Interim Progress Report on the Ecosystem Management Emulating Natural Disturbance (EMEND) Project

(For EMEND work associated with FRIAA funding)

1 January 2005 – 31 October 2005

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Contents

1. Overview of EMEND Research 2005.

There are two principal components to field research at the Ecosystem Management Emulating Natural Disturbance (EMEND) site: 1) collection of experiment-wide or "Core" data, done primarily by the centralized research group ("Core Crew"), as required to ensure that comparisons of all treatments can be made over all 4 forest types; and 2) research planned and executed by researchers interested in using EMEND as a template for their work. Work carried out under category 2 is comprised mostly of projects by graduate students and by research scientists interested in questions other than the experiment-wide questions addressed in the core research. Support provided by the Forest Research Improvement Association of Alberta (FRIAA) is aimed mainly at the Core work although limited financial support is provided for category 2 projects through i) Core Crew assistance to individual projects, ii) provision of the majority of camp costs, and iii) a number of small top-up grants for researchers working at EMEND to encourage a full research profile. FRIAA support is the essential basis for the experiment-wide work at EMEND but it also encourages an extensive range of category 2 work at our site.

This report provides details on the research activities of the EMEND Core Crew and the EMEND camp facility usage for the period 1 January through 31 October 2005. Additionally, updates on category 2 research and technology transfer activities are provided.

2. EMEND Core Personnel.

The EMEND “Core Crew” is responsible for the collection, organization, and analysis of experiment-wide data as well as the coordination and administration of research at EMEND. The crew consists of the EMEND Field Coordinator, the EMEND Data Manager (full-time positions), and a temporary summer staff of undergraduate university and college students. The summer Core Crew positions remain highly sought after positions and this year there were applications from students in Alberta, British Columbia, Ontario, Quebec and New Brunswick.

The 2005 Core Crew consisted of 8 personnel. Jason Edwards served a fifth year as EMEND Field Coordinator and Charlene Hahn carried out her fourth year as EMEND Data Coordinator. Ashlee Jollymore (McGill University), Dan Jensen (University of Alberta [UofA]), Christine Hiebert (UofA), Rachel Hofman (UofA), Savanna Rave (UofA), and Stuart Morrison (Lakeland College) all served as summer Core Crew members from 1 May until 31 August. Dominique Perez-Parada (Canadian Forest Service [CFS]) volunteered with the Core Crew for a few weeks in August.

EMEND continued its collaboration with the Boreal Forest Research Centre (Northern Alberta Institute of Technology, Peace River Campus) by taking on two local high school students as members of the Core Crew. Lisa Roy and Nathan Stilwell spent 4 weeks at EMEND. Funds to hire Roy and Stilwell were provided by the Boreal Forest Research Centre. This collaboration allows EMEND educate local students on our research program and provide them with direction on future education options. To date, EMEND has provided this opportunity to six local high school students.

2.1 EMEND Field Coordinator Activities.

The full-time EMEND Field Coordinator position is currently supported through the EMEND FRIAA budget. Jason Edwards has held the position of EMEND Field Coordinator since 2001. This position is responsible for supervising the summer Core Crew, for the day-to-day administration of the EMEND Project, and for representing EMEND at conferences and meetings.

Approximately 55% of Edwards' time from 1 January to 30 September was spent on tasks related to fieldwork. These tasks included supervising the summer Core Crew, managing the field camp use, maintaining field equipment, and conducting field surveys (see section **3. Summer Core Crew Activities** for survey details).

Approximately 30% of Edwards' time was allocated to EMEND Project administration tasks. These tasks included meetings, workshops, hiring Core Crew, summer fieldwork preparations, map updates, website updates, report writing, and grant development. Edwards represented EMEND at two major conferences since January. He presented posters at the Western Forest Insect Work Conference (WFIWC) in Vicotoria, BC and at the North American Forest Ecology Workshop (NAFEW) in Aylmer, QC.

The remaining 15% of Edwards' time was dedicated to the new EMEND Research Facility development. Numerous meetings were required to establish budgets, select the facility location, and purchase the structures and equipment.

2.2 EMEND Data Manager Activities.

The full-time EMEND Data Manager position is also currently supported through the EMEND FRIAA budget. The Data Manager is primarily responsible for compiling, validating all data collected by the summer Core Crew and is also responsible for assisting the Field Coordinator with field surveys, hiring and supervising the summer Core Crew, and organizing the annual EMEND workshop. Charlene Hahn has held this position since 2002.

Approximately 45% of Hahn's time was committed to fieldwork. Her fieldwork includes time spent collecting data as well as managing the data collected during the summer and assisting Edwards with managing the core crew and research camp.

Hahn dedicated 25% of her time validating and proofing data for the EMEND database. As of April 2005, all pre-2005 data in the EMEND Database is considered validated.

Hahn allocated the remaining 30% of her time to the EMEND Productivity and Biomass project. Hahn continued to develop allometric equations for above- and below-ground tree biomass. She also developed protocols for measuring tree fine root biomass from soil samples collected in 1999 and supervised two research assistants (hired with non-FRIAA monies) to process these samples.

3. Summer Core Crew Activities (1 May 2005 – 31 August 2005).

The summer Core Crew worked a total of 597 person-days at the EMEND site during 2005. This time was spread among several activities including site orientation, safety training, working on experiment-wide projects, and assisting with category 2 research. The following three sections of this report describe the Core Crew activities for summer 2005.

3.1. Experiment-wide (Category 1) Research.

The majority of Core Crew time, approximately 96%, during summer 2005 was spent working on four experiment-wide projects: forest productivity estimates, coarse woody debris surveys, soil sampling, and moth biodiversity collections. Descriptions of the work completed on these projects are provided below and Core Crew work time allocations are detailed in Table 1.

i) *Forest Productivity Estimates (Shrub Biomass).*

The focus of this study is to estimate above- and below-ground biomass of trees and shrubs at the EMEND site. There are three main facets of the study: 1) tree mensuration survey, 2) shrub biomass survey, and 3) development of above- and below-ground biomass estimators for trees and shrubs. Dr. Jan Volney, CFS, and Dr. John Spence, UofA, co-lead the forest productivity estimates study.

Core Crew 2005 concentrated on the shrub biomass survey portion of this study. Core Crew allotted 228.25 person-days to assess all 1200 permanent 10 x 2 meter shrub biomass plots. Over 25000 shrub stems were assessed for species, location (corridor or leave strip), diameter at 30 cm above ground, total stem length, and status (alive or dead). Any indication of stem browsing, breakage, or shoot blight (*Venturia* spp.) was also noted. Only stems greater than 1.00cm diameter at 30cm above ground were included in the survey. Tree species were included as shrubs if the diameter at breast height (DBH) was less than 5cm. Detailed methods for the snag survey are included in **Appendix 2 – EMEND Core Study Methods**.

ii) Fate of Snags and Dynamics of Coarse Woody Debris (CWD).

This year marked the continuation of the fifth-year post-harvest survey of coarse woody debris at EMEND. The coarse woody debris study consists of two aspects: a) standing coarse woody debris (snags) assessment, and b) downed CWD survey (completed 2004). Both aspects are combined to develop an understanding of the fate and function of residual material left in the wake of harvests or natural disturbances, a central focus of the EMEND project. Dr. David Langor, CFS, and Daryl Williams, CFS, supervise this work.

This year's work concentrated on standing coarse woody debris (snags) density, volume, and condition estimates. The 2005 snag survey was conducted on all 600 permanent 40 x 10 meter snag plots and consumed 122.75 person-days of Core Crew time. Approximately 3500 snags were assessed for status (dead or fallen), DBH (1.3 m above germination point), height, height class, percent bark cover, and decay class. Detailed methods for the snag survey are included in **Appendix 2 – EMEND Core**

Study Methods. All heights were assessed using a Vertex III hypsometer. No 40 x 10 meter North and East snag plots were assessed following the decision in 2004 to eliminate these plots (see Interim Progress Report on the EMEND Project 2004).

iii) Soils and Nutrient Dynamics.

The fifth-year post-harvest soil and nutrient dynamics sampling was initiated this summer under the direction of Dr. Barbara Kishchuk, CFS. Soil sampling was done to gather information on various physical and chemical soil properties including, but not limited to: bulk density, pH, total nitrogen, extractable phosphorus, extractable sulfur, carbon, cation exchange capacity (CEC), exchangeable cations, extractable nitrogen (NO3 and NH4) on forest floor and mineral soil, and total Ca, Mg, Na K, Mn, P, S, Al and Fe on forest floor material only. Both forest floor and mineral samples were taken, and were brought back to the lab for analysis. All sampling stations (6 per compartment) were located near the permanent soil plot markers along each of the 40 x 10 meter permanent mensuration plots. Detailed methods for the Soil and Nutrient Dynamics study can be found in Kishchuk (2004).

Only the Aspen-dominated and Conifer-dominated compartments were completely sampled this summer. Sampling these stands utilized 59.75 person-days of Core Crew time. The remaining Aspen with Spruce understory and Mixedwood stands will be completed next summer. All slash-burn compartments will also be sampled next year as none were completed this summer.

Edwards and Hahn will process the bulk density samples this winter. The chemistry samples are stored in a freezer at the Northern Forestry Centre, Edmonton, and will be analyzed at a future date.

iv) Lepidoptera (moth) Biodiversity.

The fifth-year post-harvest moth biodiversity survey was conducted this summer. Esther Kamunya, a new PhD student from UofA, headed the survey. Kamunya's project is a continuation of Louis Morneau's research from 1998-2001. Core Crew provided her with 36.75 person-days of assistance with setting and collecting light traps. Although this is a graduate student study, we have classed it as category 1 core work since this year focused on experiment-wide, baseline biodiversity work. The experiment-wide collection of Lepidoptera will continue next summer. Details of Kamunya's project are outlined in section **6. Graduate Student and Category 2 Research Updates** of this report.

