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Dynamics of arthropod assemblages in forests managed to emulate natural disturbance (BUGS)

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DYNAMICS OF ARTHROPOD ASSEMBLAGES IN FORESTS MANAGED TO EMULATE NATURAL DISTURBANCE (BUGS)

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— EXECUTIVE SUMMARY —

1. This study provides the first systematically and concurrently collected data about the diversity and ecological importance of a number of arthropod groups [epigaeic (= litter dwelling) spiders, saproxylic (= feed on, breed in or need dead or dying wood) beetles, moths, parasitoids and bumble bees and soil] in the northern mixedwood forest. Work on other arthropod groups is now underway. More than 500 individual species have been considered by the theses produced under this grant, although not all of this information is presented here. For some of the species considered, the work at EMEND will likely be the best source of biological information about boreal forest populations. A central and enduring aspect of this research is to establish reliable baseline against which meaningful inferences about faunal change may be drawn. In an environment where both forest companies and governments have pledged that harvesting activities will not result in extirpation of a single species, the critical importance of such inventory information should not be underestimated.

2. An ultimate goal for these data are to use them to model the relationships between arthropod diversity and net primary productivity, especially for understanding the potential trade-offs. In other words, we want to know what the productivity costs will be for cutting and regenerating in ways that maximize biotic conservation values. There is no rationale way to plan and optimize strategies for using renewable natural resources without such information.

3. Logging at intermediate levels increased the number of bumblebees, and increased the species diversity and density of plants that bumble bees visit (relative to unlogged control sites). But the distribution of bees across resources is not even. The effect of this mismatch is conjectured to be twofold: by disproportionately visiting plants in logged areas (where flowers are most common), bees experience higher levels of competition for nectar and pollen, and on average do more poorly than if they more evenly "matched" resources and foraging pressure. By being visited disproportionately less often, and with no year to year increases in the total abundance of pollinators, plants in unlogged control areas may experience diminished pollination service, possibly leading to a decline in fitness. Logged areas may therefore act over the short term as pollinator attractors that negatively impact plants in pristine areas. However, it is clear that sites subjected to partial cut logging should be highly attractive to pollinators and that this will presumably promote floral responses that promote succession. Over the longer term greater success of colonies in these sites should increase the regional numbers of bees and promote a better fit to the overall distribution of floral resources.

4. Prior to EMEND harvest treatments, stand type had a significant effect on the distribution of the ambrosia beetle *T. lineatum,* with higher trap catches in conifer dominated stands. Following harvest, abundance of suitable habitats appeared to have a stronger influence on the distribution of *T. lineatum.* Numbers of *T. lineatum* were

higher where habitat (conifer stumps) and host trees (conifer dominated stands) were more abundant. Furthermore, the effect of stand density on the movement of beetles was minimal since residual level had no effect on capture rate in deciduous dominated stands where the effect of stand density is expected to be clearest due to the lack of suitable habitat in all residual levels. Further investigation of the physical structure of the landscape also showed no significant effect on the movement of *T. lineatum.* No significant difference in the number of beetles captured was found between the 5m machine corridors created by the partial harvesting method, and 15-m retention. Thus, it appears that partial cut harvesting will not exacerbate problems with potential pests like this ambrosia beetle and other scolytids by promoting access to stands.

5. Nearly 300 species of macrolepidopterans have been collected from the EMEND site, effectively establishing a baseline for future assessments of effects. One year following partial cutting, moth species richness and particularly moth trap catch were negatively affected by changed environmental conditions in residual stands. The moth community was more different between sites as the degree of disturbance increased. Moth families were differentially affected by disturbance. Moths in the Family Geometridae were quite sensitive to the effects of partial cut harvest and this family of delicate poor-dispersing species has excellent potential as an indicator of non-disturbed forest or of forest recovery after disturbance. This study revealed an unexpected reduction of moth captures by light traps on our relatively small blocks. Thus, as reported by several other recent studies, recovery of moth populations may depend on the existence of suitable corridors to ‘source’ habitats as much as the recovery of within stand vegetation structure and composition.

6. The spruce beetle was found to be parasitized by four species of hymenopteran parasitoids at EMEND. These parasitoids have different optima and thus collectively exert control on populations of this potentially serious pest over a wide range of conditions. Partial cutting allows parasitoids to access spruce beetle larvae on the bottoms of logs, thus eliminating an important refuge against naturally enemies that is used by this pest. With effective management of slash, response of these naturally occurring biological control agents should be sufficient to constrain spruce beetle outbreaks under partial cutting regimes.

7. The ground-dwelling spider community has been inventoried at EMEND and found to include at least 164 species. These species show remarkable sensitivity to microhabitat variation and, as such, have excellent potential for development as indicators. This taxon could be used to ensure that regenerating stands are developing the full range of microhabitat variation that characterizes stands before harvest. Because spiders are predators on many potential pest species, their community structure may be functionally important in forest situations as well.

8. Graduate programs of 3 MSc (Jane Park, Julie Wesley and Louis Morneau) and 2 PhD (Christopher Buddle and David Shorthouse) were funded under this grant. Park, Morneau, and Buddle are all now employed in forest entomology and Wesley is working in an adjacent area for the Canadian Food Inspection Agency that carries the Canadian mandate for defense against importation and establishment of exotic species from abroad. All three MSc students had fulltime permanent jobs before defending their theses and Buddle was appointed as Professor of Forest Entomology at McGill University after a short PDF at Miami University. Shorthouse is presently writing his

thesis and is expected to finish in summer 2003 well within the normal 5-year timeframe that characterizes PhDs in the Department of Biological Sciences. Thus, this grant has been highly successful in terms of training HQP.

9. Published and other output from the grant to date are listed in Appendix I. Publications from all theses except Dr. Buddle's remain to appear. Many are in preparation.

DYNAMICS OF ARTHROPOD ASSEMBLAGES IN FORESTS
MANAGED TO EMULATE NATURAL DISTURBANCE (BUGS)

1. Introduction. The boreal zone harbors a diverse but poorly known invertebrate fauna. Arthropods are especially numerous and understudied, including *c.* 22K species of insects (Danks & Foottit 1989). Some phytophagous species are known to profoundly influence boreal landscapes and forest management priorities through effects on large and economically valuable host-plants (Holling 1992). For example, consideration of the spruce budworm is essential throughout the range of its principal host, white spruce. Because of clear economic importance, "the budworm" has been well enough studied to reveal adaptive features (e.g., Volney 1985; Volney & Cerezke 1992; Weber et al. 1997) and place it's activities in a natural disturbance context (e.g., Morin et al. 1993; Bergeron & Harvey 1997). However, such detailed information is missing for most Canadian arthropods. We know little more than names of described species not recognized as pests in our primeval forests, and *c.* 45% of boreal insect species are estimated to be unknown to science (Danks 1979; Danks & Foottit 1989). In short, understanding of boreal arthropod diversity, spatio-temporal variation, and ecological significance is far too rudimentary to support effective, well-informed ecosystem management. Managing forested lands to maintain biodiversity presumes that we understand that biodiversity, a connection not apparently reflected in today's pronouncements about criteria and indicators or in the views of enthusiasts impressed because we know much about the few hundred species of boreal birds and mammals. As with of icebergs, conclusions about safe practices with respect to biodiversity based on knowledge of the apparent tip are not recommended.

Information on insects from forests in Europe suggests that the shortcoming of knowledge is serious from the biodiversity perspective (Warren & Key 1991). For example, linkages between insects and lichens or fungi have been valuable in developing whole-forest management strategies. Regenerated coniferous forests in Sweden hold significantly fewer canopy-dwelling invertebrates important as food for passerine birds than do never-cut forests (Pettersson et al. 1995). Reductions in passerine populations have been attributed to changes associated with stand structure, and loss of lichens that are essential food or habitat for arthropods. Kaila et al. (1994) have revealed associations between saproxylic beetles and infection of birch trees by particular species of polypore fungi. Siitonen (1994) collected >200 species of saproxylic species (those using coarse woody material [CWM] as habitat) from old forests in Finland and showed their importance in relation to both faunal conservation and nutrient cycling (see also Muona & Rutanen 1994; Siitonen and Martikainen 1994). This sort of research has been featured in several recent conferences showcasing the modern ecosystem management approach being developed by Fennoscandians, our primary competitors on international pulp and paper markets.

Few broad faunal studies have been conducted in western Canada forests. We do know that only *c.* 15% of ground-beetle species in old-growth lodgepole pine stands (>90 yrs) recolonize regenerating stands up to 35 yrs after harvest (Niemelä et al. 1993; Spence et al. 1996), but this taxon appears to recover rapidly after wildfire in the mixedwood (Holliday 1991, 1992; Langor et al. 1993; Spence et al. 1997; Gandhi et al. 2001). Other litter-dwelling beetles and saproxylic insects seem more sensitive to stand age and structure than ground-beetles (Spence et al. 1997; Hammond 1997; Hammond et al. in prep). However, present knowledge is insufficient to predict how forestry activities underway will affect dynamics of potential pests, or impact species that maintain critical ecological functions. Management to emulate natural disturbance (ND) regimes provides the best insurance policy to retain species about which we have so little information (Hunter 1993). However, data are urgently required guide development of ND-based management that will not adversely affect boreal arthropods or alter their effects on forest systems in unanticipated or undesirable ways.

Disturbances such as harvesting and fire change physical, chemical, and biological factors in the litter, soil and coarse woody debris. These, in turn, modify habitats for invertebrates. Many studies show dramatic effects of logging on invertebrate communities (these effects reviewed in Spence et al. 1997) but there are only few North American studies of the direct effects of wildfire (Holliday 1991, 1992; Buddle et al. 2000, Gandhi et al. 2001). Thus, critical biotic components may be at risk on landscapes harvested without detailed consideration of faunal components and associated ecological process, no matter what pattern of cutting is adopted. We must determine if succession from logged sites generates forest structure suitable as habitat for a normal range of mixedwood biota, especially species characteristic of older stands. Buddle et al. (2000) approached this objective with a chronosequence study, but were limited to a 30 year post-harvest time-frame, as will be a problem for all chronosequence studies conducted on the boreal plain.

Linkage of rare or threatened species in trophic webs is a feature of recent work (Martikainen et al. 1997). However, such trophic webs are sensitive to fine-scale variation in habitat structure. For example, the lichen, *Lobaria pulmonaria*, is a good predictor for the presence of red-listed lichen species in Sweden, but is only weakly correlated with red-listed beetles using dead wood as habitat (Nilsson et al. 1995). Because diversity hot-spots for various taxa are not spatially congruent (Prendergast et al. 1993) a few reserves are unlikely to maintain a full complement of biota. Understanding such linkages and their dynamics during recovery from disturbances provides basic underpinning for bio-sensitive forestry practices on the extensive land base. If stand-level processes mediated by arthropods lead to less food for larger wildlife, their population sizes will surely decrease, no matter how pattern of harvest is optimized on the landscape scale.

2. Objectives. We conducted a comprehensive study of selected arthropod assemblages at the EMEND site to understand their diversity in northern mixedwood forests and their initial responses to disturbance caused by partial retention harvests. Our long-term goal is to understand all biodiversity elements on this limited land base as fully as possible and to use data about multiple-taxon biodiversity responses in cost-benefit modeling of trade-offs between biodiversity, productivity and other values, as appropriate in support of approaches to extensive management. However, long-term data sets are required for this task and only the initial responses to disturbance are available at present. Furthermore fire is one obvious control, against which effects of harvest should be compared under a natural disturbance approach. Although whole compartment burns are in the overall EMEND design, and as of this date we still pursue their delivery, a series of unusually dry years since the initiation of EMEND have constrained delivery of these burns to just two compartments providing insufficient opportunities for incorporation into the work sponsored by the grant considered here (BUGS). Research conducted under terms of this SFMN grant have focused on bumble bees, carabid beetles, ground-dwelling spiders, saproxylic beetles, lepidopterans and parasitoids of lepidopterans and bark beetles, and have dealt specifically with the following questions for which we can provide tentative answers now:

1) Is cover-type diversity significant for maintaining faunal diversity in western mixed-wood forests?

2) How comparable are the trajectories of representative arthropod assemblages in response to green tree retention harvest treatments imposed in the EMEND experiment?

3) What species consistently show measurable population responses to disturbance, so as to be valuable as possible "indicators" during extensive monitoring?

4) Are insect-natural enemy relationships altered by stand structure and spacing in ways that could significantly affect vulnerability of regenerating stands to pests?

5) Are functional aspects of forest arthropod activity significantly altered by the variable retention harvest systems imposed at EMEND?

3. The EMEND Experimental Templet. The “natural disturbance (ND) paradigm” for management of the boreal forest leads away from 100% removal toward some retention of residual trees on the landscape. Effects of size and landscape distribution of cut-blocks with residual patches have been and are being studied in Alberta and elsewhere. However, the essential stand-level question of “how much residual is enough to protect critical aspects of ecosystem function?” has received scant attention, although ‘thresholds’ has now become the buzzword of the day. Thus, there is little scientific basis to guide management of stand structure under extensive management. Retention of either green-tree or dead residual promotes for whole-forest regeneration. Therefore, sustainability depends on connecting harvest techniques to ecologically-sensitive silviculture within the realm of social and economic constraint. Social and economic constraints are not necessarily fixed but experience teaches that they do not move in the absence of compelling evidence. EMEND will provide such evidence.

The work reported here was executed at EMEND (Ecosystem Management by Emulating Natural Disturbance) (Spence *et al.* 1999), a large-scale multidisciplinary harvest-silviculture experiment in the boreal mixedwood forest of Alberta, 85 km northwest of Peace River (56º44'N, 118º20'W).. The site is in the Lower Foothills natural subregion (Beckingham et al. 1996) of the Boreal Forest region (Rowe, 1972) characterised by trembling aspen, *Populus tremuloides* Michaux, balsam poplar, *Populus balsamifera* L., white spruce, *Picea glauca* (Moench) Voss and black spruce, *Picea mariana* (Miller) B.S.P. (Johnson *et al.* 1995). Vegetation in the area grows on fine-textured luvisolic soils (B. Kishchuk, pers. comm.). Most of the BUGS work was conducted during the pre-harvest year (1998) and the two seasons (1999-2000) immediately following harvest. Primary research under BUGS focused on behaviour of response variables in response to harvest, without further intervention.

The EMEND experiment was designed to explore the interaction between stand cover-type, forest harvesting and prescribed wildfire through stand-level manipulations of standing green-tree retention. In 1997, composite forest polygons were selected from the Alberta Vegetation Inventory (AVI) maps within the Forest Management Agreement area granted to Daishowa-Marubeni International. These stands were selected to provide 3 replicates of 4 reasonably well defined stand cover-types based on field surveys of candidate stands. Stands were selected so as to minimize variation among cover-type replicates with respect to ecological site classification (Beckingham et al. 1996), stand age, and canopy and understory vegetation. Based on the relative proportions of deciduous (*Populus* spp.) and coniferous (*Picea* species) in the overstory, these four dominant stand cover-types were classified as 1) deciduous dominated (DDOM) with less than 30% coniferous trees in the canopy, 2) deciduous with an understory of white spruce (*Picea glauca* (Moench) Voss) (DDOMU), 3) mixed canopy with approximately equal proportions deciduous and coniferous component in the canopy (MX), and 4) conifer dominated (CDOM) with conifers representing greater than 70% of the canopy.

Harvesting treatments consisted of retention strip-cuts that left 100% (uncut control), 75%, 50%, 20%, 10% in 10-ha compartments within replicate stands. These strip cuts were oriented in a north/south direction to reduce effects of varying orientation on responses. There was an additional clear-cut treatment that left 0-2% (clearcut) of standing residual stems dispersed throughout the compartment. Within each harvested compartment, 2 elliptical retention patches (0.20 and 0.46 ha) were also left to distinguish the response of species to aggregated and dispersed retention. Harvesting treatments were replicated 3 times within each cover type resulting in 72 harvested compartments including uncut controls. The remaining compartments were allocated for prescribed burns and slash burn treatments (10% dispersed retention followed by low intensity prescribed burn). Harvesting treatments were applied in the winter of 1998-1999. Details of the study sites, and their spatial arrangement, are described in at the EMEND web site (www.biology.ualberta.ca/emend/emend.html).

4. Arthropod Studies Conducted under BUGS. Under the terms of BUGS, fieldwork for 5 studies of arthropod communities were undertaken at EMEND during 1998-2000. This report summarizes the general outcomes to date, although some aspects of the data continue to elaborated as identification of specimens is finished and the final analyses have not been executed. The studies were as follows:

1) An investigation of the effects of partial cut harvesting on pollinator (bumble bee) communities was undertaken by Dr. R. Cartar and a series of undergraduate students from the Department of Biological Sciences, University of Lethbridge.
2) Jane Park completed (October 2002) an MSc degree about the response of bark and ambrosia beetles to the EMEND treatments. This work was supervised by Dr. Mary Reid of the Department of Biological Sciences at the University of Calgary.
3) Louis Morneau completed (January 2002) an MSc degree about the responses of the macro-moth community to the EMEND treatments. This work was Co-Supervised by Drs. John Spence (University of Alberta) and Jan Volney (Canadian Forest Service) through the Department of Biological Sciences at the University of Alberta.
4) Julia Dunlop completed (September 2002) an MSc degree about the responses of parasitoids to the EMEND treatments and the possible implications for spruce beetle outbreatks. This work was Co-Supervised by Drs. John Spence and David Langor (Canadian Forest Service) through the Department of Biological Sciences at the University of Alberta.
5) David Shorthouse is in the writing phase of a doctoral program working on the effects of the EMEND treatments on spider communities. We expect a completed thesis in the summer of 2003. This work is being Co-Supervised by

Drs. John Spence and Jan Volney through the Department of Biological Sciences at the University of Alberta.

Other entomological work was begun under the terms of BUGS but has been carried forward under the umbrella of other SFMN grants. Results of these projects will thus be reported elsewhere. In this report we focus on reviewing the highlights of the above-mentioned five projects, all of which were initiated in 1998, the first year of the grant period. The studies are summarized in the order given above.

5. Effects of boreal forest logging on habitat use by bumble bees. R. Cartar and his undergraduate student associates studied 50 experimental compartments of 8 to 10 ha, 25 of each in 2 habitat types (DDOM and DDOMU). Each habitat type contained 3 compartments each of 5 logging levels (defined by % trees remaining after logging: 0%, 10%, 20%, 50%, and 75%), and 10 compartments each of control (unlogged) sites.

Each compartment contained one or more baseline transects, of roughly 0.5 m width. Bees and plants along these transects were surveyed by walking slowly along each (Banaszak 1980, Teräs 1983), two to four times over the summer (census dates ± range in days: 1998: 1st, 6 July ± 13; 2nd, 21 July ± 16; 3rd, 26 July ± 3; 1999: 1st, 24 June ± 8, 2nd, 10 July ± 9; 3rd, 28 July ± 12, 4th, 10 August ± 7). In each survey, bumble bees were counted and identified to species and sex, and the species and number of open flowers of plant species visited by bumble bees were counted over four 1 m stretches along a randomly determined side of the baseline, measured within each 20 m interval (1998), or over a 2 m wide band along the baseline (1999). Flowers were summed across all species to generate an overall measure of flower abundance in a compartment. This ignores obvious among-species differences in pollen and nectar production. But lacking information for all species on pollen and nectar production, this seemed like a reasonable approximation of floral rewards. Of the 15 plant species censused (Table 1), individual flowers were counted in all but one: the small-flowered *Trifolium*, whose inflorescences were counted as flowers. In a similar manner, bees were combined in most analyses without regard to species or caste, because many individuals (20%) were seen too briefly to allow a species identification. Six species of bumble bees were encountered on censuses (Table 1). One person collected data in each summer, but observers differed between years.

Where necessary, variables were transformed to normality. Data were tabulated at the level of the compartment, census number, and year. Counts of bees and plants were scaled to baseline transect length, which differed among compartments. This scaling was done differently in the 3 major classes of analysis performed here. Analyses of changes in bee density, plant diversity, and flower density are ANCOVAs, using the length of baselines in each compartment as a covariate. Analyses of changes in bee and plant community structure are MANOVAs, where the Ys are calculated as number of each bee or plant species/km of transect. Regressions relating bee abundance to plant abundance involve error in both X and Y variables, so orthogonal (principal component) regressions with univariate variance ratios (JMP 2000) were used.

Results. Data from the pre-logging (control) year, 1998, were used primarily to verify that compartments did not differ according to their eventual experimental logging treatment. Using the pre-logging control in this (conservative) way, as opposed to a pre-post design, is desirable because plant data were collected differently in each year, and observers differed between years. Although bees, plant species, and flowers differed in abundance between habitats (Fig. 1), there were no differences among compartments acccording to their eventual experimental treatment (ANCOVAs with the main effects habitat, census number, and eventual treatment, and their interactions, and the covariate baseline length (transformed to normality by $-\text{length}^{-0.4}$); effect of eventual treatment $P>0.1$).

If we accept that bees were equally detectable in both years, then there is no difference in overall abundance of bees from one year to the next (ANCOVA predicting ln(1+#bees) from year, habitat, year * habitat, census and $-\text{baselineline}^{-0.4}$; year effect $F_{1,306}= 0.12$, $P=0.73$); least square means ±SE, 1998: 0.507±0.067; 1999: 0.535±0.050). Any differences in bee density detected in comparisons between logging treatments therefore reflect relative distribution of the same number of bees across differences in their floral resources,.

How did logging affect the plant and bee communities? Overall, it quantitatively changed the structure (i.e., species composition and abundance) of the plant community (MANOVA of the ln-transformed numbers of flowers of 14 of the plant species listed in Table 1 vs. habitat, logging treatment, and their interaction; overall model Wilks' $\text{lamba}_{165,1504} = 0.194$, $P<0.0001$; logging treatment Wilks' $\text{lambda}_{75,799} = 0.380$, $P<0.0001$). In particular, the plant community in the 0%, 75%, and 100% treatments are significantly unique from each other, while the communities in the 10%, 20% and 50% treatments form a separate, similar group (Fig. 2). In contrast, logging had no detectable impact on the species composition and abundance of the 3 most common bee species (i.e., *Bombus flavifrons*, *B. terricola*, and *B. vagans*; MANOVA of the ln-transformed numbers of bees of the 3 bee species vs. habitat, logging treatment, and their interaction; overall model Wilks' $\text{lamba}_{33,142} = 0.837$, $P=0.72$; logging treatment Wilks' $\text{lambda}_{15,133} = 1.056$, $P=0.40$).

When we reduce the taxonomic resolution by examining total densities of all bee and plants, regardless of species, and numbers of species, we see an effect of logging on both bees and plants (Fig. 3). Overall, intermediate levels of logging appear to increase both plant and bee densities, and plant species diversity (Fig. 3).

How did logging affect the distribution of bees across their floral resources? The null hypothesis for this situation would be that bees distribute themselves across their resources according to an ideal free distribution (IFD), an equilibrium where the slope of the regression of bees on resources is 1. At an IFD, each bee in the overall study area would receive an equal rate of return, regardless of the local resource density in their current compartment. To test for an IFD, I used transformed measures of bee and flower abundances used in the ANCOVAs shown in Fig. 3, and standardized them (producing a dimensionless variable with a mean of zero and SD of 1). A slope of 1 between these standardized variables implies an IFD. In 1998 (i.e., before logging), there was indeed an IFD of bees (Fig. 4).

Following logging, the slopes of the bee-abundance regressions were greater than 1 for all logged groups (Fig. 5; but their 95% CIs all overlapped 1), but equal to 1 in the unlogged group (Fig. 5). Collectively, these five slopes of greater than 1 represent a significant deviation from 1 (sign test, one-tailed $P=0.031$). Another potentially more powerful way to consider this problem is to pool data from all 5 tree removal treatments, and test whether the fitted line has a slope of greater than one (Fig. 6). This was indeed the case (Fig. 6). Collectively, these regressions show that bees evenly match resources under natural conditions (1998 and 1999 100% treatment), but that following logging they "overmatch" (Tregenza 1995), in that too many bees visit compartments with many flowers, and too few bees visit compartments of the same treatment with few flowers.

Discussion. Overall, this paper detects strong effects of logging on the community of bumble bees, and the plants that they typically visit. The frequencies of individual bee species did not vary among treatments, but the frequencies of plant species did (Fig. 2). Generally speaking, intermediate levels of logging (i.e., leaving between roughly 50% of the original trees unlogged) produced a larger plant and bumble bee community (Fig. 3). It seems that the opportunities for understory plants favoured by bees are increased by moderate levels of logging. Results from 1998 demonstrate that the effects of logging detected in 1999 were not a simple consequence of initial differences among compartments.

While flower abundance and diversity was higher in logged sites (Fig. 3), there was no area-wide numerical response from the bumble bee community: the overall density of bees in 1998 (before logging) and 1999 (after logging) was similar. What changed between 1998 and 1999 was where the bees chose to forage. Because bumble bees travel many kms from their nest, the bees in this study can therefore have individually experienced all of the logging regimes produced in this experiment. In 1998, bees conformed to an IFD, meaning that the abundance of bees matched the abundance of plants, such that bee foraging success was presumably equivalent regardless of where they foraged. In 1999, bees in logged habitat did not conform to an IFD: they "overmatched" (i.e., slope >1, Fig. 6), such that compartments with high densities of flowers contained more bees than merited based on the quantity of resources, and compartments with low densities of flowers contained fewer bees than would be expected from the quantity of resources. A fascinating consequence of this overmatching may be that plants in low density compartments may experience pollinator limitation and Allee effects, while the converse would be true of plants in high density compartments. In this same situation, bees foraging in low density compartments would have higher fitness than bees foraging in high density compartments, who would experience higher levels of competition for pollen and nectar.

It appears that the bumble bee community, which thrives on the denser aggregations of flowers that follow disturbances such as fire, windthrow, or clearcut logging, is slightly enhanced by intermediate levels of logging. There do not appear to be any habitat-specialist species of bumble bees in this community, e.g., those that are found only in undisturbed forest. This is in contrast with many other arthropod taxa (Niemelä 1997), and may be a consequence of the wide foraging ranges of individual bees (Heinrich 1978, Osborne et al. 1999). The impact of logging on plants that bees visit is more dramatic: the nature of the community is fundamentally different following logging (Fig. 2). Given that interspecific competition among bumble bees is mediated through tongue length (Inouye 1980, Harder 1985), and given that floral traits differ between logged and unlogged communities, it is likely that a shift in the bee community will eventually manifest itself.

The apparent enhancement of the pollination community by logging may be less positive than it seems. By being visited disproportionately less often, and with no year to year increases in the total abundance of pollinators, plants in unlogged control areas could obtain diminished pollination service, possibly leading to a decline of their fitness. The proximity of logging to prisitine areas may therefore act as pollinator "attractors" that negatively impact plants in the pristine areas. These kinds of potential edge effects between logged and pristine habitats deserve further attention.

6. Response of the bark beetle, *Trypodendron lineatum*, to partial cut harvest. Jane Park (MSc Student) and Mary Reid of the University of Calgary studied the effects of conifer abundance, habitat abundance, and matrix characteristics on the distribution and movement of bark beetles, with special attention on *Trypodendron lineatum*. *T. lineatum* is a small and very abundant boreal ambrosia beetle that quickly colonizes recently dead or dying coniferous wood. For this study, Park & Reid used four EMEND residual levels (excluding clear cuts) as well as uncut compartments as controls (100% residual). Within each harvest treatment, 5m '*machine corridors*', where all vegetation was removed (75% compartments had only machine corridors), and 15m '*retention strips*', where the remaining selected felling was carried out, were cut.

To distinguish the effect of conifer abundance alone on the distribution of *T. lineatum*, beetles were sampled during the summer of 1998, prior to harvesting. Thirty-two baited 12-funnel Lindgren traps (Lindgren, 1983) were erected in 6 DDOM stands, 6 DDOMU stands, 12 MIXED stands, and 8 CDOM stands. Traps were centrally located at a height of approximately 1.5m from the ground. Traps were baited with ethanol and alpha pinene (release rate for both ethanol and alpha pinene were 1 g /day), and emptied every two weeks between 31 May 1998 and 3 August 1998.

Harvesting occurred in the winter logging season of 1998. This provided large differences in the actual abundance of habitat among stands, since *T. lineatum* inhabit stumps, as well as altering the physical structure of the forest matrix. In 1999 and 2000, baited 12-funnel Lindgren traps were placed in each 10%, 20%, 50% and control compartment in all stand types for a total of 48 traps. The same trap locations were used in both years. Each trap was baited with alpha pinene (host kairomone) released at a rate of 100-150 mg/day from a 15 ml bottle attached to each trap. Alpha pinene was used since previous studies have shown that *T. lineatum* are attracted to alpha-pinene during dispersal (Bauer and Vité, 1975; Salom and M^{c}Lean, 1988, Lindelow et. al, 1992). Traps were placed at least 50-100m away from the compartment edge to avoid edge effects. Furthermore, all traps were placed within the 15m retention strips since other studies have shown that bark beetles can orient to host kairomones and pheromones better in closed forests where wind speeds are lower (Salom and McLean, 1991). In 1999, traps were emptied every two weeks from 09 May 1999 to 08 August 1999. This sampling period was chosen since it encompasses the dispersal periods for many boreal scolytid species. In 2000, *T. lineatum* were collected from 09 May 2000 and 27 June 2000, since 1999 data showed that this species' peak dispersal occurred between 09 May 1999 to 14 June 1999. Samples were stored in plastic bags, frozen and examined in the laboratory. All scolytids in each sample were counted and identified to species (Bright, 1976).

