THE IMPACT OF FOREST HARVESTING ON FOREST FLOOR COLEOPTERA OF BALSAM FIR FORESTS OF WESTERN NEWFOUNDLAND

MEGAN ELAINE McCARTHY

THE IMPACT OF FOREST HARVESTING ON FOREST FLOOR COLEOPTERA OF BALSAM FIR FORESTS OF WESTERN NEWFOUNDLAND

By

Megan Elaine McCarthy

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ABSTRACT

The beetle fauna of old growth and previously harvested balsam fir forests of western Newfoundland was investigated from 1992 to 1994. Pitfall traps were placed in replicate sites of 40 year old, 60 year old and old growth forest stands of dry and moist fir forests. Over 20, 000 beetles comprising 122 species were collected. Principle components analysis separated old growth sites from previously cut sites and dry forest sites from moist sites. Out of 122 species collected, 70 species were found in abundances of 5 or more individuals in total over the entire sampling period. Six of these species were found only in old growth forest stands, 6 were significantly more abundant in those stands, while 10 species were significantly more abundant in the previously cut stands. Four species were significantly more abundant in the 40 year old stands, while 2 species were significantly more abundant in the old growth and 60 year old stands, indicating possible recovery to old growth abundances 60 years after forest harvesting for some species.

The old growth stands contained more and larger fallen logs, more mosses and *Lycopodium*, and a more open canopy. The difference in beetle composition between the old growth and previously cut sites may be a result of differences in the amount of suitable microhabitat, such as fallen logs and the low dispersal ability of many old growth forest species. The results of the study would suggest that forest harvesting rotations of 60 years may cause the extinction of some beetle species which are specialists in old growth forests.

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1.0 INTRODUCTION

This study examined the forest floor Coleoptera within the boreal forest of the Island of Newfoundland. Beetles are an important part of the boreal forest ecosystem. They inhabit a wide variety of microhabitats within the boreal forest and may be phytophagous, carnivorous, fungivorous, or various combinations thereof. Some carabids and staphylinids inhabit the leaf litter, feeding on fungus or preying on mites, collembola, snails, or other insects and their larvae (Bell, 1990). Other staphylinids live on dung or rotting mushrooms, while some live under rotten or loose bark on decaying logs (Newton, 1990). Members of the families Leiodidae and Ptiliidae feed on fungus, slime molds and rotting vegetable matter (Downie and Arnett, 1996), while members of the superfamily Curculionoidea are herbivores and attack the inner bark of living trees, or feed on small shrubs and other vegetation (Downie and Arnett, 1996). Beetles also serve as prey for other organisms, such as birds, bats and small insectivores, as well as spiders, ants, centipedes and even other beetles (Crowson, 1981).

Many studies have been done recently on the impact of forest harvesting on the organisms within boreal (Niemelä et al., 1993), temperate (Chandler and Peck, 1992) and wet temperate (Michaels and McQuillan, 1995) forests. It is perhaps obvious to most that clear-cutting has an immediate effect on flora and fauna; species adapted for life in a humid, shady, forested environment would likely be unable to survive the direct sunlight and dry air of an open area. Many forest organisms would be replaced by those suited to open ground and more extreme environmental conditions. It might also be assumed that if secondary succession were allowed to occur, or if saplings were replanted in that area, the flora and fauna would gradually revert back to shade tolerant forest species once again.

This study examined the beetle fauna of two balsam fir (*Abies balsamea*) forest types (*Dryopteris*-Balsam fir and *Equisetum-Rubus*-Balsam fir), to test the hypothesis that beetle species community composition and abundance differs among old growth forest and 40- and 60-year-old post-harvest forests. Balsam fir reaches maturity, in the forestry sense, at an age of 70 to 100 years, depending on the site conditions (Page et al., 1974). They can reach an age of 150 years, but generally lose vigour before 90 years (Preston, 1989), so balsam fir forest referred to as 'old growth' contains many trees that are not much older than trees in the 60-year-old post-harvest forest. The difference is that the old growth forest has never been subject to clear cutting and is representative of the natural life cycle of a balsam fir forest, with trees of all different ages. The 60-year-old forest is an even aged stand of trees that have regrown after an episode of clear cutting in the early 1930s. The same is true of the 40-year-old forest, which was clear-cut in the early 1950s.

Several studies have found lower beetle diversities in 40-year-old forests than in old growth forests (Chandler, 1987; Chandler and Peck, 1992). Studies have also shown that some beetle species and the overall beetle abundance may recover from forest harvesting, but some species are restricted to old growth forest and are replaced in mature, previously cut forests by different species (Väisänen et al., 1993; Neimelä et al., 1988).

2.0 MATERIALS AND METHODS

2.1 Study Sites

Sampling took place in balsam fir (*Abies balsamea*) forest on the west coast of Newfoundland, between 10 and 40 km south of Corner Brook (Figure 1). Three different aged forests were studied. The old growth forest was between Grand Lake and Little Grand Lake, the 40-year-old forest was west of Little Cook's Pond, near Logger's School Road and the 60-year-old forest was about 10 km south of Corner Brook, on either side of the Trans Canada Highway. Within each different aged forest, two replicate sites of *Dryopteris*-Balsam fir forest type (FD) (Figure 2) and two replicate sites of *Equisetum-Rubus*-Balsam fir forest type (FE) (Figure 3) were selected. These two forest types are characterized by their understorey vegetation and soil profile, as defined by Meades and Moores (1989) (Table 1, Figure 4). In total, twelve sites were sampled; two old growth FD sites (FDO-1 and FDO-2), two 40-year-old FD sites (FD40-3 and FD40-4), two 60-year-old FD sites (FD60-5 and FD60-6), two old growth FE sites (FEO-7 and FEO-8), two 40-year-old FE sites (FE40-9 and FE40-10) and two 60-year-old FE sites (FE60-11 and FE60-12). Each pair of sites was referred to as a stand (Table 2).

2.2 Climate

The study sites are located in the Southwestern Newfoundland Ecoregion, within the Boreal Shield Ecozone, as defined by the Ecological Stratification Working Group (1996). This ecoregion is found at the northeastern limit of the Appalachian mountain chain, named the Long Range Mountains. The study sites are along the west side of these

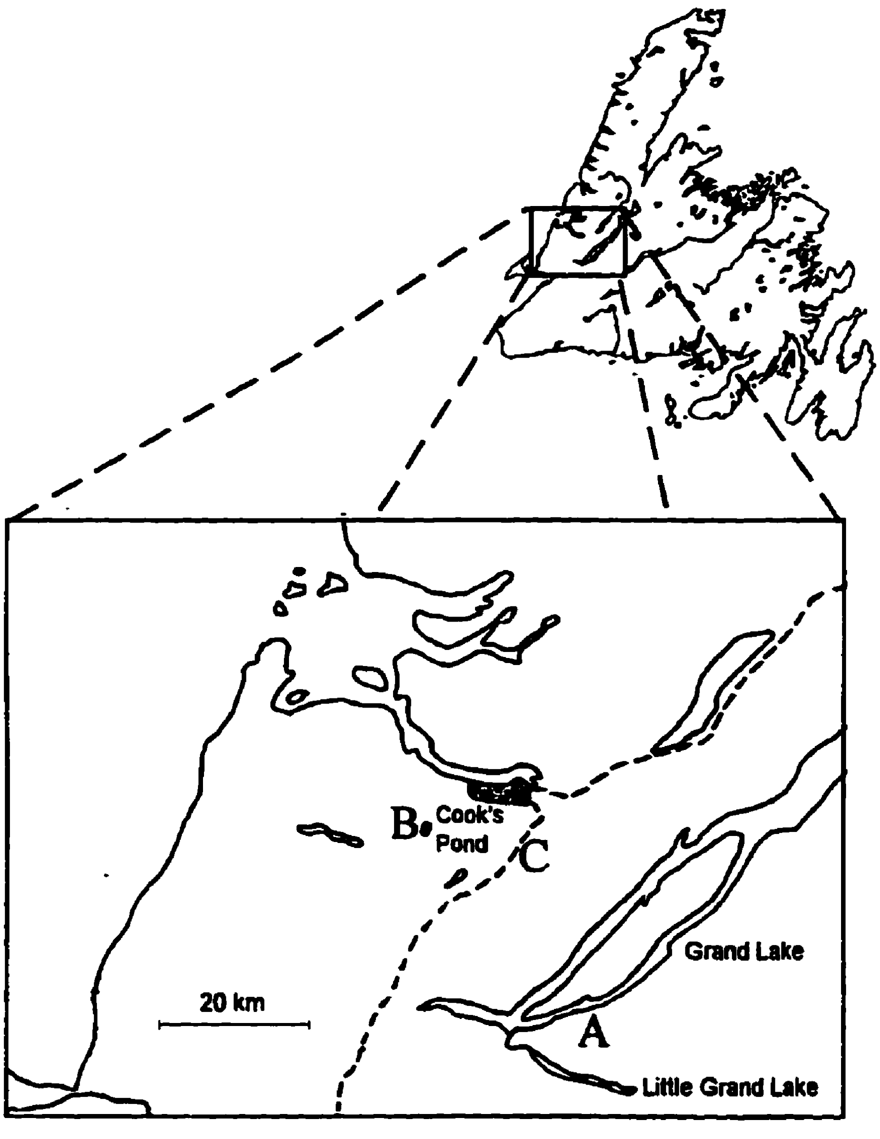


Figure 1. Map of Newfoundland and the west coast near Corner Brook (shaded area) showing the location of the study sites. A = old growth forest, B = 40-year-old forest and C = 60-year-old forest; dashed line = Trans Canada Highway.

Figure 2. Site FDO-2, one of the old growth *Dryopteris*-Balsam fir sites.

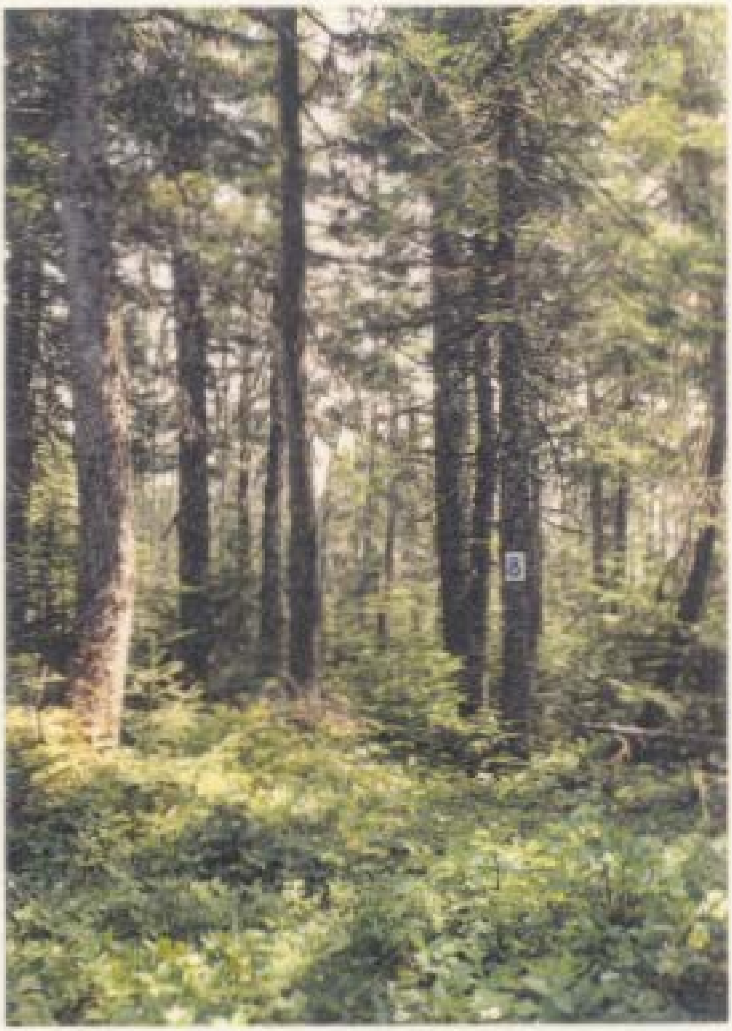


Figure 3. Site FEO-8, one of the old growth *Equisetum-Rubus*-Balsam fir sites.

Table 1. Some characteristics of types *Equisetum-Rubus*-Balsam fir and *Dryopteris*-Balsam fir, as defined by Meades and Moores (1989).

Characteristics	*Equisetum-Rubus*-Balsam fir (FE)	*Dryopteris*-Balsam fir (FD)
Topography	found on lower concave slopes	found on mid to upper slopes
Fertility	medium rich to rich	rich to very rich
Moisture	somewhat wet to wet	somewhat moist
Litter layer	shallow litter and muck surface - organic horizon developed mainly from mosses and sedges; poor drainage conditions, moderately decomposed	deep litter layer organic horizon developed mainly from leaves, needles and twigs
Understorey vegetation	herb rich; major indicator species are *Rubus pubescens, Equisetum sylvaticum, Dryopteris disjuncta*	fern rich; mosses sparse, main indicator species is *Dryopteris spinulosa* at 75-95% cover

Figure 4. The upper picture shows the typical understorey vegetation of a *Dryopteris*-Balsam fir forest type, FDO-2. The lower picture shows the typical understorey vegetation of an *Equisetum-Rubus*- Balsam fir forest type, FEO-8.

Table 2. Brief descriptions and locations of each stand. The terms 'type', 'stand' and 'site' were used to refer to these specific locations or group of locations.

TYPE	*Dryopteris*-Balsam fir			*Equisetum-Rubus*-Balsam fir		
AGE	old growth	~ 40 yrs post cut	~ 60 yrs post cut	old growth	~ 40 yrs post cut	~ 60 yrs post cut
STAND	FDO	FD40	FD60	FEO	FE40	FE60
SITES	1, 2	3, 4	5, 6	7, 8	9, 10	11, 12
LATITUDE (N)	48°39'	48°52'	48°52'	48°39'	48°52'	48°51'
LONGITUDE (W)	57°47'	58°05'	57°56'	57°47'	58°05'	57°56'
ELEVATION	300 - 350	225 - 300	300	200 - 350	250	300

mountains, which provide protection in the spring and early summer from the cold northeasterly winds associated with the Labrador Current, resulting in a longer frost free season than the remainder of the island (Damman, 1983). The soils of this ecoregion are also more fertile than in other parts of Newfoundland, therefore this is the most favourable part of the island for plant growth (Damman, 1983). The mean annual precipitation is moderate near sea level, ranging between 1000 - 1200 mm (Ecological Stratification Working Group, 1996), but increases rapidly with elevation, up to at least 1600 mm (Banfield, 1983). The winters are cold and snowy, with a mean winter temperature of -3.5 °C (Ecological Stratification Working Group, 1996) and continuous and complete snow cover normally from December until at least April (Banfield, 1983). Snow patches may be present in the forests of the lowlands until late May (Damman, 1983). The summers are moderately warm and sunny with a mean temperature of 12 °C, but with maxima up to 30 °C in sheltered valleys (Banfield, 1983). Figure 5 shows monthly precipitation means, mean daily temperatures and snowfall in the west coast region during the study period.

2.3 Vegetation Data

Vegetation data were provided for the FD sites by Dr. Ian Thompson, Forestry Canada, in 1992. These data were collected using a 2 m^2 quadrate within which the percentage of the soil surface covered by each of the principle vegetation types was estimated. Vegetation types included ground lichens, *Sphagnum* mosses, feather mosses, *Lycopodium,* low and tall ferns, grasses, herbaceous plants, low and medium shrubs (up to

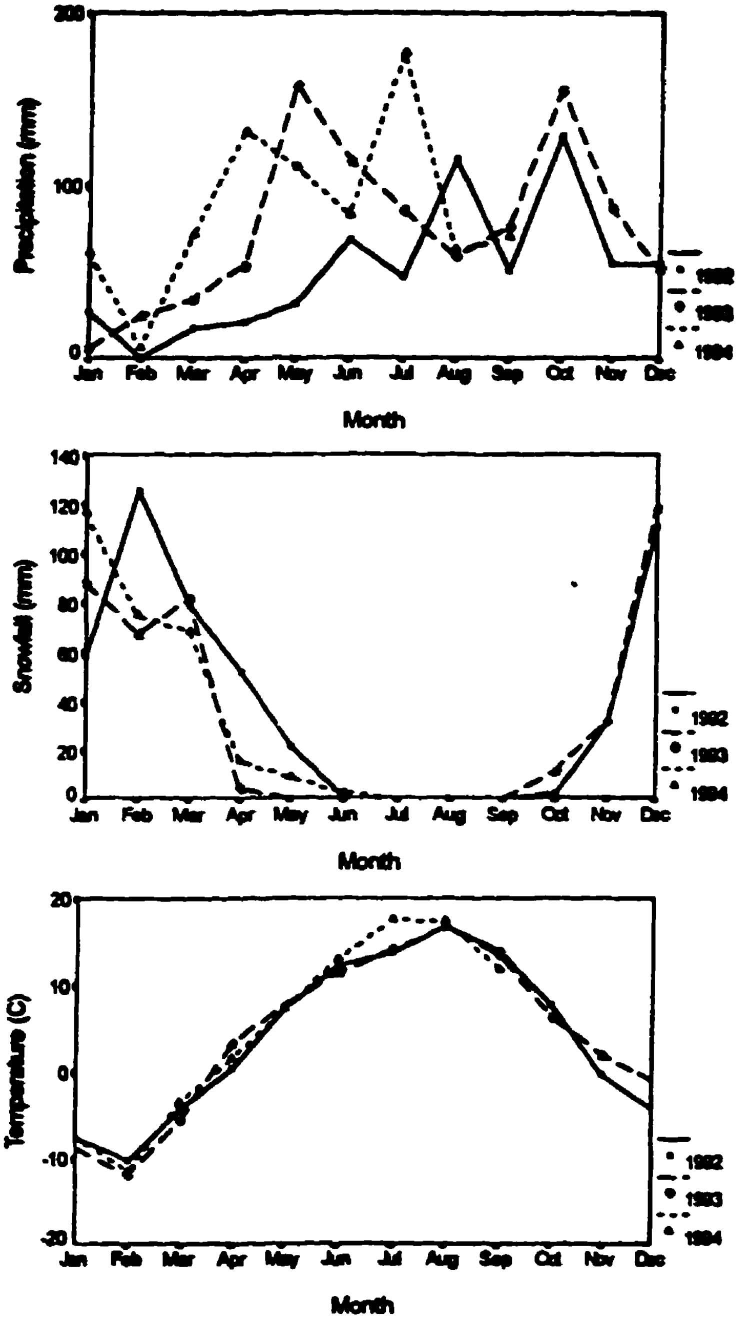


Figure 5. Mean monthly weather conditions at the Corner Brook Atmospheric Environment Service weather station (~ 48⁰ 56.00' N, 57⁰ 54.50' W) for 1992-1994 (Dwyer, 1995).

1 m tall), fern, conifer and deciduous litter, slash (woody debris <5 cm in diameter) and logs (woody debris >5 cm in diameter). Other variables measured were the mean diameter (cm) of the logs on each plot, the percent canopy closure, the density/ m^2 of shrubs (1 to 3 m tall), saplings (taller than 3 m, but < 10 cm diameter at breast height, DBH) and trees (> 10 cm DBH), the percentage of shrubs, saplings and trees that were deciduous, and the density/ m^2 of dead standing trees. Unfortunately, vegetation data was not available for the FE sites.

2.4 Beetle Sampling Method

Beetles were collected using pitfall traps (Figure 6). Each pitfall trap consisted of a plastic flower pot, 12.8 cm in diameter and 13.5 cm deep, placed in the ground so that the rim of the pot was level with the soil surface. Another smaller, plastic pot, 11.5 cm in diameter and 6.8 cm deep with a small wire handle attached to it was placed inside the first and propylene or ethylene glycol was added to a depth of about 4 cm. The small inner pot could then be easily removed without disturbing the trap or the ground around the trap.

Ethylene glycol was used as a preservative in 1992, but in subsequent years it was replaced with propylene glycol. The first year several traps were pulled out and emptied, presumably by bears or foxes which may have drunk the preservative. Ethylene glycol is extremely toxic, so a switch was made in 1993 to propylene glycol, which is non-toxic. Propylene glycol also seemed to preserve the specimens better, especially the slug by-catch, which made sieving and sorting the samples much easier. Each trap had a cover made from a 20.5 x 20.5 cm piece of plywood with an 8 cm nail in each corner which

Figure 6. Pitfall trap, consisting of flower pot and plastic inner pot, used to collect beetles. The traps normally contained preservative, which is not shown in this picture.

supported the cover about 4 - 6 cm above the trap. This kept rain from flooding the trap or diluting the preservative.

Twenty pitfall traps were set out at each of the twelve sites. They were placed about 2 to 3 m apart along a transect through each site, with the first trap in each series being at least 10 to 15 m in from the edge of the forest. Traps were placed in FD sites in the summers of 1992 and 1993, and in the FE sites in 1994. The trapping schedule for each site over the three years of the study is given in Table 3. For example, in site FDO-1 in 1992, 20 traps were put into the ground on June 24 and emptied on three occasions, July 15, August 25 and August 29. However, on August 25 it was noted that one of the traps had been disturbed by an animal, so only 19 traps were functioning between July 15 and August 25.