3.2. Category 2 Research.

Core Crew assistance to Category 2 research was limited this year. Only 22.25 person-days were allocated to such research. Core Crew allocations to each Category 2 project are summarized in Table 2.

i) Fire Ecology

Edwards and Hahn assisted CFS in observing the three slash burns conducted by Alberta Sustainable Resource Development (ASRD) in May. Rates of spread, flame height, and weather conditions were noted. Depth of burn and fuel load measurements were taken after the burn. All data have been forwarded to Peter Bothwell, CFS, for analyses. A total of 15.75 person-days were allocated to the EMEND Fire Ecology project.

ii) White Spruce Regeneration
Core Crew provided 1.5 person-days of assistance to the White Spruce Regeneration project (Stewart, CFS) to aid with the removal of seed traps.

iii) Graduate Student / Postdoctoral Research Assistance
Core Crew provided 5.0 person-days of assistance to Colin Bergeron (PhD, UofA) and Matti Koivula (Post-doctoral Fellow, UofA) for the set-up and collection of epigaeic beetle studies. Although neither of these studies was focused directly on EMEND, assistance was provided to ensure both researchers met the EMEND "no working alone" safety protocol.

3.3 Other Core Crew Tasks.

EMEND puts a priority on maintaining a safe worksite. As such, a significant portion of Core Crew time, about 30 person-days, was spent on training activities this summer. Training included site orientation, defensive driving courses, ATV certification, bear awareness, mock emergency response drill, and monthly safety meetings.

Infrastructure related activities, including camp setup/takedown, equipment maintenance, and trips to Peace River to repair and replace equipment, used about 40 person-days of Core Crew time. Edwards also spent about 12 person-days on inspections and setup of the new EMEND Research Facility. About 10 person-days were allocated to assisting the camp cook prepare food during the prescribed fires as the Core Crew was not allowed to work in the field during the burns due to safety concerns.

Over 29 person-days of Core Crew time were allocated to office work. This time is limited to Hahn's efforts to manage incoming data from the summer fieldwork and Edwards' efforts in managing the camp facilities.

4. EMEND Camp Facilities and Research Equipment.

Whitemud Wilderness Outfitters of Peace River, Alberta was contracted to provide camp services again this summer. Camp was open from 5 May until 31 August. The camp was used for 1128 nights, down 27 nights from 2004. Overall, 35 EMEND-affiliated personnel (not-including 30 ASRD fire crew personnel) used the camp facilities this summer. Breakdowns of camp usage are provided in Tables 3 and 4.

The new EMEND Research Facility was built and installed this summer. The new facility is located 10km west of Highway 35 along the Sulphur Lake Road (Township road 874). The central land location is NE 23-87-25-W5M. This site is approximately 40km away from the EMEND research site. The facility will house up to 30 researchers, 10 inside the structure and an additional 20 in canvas-covered wooden tents. Unfortunately, the facility was not functional until mid-September and so was not available for use by the summer Core Crew. A number of EMEND associated researchers used the new Research Facility for a total of 61 nights throughout September and October. This usage is summarized in Table 5.

EMEND Core Crew used three vehicles and eleven quads this summer. All three vehicles were rented from the UofA. Core Crew borrowed two quads from Canfor and three quads from DMI; the remaining six quads were allocated to EMEND by John Spence, UofA. Core Crew vehicle usage and camp fuel usage are summarized in Table 6.

John Spence purchased three Dell Axim Personal Data Assistants (PDAs) for the EMEND Core Crew in April 2005. These PDAs were used to collect all Core data during the 2005 field season. This method of data collection greatly reduced the data entry and proofing time as the data files can be directly downloaded to the EMEND desktop computer in a format compatible with the EMEND database. In fact, all Core data has already been entered, a process that takes Hahn about two months to complete in the fall.

5. EMEND Research Personnel.

A total of four graduate students conducted fieldwork at EMEND this past summer. Richard Caners and Virginia Chavez continued with their PhD programs on bryophyte (moss) communities and understory vegetation competition respectively. Colin Bergeron continued his PhD study on fire history and arthropod communities. Esther Kamunya, a PhD student from UofA, joined the EMEND research team this summer to study the post-harvest Lepidoptera (moth) communities. EMEND also welcomes Mathew Swallow, a Masters student from UofA, who is studying soil chemistry and nutrient cycling in slash harvest/burns. A number of graduate students are nearing completion of their studies. A summary of the status of EMEND graduate students is found in Tables 8 and 9. No changes to senior research personnel occurred between 1 January and 31 October 2005.

6. Graduate Student and Category 2 Research Updates.

The following sections provide updates to a number of on going research projects at EMEND. The list of projects is not inclusive as updates are provided only for those researchers who submitted them.

6.1. Patterns of bryophyte diversity in response to partial harvesting in northern mixedwood boreal forests.

Richard Caners[1] (PhD Candidate).

Supervisors: Dr. Ellen Macdonald[1] and Dr. René Belland[1,2]

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[2]Devonian Botanic Garden, University of Alberta, Edmonton, AB T6G 2E1

This study is examining the effects of partial forest harvesting on bryophyte (moss, liverwort, and hornwort) diversity in mixedwood boreal forests of northern Alberta. Bryophytes constitute an important component of the plant diversity in northern forests, and are key to a wide variety of ecosystem functions. Given that many bryophytes are sensitive to habitat change and are commonly dispersal-limited, forest harvesting may have long-term implications for bryophyte persistence over large areas. Study objectives are to describe the mechanisms driving the response and reassembly of bryophytes after harvest across different forest types and harvest intensities. Research will examine the effects of structural retention on substrate availability, bryophyte diversity, and species patterns at multiple spatial scales.

Over the 2005 field season, bryophyte species diversity and forest structure were enumerated in 50 m^2 circular plots for coniferous-dominated forest compartments that were experimentally harvested in 1998 at 10, 50, and 75 percent canopy retention, with non-harvested compartments serving as controls. Six plots were randomly established and enumerated in each of 12 compartments (4 levels of retention x 3 replicate compartments), for a total of 72 sampled plots. Within each plot, tree density and basal area were enumerated, and woody debris was assessed using two orthogonal line intercepts. Vascular and non-vascular species richness and abundance were measured in 1x1 m subplots positioned at the centre of each circular plot, with shrub density and cover measured in 10 m^2 circular plots centred on each subplot. Shoots of *Hylocomium splendens* were collected to determine the length of recent segment growth as a surrogate measure of local growing conditions. Subplots were divided into grids of 25, 20x20 cm cells to examine the effects of harvest intensity on the distribution and abundance of substrates, and the diversity and associations of bryophytes at different spatial scales. Species diversity was determined at a larger (operational) scale in 1256 m^2 circular plots centred on each of the smaller circular plots.

Mineral soil samples were collected at a depth of 0-5 cm from the centre of each 1x1 m subplot to assess the diversity of the bryophyte diaspore bank. Samples are being germinated under different light intensities for future comparison with physical and chemical properties of the soil, prevailing stand structure, and the extant bryophyte flora.

All of the above measures were previously assessed for mixed-coniferous forest compartments in 2004. Field sampling for the third (2006) field season will examine the efficacy of 0.5 ha and 0.2 ha ellipses at maintaining bryophyte diversity on the landscape for the different canopy type – harvest intensity treatment combinations. The spatial pattern of forest floor bryophytes will be assessed in unharvested compartments using transects of contiguous quadrats. Within each quadrat, biotic and abiotic factors will be measured to determine their roles in the spatial structuring of forest floor bryophyte communities.

6.2. Patterns and causes of variation in understory plant diversity and composition in the mixed-wood boreal forest of Alberta.

Virginia Chavez[1] (Ph.D. Provisional Candidate).

Supervisor: Dr. Ellen Macdonald[1]
[1]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1

Canopy trees play an important role in determining understory diversity patterns as they modify the soil moisture, nutrients, temperature, microbial activity and light availability of the micro environment where understory species grow. There is still, however, much work needed to adequately understand the influence of above and below ground resources on understory species composition and diversity (species relative abundance and richness) within mixedwood stands in the boreal forest of Alberta. This study aims to contribute to the understanding of the patterns and causes of diversity variation in understory plant communities in the mixedwood boreal forest. It addresses (i) the effect of abiotic factors (light, soil macronutrients and pH) on understory diversity and composition in relation to canopy composition; (ii) spatial patterns of understory diversity and composition and; (iii) the effect of plant interactions (competition and facilitation) on understory diversity and composition. This study has been divided into three sub-studies, data collection for two of them has been carried out at EMEND since the summer of 2004 and will be concluded during the summer of 2006.

Throughout the summer of 2005, data was collected at the control mixedwood stands of EMEND in order to investigate the role of understory competition and facilitation on plant diversity. This included understory vegetation cover estimation, shrub health assessment and soil samples collection in order to analyze for pH. Likewise, resin bags were buried at the centre of each plot in order to analyze for soil NO_3, NH_4, PO_4, Mg, Ca and K and two leaf-on hemispherical photos were taken in order to assess the amount of direct and diffuse light coming to each plot during the leaf-on months (May-September). Finally, during October of 2005 two leaf-off hemispherical photos were taken at each plot in order to assess the amount of direct and diffuse light during the leaf-off moths (October-April).

6.3. Linking changes in the soil microbial community with changes in soil C chemistry following timber harvesting in the boreal mixedwood forests of northwestern Alberta.

Kirsten Hannam[1] (PhD Candidate).

Supervisors: Dr. Sylvie Quideau[1] and Dr. Barbara Kishchuk[2]
[1]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1
[2]Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.

