4.1 ± 1.8	2.4 ± 0.2
Opilionida	0.3 ± 0.1	0.1 ± 0.02	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.03
Acarina	19.5 ± 8.2	21.6 ± 10.1	12.2 ± 2.5	14.8 ± 4.5	10.1 ± 1.6
Diplopoda	2.6 ± 0.4	1.9 ± 0.3	2.3 ± 0.7	2.8 ± 0.8	2.4 ± 0.3
Collembola	57.2 ± 12.6	50.1 ± 9.7	41.5 ± 7.3	59.7 ± 13.2	39.2 ± 6.4
Orthoptera	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.4 ± 0.1
Psocoptera	0.5 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.04	0.3 ± 0.1
Homoptera	0.8 ± 0.2	1.6 ± 0.3	1.5 ± 0.3	1.3 ± 0.3	2.3 ± 0.9
Heteroptera	0.2 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.8 ± 0.6	0.4 ± 0.1
Thysanoptera	0.2 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1
Coleoptera	3.5 ± 0.9	4.5 ± 0.7	4.4 ± 0.7	5.2 ± 0.7	4.5 ± 0.3
Diptera	21.5 ± 1.0	27.9 ± 1.7	25.4 ± 0.9	26.4 ± 3.2	27.5 ± 3.7
Lepidoptera	0.6 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1
Hymenoptera	5.0 ± 1.1	7.5 ± 1.2	7.0 ± 1.1	7.2 ± 1.3	8.4 ± 1.5
Others[a]	0.2 ± 0.1	0.5 ± 0.1	1.2 ± 0.1	0.6 ± 0.3	0.3 ± 0.1
Total	111.8 ± 20.5	120.1 ± 15.5	99.7 ± 8.5	124.7 ± 14.6	93.2 ± 3.3

*Significant treatment effect, Friedman's test, $P < 0.05$.

[a] Includes Phasmatodea, Mecoptera, Neuroptera, Chilopoda and Isopoda.

$P < 0.05$). Other vegetation variables, as well as duff depth and composition, showed no significant differences among treatments.

General abundance of arthropods

No significant treatment effect was found in the total abundance of arthropods (Table 2). When data were analyzed by year, only dipterans caught in pitfall traps during 1999 were found to be significantly more abundant in Treatment A plots than in the other treated or control plots ($X^2 = 10.85$, $P < 0.05$). When years were combined, results showed no significant difference in the total abundance of arthropods in sweepnet ($X^2 = 0.80$, $P > 0.05$) or pitfall ($X^2 = 3.80$, $P > 0.05$) samples. There was, however, a treatment effect on the abundance of Coleoptera ($X^2 = 10.00$, $P < 0.05$) and Heteroptera ($X^2 = 11.40$, $P < 0.05$) in sweepnet samples, where the lowest abundance was recorded in control plots and the highest in plots treated with group shelterwood removal (Treatments C and D), especially in Treatment D plots where the understory was also removed (Table 2). The abundance of

Homoptera was also the lowest in the control plots and highest in Treatment D plots, but the difference was not statistically significant in sweepnet ($X^2 = 8.45$, $P > 0.05$) or pitfall ($X^2 = 7.75$, $P > 0.05$) samples.