To determine whether stand composition or habitat abundance was the main determinant of *T. lineatum* abundance, relationships between the proportion of spruce in a compartment and of the number of stumps on the number of beetles captured were determined. We used the proportion of spruce in a compartment as an estimate of the likelihood that suitable habitat exists within a compartment (effect of stand type). The proportion of spruce within a stand was estimated from ground surveys of species composition, in each stand. These data were obtained from data obtained from the EMEND project core database. The estimated number of conifer stumps (i.e. habitat abundance) per compartment was calculated from the proportion of conifers in each stand multiplied by the proportion of trees felled during harvest (residual level). This estimate of habitat abundance was used since *T. lineatum* use stumps as habitat patches. Furthermore, stumps can be assured to be suitable for colonisation since all trees were felled in the 1998 logging season.

The matrix through which *T. lineatum* disperses was examined with respect to the harvest treatments. Each residual level represents a given stand density though which beetles must fly. 10% compartments represent the thinnest stands while uncut compartments represented dense stands. To further examine the influence of the physical structure of the forest on the movement of *T. lineatum*, the abundance of beetles in machine corridors and retention strips was compared. The residual harvest treatments resulted in 5 m machine corridors in which all vegetation was removed (a total of approximately 25% of all vegetation within the compartment), and 15 m retention strips where the remainder of the residual treatment was carried out. A consequence of this harvest regime was a distinct pattern of densely vegetated and unvegetated linear strips, particularly in the 75% residual compartments where the retention strips were left fully intact. To determine whether *T. lineatum* used machine corridors as corridors for movement, baited (alpha pinene) traps were placed in the three conifer-dominated 75% residual compartments. In each compartment, 6 baited traps were erected, with 3 being placed within retention strips and 3 being placed in machine corridors.

Traps were also set up along 3 seismic lines and within 3 adjacent forests. The seismic lines used did not contain any suitable habitat, therefore, if *T. lineatum* altered their movements along these corridors, it would be primarily due to physical structure. However, catches in these traps were extremely variable with 16 of the 24 traps failing to catch any beetles, and 1 trap catching 316 of the total 337 beetles caught during the entire sampling period. Therefore, the data were not analysed further.

All ANOVAs, Tukey-Kramer tests and regressions were performed on JMP® Version 3.0 (SAS institute, 1995). We used an alpha of 0.05 for all analyses. For the data analysis we used the sum of all beetles caught in each compartment over the whole sample period. The sums of all sample dates were used since the objective of the study was not to examine temporal variations in insect abundance, which may be due to meteorological influences, but to examine overall insect changes in population density. Least square means were used for the Tukey-Kramer tests. All data were appropriately transformed (natural log, reciprocal, or arcsine square root), as required to meet assumptions of normality.

Results. Because replicates within each stand type did not have equal numbers of traps, the means of all traps in each replicate were used to analyse data about *T. lineatum*. A 2-way ANOVA (stand type and replicate) determined that stand type had a significant effect on the number of *T. lineatum* caught (R^2=0.68, $F_{3,12}$=5.6124, $p_{\text{stand type}}$<0.02; Fig. 7). Replicate had no effect on the number of beetles caught (p>0.05). Beetles were more abundant in conifer-dominated stands compared to all other stand types (Tukey-Kramer HSD, p<0.05).

To examine the response of *T. lineatum* to the landscape following harvest (1999-2000), we used a three-way nested ANOVA (Factors: residual level, stand type, and year, with replicate nested within stand type). Neither replicate nor year significantly affected the number of *T. lineatum* caught (p>0.05). However, the interaction between stand type and residual level did have a significant effect on the number of beetles caught (R^2=0.62, $F_{9,95}$=2.98, p<0.005). To examine the nature of this interaction more carefully, we analysed the effect of residual level on trap catches within each stand type using one-way ANOVAs and Tukey-Kramer tests (Fig. 8). These analyses, though less powerful than the whole model, allowed us to determine the properties of the interaction. Analyses of the different stand types showed that residual level had no effect on trap catches in DDOM stands (ANOVA-R^2=0.098, $F_{3,23}$=0.72, p>0.5). In DDOMU stands, 10%, 20% and control compartments caught significantly more beetles than 50% compartments (ANOVA-R^2=0.41, $F_{3,23}$=4.65, p<0.02; T-K HSD-p<0.05). In MIXED stands, 10% and 50% compartments caught significantly more *T. lineatum* than controls, while 20% compartments did not differ significantly from all other residual levels including controls (ANOVA- $R^2=0.43$, $F_{3,23}=5.12$, $p<0.009$; T-K HSD-$p<0.05$). Finally, in CDOM stands, trap catches in both 20% and 50% compartments were significantly higher than control compartments, while 10% compartments did not differ significantly from all other residual levels (ANOVA- $R^2=0.49$, $F_{3,23}=6.45$, $p<0.004$; T-K HSD-$p<0.05$). Therefore, habitat abundance appeared to have a stronger effect on the distribution of *T. lineatum* since a significant effect of residual level in DDOM stands would indicate an effect of physical structure.

To directly test whether the *T. lineatum* distribution was influenced by the increase in the abundance of suitable habitat following harvest, trap catches were examined with respect to estimated stump density in each compartment. The number of *T. lineatum* increased with increased numbers of conifer stumps in both years following harvest (1999-$R^2=0.33$, $F_{1,47}=22.52$, $p<0.0001$; 2000-$R^2=0.29$, $F_{1,47}=19.07$, $p<0.0001$, Fig. 9). The data were natural log transformed to meet assumptions of normality. The presence of a significant effect of stump density in 2000 indicates a potential link to beetles originating from within compartments. Stumps no longer available (due to desiccation) to *T. lineatum* in the second year following harvest may act as sources of beetles dispersing in the second year.

To further examine the potential role of physical structure of the forest on the movement and distribution of *T. lineatum* catches from machine corridors and retention strips were compared using a 2-way ANOVA with trap type (machine corridor/retention strip) and replicate. The data were natural log transformed to meet assumptions of normality. There was no significant effect of trap type or replicate on the number of *T. lineatum* caught ($R^2=0.14$, $F_{2,\ 17}=2.22$, $p>0.1$; $\text{mean}_{\text{MachineCorridor}}=8.95\pm0.55$, $\text{mean}_{\text{RetentionStrip}}=7.79\pm0.55$).

Discussion. Most models of insect habitat selection assume random search (Rogers, 1972). However, searching for habitat randomly may lead to fewer encounters with habitat patches if habitat is spatially clumped. As early as 1935, Salt proposed non-random host search by parasitic insects, such that parasites may seek areas with an abundant supply of hosts and ignore areas where hosts are rare or absent. Since then, several parasitic species have been found to be attracted to areas with high host densities (Chamberlin and Tenhet, 1926; Clausen, 1940; Doutt, 1964; Varley, 1941; Schroeder, 1969; Spradbury, 1969; Hassell, 1986). Furthermore, the resource concentration hypothesis, proposes that herbivorous insects accumulate where host plants are abundant. Many studies have supported this hypothesis (Monteith, 1960; Watt, 1964, 1965; Douwes, 1968; Bach, 1984; Turchin, 1988; Andow, 1990). Bark and ambrosia beetles that are able to detect their habitat from some distance away likely search non-randomly as well. Most scolytids have a limited dispersal period during which they must find suitable habitat (Byers, 1996). Finding suitable habitat quickly is beneficial since hibernation and dispersal depletes up to one half of an individual's fat reserves leaving only one half to consume during reproduction (Nijholt, 1967). In addition to the energy constraints faced by dispersing *T. lineatum,* the habitat for *T. lineatum* (conifer wood and stumps) is often unevenly distributed across the landscape making it difficult to find.

In a pre-harvest landscape, heterogeneity on the landscape is primarily due to stand level differences such as stand composition. Furthermore, habitat is likely to be more widely distributed across the landscape, since most inputs of coarse woody debris habitat are from natural mortality. If few actual habitat patches exist, the chemical signals within a stand may be too weak to detect. Furthermore, deciduous trees may themselves be a deterrent. Borden et al. (1997) found a 63-78% reduction in trap catches of *T. lineatum* when deciduous volatiles were placed on traps. Prior to harvesting in 1998, *T. lineatum* were scarce in stands containing few host trees (DDOM) and were most abundant in stands with many host trees (CDOM). By concentrating dispersal in areas with many host trees, individuals maximise the likelihood of finding suitable habitat.

The strength of the olfactory cue may also be influenced by the quantity of suitable habitat in an area. Consequently, a stand containing large amounts of fallen conifer wood may release higher quantities of these volatiles than one with less felled wood. Following harvest, there is a major increase the quantity of coarse woody debris and stumps across the landscape. Moreover, there may be patches across the landscape where large quantities of coarse woody debris can be found. Individuals of *T. lineatum* are known to prefer stumps to logs (Schroeder et al., 1999). Therefore, harvesting creates areas where habitat is concentrated on the landscape. Catches of *T. lineatum* were higher in compartments containing large quantities of suitable habitat (conifer stumps) in both 1999 and 2000. In 1999, this was most likely because the beetles altered their movement based on habitat abundance, given that beetles were presumably evenly distributed with respect to future harvest level prior to harvest. In 2000, beetle abundance likely reflected the production of beetles in the previous year, which would have been higher in stands with more abundant habitat, but may also have been influenced by the continued attraction of beetles for stands with more habitat. In general, these results establish that *T. lineatum* do not search for habitat randomly. Instead, they follow the predictions of the resource concentration hypothesis and move in response to areas containing higher quantities of habitat.

The influence of stand density on the movement of bark beetles has not been examined thoroughly. Data from studies by Salom and McLean (1991) and Hindmarch and Reid (2001) produced conflicting results. In one case, *T. lineatum* avoided open areas and preferred closed forests due to an increase in their ability to detect host chemical (Salom and M^{c}Lean, 1991). However, Hindmarch and Reid (2001) showed that *T. lineatum* were more common in thinned forests, apparently due to beneficial microclimatological attributes and wind-assisted search. However, examination of the significant interaction between stand type and residual level showed no effect of residual level (thinning) on the catches of bark beetles in DDOM stands. In these stands, the effect of physical structure is expected to be most obvious due to the lack of suitable habitat in all residual levels.

Furthermore, major structural features such as machine corridors created by some partial cutting regimes have also been hypothesised to affect the movement of insects by either increasing wind assisted movement, or hindering olfactory detection due to increased wind velocity. For example, Sutcliffe and Thomas (1996) found that ringlet butterflies (Aphantopus hyperantus) used open corridors as flyways between fields and glades. However, Hill (1995) found that linear strips of intact rainforest acted as dispersal corridors for several insects. Salom and M^{c}Lean (1991) studied the movement of *T. lineatum* along roads and found that there were no significant differences in flight along roads versus in the forest. The results of our study confirm that *T. lineatum* do not use open corridors as flyways, as no significant differences were found between machine corridors and retention strips.

Although it has been known for some time that the dispersal of *T. lineatum* is influenced by environmental factors (Salom and McLean, 1989, 1990, 1991a,b), this study shows that *T. lineatum* also alters it movement in response to habitat distribution and landscape structure. The propensity for *T. lineatum* to aggregate where large quantities of habitat exist is of particular interest considering the increase in logging over the past decade. If *T. lineatum* are not evenly distributed across the landscape, rarely travel in deciduous stands, and accumulate in areas containing large amounts of habitat (stumps, logs) and conifer dominated stands, the distribution of conifer stands and cut blocks may influence the likelihood that harvested wood is infested. Higher numbers of *T. lineatum* where more suitable habitat is located support the resource concentration hypothesis. Further research on the dispersal ability of this species through heterogeneous landscape as well as energy costs associated with dispersal will elucidate the trade-offs between search efficiency and habitat selection.

7. Partial Cutting Impacts on a Moth Community. MSc student Louis Morneau, Jan Volney and John Spence studied moth community responses to the EMEND treatments. Experiments to evaluate effects of disturbance can be used to evaluate various potential indicator groups in relation to development of operational thresholds. Arthropods are usually considered a good indicator of disturbance as they react rapidly to changes in their environment (Kremen *et al.* 1993; Spence *et al.* 1996; Buddle *et al.* 2000). This is especially true for the insect order Lepidoptera, the moths and butterflies, which are diverse and numerous in northern forests. The night flying moths are increasingly well known both taxonomically and ecologically, quite easy to sample, and their larval populations are tightly linked to significant impacts on forest growth and yield making it a suitable indicator group (see review on criteria by McGeoch 1998). Wood fibre losses to insects in the western boreal forest are primarily caused by lepidopteran defoliators (Volney & Mallet 1998) believed to regulate forest primary production (Mattson & Addy 1975) in the long term. Understanding species dynamics of this taxon at the community level is thus both significant as a contribution to understanding ecosystem processes and relevant to the other objectives of forest management.

The major immediate impact of forest harvesting on Lepidoptera is removal of potential habitat. Are the moths affected by fragmentation? We can investigate this by contrasting species occurrence in undisturbed or habitats newly created by forest harvesting. Habitat use is defined here as the utilisation of homogeneous forest compartments by moths. Lepidoptera are highly mobile, flying organisms. As such, they will disperse through forest stands looking for mates, egg-laying spots, nectar-feeding plants, cover or simply corridors to travel (Young 1997).

The immediate impact of disturbance (winter logging in this study) will be felt differently between early and late season breeders as the first ones will spend the winter as pupae and emerge in the spring while the late season breeders will spend the winter as eggs or young larvae. A portion of the late season breeders will be removed from the forest by the tree harvesting and those lefts would be subjected to different environmental conditions affecting their development and survival.

Lepidoptera is a well-studied insect Order. Consequently, a large amount of information is known on the biology of the different families, genera and species. It is thus possible to look at the community from different perspectives. The host-plant range relates to many other aspects of moth biology and is thus useful to look at disturbance impacts on lepidopterans. Also, different moth families might have a different response to disturbance. Species in the same family usually share some common traits (feeding, body structure, and behaviour). Thus, a species of Geometridae (external feeders as larvae, slender-bodied, broad-winged and rather delicate as adults) is more likely to react to a severe removal of habitat than a Sphingidae (stout-bodied strong fliers). Families with feeding adults might be affected more by the immediate destruction caused by clearcutting of flowering plants that are nectar sources than non-feeding families (e.g. Lasiocampidae, Saturniidae).

Our work on moths was restricted to four of the seven EMEND treatments: partial cutting resulting in 20% and 50% residual structure compartments (RSC), a control to be used for prescribed burning in the near future, and an unharvested control. Each treatment was replicated twice within cover type for a total of 24 sites. Light trapping was used to sample the moth community. Light traps (Bioquip, CA, USA) with 12 volts U-shaped UV lights running on batteries and equipped with photoelectric detectors to activate the light bulbs were used. Traps were standardised at a height of 2m on tripods and photosensors were oriented North. The moth community was sampled before (1998) and after disturbance by winter logging (1999). Trapping occurred every 8-10 days, depending on local weather conditions, from May to mid-September for a total of 14 trapping nights per year. 16 traps were used to sample 24 sites using a partial replication design. Thus, replicate one consisted of 12 sites sampled every trapping night. Replicate two consisted of 12 sites, four of which were sampled on any trapping night. Thus, over three trapping nights, all sites would be sampled twice, covering the range of forest types and treatments considered.

Many factors affect light trapping catches: temperature, humidity, wind, moonlight, proximity to vegetation, height of trap above ground, trap design and light source (Young 1997, Wallner *et al.* 1995). However, most of these factors were not considered as problematic in this study since they were similar at all sites on any given sampling night thus affecting each catch in the same way. Therefore, problems related to weather factors and trap design were overcome by standardising sampling techniques and trapping nights. Only structural site factors were considered for their potential effect on trap catch: basal area, reflecting tree density and canopy cover after thinning, slope and understory vegetation height. The understory vegetation density was also measured indirectly with a light interception experiment. A laser pointer was used at night to aim at the light trap bulb from 36 different points around a circle. The experiment was repeated on circles of 5, 10 and 20-meters radii centred on the trap.

Moths were collected in paper bags during the day following a light-trapping session and frozen at the EMEND field laboratory before being processed. Moths were sorted to morphospecies based on external characters and genitalia dissection when needed. Identifications were done using up-to-date literature, the Canadian Forest Service arthropod collection at the Northern Forestry Centre (Edmonton, Alberta, Canada), and advice from local lepidopterists. Voucher specimens were deposited in the NoFC collection. Classification followed Hodges (1983) and more recent publications (Handfield 1999). Bowman's work (1951) was also consulted.

Species were classified based on their trap catch in four categories of habitat use as generalist, deciduous specialist, coniferous specialist or unknown. Generalists are species using all cover types as habitat or, as defined by Andrén (1994), species that use several habitats in the landscape although they may differ in suitability. They were found in large numbers in most sites. Deciduous and spruce specialists were species only or mostly found where aspen and spruce, respectively, account for a large proportion of the forest stand. Lastly, species with unknown habitat were not abundant enough to be assigned to one of the above category.

Species were classified as mono-, oligo- or polyphagous species based on literature (Handfield 1999, Miller & Hammond 2000). Monophagous species have one or several closely related host plants, usually in the same genus. Good examples would be the beggar, *Eubaphe mendica* Walker, feeding exclusively on violets (*Viola* spp.) in northern Alberta or the grey scoopwing, *Callizia amorata* Packard, feeding on honeysuckle

(*Lonicera* spp.). Oligophagous species have several host plants all belonging to the same family. The willow sphinx, *Smerinthus cerisyi* (Kirby), is in that category as it feeds on willows and poplars, which are plants in the Salicaceae. Polyphagous species feed and use plants from more than one family. The small engrailed, *Ectropis crepuscularia* (D.&S.) is really polyphagous, feeding on more than 70 species of plants (Handfield 1999).

The effects of harvesting on feeding guilds in the moth community was also investigated. Species using the same resources are more likely to react in a similar way to disturbance. Species were classified based on current literature (Handfield 1999, Miller & Hammond 2000) in ten guilds: 1. Herb and grass feeders, 2. Woody plants generalists, 3. Low and non-woody plants generalists, 4. Fungus and dead leaves feeders, 5. Salicaceae (poplars & willows) specialists, 6. Deciduous trees feeders, 7. Conifer feeders, 8. Lichen feeders, 9. Root feeders and 10. Generalists. Three years of data were used for this analysis (1998 to 2000).

Differences in moth species richness and trap catch between forest types, treatments, years and by moth families were analysed using one-way analysis of variance (ANOVA) with repeated measures (Zar 1996) in SPSS (1999) and SAS (1999). Because it is conservative and does not require equal sample size (Zar 1996), Scheffe's multiple comparison test was used to examine significant differences between means from the ANOVA. A correlation analysis was performed to test if specific site characteristics (basal area, understory vegetation height and slope) affected 1999 catch size. Non-metric multidimensional scaling (NMS) was chosen to analyse differences in species composition, as used successfully by Work and McCullough (2000) to analyse Lepidoptera assemblages. It is often the method of choice for graphical representation of community relationships and has been used to associate species composition with disturbance effect (Clarke 1993). This iterative method ranks data on a number of axes minimising "stress" which is the departure from monotonicity between distance in the original matrix and distance in the ordination space. The Bray-Curtis coefficient of dissimilarity was used to measure distances in the original ordination space because it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune & Mefford 1999) compared to other distance measures.

Results. The lepidopteran community in the stands examined at EMEND, based on light trapping, netting and rearing of hand collected larvae, comprised 309 species. No doubt the whole community is larger than this, but for the purposes of this report the light trap catches of 273 species were examined. These included macrolepidopterans (higher Ditrysia: Superfamilies Geometroidea to Noctuoidea) and pest microlepidopterans (e.g. large aspen tortrix, *Choristoneura conflictana* Walker). Light traps yielded 12,856 moths on 213 trap-nights in 1998 and 8927 moths on 196 trap-nights in 1999. Total richness was 215 species in 1998 and 242 species in 1999 with 67% species overlap between years. Geometridae and Noctuidae, the two largest families of macromoths, dominated the moth community in the number of genera and number of species (Table 2).

Species richness and moth trap catches were comparable among forest types investigated and years (Tables 3 and 4). Species overlap ranged from 59 to 68% among three forest types, indicating a large group of shared species. Singletons, species with only one occurrence, totalled 31 in 1998 and 40 in 1999. No species with 5 specimens or more were found only in one forest type. However, some species were found preferentially in certain forest types (see habitat use section below).

In 1999, both moth trap catch and species richness were significantly higher in control sites than in disturbed sites (Tables 4 and 8). Unlike in the 20% RSCs, species richness in 50% RSCs was not significantly different from that in control compartments. Also, lower species richness in the harvested compartments was not a reflection of the low moth trap catch because the rarefaction curve was steeper in harvested compartments (Fig. 10). Equal sample size would even yield more species (but fewer specimens per species) in harvested sites compared to unharvested sites.

Even two years of trapping were not enough to capture the entire range of species present at EMEND sites as shown by the overall species accumulation curve (Fig. 11). However, goals of this study mainly concentrated on the response of species to disturbance in relation to control sites and an exhaustive list of the lepidopteran fauna was thus not critical to meet our short-term objectives. Furthermore, the main species have all been identified considering that the curves are beyond inflexion point on the species accumulation curve (Fig. 10).

Correlation analysis done on the 1999 data showed that basal area correlated positively with catch size ($r=0.552$, $p<0.01$) and that the average height of understory vegetation was negatively correlated ($r=-0.632$, $p<0.01$) to catch size and independent of cover type (Table 5). Slope had no significant effect on catch size. The light interception by vegetation significantly increased as you go from 5 to 10 meters and from 10 to 20 meters away from the light trap (Fig. 12).

Based on trap catch over two years, 111 macro-moths species (43%) were classified in a habitat use category. Of these, 64% were generalists, 20% were deciduous forest specialists and spruce forest specialists accounted for the other 16%. The community is not clearly dominated by generalist species as expected, partly due to the large numbers of unclassified moths. The undisturbed community (1998) appeared somewhat different between deciduous dominated stands and stands with a coniferous component as shown on a three-dimensional NMS graph (Fig. 13) where the two groups are separated. Conifer specialists such as *Xestia mixta* (Walker)*, X. perquiritata* (Morris)*, Feralia comstocki* Grote and *Panthea acronyctoides* (Walker) were responsible for this forest type clustering. Also, certain species dependant on spruce or spruce-related resources (mosses, lichens…) such as *Eilema bicolor* (Grote) and *Idia americalis* (Guenée), both lichen feeders on coniferous trees, were two to ten times more abundant in stands containing spruce than in pure deciduous tree species stands.

Moths are often classified in different families based on their structural similarity. Noctuid moths are generally robust-bodied, strong fliers, thus more likely to have greater mobility than most geometrid moths. By contrast, geometrid moths have a higher wing to body size ratio and a slower, less efficient flight. Therefore, less mobile moths are less likely to venture outside their natural environment (e.g., forests, marshes, grass fields). One year after disturbance, the relative percentage of noctuids caught increased from 29% to 38%. Conversely, the relative percentage of geometrids fell from 52% down to 31% after disturbance. However, between-years comparisons are often subject to large fluctuations in numbers (Rejmánek and Spitzer 1982) and composition (Sample *et al.*). We can investigate changes between treatments in one given year to factor out those yearly fluctuations. Significant decreases in trap catch in treated compartments appeared in three lepidopteran families: Noctuidae ($p<<0.001$), Geometridae ($p<0.001$), and Uraniidae ($p=0.003$) (Table 6). Negative changes were also found in species richness of families Geometridae ($p<<0.001$) and Notodontidae ($p=0.038$) (Table 7).

There were significantly more species in the control sites than in the partial cutting treatments (Tables 4 and 8). Moreover, trap catch of generalists did not increase with thinning intensity as predicted but slightly decreased (Table 9). Data on number of individuals did show a higher proportion of spruce specialists in the 20% RSC. This increase was driven by three noctuid species: *Xylena thoracica* (Putnam-Cramer), *Nycteola frigidana* (Walker), and *Platyperigea montana* (Bremer).

The moth assemblage was affected by disturbance (Fig. 14). The left-to-right separation of the disturbance gradient (axis 1) explained most of the variation (R^2=0.687) in rank similarities between sites. The moth communities in control sites clustered tightly together in comparison to those in the disturbed sites plotted in the ordination space. The 50% RSC were almost all located between the two other treatments, leaving 20% RSC farther away from the control. They were also more dispersed in the ordination space than the others. Moth assemblages were thus less similar between the control and the highest level of disturbance, with those 50% RSC in between.

Proportions of moths classified into the three host-plant range classes were similar between both years based on number of species (Table 10). About half the community is dominated by polyphagous species. However, the trap catch of monophagous species in harvested stands decreased by half following 1999 partial cutting (Table 11). Trap catch of oligophagous species slightly increased with the amount of disturbance. Indeed, this trend was driven by species having Salicaceae plants as their main host plants. Sixty percent of the moths caught in 20% RSC were in that last category. Information was available for 261 Lepidoptera species trapped.

Control sites had proportionally more species of the woody plants, deciduous trees, conifers and lichens feeding guilds than partially cut sites two years post-harvest (Fig. 15). However, herb and grass, Salicaceae and generalist feeders species were more numerous in disturbed sites than in controls. Proportions of species in other guilds were not affected significantly.

Discussion. There was no difference in moth trap catch and richness between the three cover types investigated over two years. As hypothesised, each forest type shared many common species although no species with more than four specimens were found uniquely in one forest type. In our study, at least 35% of the species found relied on understory plants as caterpillars, another 50% of the species had at least some of their host plants in the understory, and many adult species fed on nectar from flowering plants. The relative homogeneity of the understory vegetation composition across cover types (EMEND core study 1998) might explain this large proportion of shared species. Moreover the slow response of vegetation one year after disturbance occurred (Dyrness 1973) might explain the lack of difference between years.

Partial cutting had an adverse effect on moth species richness and trap catch. Trap catch was particularly influenced by forest harvesting as both treatments (20 and 50% residual structure) had a significantly lower moth count. Moth richness was only significantly lower in 20% RSC compared to uncut sites.

A recent cut was thus affecting more the number of moths flying through a stand than the actual number of species.

Over the long run in harvested stands, plant species richness would return to pre-disturbance levels (Halpern and Spies 1995). Plant richness might even be higher following partial cutting due to a higher vertical and horizontal spatial heterogeneity (Shafi and Yarranton 1973). New plants would then attract more moth species. Indeed, the most important factor determining woodland moth species richness was the plant species richness in a study by Usher & Keiller (1998).

Species richness and catch per trap-night were highly correlated in our study (ρ=0.89, p<0.01) as also shown in another study by Daily and Ehrlich (1996). However, lower species richness in disturbed sites was not a sampling artifact caused by lower moth abundance. Indeed rarefaction curves show, for the same sample size, a faster accumulation of moth species in 20% and 50% RSC (Fig. 10).

Thinning probably affected the moth community mainly by changing local conditions in the first year: reducing the amount of canopy cover, increasing air circulation (affecting temperature and wind), precipitation reaching the forest floor and solar radiation penetrating the stand (Safranyik *et al.* 1998). Environmental conditions thus created were obviously harsher for moths of the forest interior. A partially cut, open stand was more subject to larger fluctuations in microclimate than a stand with an intact canopy acting as a buffer for understory microclimate. This resulted in an increase in the number of moths caught. However, a higher understory vegetation height potentially reduced the efficiency of the light trap by intercepting light transmission thus resulting in a lower number of specimens caught. The light interception by vegetation was expectedly higher as you move farther away from the trap. The height of the understory vegetation was independent of cover type. Consequently moth assemblage was not biased by this factor at the stand level. Thinning might also modify other factors affecting lepidopteran populations such as predation, parasitism and disease. A study by Grusheky *et al.* (1998) showed no significant effect of thinning on predation of larvae and pupae of a polyphagous species, the gypsy moth, by small mammal predators (although the population of the latter was increased). Similarly, Liebhold *et al.* (1998) reported no observable effect of thinning on rates of parasitism or disease in gypsy moth populations. Unfortunately, this outbreaking insect is atypical of most lepidopterans. Predation, parasitism and disease data are thus needed on other species in thinned and unthinned stands to evaluate if there is a significant difference between the two conditions.

The moth community is dominated by habitat generalist species. The pre-disturbance community was more similar between the two cover types with a spruce component (under- and overstory) (Fig. 13). This was caused by the presence of conifer specialists and species dependant on spruce-related resources (Roberts 1996).