I spent most of the summer working on data entry and analysis for upcoming chapters of my thesis. However, I attended a course on Disturbance Dynamics in the Boreal

Forest, put on by Hugo Asselin and Bernhard Deneller from the University of Quebec at Abitibi-Temiscamingue, from June 5th - 11th. The course was sponsored by the SFMN. I ran an experiment in the lab comparing two methods for assessing the functional diversity of soil microbes, with Lucero Mariani, in July. I presented an oral paper at the Ecological Society of America meeting in Montreal (August 6th-12th) entitled 'The influence of above- and below-ground inputs on forest soil characteristics: a reciprocal transfer study'. I also worked on the revisions of the paper that just got published in CJFR. I guess that's about it! In case you want to include it, I recently returned from the 2nd international conference on 'Mechanisms of organic matter stabilization and destabilization in soils' (Oct 9-13), where I presented a poster 'Organic matter and microbial community composition of boreal forest floors as influenced by clearcutting'. I'm hoping to defend by mid-April.

6.4. Nitrogen transformations in boreal mixedwoods.

Lucie Jerabkova[1] (PhD Candidate).

Supervisors: Dr. Cindy Prescott[1] and Dr. Barbara Kishchuk[2]
[1]Department of Forest Sciences, University of British Columbia, Vancouver, BC
[2]Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.

I finalized data analysis, summarized the results and prepared four manuscripts; three as regular papers and one as a short communication. The PhD thesis which these are part of will be finished by the end of the year.

The first manuscript "Jerabkova, L., Prescott, C.E. and Kishchuk, B.E. Nitrogen availability in soil and forest floors of contrasting types of boreal mixedwood forests" - has been accepted for publication in CJFR, others are in review.

6.5. Dynamics of a Lepidoptera (moth) community in managed boreal forests of North Western Alberta, Canada.

Esther Kamunya[1] (PhD Student).

Supervisors: John Spence[1] and Jan Volney[2].
[1]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1
2Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre.

My project seeks to evaluate and investigate the impact of forest harvesting methods on boreal lepidopteran community assemblages. In this study I seek to examine, analyze and interpret patterns of species abundance, diversity and community assemblages of moths in response to post harvest forest regeneration over a period of 3 years. Pre-harvest and 2 year post-harvest sampling of moths was done and documented by Morneau (2002) while I did a 5 year post harvest sampling in 2005 (unpublished data). The study's specific objectives include:

1. To determine post treatment moth assemblages at the EMEND research site (described below) and to evaluate treatment effects on relative abundance (number of individuals), species richness (number of species), evenness (species distribution within sample: rareness and commonness), diversity (Shannon Weiner and Simpson Yule diversity indices), community assemblages (composition), as well as indicator species
2. To determine post treatment defoliator assemblages (Caterpillars) associated with understory vegetation at EMEND and to evaluate treatment effect on richness, species diversity, functional diversity and species composition
3. To determine the parasitoid complex of selected understory larval species at EMEND and evaluate treatment effect on these complexes.
4. To investigate the effect of post treatment vegetation regeneration on trophic interactions of selected species in the study (host plants, caterpillars and parasitoids)

From the larger EMEND experiment two cover types partitioned based on canopy composition of stands before harvest into confer dominated (>70%) and deciduous dominated (>70%) and two harvesting regimes of 8-10 ha compartments each harvested leaving one of the following proportions of residual stand (green tree retention): 20% and 50% were selected for sampling. Treatment effects (harvesting) will be interpreted in relation to the control of unharvested stands of the two cover types (with 100% residual). Adult moths were sampled by light trapping with one trap per compartment in the summer (June-August) of 2006. Trap catches were transferred into paper bags and frozen for processing. Laboratory work is going on where moths are being sorted and identified to species to allow data analysis and comparisons. Understory larval communities were also searched for Caterpillars from 25m radius area around each light trap tripod. Caterpillars were reared in the lab and fed with host plant material until pupation. Moths that emerged were frozen for identification and further analysis. No parasitoids emerged from 2005 reared samples.

6.6. Avian Diversity Study

Fiona Schmiegelow[1].

[1]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1

The fifth-year post-harvest avian diversity study was complete this past summer. Three point-counts were conducted throughout the summer in all control and harvest treatments. Burn and slash-burn treatments were not surveyed.

6.7. White Spruce Regeneration Study.

Jim Stewart[1].

[1]Forest Ecology and Silviculture Research Group, Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada.

Spring of 2005 marked the end of a 6-year program of studies on white spruce regeneration at the EMEND site. In the spring, we did our final seed trap counts and removed the traps from the field. We also decommissioned the common garden from our snow-seedling study. Some of the seedlings have been left for planting around the new camp. We intend to continue annual cone crop counts, and did carry this out in September.

7. Prescribed Fires.

ASRD personnel successfully completed the remaining three slash burn treatments in May. Compartment 942 was burned on 12 May and compartments 858, and 856 were burned on 13 May. Edwards, Hahn, and Hiebert observed the burns to collect data on rates of spread and flame heights and to photograph the fires. Peter Bothwell, CFS, is currently analyzing the burn data.

An attempt to burn standing timber compartment 857 was made on 14 May. However, conditions were not favourable and very low rates of spread and burn coverage were noted. Edwards called the burn off after 20 minutes. Only the first 5 meters of the east and north compartment perimeters were burnt.

Burn conditions at the EMEND site were monitored continuously by CFS and ASRD personnel throughout the 2005 summer. No favourable burn conditions occurred in 2005 other than the few days in May when the slash burns were conducted. EMEND and ASRD will continue with efforts to burn standing timber stands in 2006.

8. Administrative and Organizational Items.

8.1. Annual EMEND Workshop.

The annual EMEND Workshop was held on 2-3 May 2005 at the Northern Forestry Centre, Edmonton, Alberta. This workshop brings together all the researchers, graduate students, and industry personnel involved in the EMEND project to discuss important matters regarding the EMEND project. The workshop focused on aligning EMEND research with the proposed Alberta Government forest planning standards as well as updating industry and government partners with EMEND research findings to date. A copy of the workshop program is included in Appendix 3.

8.2. Technology Transfer Activities.

i) EMEND Tours

Only one tour was conducted at EMEND this summer. DMI Woodlands staff from Peace River were shown around the EMEND research site on 8 July.

—add Canfor public Advisory Tour April 1st.

ii) *EMEND Web Site*.

The EMEND website is operated and maintained by EMEND Field Coordinator, Jason Edwards. Updates and new features are being added to the website on a continual basis. The website continues to be one the project's prominent methods of information distribution. The EMEND website address is as follows: http://www.biology.ualberta.ca/emend/index.htm.

8.3. EMEND Database Progress.

Brad Tomm continues to compile EMEND data into a comprehensive database. It should be noted that Tomm is a Canadian Forestry Service employee and his time is provided to EMEND through CFS funds. The primary focus of the EMEND Database is to archive research data collected at the EMEND study area that is easily accessible for analysis and to provide a platform where data summaries, with the permission of the researcher responsible for the data, may be shared amongst fellow researchers.

The EMEND Database currently consists of sixteen datasets being contributed by eight researchers. The 'Main Support Information', 'Ecosite Classification', 'Permanent Tree Plot', 'Permanent Shrub Plot', 'Understory Vegetation', 'Coarse Woody Debris', 'Snag Plot', and the 'Nearest Neighbor Snags' datasets have been established and continue to have subsequent survey data added. Metadata for these datasets has been drafted and will be finalized in the winter of 2005. These datasets have compartmental level summaries available to other EMEND researchers. The 'Tree Productivity', 'Shrub Productivity', 'Soil Chemistry', 'Foliage Chemistry', 'Growth and Yield Plots', 'Compartment Tree Age', 'Weather', and 'Hydrology' datasets are currently restricted to the researchers responsible for the data or are still being developed and will be available at a later date. The metadata for these datasets will be written as the datasets are incorporated into the EMEND Database.

External requests for data from the EMEND Database by other EMEND researchers continues to increase as more datasets become available and post-harvest surveys are being completed. There have been 28 formal requests, from 14 different EMEND researchers, for data summaries since the development of the database in 2002. These data summaries have provided valuable up to date information, in a timely manner, to assist fellow researchers with their individual research projects.

Hahn and Edwards will continue to encourage researchers to submit their data to the database. Formal "contracts" requiring researchers to submit their data at the completion of their project are currently under development and will be available to new EMEND researchers starting in 2006.

8.4. Publications and Theses.

Cartar, R.V. 2005. Short-term effects of experimental boreal forest logging disturbance on bumble bees, bumble bee-pollinated flowers and the bee-flower match. Biodiversity and Conservation 14: 1895-1907.

Hannam, K.D., S.A. Quideau, B.E. Kishchuk, S.-W. Oh, R.E. Wasylishen. 2005. Forest-floor chemical properties are altered by clear-cutting in boreal mixedwood forest stands dominated by trembling aspen and white spruce. Canadian Journal of Forest Research 35: 2457-2468.

Harrison, R.B., F.K.A. Schmiegelow, R. Naidoo. 2005. Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types. Canadian Journal of Forest Research 35: 1553-1567.

Jerabkova, L., C.E. Prescott, B.E. Kishchuk. 2005. Nitrogen availability in soil and forest floors of contrasting types of boreal mixedwood forests. Canadian Journal of Forest Research (accepted).

Kishchuk, B.E. 2004. *Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta.* Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Information Report Nor-X-397.

Lazaruk, L.W., G. Kernaghan, S.E. Macdonald, D. Khasa. 2005. Effects of partial cutting on the ectomycorrhizae of *Picea glauca* forests in northwestern Alberta. Canadian Journal of Forest Research 35: 1442-1454.

Phillips, E. 2004. *Harvesting to emulate natural disturbance: EMEND harvesting costs and productivity.* FERIC Advantage. Vol. 5 No. 26, September 2004. 22pp.