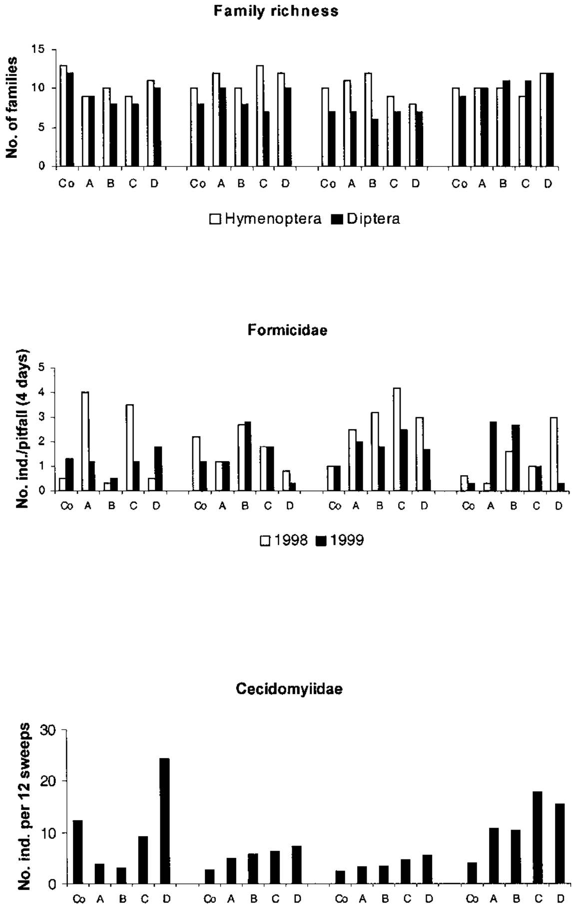
Family richness and abundance

Hymenoptera and Diptera were represented by 23 families each in sweepnet samples during 1999, and there were no significant differences in the number of Hymenoptera ($X^2 = 0.9$, $P > 0.5$) and Diptera ($X^2 = 3.95$, $P > 0.5$) families among treatments (Figure 1). Platygastridae was the most common hymenopteran family collected whereas Cecidomyiidae and Sciaridae were the most abundant dipteran families collected. The abundance of ants (Formicidae) was low, ranging from 0.3 to 4.2 individuals per pitfall trap/4 days in 1998 and 0.3–2.8 in 1999; no significant differences were observed among treatments (1998, $X^2 = 2.35$, $P > 0.5$; 1999, $X^2 = 2.65$, $P > 0.5$) (Figure 1). Of the most common families, Cecidomyiidae had the lowest abundance in the control plots for all blocks except one, and was less abundant in plots treated with uniform shelterwood removal than in those subjected to group shelterwood removal ($X^2 = 10.8$, $P < 0.05$) (Figure 1). The abundance of other dipteran or hymenopteran families did not differ statistically among the treatments.

Richness and abundance of carabid beetles

A total of 21 species of carabid beetles, representing 14 genera, were caught in pitfall traps in the study site (Table 3). There was no significant effect of the treatments on species richness ($X^2 = 1.50$, $P > 0.5$) and abundance ($X^2 = 4.15$, $P > 0.1$) of carabid beetles. Control plots supported the greatest proportion of large-sized beetles followed by plots with uniform shelterwood removal (Treatments A and B) and plots with group shelterwood removal (Treatments C and D) (Figure 2). The opposite pattern was found for small-sized beetles.

Prey-type groups


Family richness

Formicidae

Cecidomyiidae

Figure 1. The number of Hymenoptera and Diptera families caught in sweepnet samples in 1999, and the abundance of Formicidae (Hymenoptera) and Cecidomyiidae (Diptera) in four blocks and five treatments conducted to encourage natural regeneration under planted conifers in southern Ontario, Canada. Co: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal.

There were fewer soft-bodied arthropods in the control than in the treated plots during 1999. However, Friedman's test revealed no significant differences in the abundance of soft-bodied (Sweepnet samples: $X^2 = 5.80$, $P > 0.05$; Pitfall samples: $X^2 = 1.35$, $P > 0.05$) and hard-bodied (Sweepnet samples: $X^2 = 5.0$, $P > 0.05$; Pitfall samples: $X^2 = 1.40$, $P > 0.05$) arthropods among treatments for all years combined (Figure 3). There was a treatment effect on the number of small-sized arthropods collected in sweepnet samples in 1999 ($X^2 = 11.50$, $P < 0.05$), where plots subjected to understory and group overstory removal

Table 3. Species of carabid beetles and the total number of individuals caught in experimental plots in southern Ontario during July 1998 and 1999. Control: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal

	Treatments				
Species of carabid beetles	Control	A	B	C	D
Myas cyanescens	5	6	8	3	3
Pterostichus pensylvanicus	3	9	4	2	3
Pterostichus corocinus	5	5	4	2	1
Carabus limbatus	13	5	0	0	2
Synuchus impunctatus	0	6	4	0	4
Carabus nemoralis	4	1	2	1	0
Agonum retractum	0	1	4	0	4
Pseudamara arenaria	0	1	1	1	4
Sphaeroderus canadensis	1	0	2	2	1
Chlaenius emarginatus	0	0	1	0	3
Sphaeroderus lecontei	1	1	1	0	0
Microlestes linearsis	0	0	0	1	1
Pterostichus melanarius	1	0	0	1	0
Amara quenseli	0	0	0	0	1
Bembidion mimus	0	0	0	1	0
Cymindis cribricollis	0	0	0	1	0
Harpalus pleuriticus	0	0	0	0	1
Harpalus fallax	0	0	0	1	0
Notophilus aeneus	0	0	1	0	0
Pterostichus axodus	0	0	0	1	0
Pterostichus mutus	0	1	0	0	0

(Treatment D) supported more small-sized arthropods than plots subjected to other treatments. When the two years were combined, however, there was no treatment effect on the abundance of arthropods <3 mm in length (Sweepnet samples: $X^2 = 3.25$, $P > 0.05$; Pitfall samples: $X^2 = 2.60$, $P > 0.05$) and >3 mm in length (Sweepnet samples: $X^2 = 5.85$, $P > 0.05$; Pitfall samples: $X^2 = 5.05$, $P > 0.05$) (Figure 3).

Trophic groups

There was a significant treatment effect on the abundance of herbivores where higher numbers were caught in Treatment D plots and lower numbers in the control plots during 1998 ($X^2 = 11.20$, $P < 0.01$) (Figure 4). In 1999, much higher numbers of herbivores were caught by the sweepnets in Treatment D plots than in the other plots for all blocks except one; differences were not significant

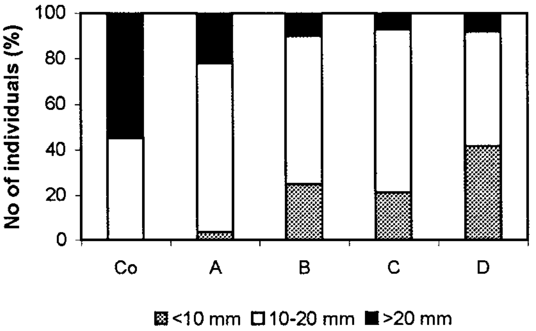


Figure 2. Relative frequency of carabid beetles grouped by body length in plots where silvicultural treatments were conducted to encourage natural regeneration. Co: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal.

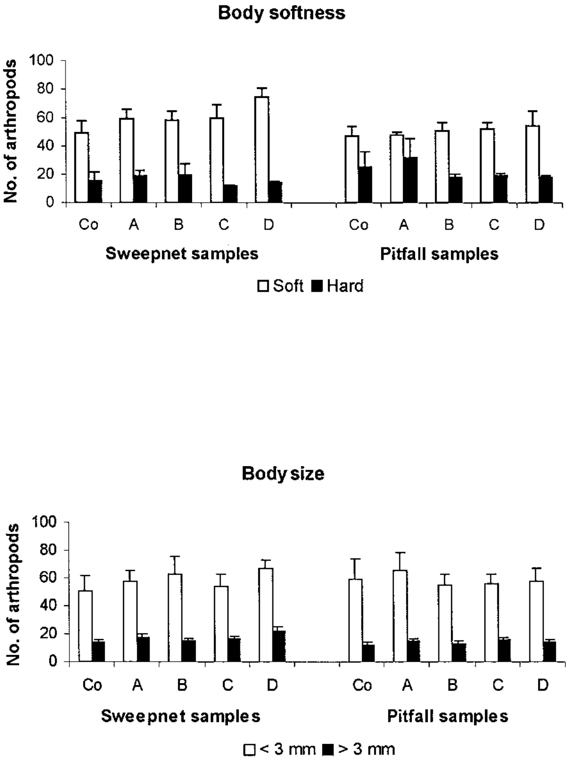


Figure 3. Number of arthopods, grouped by body softness and body size (±SE, $n = 4$), caught per 12 sweeps and per pitfall trap/4 days (1998 and 1999 combined) in plots where different treatments were used to encourage natural regeneration of the deciduous forest under planted conifers in southern Ontario, Canada. Co: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal.