Judging from their structure, certain groups of moths should be more mobile than others (Nieminen *et al.* 1999). Moth flight ability may influence resilience to changing environmental conditions. In 1999, between-site differences across treatments clearly showed a differential effect of environmental conditions on certain moth families. Partial cutting negatively affected trap catches of Noctuidae, Geometridae, Uraniidae and species richness of Geometridae and Notodontidae. Significant changes in these last two families occurred only between control and 20% RSC. All other negative impacts were significant between control and disturbed sites. The Uraniidae, represented by only one monophagous species, *Callizia amorata* Packard, was probably affected by impact of thinning on its host plant: bracted honeysuckle (*Lonicera involucrata* (Richards.) Banks). This plant is known to grow on moist or wet soils in forests, clearings, swamps and thickets (Johnson *et al.* 1995). The experimental compartments might have been too small (8-10 hectares) to affect catches of larger moths that are generally highly mobile such as hawkmoths (Scoble 1995), family Sphingidae (p=0.23). Two species in the genus *Smerinthus* Latreille, characterised by non-functional mouthparts, accounted for 99.9% of the hawkmoths trapped. Their size and lack of feeding may explain their lack of response to partial cutting because, as strong fliers not needing any nectar source, disturbed sites would not be limiting to them. Between-year differences seemed to indicate a decrease in overall geometrid trap catch compared to noctuids, which are robust-bodied, hence thought to be strong fliers. Thus, moth body size, feeding specificity, and flight capability all influenced the habitat use by different moth species.

There was only a slight evidence of an increase in habitat generalist species following different treatments as hypothesised. The plant community probably did not change enough in the year following winter harvesting to drive a change in moth species composition. A study by Halpern and Spies (1995) in which understory plant richness decreased by 24-29% after one growing season post-logging showed that losses in plant species diversity were short-lived and plant species richness exceeded pre-harvest levels within one to three years. In another study by Peterson and Pickett (1995), it similarly took two growing seasons after an old-growth forest blowdown to see an increase in plant richness. Also, invading plant species were not found until 2 years after logging in old-growth Pacific forests (Dyrness 1973). Finally, Thomas *et al.* (1999) demonstrated that twelve to sixteen years after thinning, understory plant cover and richness were higher, especially for the herb and shrub-layer. In our study, delayed disturbance effects on understory plants community is reflected in the moth community as changes in species richness by treatment for different feeding guilds (discussed in the next section).

Some species of moths might be adapted for taking advantage of ephemeral habitats, responding rapidly to change (Woiwod & Stewart 1990). Moths caught in harvested and control compartments were thus compared. There was little evidence that species took advantage of newly created ephemeral conditions in the year following disturbance. Instead, some species were relatively more abundant than others because of their resilience to environmental changes following disturbance. The post-disturbance NMS analysis clearly shows disturbance impact on moths based on their species composition: control sites are clustering tightly together, reflecting a more similar moth community than in disturbed sites. The increase in the number of spruce specialist species in highly disturbed sites with only 20% residual structure was driven by three noctuid species. An increase in abundance of these species could be explained by their association with open woodlands for *Xylena thoracica* (Putnam-Cramer) and other factors not measured here such as more humid woodlands for *Platyperigea montana* (Bremer) and *Nycteola frigidana* (Walker) (Handfield 1999).

The moth community at EMEND appears organised to exploit a broad defoliator niche by using diverse host-plant range and feeding strategies. For noctuids our host-plant range proportions were similar to a British study (Inkinen 1994). In general, monophagous species were less abundant than oligo- and polyphagous species. It is expected since larger moths tend to be more polyphagous and better dispersers while monophagous species are known to migrate less (Nieminen *et al.* 1999) and are believed to be more sensitive to disturbance. Thus, polyphagous species would travel more through recently disturbed habitats than monophagous species. Also, oligophagous species were slightly more abundant in disturbed sites than in control sites. One-year old aspen suckers following harvesting most probably drew them to those sites as many of these species fed on Salicaceae plants and used them to lay their eggs.

Lack of a large difference between host-plant proportions after disturbance probably reflected a delay in moth response to disturbance. Indeed, many moths flying in 1999 were already pupating when the partial cutting occurred in the winter of the preceding year. Thus larvae were not exposed to thinned stand conditions and changes in environmental conditions would not be fully reflected on the moth community before summer 2000, two years after the cut.

Feeding guilds can be used to indirectly examine disturbance impact on plants using two years of post-disturbance data. An increase in the number of generalist moth species was caused by the short-term increase in plant species richness following harvesting. The greater number of host plants present attracted more moth species. Also, the increase in species richness found in disturbed sites for moths feeding on herb, grass, and plants of the Salicaceae family was caused by the invasion of the stands by herb, grass and pioneer tree species such as aspen suckers. Disturbance reduced cover of both deciduous and coniferous trees, woody plants and lichen on trees which explained why moth species classified in those feeding guilds were found in lower proportions on partially cut stands.

Conclusion. Moth species richness and trap catch before disturbance was similar between the three forest types investigated. Moth species assemblages were also quite similar between forest types although stands with a spruce component were more similar together due to the presence of a few spruce specialist species. The moth community was dominated by habitat generalist species.

One year following partial cutting, moth species richness and particularly moth trap catch were negatively affected by changed environmental conditions in residual stands. The moth community was more different between sites as the degree of disturbance increased. Moth families were differentially affected by disturbance. Small-bodied moths such as loopers (family Geometridae) were affected more negatively than others. No species had a positive response one year after cut when the plant community did not have one full growing season yet to react to disturbance. However, data collected two years after cut showed that moths, once grouped by feeding guild, had a differential response to partial cutting. Species feeding on early successional plants or having a broad selection of host plants were more diverse in disturbed sites compared to uncut sites. The opposite was also true for species feeding on shrubs, and on deciduous and coniferous trees.

The moth community should return to pre-disturbance conditions with time. Partial cutting showed that many moth species would still be using disturbed habitat in a significant way. It might even be a good compromise to clearcutting after more studies are done on the subject. In the long run, partial cutting might even increase moth species diversity by increasing spatial heterogeneity and consequently plant diversity, an important determinant of moth species richness. Other factors like parasitism, predation, and occurrence of disease should also be monitored after partial cutting as they may be major actors affecting the moth community.

8. Impact of variable retention harvesting on spruce beetle parasitoids. MSc student, Julia Wesley, John Spence and David Langor have studied how natural enemies of the spruce beetle, *Dendroctonus rufipennis* (Kirby), responded to the EMEND treatements. The spruce beetle is one of the most destructive pests of mature spruce (*Picea* spp.) in North America (Humphreys and Safranyik 1993, Schmid and Frye 1977, Werner *et al.* 1977). Periodic, dramatic outbreaks can cause up to 95% mortality of mature trees within some stands, and can cover tens of thousands of adjoining acres of white spruce (Packee 1997; Schmid and Frye 1977). From 1974 to 1999, an estimated 3 billion board feet of lumber in British Columbia and 2 billion board feet in Alaska were lost to this beetle (Holsten *et al.* 1997). Spruce beetle outbreaks can be more important than other disturbances, including fire, in influencing the ecology of spruce forests (Veblen *et al.* 1994). The creation of large amounts of fallen host material following large-scale windfall, accumulation of logging residues and road-building favors rapid increases in local populations of *D. rufipennis.* Such events often precipitate outbreaks in adjacent stands (Reynolds and Holsten 1994; Wygant and Lejeune 1967), but this is not always the case (Safranyik 1989). It appears necessary that adjacent stands are stressed and susceptible to beetle attacks in order for an outbreak to occur (Safranyik 1989; Safranyik *et al.* 1983). Many aspects of the epidemiology of *D. rufipennis* are still poorly understood, and the possibility that variable retention harvests could stimulate outbreaks should be tested.

Of the 4 stand types included in EMEND; only conifer-dominated stands were selected for study as these are the stands most frequented by *D. rufipennis*. This work was limited to three harvesting treatments [clear-cut, 20% residual (live number of standing trees) and 50% residual as well as uncut controls] and included three replicates of each treatment, thus spanning a total of 12 of EMEND's 10 hectare compartments. A pre-treatment survey indicated that *D. rufipennis*-infested host material, mainly fallen logs, was present in all stands, and *D. rufipennis* populations were low.

Sampling of *D. rufipennis* and its parasitoids in bark commenced in 1999, immediately following application of harvesting treatments. As there was no assurance that sufficient and suitable *D. rufipennis*-infested material would be present in all treatments and replicates following harvesting, it was necessary to translocate spruce beetle-infested logs from off site into the study compartments. This approach also minimized effects of confounding factors such as tree diameter, phloem thickness and attack density, all of which are hypothesized to affect parasitism (Dahlsten 1982). In late April 1999, about 2 weeks before the start of the *D. rufipennis* flight period, 56 white spruce trees with a diameter at 1.3 m above ground of 34-40 cm (average 37.1 ± 0.2 cm) were felled in stands located about 10 kilometers south and north of the EMEND site. These trees were baited with *D. rufipennis* pheromone lures (Pherotech Ltd.) to encourage attack. In mid-June, following peak *D. rufipennis* attack but preceding parasitoid activity, 1.5 m-long bolts were cut from baited trees. Bolts chosen for use in the experiment were similar in terms of diameter (33.0 ± 3.3 cm), phloem thickness (2.8 ± 0.1 mm) and *D. rufipennis* attack density (approximately 30 entrance holes per m^2 of bark).

After translocation to study compartments, two bolts were placed end-to-end to form a 3 m-long 'log' with the long axis oriented north – south. The bark surfaces of the bolts were aligned to maintain the same orientation with respect to the ground as at the time of attack. In each of the 12 treatment or control compartments, three 'logs' were placed at least 50 m apart and 50 m from the stand edge. In most stands bolts were located in areas where there were residual trees to provide shade, although this was not possible in clear cuts.

Every two weeks spruce bark samples were removed from each log in all compartments. Because the summer was relatively cool in 1999, some individuals of *D. rufipennis* in this cohort required 2 years to complete development. Hence, sampling continued through the 2 post-treatment seasons, from 6 July to 11 September 1999 and from 10 May to 21 August 2000. Square bark samples of 100 cm^2 were cut from the top, two sides (east and west), and bottom of each log using a masonry chisel and hammer. Although it was necessary to roll the logs to sample from the underside, they were returned to their original orientation immediately after the sample was removed. Bark samples, and any specimens remaining on the log surface after bark removal, were placed in large petri dishes, transported to the field laboratory and stored in a refrigerator for no more than 3 days before processing.

Each *D. rufipennis* individual in these samples was tallied as live, parasitised or killed by other agents. A spruce beetle larva was considered parasitised if it had a parasitoid larva or pupa on or near it, or was paralyzed (often indicated by a scar) but with no parasitoid located nearby

In 1998, a diet and protocol was developed to allow rearing of larval and pupal parasitoids to adulthood to facilitate identification (see Wesley 2002). In 1999, parasitised spruce beetle larvae and their associated parasitoids were removed from bark samples and placed on a rearing medium developed from Robertson's (1979) spruce budworm diet by removing selected nutritive ingredients (Appendix 1). The medium was designed to maintain moisture but provide a bacteria- and fungus-free environment. About 3-4 ml of medium was poured into 10 mL plastic container fitted with a cardboard lid. Medium was made prior to use and frozen in rearing containers until needed. Generally, one parasitoid with its host was placed in each rearing container, except that in the case of superparasitism, all parasitoids from the same host were placed in one rearing container. Containers with parasitoid specimens were placed on shelves at ambient temperature and covered by dark bags to exclude light. Parasitoid rearing containers were checked daily and emerged parasitoids were placed in 75% ethanol for later identification. In October, containers with cocoons from which there was no emergence were placed in dark bags and held in cold storage (-3^0 C) to break diapause. In March 1999, parasitoids were returned to room temperature and adults began emerging after 2 weeks. Dead larvae and live adult parasitoids were preserved in 75% ethanol for subsequent identification. Dead larvae were later identified using mandibular characteristics (Appendix 2). Adult parasitoid specimens were identified using voucher specimens at the Northern Forestry Center museum in Edmonton, Alberta and identifications were verified by Gary Gibson, Henri Goulet and John Huber at the Canadian National Collection in Ottawa, Ontario.

As only 1.6% of overall parasitism occurred on second instar *D. rufipennis* larvae, and dead second instars were often hard to locate, percent parasitism was calculated only for third larval and later instars (hereafter referred to as 'available hosts'). Thus, percent parasitism within a sample was estimated as 100(P/T), where P is the number of parasitised available hosts and T is the total number of live and dead available hosts.

Spruce beetle development was described and compared among samples and treatments with a development index. Instars were assigned the values one to seven for eggs, first, second, third, and fourth larval instars, pupae and adults, respectively. The development index was calculated as the average instar in the sample.

A variety of approaches were used to obtain information about spruce beetle and parasitoid emergence and flight phenology and about parasitoid oviposition. Following capture, insects were preserved in 75% ethanol pending identification.

Eight Lindgren funnel traps (Lindgren 1983) containing propylene glycol as a preservative were suspended 4 m from the ground in uncut conifer- dominated forest surrounding the EMEND site and baited with *D. rufipennis* lures containing α-pinene and frontalin (Phero Tech Inc.). Traps were checked and captured insects were removed every 2 weeks from May 11 to September 12, 1999.

In control compartments, 13 bright yellow 4x6 inch sticky traps (Moeck *et al.* 1981; from Phero Tech Inc.) were hung by wire perpendicularly to the *P. glauca* log side on felled trees and stumps baited with spruce beetle pheromone lures. Traps were deployed on July 17, 1999, after peak *D. rufipennis* flight was completed, and collected every 2 weeks until August 20, 1999. After removal, traps were wrapped in wax paper and frozen for later tally and identification of parasitoids.

Emergence traps (Langor and Raske 1987), which each sample a 100 cm^2 circular area and use propylene glycol as a preservative, were attached to spruce beetle-infested trees and emptied every 2 weeks. In 1999, 24 emergence traps were placed on each of 12 translocated logs into treatments and these were monitored from July 4 - September 12, 1999 and from May 10 to August 8, 2000. Also in 1999, 12 emergence traps were placed on a girdled standing tree and 20 traps on a log during the second year following *D. rufipennis* attack.

Activity of *D. rufipennis* parasitoids was recorded for the surface of the translocated logs and observed during sampling in 1999 and 2000 was recorded. In addition to these casual observations, structured observation times were scheduled for all 9 translocated logs in control compartments and for 3 translocated logs in one 20% residual compartment (these compartments were chosen for regular observations because parasitoids were more frequently observed there). On each log two people made simultaneous observations for fifteen minutes once per week from 6 July to 11 September 1999 and from 10 May to 21 August 2000 to record incidence and behavioral information about the parasitoids. Observations of parasitoids were conducted on all days that samples were collected except when it was raining, in which case parasitoid observations were rescheduled for the next rain free date. Parasitoid specimens that were not identified during bark activity observations were collected using aspirators (Bioquip), identified at close range and immediately returned to the environment.

All analyses were done using SPSS 10.0.5 (SPSS Inc. 1999). Composition of parasitoid assemblages was compared among treatments and among log surfaces using Chi square tests. First, tests were applied to data on the number of parasitised hosts in bark samples attributable to each parasitoid species. Second, as one species was a superparasitoid, X^2 tests were also applied to data on the number of parasitoid larvae/pupae of each species found in bark samples. For all X^2 tests, data for *R. xylophagorum* and *D. dendroctoni* were combined since there were fewer than 5 individuals from each species reared from each treatment and bark surface location.

The relationship between brood density of *D. rufipennis* and percent parasitism in each treatment and log surface for August 17, 1999 (the date when maximum parasitism was achieved) was examined graphically but could not be tested statistically. Residuals for these samples could not be normalized even by transformation and a high proportion of samples had either no parasitism or available hosts present, therefore, was not possible. Many of the cells in the contingency table had expected values less than 5, also eliminating Chi squared analyses (X^2).

Comparison of overall percent parasitism among treatments and sample locations could not be accomplished with ANOVA as ca. 80% of samples had no parasitism and residuals could not be normalized by transformation (arcsine square root, natural log). Thus, for purposes of analyses, parasitism in these samples was separated into two components: 1) probability of sample discovery by parasitoids and 2) conditional probability of parasitism, given discovery. Data from all treatments and log surfaces combined were subjected to regression analysis to determine if there was a relationship between density of available hosts and the proportion of samples discovered, but data points were too few to allow regression to be applied to each treatment individually. Thus, chi squared analyses (X^2) were used to examine individually the effect of treatment and log surface on proportion of samples discovered by parasitoids. For those samples discovered by parasitoids, ANOVA (General Linear Model) was used to analyze parasitism patterns among discovered samples using treatment and log surface as the main effects and beetle density as a covariate. Data for ANOVA had normal residuals so no data transformation was required. For each sample date, the *D. rufipennis* development index (non-transformed) was compared among treatments and log surfaces using ANOVA (General Linear Model). Bonferroni pre-planned pairwise comparisons were used to detect differences between treatments and log surfaces for development index.

Results. The first bark samples were taken on July 6, 1999, two weeks after logs were moved into the stands. At this time there was no significant difference in beetle development among treatments and most of the *D. rufipennis* progeny were represented by 1st instar larvae (Table 12). On both July 19 and August 2, development was significantly slower in control stands than in harvested stands (Table 12a). By August 17, most of the beetle population was represented by third larval or later instars and there was a strong effect of treatment on development. At this time spruce beetle progeny in uncut stands were significantly less developed than in all harvested stands, and development in clear cuts was significantly more advanced than in all other compartments (Table 12a). Since after August 17 there was untallied adult emergence from some samples and thus, it was no longer possible to calculate reliable development indices for these samples.

Beetle development pooled over all treatments was similar on all surfaces of the logs on July 6 (Table 12b), but by August 17, larvae on the top surfaces of logs had developed significantly faster than those at the log bottom. There was no significant interaction between treatment and log surface for August 17, 1999.

On August 17, the number of available spruce beetle hosts was similar for clear cut and 20% treatments but increased in 50% residual and control compartments, and this pattern was generally evident for all log surfaces (Fig. 16). In all treatments the majority of available beetles were located in the bottom of logs (Fig. 16a). Clear-cut and 20% treatments had a similar proportion of overall available host in the lower surface, but the proportion of available host in other surfaces increased in 50% residual and control compartments.

Four species of parasitoids were found associated with *D. rufipennis*: two braconids, *Coeloides rufovariegatus* (Provancher) and *Bracon tenuis* Muesebeck & Walley, and two pteromalids, *Roptrocerus xylophagorum* (Ratzeburg) and *Dinotiscus dendroctoni* (Ashmead). Overall, only 72% of the parasitised *D. rufipennis* could be attributed to a parasitoid species as some parasitoid larvae were unidentifiable or the host was only paralyzed with no eggs or larvae found on or near it.

The highest number of parasitised available hosts occurred in control treatments and parasitism decreased as the treatment areas became less shaded (Fig. 16b). Of the parasitism that could be attributed to parasitoid species, 49.0%, 36.6%, 9.8% and 4.6%, respectively, were caused *C. rufovariegatus, B. tenuis, R. xylophagorum, and D. dendroctoni* (Fig. 17a). The proportion of spruce beetle parasitism attributable to the four parasitoid species varied significantly among treatments ($\chi^2 = 39.7$, df=6, $P < 0.001$). *Coeloides rufovariegatus* was the most common parasitoid in clear cuts and controls and *B. tenuis* was the most abundant in the 20% and 50% residual treatments (Fig. 17a). *Roptrocerus xylophagorum* was proportionately much more abundant in clear cuts than in the other treatments (Fig. 17a).

All four parasitoid species are ectoparasitic and only one parasitoid was found per host for *C. rufovariegatus* and the two pteromalid species. *Bracon tenuis*, however, is a superparasitoid with an average of 2.4 (± 0.16) larvae found per host (range was 1-9). Of the total number of parasitoid larvae sampled in 1999, *C. rufovariegatus, B. tenuis, R. xylophagorum* and *D. dendroctoni* comprised 32.8%, 56.7%, 6.7% and 3.9%, respectively (see Total in Fig. 17). Thus, the proportional representation by *B. tenuis* in the parasitoid assemblages was much higher than the proportion of parasitised hosts attributed to that species. The proportional representation by the four parasitoid species within the total parasitoid population varied significantly among treatments ($X^2 = 106.2$, df=6, P< 0.001). Provided that mortality is equivalent among all parasitoid species during development, *C. rufovariegatus* will be the dominant species emerging from spruce beetle populations in clear cuts, *B. tenuis* will dominate emerging parasitoids in 20% and 50% residual treatments, and these species will be in almost equal abundance in controls (Fig. 17). Proportionately, *R. xylophagorum* will be much more abundant in clear cuts than in other treatments.

The distribution of parasitism events around the log surface was congruent with the distribution of available hosts (Fig. 16) in clear cut and 20% residual treatments; however, as the percent residual increased, parasitism events occurred primarily on the sides and tops of logs (Fig. 16). Individual parasitoid species were associated with various parts of the logs during oviposition ($X^2 = 71.1$, df=6, $P < 0.001$). *Roptrocerus xylophagorum* was the dominant parasitoid attacking tops of logs, despite the fact that it was one of the least abundant parasitoids; *C. rufovariegatus* was found predominantly on the sides of logs, and caused over 70% of the parasitism events; and *B. tenuis* were most common on the bottoms of logs (Table 13). A similar pattern was evident for the number of parasitoid progeny produced on different log surfaces ($X^2 = 131.7$, df=6, $P < 0.001$) (Fig. 17b).

Parasitism of *D. rufipennis* was first noted on July 19, 1999 in the three harvesting treatments and on August 7 in the controls (Fig. 18), and most parasitism had accrued by the August 17 sample date as no new cases of parasitism were encountered after this date (note data for parasitism and number of parasitised hosts in Fig. 18). Emergence of new brood adults had commenced in all treatments by August 29 (note decline in number of available beetles from Aug. 17 to Aug. 29 (Fig. 18)), but these adults were not tallied. Thus percent parasitism could be estimated only for those samples taken on August 17. Of the 144 samples taken on this date, 77 contained available hosts and could be analyzed. Parasitism was sub-divided into two components for examination. First, the chance of sample discovery by parasitoids was compared among treatments using the 77 samples containing available hosts. Then conditional probability of parasitism given discovery was compared among treatments using the 35 samples that sustained parasitism.

Overall, only 45% of samples with available beetles were discovered by parasitoids and the chances of sample discovery did not vary significantly among harvesting treatments (Table 14a; $\chi^2 = 0.27$, df=3, $P = 0.970$) or around the circumference of logs (Table 14b; $X^2 = 2.49$, df=3, $P = 0.477$). Regression analysis showed that there was no relationship between density of available hosts and probability of discovery ($R^2 = 0.003$, $P = 0.670$).

Within samples containing parasitism there was a significant inverse relationship between density of available hosts and percent parasitism ($R^2 = 0.896$, $P < 0.001$), and for this reason density of available hosts was included as a covariate in the analysis of variance to assess treatment effects on percent parasitism in discovered samples.

Although percent parasitism appear to vary from 34.5% to 54.5% in different treatments (Table 15a) this variation was not significant ($F_{3,\ 31}$ = 0.67, *P* = 0.581). Observed percent parasitism was highest on hosts in the top surface (74%) and lowest for those in the bottom surface (32%), but overall this was not significant (Table 15b, $F_{3,\ 31}$ = 0.73, *P* = 0.546). As the earlier regression of percent parasitism and available host density suggested, available beetle density was a significant factor determining parasitism proportion in each sample (Table 15, $F_{3,\ 31}$ = 22.20, *P* < 0.001), but the interactions between host density and the main effects were insignificant.

Flight and oviposition of parasitoids peaked in early August (Fig. 15), when spruce beetle progeny were mainly third and fourth larval instars (Fig. 14), and number of parasitoid larvae in bark samples peaked in mid-August. The fourth larval instar was the most severely affected by each parasitoid species (Table 16), and overall this instar experienced almost 75% of the total parasitism events. *Coeloides rufovariegatus* was the most abundantly captured and observed species, it's flight period extended from early July to mid-September (Fig. 19a). The other species appeared to have shorter flight periods, extending from mid-to-late July to mid-August. *Bracon tenuis* was rarely caught in traps, although it was relatively abundant in bark samples. After mid-August, there was little accrual of parasitism as indicated by bark samples. Thus, parasitoids flying in late August and September were probably those finished reproducing or the next generation of parasitoid adults that had completed development and emerged. Although some parasitoids did emerge in August and September 1999, these were not tallied, but comparison of the average number of parasitoids in samples from August 17, 1999 to May 10, 2000 suggests that as many as 75% of parasitoids emerged before winter (Table. 17). There was no evidence that these emerged parasitoids reproduced on spruce beetle hosts in the year of emergence. Some larvae of all species overwintered in the logs. No parasitoids emerged from sample logs during winter and spring until mid June 2000.

Only *C. rufovariegatus* was observed sufficiently often to provide reliable data on behavior. It appears that some mating occurs on the bark surface (observed once). On one occasion, a mating swarm of *C. rufovariegatus* was observed on the bark surface of a spruce log. The swarm had approximately 20 males tightly grouped around 1 female. The group of parasitoids flew away after a brief observation period.

During oviposition, females antennated over an area on the bark surface, alternately touching their antennal tips to the bark surface. An area as small as 5 cm^2 was communally shared with up to 5 other antennating *C. rufovariegatus* females without evidence of aggression or territoriality. When a female determined that a oviposition site was suitable, she probed the bark several times with a vertically oriented ovipositor, apparently to determine exact placement. Then, she placed her ovipositor at right angles to the bark surface and drilled. The female's abdomen pulsated as the ovipositor entered the bark, a process that may last 3-6 minutes, depending on the bark and phloem thickness. After a female of *C. rufovariegatus* had inserted her ovipositor into the bark, the ovipositor was removed with the same pulsating abdomen motion and about the same time as required for ovipositor insertion. Before the ovipositor was entirely removed from the bark it could be oriented to a different angle and inserted into the bark a second time. This procedure was done without the female assuming another body position. After ovipositor insertion and removal, the female then turned her body approximately 90^{o} (clockwise usually), relocated the oviposition site with her ovipositor and inserted the ovipositor into the bark again, using the same pulsating motion of the abdomen. This second drilling took about the same time as the initial bark entrance and removal. After this ovipositor insertion and removal a female cleaned her ovipositor with her hind legs while remaining in the same location. After cleaning the female remained motionless for 3 minutes before repeating the oviposition site location procedures a second time. This highly stereotyped procedure was observed in the field five times.

There was evidence of interference competition between *C. rufovariegatus* and *D. dendroctoni*. When *D. dendroctoni* encroached on a *C. rufovariegatus* female*,* the *C. rufovariegatus* defender either chased the invader away or rammed it until it was dislodged from the bark surface. Females of *C. rufovariegatus* interrupted site selection or oviposition behavior to chase off *D. dendroctoni* in both encounters observed.

Discussion. The life cycle of the spruce beetle varies from 1-3 years, depending on temperature conditions, but the 2-year cycle is most common in western Canada (Safranyik 1989). Rate of larval development, and hence the length of the life cycle, is a function of phloem temperature, which is strongly influenced by solar radiation (Werner and Holsten 1983, 1985; Hansen *et al*. 2001a). Thus, it is common that different parts of the same tree or log may have univoltine or bivoltine beetles, depending on exposure to direct solar radiation (Safranyik 1989). Although spruce beetle development was at about the same stage on all log surfaces and in all sample logs at the time that they were translocated to treatment and control compartments, differences in exposure to sunlight resulted in differences in development rate. By August 17, beetles had developed significantly faster in clear cuts and in the top surfaces of logs. An unestimated proportion of the beetle population completed development to adulthood within one year, and it is reasonable to expect that the proportion of univoltine beetles increased with the amount of sun-exposure. Safranyik *et al*. (1983) reported 66% of beetles in logging residual and 22% of beetles in windfall had a 1-year life cycle. As spruce beetle epidemiology appears to be in part influenced by proportion of beetles which are univoltine (Safranyik et al. 1983; Reynolds and Holsten 1994), forest managers must be aware of the potential consequences of management activities in spruce forests which increased availability of suitable host material and rate of beetle development. A temperature-based model to predict proportion of univoltine spruce beetles may help identify risk and aid management decisions (Hansen *et al*. 2001b).

The density of available spruce beetle hosts available for parasitism on August 17 was likely largely influenced by the original density of eggs laid, development rate and mortality by other agents. Although the relative importance of these three factors (and perhaps others) could not be separated in this study, the end result was that the lowest density of available hosts was available in clear cut and 20% residual compartments, and within these compartments almost all available hosts were located in the lower surface of logs, thereby limiting the action of parasitoids to these surfaces. As the amount of stand residual, and hence shading, increased, so did the overall density of available hosts, and increasingly more hosts were available on the sides and tops of logs, providing more opportunity for parasitoids to distribute themselves around the circumference of logs.