Another twelve pitfall traps, 4 of which were baited with un-cooked ground beef, were set out in one of the sites, FD60-6, in 1994 from July 28 to August 6. The bait was placed in a small plastic cup tacked to the underside of the wooden covers. Any beetle species strongly associated to carrion were to be excluded from further analysis, since the 60-year-old sites contained more slugs (E. Goudie, pers comm.), which often fouled the pitfall traps, attracting certain beetle species in disproportionate numbers.

2.5 Beetle Identification

The contents from each pitfall trap were sieved and stored in vials of 70% ethanol until they could be examined under a dissecting microscope. Identifications were made by David Larson and Megan McCarthy with the help of available literature and a reference

Table 3. The sampling timetable for each site in 1992, 1993 and 1994.

SITE	YEAR	sampling dates	# of days	# of traps
FDO-1	1992	June 24 - July 15	21	20
		July 15 - August 25	41	19
		August 25 - 29	4	20
	1993	June 8 - July 13	35	12
		July 13 - August 24	42	20
FDO-2	1992	June 24 - July 15	21	19
		July 15 - August 25	41	20
		August 25 - 29	4	20
	1993	June 8 - July 13	35	20
		July 13 - August 24	42	5
FD40-3	1992	June 25 - July 23	28	11
		July 23 - 30	7	20
		July 30 - August 21	22	20
		August 21 - 31	10	19
	1993	June 1 - 14	13	20
		June 14 - July 6	22	19
		July 6 - 19	13	20
		July 19 - August 17	29	20
		August 17 - 27	10	20
FD40-4	1992	June 25 - July 23	28	20
		July 23 - 30	7	20
		July 30 - August 21	22	20
		August 21 - 31	10	15
	1993	June 1 - 14	13	20
		June 14 - July 6	22	20
		July 6 - 19	13	20
		July 19 - August 17	29	20
		August 17 - 27	10	20
FD60-5	1992	June 25 - July 24	29	20
		July 24 - 29	5	20
		July 29 - August 21	23	20
		August 21 - 31	10	20
	1993	June 1 - 14	13	20
		June 14 - July 6	22	20
		July 6 - 19	13	19
		July 19 - August 17	29	19
		August 17 - 27	10	19
FD60-6	1992	June 25 - July 17	22	20
		July 17 - 29	12	20
		July 29 - August 25	27	20

Table 3, contd.

FD60-6 (contd.)		August 25 - 29	4	20
	1993	June 1 - 14	13	20
		June 14 - July 6	22	20
		July 6 - 19	13	20
		July 19 - August 17	29	20
		August 17 - 27	10	20
FEO-7	1994	July 5 - 27	22	20
		July 27 - August 6	10	20
		August 6 - 22	16	20
		August 22 - September 1	10	20
FEO-8	1994	July 5 - 27	22	20
		July 27 - August 6	10	20
		August 6 - 22	16	10
		August 22 - September 1	10	20
FE40-9	1994	July 4 - 10	6	19
		July 10 - August 8	29	18
		August 8 - 22	14	20
		August 22 - September 1	10	20
FE40-10	1994	July 4 - 10	6	20
		July 10 - August 8	29	20
		August 8 - 22	14	20
		August 22 - September 1	10	20
FE60-11	1994	June 28 - July 13	15	20
		July 13 - 28	15	20
		July 28 - August 10	13	20
		August 10 - 23	13	20
		August 23 - September 1	9	20
FE60-12	1994	June 28 - July 13	15	20
		July 13 - 28	15	20
		July 28 - August 10	13	20
		August 10 - 23	13	20
		August 23 - September 1	9	20

collection was sent to the Agriculture Canada Centre for Land and Biological Resources Research, Ottawa (CLBRR) for confirmation of identification. Voucher collections were deposited in the Canadian National Collection of Insects (CLBRR) and in the Department of Biology, Memorial University of Newfoundland insect collection.

2.6 Statistical Analyses

The mean values of the vegetation data from the FD sites was analysed using principle components analysis (SPSS, 1994). This is a method of breaking down a resemblance matrix into a set of perpendicular axes or components, each of which accounts for a certain amount of variance within the data set (Ludwig and Reynolds, 1988). The axes are extracted in descending order of magnitude, so the first few axes represent the largest percentage of the total variation that can be explained (Ludwig and Reynolds, 1988). In this study, the first three axes, referred to as factors, were extracted to determine the amount of variance that was contributed by each vegetation characteristic. The first three factors for each site were then graphed in a 3-D scatterplot.

Comparisons of beetle species richness within each stand were made using RAREFACT (Krebs, 1991). Rarefaction curves estimate the expected number of species in a random sample of individuals taken from a collection (Krebs, 1989). Cluster analysis was conducted using species presence or absence data for each site (SPSS, 1994). The cluster method used was between groups linkage on the squared Euclidean distances of the binary data.

The number of traps and the number of collecting days varied from site to site due to the remoteness of some sites and the occasional destruction of traps by mammals. Therefore, the numbers of beetles of each species were grouped by site, stand, trap number or date of collection, depending on the type of analysis, and standardized as individuals per trap per night. These numbers were then multiplied by a factor of 100, 200 or 1000, which was a simple approximation of a typical number of trap-nights, depending on how the data was originally grouped.

Principle components analysis (SPSS, 1994) was carried out on the data set grouped by site as individuals per trap per night x 1000. This determined which sites were most alike according to how much variance each beetle species contributed to the data set. The first three factors calculated from this data for each site were graphed in a 3-D scatterplot.

The more numerous beetle species (those in which 5 or more individuals were collected over the entire sampling period and over all sites) were also examined to compare their mean abundances in the old growth stands versus the previously cut stands. The data set was grouped by stand and trap number as individuals per trap per night x 100, and each stand was compared to the other stands within a given forest type using the Mann-Whitney U-test (SPSS, 1994). This is a non-parametric method of comparing two data sets, by pooling the data, giving each variate a rank, then comparing the total ranks of the two data sets (Sokal and Rohlf, 1981). Non-parametric methods are suitable for this data set because no assumptions are made about the distribution of the populations, and since the variates are ranked, the null hypothesis is not concerned with specific parameters, but only with the relative position of the variates (Sokal and Rohlf, 1981).

The Mann-Whitney U-test was also used to compare the seasonal abundances of the more numerous beetle species. The data set was split into early and late summer groups and standardized as individuals per trap per night x 200. Since the collecting dates were variable, sites or stands that were sampled at different times were tested separately. The dates used to separate the early summer samples from the late summer samples were July 15 for FDO in 1992, July 13 for FDO in 1993, July 23 for FD40 in 1992, July 24 for FD60-5 in 1992, July 17 for FD60-6 in 1992, July 19 for both FD40 and FD60 combined in 1993, July 27 for FEO, July 10 for FE40 and July 13 for FE60. The sites were also pooled to compare early and late summer abundances, but only species that were active either very early or very late in the summer showed this significantly because of overlapping dates when all sites are pooled.

Since species of the sub-family Aleocharine (Staphylinidae) were difficult to identify, the contents from the twenty traps within each site and at each sampling date were combined so more specimens could be compared with one another. These species were also tested using the Mann-Whitney U test to compare the stands and seasonal abundance, but the data set was grouped according to stand and sampling date (not trap number) and standardized as individuals per trap per night x 1000.

3.0 RESULTS

3.1 Vegetation characteristics

Table 4 lists the mean values of the vegetation characteristics of each FD site. A principle components analysis of this data separated the FDO stand from the cut stands along factor 1 with a high negative loading (Figure 7). This factor accounted for 35.4 percent of the variation in the data. Factors 2 and 3 showed variation between sites within the same stand. These two factors account for 26.2 percent and 16.2 percent of the variation in the data, respectively. Table 5 lists the loading scores (eigenvectors) of the vegetation characteristics on the first three factors calculated from the principle components analysis. The *Sphagnum* mosses, feather mosses and *Lycopodium* all have a high negative loading on factor one, along with the percent cover of fallen logs and the log diameter, indicating higher values in the FDO sites. The lichens, tall ferns and deciduous leaf litter, as well as the percent canopy closure, the shrub and sapling densities and the percentage of shrubs that were deciduous all have a high positive loading on factor one, indicating higher values in the FD40 and FD60 sites.

3.2 Mean abundances of beetle species

The number of individuals per trap per night x 1000 of each beetle species in each stand are listed in Table 6. Species representing 28 families were collected; the three most abundant families were the Staphylinidae, with 79.5 % of the total number of individuals collected, the Carabidae, with 9.0 %, and the Ptiliidae, with 7.7%.

Table 4. Mean values for vegetation characteristics of the FD sites. Data courtesy Ian Thompson, Canadian Forest Service.

Vegetation Characteristics	FDO-1	FDO-2	FD40-3	FD40-4	FD60-5	FD60-6
ground lichens (% cover)	.02	0	.04	.12	.10	.02
Sphagnum mosses (% cover)	5.16	5.72	.20	.44	.94	.20
feather mosses (% cover)	48.54	50.84	26.64	30.42	19.04	38.96
Lycopodium (% cover)	.06	0	0	0	0	0
low ferns (% cover)	26.32	16.72	14.12	23.10	24.46	31.71
tall ferns (% cover)	4.46	8.32	9.76	12.92	16.54	5.24
grasses (% cover)	.10	0	.02	.06	0	0
herbaceous plants (% cover)	24.22	16.02	27.34	19.74	22.74	14.04
low shrubs (% cover)	6.14	3.96	6.24	1.78	4.94	9.18
medium shrubs (% cover)	.90	.34	3.38	.34	1.46	4.78
fern litter (% cover)	8.42	1.10	.30	0	.04	7.39
coniferous litter (% cover)	13.04	8.90	17.18	17.08	6.26	26.92
deciduous litter (% cover)	8.80	16.56	15.68	19.26	62.70	13.20
slash (woody debris < 5cm diameter) (% cover)	10.70	6.54	6.78	7.02	8.16	11.02
logs (woody debris > 5cm diameter) (% cover)	5.10	9.68	4.66	4.82	2.24	2.67
log diameter (cm)	7.52	13.18	4.72	7.32	3.46	6.00
% canopy closure	63.12	73.90	69.54	79.12	78.62	75.53
shrub density	.13	.06	.19	.12	.49	.24
% deciduous shrubs	.22	.04	.56	.01	.68	.55
sapling density	.04	.04	.09	.14	.21	.14
% deciduous saplings	<.01	.01	.17	.11	.07	.35
tree density	.12	.09	.22	.31	.12	.17
% deciduous trees	.10	<.01	.07	.05	.03	.01
dead standing tree density	.09	.15	.20	.13	.15	.12

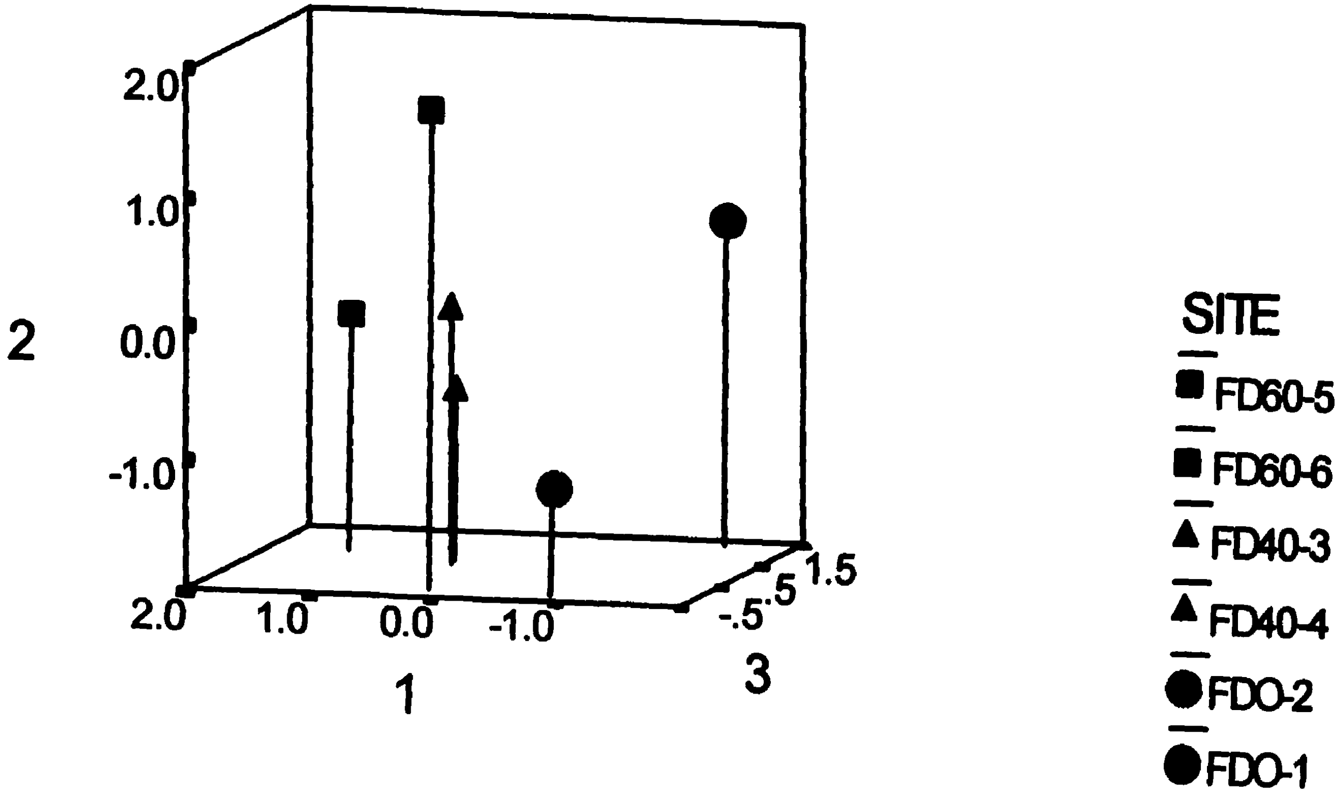


Figure 7. A scatterplot of the first three principle components factors (1, 2 and 3) calculated from the vegetation data from the FD sites.

Table 5. The first three principle components factors calculated from the vegetation data from the FD sites.

Vegetation Character	Factor 1	Factor 2	Factor 3
ground lichens	**.71082**	-.27599	.40240
Sphagnum mosses	**-.83186**	-.33079	.03151
feather mosses	**-.94526**	.04298	-.27877
Lycopodium	**-.69229**	.24110	**.66664**
low ferns	.02844	**.74507**	.09120
tall ferns	**.80322**	-.53830	.18950
grasses	-.53775	.02652	**.72463**
hebaceous plants	.12404	-.17663	**.77525**
low shrubs	-.06130	**.88477**	-.17441
medium shrubs	.29535	**.79823**	-.32160
fern litter	-.58382	**.77992**	.11431
conifer litter	-.00645	**.72886**	-.34845
deciduous litter	**.74929**	-.22431	.23051
slash	-.26164	**.88347**	.20143
fallen logs	**-.65726**	**-.64256**	-.37999
log diameter	**-.71193**	-.46030	-.49374
canopy closure	**.72966**	-.22904	-.42248
shrub density	**.77906**	.23196	.27160
% deciduous shrubs	**.61997**	.53758	.11322
sapling density	**.91968**	.14656	.08411
% deciduous saplings	.37500	**.73591**	-.45947
tree density	.35639	-.03800	.08574
% deciduous trees	-.32460	.11473	**.84856**
dead standing tree density	.48062	-.42285	-.26899

Table 6. The number of individuals per trap per night x 1000 of adults of beetle species in each forest stand.

SPECIES	FDO	FD40	FD60	FEO	FE40	FE60
CARABIDAE						
Sphaeroderus nitidicollis Chevrolat	0.6	0	0	0.9	1.7	0
Clivina fossor (Linnaeus)	0	0	0.2	0	0	0
Trechus apicalis Motschulsky	5.9	0	5.6	5.6	7.8	8.1
T. crassiscapus Lindroth	0.4	0	2.8	0	1.7	0.8
Bembidion wingatei Bland	61.1	72.4	52.7	0	10.9	7.3
Pterostichus adstrictus Eschscholtz	17.9	0.5	0	1.4	0	0
P. coracinus (Newman)	5.3	2.1	1.5	32.4	12.6	10.4
P. melanarius (Illiger)	0	0	1.2	0	0	0.8
P. punctatissimus (Randall)	3.6	8.8	0.5	5.1	9.6	5.8
Harpalus nigritarsus C.R. Sahlberg	0	0	0	1.4	0	0
Calathus ingratus Dejean	1.1	0	0	0	0	0
C. advena (LeConte)	12.4	0	0	0	0	0
Platynus decentis (Say)	34.5	0	0	0.5	0	0
DYTISCIDAE						
Hydroporus paugus Fall	0	0	0	0.5	0	0
PTILIIDAE						
Ptenidium species #1	0	0	0	13.0	32.7	138.1
Millidium mintissimum (Ljungh)	6.7	1.7	2.0	3.2	0.4	0
Acrotrichus species #1	38.8	89.6	46.6	10.2	17.0	8.1
LEIODIDAE						
Leiodes assimilis (LeConte)	0	0	0	5.1	0	0.4
Agathidium species #1	3.2	0	0	0.5	0	0
LEPTODIRIDAE						
Colon magnicolle Mannerheim	0	0.2	1.8	0.5	0	0.8

Catops basillaris Say	0.4	2.1	22.4	0.9	13.9	33.5
SCYDMAENIDAE						
Stenichnus species #1	2.3	0	0	0.5	0	0
MICROPEPLIDAE						
Micropeplus laticollis Mäklin	0.8	0.2	0	0	0	0
SILPHIDAE						
Nicrophorus defodiens Mannerheim	0.2	0.3	1.2	0	2.2	1.9
N. sayi Castelnau	0	0.3	1.3	0	0	0
STAPHYLINIDAE						
Megarthrus americanus Sachse	0	0.5	2.1	0	1.7	1.5
Proteinus limbatus Mäklin	89.9	233.3	61.1	1.4	60.5	48.5
Eusphalerum pothos (Mannerheim)	0	0.3	0.8	0.5	2.2	0.8
Elonium diffusum (Fauvel)	144.1	496.9	89.7	34.3	134.6	31.9
Omalium rivulare (Paykull)	0.4	0.3	1.3	0	0.4	0
O. species #2	0.2	0	3.5	0	0.4	3.5
O. species #3	0.8	0.3	1.5	0	0	0.4
Brathinus nitidus LeConte	0	0	0	23.6	0.4	0
Acidota subcarinata Erichson	4.0	0.3	0.7	6.5	3.0	5.0
Olophrum consimile (Gyllenhal)	0	0	0	0.9	3.0	2.7
O. rotundicolle (C.R. Sahlberg)	1.7	0.2	0.3	41.7	0.4	0.4
Arpedium cribratum Fauvel	0	47.2	0.3	0.5	0	0
Lesteva pallipes LeConte	0	0	0	31.5	0	0
Siagonium americanum Melsheimer	0.2	0	0	0	0	0
Oxytelus fuscipennis Mannerheim	2.1	0.2	12.2	9.7	2.2	21.2
Pseudopsis subulata Herman	11.4	42.4	44.2	0	18.3	51.2
Tachinus basalis Erichson	1.5	0.5	2.1	0	0.4	1.9
T. elongatus Gyllenhal	11.4	0.2	3.0	0.9	0	1.9
T. frigidus Erichson	146.8	42.1	7.4	5.6	9.1	3.8

T. quebecensis Robert	25.7	29.7	3.3	0	3.0	1.2
T. tachyporoides Horn	0	0.2	0.2	0	4.4	0.8
T. thruppi Hatch	0	5.3	2.5	2.3	0	2.3
Tachyporus nitidulus (Fabricius)	0	0	1.3	0	0	0.8
Sepedophilus testaceus (Fabricius)	0	0.2	0	0	0	0
Lordithon facilis (Casey)	0.6	4.6	0.2	0	0	0.4
L. thoracicus (Fabricius)	0.2	0.3	0	0	0	0
L. fungicola Campbell	41.9	20.6	3.6	5.6	8.7	4.2
Mycetoporus horni Bernhauer and Schubert	0.2	0	0	0	0	0
Ischnosoma fimbriatum Campbell	1.7	2.1	0.3	1.9	2.6	0.4
I. splendidum (Gravenhorst)	9.9	0.2	2.5	6.0	1.7	5.4
Oxypoda species #1	97.5	75.4	15.5	2.3	76.7	49.6
O. species #2	2.7	3.4	1.8	2.8	3.0	2.3
Gyrophaena species #1	0	0.3	0.2	0	0	0
Aleocharinae species #4	172.3	7.6	16.0	0.9	0.9	19.2
Aleocharinae species #5	5.9	2.1	0.5	0.9	1.3	0
Aleocharinae species #6	12.4	2.4	71.4	39.4	36.1	164.2
Aleocharinae species #7	0	0	0	0.9	0	0
Aleocharinae species #8	0	7.2	5.6	1.4	4.4	3.1
Other Aleocharinae species	93.9	57.0	30.8	36.6	79.3	80.4
Stenus egenulus Puthz	9.3	0	0.3	0	0	0.4
Euaesthetus species #1	0.4	0	0	0	0	0
Lathrobium fauveli Duvivier	0.2	0.2	0.3	0	1.3	1.5
L. fulvipenne (Gravenhorst)	0	0	1.0	0	0	0
L. washingtoni Casey	0	0	0.3	0	0	0.4
Philonthus seigwaldii Mannerheim	0.6	0.3	0.3	0.9	0.4	0.8
Gabrius brevipennis (Horn)	2.7	0	0.2	0.5	1.3	0
Ontholestes cingulatus (Gravenhorst)	0	0	0.2	0	0	0

Table 6, contd.