8.5. Talks of Interest and Poster Presentations.

Bergeron C., J.R. Spence, W.J.A. Volney. Do humans and beetles see the same forest? Western Forest Insect Work Conference, Victoria, British Columbia, March 28-31, 2005 (Oral Presentation).

Bergeron, C., J.R. Spence, W.J.A. Volney. Linking natural disturbances, forest composition and structure and insect biodiversity: an example from the boreal mixedwood forest. North American Forest Ecology Workshop, Aylmer, Quebec, June 12-16, 2005. (Oral Presentation).

Bergeron C., J.R. Spence, W.J.A. Volney. Ground-dwelling beetles and forest mosaic. Entomological Society of Canada / Entomological Society of Alberta Joint Annual Meeting, Canmore, Alberta, November 2-5, 2005. (Oral Presentation).

Bergeron, C., J.R. Spence. Pitfall trap depth in 3 forest habitats. Entomological Society of Canada / Entomological Society of Alberta Joint Annual Meeting, Canmore, Alberta, November 2-5, 2005. (Poster Presentation).

Edwards, J.E., J.R. Spence, W.J.A. Volney, T.T. Work, D. Shorthouse. Arthropod diversity of the Ecosystem Management Emulating Natural Disturbance (EMEND) Project. Western Forest Insect Work Conference, Victoria, British Columbia, March 28-31, 2005. (Poster Presentation).

Edwards, J.E., J.R. Spence, W.J.A. Volney. An overview of the Ecosystem Management Emulating Natural Disturbance (EMEND) project. . North American

Forest Ecology Workshop, Aylmer, Quebec, June 12-16, 2005. (Poster Presentation).

Hannam, K., S.A. Quideau, B.E. Kishchuk. The influence of above- and below-ground Inputs on forest soil characteristics: a reciprocal transfer study. Ecological Society of America annual meeting, Montreal, QC, August 6-12, 2005. (Oral Presentation).

Hannam, K., S.A. Quideau, B.E. Kishchuk. Organic matter and microbial community composition of boreal forest floors as influenced by clearcutting. 2nd international conference on 'Mechanisms of organic matter stabilization and destabilization in soils, October 9-13, 2005. (Poster Presentation).

Jacobs, J.M., D.W. Langor, J. Hammond, J.R. Spence. Maintaining saproxylic beetles in the western Canadian mixedwood: priorities and surprises. North American Forest Ecology Workshop, Aylmer, Quebec, June 12-16, 2005. (Oral Presentation).

Jacobs, J.M., J.R. Spence, D.W. Langor. Breaking down the break-down: The rise and fall of beetle empires. Entomological Society of Canada / Entomological Society of Alberta Joint Annual Meeting, Canmore, Alberta, November 2-5, 2005. (Oral Presentation).

Jacobs, J.M.. Habitat utilization of the pyrophilous beetle *Sericoda quadipunctata* (Carabidae) in burned white spruce stands. Entomological Society of Canada / Entomological Society of Alberta Joint Annual Meeting, Canmore, Alberta, November 2-5, 2005. (Poster Presentation).

Jerabkova, L. and Prescott, C.E. Is soil nitrogen availability in boreal mixedwoods related to proportion of broadleaves? CONFOR, Montmorency, Quebec, February 2005. (Oral Presentation).

Jerabkova, L. and Prescott, C.E. Effect of variable retention harvesting on nitrogen availability in forest floor and mineral soil of three types of boreal mixedwood forests. CSSS Annual Meeting, Halifax, N.S., May 2005. (Oral Presentation).

Jerabkova, L. and Prescott, C.E. Nitrate in boreal mixedwoods. Ecological Society of America annual meeting, Montreal, QC, August 6-12, 2005. (Poster Presentation).

Jerabkova, L. and Prescott, C.E. Post-harvest nitrate dynamics in aspen and spruce boreal mixedwood forests. Forest Biology Symposium, University of Victoria, Victoria, BC, November 9, 2005. (Poster Presentation).

Kamunya, Esther, J.R. Spence, W.J.A. Volney. Dynamics of a Lepidopteran (moth) community in managed boreal forests of northwestern Alberta, Canada. Entomological Society of Canada / Entomological Society of Alberta Joint Annual Meeting, Canmore, Alberta, November 2-5, 2005. (Poster Presentation).

Spence, J.R., W.A.J. Volney, S.E. Macdonald. Development, structure and early results of the EMEND experiment. North American Forest Ecology Workshop, Aylmer, Quebec, June 12-16, 2005. (Oral Presentation).

Work, T.T., C.M. Buddle, S. Brais, J.R. Spence, WJA Volney. Effectiveness of variable retention harvesting for the maintenance of arthropod biodiversity in boreal mixedwood forests across Canada. North American Forest Ecology Workshop, Aylmer, Quebec, June 12-16, 2005. (Oral Presentation).

9. Literature Cited.

Kishchuk, B.E. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-397.

Appendix 1: Tables.

Table 1. Summary of EMEND core crew work completed for core (Category 1) research from May 6 – August 31, 2005.

Project	Work Description	Total Number of Person Days of Core Crew Activity	% of Total Category 1 Person Days	% of Total Person Days
Forest Productivity Estimates (Jan Volney/John Spence)	- Shrub biomass data collection in all compartments	228.25	39.7	38.2
Snags Dynamics (Dave Langor/Daryl Williams)	- Standing snag assessment in all compartments	122.75	21.4	20.6
Training, Orientation and Infrastructure Activities	- Bear awareness course - Quad safety course - Emergency response training and mock drill - Orientations - Quad maintenance, vehicle maintenance, equipment purchases/maintenance, camp set-up/take-down - Inspections and set up for new camp - Tours of EMEND	92.50	16.1	15.5
Soils and Nutrient Cycling (Barbara Kishchuk)	- Soil sample collections for bulk density and chemistry in all deciduous- and coniferous-dominated (Ddom and Cdom) compartments	59.75	10.4	10.0
Moth Diversity (John Spence/Esther Kamunya)	- Light trap collections	36.75	6.4	6.2
Office Work	- Data validation and management - Camp organization	29.75	5.2	5.0
Tree Plot and Compartment Maintenance	- Mapping standing timber burn plots	5.0	0.9	0.8
	Total:	**574.75**	**100.0**	**96.3**

Table 2. Summary of EMEND core crew assistance provided for non-core (Category 2) research from May 6 – August 31, 2005.

Project	Work Description	Total Number of Person Days of Core Crew Activity	% of Total Category 2 Person Days	% of Total Person Days
Fire Ecology (Peter Bothwell)	- Observation and documentation of burning in deciduous-dominated (Ddom) slash-burn compartments - Fuel line and depth-of-burn measurements in Ddom slash-burn compartments	15.75	70.8	2.6
Arthropods (Colin Bergeron/Matti Koivula)	- Pitfall trap collections - Enclosures set up	5.0	22.5	0.8
Silviculture (Jim Stewart)	- Removal of seed traps	1.5	6.7	0.3
	Total :	**22.25**	**100.0**	**3.7**

Table 3. Number of person-days EMEND camp was used by individuals involved in core (Category 1) research from May 6 - August 31, 2005.

				Number of Days at EMEND Camp				
Project	**Camp User**	**Affiliation**	**Title**	**May**	**Jun**	**Jul**	**Aug**	**Total**
Core Crew	Edwards, Jason	Field Coordinator	Field Coordinator	21	14	20	23	78
	Hahn, Charlene	U of A	Data Manager	18	23	23	24	88
	Hiebert, Christine	U of A	Core Crew	21	23	20	23	87
	Hofman, Rachel	U of A	Core Crew	18	23	23	24	88
	Jensen, Dan	U of A	Core Crew	18	23	23	22	86
	Jollymore, Ashlee	U of A	Core Crew	21	22	17	15	75
	Morrison, Stuart	U of A	Core Crew	7	23	27	17	74
	Perez-Parada, Dominique	CFS (volunteer)	Core Crew	0	0	5	10	15
	Rave, Savanna	U of A	Core Crew	0	22	19	20	61
	Roy, Lisa	U of A	Core Crew (high school)	0	0	18	3	21
	Stilwell, Nathan	U of A	Core Crew (high school)	0	0	18	5	23
							Subtotal:	**696**
Soils and Nutrient Cycling	Blank, Martin	CFS	Technician	0	0	0	3	3
	Kishchuk, Barbara	CFS	Researcher	0	0	0	3	3
							Subtotal:	**6**
Category 1 Research Projects - Monthly Totals:				**124**	**173**	**213**	**192**	**702**

Table 4. Number of person-days EMEND camp was used by individuals involved in non-core (category 2) research from May 6 - August 31, 2005.