Except for *B. tenuis*, the parasitoid species found attacking the *D. rufipennis* in this study have also been reported from *D. rufipennis* in Alaska and Colorado (Bushing 1965; DeLeon 1935; Gara *et al.* 1995; Krombein 1958; Massey and Wygant 1954; McCambridge and Knight 1972; Peck 1963). Gara *et al.* (1995) noted that *Bracon* sp. was reared in association with *D. rufipennis* in Alaska, but the individuals were not identified to species. McCambridge and Knight (1972) report that parasitism in Colorado was mostly by *C. rufovariegatus* and resulted in 0.4 – 6.1% *D. rufipennis* mortality. Also in Colorado, Massey and Wygant (1954) reported that *C. rufovariegatus* was the most important parasitoid of spruce beetle larvae, but *D. dendroctoni* and *R. xylophagorum* were also effective parasitoids. In Alaska, Gara *et al.* (1995) found *R. xylophagorum* to be the most abundant spruce beetle parasitoid, followed by *D. dendroctoni* and *C. rufovariegatus*. Although other authors (e.g., Gara *et al*. 1995) have reported many other parasitoid species associated with *D. rufipennis*, in all cases parasitoids were reared from bolts infested by *D. rufipennis* and other scolytid species. Thus, specific host-parasitoid relationships could not be ascertained. The current study is the first to clearly establish specific spruce beetle-parasitoid relationships.

In 1999, *C. rufovariegatus* was the dominant parasitoid in terms of impact on *D. rufipennis*, and accounted for 49.0% of the total recognizable parasitism. This species had the longest flight period and was the most aggressive parasitoid on the bark surface, which may contribute to its success. However, assuming similar survival among larvae of all parasitoid species, the superparasitoid, *B. tenuis*, was the most abundant parasitoid at emergence; in the first post-treatment parasitoid generation 56.7% of parasitoid larvae found were of this species. It may be, therefore, that the relative abundance and impact of the four parasitoid species will change over time at the EMEND site, but this depends very much on relative fecundity, survival and propensity to attack other host species (all are bark beetle generalists and some even attack other families of wood-boring beetles) (Dahlsten 1982).

The high variability of proportional abundance of the four parasitoid species around the circumference of logs may reflect active choices for oviposition sites rather than differential mortality, as mortality of parasitoids was very low (no cases of mortality were observed). In terms of overall parasitism, a null hypothesis might reasonably predict that spatial patterns in percent parasitism would be congruent with the distribution of available hosts. Specifically, this hypothesis would then predict that control compartments and the bottom log surfaces should be best for parasitoids. Parasitism was indeed highest in control compartments, but in these compartments the strongly inverse relationship between host density and percent parasitism suggests that hosts in bottoms of logs may be underutilized, perhaps because the microhabitat is not ideal for parasitoids. Alternatively, this pattern of host utilization may simply be an outcome of parasitoid landing and host searching patterns. Parasitoids were observed to land on the top surfaces of logs initially and commence searching and ovipositing there, eventually moving down the sides and to the bottoms. By the time parasitoids reached the bottom of the logs, they likely had fewer eggs to lay but there was greater host availability, resulting in under utilization and low percent parasitism. However, parasitism patterns are best understood when the activities of different parasitoid species are examined individually, both in terms of percent parasitism and number of parasitism events.

Although *C. rufovariegatus* caused over 70% of the total parasitism on the sides of logs, the number of parasitism events caused by this species was the same on sides and bottoms. Thus, there is no compelling evidence to suggest that *C. rufovariegatus* was most common on log sides over bottoms; however, the relative rarity of this parasitoid in the tops of logs suggests that this is not a chosen oviposition location or that females are not as efficient at locating hosts when host density is very low. All other three parasitoid species showed strong affinity for the bottom surfaces of logs, as indicated by number of parasitism events. *Bracon tenuis* exhibited the strongest correlation with log bottoms, accounting for 54% of total parasitism events on that surface and 75% of all parasitism events by that species. Additionally, *R. xylophagorum* was proportionately most abundant in the tops of logs and clear-cut areas, suggesting that this species chooses sun-exposed habitats. There is little information available on the best microhabitat for bark beetle parasitoids; however, there is evidence that due to physical limitations of ovipositor length, parasitoid success and spatial distribution on trees may be limited by bark thickness (Ball and Dahlsten 1973; Dahlsten and Stephen 1974). However, some parasitoids with short ovipositors, e.g. *R. xylophagorum*, are able to enter bark beetle galleries to seek hosts and are not limited to oviposition through the bark (Berisford *et al*. 1970; Dahlsten and Bushing 1970; Reid 1957).

The flight periods of all four species overlap with the occurrence of third larval and later instars of *D. rufipennis*. As parasitoid larvae must develop on one host there are advantages (e.g., survival & fecundity of the F1 generation) to attacking the largest host, and synchrony between availability of the largest host instars and peak flight of parasitoids is a general pattern (Camors and Payne 1973; Dahlsten 1982; Dixon and Payne 1979; Edson 1978; Stephen and Dahlsten 1976). Parasitoids *C. rufovariegatus* and *B. tenuis* began emerging in late August but emergence phenology was not monitored. It is not known if these emerged individuals have an obligatory diapause, but the fact that no additional parasitism accrued on spruce beetle larvae after August 17 suggests that they are not actively seeking new hosts and may simply feed on nectar (Kevan *et al*. 1993; Syme 1975) and overwinter. Adults may be long-lived as females of *Coeloides brunneri* Viereck survived an average of 32.9 days and males 22.2 days on a honey diet at room temperature (Ryan and Rudinsky 1962).

C. rufovariegatus, R. xylophagorum and *D. dendroctoni* have broad host ranges (Dahlsten 1982), including many other bark beetle species. Thus the impact of these species on spruce beetle may be influenced by the abundance of other bark beetles in the same logs and stands.

Although there is biological utility in sub-dividing parasitism to first examine chances of patch discovery and then parasitism within discovered patches (Kreuss and Tscharntke 1994; Morrison and Strong 1981; Roland and Taylor 1995), insufficient information is available to adequately define the spatial and temporal parameters of a patch from the functional viewpoint of spruce beetle parasitoids. In this study, the 100 cm^2 circular bark samples were used as a rough proxy of patch, without knowing if parasitoids respond to host density at this scale. Nonetheless, the lack of treatment effects on probability of discovery by parasitoids, and the lack of a relationship between available host density and chances of discovery (all treatments combined), suggests that *D. rufipennis* parasitoids use cues other than host density to select oviposition sites. For example, the large amount of logging slash present immediately following harvest may attract parasitoids (Dahlsten 1982). Also, although all four parasitoid species were present in all treatments, the degree of sun-exposure seems to have influenced the relative abundance of the species, and hence the chances of patch discovery by individual parasitoid species. Generally, it is believed that parasitoids are initially attracted to the host habitat and then to the host, which they then choose to accept or reject. (Doutt 1965; Richerson and Borden 1972a). Thus, sample discovery for each treatment depends on a complicated set of decisions by the parasitoids and much behavioral work is needed to ascertain how parasitoids select patches and hosts.

Parameters that determine whether parasitoids oviposit and the amount of reproductive effort invested in a host patch are also little understood (Waage and Greathead 1986; Richerson and Borden 1972b). Studies conducted on *Coeloides* spp. indicated that parasitoids which oviposit through bark may use cues like infrared radiation from host muscle or, less likely, sound or vibration from host feeding or host odor (DeLeon 1935; Richerson and Borden 1971, 1972a, b; Ryan and Rudinsky 1962).

My observations suggest that antennae are an important tool to help *C. rufovariegatus* identify oviposition sites.

The significant inverse relationship between beetle density and percent parasitism proportion largely reflects the pattern in 50% residual and control compartments as parasitism events in these compartments comprised 71.8% of the total number of events. This relationship suggests that even though all treatments may have an equal chance of discovery, a beetle larva feeding in a high density patch is less likely to be parasitised than if feeding in an area where density is low. Thus, there may be a significant benefit to host clumping, as has been demonstrated in other host-parasitoid systems (Brown and Cameron 1979; Burnett 1958; Hirose *et al.* 1976; Morrison *et al.* 1980; Reeks 1953).

Conclusion: Although there was no overall impact of harvesting treatment on percent parasitism in discovered samples, there was some evidence of treatment effects on the distribution of parasitism around the circumference of logs. In control stands, which represent the usual stand conditions for *D. rufipennis* populations, parasitism was concentrated on the top and sides of logs although the densities of available beetles were highest on bottoms. It may be that in control stands the bottoms of logs are too shaded and cool for optimum parasitoid development. Thus, concentration of *D. rufipennis* oviposition on lower surfaces of logs may be a parasitoid-avoidance mechanism. However, as stands are increasingly opened up by harvesting, parasitoids increasingly utilize hosts in the bottom surface of each bolt. These results suggest that partial harvesting of stands may be detrimental to *D. rufipennis* as the increased exposure of breeding material makes exposed surfaces less suitable for beetle development and survival and also makes the lower surface more susceptible to parasitism. However, these disadvantages may be partially offset by the faster development of *D. rufipennis* and the fact that a higher proportion of beetles are univoltine than in more shaded stands (Safranyik *et al*. 1983).

At least four parasitoids contribute to the environmental resistance that keeps populations of *Dendroctonus rufipennis* (Kirby) in check in northwestern Alberta. *Coeloides rufovariegatus* (Provancher) (Ichneumonoidea: Braconidae) was the most common parasitoid, *Bracon tenuis* Muesebeck & Walley (Ichneumonoidea: Braconidae) was the second most abundant parasitoid and was reared more successfully than *C. rufovariegatus*. Smaller proportions of beetles were parasitised by *Roptrocerus xylophagoru*m (Ratzeburg) (Chalcidoidea: Pteromalidae) and *Dinotiscus dendroctoni* (Ashmead) (Chalcidoidea: Pteromalidae). Fourth instar *D. rufipennis* larvae were the instar that was parasitised (74.6%) most often. Discovery of spruce beetles by parasitoids was not affected by harvest treatment or host density, but among samples with parasitism there was a significant inverse relationship between available host density and percent parasitism. Parasitism did not differ with respect to treatment or position on log surface but beetle number was significantly correlated with parasitism in each sample.

9. Boreal Spiders as Indicators of Forest Disturbance and Management. David Shorthouse, a PhD student in the Department of Biological Sciences, has studied the impacts of harvesting on spider communities at EMEND under the supervision of John Spence and Jan Volney. The value of spiders as indicators is supported by three observations. First, spiders are generally abundant in terrestrial communities ensuring large enough samples for numerical analyses. Second, they have a variety of forms to fulfill a variety of ecological niches. And third, the order is small enough so that a working knowledge of the taxonomy is not beyond the capabilities of a single worker.

Spiders have been studied in relation to clear-cutting (McIver *et al.* 1992), fire (Johnson 1995, Koponen 1995, Koponen 1993, Aitchison-Benell 1994, Hauge and Kvamme 1983, Huhta 1971), managed forests (Pajunen *et al.* 1995), and succession (Bultman 1980). However, integrated experimental studies tying all these processes together have not been published. Also surprising is our ignorance of fundamental boreal forest spider diversity (Danks and Foottit 1989). The purpose of this study is twofold: 1) to assess litter spider biodiversity in the boreal mixedwood forest within the EMEND experiment and, 2) to examine the relationship between tree cover classification and harvest treatment on spider assemblages. At this point in time it is not possible to give a full account of the treatment effects as the study is still in progress toward completion of Mr. Shorthouse's doctoral degree, expected during summer 2003 and well within the normal 5 year framework of doctoral dissertations in the Department of Biological Sciences.

Spiders are upper trophic level arthropods that provide significant functional linkages between smaller arthropods and larger animals, like birds, generally valued by the public (Moulder and Reichle 1979, Mason *et al.* 1997). A major shift in the structure of their assemblage undoubtedly shifts the activity patterns of their prey and those that prey upon them. Because spiders are agile and short-lived, they respond quickly to disturbances (Crawford *el al.* 1995). On the other hand, most understory plant species are perennial. Their distribution patterns do not reflect short-term changes in habitat quality, nor can they be good early predictors of habitat change. Consequently, litter spider composition may be more useful than plants as a bioassay of forest floor habitat quality.

Ground-dwelling spiders were passively captured in pitfall traps throughout the pre-harvest season (summer 1998), the first post-harvest season (summer 1999), and the second post-harvest season (summer 2000).

Prior to harvest, 72 pitfall traps were arranged in transects of 6 traps in each of four replicated cover types, deciduous-dominant (DDOM), deciduous-dominant with a coniferous understory (DDOMU), mixed (MX), and conifer-dominant (CDOM). Traps were emptied approximately once every three weeks.

After harvest (summer 1999 and 2000), pitfall traps were installed in pairs in established tree plots in each of the 100, 10 ha compartments. In each of the harvested compartments, one trap was installed in the middle of a machine corridor, while the second was installed in the middle of a vegetation strip. In control and clearcut compartments, pitfall traps were installed at opposite ends of established tree plots. A team of undergraduate students recorded vegetation data and GIS coordinates for each tree plot. Pitfall trap contents were collected approximately once every three weeks throughout both post-harvest seasons.

Additional pitfall trapping regimes were established during the first and third post-harvest seasons to address potential edge effects and preferential spider movement between harvested and un-harvested areas. Transects were established through elliptical reserves in mixed stand clearcuts summer 1999 (see Fig. 20). In summer 2001, directional pitfall traps consisting of traps nestled at the apex of folded polyethylene sheets, were installed in transects between harvested deciduous-dominant stands and their surrounding, uncut buffers. In conjunction with this latter design, female wolf spiders (Lycosidae: *Pardosa moesta* Banks) carrying egg sacs were tracked at the transition between deciduous-dominant clearcuts and their buffers to estimate the redistribution of their populations. The specimens and data from these studies will not be presented here.

Results. Seventy-two pre-treatment pitfall traps were maintained summer 1998, while sampling was intensified to 704 post-treatment pitfall traps summer 1999 and 2000. This represents perhaps the largest systematic sampling regimes in Canada's boreal forests. Spiders from pre-treatment season and the 1999 post-treatment season have been identified to species, while identifications for the 2000 post-treatment season are 50% complete. The remaining specimens will be identified by end December 2001. To date, 143 species and 30,734 specimens have been identified. Few species will be added to this list because the rarefaction of subsamples approaches a species richness asymptote (Fig. 20). Indeed, the Chao1 estimate of true species richness (Chao, 1984) was 164±8. The results that follow are from the 1999 collecting season. The majority of these species are singletons, species represented by a single specimen, or doubletons, species represented by two specimens. Consequently, there are many new distribution records and a few undescribed species. For example, a recently described species in the Family Linyphiidae, *Maro amplus* Dondale & Buckle, is well represented and a paratype collected from this sampling protocol rests in the Canadian National Collection in Ottawa (Dondale & Buckle 2001).

Spider assemblages responded to cover type and treatment, particularly the latter. As a group, spiders (pooled by treatment replicate) were less abundant in deciduous-dominant stands with a coniferous understory than in deciduous-dominant stands without a coniferous understory ($F_{3,35}$=20.78,s p<0.05) (Fig. 21). Species richness was not significantly affected by harvesting intensity (Fig. 22). However, the greatest number of species was trapped in stands of intermediate harvest intensity, 10%, 20%, and 50% residual standing trees. On the other hand, spider abundance closely mirrored forest harvest intensity. Greater harvesting intensity resulted in greater spider abundance (Fig. 23). In particular, spiders were significantly more abundance in clearcut treatments ($F_{5,35}$=50.17, p<0.01). This counter-intuitive response is largely due to the extraordinary abundance of one active member of the family Lycosidae, *Pardosa moesta* Banks. Over 5,000 specimens of *P. moesta*, or 26% of all spiders, were collected predominantly in clearcut stands ($F_{5,35}$=24.81, p<0.01) (Fig. 24). Prior to harvesting however, the relative abundance of *P. moesta* was less than 1%. On the other hand, more cryptic spiders responded in reverse. Spiders in the superfamily Linyphiidae were most abundant in control treatments than all other treatments, although this response was not significant (Fig. 25). Close to 50% of all spiders were linyphiids prior to harvesting; after harvesting however, the relative abundance of linyphiids dropped to 22%.

The preceding analyses of variance assumed that samples, in this case collections from pitfall traps pooled by treatment replicate, are independent from one another. However, *P. moesta* abundance isoclines created using ArcView spatial tools reveal elevated concentrations of abundance in regions of the EMEND project, particularly in the vicinity of intensely harvested compartments (Fig. 26). Spiders in adjoining control and moderately harvested compartments may be affected by their proximity to elevated pockets of abundance. In other words, treatment replicates may not be independent from one another as assumed, thus violating an assumption of analysis of variance.

Nonmetric multidimensional scaling of spider scores pooled by treatment replicate demonstrates clusters of spider scores from clearcuts and 10% residual treatments (Fig. 27). Scores from other treatment levels are variably distributed in multidimensional space. This multidimensional technique also revealed an unknown source of variance, linked to the geographical distance between replicates.

In order to eliminate concerns over spatial autocorrelation of samples, partial Mantel tests were employed (Legendre and Fortin 1989, Mantel 1967) (Fig. 28). Partial Mantel tests revealed a significant correlation between cover type and the spider assemblage (r=0.19, *p*<0.01) and harvesting treatment levels and the spider assemblage (r=0.20, *p*<0.01). There was also a significant interaction between harvesting treatment level and cover type on the spider assemblage (r=0.19, *p*<0.01). An attempt was made to examine the source of this interaction by reconfiguring design matrices to allow sequential comparison of the spider assemblage from specific treatment levels to the clearcut treatment. The resultant array of partial Mantel r values revealed inconclusive patterns.

Correlation between environmental parameters and spider assemblages is also facilitated with Mantel tests. Instead of an experimental design matrix in this case, Euclidian distance matrices of overstory percent cover, tree diameter at breast height, understory percent cover, and course woody debris were substituted. A team of undergraduates collected these data in the vicinity of each pitfall trap. Results indicate a strong correlation between the spider assemblage and understory percent cover (r=-0.011, *p*<0.01) and a weak correlation between the spider assemblage and overstory percent cover (r=-0.07, *p*<0.05). The remaining correlations were not statistically significant (Fig. 29).

Discussion. There is always concern in invertebrate biodiversity assessments that too few species have been collected to obtain a representative snapshot of the residents in the area of interest or to answer questions about impacts to biodiversity. It can be safely assumed in the present study however that over 85% of the potential number of species has been collected (Fig. 20).

After one winter post-harvest, spider assemblages showed considerable response to the harvesting treatment levels. Species richness was not significantly affected by harvesting (Fig. 22). However, overall abundance increased in a linear fashion with harvest intensity (Fig. 23). This contrasts the community response in Appalachian forests post-clearcut where the abundance of hunting spiders remained unchanged whereas species richness increased (Coyle 1981). Unlike the present collection, few actively hunting species were represented in the Appalachian collection largely because of differing sampling protocols. The discrepancy in species richness and abundance between harvesting treatment levels in the present study is a result of a handful of species in the Family Lycosidae. In particular, *Pardosa moesta* Banks abundance dramatically increases with canopy openings (Fig. 24) . McIver *et al.* (1992) found a very similar pattern in differently aged post-clearcut coniferous forests in Oregon. Young, herb-covered clearcuts supported a greater number and proportion of species in the Family Lycosidae than did tree-dominated 30-year-old clearcuts. They attributed these differences primarily to microenvironmental extremes in clearcut stands. Actively hunting cursorial spiders are likely resistant to desiccation and temperature extremes typical in clearcut stands as are dune-inhabiting spiders (Almquist 1973). Conversely, McIver *et al.* (1992) also found that cryptic spiders such as those in the superfamily Linyphiidae are proportionately more common in closed canopy stands with thicker litter layers and stable microenvironmental conditions. Analyses of community assemblage across treatment levels revealed homogenous species assemblages in clearcuts to increasingly heterogenous species assemblages in control stands (Fig. 27), consistent with McIver *et al.* (1992).

Large experiments like EMEND likely support many independent populations of spiders, each of which respond to adjacency to harvest disturbance. Indeed, *P. moesta* cluster around clearcut stands (Fig. 26), which undoubtedly influence populations in treatments adjacent to these clearcuts. Consequently, treatment levels may not be considered independent, thus violating one assumption of traditional analysis of variance. An alternative to traditional statistics that eliminates spatial autocorrelation is the partial Mantel test (Fig. 28). Spider assemblages were significantly correlated to cover type and treatment level. The partial Mantel test also revealed a significant interaction between cover type and treatment level on spider assemblages, although the source of this interaction remains unclear. Substituting environmental matrices for experimental design matrices revealed that spider assemblages responded to varying percent cover in understory and overstory vegetation. However, variance in percent cover of coarse woody material across the EMEND experiment explained little in the variance in spider assemblages (Fig. 29). This result is not surprising because coarse woody debris was defined as fallen logs greater than 7 cm in diameter. Debris complexity was not measured. It is more likely that epigeic spiders use fine debris and complex debris architecture to support their hunting and resting behaviours (Draney *pers. comm.*). Cryptic, web-building spiders that are often collected in pitfall traps use the three-dimensional array of debris as attachment points for their webs. Abundant attachment points results in greater numbers and species richness of these spiders as experimentally shown by Hatley & MacMahon (1980).

Conclusions. These results contribute to a basic understanding of boreal forest spider biology and diversity and provide some biological facts for the largely socio-political discussion about forest sustainability and biodiversity. Epigaeic spiders are not presently integrated into forest management protocols. However, they are easily sampled using standard pitfall traps and identification to the level of species is not insurmountable. Atypical assemblages may forewarn forest managers of insufficient microhabitat variation to conserve and maintain other invertebrate assemblages. Spiders exert a predatory stabilizing influence on invertebrate communities. Consequently, they influence the severity of damaging insect outbreaks, the breakdown of coarse woody material, and ultimately, forest net primary productivity. These results will also provide a basis for modeling trade-off between biodiversity and mixedwood forest productivity.

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Table 1. List of bumble bee and plant species encountered in cencuses at EMEND (1998-1999).

Bumblebee Taxa

Bombus flavifrons
B. mixtus
B. perplexus
B. sylvicola
B. terricola
B. vagans

Plant Taxa

Arnica spp.
Aster conspicuous
Astragalus americanus
Astragalus canadensis
Delphinium glaucum
Epilobium angustifolium
Lathyrus ochroleucus
Lonicera dioica
Maianthemum canadense
Mertensia paniculata
Pyrola asarifolia
Rosa spp.
Solidago canadensis
Trifolium hybridum
Vicia americana

Table 2. Total number of moth individuals, species and genera captured by light trapping at all study locations on the EMEND site during1998-99.

Family	**Individuals**	**Genera**	**Species**
Geometridae	8388	58	83
Noctuidae	6437	86	138
Sphingidae	1717	3	4
Notodontidae	650	6	11
Lasiocampidae	507	2	2
Uraniidae	313	1	1
Arctiidae	263	10	12
Drepanidae	163	5	6
Hepialidae	43	2	2
Lymantriidae	21	1	1
Saturniidae	6	1	1

Table 3. ANOVA table of moth species richness and trap catch between cover types in undisturbed forest (1998).

Source of variation	d.f.	MS	F	P
Moth richness				
Cover type	2	79.8	1.32	0.32
Error	9	60.5		
Moth trap catch				
Cover type	2	2813.8	0.60	0.57
Error	9	4685.6		

Table 4. ANOVA table of moth species richness and trap catch between cover types and treatments in 1999.

Source of variation	d.f.	MS	F	P
Moth richness				
Cover type	2	5.9	0.06	0.95
Treatment	2	1248.4	11.96	0.01*
Error	7	104.4		
Moth trap catch				
Cover type	2	3625.4	0.43	0.67
Treatment	2	49630.1	5.91	0.03*
Error	7	8394.5		

Table 5. Average understory vegetation height by cover type (1998) (N=2211).

Cover type	Height (m ± SD)
Deciduous	2.26 ± 0.93
Mixed	2.17 ± 1.34
Coniferous	2.36 ± 1.31

Table 6. ANOVA table - Treatment impact on **moth trap catch** by family (N=12).

Source of variation	d.f.	MS	F	P
Noctuidae				
Treatment	2	46232.17	24.33	0.000*
Error	9	1899.93		
Geometridae				
Treatment	2	49760.33	15.65	0.001*
Error	9	3179.26		
Notodontidae				
Treatment	2	40.13	1.41	0.293
Error	9	28.44		
Sphingidae				
Treatment	2	85.13	3.11	0.094
Error	9	27.41		
Lasiocampidae				
Treatment	2	1339.13	2.14	0.174
Error	9	626.30		
Arctiidae				
Treatment	2	16.50	0.69	0.525
Error	9	23.86		
Drepanidae				
Treatment	2	18.00	1.06	0.386
Error	9	16.96		
Uraniidae				
Treatment	2	155.79	12.16	0.003*
Error	9	12.82		

Table 7. ANOVA table - Treatment impact on **moth species richness** by family (N=12).

Source of variation	**d.f.**	**MS**	**F**	**P**
Noctuidae				
Treatment	2	116.13	2.04	0.186
Error	9	56.96		
Geometridae				
Treatment	2	572.38	14.80	0.001*
Error	9	38.69		
Notodontidae				
Treatment	2	8.17	4.79	0.038*
Error	9	1.70		
Sphingidae				
Treatment	2	0.38	0.81	0.475
Error	9	0.46		
Lasiocampidae				
Treatment	2	1.83	4.13	0.054
Error	9	0.44		
Arctiidae				
Treatment	2	2.83	2.13	0.175
Error	9	1.50		
Drepanidae				
Treatment	2	2.75	1.83	0.215
Error	9	1.33		
Uraniidae				
Treatment	2	0.46	3.09	0.095
Error	9	0.15		

Table 8. Total number of species and individuals trapped by forest type and treatments during **1999**. Numbers with the same letters indicate no significant difference based on Scheffé's multiple comparisons test ($p<0.05$) (N=12).

Forest types and treatments	**Richness** Mean ± SE	**Trap catch** Mean ± SE
Deciduous	83.3 ± 17.4^{a}	56.1 ± 15.9^{a}
Mixed	89.0 ± 4.9^{a}	42.1 ± 9.9^{a}
Coniferous	83.3 ± 12.3^{a}	36.0 ± 9.5^{a}
CONTROL	101.7 ± 5.9^{b}	74.0 ± 13.9^{b}
50% RESIDUAL	76.0 ± 9.1^{a,b}	20.1 ± 4.8^{a}
20% RESIDUAL	61.3 ± 10.5^{a}	10.8 ± 2.6^{a}

Table 9. Number of moths caught in 1999 in each habitat use classes by treatment. Number of individuals in each class is found between brackets following each percent representation.

Moth habitat use classes	**CONTROL**	**50% RSC**	**20% RSC**
Generalist	60.0%	58.5%	52.9%
Deciduous spec.	21.8%	13.1%	12.1%
Coniferous spec.	6.4%	6.2%	14.2%
Unknown	11.8%	22.2%	20.9%
Total	100.0%	100.0%	100.0%

Table 10. Number of moth species in each host-plant range by year.

Host-plant range	**1998**	**1999**	**Total**
Polyphagous	104 spp.	119 spp.	156 spp.
Oligophagous	48 spp.	55 spp.	66 spp.
Monophagous	28 spp.	29 spp.	38 spp.

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Table 11. Moths' relative host-plant range proportions between treatments by species richness and abundance (1999).

Richness	**CONTROL**	**50% RSC**	**20% RSC**
Polyphagous	58.0%	59.3%	65.2%
Oligophagous	26.6%	27.9%	21.7%
Monophagous	15.4%	12.8%	13.0%

Abundance	**CONTROL**	**50% RSC**	**20% RSC**
Polyphagous	63.3%	65.0%	60.7%
Oligophagous	22.1%	27.1%	31.3%
Monophagous	14.6%	7.9%	8.0%

Table 12. Average development index (± SE) of *Dendroctonus rufipennis* in: A) harvesting treatments and; B) different log surfaces pooled across treatments in 1999. In columns with significant main effects as determined by ANOVA (P=0.05), cells with the same letter indicate no significant difference (Bonferroni tests).