Quedius labradorensis Smetana	0	0	0	0.9	0	0
Q. densiventris (Casey)	80.2	1.7	6.8	0	2.6	4.2
Q. fulvicollis (Stephens)	5.7	0.3	2.5	2.3	0.4	1.5
Atrecus macrocephalus (Nordmann)	0.6	0.7	0.2	0	0	0
PSELAPHIDAE						
Lucifotychus testaceus (Casey)	0	0	0.2	0.5	0.4	0
HYDROPHILIDAE						
Anacaena limbata (Fabricius)	0	0	0.2	0	0	0
Cymbiodyta vindicata Fall	0.2	0	0	0	0	0
Cercyon haemorrhoidalis (Fabricius)	0	0.2	0.2	1.4	0	0.4
C. minusculus Melsheimer	0	0.2	0	0	0	0
Cryptopleurum minutum (Fabricius)	0	0	0.2	0	0	0
SCARABAEIDAE						
Aegialia rufescens Horn	0.8	1.7	1.6	0	0.4	0.4
Aphodius leopardus Horn	0	0	0	0.9	0	0
A. borealis Gyllenhal	0	0	0	0.9	0	0
Geotrupes stercorarius (Linnaeus)	0	0	0.5	0	0	0
ELATERIDAE						
Hypnoidus bicolor (Eschscholtz)	0	0	0	0.5	0	0
Ctenicera nitidula (LeConte)	0	0.3	0.2	0	0	0
C. pygmaea (Van Dyke)	0.2	0	0.3	0	0	0.4
C. spinosa (LeConte)	0.8	0	0.2	0	0.4	0.4
Eanus maculipennis LeConte	0	0	0	0	0	0.4
EUCNEMIDAE						
Epiphanis cornutus Eschscholtz	0.2	0	0	0	0	0
CANTHARIDAE						
Podabrus species #1	2.3	0.5	0.3	0.5	0	1.2
P. species #2	0.2	0.3	0.3	0	0	0.8

Malthodes species #1	0	0	0.2	0	0	0.8
PTINIDAE						
Ptinus raptor Sturm	0	0	0	0.5	0	0
NITIDULIDAE						
Epuraea truncatella Mannerheim	0	0.2	0	0	0	0
Omosita discoidea (Fabricius)	0	0	0.5	0	0	0.4
Nitidulidae species #3	0	0.3	2.0	0	0.4	0.4
RHIZOPHAGIDAE						
Rhizophagus dimidiatus Mannerheim	0.2	0.2	0	0	0	0
CRYPTOPHAGIDAE						
Caenoscelis species #1	0.2	0	0.2	0	0	0
Atomaria species #1	10.7	0.9	1.0	0	0.4	1.9
LATHRIDIIDAE						
Stephostethus species #1	0.2	0.2	2.3	0	0	0.4
CIIDAE						
Cis species #1	0.2	0	0.2	0	0	0
MELANDRYIDAE						
Melandrya labiata Say	0	0	0.2	0	0	0
Zilora hispida LeConte	0	0	0	0	0	0.4
Prothalpia undata LeConte	0	0.2	0	0	0	0
Serropalpus coxalis Mank	0	0	0.2	0	0	0.4
ZOPHERIDAE						
Phellopsis obcordata (Kirby)	1.1	0.2	1.5	0.5	0	0.4
TENEBRIONIDAE						
Bius estriatus LeConte	0	0.2	0	0	0	0
CEPHALOIDAE						
Cephaloon ungulare LeConte	0.2	0	0	0	0	0
PYROCHROIDAE						

Table 6, contd.

Dendroides concolor (Newman)	0.2	0	0	0	0	0
SCRAPTIIDAE						
Anaspis rufa Say	0	0	0	0	0	0.4
CERAMBYCIDAE						
Evodinus monticola (Randall)	0	0.2	0.3	0	0	0
CHRYSOMELIDAE						
Syneta extorris W.J. Brown	0	0	0.3	0.5	0	0
CURCULIONIDAE						
Otiorhynchus sulcatus (Fabricius)	0	0	0.3	0	0	0
Hylobius warreni Wood	4.0	10.6	9.4	0.5	1.7	2.3
Pissodes similis Hopkins	0	0.2	0.2	0	0	0
Rhyncolus brunneus Mannerheim	2.5	0.5	0.5	2.3	0.9	0.4
SCOLYTIDAE						
Phloeotribus piceae Swaine	0	0	0	0	0	0.4
Trypodendron lineatum (Olivier)	0.2	0	0.2	0	0	0
Xyleborus species #1	0.2	0	0	0	0	0.8

The experimental pitfall traps containing un-cooked ground beef showed that the beetle genera *Catops*, *Cercyon* and *Nicrophorus* are strongly attracted to carrion (Table 7). These beetles were therefore excluded from further analysis. *Hydroporus paugus* and *Ptinus raptor* were also excluded because the habitat in which they are normally found is very different from forest floor leaf litter, *H. paugus* being aquatic and *P. raptor* being a pest of stored grain. This is also reflected in the very low numbers in which these two species were caught. With these species excluded, over the entire study period (23 698 trap nights), a total of 20 292 beetles, representing 115 species were caught (Table 8).

3.3 Rarefaction

The beetle species richness of each forest stand was compared using rarefaction (Figure 8). Both the FD40 and FE40 forest stands showed the lowest richness within their respective forest types. However, in the FD forest type, the 60 year old stand showed the highest richness, whereas in the FE type, the old growth stand showed the highest richness.

3.4 Cluster Analysis

Figure 9 shows the heirarchical cluster analysis calculated from the presence or absence of each beetle species, grouped by site. Most of the replicate sites grouped together, except for FE60-11 and FE60-12. FE60-12 grouped with the FE40 sites, then the 40 year old sites together formed a larger cluster. The FDO sites then grouped with this large cluster. FE60-11 clustered with the FD60 sites. The FEO sites were not closely associated with any of the other sites.

Table 7. Numbers of beetles found in twelve pitfall traps, four of which were baited with un-cooked ground beef (marked by *), that were set out in FD60-6 from July 28 to August 6, 1994.

Pitfall #	*Catops basilaris*	*Cercyon haemorrhoidalis*	*Nicrophorus defodiens*	*Nicrophorus sayi*
1	0	0	0	0
2*	443	1	2	5
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0
6*	289	5	5	5
7*	252	3	7	4
8	0	0	0	0
9	0	0	0	0
10	0	0	0	0
11*	265	4	1	2
12	0	0	0	0

Table 8. The number of species, individuals and trap nights for the six forest stands, with obvious carrion feeding species excluded.

STAND	no. of species	no. of individuals	no. of trap nights
FDO	68	5692	4748
FD40	60	7449	5826
FD60	78	3252	6068
FEO	51	755	2160
FE40	47	1296	2296
FE60	63	1848	2600
TOTAL	115	20 292	23 698

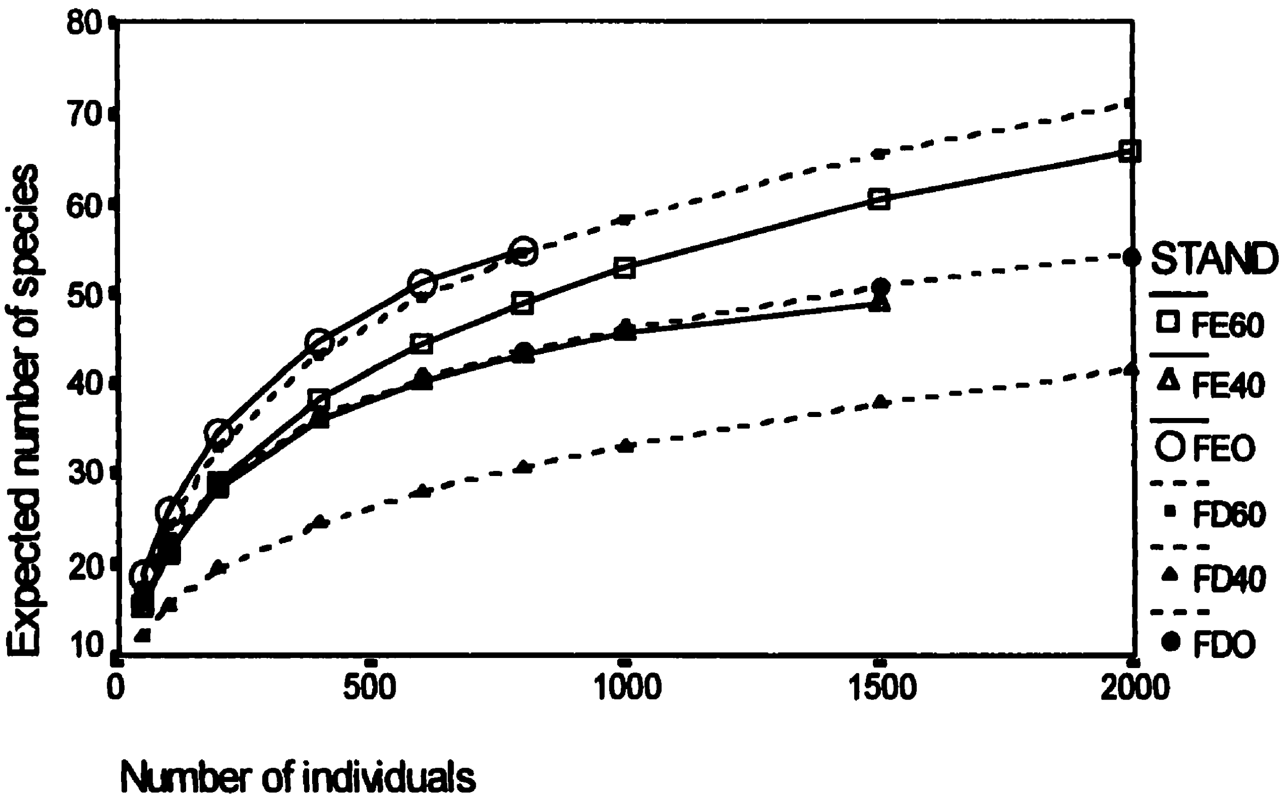


Figure 8. The expected number of species per number of individuals, calculated from RAREFACT (Krebs, 1991) for each stand.

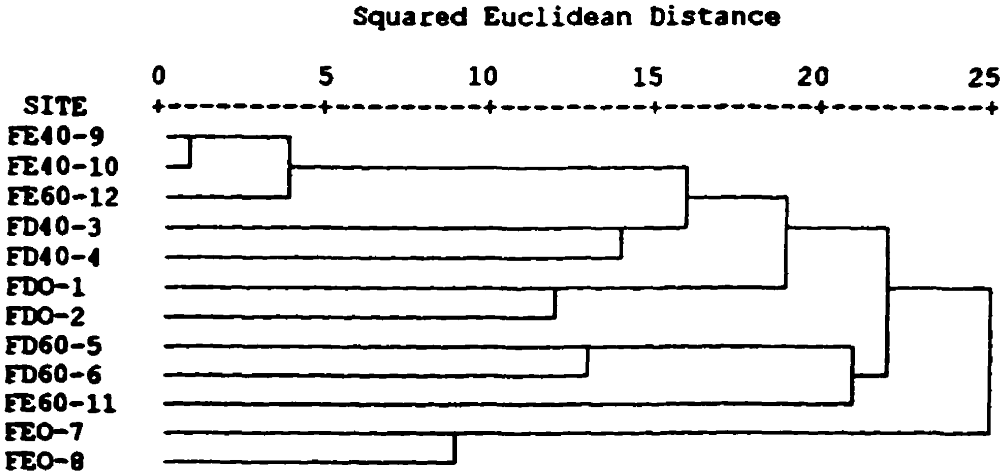


Figure 9. Hierarchical cluster analysis of the twelve study sites based on presence or absence of beetle species.

3.5 Principle Components Analysis

Principal components analysis was performed on the beetle data grouped by site and standardized as individuals per trap per night x 1000 (Figure 10). The FDO sites separated from the others along factor 1, with a high positive loading. This factor accounted for 19.8 % of the variation in the data. Factor 2 accounted for 15.1 % of the variation in the data. The FEO sites had a high negative loading along this factor, while the FD40 and FD60 sites had a high positive loading. Factor 3 showed the variation within the FDO and the FD60 sites, but also separated the FD40 sites from those older sites. This factor accounted for 13.6 % of the variation in the data. Together, the first three factors accounted for 48.5 % of the variation among the sites. The beetle species that had the highest loading scores (eigenvectors with a value of 0.6 and above or -0.6 and below) along the first factor are listed in Table 9, while those that had the highest loadings on the second and third factors are listed in Table 10.

The first principle components factor of the beetle data was plotted against that of the vegetation data, both from the FD sites only, which shows a clear separation of the different aged stands for that forest type (Figure 11).

3.6 Trends in Beetle Abundances

The beetle species that comprised 1% or more of the total number of individuals collected within each stand are listed in Tables 11 and 12. These tables show that the most abundant beetle species were different from stand to stand. *Pterostichus adstrictus, Platynus decentis* and *Calathus advena* were very abundant in FDO, but were absent or

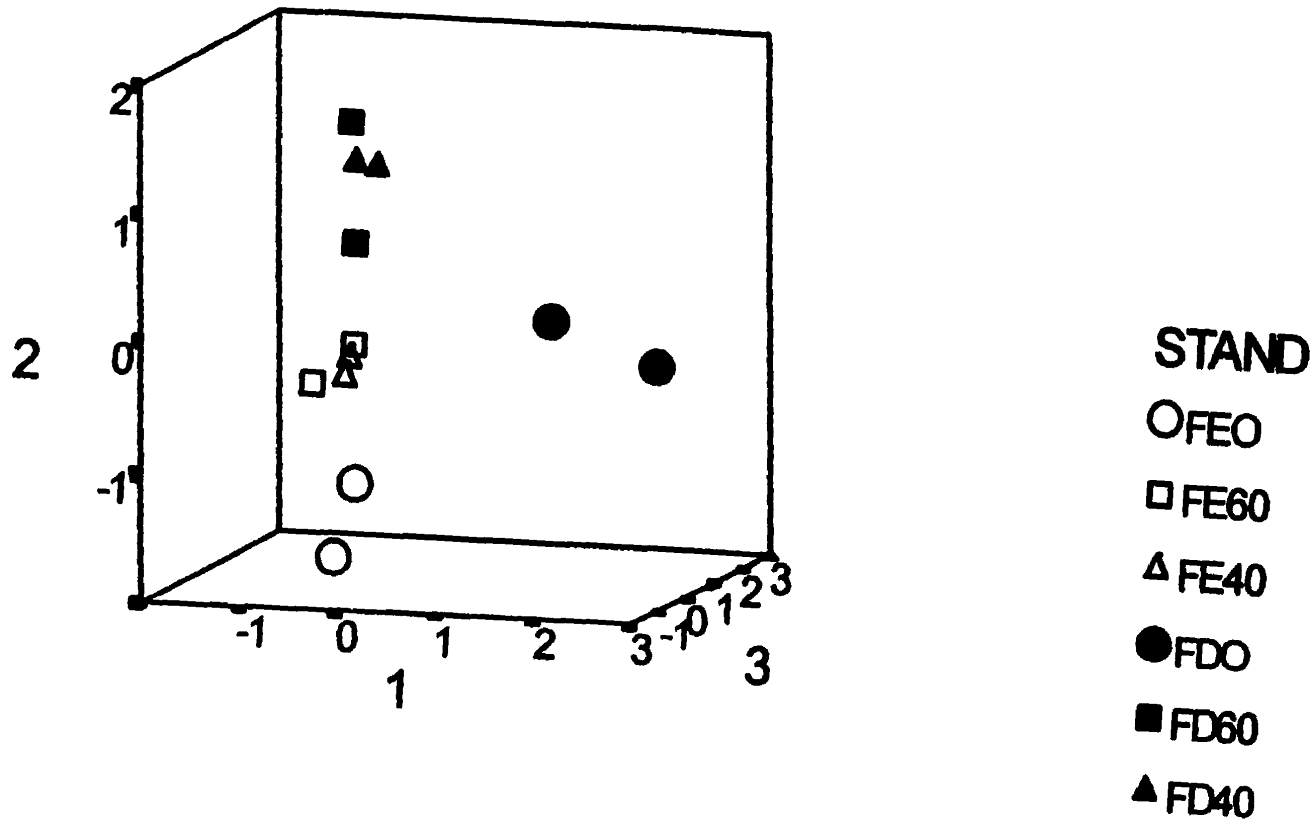


Figure 10. A scatterplot of the first three principle components factors (1, 2 and 3) calculated from the standardized beetle data from all sites.

Table 9. **The beetle species that showed the highest loading on the first principle components factor.**

SPECIES	FACTOR 1	SPECIES	FACTOR 1
Lordithon fungicola	.94265	*Micropeplus laticollis*	.71622
Quedius densiventris	.94085	*Calathus ingratus*	.70772
Agathidium sp. #1	.91474	*Cephaloon ungulare*	.70772
Tachinus frigidus	.90243	*Mycetoporus horni*	.70772
Aleocharinae sp. #4	.89511	*Atomaria* sp. #1	.70408
Aleocharinae sp. #5	.87959	*Millidium minutissimum*	.70400
Calathus advena	.86926	*Quedius fulvicollis*	.70175
Tachinus elongatus	.85672	*Stenichnus* sp. #1	.69812
Platynus decentis	.79892	*Ischnosoma splendidum*	.64560
Stenus egenulus	.78568	*Gabrius brevipennis*	.63962
Pterostichus adstrictus	.76147	*Rhyncolus brunneus*	.62719
Podabrus sp. #1	.71944	*Rhizophagus dimidiatus*	.62719

Table 10. The beetle species that showed the highest loading on the second and third principle components factors.

SPECIES	FACTOR 2	SPECIES	FACTOR 2
Gyrophaena sp. #1	.84056	*Olophrum rotundicolle*	-.67853
Acidota subcarinata	-.82595	*Quedius labradorensis*	-.67453
Pterostichus coracinus	-.81276	*Leiodes assimilis*	-.65000
Acrotrichus sp. #1	.79870	*Evodinus monticola*	.64793
Bembidion wingatei	.79509	*Pseudopsis subulata*	.63599
Proteinus limbatus	.78415	*Hylobius warreni*	.63121
Aegialia rufescens	.72533	*Trechus apicalis*	-.62411
Aleocharinae sp. #8	.68761	*Brathinus nitidus*	-.62334
Elonium diffusum	.68554	*Ctenicera nitidula*	.60337

SPECIES	FACTOR 3	SPECIES	FACTOR 3
Cis sp. #1	.82502	*Cryptopleurum minutum*	.69741
Phellopsis obcordata	.80947	*Melandrya labiata*	.69741
Tachinus basalis	.77062	*Ontholestes cingulatus*	.69741
Oxypoda sp. #2	-.76723	*Otiorhynchus sulcatus*	.69741
Ctenicera pygmaea	.76110	*Geotrupes stercorarius*	.68738
Omalium sp. #2	.72249	*Pterostichus melanarius*	.64508
Lathrobium fulvipenne	.71331	*Colon magnicolle*	.63454

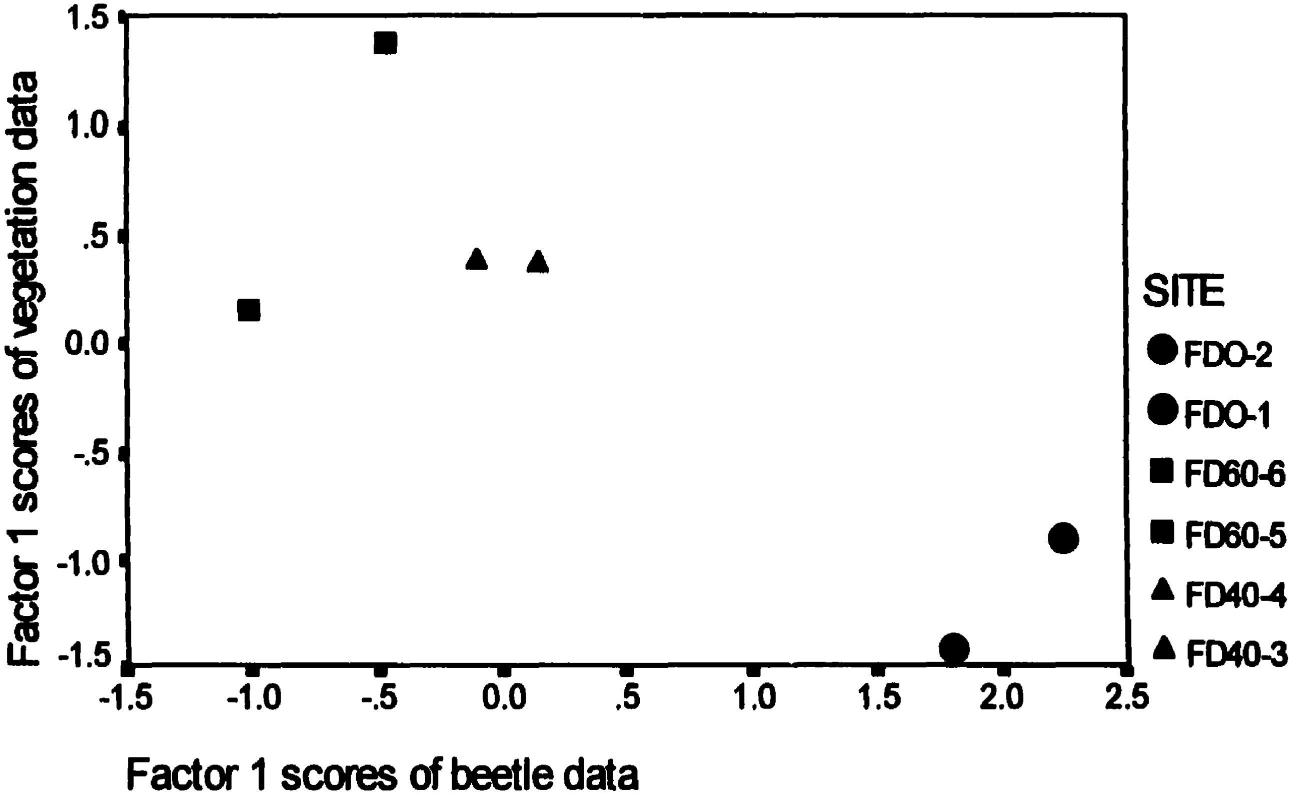


Figure 11. A scatterplot of the first principle components factor of the beetle data and the first principle components factor of the vegetation data.