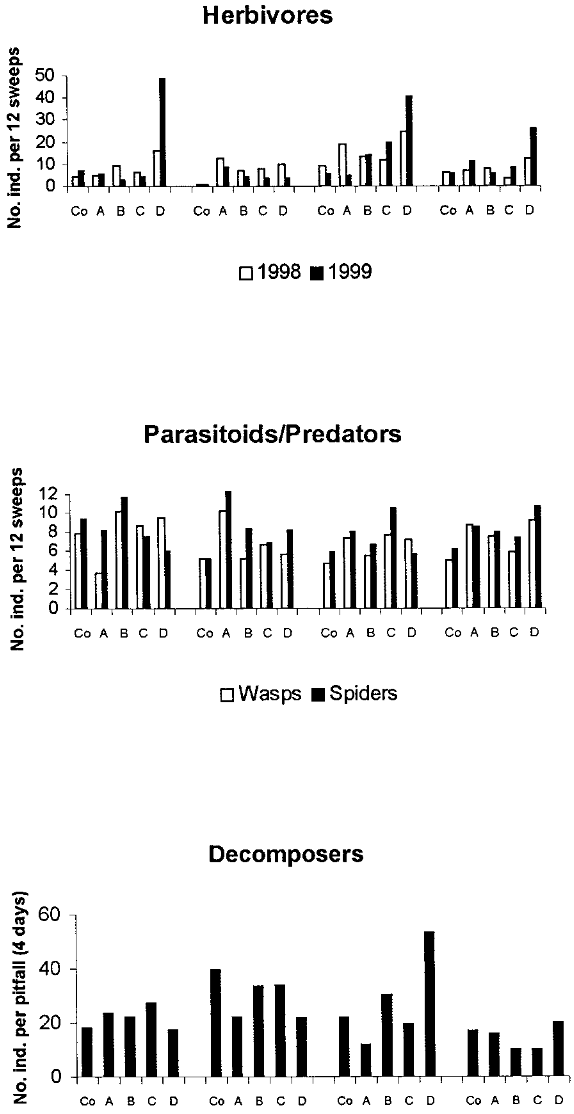


Figure 4. The abundance of herbivores, parasitoid wasps, predators (spiders) and decomposers (Collembola) in four blocks and five treatments conducted to encourage natural regeneration of the deciduous forest under planted conifer in Canada. Co: no treatment; Treatment A: uniform shelterwood removal; B: uniform shelterwood removal and understory removal; C: group shelterwood removal; D: group shelterwood removal and understory removal.

in that year ($X^2 = 2.10$, $P > 0.5$). Results revealed no treatment effect on the abundance of parasitoid wasps (1998, $X^2 = 4.55$, $P > 0.1$; 1999, $X^2 = 4.15$, $P > 0.1$), decomposers (Collembola) (1998, $X^2 = 1.60$, $P > 0.5$; 1999, $X^2 = 6.20$, $P > 0.1$) and spider predators (1998, $X^2 = 2.30$, $P > 0.5$; 1999, $X^2 = 1.80$, $P > 0.5$) (Figure 4).

Discussion

The process of conversion from red pine plantations to deciduous forests had different effects on the various insect taxa of the understory shortly after silvicultural treatment. Our regimes reduced canopy cover, especially in those plots treated with group shelterwood removal, and increased herbaceous cover and reduced sapling height, primarily in plots where the understory was removed. The abundances of Homoptera, Heteroptera and Coleoptera were all affected by the treatments and were highest in plots with group overstory and understory removal, and lower in the control conifer plantations than in any of the treated plantations undergoing conversion. In contrast to our conifer plantations, abundances of Coleoptera and Heteroptera (unlike Homoptera) were lower in small-sized patches or gaps (such as those created in our study by the group shelterwood removal) than in a comparative deciduous forest in the Southern Appalachian Mountains (Shure and Phillips 1991). In tropical forests, the response of arthropods to overstory and understory removal also varies depending on the insect taxa under study. Watt et al. (1997) found the abundance of leaf-litter ants to be higher in sites where there had been partial mechanical clearance (mechanical removal of most of the understory and 50% of the canopy) or partial manual clearance (manual removal of some understory) than in uncleared forest plots. In contrast, they reported fewer species and lower numbers of butterflies in partially cleared plots than in natural forest plots. We found no difference in the total abundance of arthropods among our different silvicultural treatments, even though in our previous work from the boreal forest, we observed general arthropod abundance to decline significantly following an extreme reduction in understory cover (Bellocq et al. 2001).