A)

Treatment	**July 6**	**July 19**	**August 2**	**August 17**
CLEAR CUT	1.20 ± 0.13	2.12 ± 0.19^b	3.78 ± 0.14^b	5.11 ± 0.21^c
20% residual	1.00 ± 0.00	2.24 ± 0.12^b	3.58 ± 0.12^b	4.38 ± 0.23^b
50% residual	1.00 ± 0.00	2.24 ± 0.14^b	3.43 ± 0.11^b	4.37 ± 0.19^b
Control	1.01 ± 0.01	1.66 ± 0.09^a	2.97 ± 0.08^a	3.91 ± 0.09^a
	$F_{3,46}$=2.46, P=0.080	$F_{3,83}$=4.74, P=0.005	$F_{3,71}$=8.34, P<0.001	$F_{3,61}$=8.05, P<0.000

B)

Log Surface	**July 6**	**July 19**	**August 2**	**August 17**
TOP	1.00 ± 0.00	1.72 ± 0.17	2.90 ± 0.18	4.70 ± 0.37^b
East	1.01 ± 0.01	2.07 ± 0.16	3.47 ± 0.12	4.19 ± 0.18^a
Bottom	1.03 ± 0.03	2.02 ± 0.12	3.34 ± 0.11	4.27 ± 0.14^a
West	1.11 ± 0.09	2.19 ± 0.12	3.26 ± 0.13	4.10 ± 0.12^a
	$F_{3,46}$=1.68, P=0.191	$F_{3,83}$=1.20, P=0.315	$F_{3,71}$=1.24, P=0.303	$F_{3,61}$=4.74, P=0.005

Table 13. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species for each log surface.

Parasitoid Species	*Log Surfaces*				
	Top	*East*	*Bottom*	*West*	TOTAL
Coeloides rufovariegatus	6 (4.0%)	47 (31.3)	48 (32.0)	49 (32.7)	150
Bracon tenuis	3 (2.7%)	13 (11.6%)	84 (75.0%)	12 (10.7%)	112
Roptrocerus xylophagorum	7 (23.3%)	3 (10.0%)	14 (46.7%)	6 (20.0%)	30
Dinotiscus dendroctoni	2 (14.3%)	2 (14.3%)	9 (64.3%)	1 (7.1%)	14
Total	18 (5.9%)	65 (21.2%)	155 (50.7%)	68 (22.2%)	306 (100.0%)

Table 14. Number of 100 cm^2 bark samples containing available *D. rufipennis* hosts discovered by parasitoids in each a) treatment and b) log surface.

A)

Treatment	**Discovered**	**Not Discovered**	**Total**
CLEAR CUT	5	7	12
20% residual	4	6	10
50% residual	11	12	23
Control	15	17	32
Total	35	42	77

B)

Log Surface	**Discovered**	**Not Discovered**	**Total**
TOP	6	3	9
East	8	10	18
Bottom	13	21	34
West	8	8	16
Total	35	42	77

Table 15. Mean parasitism proportion (± SE) for available beetles contained in discovered log samples in each a) treatment ($F_{3, 31}$= 0.667, P = 0.581) and b) log surface ($F_{3, 31}$ = 0.727, P = 0.546). Beetle density was used as a covariate in this Univariate GLM ($F_{1, 33}$ = 22.202, P < 0.001).

A)

Treatment	**Mean % (± SE)**
CLEAR CUT	43.2 ± 14.9
20% residual	34.5 ± 22.4
50% residual	45.5 ± 11.3
Control	54.5 ± 7.4
Total	47.8 ± 5.6

B)

Log Surface	**Mean % (± SE)**
TOP	74.3 ± 12.0
East	48.6 ± 9.8
Bottom	32.1 ± 9.1
West	52.5 ± 11.3
Total	47.8 ± 5.6

Table16. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species.

Parasitoid Species	*Beetle Instar or Stage*					
	Second Instar	*Third Instar*	*Fourth Instar*	*Pupa*	TENERAL	**Total**
Unknown	4 (3.6%)	32 (28.6%)	74 (66.1%)	1 (0.9%)	1 (0.9%)	112
Coeloides rufovariegatus	1 (1.0%)	23 (23.7%)	73 (75.3%)	0 (0.0%)	0 (0.0%)	97
Bracon tenuis	1 (1.2%)	15 (18.3%)	66 (80.5%)	0 (0.0%)	0 (0.0%)	82
Roptrocerus xylophagorum	1 (4.3%)	2 (8.7%)	18 (78.3%)	2 (8.7%)	0 (0.0%)	23
Dinotiscus dendroctoni	0 (0.0%)	0 (0.0%)	13 (100%)	0 (0.0%)	0 (0.0%)	13
Total	7 (2.1%)	72 (22.0%)	244 (74.6%)	3 (0.9%)	1 (0.3%)	327 (100.0%)

Table 17. Number of parasitoid larvae and cocoons collected and reared from all 100 cm^2 bark samples in treatments and controls for 4 sample dates.

	Treatment				
Sample Date	**Clear Cut**	**20% Residual**	**50% Residual**	**Control**	**Total**
17-AUG-99	19	7	33	60	119
29-AUG-99	11	13	20	32	76
11-SEP-99	10	2	14	17	43
10-MAY-00	1	5	3	21	30

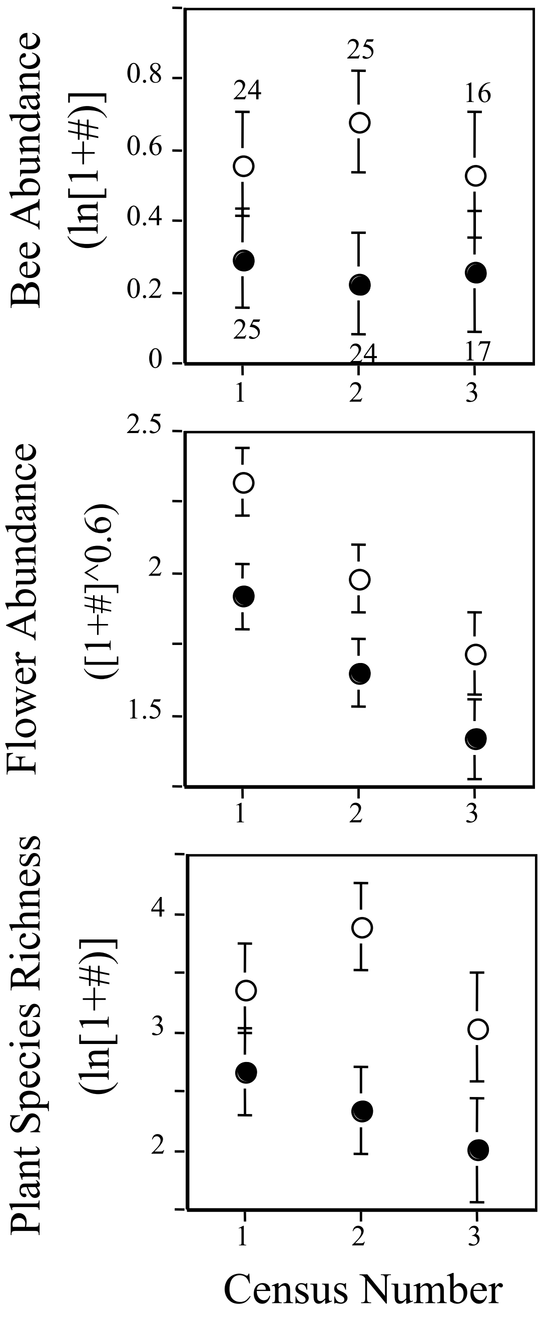
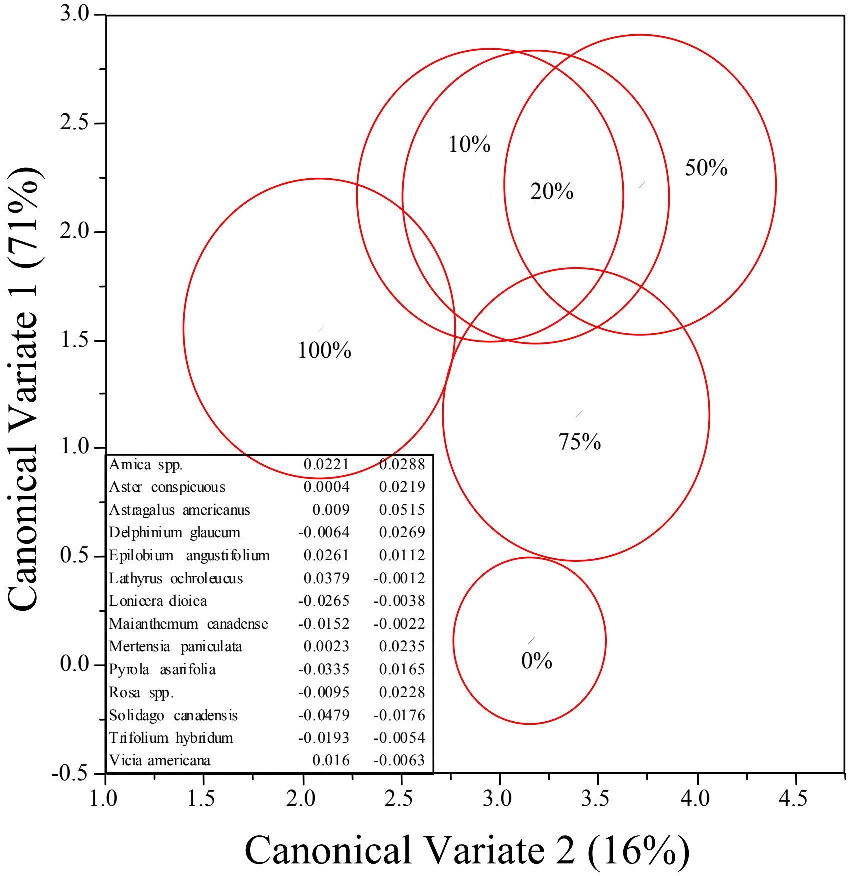


Figure 1. Habitat and seasonal trends in bee abundance, plant species richness, and flower abundance at ADOM (open circles) and ADOU-U (black circles) habitats. Least square means ≠ 1 SE are plotted. Sample sizes are shown in the top graph. Habitats are significantly different (P<0.01) in all 3 instances, and censuses are different only for number of plant species (P<0.001).



Arnica spp.	0.0221	0.0288
Aster conspicuous	0.0004	0.0219
Astragalus americanus	0.009	0.0515
Delphinium glaucum	-0.0064	0.0269
Epilobium angustifolium	0.0261	0.0112
Lathyrus ochroleucus	0.0379	-0.0012
Lonicera dioica	-0.0265	-0.0038
Maianthemum canadense	-0.0152	-0.0022
Mertensia paniculata	0.0023	0.0235
Pyrola asarifolia	-0.0335	0.0165
Rosa spp.	-0.0095	0.0228
Solidago canadensis	-0.0479	-0.0176
Trifolium hybridum	-0.0193	-0.0054
Vicia americana	0.016	-0.0063

Figure 2. Multivariate description of the plant community in 1999, following logging of different intensities (percentages indicate % trees remaining after logging). The first 2 canonical variates explain 87% of the variation in the 14 species' flower abundances. Centroids indicate 95% confidence intervals for each of the groups. Inset shows the loadings of the original variables on the first two eigenvectors.

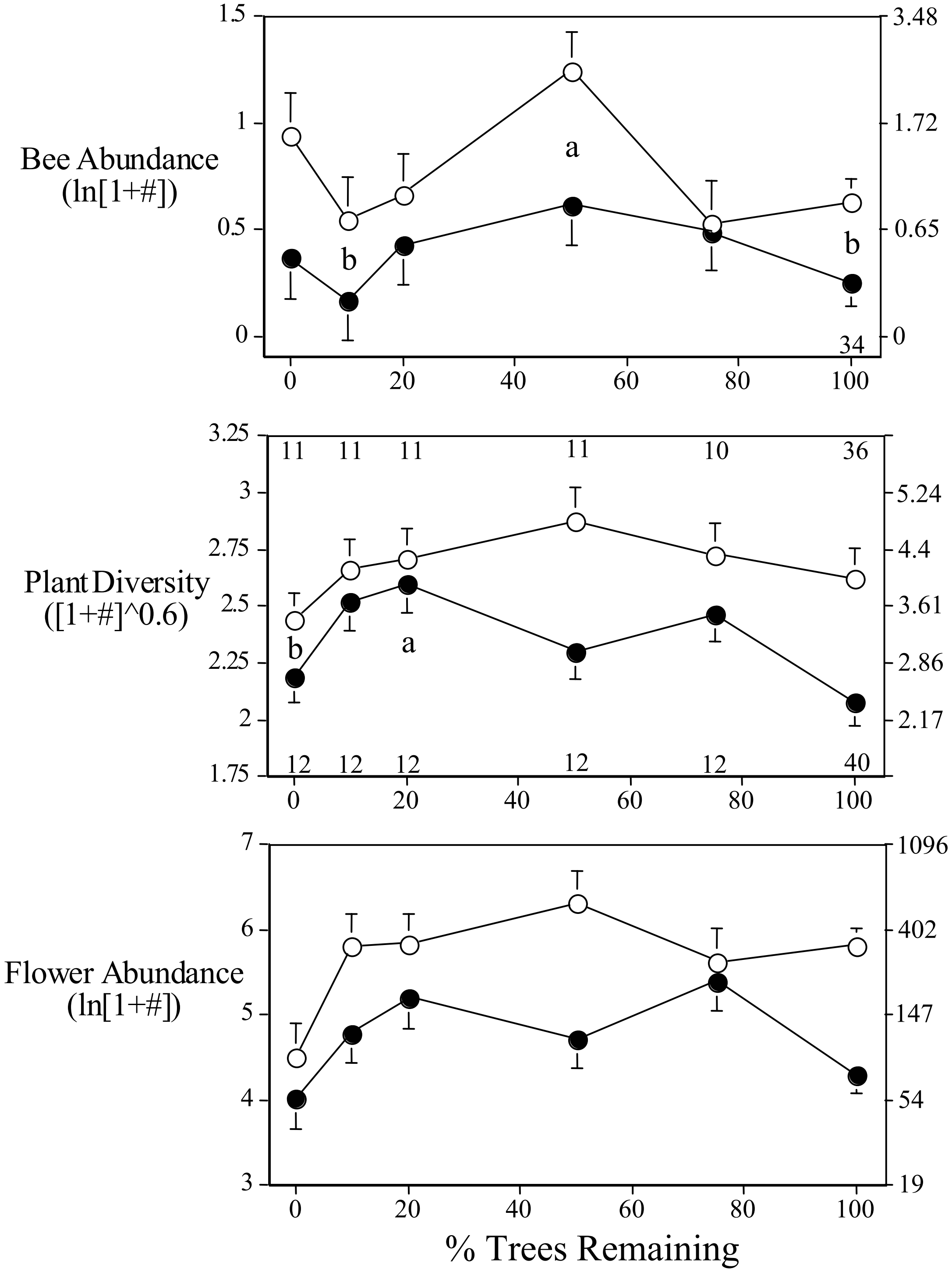


Figure 3. Changes in bumble bee abundance, plant diversity, and flower abundance following logging in ADOM (open circles) and ADOU-U (black circles) habitats. Least square means ± 1 SE are plotted. These least square means are from ANCOVAs where habitat, census, logging treatment, and their interactions are the main effects, and -baseline length$^{-0.4}$ is the covariate. In all ANCOVAs the non-significant 3-way interaction was removed for clarity.

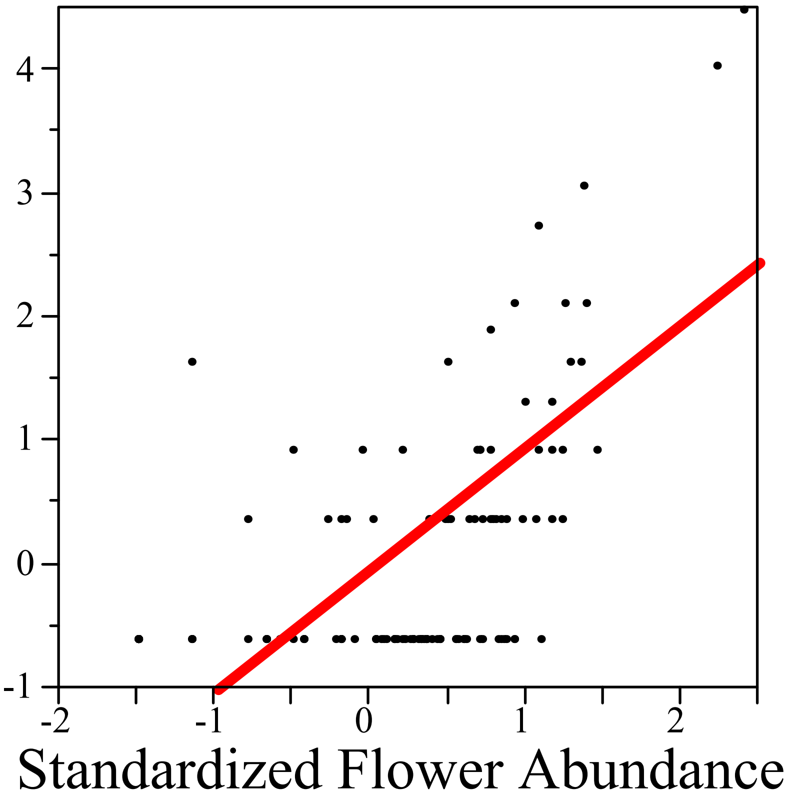


Figure 4. The distribution of bees across flowers in 1998 (before logging). Data from the 2 habitats are pooled, since there was no significant interaction habitat by flower abundance (ANCOVA, interaction $F_{1,128}$=3.10, P=0.081). The fitted orthogonal regression line has a slope of 0.995 (r=0.577, n=131, P<0.0001), which rounds to the predicted slope of 1.0.

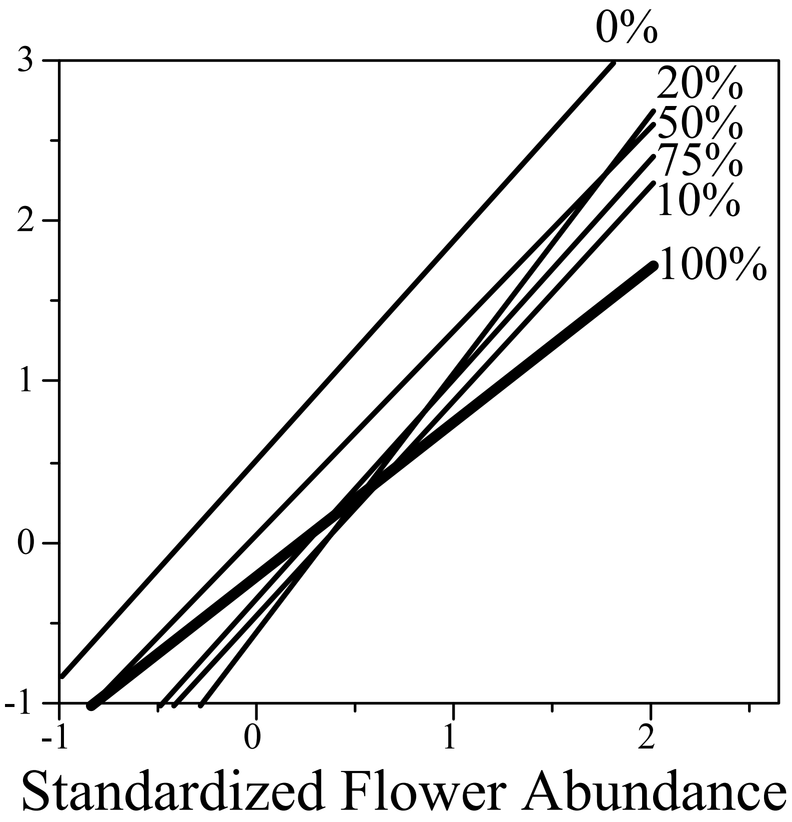


Figure 5. The distribution of bees across flowers in 1999 (after logging). Data from the 2 habitats are pooled, since there was no significant interaction habitat by flower abundance (ANCOVA, interaction $F_{1,180}$=0.54, P=0.46). A separate orthogonal regression line is fitted for each logging treatment. The slope of the control (unlogged, 100%) treatment is 0.957, which is close to the IFD prediction of 1. The slopes of all 5 treatments involving logging are greater than one (ranging from 1.27 to 1.60). Data points are omitted for clarity.

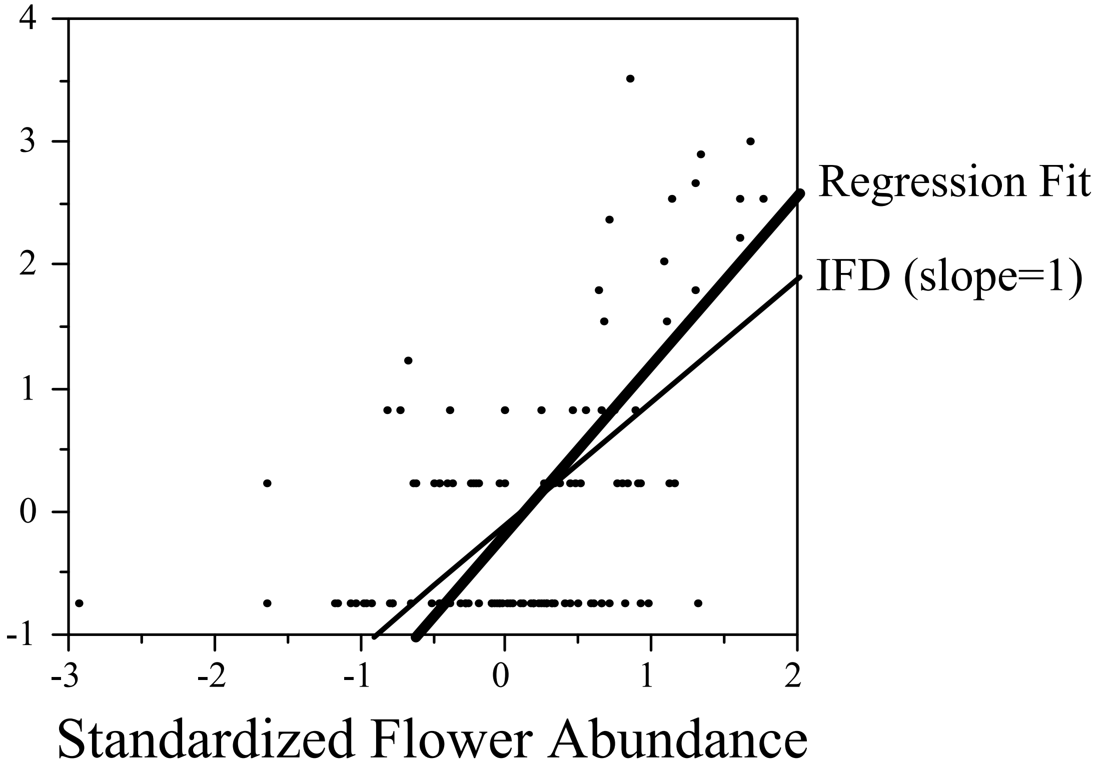


Figure 6. The distribution of bees across flowers in 1999 (after logging). Data from the 5 logging treatments are pooled (i.e., unlogged control treatment is not in this analysis). The fitted orthogonal regression line has a slope of 1.366 (r=0.523, n=68, P<0.0001), which is significantly greater than 1 (one-tailed P=0.0285).

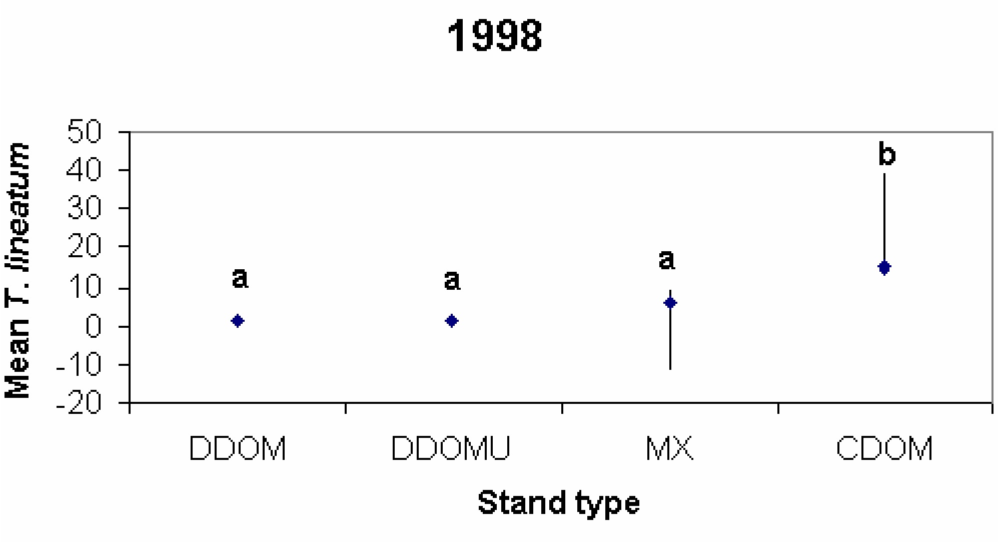


Figure 7. Mean number of *T. lineatum*captured by stand type prior to harvest (1998). Data were reciprocal transformed to meet assumptions of normality. Similar letters indicate non significant differences (Tukey-Kramer HSD- $p<0.05$).

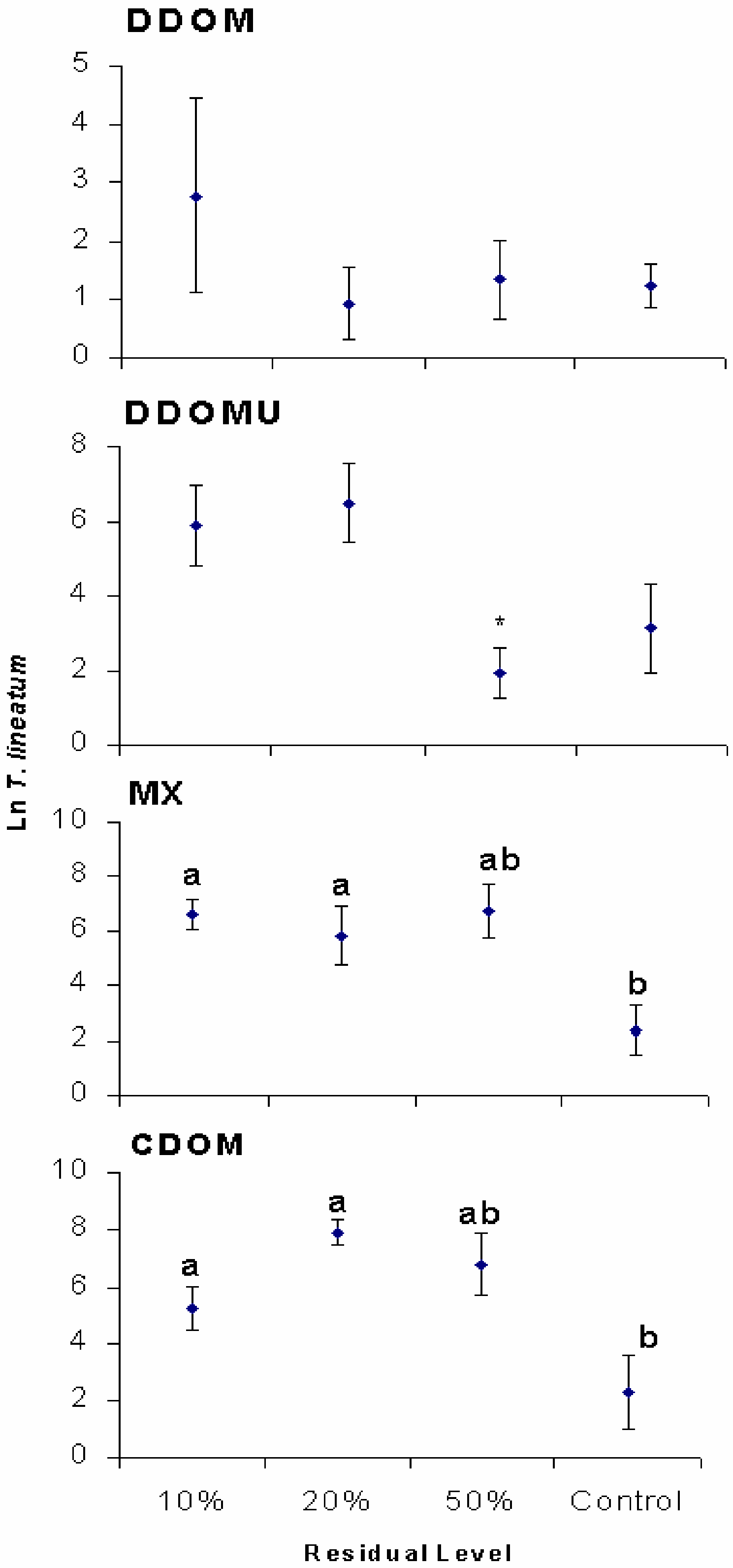


Figure 8- Mean number of captured *T. lineatum* by residual level separated by stand type 1999 and 2000 data combined. Data were natural log transformed to meet assumptions of normality. Asterisks and letters indicate significant differences (Tukey-Kramer HSD - $p<0.05$) Similar letters show non-significant differences). Note different scales on y-axes.