Table 11. Species that make up at least 1% (in bold) of the total number of beetles for each FD stand.

SPECIES	FDO(%)	FD40(%)	FD60(%)
Tachinus frigidus	**12.2**	**3.3**	**1.4**
Elonium diffusum	**12.0**	**38.9**	**16.7**
Oxypoda sp. #1	**8.1**	**5.9**	**2.9**
Aleocharinae spp.	**7.8**	**4.5**	**5.8**
Proteinus limbatus	**7.5**	**18.2**	**11.4**
Bembidion wingatei	**5.1**	**5.7**	**9.8**
Acrotrichus sp. #1	**3.2**	**7.0**	**8.7**
Aleocharinae sp. #4	**14.3**	<1%	**3.0**
Quedius densiventris	**6.7**	<1%	**1.3**
Aleocharinae sp. #6	**1.0**	<1%	**13.3**
Pterostichus adstrictus	**1.5**	<1%	0
Lordithon fungicola	**3.5**	**1.6**	<1%
Tachinus quebecensis	**2.1**	**2.3**	<1%
Platynus decentis	**3.0**	0	0
Calathus advena	**1.0**	0	0
Arpedium cribratum	0	**3.7**	<1%
Pseudopsis subulata	<1%	**3.3**	**8.2**
Oxytellus fuscipennis	<1%	<1%	**2.3**
Hylobius warreni	<1%	<1%	**1.8**
Trechus apicalis	<1%	0	**1.0**
Aleocharinae sp. #8	0	<1%	**1.0**
% Total of spp. ≥ 1%	**89.2**	**94.4**	**88.6**

Table 12. Species that make up at least 1% (in bold) of the total number of beetles for each FE stand.

SPECIES	FEO(%)	FE40(%)	FE60(%)
Aleocharinae sp. #6	**11.3**	**6.4**	**23.1**
Aleocharinae spp.	**10.5**	**14.0**	**11.3**
Elonium diffusum	**9.8**	**23.8**	**4.5**
Pterostichus coracinus	**9.3**	**2.2**	**1.5**
Ptenidium sp. #1	**3.7**	**5.8**	**19.4**
Acrotrichus sp. #1	**2.9**	**3.0**	**1.1**
Trechus apicalis	**1.6**	**1.4**	**1.1**
Lordithon fungicola	**1.6**	**1.5**	<1%
Tachinus frigidus	**1.6**	**1.6**	<1%
Pterostichus punctatissimus	**1.5**	**1.7**	<1%
Oxytellus fuscipennis	**2.8**	<1%	**3.0**
Brathinus nitidus	**6.8**	<1%	0
Olophrum rotundicolle	**11.9**	<1%	<1%
Acidota subcarinata	**1.9**	<1%	<1%
Ischnosoma splendidum	**1.7**	<1%	<1%
Leiodes assimilis	**1.5**	0	<1%
Lesteva pallipes	**9.0**	0	0
Oxypoda sp. #1	<1%	**13.6**	**7.0**
Proteinus limbatus	<1%	**10.7**	**6.8**
Pseudopsis subulata	0	**3.2**	**7.2**
Bembidion wingatei	0	**1.9**	**1.0**
Aleocharinae sp. #4	<1%	<1%	**2.7**
% Total of spp. ≥ 1%	**89.1**	**91.0**	**89.8**

found in low abundances in FD40 and FD60. Likewise, 5 species that were abundant in FD40 and FD60 were not as abundant in FDO. The FE forest type showed the same pattern. Six species that were highly abundant in FEO were found in low abundances in FE40 and FE60, while these stands had 5 abundant species that were of low abundance in FEO. In total, there were 15 species out of 68 in FDO and 17 species out of 51 in FEO that contained 1% or more of the total number of individuals, but only 6 of these abundant species were common to both stands. There were 11 species out of 60 in FD40 and 14 species out of 47 in FE40 that were very abundant. However, 9 of these species were common to both stands. FD60 contained 15 abundant species out of 78 and FE60 contained 13 abundant species out of 63, with 11 species common to both stands.

Of the 115 beetle species examined in this study, 70 species each had an abundance of 5 or more individuals, when totalled over all stands and over the entire study period. Non-parametric Mann-Whitney U tests were calculated on the number of beetle individuals per trap per night x 100, split according to stand and trap number, to compare the stands within each forest type. The results of these tests are shown in Table 13. Six species, *Platynus decentis*, *Lesteva pallipes*, *Calathus advena*, *Agathidium* sp. #1, *Stenichnus* sp. #1, and *Calathus ingratus*, were found only in the old growth stands (Figure 12). Three species, *Pterostichus coracinus*, *Brathinus nitidus*, and *Leiodes assimilis* were significantly more abundant in the old growth stands (Figure 13). *Pseudopsis subulata* was significantly more abundant in the previously cut stands and *Ptenidium* sp. #1, *Omalium* sp. #2 and *Lathrobium fulvipenne* were significantly

Table 13. **Results of the Mann-Whitney U tests comparing stands within each forest type. Stands identified within the table have significantly more individuals (at p < .05). ns = stands not significantly different, 0 = no specimens present in compared stands.**

SPECIES	FDO vs. FD40	FDO vs. FD60	FD40 vs. FD60	FEO vs. FE40	FEO vs. FE60	FE40 vs. FE60
Platynus decentis	FDO	FDO	0	ns	ns	0
Lesteva pallipes	0	0	0	FEO	FEO	0
Calathus advena	FDO	FDO	0	0	0	0
Agathidium sp. #1	FDO	FDO	0	ns	ns	0
Stenichnus sp. #1	FDO	FDO	0	ns	ns	0
Calathus ingratus	FDO	FDO	0	0	0	0
Pterostichus coracinus	FDO	FDO	ns	FEO	FEO	ns
Brathinus nitidus	0	0	0	FEO	FEO	ns
Leiodes assimilis	0	0	0	FEO	FEO	ns
Pseudopsis subulata	FD40	FD60	ns	FE40	FE60	FE60
Ptenidium sp #1	0	0	0	ns	FE60	FE60
Omalium sp. #2	ns	FD60	FD60	ns	FE60	FE60
Lathrobium fulvipenne	0	FD60	FD60	0	0	0
Lordithon fungicola	FDO	FDO	ns	ns	ns	ns
Pterostichus adstrictus	FDO	FDO	ns	ns	ns	0
Acidota subcarinata	FDO	FDO	ns	ns	ns	ns
Stenus egenulus	FDO	FDO	ns	0	ns	ns
Rhyncolus brunneus	FDO	FDO	ns	ns	ns	ns
Gabrius brevipennis	FDO	FDO	ns	ns	ns	ns

Table 13, contd.

Ischnosoma splendidum	FDO	FDO	FD60	ns	ns	FE60
Tachinus elongatus	FDO	FDO	FD60	ns	ns	FE60
Atomaria sp. #1	FDO	FDO	ns	ns	FE60	ns
Olophrum rotundicolle	FDO	ns	ns	FEO	FEO	ns
Hylobius warreni	FD40	FD60	ns	ns	ns	ns
Stephostethus sp. #1	ns	FD60	FD60	0	ns	ns
Nitidulidae sp. #3	ns	FD60	FD60	ns	ns	ns
Colon magnicolle	ns	FD60	FD60	ns	ns	ns
Tachinus nitidulus	0	FD60	FD60	0	ns	ns
Pterostichus melanarius	0	FD60	FD60	0	ns	ns
Trechus crassiscapus	ns	FD60	FD60	FE40	ns	ns
Elonium diffusum	FD40	ns	FD40	ns	ns	ns
Acrotrichus sp. #1	FD40	ns	FD40	ns	ns	ns
Arpedium cribratum	FD40	ns	FD40	ns	ns	0
Pterostichus punctatissimus	FD40	FDO	FD40	ns	ns	ns
Lordithon facilis	FD40	ns	FD40	0	ns	ns
Trechus apicalis	FDO	ns	FD60	ns	ns	ns
Quedius fulvicollis	FDO	ns	FD60	ns	ns	ns
Tachinus quebecensis	ns	FDO	FD40	FE40	ns	ns
Proteinus limbatus	FD40	ns	FD40	FE40	FE60	ns
Bembidion wingatei	ns	FDO	FD40	FE40	FE60	ns
Tachinus frigidus	FDO	FDO	FD40	FE40	ns	FE40
Quedius densiventris	FDO	FDO	FD60	FE40	FE60	ns
Oxytelus fuscipennis	ns	FD60	FD60	FEO	ns	FE60
Ctenicera spinosa	FDO	ns	ns	ns	ns	ns

Table 13, contd.

Millidium minutissimum	FDO	ns	ns	ns	FEO	ns
Podabrus sp. #1	ns	FDO	ns	ns	ns	FE60
Olophrum consimilie	0	0	0	FE40	ns	ns
Tachinus tachyporoides	ns	ns	ns	FE40	ns	ns
Ischnosoma fimbriatum	ns	ns	FD40	ns	ns	ns
Sphaeroderus nitidicollis	ns	ns	0	ns	ns	FE40
Tachinus thruppi	ns	FD60	FD40	ns	ns	FE60
Tachinus basilis	ns	ns	ns	ns	FE60	ns
Megarthrus americanus	ns	FD60	ns	ns	ns	ns
Eusphalerum pothos	ns	FD60	ns	ns	ns	ns
Phelopsis obcordata	ns	ns	FD60	ns	ns	ns
Agialia rufescens	ns	ns	ns	ns	ns	ns
Omalium sp. #3	ns	ns	ns	0	ns	ns
Omalium rivulare	ns	ns	ns	ns	0	ns
Philonthus seigwaldii	ns	ns	ns	ns	ns	ns
Lathrobium fauveli	ns	ns	ns	ns	ns	ns
Atrecus macrocephalus	ns	ns	ns	0	0	0
Podabrus sp. #2	ns	ns	ns	0	ns	ns
Micropeplus laticollis	ns	ns	ns	0	0	0

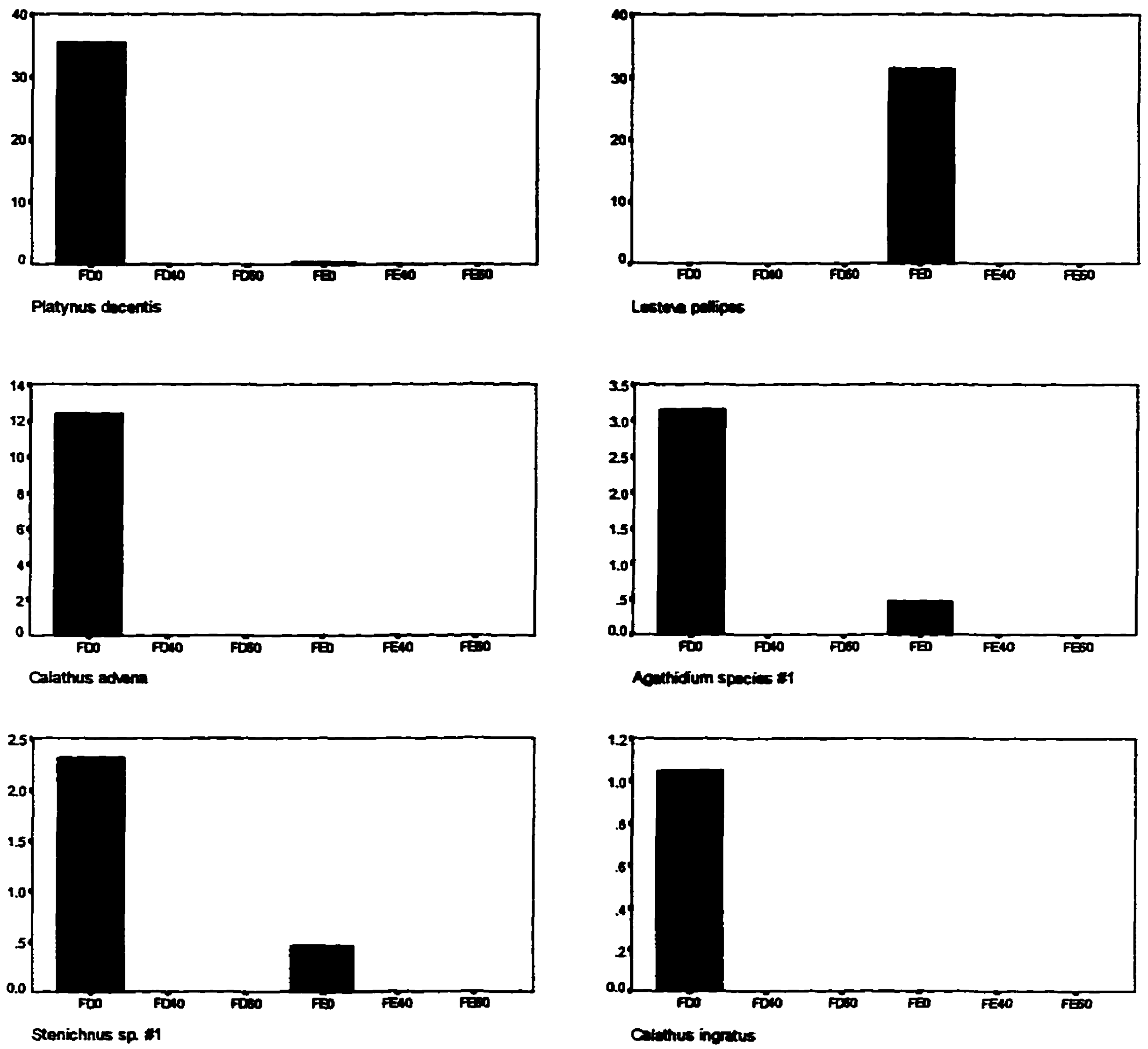
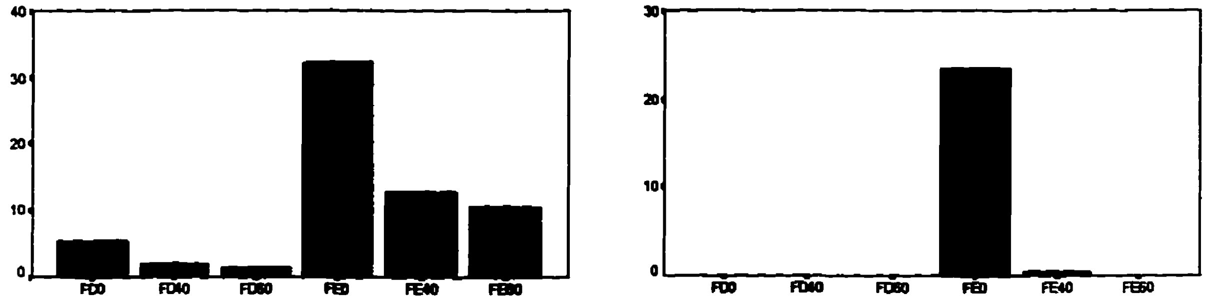
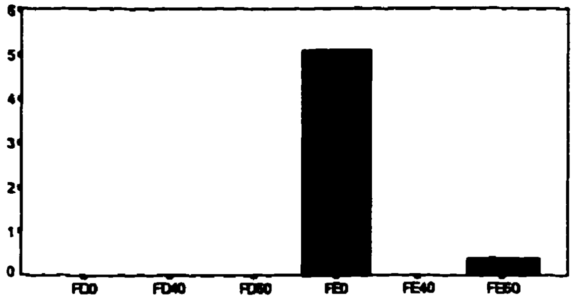


Figure 12. Six species found only in the old growth stands. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.



Pterostichus coracinus

Brathinus nitidus



Leiodes assimilis

Figure 13. Three species that were significantly more abundant in the old growth stands. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.

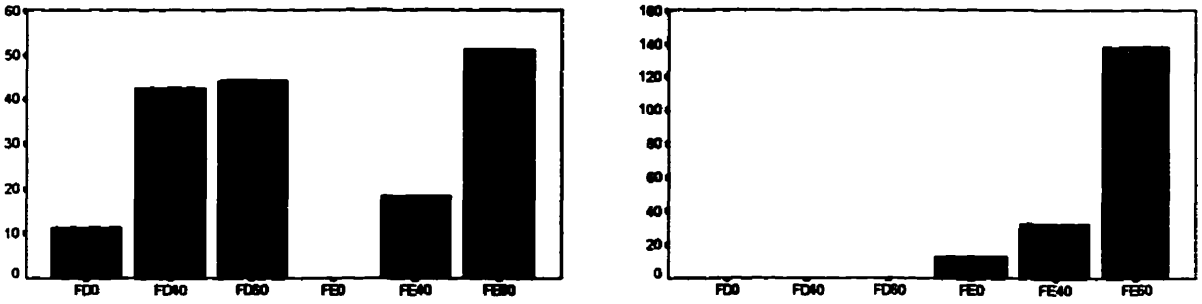
more abundant in the 60 year old stands (Figure 14). Some species showed significant differences between stands only in the FD forest type. Six species, *Lordithon fungicola, Pterostichus adstrictus, Acidota subcarinata, Stenus egenulus, Rhyncolus brunneus* and *Gabrius brevipennis* were significantly more abundant in FDO (Figure 15). Four species, *Stephostethus* sp. #1, Nitidulidae sp. #3, *Colon magnicolle, Tachinus nitidulis* and *Pterostichus melanarius* were significantly more abundant in FD60, while *Hylobius warreni* was significantly more abundant in both previously cut FD stands (Figure 16). Four species, *Elonium diffusum, Acrotrichus* sp. #1, *Arpedium cribratum* and *Lordithon facilis* were significantly more abundant in FD40 (Figure 17). *Quedius fulvicollis* and *Trechus apicalis* were significantly more abundant in FDO and FD60 (Figure 17).

The results of the Mann-Whitney U tests for the Aleocharinae species can be found in Table 14.

3.7 Seasonal abundances and species notes

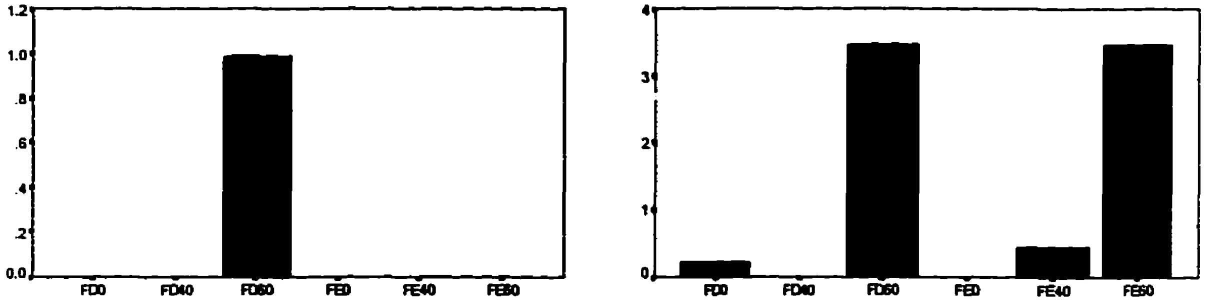
Twelve species were found to be significantly more abundant in early summer, while 19 species were significantly more abundant in late summer (Tables 15 and 16).

Brief descriptions of the usual habitat and distribution of each species, as well as the stands each species was found in are in Appendix 1. Thirteen species were known to be Holarctic, 26 were found only in eastern North America and 48 were Nearctic (Table 17).