				Number of Days at EMEND Camp				
Project	**Camp User**	**Affiliation**	**Title**	**May**	**Jun**	**Jul**	**Aug**	**Total**
Vegetation Structure	Bodeux, Brett	U of A	Research Assistant	0	21	18	23	**62**
	Caners, Richard	U of A	Ph. D. Candidate	0	21	18	23	**62**
	Chavez, Virginia	U of A	Ph. D. Candidate	0	9	23	4	**36**
	Mathew, Nicole	U of A	Research Assistant	0	9	23	4	**36**
	Present, Peter	U of A	Technician	4	0	0	0	**4**
							Subtotal:	**200**
Fire	ASRD Fire Crew	ASRD		89	0	0	0	**89**
	Bothwell, Pete	CFS	Technician	2	0	0	0	**2**
							Subtotal	**91**
Arthropods	Bergeron, Colin	U of A	Ph. D. Candidate	8	5	2	6	**21**
	Brown, Anna	U of A	Research Assistant	0	2	2	0	**4**
	Deshene, Andrea	U of A	Research Assistant	3	0	0	0	**3**
	Esch, Evan	U of A	Research Assistant	0	0	2	3	**5**
	Jacobs, Josh	U of A	Technician	3	2	0	3	**8**
	Kamunya, Esther	U of A	Ph. D. Student	8	12	7	7	**34**
	Koivula, Matti	U of A	Researcher	3	2	2	0	**7**
	Pawluk, Kylee	U of A	Research Assistant	3	0	0	0	**3**
							Subtotal	**85**
Avian Diversity	Slater, Simon	U of A	Technician	6	6	0	0	**12**
	St. Laurent, Kathy	U of A	Technician	6	6	0	0	**12**
	Young, Lasha	U of A	Technician	6	6	0	0	**12**
							Subtotal	**36**

Table 4. Continued

				Number of Days at EMEND Camp				
Project	**Camp User**	**Affiliation**	**Title**	**May**	**Jun**	**Jul**	**Aug**	**Total**
Soils and Nutrient Cycling	Mackenzie, Derek	U of A	Post Doctoral Fellow	0	0	0	5	**5**
	Swallow, Matthew	U of A	MSc. Student	0	0	0	5	**5**
							Subtotal	**10**
Silviculture	Jones, Travis	CFS	Technician	2	0	0	0	**2**
	Stewart, Jim	CFS	Researcher	2	0	0	0	**2**
							Subtotal	**4**
			Category 2 Research Projects - Monthly Totals:	**145**	**101**	**97**	**83**	**426**

Table 5. Number of nights EMEND Research Facility was used from September 14 – October 31, 2005.

Project	**Camp User**	**Affiliation**	**Title**	**Number of Nights**
Core Crew	Edwards. Jason	U of A	Field Coordinator	14
	Hahn, Charlene	U of A	Data Manager	14
Hydrology	Newman, Sharon	ARC	Technician	2
	Twitchell, Colin	ARC	Technician	2
Silviculture	Jones, Travis	CFS	Technician	3
	Noble, Richard	CFS	Technician	3
	Stewart, Jim	CFS	Researcher	3
Vegetation Structure	Chavez, Virginia	UofA	Ph. D. Candidate	10
	Present, Peter	UofA	Technician	10
			Total:	61

Table 6. EMEND Core vehicle mileage and camp fuel usage from May 6 – August 31, 2005.

Vehicle	Total Kilometers	Total Fuel Used (L)
Trucks		
U of A #298 (Suburban)	5,058	70.0
U of A #290 (Yukon)	11,692	+
Budget Van	5,346	+
Quads		
Canfor Green 400	577	96.0
Canfor Red 400	244	38.5
DMI Red 350 (Lic.# PJ764)	471	50.5
DMI Red 450 (Lic.# PJ766)	1,454	130.0
DMI Yellow 350 (Lic.# PJ769)	924	74.3
U of A Red 250 (Lic.# SL474)	800*	61.0
U of A Red 250 (Lic.# SL475)	950*	73.0
U of A Yellow 500 (Lic # US952)	756	70.5
U of A Yellow 500 (Lic # US953)	620	55.5
U of A Yellow 500 (Lic # US954)	1,083	91.7
U of A Yellow 500 (Lic # US955)	858	57.3

+ No camp fuel used in these vehicles; *These U of A quads do not have odometers; mileage has been estimated based on fuel consumption.

Table 7. EMEND camp fuel use by work group.

Work Group	Fuel Used (L)	% Total Fuel Use
EMEND Core	868.3	66.3
Vegetation Structure (MacDonald)	225.2	17.2
Arthropods (Spence)	96.5	7.4
Avian Diversity (Schmiegelow)	79.0	6.0
Silviculture (Stewart)	21.0	1.6
Fire (Bothwell)	20.0	1.5
Total	**1310.0**	**100.0**

Table 8. EMEND master student project status.

Student	Affiliation	Project Title	Project Status
Berger (nee Becker), Carrie	University of Minnesota	Modeling early regeneration processes in mixed-species forests of Alberta.	Defended Spring 2002
Cuthbertson, Lisa	University of Alberta	Spatial patterns of *Armillaria*.	Defended 25 September, 2001
Wesley (nee Dunlop), Julia	University of Alberta	Effects of forest harvesting on spruce beetle parasitoids.	Defended 19 September, 2002
Fenniak, Treena	University of Alberta	Understory vascular plant regeneration following disturbance.	Defended August 2001
Frey, Brent	University of Alberta	Effects of forest floor disturbance and canopy removal on soil nutrient dynamics and response of *Calamagrostis canadensis*, *Epilobium angustifolium*, and *Picea glauca* seedlings.	Defended September 2001
Harrison, Bruce	University of Alberta	Response of boreal forest birds to experimental harvest and burning.	Defended 31 October, 2001
Jacobs, Josh	University of Alberta	Saproxylic beetles and coarse woody debris.	Defended 29 September, 2004
Kembel, Steven	University of Alberta	Spatial patterns of boreal canopies, understory communities, and tree regeneration.	Defended September 2001
Lazaruk, Lance	University of Alberta	The impact of silvicultural practices on the abundance and biodiversity of ectomycorrhizae in a boreal forest ecosystem.	Defended February 2002
Lindo, Zoë	University of Calgary	Harvesting effects on soil mesofauna and decomposition /nutrient cycling processes in aspen and spruce stands of the boreal mixed-wood forest.	Defended 2003

Table 8. Continued

Student	Affiliation	Project Title	Progress
Martin, René	University of British Columbia	Reproductive responses of bunchberry (*Cornus Canadensis)* to disturbance in a managed forest.	Defended 2000
Mills, Suzanne	University of Alberta	Distribution of bryophyte species diversity in relation to microsite and moisture availability at 2 scales within conifer dominated boreal forests.	Defended August 2001
Morneau, Louis	University of Alberta	Lepidoptera diversity following fire and harvesting.	Defended January 2002
Park, Jane	University of Calgary	Movement and settlement of bark beetles in a heterogeneous landscape.	Defended Summer 2002
Patriquin, Krista	University of Calgary	Impacts of fire and harvesting on the foraging ecology of forest dwelling bats.	Defended June 2001
Swallow, Mathew	University of Alberta	Title Unknown	Data Collection

Table 9. EMEND doctoral student project status.

Student	Affiliation	Project Title	Progress
Bergeron, Colin	University of Alberta	Effect of fire behavior on dynamic associations of insects and plants at the landscape level.	Data collection
Caners, Richard	University of Alberta	Patterns of bryophyte diversity in response to partial harvesting in northern mixedwood boreal forests.	Data collection
Chavez, Virginia	University of Alberta	Patterns and causes of variation in understory plant diversity and composition in the mixed-wood boreal forest of Alberta.	Data Collection
Hannam, Kirsten	University of Alberta	Linking changes in the soil microbial community with changes in soil C chemistry following timber harvesting in the boreal mixedwood forests of northwestern Alberta.	Writing Thesis
Jerabkova, Lucie	University of British Columbia	Nitrogen transformations in boreal mixedwoods.	Writing Thesis
Kamunya, Esther	University of Alberta	Dynamics of a Lepidoptera (moth) community in managed boreal forests of North Western Alberta, Canada.	Data collection
Shorthouse, David	University of Alberta	Boreal spiders as bioindicators of forest disturbance and management.	Writing Thesis

Appendix 2: EMEND Core Study Methods

EMEND Permanent Shrub Plot Survey Methods

Revised: March 4, 2004

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EMEND (Ecosystem Management Emulating Natural Disturbances) Database
Permanent Shrub Plot Data Set
Date Issued:

Introduction:

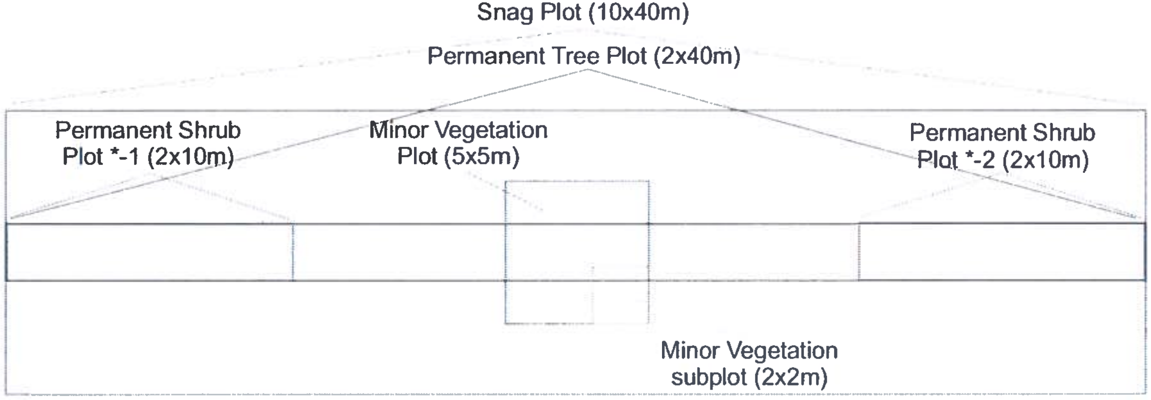
The goal of the research is to monitor the structure and the rate of change of biomass in the shrub component of a forest stand when subjected to various harvesting treatments so as to determine which treatment best emulates a natural fire disturbance. A survey to identify the species, height and diameter at 0.3 m above the point of germination for shrubs was conducted at EMEND in each compartment.