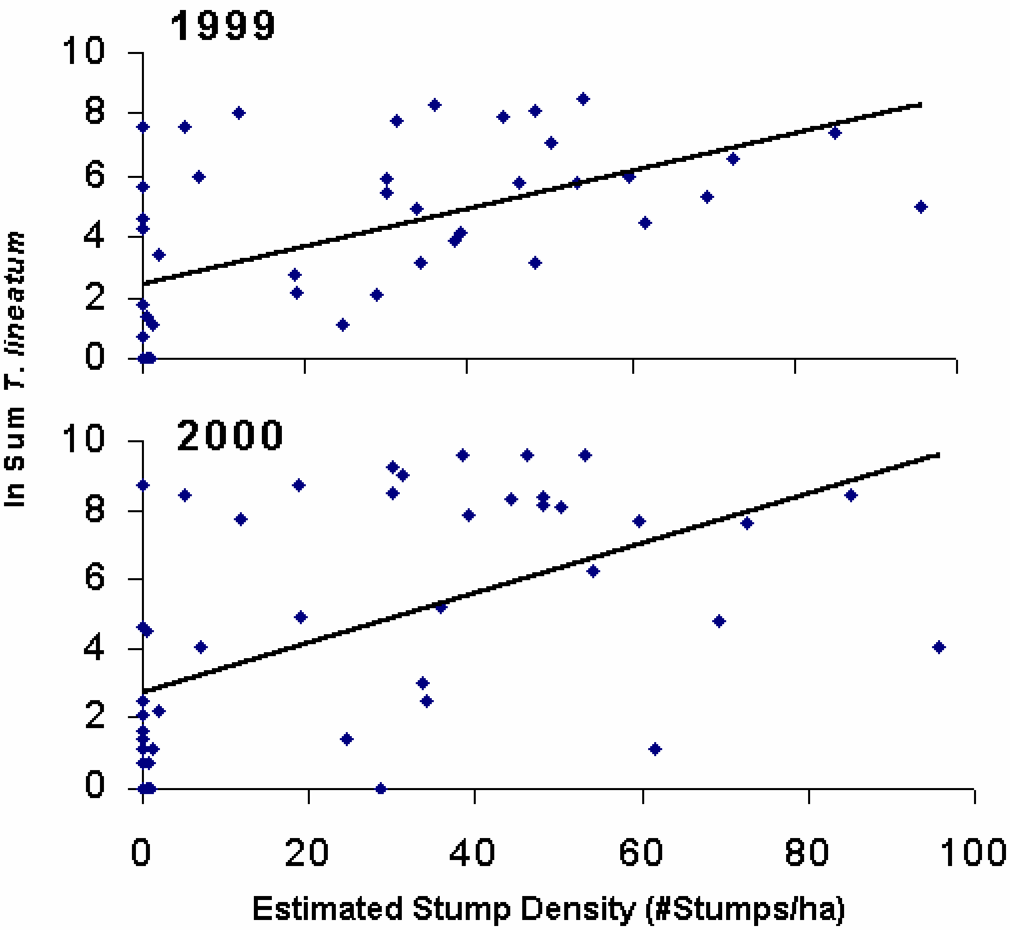


Figure 9. Number of *T. lineatum* captured by estimated stump density in both years following harvest. Data were natural log transformed to meet assumptions of normality.

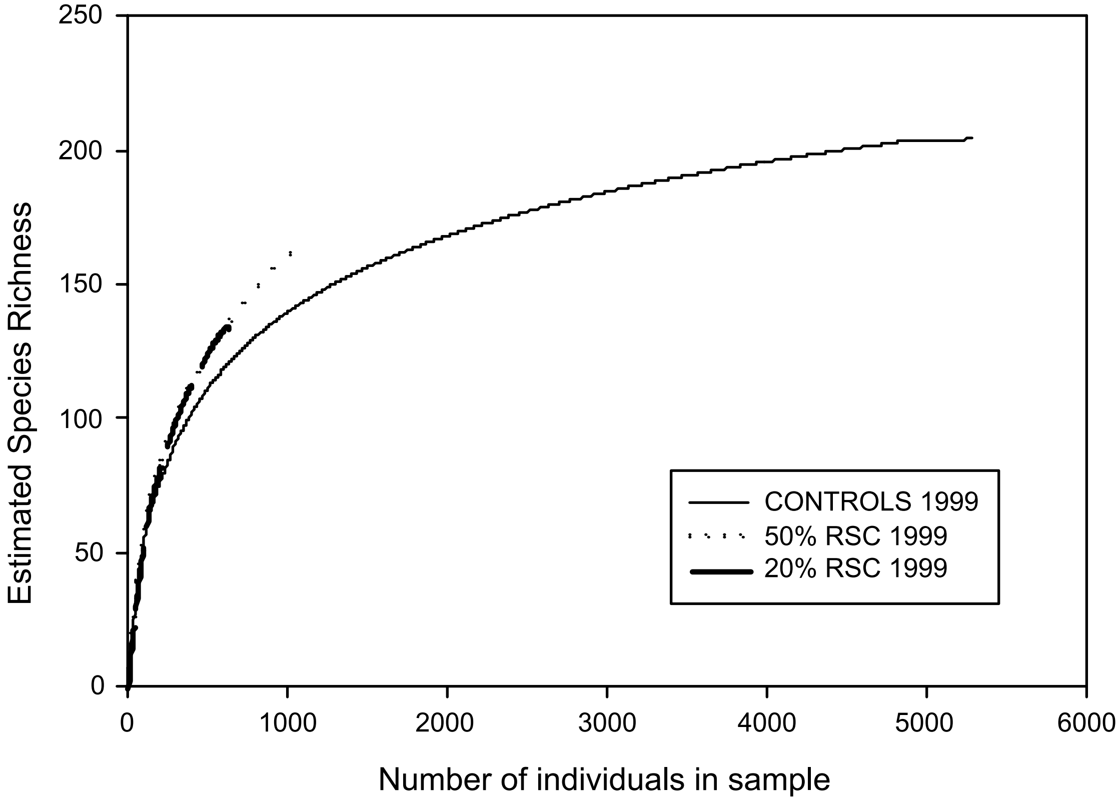


Figure 10. Rarefaction curves of the macromoth community in three different treatments (1999).

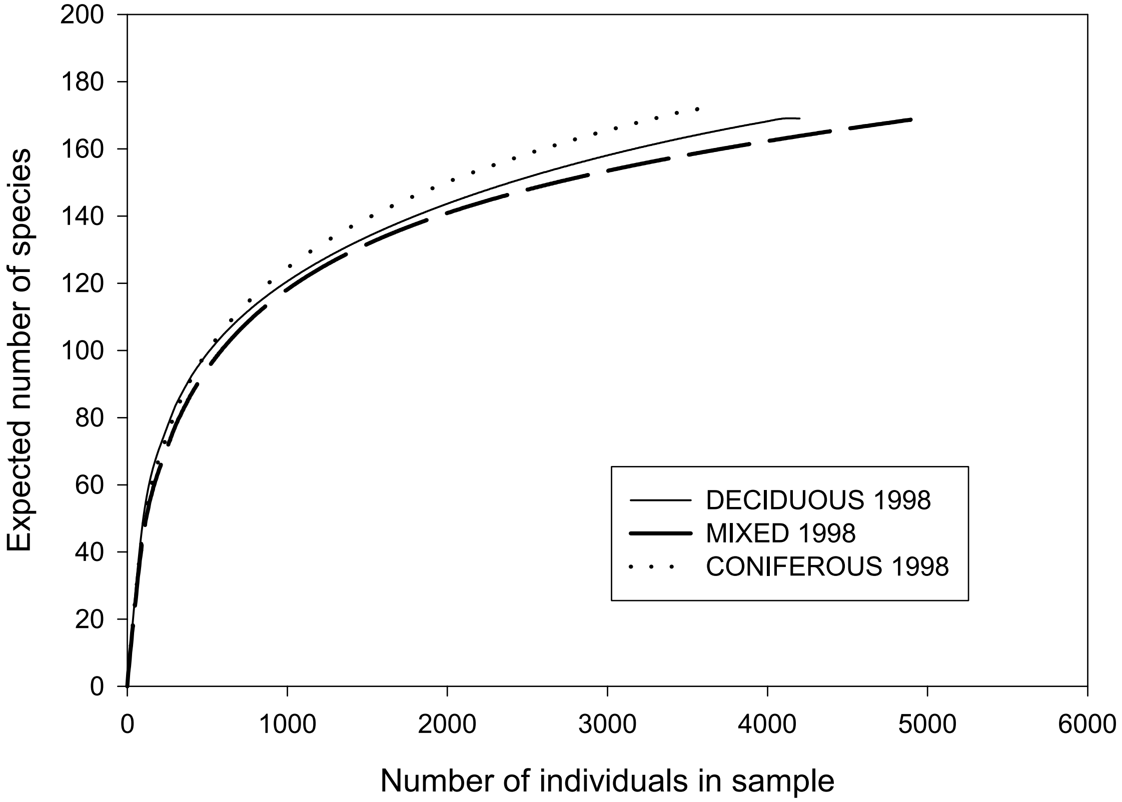


Figure 11. Rarefaction curves for the macromoth community in three forest types (1998).

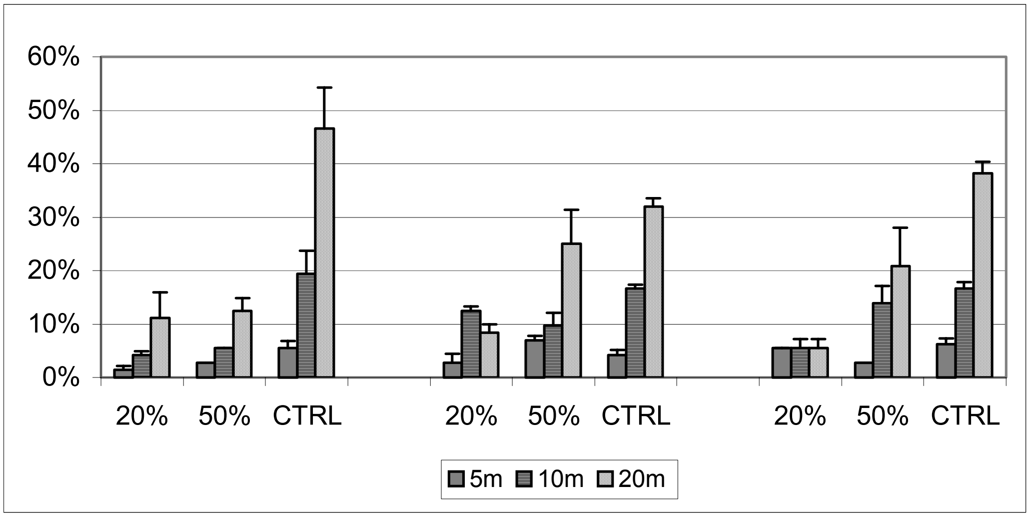


Figure 12. Vegetation interference to light by cover type and treatment (1999).

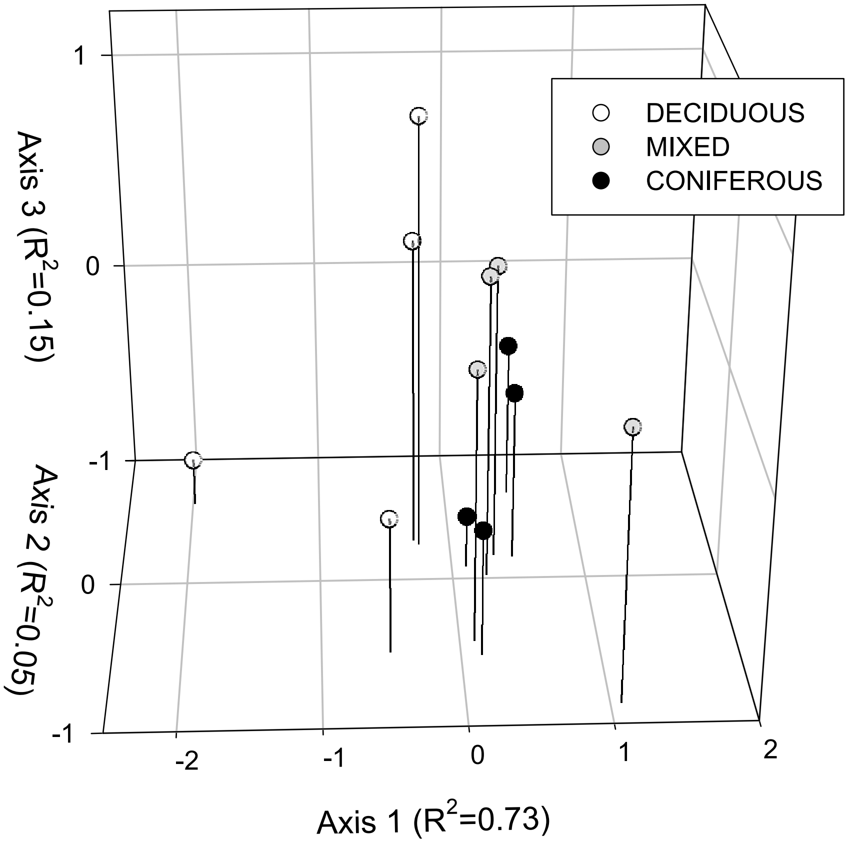


Figure 13. Three-dimensional solution of NMS pre-disturbance moth community (1998) by forest type (R^2_{tot}=0.928, stress=4.9%).

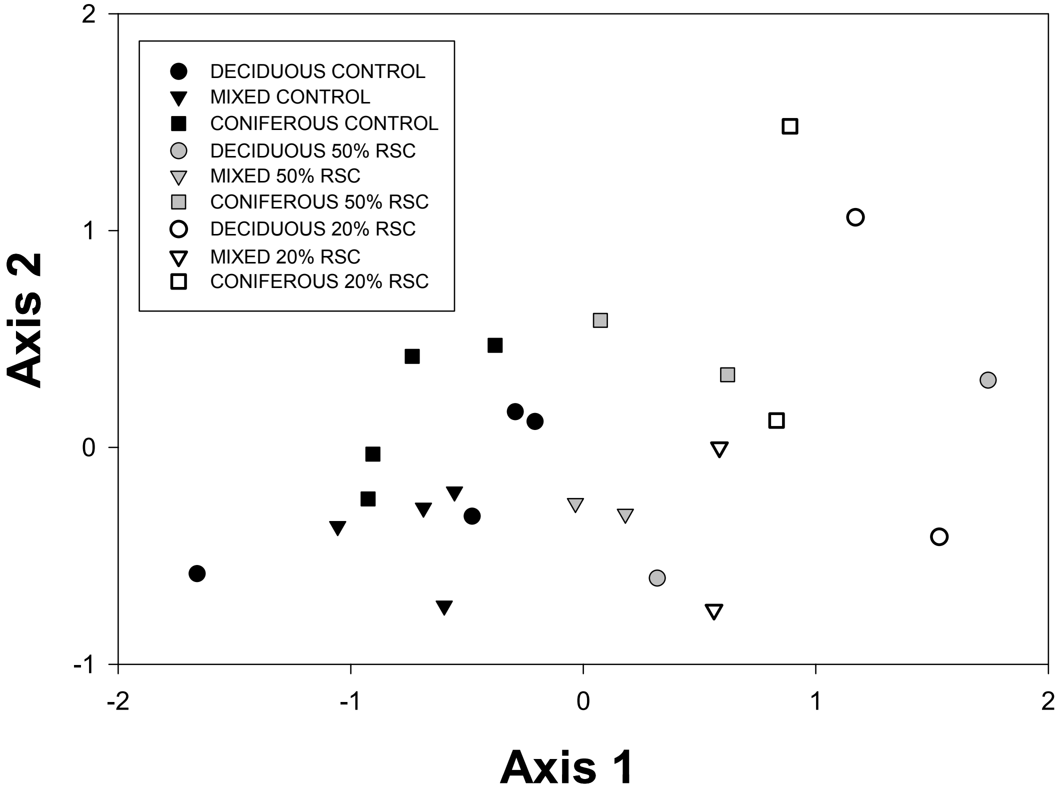


Figure 14. Two-dimensional solution of NMS post-disturbance moth community (1999) by forest type and treatment (R^2_{tot}=, stress=%).

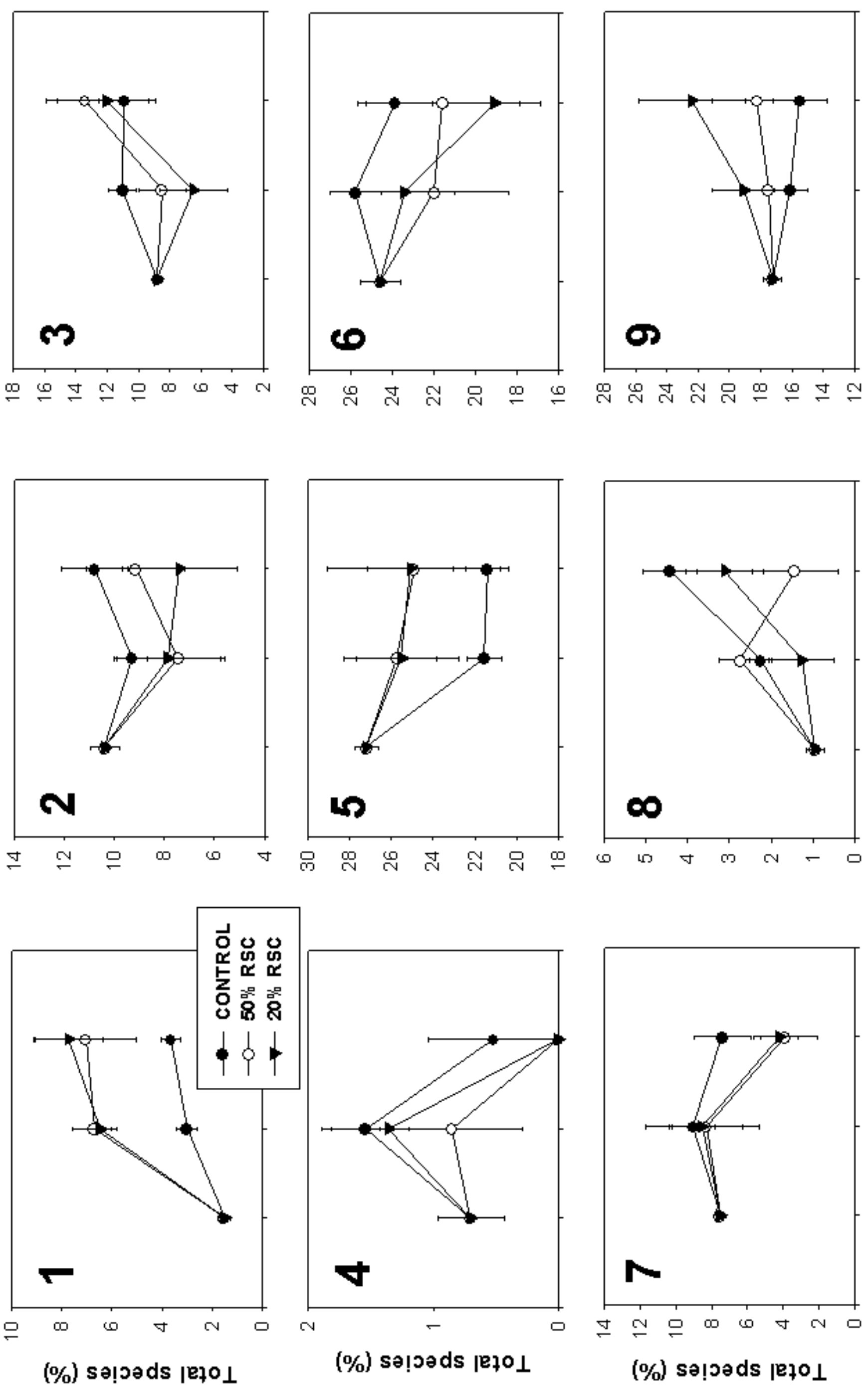


Figure 15. Percentage of moth species in each feeding guild by treatment from 1998 to 2000. The guilds are: 1. Herb and grass feeders, 2. Woody plants generalists, 3. Low and non-woody plants generalists, 4. Fungus and dead leaves feeders, 5. Salicaceae (poplars & willows) specialists, 6. Deciduous trees feeders, 7. Conifer feeders, 8. Lichen feeders, and 9. Generalists.

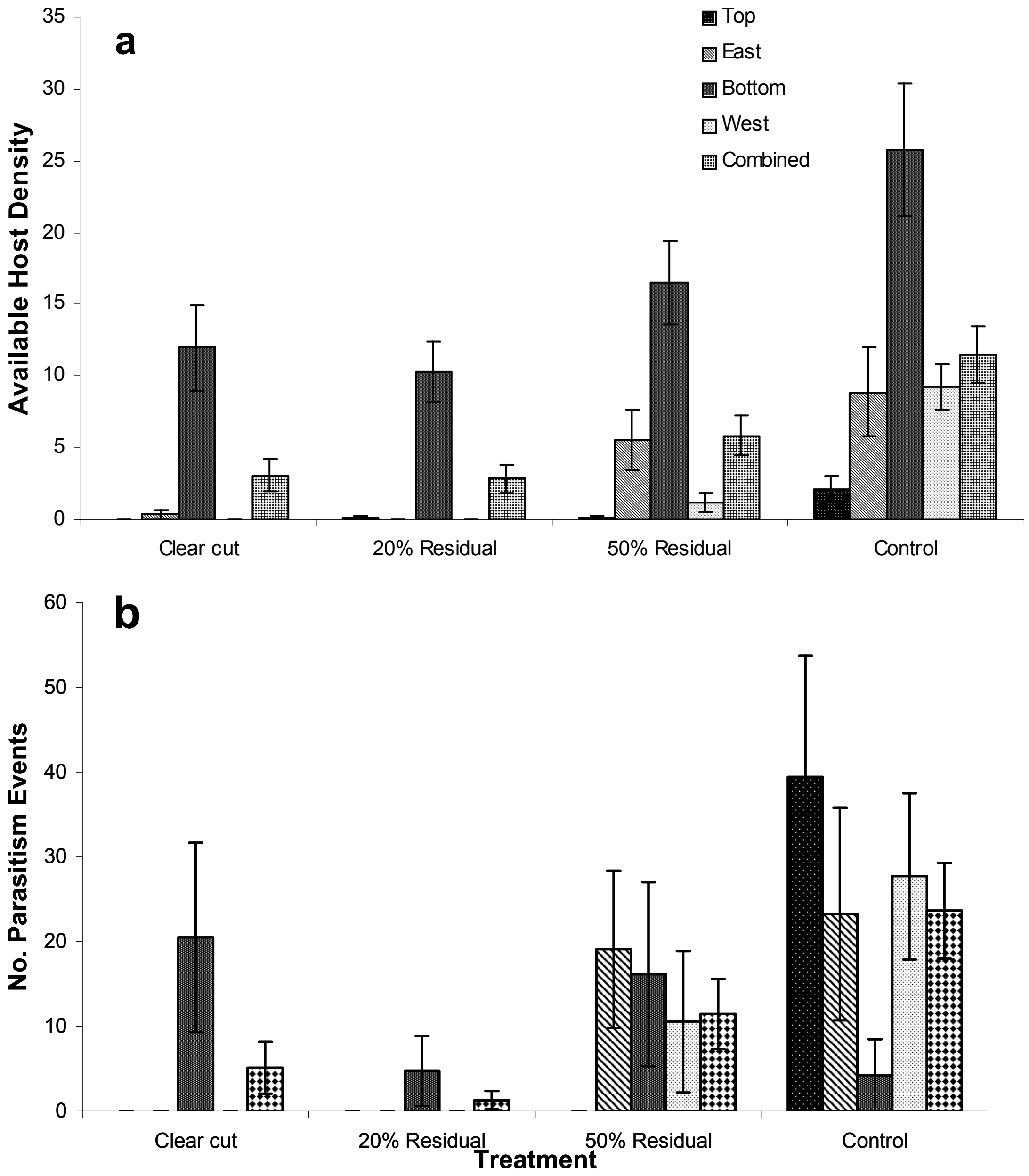


Figure 16. Comparisons of means (± SE) density (per 100 cm^2) of: a) available hosts and; b) number of parasitised available hosts for each treatment and log surface. Data represent all 144 bark samples collected on August 17, 1999.

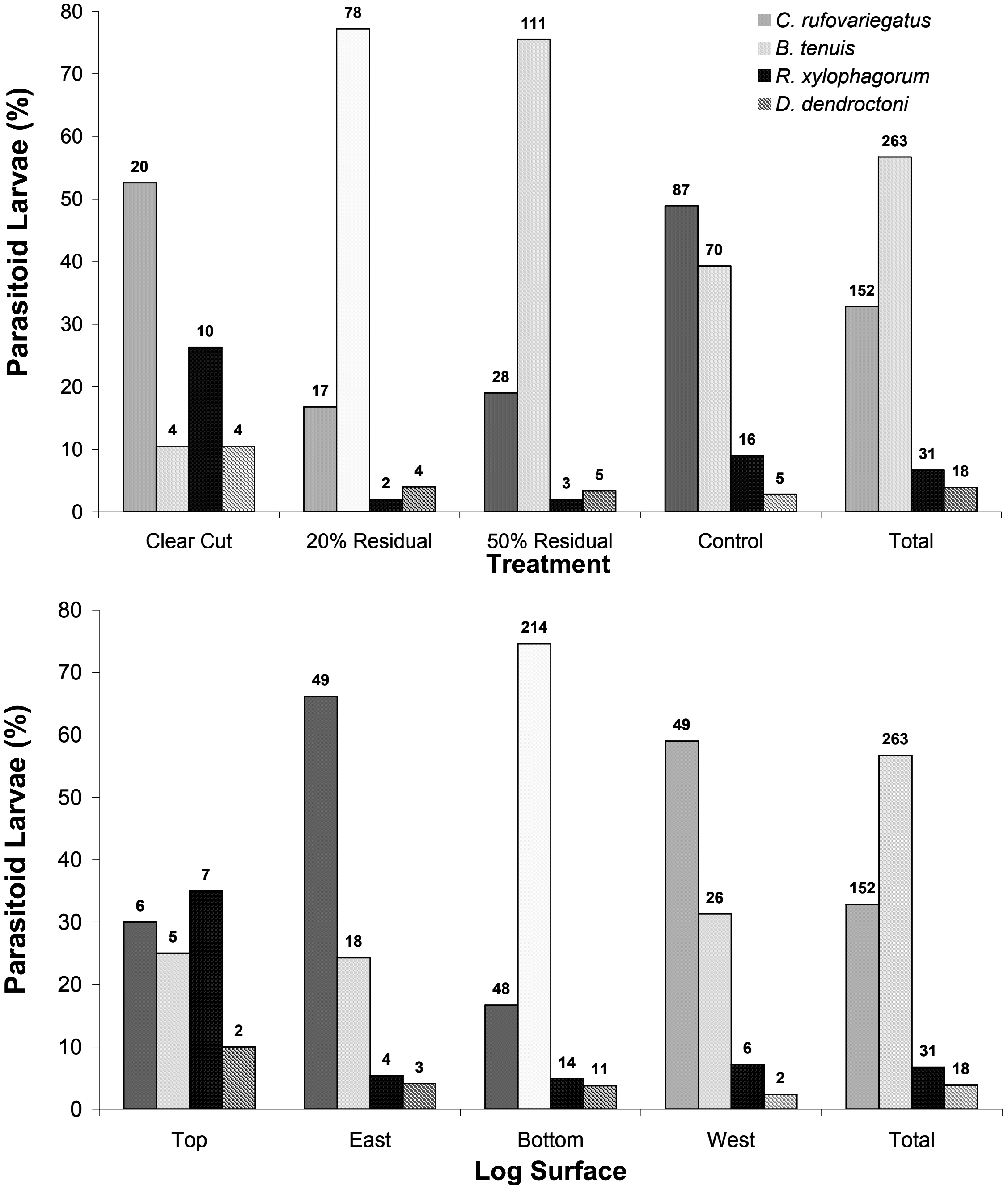


Figure 17. Percent of parasitoid larvae in samples collected from July 19, 1999 to July 21, 2000 represented by different species, partitioned by: a) harvesting treatment; and b) log surface. Number of parasitoid individuals is indicated at the top of each bar.