Pseudopsis subulata

Ptenidium sp. #1



Lathrobium fulvipenne

Omalium species #2

Figure 14. One species that was significantly more abundant in the previously cut stands and 3 species that were significantly more abundant in the 60 year old stands. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.

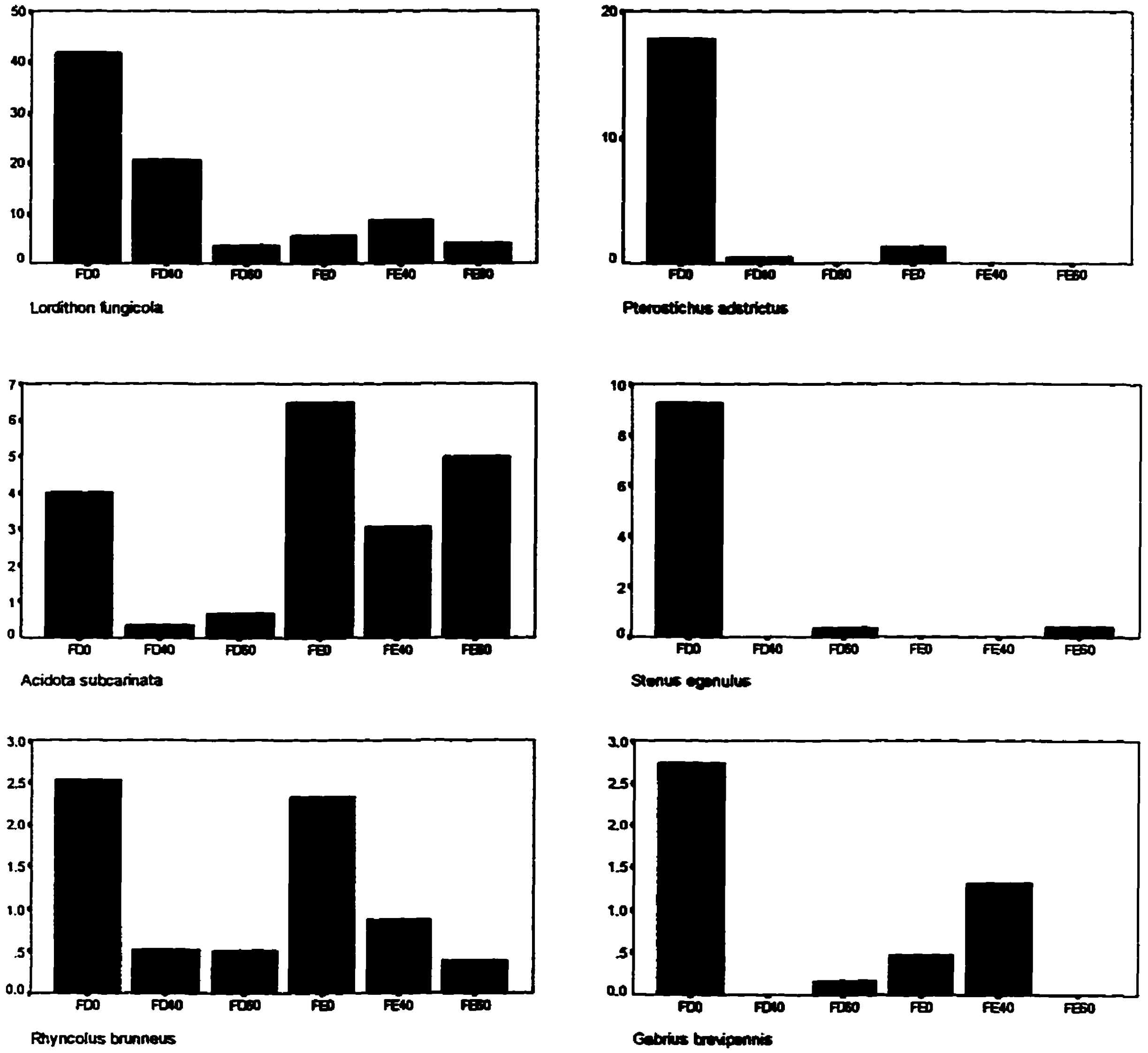


Figure 15. Six species that were significantly more abundant in FDO than in the other FD stands. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.

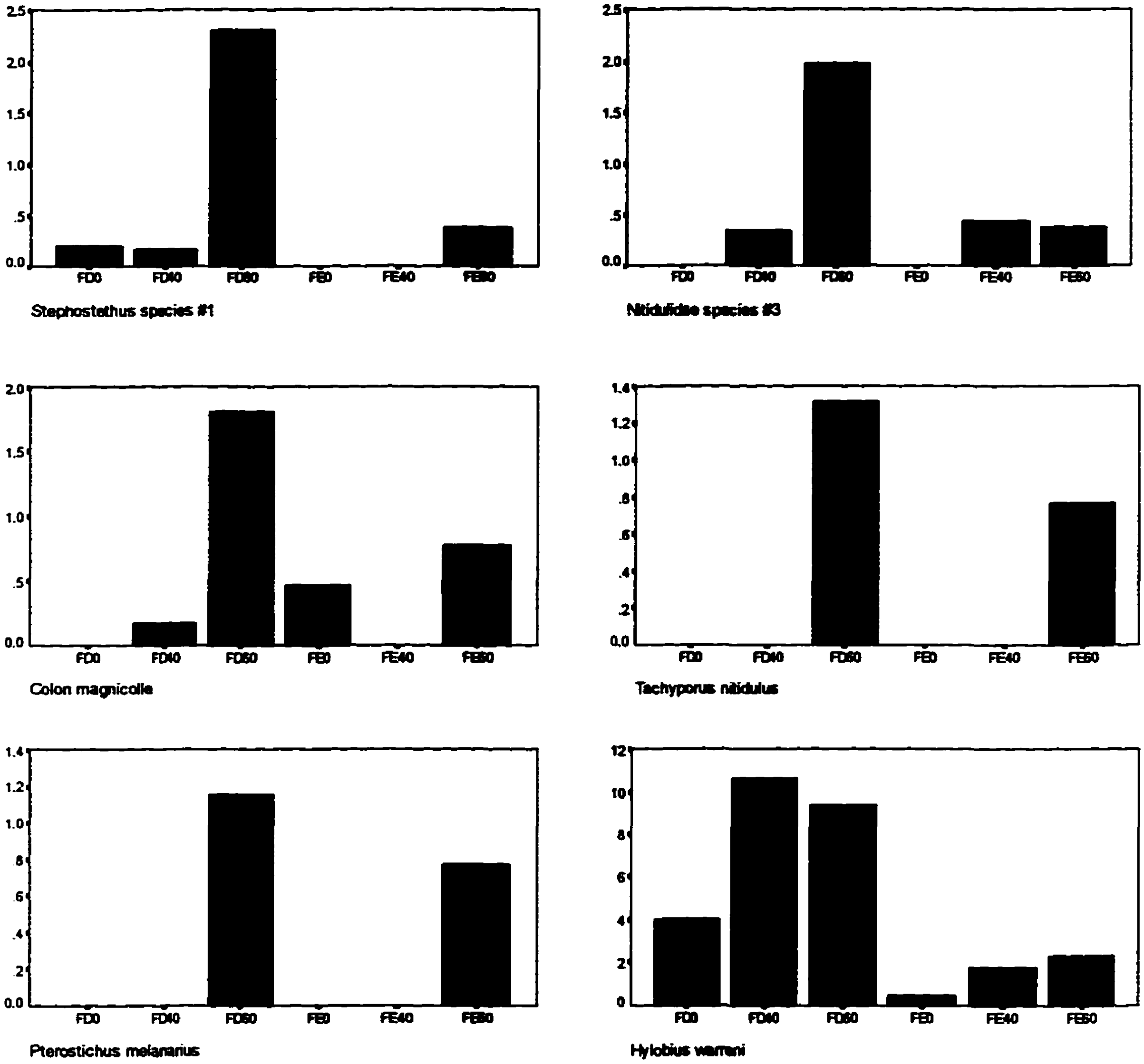


Figure 16. Five species that were significantly more abundant in FD60 than in the other FD stands and 1 species that was significantly more abundant in both previously cut FD stands. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.

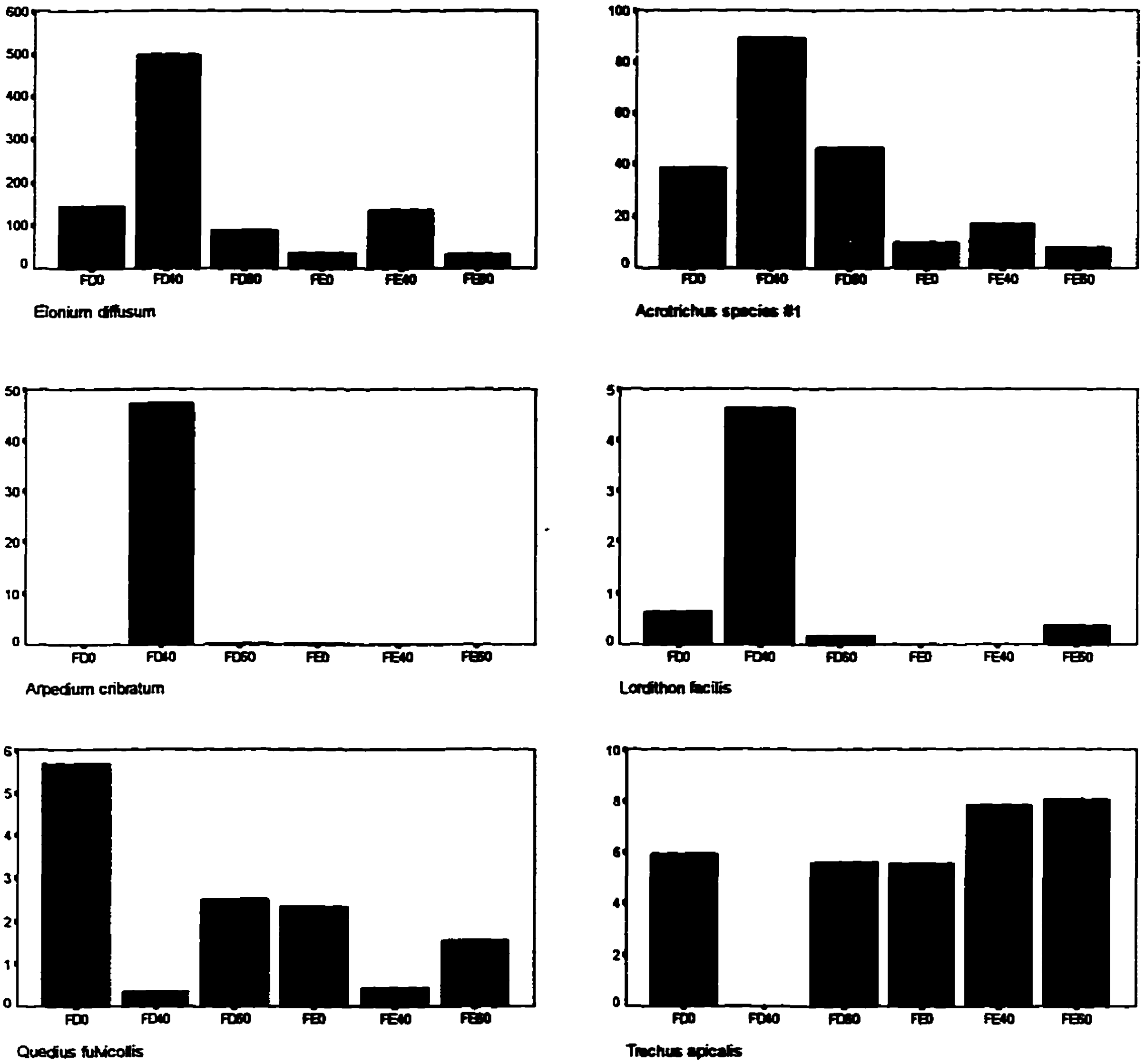


Figure 17. Four species that were significantly more abundant in FD40 than in the other FD stands and 2 species that were significantly more abundant in FDO and FD60 than in FD40. Stands are along the x axis and the number of individuals per trap per night x 1000 is on the y axis.

Table 14. **Results of the Mann-Whitney U tests for the Aleocharinae comparing stands within each forest type. Stands identified within the table have significantly more individuals (at p > .05). ns = stands not significantly different.**

SPECIES	FDO vs. FD40	FDO vs. FD60	FD40 vs. FD60	FEO vs. FE40	FEO vs. FE60	FE40 vs. FE60
Oxypoda sp. #1	ns	FDO	ns	FE40	FE60	ns
Oxypoda sp. #2	ns	ns	ns	ns	ns	ns
Aleocharinae sp. #4	FDO	FDO	ns	ns	FE60	FE60
Aleocharinae sp. #5	ns	FDO	ns	ns	ns	FE40
Aleocharinae sp. #6	ns	ns	ns	ns	ns	ns
Aleocharinae sp. #8	FD40	FD60	ns	ns	ns	ns
Aleocharinae spp.	ns	ns	ns	FE40	FE60	ns

Table 15. **Results of the Mann-Whitney U tests comparing early and late summer beetle abundances for each site or group of sites. *A* = FDO in 1992, *B* = FD40 in 1992, *C* = FD60-5 in 1992, *D* = FD60-6 in 1992, *E* = FDO in 1993, *F* = FD40 and FD60 in 1993, *G* = FEO, *H* = FE40, *I* = FE60 and *J* = all sites pooled. E = species significantly more abundant (at $p < .05$) in early summer, L = species significantly more abundant in late summer, ns = early and late summer not significantly different, 0 = no specimens present in tested site or group of sites.**

SPECIES	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*
Arpedium cribratum	0	0	0	0	0	E	ns	0	0	E
Atomaria sp. #1	ns	ns	ns	0	E	ns	0	ns	ns	E
Bembidion wingatei	ns	E	E	ns	E	E	0	ns	ns	E
Calathus ingratus	ns	0	0	0	ns	0	0	0	0	E
Hylobius warreni	ns	E	ns	E	ns	E	ns	ns	ns	E
Omalium sp. #3	E	ns	ns	ns	0	E	0	0	ns	E
Platynus decentis	E	0	0	0	E	0	ns	0	0	E
Pterostichus adstrictus	E	ns	0	0	E	0	ns	0	0	E
Pterostichus coracinus	ns	ns	ns	ns	E	E	E	ns	ns	E
Stenus egenulus	ns	0	0	ns	E	ns	0	0	ns	E
Tachyporus nitidulus	0	0	E	0	0	ns	0	0	ns	E
Acidota subcarinata	ns	0	ns	0	L	ns	ns	ns	L	L
Brathinus nitidus	0	0	0	0	0	0	ns	ns	0	L
Elonium diffusum	L	L	L	L	L	L	L	L	L	L
Micropeplus laticollis	ns	0	0	0	0	ns	0	0	0	L
Olophrum consimilie	0	0	0	0	0	0	ns	L	ns	L
Olophrum rotundicolle	ns	0	0	0	ns	ns	L	ns	ns	L
Oxytelus fuscipennis	ns	0	L	ns	ns	L	ns	L	L	L
Proteinus limbatus	L	L	L	L	L	L	ns	L	ns	L

Table 15, contd.

Pseudopsis subulata	ns	L	ns	L	ns	ns	0	L	L	L
Ptenidium sp. #1	0	0	0	0	0	0	L	L	L	L
Millidium minutissimum	L	L	L	ns	ns	L	ns	ns	0	L
Sphaeroderus nitidicollis	ns	0	0	0	ns	0	ns	L	0	L
Tachinus basalis	L	ns	ns	L	ns	ns	0	ns	ns	L
Tachinus frigidus	L	L	ns	L	L	L	ns	L	ns	L
Tachinus quebecensis	L	L	ns	L	L	L	0	L	ns	L
Tachinus thruppi	0	0	ns	ns	0	L	ns	0	L	L
Acrotrichus sp. #1	L	L	ns	ns	ns	E	ns	ns	ns	ns
Aegialia rufescens	ns	ns	ns	ns	ns	ns	0	ns	ns	ns
Agathidium sp. #1	ns	0	0	0	ns	0	ns	0	0	ns
Atrecus macrocephalus	ns	ns	0	0	ns	ns	0	0	0	ns
Calathus advena	ns	0	0	0	ns	0	0	0	0	ns
Colon magnicolle	0	ns	ns	ns	0	ns	ns	0	ns	ns
Ctenicera spinosa	ns	0	ns	0	ns	0	0	ns	ns	ns
Eusphalerum pothos	0	ns	ns	ns	0	0	ns	ns	ns	ns
Gabrius brevipennis	ns	0	0	ns	E	0	ns	ns	0	ns
Ischnosoma fimbriatum	ns	ns	0	ns	ns	ns	ns	ns	ns	ns
Ischnosoma splendidum	ns	ns	ns	ns	ns	ns	E	ns	ns	ns
Lathrobium fauveli	ns	ns	0	ns	0	ns	0	ns	ns	ns
Lathrobium fulvicollis	0	0	ns	ns	0	ns	0	0	0	ns
Leiodes assimilis	0	0	0	0	0	0	ns	0	ns	ns
Lordithon facilis	0	0	ns	0	ns	ns	0	0	ns	ns
Lordithon fungicola	L	ns	ns	ns	ns	E	ns	L	ns	ns
Megarthrus americanus	0	ns	ns	ns	0	ns	0	ns	ns	ns

Table 15, contd.

Nitidulidae sp. #3	0	0	ns	ns	0	E	0	ns	ns	ns
Lesteva pallipes	0	0	0	0	0	0	L	0	0	ns
Tachinus tachyporoides	0	0	0	0	0	ns	0	ns	ns	ns
Omalium rivulare	ns	ns	ns	0	ns	ns	0	ns	0	ns
Omalium sp. #2	ns	0	ns	ns	0	ns	0	ns	L	ns
Phellopsis obcordata	ns	ns	0	E	ns	ns	ns	0	ns	ns
Philonthus seigwaldii	ns	0	ns	0	ns	ns	ns	ns	ns	ns
Podabrus sp. #1	ns	ns	0	0	ns	E	ns	0	ns	ns
Podabrus sp. #2	ns	ns	ns	0	0	ns	0	0	ns	ns
Pterostichus melanarius	0	0	ns	L	0	ns	0	0	ns	ns
Pterostichus punctatissimus	ns	ns	ns	ns	E	E	ns	ns	ns	ns
Quedius densiventris	ns	ns	ns	ns	E	ns	0	ns	ns	ns
Quedius fulvicollis	ns	0	ns	ns	ns	ns	ns	ns	ns	ns
Rhyncolus brunneus	ns	ns	0	0	ns	E	ns	ns	ns	ns
Stenichnus sp. #1	L	0	0	0	ns	0	ns	0	0	ns
Stephostethus sp. #1	0	0	L	ns	ns	ns	0	0	ns	ns
Tachinus elongatus	L	0	E	0	E	ns	ns	0	ns	ns
Trechus apicalis	ns	0	ns	ns	ns	ns	ns	ns	ns	ns
Trechus crassiscapus	ns	0	ns	ns	0	0	0	L	ns	ns

Table 16. **Results of the Mann- Whitney U tests comparing early and late summer Aleocharinae abundances for each site or group of sites. *A* = FDO in 1992, *B* = FD40 in 1992, *C* = FD60-5 in 1992, *D* = FD60-6 in 1992, *E* = FDO in 1993, *F* = FD40 and FD60 in 1993, *G* = FEO, *H* = FE40, *I* = FE60 and *J* = all sites pooled. E = species significantly more abundant (at p < .05) in early summer, L = species significantly more abundant in late summer, ns = early and late summer not significantly different and 0 = no specimens present in tested site or group of sites.**

SPECIES	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*
Oxypoda sp. #1	ns	ns	ns	ns	ns	L	ns	L	ns	L
Oxypoda sp. #2	ns	ns	ns	0	ns	ns	E	E	ns	ns
Aleocharinae sp. #4	ns	ns	ns	ns	ns	ns	ns	E	ns	E
Aleocharinae sp. #5	ns	ns	0	0	ns	ns	ns	ns	0	ns
Aleocharinae sp. #6	ns	0	0	L	ns	L	ns	L	L	L
Aleocharinae sp. #8	0	E	ns	ns	0	ns	ns	ns	ns	ns
Aleocharinae spp.	ns	ns	ns	L	ns	L	E	ns	ns	L

Table 17. The known distributions of beetle species found in the present study. Beetles that were identified to genus only are not included.

DISTRIBUTION	number of species
eastern North America	26
Nearctic	48
Holarctic	13
Introduced to eastern North America	2
Introduced to North America	10
May be introduced to North America	1

4.0 DISCUSSION

4.1 Efficiency of pitfall trapping

There has been much debate over the efficiency of pitfall traping and numerous studies have been done on different types of traps, in different habitats. Luff (1975) found that plastic traps were less efficient than glass ones, but plastic traps were used in this study because they are much lighter and less fragile than glass jars. They are also more compact since they can be easily stacked, one inside the other. Twenty pitfall traps, twenty wooden rain covers and two litres of preservative were carried into each site and although all of the forest sites were near logging roads, some required a five to ten minute walk through heavy brush and up (or down) steep embankments.