Plot Location and Size:

A permanent shrub plot (measuring 2x10 m) was located and overlaid at the start and end of each permanent tree plot in a compartment, therefore, twelve permanent shrub plots were established in each compartment for a total of 1200 plots in the EMEND project. With one measuring tape run the mid-line (as accurately as possible) from the start to the end of the 2 x 40 m permanent tree plot. Extra care needs to be exercised to get as close as possible to the mid-line. Create the 2 x 10 m plot box using the second measuring tape with one metre of the plot box on each side of permanent tree plot mid-line (figure 1). Put a pigtail marked with blue flagging tape at the end of each shrub sub-plot. All permanent shrub plots located at the start of the permanent tree plot were numbered with the 'permanent tree plot number'-1 (eg. 1-1 is the permanent shrub plot located at the start of the permanent tree plot). Permanent shrub plots located at the end of the permanent tree plot were numbered with the 'permanent tree plot number'-2 (eg. 1-2 is the permanent shrub plot located at the end of the permanent tree plot). The mid-line UTM coordinates for the start and end of each plot was determined in SAS using the coordinates provided for the associated permanent tree plot. After the treatments were conducted in the winter of 1998 some plots were destroyed beyond the limits of the prescribed treatment and were therefore replaced. In 1999, new shrub plots were established where required to replace those that were destroyed in order to maintain the twelve plots per compartment design.

Each plot was assessed for the percentage falling in a machine corridor, vegetation strip, or clear-cut in 2001/2002.

Figure 1.



The difficulty in conducting the prescribed "burn" treatments has resulted in 14 compartments having their prescribed treatment revised. Each of the designated compartments was split in half, thereby creating two new compartments. From the original compartment, one half was treated with a 10% Residual Slash Harvest and the other half was treated with a 10% Residual Slash/Burn Harvest. Six permanent shrub plots were retained or re-established in each of these new compartments.

Shrub Data Collection:

The permanent shrub plot was used to assess the species, height, diameter at 0.3 m, and status of each individual shrub within the plot. For a shrub stem to be considered "on-plot" it must be rooted inside the permanent shrub plot. A shrub stem can be rooted inside the plot and be leaning out. All tree and shrub species with a diameter greater that 1.00 cm at a height of 0.3m, but less than 5.0 cm in DBH were assessed regardless if they share the same base. In 2001/2002 shrubs were also assessed for presence browsing, lean, and broken stems.

"Some areas around the EMEND site were observed to be heavily browsed by ungulates (moose and deer). As such, a survey, done in conjunction with the shrub biomass project, was conducted to estimate the amount of ungulate browsing at the EMEND site. Each shrub was measured in the shrub biomass study (shrubs of diameter greater than or equal to 1.00 cm at 30cm above ground) was assessed for any indication of browsing. Browsing was defined as any twig or branch that appeared cleanly snipped off. In addition, a count of all shrubs under 1.00 cm diameter at 30 cm above ground but greater than 30 cm tall was conducted and all counted shrubs were assessed for browsing." (EMEND Interim Report 2001). Defoliated leaves and leaves removed at petiole are not considered evidence of browsing. All shrubs were assessed for browsing and recorded as yes or no. Initial analysis of the 2001 Shrub "Browsing" data of stems <1.00 cm in diameter indicated non-significant results and as such, no 2002 shrub browsing data for stems <1.00 cm in diameter was collected.

In 1998, a survey of shrubs in the permanent shrub plots was conducted in all compartments. In 2001/2002, permanent shrub plots were reassessed for the first time following the experimental treatments. New permanent shrub plots were established in permanent tree plots that were set up to replace those plots that were damaged during the experimental treatment. In 2001, deciduous and coniferous compartments were assessed. In 2002, mixed-wood and deciduous dominant with coniferous under-story compartments were assessed. Permanent shrub plot surveys will continue on a 3-year cycle with the next assessment scheduled for 2004.

Data Quality and Assurance:

In some compartments it was difficult to differentiate between the vegetation (retention) strips and the corridors (eg. in 10% and 20% treatments). VEG TOTAL and COR TOTAL values may thus seem strange for some shrub plots in these compartments. In addition, some plots in higher retentions (eg. 50%, 75% and Burns) had COR TOTAL values that were high (or, in the case of burns, present when they should not have been). Smaller variations in corridor width for plots in 50% and 75% residuals were normally due to minute inconsistencies during harvesting. Larger variations were most often due to factors such as adjacency to compartment boundaries or ellipses.

Some shrubs in the data set seem unusually short when compared with their corresponding diameters. These shrubs were most likely broken, but the absence of being indicated as broken is likely a result of recording error.

No program has been established to cross-check the quality assurance and control of the data being collected in the field for the permanent shrub plots. Field data is subjected to a series of SAS validation programs before being incorporated into the EMEND Database.

Equipment required:

1. 40m tape
2. 30m tape
3. Metric carpenter's tape
4. 6 pigtail pegs
5. Small calipers
6. Marker
7. DBH tape.

Reference:

EMEND Interim Report 1998

EMEND Interim Report 2001

EMEND Interim Report 2002

EMEND Snag Plot Survey Methods

Revised: March 24, 2005

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EMEND (Ecosystem Management Emulating Natural Disturbances)
Database
Snag Plot Data Set
Date Issued:

Introduction:

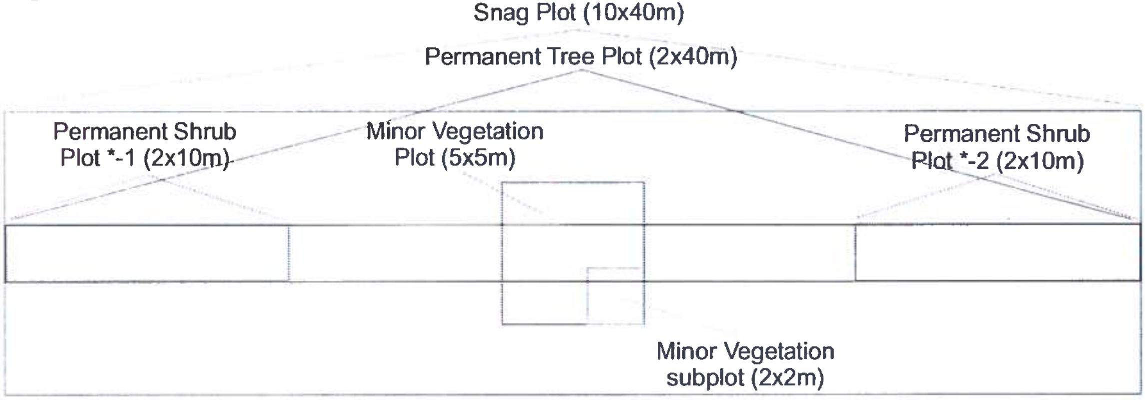
The goal of the research is to monitor the structure and the decay of the standing dead tree (snag) component of a forest stand when subjected to various harvesting treatments so as to determine which treatment best emulates a natural fire disturbance. A survey to identify the species, DBH, height, height class, percent bark retention, and decay class was conducted at EMEND in each compartment.

Plot Establishment:

The snag survey initially utilized the six permanent tree plots (measuring 2x40 m) that were randomly located within each compartment, for a total of 600 plots in the EMEND project. All permanent tree plots were established in an east-west orientation so that the are perpendicular to the north-south orientated machine corridors. A measuring tape was stretch out in a west or east direction from the plot start point for 40 meters to establish the mid-line of the plot. The mid-line UTM coordinates for the start and end of each plot was determined using a GPS unit with differentially corrected data. “A hand-held Geo Explorer II was used to collect the points to give the positions.... The data from the GPS unit was downloaded at DMI and their GPS technician...” corrected the data (EMEND Interim Report 1998). The start and end of the mid-line in each plot was marked with a pig-tail. The plot sides are 1 meter on either side of the plot mid-line for a plot width of 2 meters. “To allow greater visibility of the plot boundaries, wooden stakes painted pink were put in at the start and end of all the plots. Solid aluminum redi-rods with a length of approximately 3 feet were also pounded into the ground. The intent of the metal rods is to make a more permanent marking of the plots so that they ca be re-located in the future" (EMEND Interim Report 1999). In 1998, the plots were number 1 – 6, but after the treatments were conducted in the winter of 1998 some plots were destroyed beyond the limits of the prescribed treatment and were therefore replaced. In 1999, plots numbering 7 – 9 were established where required to replace those that were destroyed in order to maintain the six plots per compartment design. "The first tree plot is usually located from a baseline. Double pink ribbon on a tree on the baseline indicates the start of the trail to the first plot. A trail in pink X's (marked on trees) lead the way between each plot" (EMEND Interim Report 1998).

In 2000, it was decided that the permanent tree plots did not provide a sufficient sample area to survey snags. An expanded snag plot design (10 m x 40 m) was overlaid on the existing permanent tree plot. Figure 1 illustrates the layout of the snag plot in relation to permanent tree, permanent shrub, and minor vegetation plots.

Figure 1.



The difficulty in conducting the prescribed "burn" treatments has resulted in 14 compartments having their prescribed treatment revised in 2002. Each of the designated compartments was split in half, thereby creating two new compartments. From the original compartment, one half was treated with a 10% Residual Slash Harvest and the other half was treated with a 10% Residual Slash/Burn Harvest. Three snag plots were retained or re-established in each side of these new compartments.

Plot Tree Numbering:

All standing dead trees rooted or not rooted (snags) meeting the following criteria of DBH >=7.0cm, height >=1.3m, and lean $<45^{\circ}$ from vertical were assessed. The compartment number, plot number, tree number, and species was recorded. Appendix 1 lists the coding used to identify tree species. Once the experimental treatment was conducted in the compartment a unique metal tree tag was attached to each tree still standing with electrical phone wire at DBH. This metal tree tag number is now used to identify the tree. New snags since the last assessment will be added to the data and tagged with a unique metal tree tag.