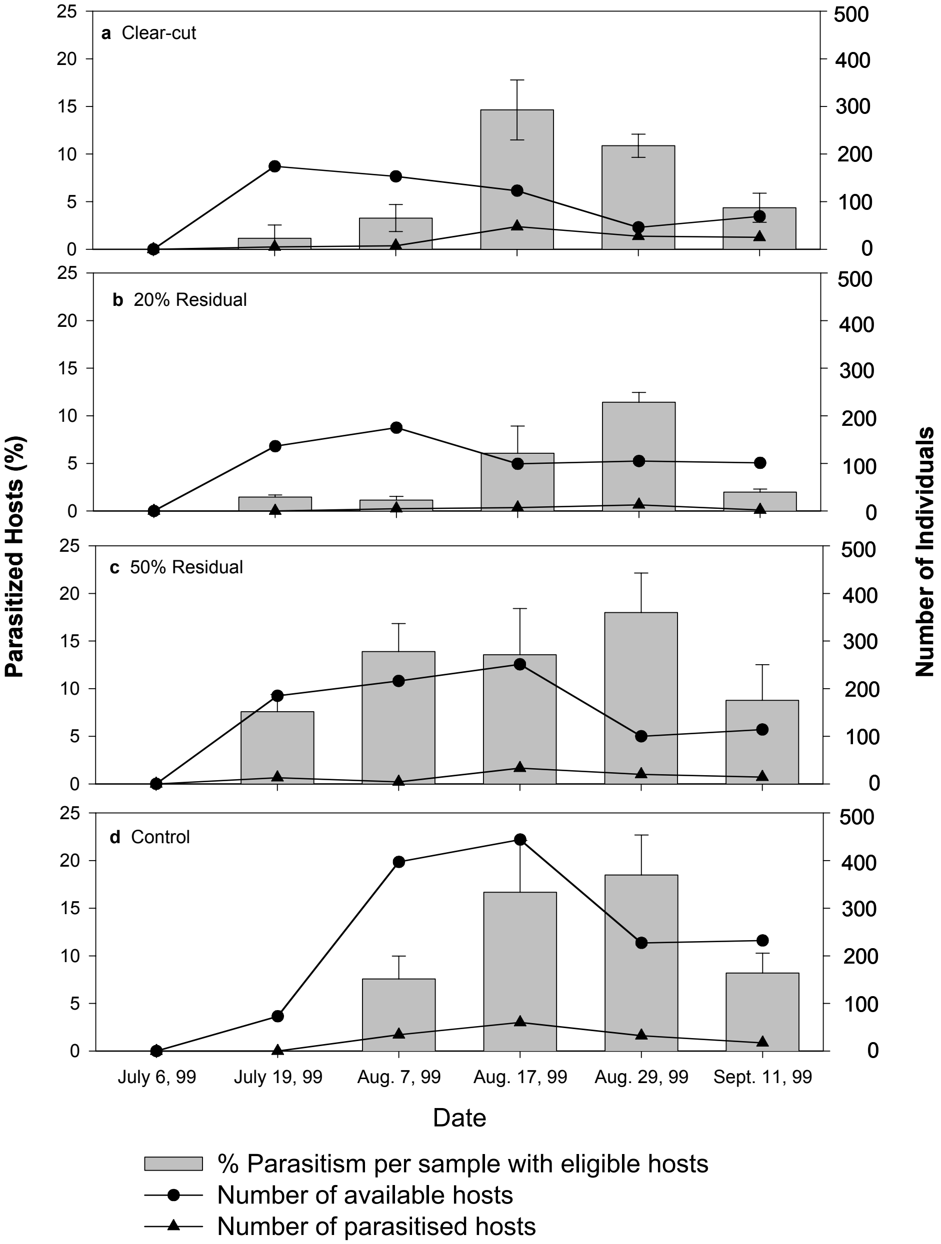


Figure. 18. Comparisons of means (± SE) % parasitism per sample containing available beetle hosts, total number of parasitised hosts, and total of available hosts for a) clear-cut, b) 20% residual, c) 50% residual, and d) control compartments.

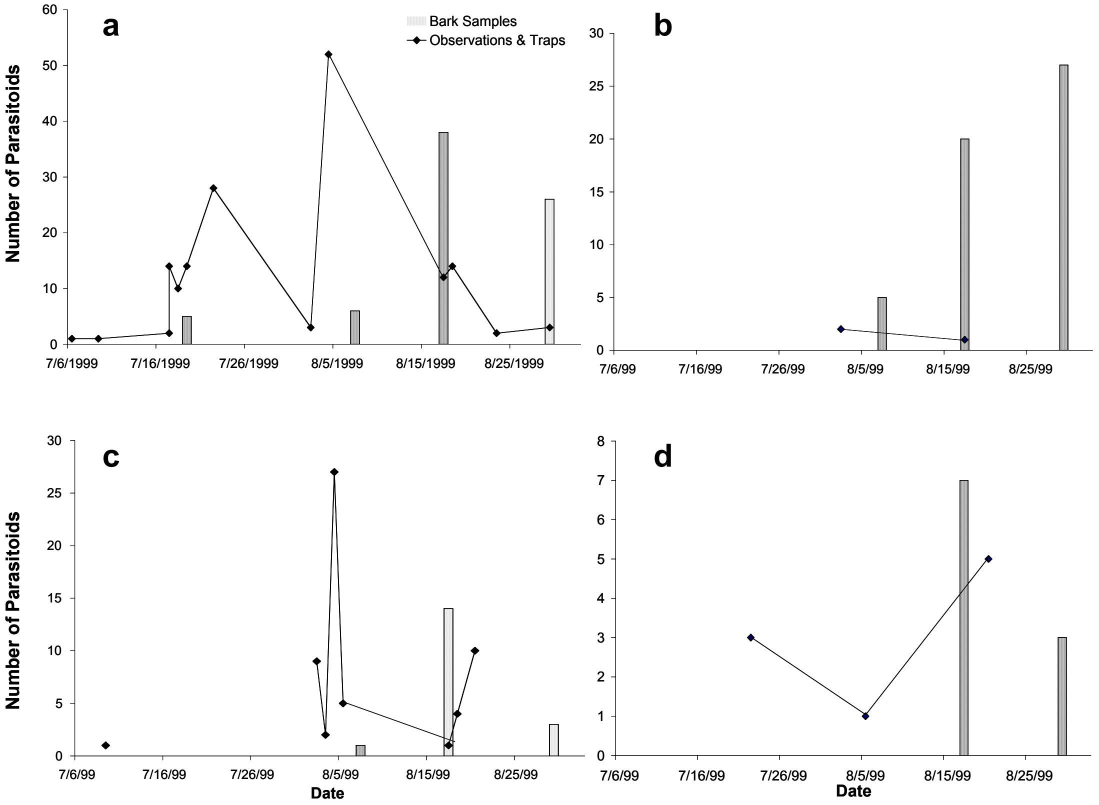


Figure 19. Flight activities for parasitoids based on combined observations of specimens on logs and in Lindgren funnel, emergence and sticky traps and number of parasitoids present in 144 bark samples for each date (all treatment and log surfaces combined) for a) *Coeloides rufovariegatus*, b) *Bracon tenuis*, c) *Roptrocerus rufovariegatus*, and d) *Dinotiscus dendroctoni*.

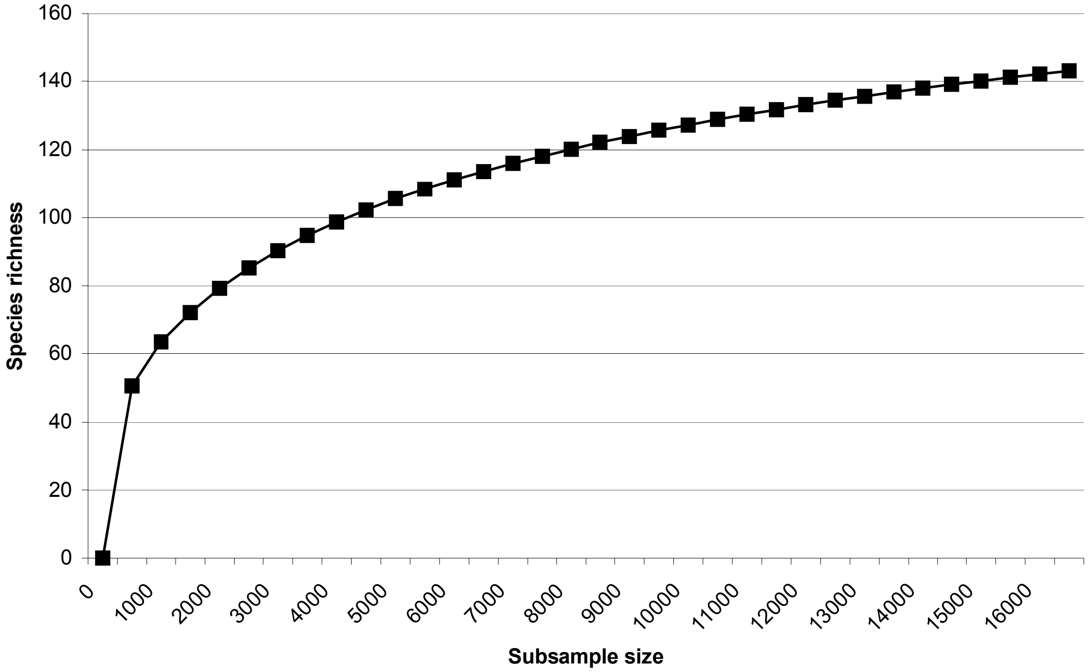


Figure 20. Rarefaction of subsamples of spiders.

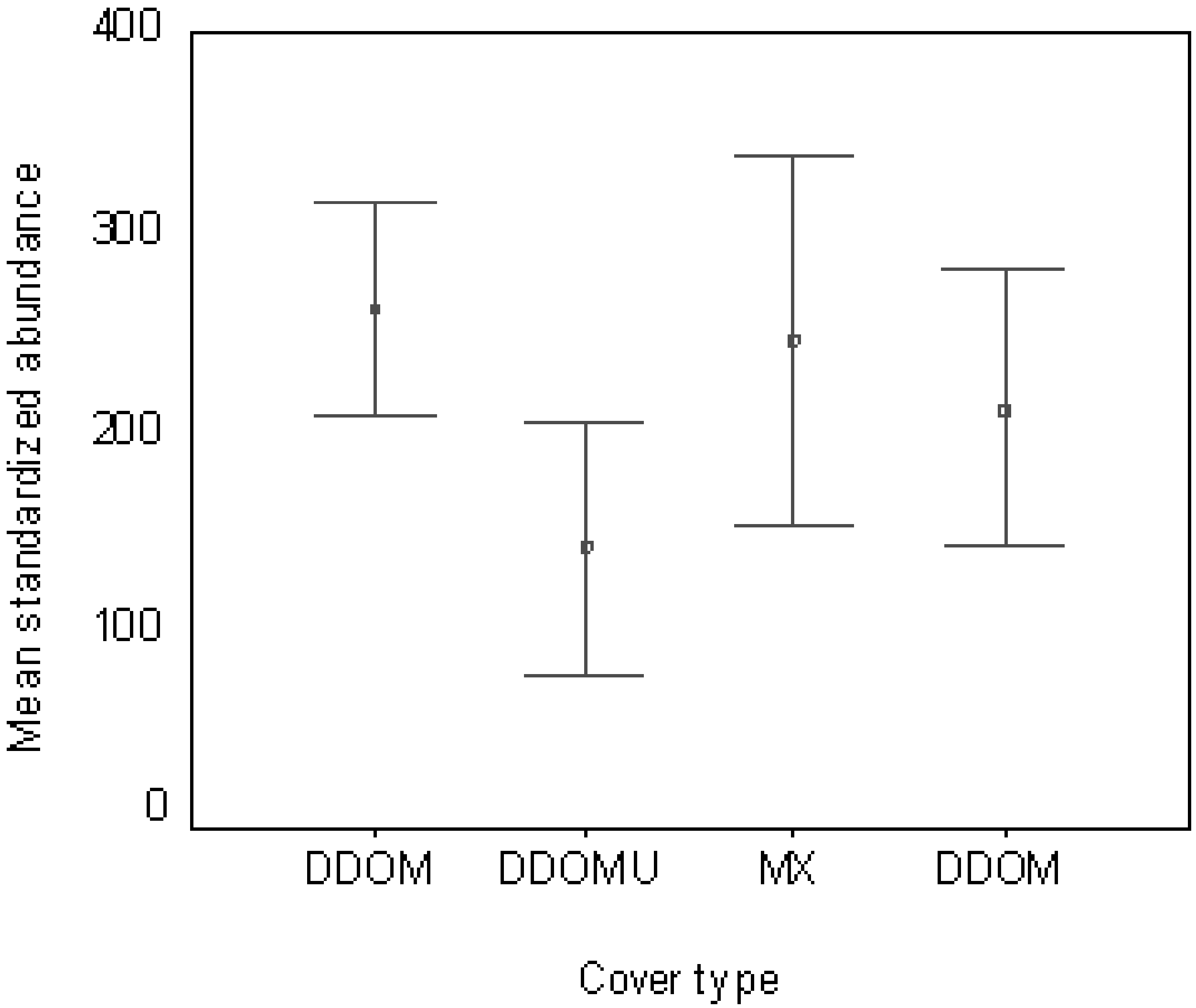


Figure 21. Mean standardized abundance (±SE) of all spiders across cover types from summer 1999.

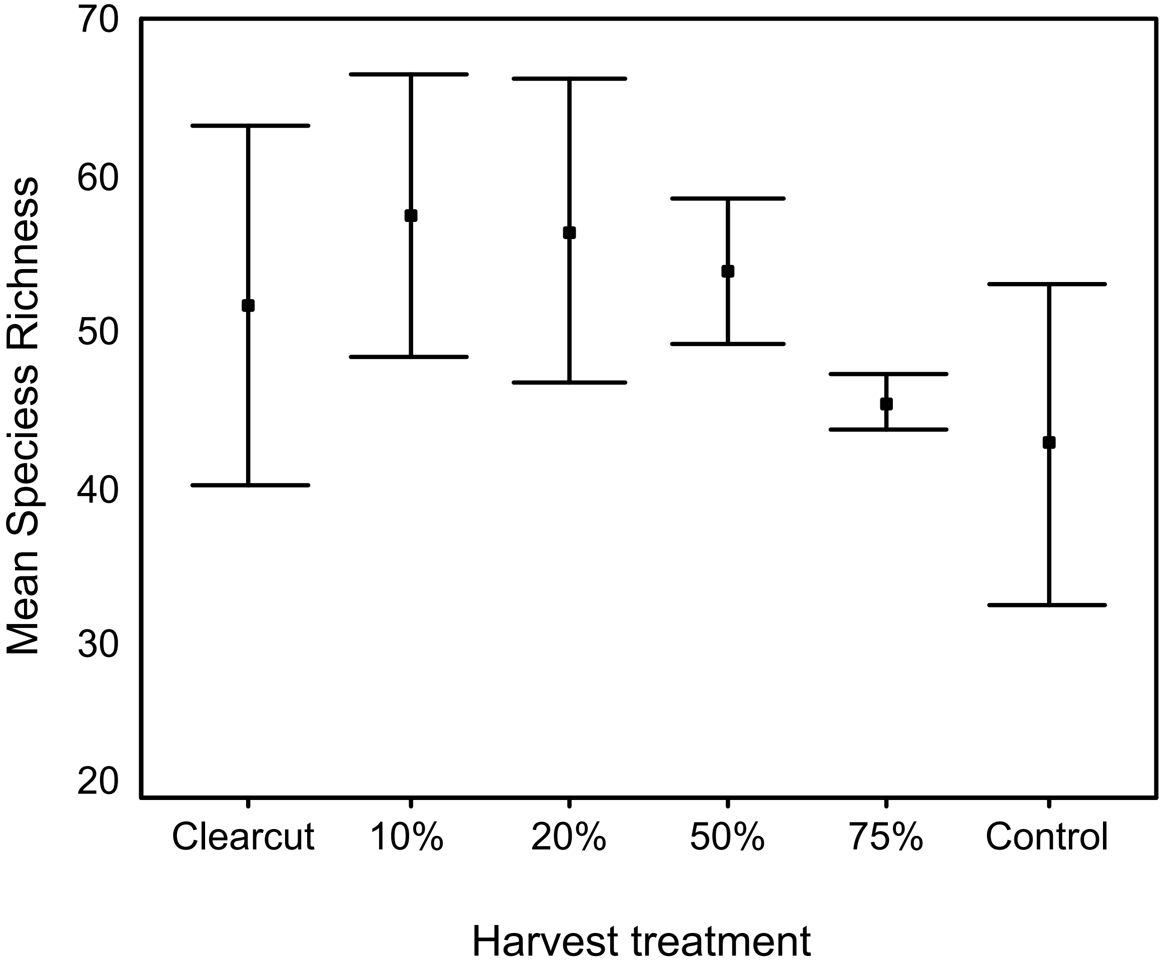


Figure 22. Mean spider species richness (±SE) across treatment from summer 1999.

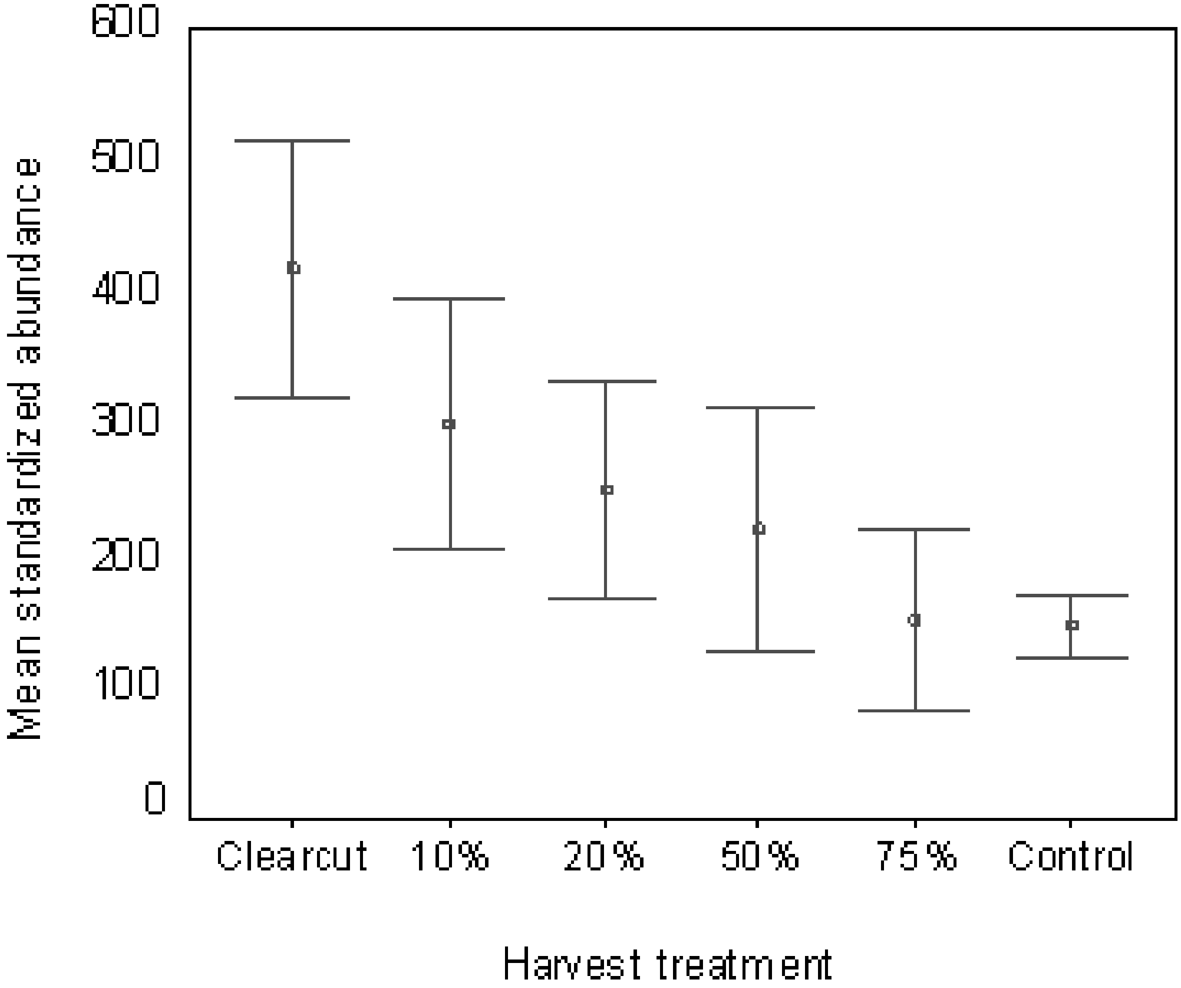


Figure 23. Mean standardized abundance (±SE) of all spiders across treatment from summer 1999.

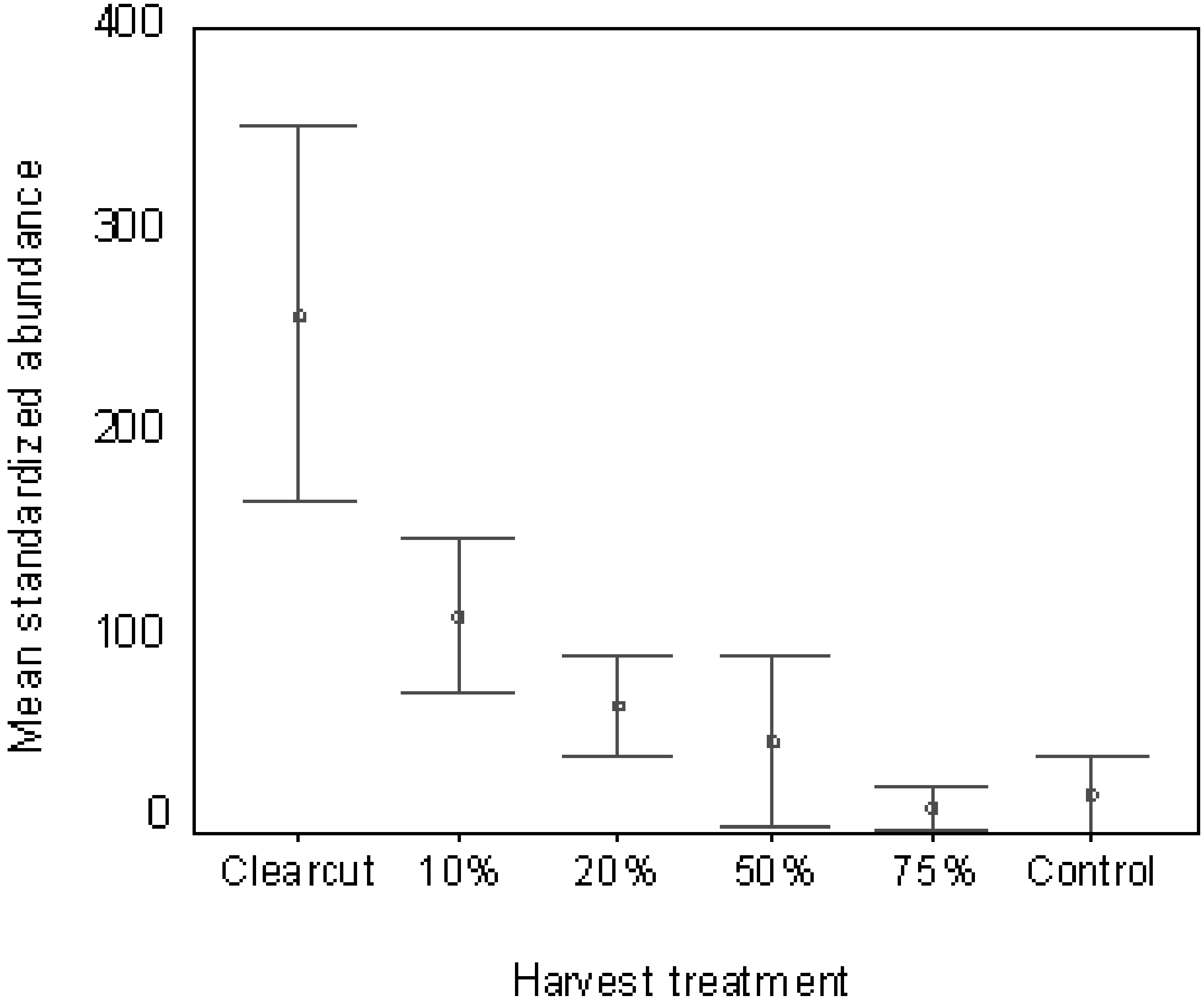


Figure 24. Mean standardized abundance (±SE) of *Pardosa moesta* Banks across cover type and treatment from summer 1999.

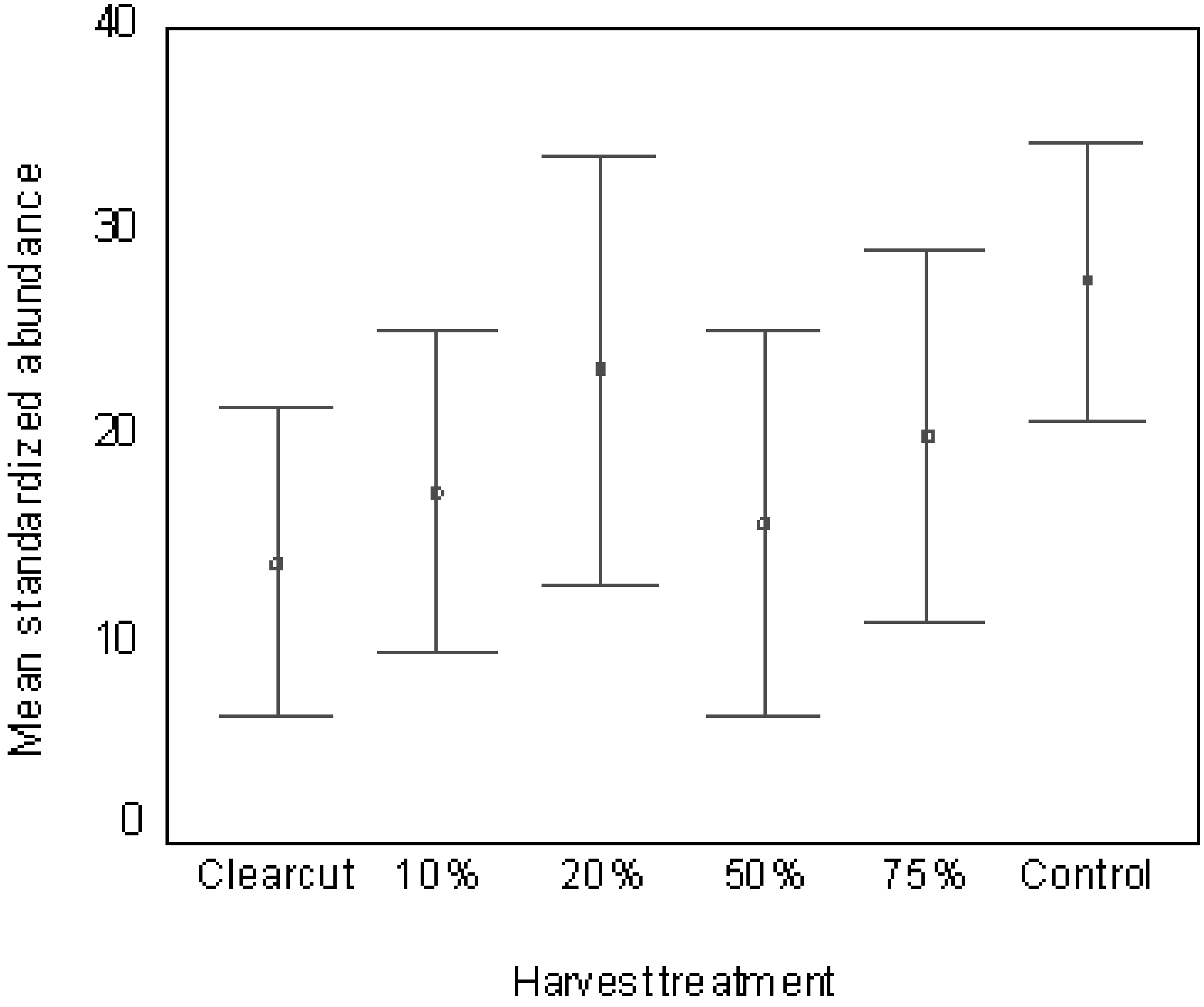


Figure 25. Mean standardized abundance (±SE) of Linyphiidae across all treatments from summer 1999.