Holopainen (1992) compared water filled traps with those filled with ethylene glycol. Some species of carabids were caught more frequently in traps filled with ethylene glycol, while some species were caught equally in both types of traps. However, it was unclear whether the higher catches were due to an attractive effect of ethylene glycol or the greater killing efficiency of this preservative as compared to water (Holopainen, 1992). Overall, more beetle specimens were caught in this study in 1992, when ethylene glycol was used as preservative, than in 1993 or 1994, when propylene glycol was used. This may, however, be simply due to natural yearly variations in abundance.

Greenslade (1964) concluded that pitfall traps could not properly be used for a quantitative assessment of the carabid fauna of any one habitat, nor for comparisons of the numbers of any one species in different habitats. However, this was based on three experiments; one using a grid of nine pitfall traps in grass heath, one with a grid of four traps in beach woodland and one with a transect of five traps through different leaf litter depths under beach, all of which have rather small sample sizes.

Spence and Niemelä (1994) found more large bodied than small bodied species of carabids in pitfall traps with a diameter of 11.2 cm. For example, more specimens of *Pterostichus adstrictus* (body length 10.9 mm) were collected in their traps than *Agonum retractum* (6.7 mm). They also found that although large pitfall traps failed to catch small beetles, quadrat sampling missed some species of large carabids and was much more time consuming than pitfall trapping. The traps used in the present study were 12.8 cm in diameter, yet they caught many species of small beetles in quite high abundances. The most abundant beetle caught (4596 specimens) was *Elonium diffusum*, a staphylinid which is only about 2.5 mm long. Two species of feather-wing beetles, *Acrotrichus* sp. and *Ptenidium* sp., both around 1 mm long, were among the top twenty most abundant beetles, along with large carabid species such as *Pterostichus coracinus*, which is about 18 mm long. In fact, 1076 *Bembidion wingatei* (6 mm) were collected in all sites over the entire sampling period as compared to 172 *Pterostichus coracinus* (18 mm), results opposite to those found by Spence and Niemelä (1994).

Baars (1979) concluded that continuous pitfall sampling summed over the whole activity period could give a reliable measure of the sizes of carabid populations in several habitats. Many beetle species collected in the present study were significantly more abundant in early or late summer. However, samples were taken from the pitfall traps continuously throughout the summer in all three years and seemed to adequately encompass the activity periods of most species. Snider and Snider (1986) found that pitfall traping could be used to compare the faunas of two sites, as long as their habitat and climate characteristics are closely similar, which is the case for the sites in the present study.

4.2 Vegetation Characteristics

The vegetation characteristics of the old growth FD stand were somewhat different from the previously cut FD stands. FDO had a greater percent cover of *Sphagnum* mosses, feather mosses and *Lycopodium*, while FD40 and FD60 had more lichens, mostly *Cladonia* species. Gustafsson and Hallingbäck (1988) found that overall species numbers and total cover of bryophytes were somewhat higher in a virgin stand of *Picea abies* than in managed stands. However, most of the difference was due to rare hepatics or liverworts, species that didn't occur in the present study. Söderström (1988) found that *Cladonia* species, were predominant in a managed *Picea abies* stand when compared with an old natural stand, but so too were feather mosses, while the present study found more feather mosses in the old growth stand.

Söderström (1988) also found that the managed stand had a more uneven supply of fallen logs in different decay stages. The present study found more fallen logs, and with a larger diameter, in the FDO stand. However, there wasn't a large difference in the density of dead standing trees between the FDO stand and the FD40 and FD60 stands. Trees in previously cut stands are nearly all the same age , whereas old growth stands have trees of different stages of maturity. New fallen logs are also created regularly due to the dynamics of natural forests in late successional stages (Söderström, 1988). It has been found that in northern hardwood forests, the amount of downed wood declines within 20 - 30 years after logging, remains low for up to an additional 30 years, then increases and stabilizes at a much higher level after 100 years (Gore and Patterson, 1986).

Söderström (1988) concluded that the difference in bryophyte species and abundances between the old natural and managed spruce stands was due to more and larger fallen logs in the natural stand, and also to a higher relative humidity. The managed stands in his study were regularly thinned and were exposed to drought more often than the natural stand. However, old growth stands usually consist of patches of different ages and degrees of crown cover, as well as open gaps caused by the death of old trees (Andersson and Hytteborn, 1991), so areas of both high and low humidity may occur in different parts of an old growth forest. In the present study the canopy was indeed more open in the FDO stand, but it is unknown whether or not the previously cut stands were ever thinned. No vegetation data was available for the FE stands.

4.3 Beetle species composition

4.3.1 Differences between forest types

Comparisons between the two forest types must be made with caution as the FD stands were sampled in 1992 and 1993, while the FE stands were sampled in 1994. However, there were differences between the two forest types. The rarefaction graph showed that the FE stands, as a whole, showed slightly higher beetle species richness than the FD stands. Principle components analysis separated the FE stands from the FD stands along factor 2. This analysis also showed that the previously cut FD and FE stands were more alike than the old growth FD and FE stands. FDO and FEO had 6 species in common out of the 26 species that made up 1% or more of the total number of beetle individuals in each of these stands. However, FD40 and FE40 had 9 species in common out of the 16 most abundant beetles in each stand, and FD60 and FE60 had 11 species in common out of 17. This indicates that the old growth forest types each contain a distinctive beetle fauna, while the beetle faunas of the previously cut forest types are more alike.

Calathus advena, C. ingratus, Atrecus macrocephalus, Lathrobium fulvipenne and *Micropeplus laticollis* were found only in the FD stands, while *Ptenidium* sp. #1, *Lesteva pallipes, Brathinus nitidus, Olophrum consimilie* and *Leiodes assimilis* were found only in the FE stands. The FE forest type was much wetter than the FD type, with different soil layers and different plant species in the understorey vegetation (Meades and Moores, 1989). It might be expected that they would also differ in beetle species composition. However, both forest types showed the effects of forest harvesting, in that the species composition of the old growth stands was different than that of the previously cut stands.

4.3.2 Differences between old growth and previously cut forest

The rarefaction graph shows that the 60 year old stands and the old growth stands were more species rich than the 40 year old stands, so that in terms of beetle species diversity, the forest seems able to recover to some extent after forest harvesting. However, with regards to presence or absence of beetle species, the old growth stand, FDO, showed a closer relation to the 40 year old stands, than the 60 year old stands, as shown by the cluster analysis. The principle components analysis of the beetle data separated the old growth stands from the previously cut stands, and identified several species that were more abundant in the old growth, as well as species that were more abundant in the cut forests. Seventy species were found in abundances of 5 or more individuals over all stands throughout the entire study period. Fifteen species were found only in, or were significantly more abundant in, one or both old growth stands, while 10 species were significantly more abundant in the previously cut stands. Four species were significantly more abundant in FD40 and 2 species were least abundant in FD40. This pattern suggests that some species are affected by forest harvesting, but are able to recover.

The beetle species abundances were also compared between sites and years within each stand (Appendix 2). Sites within the same stand were significantly different for some of the species. *Platynus decentis* was significantly more abundant in site FDO-2 than in FDO-1. However, this species is often found under loose bark on dead logs (D. Larson, pers comm.) and FDO-2 contained more and larger fallen logs than FDO-1, more than any other FD site. Although there may be some variation within the stands, variation between the stands was also significant for many species, and it was this difference beteen stands that was of importance in this study.

Species that made up 1% or more of the total number of individuals were different in each stand. Some species that were very abundant in the old growth stands were not as abundant in the previously cut stands and vice versa. Studies on sub-cortical beetles in pine and spruce forests (Väisänen et al., 1993), pselaphids in mixed deciduous-coniferous forest (Chandler, 1987), and carabids in tropical *Eucalyptus* forest (Michaels and McQuillan, 1995) all found that old growth sites had equal or slightly lower species richness compared to regrowth sites, but that the species composition in regrowth was quite different from that of old growth sites.

4.3.3 Loss of suitable microhabitats

One possible reason for the difference in beetle species between the different aged forests is the loss of suitable microhabitats in the previously cut forests. There were more and larger fallen logs in the FDO stand, as well as more bryophytes, which may indicate areas of higher relative humidity (Söderström, 1988), all things which may cause certain beetle species to be restricted to old growth forests.

Chandler (1987, 1991) and Chandler and Peck (1992) compared the abundances of several families of beetles in old growth and 40 year old forests in New Hampshire. Pselaphidae species that were associated with deciduous leaf litter or found beneath bark were more abundant in the old growth site (Chandler, 1987). Several other families associated with slime molds and fungi under tree bark, such as Eucinetidae, Sphinidae, Rhizophagidae, Pyrochroidae and Melandryidae were also more abundant in old growth forest (Chandler, 1991). This is because the old growth forest had more leaf litter and rotten wood than the 40 year old forest (Chandler, 1987). These taxa were collected in flight intercept traps, since they are able fliers. They were poorly represented in the pitfall data of the present study, with the exception of *Phellopsis obcordata*, *Stephostethus* sp. #1, *Atomaria* sp. #1 and Nitidulidae sp. #3. Fifty-one out of the 68 specimens of *Atomaria* sp. #1 were found in the FDO stand, but most individuals from the other three species, 43 out of 50 specimens, were found in one or both of the 60 year old stands.

Chandler and Peck (1992) found that species of Leiodidae associated with slime molds, and those feeding on carrion and fungi, were more abundant in the old growth site than in the 40 year old site, while those presumed to feed on hypogeal fungi were equally or more abundant in the 40 year old site. Specifically, they found *Agathidium* species and *Catops basilaris* to be more abundant in the old growth site, while *Leiodes assimilis* and *Colon* species were more abundant in the 40 year old site. The present study found *Agathidium* sp. #1 to be restricted to the old growth stands, but 11 out of 12 specimens of *Leiodes assimilis* were also found in the old growth stands, while *Catops basilaris* and *Colon magnicolle* were much more abundant in the 60 year old stands. However, *Catops basilaris* is attracted to carrion and may be more abundant in the 60 year old sites because the higher incidence of slugs in those sites caused the traps to become fouled more often by decaying slugs. The results of the experiment with baited traps confirmed that *Catops basilaris* preferred traps with bait than those without.

Väisänen et al. (1993) compared the sub-cortical beetle fauna living in dead pine and spruce, of primeval and managed forests. They found only 26 species in common between the two forests, out of a total of 107 species, and of the ten most abundant species, the forests had only one in common. They also found that the primeval forest had larger fallen logs that were more extensively decayed, with looser bark and it was speculated that this was due to a higher stable air humidity (Väisänen et al., 1993). The bark of dead trees in the managed forest dried out too rapidly for many sub-cortical species.

Niemelä et al. (1988) in Finland compared the carabid beetles of several types of primeval forest to those found in adjacent managed forests. Two species occurred only in old forests, while twenty species occurred only in managed forests. A similar study in Alberta by Niemelä et al. (1993) found ten species that decreased after clear-cut logging and 27 species that appeared exclusively, or in increased abundances, in the regenerating sites. Three *Bembidion* species were found only in the regenerating sites and *Pterostichus adstrictus* was more abundant in the regenerating sites, while *Platynus decentis* and *Calathus advena* decreased after clear-cutting. *Calathus ingratus* was most abundant in a 27 year old regenerating site. In the present study, *Platynus decentis*, *Calathus advena* and *C. ingratus* were restricted to the old growth stands. *Bembidion wingatei* was significantly more abundant in FDO and FD40 within the FD stands, and in FE40 and FE60 in the FE stands. However, in contrast with the findings of Niemelä et al. (1993), *Pterostichus adstrictus* was significantly more abundant in FDO than in the previously cut FD stands. Jennings et al. (1986) also found more *P. adstrictus* in uncut spruce-fir forests in Maine, than in clear-cut strips, as well as more *P. coracinus*, *P. punctatissimus*, *Platynus decentis* and *Calathus ingratus*. Although *P. adstrictus* is known to be found in a wide range of habitats, from forest to open meadow (Lindroth, 1969), females oviposit in fallen logs (Goulet, 1974), so they may rely on old growth forest for this resource. It has been found that a local assemblage of species is sometimes an artifact of the resources and conditions of neighbouring habitats (Pulliam, 1988).

4.3.1 Dispersal ability

Another factor that may cause differences in the beetle composition between old growth and cut forests is the poor dispersal ability of some species. In a study of the changes in crabid beetle distribution in the Netherlands since 1880, Turin and den Boer (1988) found that species with low powers of dispersal were becoming progressively endangered, while the occurrences of species with high powers of dispersal were more stable or increasing. Another study in heath areas of the Netherlands (de Vries, 1994) found that species with low powers of dispersal were almost absent from small, isolated heath fragments. Eyre (1994) collected carabids in England from 160 sites of different levels of disturbance and productivity. Two groups of species that were of large size, with low dispersal ability were restricted to sites of low disturbance levels, while several groups of highly mobile species were found in sites of mid to high disturbance, or were not restricted by level of disturbance (Eyre, 1994). Halme and Niemelä (1993) compared carabid abundance in coniferous forest fragments in Finland and found four strict forest specialists restricted to the contiguous old growth forest, three of which were large bodied and short winged. They also found that invasion of species from the surrounding habitat increased as the forest fragment size decreased (Halme and Niemelä, 1993). Even in 20 year old regrowth tropical rainforest, recolonizing pioneer species were winged and non-endemic, while the two species that were restricted to old growth forest were flightless (Michaels and McQuillan, 1995). The present study contained several species restricted to, or most abundant in old growth stands, that have low powers of dispersal, including *Platynus decentis, Pterostichus adstrictus, Calathus ingratus* (Lindroth, 1963), *Brathinus nitidus* and possibly *Stenichnus* sp. #1 (Arnett, 1963). *Pterostichus melanarius* was found only in the 60 year old stands along the Trans Canada Highway. This is an introduced species in Newfoundland, with populations on the west coast of the island that are mostly macropterous (Larson and Langor, 1982).

4.4 Disturbance and species diversity

The equilibrium model of community succession states that a community that is disturbed will return to its original state and that the final climax community is the one that will have the highest species diversity (McLeod, 1980). This view has been challenged in recent years and most ecologists now feel that a non-equilibrium model better fits the processes of most communities. This states that species diversity is greatest in areas where disturbance is intermediate in frequency and severity, because these areas can accomodate both rapidly colonizing species of early successional stages and competitive, late successional species (Campbell, 1987).

This has led some researches to conclude that preservation of large expanses of old growth forest would be a wasted effort, because they contain a low diversity of species

(Middleton and Merriam, 1985), and that disturbances, such as forest harvesting activities are beneficial because they increase species diversity. This, however, still assumes that old growth forest is somehow suspended in time, pristine and unchanging.

In fact, the norm for boreal ecosystems may be disturbances (Danks and Foottit, 1989), such as windthrows, insect defoliation, fungal disease and fires, creating dead standing trees, fallen logs and gaps in the canopy that allow saplings to grow (Kuuluvainen, 1994). Balsam fir forest actually relies on periodic infestations of spruce budworm, which create openings in the forest without disturbing the soil (McLeod, 1980). Forests under the control of the logging industry are managed by policies which interrupt natural forest processes by preventing, as much as possible, all forest fires and outbreaks of insect pests or disease. Old growth stands are then labelled 'decadent' and 'over-mature' if they are not harvested regularly (Page et al., 1974). Regrowth and managed forests often consist of monocultures that are artificially thinned, with any dead wood removed, and as such are quite homogeneous (Hansson, 1992).

Old growth forests are the areas that will support the greatest diversity of species, due to their high amount of heterogeneity. Managed forests don't contain enough suitable micro-habitats for many forest species, especially if they are harvested before decaying wood and leaf litter can accumulate on the forest floor. Rotation times of 60 years are probably too short to allow many old growth specialists the opportunity to become established in regrowth forests. This may cause the extinction of some old growth species.

5.0 CONCLUSION

This study found differences in the beetle fauna of old growth, 40 year old and 60 year old balsam fir forest stands, as well as differences between the forest types. The FE forest type is slightly more species rich than the FD type. The old growth and 60 year old stands both had higher beetle species richness than the 40 year old stand, but the species composition between the stands was quite different. Seventy species were caught in abundances of 5 or more individuals over the entire sampling period. Five of these species were found only in FDO and five species were found only in FEO. *Platynus decentis, Calathus advena, C. ingratus, Agathidium* species #1, *Stenichnus* species #1 and *Lesteva pallipes* were found only in the old growth stands, while a further 9 species were most abundant in one or both old growth stands. 10 species were significantly more abundant in the previously cut stands and 6 species showed possible recovery to old growth abundances 60 years after forest harvesting.

The old growth stands had more and larger fallen logs, more *Sphagnum* mosses, feather mosses and *Lycopodium*, as well as a more open canopy than the previously cut forests. Many forest species are prevented from recolonizing regrowth forest due to the lack of available microhabitats, such as decaying logs, or to limited dispersal abilities. Increased fragmentation of forests may lead to increased invasion of species from surrounding managed forests and a decline in old growth specialists.

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PERSONAL COMMUNICATIONS

Goudie, E., Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, 1996.

Larson, D.J., Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, 1996.

APPENDIX 1

These are brief descriptions of the stands each species was found in, general habitat, and North American distribution. n = the number of individuals found in all stands over the entire sampling period. All beetles were caught in pitfall traps and all descriptions of North American distribution are from the Checklist of Beetles of Canada and Alaska (Bousquet, 1991), unless otherwise specified.

CARABIDAE Latreille, 1802

Sphaeroderus nitidicollis Chevrolat, 1829 n = 9

Found only in FDO, FEO and FE40; significantly more abundant in late summer.

A forest species, preferring rather moist places with mosses and dead leaves (Lindroth, 1969). Hindwings non-functional (Lindroth, 1963).

Eastern North America; once restricted to Newfoundland (Lindroth, 1969), now also found in Quebec.

Clivina fossor (Linnaeus), 1758 n = 1

One specimen from FD60.

On cultivated, usually clayish soil; often in parks and gardens (Lindroth, 1969). Shows wing dimorphism (Lindroth, 1969). FD60 is close to the Trans Canada Highway, so this specimen may have wandered into this site from there.

Introduced to North America (Lindroth, 1969).

Trechus apicalis Motschulsky, 1845 n = 113

Found in all stands except FD40; shows possible decrease, then recovery to former abundances 60 years after forest harvesting in the FD forest type; more abundant in FE than in FD.

Found under leaves and stones in damp situations (Downie and Arnett, 1996). Hindwings non-functional in Newfoundland specimens, but dimorphic elsewhere (Lindroth, 1963).

Holarctic.

T. crassiscapus Lindroth, 1955 n = 25

Found in FDO, FD60, FE40 and FE60; significantly more abundant in FD60 than in FDO.

Lives in small woodland swamps (Downie and Arnett, 1996). Hindwings non-functional (Lindroth, 1963).

Eastern North America (Lindroth, 1969).

Bembidion wingatei Bland, 1863 n = 1076

Found in all stands except FEO; significantly more abundant in FDO and FD40 than in FD60; more abundant in FD than FE; significantly more abundant in early summer than late summer.

Almost subterranean, occurring both under deep-lying stones in open grassland and among leaves in shady deciduous forest (Lindroth, 1969). Hindwings non-functional (Lindroth, 1963).

Eastern North America.

Pterostichus adstrictus Eschscholtz, 1823 n = 91

Found only in FDO, FD40 and FEO; significantly more abundant in FDO than in FD40; more abundant in FD than in FE; significantly more abundant in early summer than in late summer.

A common beetle in northern coniferous regions. However, it prefers open country, where the soil is moderately moist or rather dry; also on cultivated ground (Lindroth, 1969). Fully developed hindwings (Lindroth, 1963). Oviposits in decaying wood (Goulet, 1974).

Holarctic (Lindroth, 1969).

P. coracimus (Newman), 1838 n = 172

Found in all stands; significantly more abundant in both old growth stands than in the previously cut stands; more abundant in FE than in FD; significantly more abundant in early summer than in late summer.

A common species under logs and stones in woods (Downie and Arnett, 1996). Also in wet coastal areas and open fields and meadows (Lindroth, 1969). Hindwings non-functional (Lindroth, 1963).

Eastern North America.

P. melanarius (Illiger), 1798 n = 9

Found only in 60 year old stands.

In light forest and on open meadows, cultivated land, waste places (Lindroth, 1969). Shows wing dimorphism (Larson and Langor, 1982).

Introduced to North America (Lindroth, 1969).

P. punctatissimus (Randall), 1838 n = 119

Found in all stands; significantly more abundant in FD40 than in FDO and FD60, and significantly more abundant in FDO than in FD60; more abundant in FE than in FD.

In conifer or mixed forests, usually under bark and moss on tree stumps (Lindroth, 1969). Hindwings non-funtional (Lindroth, 1963).

Nearctic.

Harpalus nigritarsis C.A. Sahlberg, 1827 n = 3

Three specimens from FEO.

On open, rather dry, firm soil, mostly gravel, with dense but short vegetation (Lindroth, 1969). Wings constantly full and large (Lindroth, 1969). May have flown into this site from the gravel logging road.

Holarctic (Lindroth, 1969).

Calathus ingratus Dejean, 1828 n = 5

Found only in FDO; significantly more abundant in early summer than late summer.