Snag Data Collection:

Each snag is assessed for status (dead, fallen, cut), DBH (cm), height (m), height class (appendix 2), percent bark retention (to the nearest 20%), and decay class (appendix 3). In 1998, the height of each snag was measured. Surveys conducted in 2000, and 2001 did not measure the height of each snag, but instead assigned each snag a height class. The full height in meters was assessed again in 2004 for all snags surveyed. The height (m) should be collected for all future snag surveys. The snag plot surveys will continue on a 2-year cycle with the baseline year as 1998 and the next assessments scheduled for 2004.

Data Quality and Assurance:

Starting in 2005, all snag data was collected electronically using Dell Axim Person Data Assistants (PDAs). Electronic data collection provides the ability to bring past assessment data into the field to cross-reference and field check old data with new. Field data is subjected to a series of SAS validation programs before being incorporated into the EMEND Database.

Reference:

EMEND Interim Report 1998
EMEND Interim Report 2000
EMEND Interim Report 2001

Appendix 1. Tree Species Code List

Species	Common Name	Scientific Name	Vegetation Type
.	no trees		T
Abibal	balsam fir	Abies balsamea	T
Alncri	green alder	*Alnus crispa*	S
Alnrug	mountain alder	*Alnus rugosa*	S
Betpap	white birch	*Betula papyrifera var. papyrifera*	T
Conifer	unknown conifer species	*Conifer species*	T
Larlar	tamarack	*Larix laricina*	T
Picgla	white spruce	*Picea glauca*	T
Picmar	black spruce	*Picea mariana*	T
Picspp	spruce species	*Picea species*	T

Species	Common Name	Scientific Name	Vegetation Type
Pinban	jack pine	*Pinus banksiana*	T
Pincon	lodgepole pine	*Pinus contorta var. latifolia*	T
Pinspp	pine species	*Pinus species*	T
Popbal	balsam poplar	*Populus balsmifera*	T
Popspp	poplar species	*Populus species*	T
Poptre	trembling aspen	*Populus tremuloides*	T
Salspp	willow species	*Salix* species	S
Unk	unknown		

Appendix 2. Snag Survey Height Class Coding

Height Class	Height Class Definition
1	1.3 – 5 m
2	5 m – below canopy
3	canopy+

Appendix 3. Snag Survey Decay Class Coding

Decay Class	Decay Class Definition
.	Missing.
1	Recently dead, all twigs present, spruce with fading needles.
2	Partially rotten, major branches left, small branches mostly gone, bark still mostly intact, sound wood.
3	Rotten, missing bark in places (bark loose), no (or few) branches left.

Appendix 3: EMEND Workshop 2005 Program

Ecosystem
Management
Emulating
Natural
Disturbance

EMEND
Workshop 2005

Program and Abstracts

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2 –3 May, 2005

Northern Forestry Centre
Edmonton, Alberta, Canada

Workshop Objectives

- Provide EMEND researchers with an understanding of the Alberta Government's proposed Forest Planning Standards.
- Obtain researcher's initial feedback to these Standards considering their research results at EMEND.
- Provide a forum for current researchers and graduate students to present their research results and for new researchers to propose research ideas.
- Update researchers with current EMEND news and events.
- Showcase the EMEND Database.

Monday, May 2
Pine Room, Northern Forestry Centre
09:00 – 16:30

09:00 – 09:20 Morning coffee.

09:20 – 09:30 Welcome and opening remarks – John Spence

09:30 – 09:50 EMEND Core Work: where we are at and where we are going.
-Jason Edwards, EMEND

09:50 – 10:10 Forest industry perspectives.
-Tim Vinge, Canadian Forest Products

10:10 – 10:40 Alberta forest planning standards and required research.
- John Stadt, Alberta Sustainable Resource Development

10:40 – 11:00 Coffee break

11:00 – 11:20 EMEND coarse woody debris (CWD) dynamics.
-David Langor and Daryl Williams, Canadian Forest Service

11:20 – 11:40 White spruce regeneration in boreal mixedwood forests.
- Jim Stewart, Travis Jones, Rick Hurdle and Derek Sidders, Canadian Forest Service

11:40 – 12:00 Rare beetle species of EMEND; EMEND and SAFE Project connections.
- Tim Work, Université du Québec à Montréal

12:00 – 12:10 EMEND Database, what it is and how it's used?
- Brad Tomm, Canadian Forest Service

12:10 – 13:00 Lunch Break (Lunch provide by EMEND).

13:00 – 13:20 Are we changing soil nitrogen dynamics by harvesting in boreal mixedwoods?
- Lucie Jerabkova and Cindy E. Prescott, University of British Columbia

13:20 – 13:40 Bryophyte diversity in response to partial harvesting of northern mixedwood boreal forests.
- Richard Caners, Ellen Macdonald and René Belland, University of Alberta

13:40 – 14:00 The importance of coarse woody debris in forested landscapes.
- Josh Jacobs, University of Alberta

14:00 – 14:20 Landscape dynamics of boreal ground-dwelling beetles.
- Colin Bergeron, University of Alberta

14:20 – 14:40 Coffee break.

14:40 – 15:00 Response of bark beetles to fire in harvested forest stands.
- Dan Jensen, University of Alberta

15:00 – 15:20 Dynamics of a Lepidoptera (moth) community in managed boreal forests of Northwestern Alberta, Canada.
- Esther Kamunya, University of Alberta

15:20 – 16:30 Discussion Session
- Advancing Alberta's forest management policies and initiatives. How does EMEND fit in?

Tuesday, May 3
Pine Room, Northern Forestry Centre
09:00 – 12:00

9:00 – 12:00 EMEND workgroup sessions.
- Workgroup sessions will develop and initiate a number of objectives for the next phase of EMEND research. Session topics will include:

1) Identifying EMEND research topic gaps.
2) Constructing the EMEND Matrix.
3) Major EMEND initiatives for 2006.

Bryophyte diversity in response to partial harvesting of northern mixedwood boreal forests.

Richard Caners, Ellen Macdonald, and René Belland
Department of Renewable Resources, University of Alberta, T6G 2H1

Bryophytes (mosses, liverworts, and hornworts) constitute an important yet often overlooked component of understory plant diversity in mixedwood boreal forests, and are key to a wide variety of ecosystem functions. In these forests, diversity is largely controlled by the number, types, and properties of substrates available for colonization on the forest floor. Industrial harvesting of Alberta's northern mixedwood forests has the potential to extirpate bryophyte species from large areas through direct and indirect modifications to microclimate and available substrates. This study is examining how changes in the amount and quality of residual forest structure after harvest affects the diversity and spatial pattern of bryophytes across mixedwood stands with different canopy composition. A first field season of data collection was conducted at EMEND in 2004. Bryophyte diversity and habitat quality were enumerated in 50m^2 circular plots randomly established in mixed-coniferous (MIX) forest compartments harvested in 1998 at 100 (control), 75, 50, and 10 percent canopy retention. Six plots were enumerated in each of three compartments for each harvesting treatment, for a total of 72 plots. Within each plot, the density, cover-abundance, and basal area of canopy and subcanopy trees were enumerated, and woody debris was assessed using line transects and counts. Vascular and non-vascular species richness and abundance, substrate properties, and measures of evaporation and PAR were measured in 1x1m subplots to relate fine-scale habitat characteristics to species associations and niche breadths. The role of the mineral soil diaspore bank as a repository of bryophyte diversity is presently being examined through an analysis of its species composition. Soil samples obtained from each subplot were placed in growth cabinets in October, 2004, under two light regimes, high (300µmolm^{-2}s^{-1}) and low (30µmolm^{-2}s^{-1}) intensity. Samples will remain in the cabinets until June, 2005, or until germinated bryophytes can be identified to species. Extant bryophyte flora, stand characteristics, and the physical and chemical properties of the mineral soil and organic matter will be used to describe the diversity of germinated species. Subsequent field seasons will focus on the effects of partial harvesting in conifer-dominated (CDOM) compartments (2005), and examine the effectiveness of residual islands of habitat on the maintenance of bryophyte diversity across forest types and harvest intensities (2006). This study aims to outline the mechanisms driving the response and reassembly of bryophytes after forest harvest, providing specific guidelines to help industry set harvesting parameters that preserve critical levels of structure on the landscape.

Response of bark beetles to fire in harvested forest stands.

D.E. Jensen[1], J.R. Spence[2] and B.A. Keddie[1]
[1] *Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9*
[2]*Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E9*

Post-harvest fire has been used by forestry companies for many years to prepare stands for regeneration. Despite this, the true value of this procedure is not completely known in terms of its effect on forest biota. The diversity of bark beetles, as well as their interaction with dead wood, makes them a good indicator group to determine the effects of this practice on insect biodiversity. During the summer of 2004, I sampled bark beetle communities in six forest stands (3 conifer dominated and 3 deciduous dominated) at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site. Each 10 hectare stand was subjected to slash harvesting and subsequently half of each compartment was burned post-harvest. The effect on conifer dominated stands is apparent as the assemblages appear more similar to deciduous assemblages than unburned conifer stand assemblages. It also appears that post-harvest burning has very little effect on bark beetles assemblages in aspen dominated stands. These effects are driven by 3 major species specific responses: high catch rates in burned conifer stands, high catch rates in unburned conifer stands and even distribution among treatments.

Are we changing soil nitrogen dynamics by harvesting in boreal mixedwoods?