Ground beetles have many characteristics that make them good indicators of forest health (Refseth 1980). Previous studies have shown that major changes in the community composition and diversity of ground beetles may occur following forestry practices such as logging (Niemelä et al.

1993) and site preparation (Beaudry et al. 1997). We found no significant effect of the silvicultural treatments on species richness and abundance of carabid beetles. It seems that most changes in the ground beetle community occur when the disturbance produced by silvicultural practices is more intense than that produced in our experiment; e.g. those that affect the duff layer. Litter heterogeneity (e.g. aspen patches in pine needle litter) seems to favour diversity of carabid beetles (Niemelä et al. 1992), and in the long run, may help improve diversity in the process of stand conversion.

The silvicultural treatments for stand conversion that we examined affected herbivore abundance. Herbivores were most abundant in plots treated with understory and group overstory removal where herbaceous cover was high and canopy cover was low compared to the other treatments. Similarly, Shure and Phillips (1991) found the biomass of sap feeders (such as Homoptera) and strip feeders (such as most lepidopteran and hymenopteran larvae) to be higher in small forest openings than in a control deciduous forest. In contrast, they reported similar predator (ground spiders and carabid beetles) biomass and reduced decomposer biomass on the forest floor in forests with small openings versus control deciduous forest. It may be that microhabitat heterogeneity produced by different litter leaves will promote predatory arthropods on the forest floor (Niemelä 1997), however, we saw no such effect on the abundance of predators (spiders), parasitoids (wasps) or decomposers (Collembola) in our study.

Ants are a major food resource for amphibian species coexisting in Canadian forests, such as the American toad (*Bufo americanus*) and the Redback salamander (*Plethodon cinereus*) (Bellocq et al. 2000). Acari and Collembola primarily comprised the diet of Redback salamanders in mixed deciduous forests of Tennessee (Maglia 1996). We found low abundance of ants in the leaf litter and no effect of the treatments on the abundance of ants, Collembola or hard-bodied arthropods. In general, ranids have high dietary diversity, and have been classified as opportunistic feeders in temperate regions (Stewart and Sandison 1972; McAlpine and Dilworth 1989) including Ontario (Bellocq et al. 2000). The diet of the Wood frog (*Rana sylvatica*) includes wasps, spiders, flies and beetles (Moore and Strickland 1955; Bellocq et al. 2000), and we found no differences in the abundance of any of these arthropods among our treatments on the ground. Salamander species discriminate food by size (Tolf 1985), and different age classes within a species will feed on different prey sizes (Maglia 1996). We found no differences in prey size among treatments, except for sweepnet samples in 1999. Small-sized carabid beetles were more abundant in treated than in control plots and thus, would provide wider food-size options for wildlife under these silvicultural conditions.

Treatments to encourage natural regeneration seem to favor soft-bodied arthropods, which in turn, may benefit small mammals. Shrews are voracious insectivores living on the forest floor. Masked shrews (*Sorex cinereus*) prefer spiders and lepidopteran larvae as food in Ontario, shifting to alternative prey when the abundance of larvae decreases (Bellocq et al. 1992, 1994). Cafeteria trials showed that both Masked shrews (*S. cinereus*) and Deer mice (*Peromyscus maniculatus*) preferred soft-bodied arthropods such as larvae, spiders, moths and flies (Bellocq and Smith 1994). We found less soft-bodied arthropods in control than in treated plots suggesting that these sites are also less favourable for shrews, mice and possibly other vertebrates on which they depend.

Finally, the removal of the overstory and understory vegetation affected some insect groups living in the understory unlike those on the litter layer. The group overstory removal created small forest openings and these seemed to promote some insect groups such as Coleoptera, Heteroptera and herbivores. Although encouraging litter heterogeneity may help to increase diversity and abundance of predatory arthropods on the forest floor, the silvicultural treatments that we examined to promote natural regeneration did not seem to affect this layer and thus, produced little difference in food availability to insectivore vertebrates on the ground.

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