A common beetle of northern forests; lives among dead leaves under bushes and deciduous trees in moist or dry ground (Downie and Arnett, 1996). Wings usually highly reduced, but macropterous specimens recorded (Lindroth, 1969).

Nearctic (Lindroth, 1969).

Calathus advena (LeConte), 1848 n = 59

Found only in FDO.

Primarily a forest insect, occurring among leaves and debris, often in very shady places with little vegetation and not too much moisture (Lindroth, 1969). Mostly macropterous (Lindroth, 1969).

Nearctic (Lindroth, 1969).

Platynus decentis (Say), 1823 n = 165

Found only in old growth stands; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

A pronounced forest species, often found under bark and logs (Lindroth, 1969). Hindwings seemingly full, but so small that they cannot be functional (Lindroth, 1969).

Nearctic (Lindroth, 1969).

DYTISCIDAE Leach, 1815

Hydroporus paugus Fall, 1923 n = 1

One specimen from FEO.

Found in small ponds along margins of lakes and streams (Downie and Arnett, 1996). This specimen is probably an incidental capture.

Nearctic.

PTILIIDAE Erichson, 1845; Motschulsky 1845

No Ptiliidae have been previously recorded from Newfoundland (Bousquet, 1991). Three species were found in this study, in high abundances. Identification is difficult.

Ptenidium species #1 n = 462

Found only in FE; significantly more abundant in FE60 than in FEO and FE40; significantly more abundant in late summer.

Found in forest floor litter, compost grass piles, tree holes, nests (Dybas, 1990).

Three species known from Canada, none from Newfoundland. Identified to genus by Megan McCarthy using Dybas, 1990.

Millidium (Ptilium) minutissimum (Ljungh), date ? n = 62

Found in all stands except FE60; significantly more abudant in FDO than in FD40; more abundant in FD than in FE; significantly more abundant in late summer than in early summer.

Found in decaying vegetation and other rotting organic materials on the forest floor (Downie and Arnett, 1996).

New Newfoundland record; introduced to North America (Dybas, 1990). Identified to species by David Larson.

Acrotrichus species #1 n = 1071

Found in all stands; significantly more abundant in FD40 than in FDO and FD60; shows possible increase, then recovery to former abundances 60 years after forest harvesting; more abundant in FD than in FE.

Found in decaying floor litter, dung, compost, decaying fungi, nests, under carrion, and other debris (Dybas, 1990).

Eighteen species known from Canada, none from Newfoundland. Identified to genus by David Larson.

LEIODIDAE Fleming, 1821

Leiodes assimilis (LeConte), 1850 n = 12

Found only in FEO and FE60; significantly more abundant in FEO than in FE60.

Usually in forested habitats (Peck, 1990).

Nearctic.

Agathidium species #1 n = 16

Found only in old growth stands.

Usually found in forested habitats and on slime molds (Peck, 1990).

Seventeen species known from Canada, none from Newfoundland. Identification to genus confirmed by CLBRR, Ottawa.

LEPTODIRIDAE Solier, 1834

Colon magnicolle Mannerheim, 1853 n = 15

Found in FD40, FD60, FEO and FE60; significantly more abundant in FD60 than in FD40.

On carrion and fungi (Downie and Arnett, 1996).

Nearctic.

Catops basalaris Say, date ? n = 271

Found in all stands; more abundant in FE than in FD.

Found on carrion and fungi (Downie and Arnett, 1996).

Nearctic.

SCYDMAENIDAE Leach, 1815

Stenichnus species #1 n = 12

Found only in old growth stands.

Found under stones and bark where they live with ants or termites (Downie and Arnett, 1996).

Ten species known from Canada, none from Newfoundland. Identified to genus by David Larson.

MICROPEPLIDAE

Micropeplus laticollis Maklin, 1853 n = 5

Four specimens from FDO and one from FD40.

Found by sifting soil and tree duff (Downie and Arnett, 1996).

New Newfoundland record; Nearctic. Identified to species by David Larson.

SILPHIDAE Latreille, 1807

Nicrophorus defodiens Mannerheim, date ? n = 20

Found in all stands except FEO; more abundant in FE than in FD.

Found on carrion (Downie and Arnett, 1996).

Nearctic.

N. sayi Castelnau, date ? n = 10

Found in FD40 and FD60.

Found on carrion (Downie and Arnett, 1996).

Eastern North America.

STAPHYLINIDAE Latreille, 1802

Proteininae

Megarthrus americanus Sachse, date ? n = 24

Found only in the previously cut stands.

Found on fungi (Downie and Arnett, 1996).

New Newfoundland record; eastern North America. Identification to species confirmed by CLBRR, Ottawa.

Proteinus limbatus Mäklin, date ? n = 2425

Found in all stands; significantly more abundant in FD40 than in FDO and FD60; significantly more abundant in FE40 and FE60 than in FEO; more abundant in FD than in FE; significantly more abundant in late summer than early summer.

Habitat unknown.

New Newfoundland record; Holarctic. Identification to species confirmed by CLBRR, Ottawa.

Omaliinae

Eusphalerum pothos (Mannerheim), date ? n = 15

Found in all stands except FDO.

Common on flowers (Downie and Arnett, 1996).

Nearctic.

Elonium diffusum (Fauvel), date ? n = 4589

Found in all stands; significantly more abundant in FD40 than in FDO and FD60;

shows increase, then possible recovery to former abundances 60 years after forest harvesting; more abundant in FD than in FE; significantly more abundant in late summer than early summer.

Habitat unknown.

Eastern North America.

Omalium rivulare (Paykull), date ? n = 13

Found in FDO, FD40, FD60 and FE40.

Habitat unknown.

Introduced to North America. Nine species of *Omalium* are known from Canada, but only this species is known from Newfoundland. However, two other distinct species were found in this study. Their identification as two separate species of *Omalium* was confirmed by CLBRR, Ottawa.

Omalium species #2 n = 32

Found in FDO, FD60, FE40 and FE60.

Habitat unknown.

Omalium species #3 n = 16

Found in FDO, FD40, FD60 and FE60.

Habitat unknown.

Brathinus nitidus LeConte, 1852 n = 52

Found only in FEO and FE40; significantly more abundant in FEO than in FE40; significantly more abundant in late summer than early summer.

Poorly known; these are rare beetles found in among the roots of grass growing near water (Arnett, 1963).

Eastern North America.

Acidota subcarinata Erichson, 1840 n = 59

Found in all stands; significantly more abundant in FDO than in FD40 and FD60; more abundant in FE than in FD; significantly more abundant in late summer than early summer.

Found by sweeping undergrowth of deciduous woods, sifting dead leaves from the forest floor, and in early April from flood debris in a pine forest (Campbell, 1982b).

Eastern North America (Campbell, 1982b).

Olophrum consimile (Gyllenhal), date ? n = 16

Found only in FE; significantly more abundant in FE40 than FEO; significantly more abundant in late summer than early summer.

Found in deciduous leaf litter along streams or at the edges of ponds and lakes, small deciduous shrubs or moss growing in shallow water (Campbell, 1983).

Holarctic (Campbell, 1983).

O. rotundicolle (C.R. Sahlberg), date ? n = 103

Found in all stands; significantly more abundant in FDO than in FD40; significantly more abundant in FEO than in FE40 and FE60; more abundant in FE than in FD; significantly more abundant in late summer than early summer.

Found in moss at the edges of lakes, bogs and small streams and in moist litter

(Campbell, 1983).

Holarctic (Campbell, 1983).

Arpedium cribratum Fauvel, 1878 n = 278

Found in FD40, FD60 and FEO; significantly more abundant in FD40 than in FD60; shows possible increase, then recovery, to former abundances 60 years after forest harvesting; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

Found under cover in damp locations (Downie and Arnett, 1996).

Nearctic.

Lesteva pallipes LeConte, 1863 n = 68

Found only in FEO.

Habitat unknown.

Eastern North America.

Piestinae

Siagonium americanum Melsheimer, date ? n = 1

One specimen from FDO.

Associated with wood (Hatch, 1957).

Eastern North America.

Oxytelinae

Oxytelus fuscipennis Mannerheim, date ? n = 166

Found in all stands; significantly more abundant in FD60 than in FDO and FD40;

significantly more abundant in FEO and FE60 than in FE40; more abundant in FE than in FD; significantly more abundant in late summer than early summer.

Found mainly on dung (Newton, 1990).

New Newfoundland record; Nearctic. Identified to species by David Larson.

Pseudopsinae

Pseudopsis subulata Herman, 1975 n = 744

Found in all stands except FEO; significantly more abundant in FD40 and FD60 than in FDO; significantly more abundant in FE60 than in FE40; significantly more abundant in late summer than early summer.

Found in leaf litter of mixed broadleaf forests and in leaf litter under animal dung (Herman, 1975).

Eastern North America.

Tachyporinae

Tachinus basalis Erichson, 1840 n = 29

Found in all stands except FEO; more abundant in FD than in FE; significantly more abundant in late summer than early summer.

Found with dung, but may be taken from rotting mushrooms or under carrion (Campbell, 1973).

New Newfoundland record; Holarctic (Campbell, 1973). Identification to species confirmed by CLBRR, Ottawa.

T. elongatus Gyllenhal, 1810 n = 80

Found in all stands except FE40; significantly more abundant in FDO than in FD40 and FD60, and significantly more abundant in FD60 than FD40; more abundant in FD than in FE.

Found under stones in very damp places, in wet moss and from under damp and decayed piles of leaves or rubbish; occasionally found under dung and carrion (Campbell, 1973).

Holarctic (Campbell, 1973).

T. frigidus Erichson, 1840 n = 1030

Found in all stands; significantly more abundant in FDO than in FD40 and FD60, and significantly more abundant in FD40 than in FD60; significantly more abundant in FE40 than in FEO and FE60; more abundant in FD than in FE; significantly more abundant in late summer than early summer.

Found under various kinds of animal dung, from the mouth of mammal burrows, in leaf litter and rotting mushrooms (Campbell, 1973).

Nearctic (Campbell, 1973).

T. quebecensis Robert, 1946 n = 325

Found in all stands except FEO; significantly more abundant in FDO and FD40 than in FD60; more abundant in FD than in FE; significantly more abundant in late summer than early summer.

Found on decaying mushrooms (Campbell, 1973).

Nearctic (Campbell, 1973).

T. tachyporoides Horn, 1877 n = 14

Found only in the previously cut stands; more abundant in FE than in FD.

Found primarily in cool wet habitats (Campbell, 1973).

Nearctic (Campbell 1973).

T. thruppi Hatch, 1957 n = 57

Found in FD40, FD60, FEO and FE60; significantly more abundant in FD40 than in FD60; more abundant in FD than FE; significantly more abundant in late summer than early summer.

Habitat unknown.

Nearctic.

Tachyporus nitidulus (Fabricius), 1781 n = 10

Found only in 60 year old stands; significantly more abundant in early summer than late summer.

Found in leaf litter in wet habitats and in decaying material in hollow logs and stumps (Campbell, 1979).

Holarctic (Campbell, 1979).

Sepedophilus testaceous (Fabricius), 1792 n = 1

One specimen from FD40.

Found under loose decaying bark, in fungi or in decaying leaves and other vegetation (Downie and Arnett, 1996).

Introduced to eastern North America.

Lordithon facilis (Casey), 1884 n = 32

Found in all FD stands and FE60; significantly more abundant in FD40 than in FDO and FD60; shows possible increase, then recovery to former abundances 60 years after forest harvesting; more abundant in FD than in FE.

Found on a wide variety of mushrooms (Campbell, 1982a). They feed on the larvae of flies that eat the fungi (Downie and Arnett, 1996).

Eastern North America (Campbell, 1982a).

L. thoracicus (Fabricius), 1776 n = 3

One specimen from FDO and two from FD40.

Same habitat as above.

Holarctic (Campbell, 1982a).

L. fungicola Campbell, 1978 n = 384

Found in all stands; significantly more abundant in FDO than in FD40 and FD60; more abundant in FD than in FE.

Same habitat as above.

Nearctic (Campbell, 1982a).

Mycetoporus horni Bernhauer and Schubert, 1916 n = 1

One specimen from FDO.

Found in forest litter, moose dung, moss and rotten wood (Campbell, 1991).

Eastern North America (Campbell, 1991).

Ischnosoma fimbriatum Campbell, 1990 n = 33

Found in all stands; significantly more abundant in FD40 than FD60.

Found in forest litter, moss, rotten wood and under stones (Campbell, 1991).

Nearctic (Campbell, 1991).

I. splendidum (Gravenhorst), 1806 n = 94

Found in all stands; significantly more abundant in FDO than in FD40 and FD60, and significantly more abundant in FD60 than in FD40; significantly more abundant in FE60 than in FE40.

Found in a variety of wet habitats and from a variety of types of leaf litter in forests (Campbell, 1991).

Holarctic.

Aleocharinae

These beetles are known or suspected to feed on molds or other soil inhabiting fungi (Newton, 1990). Identification to genus by David Larson. The Aleocharinae are very difficult to identify with existing keys, however, they are widely distributed across North America. No *Oxypoda* or *Gyrophaena* species are recorded from Newfoundland (Bousquet, 1991).

Oxypoda species #1 n = 1306

Found in all stands; significantly more abundant in FDO than in FD60; significantly more abundant in FE40 and FE60 than in FEO; significantly more abundant in late summer than early summer.

O. species #2 n = 63

Found in all stands with fairly equal abundances.

Gyrophaena species #1 n = 3

Two specimens from FD40 and one from FD60.

Aleocharinae species #4 n = 1013

Found in all stands; significantly more abundant in FDO than in FD40 and FD60; significantly more abundant in FE60 than in FEO and FE40; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

Aleocharinae species #5 n = 48

Found in all stands except FE60; significantly more abundant in FDO than FD60; more abundant in FD than in FE.

Aleocharinae species #6 n = 1101

Found in all stands; more abundant in FE than FD; significantly more abundant in late summer than early summer.

Aleocharinae species #7 n = 2

Two specimens from FEO.

Aleocharinae species #8 n = 97

Found in all stands except FDO.

Other Aleocharinae species n = 1435

Found in all stands; significantly more abundant in FE40 and FE60 than FEO; significantly more abundant in late summer than early summer.

Steninae

Stenus egenulus Puthz, 1974 n = 47

Found in FDO, FD60 and FE60; significantly more abundant in FDO than in FD60; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

Found on vegetation in damp situations (Downie and Arnett, 1996).

Nearctic.

Euaesthetinae

Euaesthetus species #1 n = 2

Two specimens from FDO.

Found on flowers (Arnett, 1963), mainly in wet habitats (Newton, 1990).

Eight species known from Canada, *E. americanus* known from Newfoundland.

Paederinae

Lathrobium fauveli Duvivier, date ? n = 11

Found in all stands except FEO.

Found in damp leaf litter, moss and other debris along streams, bogs, marshes, swamps, ponds and other riparian situations (Watrous, 1980).

Eastern North America.

L. fulvipenne (Gravenhorst), date ? n = 6

Found only in FD60.

Same habitat as above.

Introduced to North America.

L. washingtoni Casey, 1905 n = 3

Two specimens from FD60 and one from FE60.

Same habitat as above.

Nearctic.

Staphylininae

Philonthus seigwaldii Mannerheim, date ? n = 12

Found in nearly equal abundances in all stands.

Found on carrion, dung and decaying vegetable materials; also occur under stones and boards (Hatch, 1957).

Nearctic.

Gabrius brevipennis (Horn), 1884 n = 18

Found in FDO, FD60, FEO and FE40; significantly more abundant in FDO than in FD60.

Habitat unknown.

Nearctic.

Ontholestes cingulatus (Gravenhorst), date ? n = 1

One specimen from FD60.

A common species on dung and decaying fungi (Downie and Arnett, 1996).

Nearctic.

Quediinae

Quedius labradorensis Smetana, 1965 n = 2

Two specimens from FEO.

Found in fallen leaves of forests with rich vegetation (Smetana, 1971).

Nearctic (Smetana, 1971).

Q. densiventris (Casey), 1915 n = 449

Found in all stands except FEO; significantly more abundant in FDO than in FD40 and FD60, and significantly more abundant in FD60 than FD40; more abundant in FD than in FE.

Found in wet biotopes of various kinds in moss, debris, under fallen leaves, etc. and often near water (Smetana, 1971).

Nearctic (Smetana, 1971).

Q. fulvicollis (Stephens), 1832 n = 54

Found in all stands; significantly more abundant in FDO and FD60 than in FD40; shows possible decrease, then recovery to former abundances 60 years after forest harvesting; more abundant in FD than in FE.

Found in wet biotopes of various kinds in moss, various debris and under fallen leaves; often in swampy and marshy biotopes in wet *Sphagnum* (Smetana, 1971).

Holarctic (Smetana, 1971).

Xantholininae

Atrecus macrocephalus (Nordmann), 1837 n = 8

Three specimens in FDO, 4 in FD40 and 1 in FD60.

Found under loose bark of dead or dying trees, usually conifers, or in the debris fallen from such trees; some in hardwoods (Downie and Arnett, 1996).

Nearctic.

PSELAPHIDAE Latreille, 1802

Lucifotychus testaceous (Casey), date ? n = 3

One specimen from FD60, one from FEO and one from FE40.

Found on mold that occurs on logs or in the forest floor (Downie and Arnett, 1996).

Eastern North America.

HYDROPHILIDAE Latrielle, 1802

Anacaena limbata (Fabricius), 1792 n = 1

One specimen from FD60.

Found in shallow standing water, along muddy shores with wet debris, wet moss and grasses, etc. (Smetana, 1988).

Introduced to North America (Smetana, 1988).

Cymbiodyta vindicata Fall, 1924 n = 1

One specimen from FDO.

Found in *Sphagnum*, humus, wet swamp grass (Smetana, 1974).

Nearctic (Smetana, 1974).

Cercyon haemorrhoidalis (Fabricius), 1775 n = 6

One specimen from FD40, one from FD60, three from FEO and one from FE60.

Found in dung of herbivorous animals, decaying fungi or other decaying plant material (Downie and Arnett, 1996).

Introduced to North America (Smetana, 1988).

C. minusculus Melsheimer, 1846 n = 1

One specimen from FD40.

Found in fermenting organic matter and litter under decaying fungus (Smetana, 1978).

Neartic.

Cryptopleurum minutum (Fabricius), 1775 n = 1

One specimen from FD60.

Found in dung of herbivorous animals, decaying fungi, or other decaying plant material (Downie and Arnett, 1996).

Introduced to North America (Smetana, 1988).

SCARABAEIDAE Latreille, 1804

Aegialia rufescens Horn, 1887 n = 26

Found in all stands except FEO; more abundant in FD than in FE.

Habitat unknown.

New Newfoundland record; Nearctic. Identification confirmed by CLBRR, Ottawa.

Aphodius borealis Gyllenhal, date ? n = 2

Two specimens from FEO.

Found in moose or caribou dung (Gordon, 1983).

Holarctic.

A. leopardus Horn, date ? n = 2

Two specimens from FEO.

Found in deer dung (Gordon, 1983).

Nearctic.

Geotrupes stercorarius (Linnaeus), 1958 n = 3

Three specimens from FD60.

Lives on horse or cow dung (Downie and Arnett, 1996).

Introduced to eastern North America.

ELATERIDAE Leach, 1815

Hypnoidus bicolor (Eschscholtz), 1829 n = 1

One specimen from FEO.

Same habitat as above.

Holarctic.

Ctenicera nitidula (LeConte), 1853 n = 3

Two specimens from FD40 and one from FD60.

Same habitat as above.

Nearctic.

C. pygmaea (Van Dyke), 1932 n = 4

One specimen from FDO, two from FD60 and one from FE60.

Same habitat as above.

Nearctic.

C. spinosa (LeConte), 1853 n = 7

Four specimens from FDO, one from FD60, one from FE40 and one from FE60.

Found under bark and stones, sitting on flowers and vegetation (Downie and Arnett, 1996).

Eastern North America.

Eanus maculipennis LeConte, 1863 n = 1

One specimen from FE60.

Same habitat as above.

Eastern North America.

EUCNEMIDAE Eschscholtz, 1829

Epiphanis cornutus Eschscholtz, 1829 n = 1

One specimen from FDO.

Found on coniferous trees (Downie and Arnett, 1996).

Nearctic.

CANTHARIDAE Imhoff, 1856

Podabrus species #1 n = 20

Found in all stands except FE40; significantly more abundant in FDO than in

FD60; significantly more abundant in FE60 than in FE40.

Found in large numbers on flowers of golderod; also on vegetation along the edges of water (Downie and Arnett, 1996).

Fifty species of *Podabrus* known from Canada, 6 from Newfoundland.

P. species #2 n = 7

One specimen from FDO, two from FD40, two from FD60 and two from FE60.

Same habitat as above.

Malthodes species #1 n = 3

One specimen from FD60 and two from FE60.

Same habitat as above.

20 species known from Canada, 3 from Newfoundland.

PTINIDAE Latreille, 1802

Ptinus raptor Sturm, date ? n = 1

One specimen from FEO.

A pest of warehouses and flower mills (Downie and Arnett, 1996). This specimen may have already been present in the pitfall trap or one of the vials before they were taken to the study site.

Introduced to North America.

NITIDULIDAE Latreille, 1802

Epuraea truncatella Mannerheim, 1846 n = 1

One specimen from FD40.