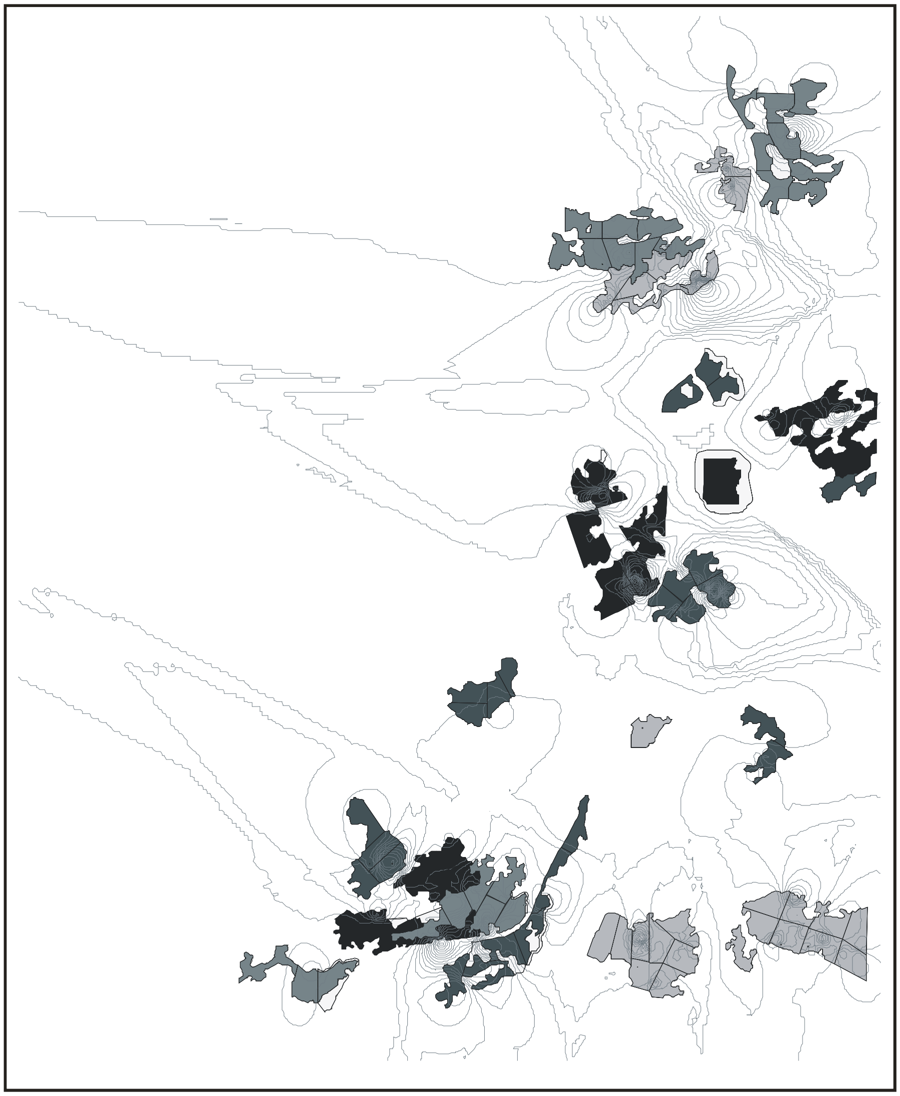


Figure 26. Isoclines of *Pardosa moesta* Banks abundance overlaying the EMEND map. Closely adjoining contour lines indicate steep gradients in abundance.

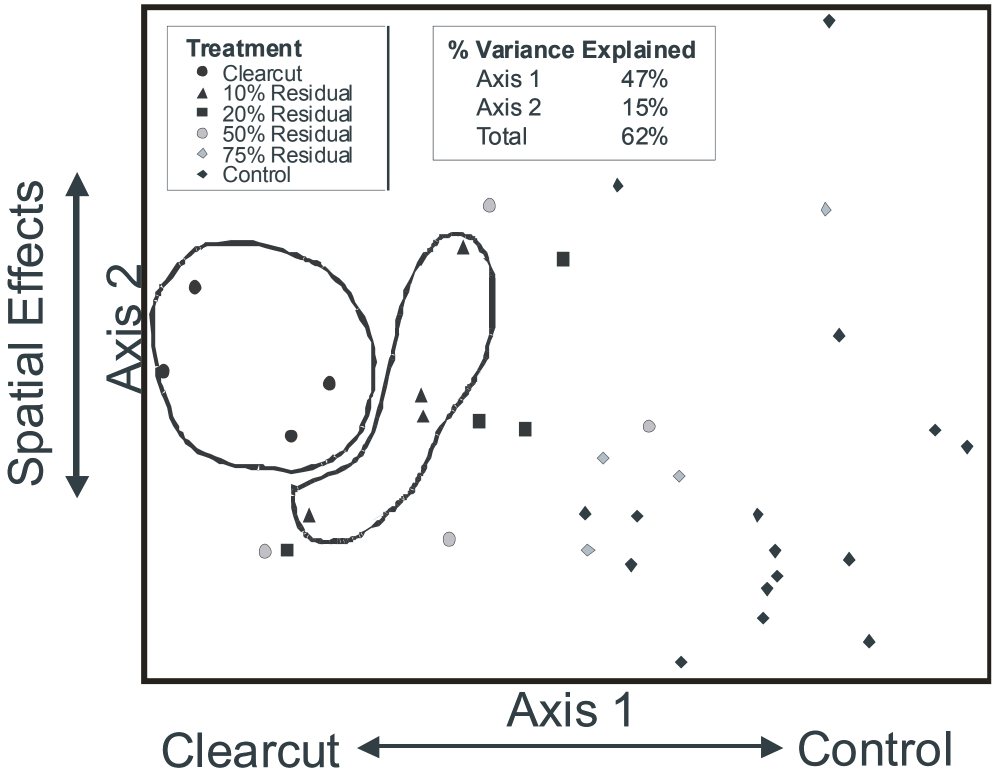


Figure 27. Nonmetric multidimensional scaling (NMS) of spider scores in each cover type coded by harvest treatment. The circular grouping denotes spider scores from clearcut stands and the polygonal grouping denotes spider scores from 10% residual stands. Axis 1 and axis 2 explain 47% and 15% of the variance in spider scores, respectively.

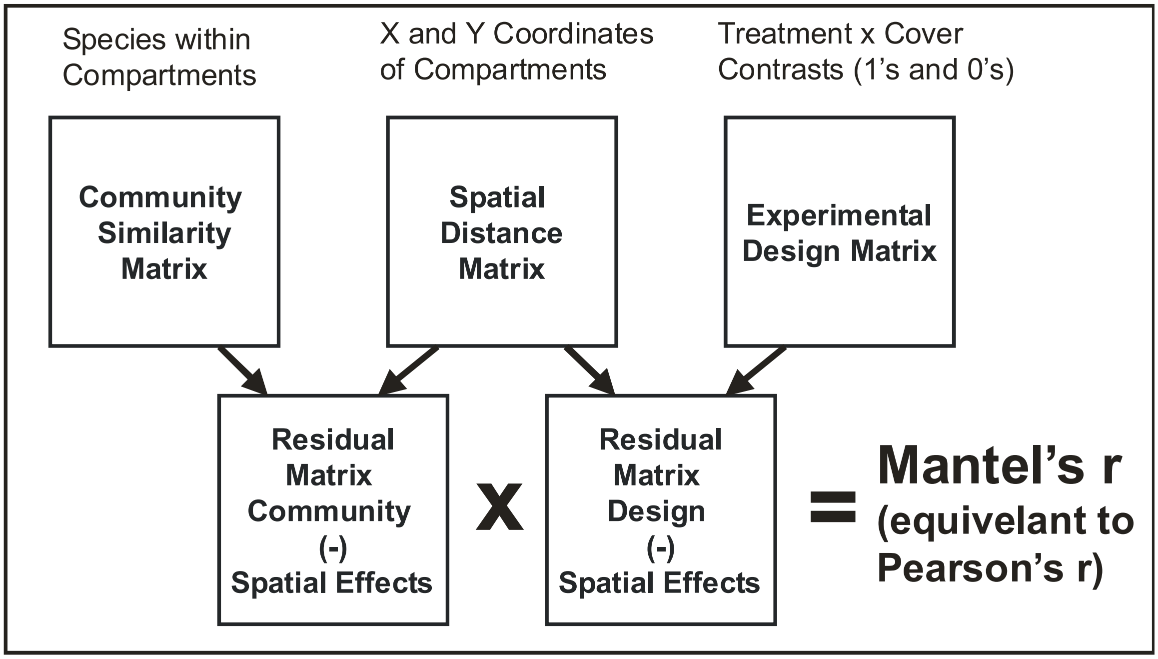


Figure 28. Graphical representation of the partial Mantel calculation. The spider community similarity matrix is first regressed onto a spatial Euclidian distance matrix. The resultant residual matrix is then regressed onto a second residual matrix constructed by regressing an experimental design matrix onto the same spatial Euclidian distance matrix.

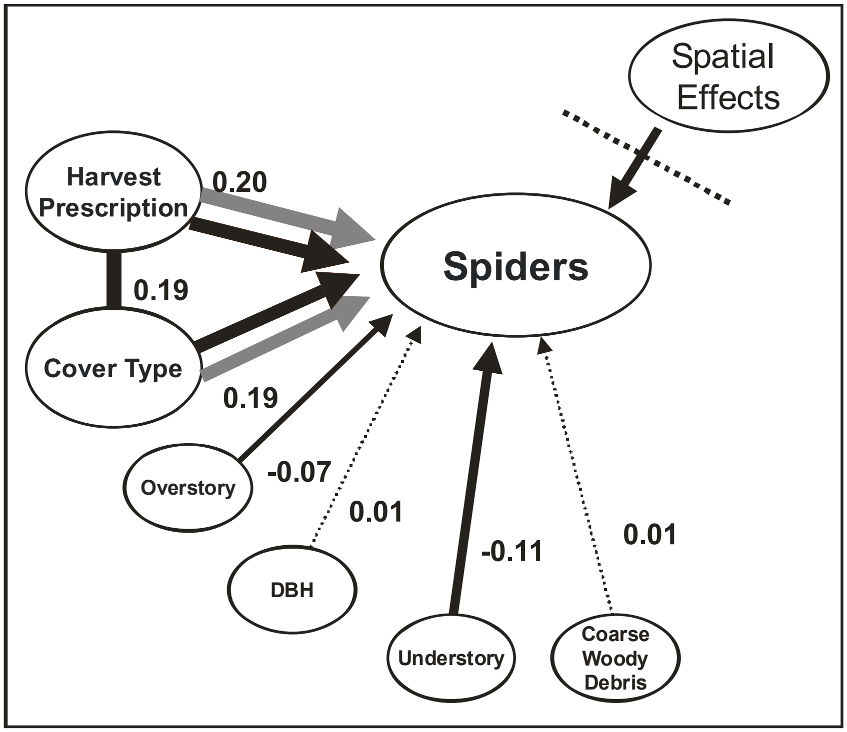


Figure 29. Representation of multiple partial Mantel tests of the correlation between the spider assemblage and the EMEND experimental design (Harvest Prescription and Cover Type) and environmental parameters (Overstory, DBH=tree diameter at breast height, Understory, and Coarse Woody Debris). Numbers are Mantel r values and the thickness of arrows represent Monte Carlo significance levels. Darkly coloured arrows indicate main effects and light coloured arrows indicate an interaction between cover type and harvest prescription on the spider assemblage.

APPENDIX I. Output from work funded under the 'BUGS' grant, as of 1 Mar 03

Refereed Publications.

Work, TT, D Shorthouse, JR Spence, WJA Volney & DW Langor. 2003. Coarse-filter Conservation Strategies in Boreal Mixedwood Forests: Initial Responses about Invertebrates from the EMEND Experiment. *Canadian Journal of Forest Research* (submitted).

Work, T., C. Buddle, L. Korinus & J. Spence. 2002. Pitfall trap size and capture of three taxa of litter-dwelling arthropods: Implications for biodiversity studies. *Environmental Entomology* **31**: 438-448.

Buddle, C. 2002. Interactions among young stages of two wolf spiders***.*** *Oikos* **99**: 130-136.

Buddle, CM. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. *Agricultural & Forest Entomology* **3**: 241-251.

Buddle, CM. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* in central Alberta, Canada. *Journal of Arachnology* **28**: 319-328.

Buddle, CM, JR Spence & DW Langor. 2000. Succession of boreal spider assemblages following wildfire and harvesting. *Ecography* **23**: 424-436.

Spence, JR. 2001. The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology and Evolution* **16**: 591-593.

Spence, JR, CM Buddle, K Gandhi, DW Langor, WJA Volney, HEJ Hammond & GR Pohl. 1999. Invertebrate biodiversity, forestry and emulation of natural disturbance: a down-to-earth perspective. pp. 80-90 in Gen. Tech. Rep. **PNW-GTR-461** (*Pacific Northwest Forest and Rangeland Soil Organism Symposium*). USDA Forest Service, Pacific Northwest Research Station, Portland, OR. 215 pp.

Volney, WJA, HEJ Hammond, DG Maynard, DA MacIsaac, KI Mallett, DW Langor, JD Johnson, GR Pohl, B Kishchuk, B Gladders, B Avery, R Chemago, T Hoffman, M Chorney, S Luchkow, M Maximchuk & JR Spence. 1999. A silvicultural experiment to mitigate pest damage. *Forestry Chronicle* **75:** 461-465.

Printed Reports

Sidders, D. and J. Spence. 2000. Ecosystem management emulating natural disturbance: Research Study and Field Guide. Sustainable Forest Management Network.

Oral Presentations

Buddle, C, DW Langor, JR Spence & GR Pohl. Successional trajectories of arthropod assemblages following wildfire and harvesting in boreal *Populus* forests. 4th Int Workshop on Disturbance Dynamics in Boreal Forests, Prince George, B.C. 9-14 Aug 2002.

Buddle, CM, JR Spence & DW Langor. "The succession of boreal forest spiders following disturbance of wildfire and clearcutting ", contributed presentation, Annual Meeting of the Ecological Society of America, Spokane, WA, USA, Aug 8-12, 1999.

Buddle, CM, JR Spence & DW Langor. Arthropod faunal recovery and timing of two-pass logging systems, invited presentation, Habitat Loss: Ecological, Evolutionary and Genetic Consequences, Helsinki, Finland, Sept 7-12, 1999.

Buddle, CM, JR Spence & DW Langor. Eipgaeic arthropod succession in boreal forests: convergence, recovery or both? Annual Meeting of the Entomological Society of Canada, Saskatoon, Sept 25-29, 1999.

Cartar, RV. Effects of boreal forest logging on bumble bee-flower relationships. Canadian Society of Zoologists. Annual Meeting. 07-11 May, 2002. University of Lethbridge.

Dunlop, J. Harvesting treatment effects on spruce beetle parasitism, EMEND Workshop, 24-25 Feb 2000.

Dunlop, J. Insect parasitoid activity on a harvested landscape, Ent 601 Seminar, 25 Nov 1999.

Dunlop, JL, DW Langor & JR Spence. Spruce beetle parasitoid response to experimental harvesting and burns, contributed presentation, Annual Meeting of the Ecological Society of America, Spokane, WA, USA, Aug 8-12, 1999.

Dunlop, JL, DW Langor & JR Spence. Spruce beetle parasitoid response to experimental harvesting and burns, contributed presentation, Annual Meeting of the Entomological Society of Canada, Saskatoon, Sept 25-29, 1999.

Dunlop, J. , D. W. Langor & J. R. Spence. Responses of defoliator parasitoids to experimental harvesting and burns,*Proc. SFMN Conference, "Science and practice: sustaining the boreal forest"*, 14-17 Feb 1999, p. 750.

Macdonald, S.E., J.R. Spence, W.J.A. Volney, D. Johnson, F.K.A. Schmiegelow, D.W. Langor, and T.T. Work. 2002. Leaky lifeboats and forest management options: the initial biotic responses to green-tree retention harvests at EMEND. Sustainable Forest Management Network Conference, "Advances in Forest Management: From Knowledge to Practice", 13-15 November 2002, Shaw Conference Centre, Edmonton, Alberta.

Miller, J. & J. Spence. 2001. Effects of forestry practices on biodiversity. 3rd North American Forest Insect Work Conference, Edmonton, Alberta, 14-18 May 2001.

Morneau, L. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. M.Sc. thesis seminar, University of Alberta, Edmonton, AB, Canada, 28 January 2002.

Morneau, L., J. Volney and J. Spence. 2000. Lepidoptera odessyes: how do ‘Leps’ deal with forest habitat structure? *Invited symposium talk*, joint meeting of the Entomological Societies of America, Canada and Quebec, Montreal, Quebec, 3-6 December 2000.

Morneau, L. Moth seasons and habitats in northern Alberta, Ent 601 Seminar, 11 Nov 1999.

Morneau, L. Hey Moth! How do you like this clear-cut?, Annual Meeting of the Entomological Society of Alberta, Waterton, Alberta, Oct 15-17, 1999 and in revised form at EMEND Workshop, 24-25 Feb 2000.

Morneau, L, JR Spence & WJA Volney. Gone with the light: A look at habitat use by moths, contributed presentation, Annual Meeting of the Ecological Society of America, Spokane, WA, USA, Aug 8-12, 1999.

Morneau, L, JR Spence & WJA Volney. A simple guide to forest defoliators, contributed presentation, Annual Meeting of the Entomological Society of Canada, Saskatoon, Sept 25-29, 1999.

Morneau, L., J. R. Spence & W.J.A. Volney. Lepidopteran community in a boreal mixed forest, *Proc. SFMN Conference, "Science and practice: sustaining the boreal forest"*, 14-17 Feb 1999, p. 786.

Morneau, L., J. R. Spence & W.J.A. Volney. Lepidoptera diversity in residual forest stands following fire and harvesting in a boreal mixedwood forest of Alberta, Annual mtg Ent. Soc. Alberta, 22-24 Oct 1998, Kannanaskis.

Morneau, L., J. R. Spence & W.J.A. Volney. The quest for lepidopteran diversity, Joint mtg Ent. Soc. Canada and Ent Soc. Quebec, 31 Oct - 4 Nov 1998, Québec.

Morneau, L., J. R. Spence & W.J.A. Volney. The quest for lepidopteran diversity, Joint mtg Ent. Soc. America and Amer. Phytopath. Soc*.* , 8-12 Nov. 1998, Las Vegas, NV.

Niemelä, J & JR Spence. Ecological effects of habitat loss and fragmentation in the boreal forest, conference section organization, moderating and summarization, Habitat Loss: Ecological, Evolutionary and Genetic Consequences, Helsinki, Finland, Sept 7-12, 1999.

Park, J., E. Crone, M. Reid. 2002. Landscape level influences on dispersal by pest insects in managed forests. Workshop on: Insect outbreaks and impacts on forest health: modeling and decision support tools for forest managers. Boreal Forest Research Centre. Peace River, AB June 2002.

Park, J. and Reid, M.L. 2001. The influence of stand composition and stand structure on the dispersal of the striped ambrosia beetle, North American Forest Insect Work Conference, Edmonton, AB.

Park J. and Reid, M.L. 2000. Distribution of bark beetles in a harvested landscape. 85th Annual Meeting of the Ecological Society of America, Snowbird, Utah.

Park, J. Distribution of bark beetles in a harvested landscape, Ecology Graduate Seminar, University of Calgary, 28 Feb 2000.

Park, J. Distribution of bark beetles in a harvested landscape, EMEND Workshop, 24-25 Feb 2000.

Park, J. Habitat selection and dispersal in bark beetles in a harvested landscape, contributed presentation, Annual Meeting of the Entomological Society of Alberta, Waterton, Alberta, Oct 15-17, 1999.

Shorthouse, DP, JJ Jacobs & TT Work. Dr. Spence's lonely heart's club band: dealing with singletons and doubletons. 50th Annual Meeting of the Entomological Society of Alberta, Lethbridge, 24-26 October 2002.

Shorthouse, DP, JR Spence & WJA Volney. Spider wanderings as correlated random walk. Annual meeting of the Entomological Society of Canada, Winnipeg, Manitoba, 5-9 Oct 2002.

Shorthouse, D. Boreal spiders as indicators of forest disturbance and management, contributed presentation, Annual Meeting of the American Arachnological Society, Lexington, KY, USA, July 15-19, 2000 .

Shorthouse, D., J. Spence & J. Volney. 2001. Untangling the threads of boreal spider bioindication. Annual meeting of the Entomological Society of Canada, Niagara Falls, Ont, 21-24 Oct 2001.

Shorthouse, D , J Spence & J Volney. Multiple scale linkages of boreal forest spiders and carabids to habitat structure modifications. *Invited symposium talk*, joint meeting of the Entomological Societies of America, Canada and Quebec, Montreal, Quebec, 3-6 December 2000.

Shorthouse, D. Boreal spiders as indicators of forest disturbance and management, EMEND Workshop, 24-25 Feb 2000.

Shorthouse, D. Effects of forest harvesting on boreal spiders, Ent 601 Seminar, 4 Nov 1999.

Shorthouse, D. Boreal spiders and carabid beetles as bioindicators of forest disturbance and management, contributed presentation, Annual Meeting of the Ecological Society of America, Spokane, WA, USA, Aug 8-12, 1999.

Shorthouse, D & KJ Cryer. Boreal spiders and carabid beetles as bioindicators of forest disturbance and management , contributed presentation, Annual Meeting of the Entomological Society of Canada, Saskatoon, Sept 25-29, 1999.

Spence, J, Jan Volney, Derek Sidders, Steve Luchkow, Tim Vinge, Frank Oberle, Dan Gilmore, J. P. Bielech, Pat Wearmouth, Jason Edwards, Peter Bothwell, David Shorthouse, Dan Wilkinson, and Suzanne Brais. The EMEND Experience. Sustainable Forest Management Network Conference, "Advances in Forest Management: From Knowledge to Practice", 13-15 November 2002, Shaw Conference Centre, Edmonton, Alberta.

Spence, J & WJA Volney. A large-scale experiment about forestry and biodiversity: the good, the bad and the useful. SFMN Variable Retention Workshop, Montreal, Quebec, 15-16 February 2002.

Spence, J. Managing risk to arthropod populations with unharvested reserves. BorNet International Conference on Biodiversity Conservation in Boreal Forests, Uppsala, Sweden, 27-28 May 2002.

Spence, J & WJA Volney. EMEND, Entomology and Evangelism. Seminar, Department of Entomology, Swedish University of Agricultural Sciences, Uppsala, Sweden, 3 June 2002.

Spence, JR, WJA Volney, B Kishchuk, DW Langor, SE Macdonald, D Sidders and TT Work. The EMEND Experiment: the basin view of a growing data ocean. 4th Int Workshop on Disturbance Dynamics in Boreal Forests, Prince George, B.C. 9-14 Aug 2002.

Spence, J & J Volney. A large-scale experiment about forestry and biodiversity: the good, the bad and the useful. Invited Plenary Address, Ecosystem Management in Boreal Forest Landscapes, Koli National Park, Finland, 27-30 May 2001.

Spence, J. Entomological communities in the biodiversity era, Annual meeting of the Entomological Society of Canada, Niagara Falls, Ont, 21-24 Oct 2001. (Invited Gold Medal Address.

Spence, J. Boreal forest stands: a key element for conserving beauty and the beasts. Boreal FSC Principle 6 Workshop, World Wildlife Fund, Toronto, Ontario, 26 March 2001.

Spence, J. & W. J. A. Volney. Development of environmental research collaboration with industry: an ounce of prevention is worth a pound of cure. 3rd North American Forest Insect Work Conference, Edmonton, Alberta, 14-18 May 2001.

Spence, J., J. Volney, D. Shorthouse and L. Morneau. The EMEND experiment: forest biodiversity conservation in context, Annual Meeting, Society for Conservation Biology, Missoula, MT, USA, 9-12 June 2000.

Spence, J. Forest management and insect biodiversity, invited symposium presentation, International Congress of Entomology, 20-26 Aug 2000, Iguassu Falls, Brazil.

Spence, JR. Sustainable Forest Management: Whats bugs got to do with it?, SFMN seminar, 25 Janurary 2000.

Spence, JR. Sustainable forest management: what's bugs got to do with it?, invited seminar, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA, 29 March 1999.

Spence, JR. Studies in arthropod biodiversity, invited presentation, SFMN Biodiversity Workshop, Rouyn-Noranda, Québec, Aug 29-31, 1999.

Spence, JR, WJA Volney, MRT Dale, BE Kishchuk, DW Langor, VJ Lieffers, SE Macdonald, DM Sidders & MG Weber. "EMENDing Boreal Forest Mangement to Minimize Habitat Loss", invited presentation, Habitat Loss: Ecological, Evolutionary and Genetic Consequences, Helsinki, Finland, Sept 7-12, 1999.

Spence, JR & WJA Volney. Around the bend with EMEND, contributed presentation, Annual Meeting of the Entomological Society of Alberta, Waterton, Alberta, Oct 15-17, 1999.

Spence, J. R. & W. J. A. Volney. You are what you eat II. Foliage, feeding, FTC and fecundity, Annual mtg Ent. Soc. Alberta, 22-24 Oct 1998, Kannanaskis.

Volney, WJA & JR Spence. 2002. Insects as disturbance agents in boreal forests. 4th Int Workshop on Disturbance Dynamics in Boreal Forests, Prince George, B.C. 9-14 Aug 2002.

Volney, J. and J. Spence. Management of forest stand structure and insect assemblages: implications for the good, the bad and the ugly, invited symposium presentation, International Congress of Entomology, 20-26 Aug 2000, Iguassu Falls, Brazil.

Volney, J. and J. Spence. Biodiversity and forest management in Populus-dominated forests of North America, invited symposium presentation, 21st Meeting of the International Poplar Commission, Portland, Oregon, USA, September 24-30, 2000.

Wesley, J. 2002. The impacts of variable retention harvesting on phytophagous insects and their parasitoids in the boreal forest, M.Sc. thesis seminar, University of Alberta, Edmonton, AB, Canada, 22 September 2002.

Work, TT, JR Spence, DP Shorthouse & K Cryer. 2002. Retention thresholds for carabid beetle communities in boreal forests. 4th Int Workshop on Disturbance Dynamics in Boreal Forests, Prince George, B.C. 9-14 Aug 2002.

Work, TT, JR Spence, WJA Volney & K Cryer. 2002. Habitat compostion versus habitat structure: evaluating coarse filter strategies for maintaining invertebrates in boreal forests. Annual meeting of the Entomological Society of Canada, Winnipeg, Manitoba, 5-9 Oct 2002.

Work, TT, D Shorthouse, JR Spence & WJA Volney. 2002. Impact of six intensities of forest harvest on rove beetle communities in western boreal forests. 50th Annual Meeting of the Entomological Society of Alberta, Lethbridge, 24-26 October 2002.

Poster Presentations

Dunlop, J., D. Langor & J. Spence. 2001. Disturbance effects on spruce beetle parasitism. 3rd North American Forest Insect Work Conference, Edmonton, Alberta, 14-18 May 2001. (Poster)

Park, Jane S., E. Crone, and M.L. Reid. 2002. Landscape level influences on dispersal by pest insects in managed forests. Poster presented at Sustainable Forest Management Network Conference, "Advances in Forest Management: From Knowledge to Practice", 13-15 November 2002, Shaw Conference Centre, Edmonton, Alberta.

Shorthouse, D.P., T.T. Work, and J.R. Spence. 2002. Multiple-scale linkages of boreal forest spiders to habitat structure modifications. Poster presented at Sustainable Forest Management Network Conference, "Advances in Forest Management: From Knowledge to Practice", 13-15 November 2002, Shaw Conference Centre, Edmonton, Alberta.

Shorthouse, D., J. Spence & T. Work. 2001. Boreal spiders as indicators of multi-scale forest structure, disturbance and biodiversity. 3rd North American Forest Insect Work Conference, Edmonton, Alberta, 14-18 May 2001. (Poster)

Shorthouse, D. Boreal forest spiders as indicators of multi-scale structure, disturbance and biodiversity. *Poster*, joint meeting of the Entomological Societies of America, Canada and Quebec, Montreal, Quebec, 3-6 December 2000.

Publications & Theses

Buddle, C. 2001. *Spider communities in boreal mixed-wood forests of Alberta: succession, species interactions and habitat utilization.* PhD Thesis, Department of Biological Sciences, University of Alberta, Edmonton. 203 p.

Morneau, L. 2002. *Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest in Alberta*. MSc Thesis, Department of Biological Sciences, University of Alberta, Edmonton. 138 p.

Park, J. 2002. *The effects of resource distribution and spatial scale on the distribution of two species of bark beetle:* Polygraphus rufipennis *(Kirby) and* Trypodendron lineatum *(Olivier) (Coleoptera: Scolytidae).* MSc Thesis, Department of Biological Sciences, University of Calgary, Calgary. 104p.

Shorthouse, D. 2003. *Boreal spiders as bioindicators of forest disturbance and management.* PhD Thesis, Department of Biological Sciences, University of Alberta, Edmonton. (in progress, expected July 2003).

Wesley (nee Dunlop), J. 2002. *The impacts of variable retention harvesting on phytophagous insects and their parasitoids in the boreal forest.* MSc Thesis, Department of Biological Sciences, University of Alberta, Edmonton. 132 p.

Student Career Placement

All four students who have to date completed their theses under the ‘Bugz’ grant have permanent jobs in their fields. All three MSc students had jobs before finishing their theses and this has slowed down bringing the work to completion.

Christopher M. Buddle is now Assistant Professor of Forest Entomology, Macdonald College, McGill University, Montreal, Quebec, hoping to join the SFMN as a researcher himself in 2003!!

Louis Morneau is now a Forest Protection Officer, Province of Quebec, Quebec City, Quebec.

Jane Park is now a Park Warden (Fire and Vegetation Management), Banff National Park, Banff, Alberta.

Julia Wesley (nee Dunlop) is now Entomologist & Inspector, Canadian Food Inspection Agency, Vancouver, B.C.