Found on decaying fungi (Downie and Arnett, 1996).

Nearctic.

Omosita discoidea (Fabricius), date ? n = 4

Three specimens from FD60 and one from FE60.

Feeds on dry carrion, bones, hides, fungi and decaying vegetation (Downie and Arnett, 1996).

Nearctic; may be introduced.

Nitidulidae species #3 n = 16

Found only in previously cut stands; significantly more abundant in FD60 than in FDO and FD40.

RHIZOPHAGIDAE Redtenbacher, 1845

Rhizophagus dimidiatus Mannerheim, 1843 n = 2

One specimen from FDO and one from FD40.

Under bark of fir, spruce and pine (Downie and Arnett, 1996).

Nearctic.

CRYPTOPHAGIDAE Kirby, 1837

Caenoscelis species #1 n = 2

One specimen from FDO and one from FD60.

Found on flowers and leaves, fungi, in rotton logs and beneath dead leaves (Downie and Arnett, 1996).

Four species known from Canada, none from Newfoundland. Identified to genus by David Larson.

Atomaria species #1 n = 68

Found in all stands except FEO; significantly more abundant in FDO than in FD40 and FD60; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

Same habitat as above.

Twenty-two species known from Canada, none from Newfoundland.

Identification to genus confirmed by CLBRR, Ottawa.

LATHRIDIIAE Reitter, 1845

Stephostethus species #1 n = 17

Found in all the FD stands and FE60; significantly more abundant in FD60 than in FDO and FD40.

Found on decaying foliage of recently fallen tree limbs (Downie and Arnett, 1996).

Seven species known from Canada, *S. lardarius* known from Newfoundland.

CIIDAE Leach, in Samouelle, 1819

Cis species #1 n = 2

One specimen from FDO and one from FD60.

Found under bark and on various fungi (Downie and Arnett, 1996).

Fifteen species known from Canada, 3 from Newfoundland.

MELANDRYIDAE Leach, 1815

Melandrya labiata Say, date ? n = 1

One specimen from FD60.

Found under loose bark, on fungi (Downie and Arnett, 1996).

Eastern North America.

Zilora hispida LeConte, 1866 n = 1

One specimen from FE60.

Found under loose bark, on fungi (Downie and Arnett, 1996).

Nearctic.

Prothalpia undata LeConte, 1862 n = 1

One specimen from FD40.

Found on fungi (Downie and Arnett, 1996).

Eastern North America.

Serropalpus coxalis Mank, date ? n = 2

One specimen from FD60 and one from FE60.

Found on coniferous trees (Downie and Arnett, 1996).

Nearctic.

ZOPHERIDAE

Phellopsis obcordata (Kirby), date ? n = 17

Found in all stands except FE40; significantly more abundant in FD60 than in FD40.

Found on bracket fungi on decaying grey birch trees (Downie and Arnett, 1996).

Nearctic.

TENEBRIONIDAE Latreille, 1802

Bius estriatus (LeConte), 1851 n = 1

One specimen from FD40.

Habitat unknown.

New Newfoundland record; Nearctic. Identified to species by David Larson.

CEPHALOIDAE LeConte, 1862

Cephaloon ungulare LeConte, 1874 n = 1

One specimen from FDO.

Found on flowers, foliage (Downie and Arnett, 1996).

Eastern North America.

PYROCHROIDAE Latreille, 1807

Dendroides concolor (Newman), date ? n = 1

One specimen from FDO.

Found under loose bark, on flowers and herbage (Downie and Arnett, 1996).

Eastern North America.

SCRAPTIIDAE

Anaspis rufa Say, date ? n = 1

One specimen from FE60.

Found on flowering shrubs (Downie and Arnett, 1996).

Nearctic.

CERAMBYCIDAE Latreille, 1802

Evodinus monticola (Randall), 1838 n = 3

One specimen from FD40 and two from FD60.

Larvae develop in various conifers (Downie and Arnett, 1996).

Eastern North America.

CHRYSOMELIDAE Latreille, 1802

Syneta extorris W.J. Brown, date ? n = 3

Two specimens from FD60 and one from FEO.

Found on species of pine and spruce (Downie and Arnett, 1996).

Eastern North America.

CURCULIONIDAE Latreille, 1802

Otiorhynchus sulcatus (Fabricius), date ? n = 2

Two specimens from FD60.

Found on strawberries and cranberries (Downie and Arnett, 1996).

Introduced to North America.

Hylobius warreni Wood, date ? n = 149

Found in all stands; significantly more abundant in FD40 and FD60 than in FDO; more abundant in FD than in FE; significantly more abundant in early summer than late summer.

Attacks inner bark and cambium of numerous pines, firs, tamarack and spruce (Downie and Arnett, 1996).

Nearctic.

Pissodes similis Hopkins, 1911 n = 2

One specimen from FD40 and one from FD60.

Found on Balsam fir (Downie and Arnett, 1996).

Nearctic.

Rhyncolus brunneus Mannerheim, date ? n = 25

Found in all stands; significantly more abundant in FDO than in FD40 and FD60.

Found on wild cherry (Downie and Arnett, 1996).

Nearctic.

SCOLYTIDAE Latreille, 1804

Phloeotribus piceae Swaine, 1911 n = 1

One specimen from FE60.

Found on species of spruce (Downie and Arnett, 1996).

New Newfoundland record; Nearctic. Identifiction to species by Megan McCarthy using Downie and Arnett, 1996.

Trypodendron lineatum (Olivier), 1795 n = 2

One specimen from FDO and one from FD60.

Found on coniferous trees (Downie and Arnett, 1996).

Nearctic.

Xyleborus species #1 n = 3

One specimen from FDO and two from FE60.

Found on hardwood trees (Downie and Arnett, 1996).

Seven species known from Canada, *X. dispar* known from Newfoundland.

APPENDIX 2

Table A.1. Results of Mann-Whitney U tests comparing between years and between sites within the old growth stands. A significant difference between sites or stands is indicated with the name of the site or stand which had significantly more of that species present. ns = compared sites or stands not significantly different, 0 = no specimens found in compared sites or stands.

SPECIES	1/92 vs. 1/93	2/92 vs. 2/93	1/92 vs. 2/92	1/93 vs. 2/93	1 vs. 2	FDO/92 vs. FDO/93	7 vs. 8
Acidota subcarinata	ns	ns	ns	1/93	ns	ns	ns
Acrotrichus sp. #1	ns	ns	2/92	ns	2	FDO/93	ns
Aegialia rufescens	ns	ns	ns	ns	ns	ns	0
Agathidium sp. #1	ns	ns	ns	ns	ns	ns	ns
Arpedium cribratum	0	0	0	0	0	0	ns
Atomaria sp. #1	ns	2/93	ns	2/93	2	FDO/93	0
Atrecus macrocephalus	ns	0	ns	ns	ns	ns	0
Bembidion wingatei	ns	ns	ns	ns	ns	ns	0
Brathinus nitidus	0	0	0	0	0	0	ns
Calathus advena	ns	2/92	ns	ns	ns	FDO/92	0
C. ingratus	0	ns	ns	ns	2	ns	0
Colon magnicolle	0	0	0	0	0	0	ns
Ctenicera spinosa	ns	ns	ns	ns	ns	ns	0
Elonium diffusum	1/92	2/92	1/92	1/93	1	FDO/92	ns
Eusphalerum pothos	0	0	0	0	0	0	ns
Gabrius brevipennis	0	ns	2/92	2/93	2	ns	ns
Hylobius warreni	ns	ns	ns	ns	ns	ns	ns
Ischnosoma fimbriatum	ns	ns	ns	ns	ns	ns	ns
I. splendidum	ns	ns	ns	ns	ns	ns	ns
Lathrobium fauveli	0	ns	ns	0	ns	ns	0

Leiodes assimilis	0	0	0	0	0	0	ns
Lesteva pallipes	0	0	0	0	0	0	8
Lordithon facilis	ns	ns	0	ns	ns	ns	0
L. fungicola	ns	2/93	ns	ns	ns	FDO/93	ns
Micropeplus laticollis	0	ns	ns	ns	ns	ns	0
Millidium minutissimum	ns	2/92	ns	ns	ns	FDO/92	8
Olophrum consimilie	0	0	0	0	0	0	ns
O. rotundicolle	ns	0	ns	1/93	1	ns	ns
Omalium flavidum	ns	ns	ns	0	ns	FDO/92	0
O. sp. #2	0	ns	ns	0	ns	ns	0
O. sp. #3	ns	ns	ns	ns	ns	ns	0
Oxytelus fuscipennis	1/93	ns	ns	ns	ns	ns	8
Phelopsis obcordata	ns	ns	ns	ns	ns	ns	ns
Philonthus seigwadii	ns	0	ns	ns	ns	ns	ns
Platynus decentis	1/92	ns	2/92	2/93	2	FDO/92	ns
Podabrus sp. #1	ns	ns	ns	ns	ns	ns	ns
P. sp. #2	ns	0	ns	0	ns	ns	0
Proteinus limbatus	ns	2/92	1/92	1/93	1	FDO/92	ns
Pseudopsis subulata	1/93	ns	ns	ns	ns	FDO/93	0
Ptenidium sp. #1	0	0	0	0	0	0	7
Pterostichus adstrictus	1/92	ns	2/92	2/93	2	ns	ns
P. coracinus	0	ns	2/92	2/93	2	ns	8
P. puntatissimus	ns	ns	2/92	ns	2	ns	ns
Quedius densiventris	ns	ns	ns	2/93	2	ns	0
Q. fulvicollis	ns	2/93	ns	ns	ns	ns	ns
Rhyncolus brunneus	ns	ns	ns	ns	ns	ns	ns
Sphaeroderus nitidicollis	ns	0	ns	ns	ns	ns	ns

Stenichnus sp. #1	0	2/92	2/92	ns	2	FDO/92	ns
Stenus egenulus	ns	ns	ns	2/93	2	ns	0
Stephostethus sp. #1	ns	0	0	ns	ns	ns	0
Tachinus basalis	ns	ns	ns	ns	ns	ns	0
T. elongatus	ns	ns	ns	ns	ns	ns	ns
T. frigidus	ns	2/92	ns	1/93	1	FDO/92	ns
T. quebecensis	1/92	2/92	1/92	1/93	1	FDO/92	0
T. thruppi	0	0	0	0	0	0	ns
Trechus apicalis	1/93	2/93	ns	ns	ns	FDO/93	ns
T. crassiscapus	ns	0	ns	0	ns	ns	0

Table A.2. Results of Mann-Whitney U tests comparing between years and between sites within the 40 year old stands. A significant difference between sites or stands is indicated with the name of the site or stand which had significantly more of that species present. ns = compared stands or sites not significantly different, 0 = no specimens found in compared sites or stands.

SPECIES	3/92 vs. 3/93	4/92 vs. 4/93	3/92 vs. 4/92	3/93 vs. 4/93	3 vs. 4	FD40/92 vs. FD40/93	9 vs. 10
Acidota subcarinata	0	ns	0	ns	ns	ns	ns
Acrotrichus sp. #1	3/93	4/92	4/92	3/93	ns	ns	ns
Aegialia rufescens	ns	ns	ns	ns	ns	ns	ns
Arpedium cribratum	3/93	4/93	0	3/93	3	FD40/93	0
Atomaria sp. #1	0	ns	ns	ns	4	ns	ns
Atrecus macrocephalus	ns	ns	ns	ns	ns	ns	0
Bembidion wingatei	ns	4/92	ns	3/93	3	FD40/92	ns
Brathinus nitidus	0	0	0	0	0	0	ns
Colon magnicolle	0	ns	ns	0	ns	ns	0
Ctenicera spinosa	0	0	0	0	0	0	ns
Elonium diffusum	3/92	4/92	ns	ns	ns	FD40/92	10
Eusphalerum pothos	0	ns	ns	0	ns	ns	9
Gabrius brevipennis	0	0	0	0	0	0	ns
Hylobius warreni	ns	ns	4/92	ns	4	ns	ns
Ischnosoma fimbriatum	3/93	ns	ns	ns	ns	ns	ns
I. splendidum	0	ns	ns	0	ns	ns	9
Lathrobium fauveli	ns	0	ns	0	ns	ns	ns
Lordithon facilis	3/93	4/93	0	ns	ns	FD40/93	0
L. fungicola	ns	4/93	ns	ns	ns	FD40/93	ns
Megarthrus americanus	ns	ns	ns	0	ns	ns	ns
Micropeplus laticollis	0	ns	0	ns	ns	ns	0

Millidium minutissimum	ns	ns	ns	ns	ns	ns	ns
Nitidulidae sp. #3	ns	ns	0	ns	ns	ns	ns
Olophrum consimilie	0	0	0	0	0	0	ns
O. rotundicolle	0	ns	0	ns	ns	ns	ns
Omalium flavidum	ns	ns	ns	0	ns	ns	0
O. sp. #2	0	0	0	0	0	0	ns
O. sp. #3	0	ns	ns	0	ns	ns	ns
Oxytelus fuscipennis	0	ns	0	ns	ns	ns	ns
Phelopsis obcordata	0	ns	ns	0	ns	ns	0
Philonthus seigwaldii	0	ns	0	ns	ns	ns	ns
Podabrus sp. #1	ns	ns	ns	ns	ns	ns	0
P. sp. #2	ns	0	ns	ns	ns	ns	0
Proteinus limbatus	3/92	4/92	ns	ns	ns	FD40/92	ns
Pseudopsis subulata	ns	4/92	4/92	ns	ns	FD40/92	ns
Ptenidium sp. #1	0	0	0	0	0	0	ns
Pterostichus adstrictus	ns	0	ns	0	ns	ns	0
P. coracinus	ns	ns	ns	ns	ns	ns	ns
P. punctatissimus	ns	ns	ns	ns	ns	ns	ns
Quedius densiventris	ns	ns	ns	ns	ns	ns	ns
Q. fulvicollis	0	ns	0	ns	ns	ns	ns
Rhyncolus brunneus	0	ns	ns	ns	ns	ns	ns
Sphaeroderus nitidicollis	0	0	0	0	0	0	ns
Stephostethus sp. #1	ns	0	0	ns	ns	ns	0
Tachinus basilis	0	ns	ns	0	ns	ns	ns
T. elongatus	0	ns	0	ns	ns	ns	0
T. frigidus	ns	4/92	ns	ns	ns	FD40/92	ns
T. quebecensis	3/92	4/92	ns	ns	ns	FD40/92	ns

T. tachyporoides	ns	0	0	ns	ns	ns	ns
T. thruppi	0	ns	0	ns	ns	ns	0
Trechus apicalis	0	0	0	0	0	0	ns
T. crassiscapus	0	0	0	0	0	0	ns

Table A.3. Results of Mann-Whitney U tests comparing between years and between sites within the 60 year old stands. A significant difference between sites or stands is indicated with the name of the site or stand which had significantly more of that species present. ns = compared sites or stands not significantly different, 0 = no specimens found in compared sites or stands.

SPECIES	5/92 vs. 5/93	6/92 vs. 6/93	5/92 vs. 6/92	5/93 vs. 6/93	5 vs. 6	FD60/92 vs. FD60/93	11 vs. 12
Acidota subcarinata	ns	ns	ns	ns	ns	ns	ns
Acrotrichus sp. #1	5/92	6/92	5/92	ns	5	FD60/92	ns
Aegialia rufescens	ns	ns	ns	ns	5	ns	ns
Arpedium cribratum	ns	0	0	ns	ns	ns	0
Atomaria sp. #1	ns	0	ns	5/93	5	ns	ns
Atrecus macrocephalus	ns	0	0	ns	ns	ns	0
Bembidion wingatei	ns	ns	5/92	5/93	5	ns	ns
Colon magnicolle	ns	ns	ns	ns	6	ns	ns
Ctenicera spinosa	ns	0	ns	0	ns	ns	ns
Elonium diffusum	5/92	6/92	5/92	ns	ns	FD60/92	ns
Eusphalerum pothos	ns	ns	ns	0	ns	FD60/92	ns
Gabrius brevipennis	0	ns	ns	0	ns	ns	0
Hylobius warreni	ns	6/92	6/92	ns	ns	FD60/92	ns
Ischnosoma fimbriatum	0	ns	ns	ns	ns	ns	ns
I. splendidum	ns	ns	ns	ns	ns	ns	ns
Lathrobium fauveli	ns	ns	ns	ns	ns	ns	ns
L. fulvipenne	ns	ns	ns	ns	ns	ns	0
Leiodes assimilis	0	0	0	0	0	0	ns
Lordithon facilis	ns	0	ns	0	ns	ns	ns
L. fungicola	ns	ns	ns	ns	ns	FD60/93	12
Megarthrus americanus	ns	ns	ns	ns	ns	ns	ns

Millidium minutissimum	5/92	ns	ns	ns	ns	FD60/92	0
Nitidulidae sp. #3	ns	ns	ns	ns	ns	FD60/92	ns
Olophrum consimilie	0	0	0	0	0	0	ns
O. rotundicolle	ns	ns	0	ns	ns	ns	ns
Omalium flavidum	ns	ns	ns	5/93	ns	ns	ns
O. sp. #2	ns	6/92	ns	ns	ns	FD60/92	ns
O. sp. #3	5/92	ns	5/92	ns	ns	ns	0
Oxytelus fuscipennis	ns	ns	5/92	5/93	5	ns	ns
Phelopsis obcordata	0	ns	6/92	6/93	6	ns	ns
Philonthus seigwaldii	ns	0	ns	0	ns	ns	ns
Podabrus sp. #1	ns	ns	0	ns	ns	ns	ns
P. sp. #2	ns	0	ns	ns	ns	ns	ns
Proteinus limbatus	5/92	ns	5/92	5/93	5	FD60/92	ns
Pseudopsis subulata	5/92	ns	ns	ns	ns	FD60/92	ns
Ptenidium sp. #1	0	0	0	0	0	0	11
Pterostichus coracinus	ns	ns	ns	ns	ns	ns	11
P. melanarius	ns	ns	ns	ns	ns	ns	ns
P. punctatissimus	ns	ns	ns	0	ns	ns	ns
Quedius densiventris	ns	ns	5/92	6/93	5	ns	12
Q. fulvicollis	ns	ns	ns	ns	ns	ns	ns
Rhyncolus brunneus	ns	ns	0	ns	ns	ns	ns
Stenus egenulus	ns	ns	ns	ns	ns	ns	ns
Stephostethus sp. #1	5/92	ns	ns	ns	ns	FD60/92	ns
Tachinus basilis	ns	ns	ns	ns	ns	FD60/92	ns
T. elongatus	5/92	0	5/92	ns	5	FD60/92	ns
T. frigidus	5/92	6/92	ns	ns	ns	FD60/92	12
T. quebecensis	ns	ns	ns	6/93	6	ns	ns

T. tachyporoides	0	ns	0	ns	ns	ns	ns
T. thruppi	ns	6/92	ns	ns	ns	ns	ns
Tachyporus nitidulis	ns	ns	5/92	ns	5	ns	ns
Trechus apicalis	ns	ns	ns	6/93	6	ns	ns
T. crassiscapus	ns	6/92	ns	0	ns	FD60/92	ns

Table A.4. Results of Mann-Whitney U tests comparing between years and between sites within each stand for the Aleocharinae. A significant difference between sites or stands is indicated with the name of the site or stand which had significantly more of that species present. ns = compared sites or stands not significantly different, 0 = no specimens found in compares sites or stands.

	Oxypoda sp. #1	*Oxypoda* sp. #2	A. sp #4	A. sp. #5	A. sp. #6	A. sp. #8	A. spp.
1/92 vs. 1/93	ns	ns	ns	ns	ns	0	ns
2/92 vs. 2/93	ns	ns	ns	ns	ns	0	ns
1/92 vs. 2/92	ns	ns	ns	ns	ns	0	ns
1/93 vs. 2/93	ns	ns	ns	ns	ns	0	ns
1 vs. 2	ns	ns	ns	ns	ns	0	ns
FDO/92 vs. FDO/93	ns	ns	ns	ns	ns	0	ns
7 vs. 8	ns	ns	ns	ns	ns	ns	ns
3/92 vs. 3/93	ns	ns	ns	ns	ns	ns	ns
4/92 vs. 4/93	ns	ns	ns	ns	ns	ns	ns
3/92 vs. 4/92	ns	4/92	ns	ns	0	ns	ns
3/93 vs. 4/93	ns	ns	3/93	ns	ns	ns	ns
3 vs. 4	ns	ns	3	ns	ns	ns	ns
FD40/92 vs. FD40/93	ns	ns	ns	ns	ns	ns	ns
9 vs. 10	ns	ns	ns	9	ns	ns	ns
5/92 vs. 5/93	ns	ns	5/93	ns	5/93	ns	ns
6/92 vs. 6/93	ns	ns	ns	ns	ns	ns	ns
5/92 vs. 6/92	ns	5/92	ns	0	ns	ns	ns
5/93 vs. 6/93	ns	ns	5/93	ns	ns	5/93	ns
5 vs. 6	ns	5	5	ns	ns	5	ns

FD60/92 vs. FD60/93	ns	ns	ns	ns	ns	ns	ns
11 vs. 12	ns	ns	ns	0	ns	ns	ns