Lucie Jerabkova and Cindy E. Prescott
Department of Forest Sciences, Faculty of Forestry, UBC, Vancouver

Clear-cutting has repeatedly resulted in increased levels of nitrate and/or available N. Soil nitrate concentrations are of particular concern because of nitrate's high mobility and associated potential for ground and surface water contamination. It has also been suggested that the higher nitrate levels in soil may hinder conifer regeneration on harvested sites. Variable-retention (VR) harvesting might eliminate some of the adverse environmental effects of clear-cutting, but its effects on nutrient cycling still need to be evaluated. In this study we compared the effects of clearcut and VR harvesting of deciduous, mixed and coniferous stands of boreal mixedwood forests on N dynamics. Our particular objectives were to assess whether clear-cut harvesting increases levels of soil nitrate and available N in boreal mixedwoods, assess whether VR harvesting has a less pronounced effect, and assess whether the response to harvesting differs among forest types. Nitrate levels were very low, without any significant differences among harvesting intensities. Harvesting also had no apparent effect on the concentrations of ammonium or soluble inorganic N (SIN). The ratio of SON/SIN and microbial C/N ratio declined in the clearcuts. Changes in both of these indices could be associated with higher N availability, but this was not reflected in the pools or net turnover rates as no differences in N mineralization and nitrification were detected among harvesting treatments. There was little evidence that clearcut harvesting of boreal mixedwoods results in significant losses of N from the system (as soil nitrate levels did not increase substantially) and thus VR harvesting is not necessary based on nutritional concerns. Attention should however be paid to the changes in tree species composition as a result of harvesting, as the three forest types showed differences in N dynamics.

Dynamics of a Lepidoptera (moth) community in managed boreal forests of Northwestern Alberta, Canada.

Esther Kamunya
Department of Renewable Resources, University of Alberta, T6G 2H1

In this study I propose to evaluate the response of Lepidoptera (moths) to forest harvesting in the mixed wood boreal of North Western Alberta. This study is part of a larger Ecosystem Management Emulating Natural Disturbance (EMEND) project initiated in 1997. Moth diversity and species assemblages will be evaluated with respect to three cover types (deciduous dominated, mixed coniferous and deciduous, and coniferous dominated stands) and three harvesting strategies (percentage green tree retention of 20%, 50% and 100% which is the control). In the summer of 2005, adult moths will be light trapped for a single night every 7-10 days and understory vegetation searched for caterpillars. Vegetation data from the EMEND data base will be used to describe habitat from which caterpillars are collected. The adults will be identified to species and the caterpillars reared. Emerging adults or parasitoids will also be identified to species. Data on adult moths, larvae and vegetation will then be summarized using different diversity measures. To test for treatment effect, pretreatment data (from EMEND data base) will be used as a co-variable. Light trap catches will be correlated with larval samples to test if light trapping is an effective way for estimating moth diversity. Moths collected in 2005 will then be subjected to an indicator species analysis. Based on these results and literature review, 2-3 indicator species for moths and understory vegetation will be selected and sampled in the subsequent years (2006-2007). Differences in selected species diversity by cover-type and treatment will be assessed with vegetation and parasitoid diversity as co-variables. Ordination techniques will be used to test for differences of moth assemblages by treatment and cover type.

White spruce regeneration in boreal mixedwood forests.

Jim Stewart, Travis Jones, Rick Hurdle, Derek Sidders
Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre

Understanding the processes that contribute to white spruce regeneration is critical to successful mixedwood management. The purpose of this project was to investigate the biological and physical processes that determine the regeneration of white spruce under different silvicultural systems in boreal mixedwoods.

A series of studies were carried out at the EMEND experimental site. Experimental factors included forest type, harvest residual, and mechanical site preparation. We hand-seeded and planted white spruce in the different combinations of the experimental factors. Measurements were made of atmospheric and soil microenvironments, cone production, natural seed rain, germinant counts, and planted stock size and physiological condition.

The best survival of seeded germinants, and growth of planted stock, was in the moderated environment provided by partial harvesting and site preparation. Spruce-dominated stands with 50% residual canopy provided the best conditions for regeneration from seed, while both spruce-dominated and poplar-dominated partial-cut stands improved growing conditions for planted seedlings. Regeneration from seed was poor and inconsistent, even with prepared microsites. Planted stock required site preparation in clearcuts, but could do well without under partial canopies. However, site preparation, particularly the warmer and drier conditions produced by mounding, significantly improved growth. Mixed microsites were also good, especially under poplar. These results support the use of partial harvesting and understory regeneration of white spruce as an alternative to clearcut-and-plant in managing boreal mixedwood forests.

EMEND Project Partners and Sponsors

Alberta Sustainable Resource Development
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Weyerhaeuser

Appendix 4: EMEND Publications 2005

Available only in print versions

Biodiversity and Conservation (2005) 14: 1895–1907
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Short-term effects of experimental boreal forest logging disturbance on bumble bees, bumble bee-pollinated flowers and the bee–flower match

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Key words: Arthropods, Boreal forest, Bumble bees, Forestry, Ideal free distribution, Logging impacts, Selective logging, Undermatching

Abstract. This study examines how, over the short term, logging affects the density of bumble bees (Apidae: *Bombus*), the understory plants commonly visited by bumble bees, and the numerical relationship between bumble bees and flowers. In the summers before and after winter logging, bumble bees and plants were surveyed in 50 deciduous stands (each of 8–10 ha) in the boreal forest of northern Alberta, Canada. Logging was replicated at three different intensities: 0, 10–20, and 50–75% of trees remaining. There were generally more bumble bees, species of bumble bee-visited plants, and flowers in moderately (50–75%) logged sites, but this pattern depended on the time of year. Before logging, bumble bees matched resources according to an ideal free distribution (IFD). Logging affected the distribution of bumble bees across floral resources: the slope of the regression relating bumble bee and flower proportions was less than one for clearcut and control treatments (i.e., undermatching), with too many bumble bees in the flower-poor compartments and too few in the flower-rich ones. Deviations from an IFD were negative in control sites, such that fewer bumble bees occurred here than warranted by flower numbers. Controlling for flower density, bumble bee density was significantly greater in clearcuts than in the other treatments. By disproportionately visiting plants in clearcuts (relative to flower density), and by undermatching, bumble bees in clearcuts should experience higher levels of competition. Conversely, the fewer (and undermatching) bumble bees in control sites (relative to flower abundances there) may cause these plants to obtain diminished pollination service. The proximity of clearcut logging to pristine areas may therefore negatively impact plants and bumble bees in the pristine areas, at least in the season immediately following logging.

Abbreviations: IFD – ideal free distribution

Introduction

The boreal forests of the northern hemisphere are being logged at an unprecedented rate, and the boreal forests of Alberta, Canada, are no exception (Schneider 2002). Except for a few beetle families (notably Scolytidae and Carabidae), the impacts of boreal forest logging on arthropod biodiversity are largely unknown. One element of the arthropod community of particular interest are the pollinators, which effect pollen transfer through their flower visiting behaviour to affect the reproductive success of plants. In the boreal forest, bumble bees (Apidae: *Bombus*) are a widespread, locally abundant and ecologically important pollinator.

Logging has the potential to affect the pollination community by changing the densities and species composition of the communities of bumble bees and plants. For example, understory flowering plants may flourish when a proportion of overstory trees are removed and opportunities for photosynthesis at the ground level increase. Alternatively, they may wither in the hot and dry conditions that often prevail in clearcuts. Similarly, certain species of insects may specialize on old-growth or disturbed habitats, such that logging changes the nature of the insect community (Grove 2002; Siira-Pietkainen et al. 2003).

Pollination systems are by their nature symbiotic, so at a subtler level logging may also affect the way the plants and pollinators interact. For example, plants growing in a clearcut might be easier for bumble bees to see at a distance, such that their flowers are visited more frequently and their pollen transported more effectively than the same species of plants in more natural denser forest. One way to measure any potential mismatch between plants and pollinators is to use an ideal free distribution (IFD; Fretwell and Lucas 1970) as the framework for comparison. Deviations from an IFD prediction that numbers of consumers should match quantities of resources can show which logging treatments have relatively more (or fewer) bumble bees (or flowers), and how logging changes the bumble bee–flower relationship.

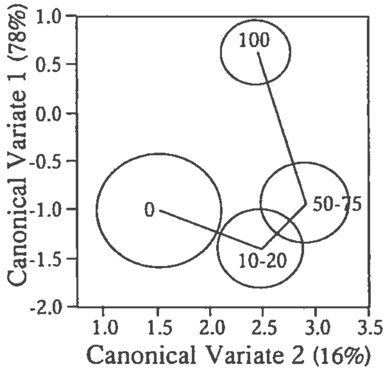
This study examines what happens in the short term to the bumble bee fauna and the plants that they pollinate when a boreal forest is logged at different intensities. I use a small-scale experiment (logging imposed on ≈9 ha-sized replicates) to examine how different intensities of logging causes changes to the density of bumble bees and species of understory plants commonly visited by bumble bees. I also look for logging-associated changes in the way that bumble bees interact with their food plants, by examining whether the distribution of bumble bees across flowers differs from an IFD.

Methods

This study was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) site in NW Alberta (56°46′N, 118°22′W). In this experimental system, I studied 50 experimental units ('compartments') of 8–10 ha distributed among stands of deciduous-dominated boreal forest. Each compartment received one of 4 logging levels (defined by % trees remaining after logging): 0% = 'clearcut' (n = 6), 10–20% (n = 12), 50–75% (n = 12), and 100% = 'control' (n = 20). Compartments occurred in contiguous clusters, with treatments being generally non-adjacent within clusters, and clusters being distributed over a roughly 16 km × 5 km area.

Each compartment contained one or more baseline transects, of roughly 0.5 m width. Bumble 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), and counting bumble bees foraging on flowers in the 1.5 m zone on each side of the transect. 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 transect, measured within each 20 m interval (1998), or over a 2 m wide band along a random side of the entire transect (1999). Because I lacked information for all species on pollen and nectar production, I summed flowers across all species to generate an overall measure of flower abundance in a compartment. Of the 15 plant species censused (Figure 1), individual flowers were counted in all but *Arnica*, *Aster*, *Maianthemum*, *Solidago*, and *Trifolium*, whose inflorescences were counted as flowers. In a similar manner, bumble 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 (*Bombus flavifrons*, *B. mixtus*, *B. perplexus*, *B. sylvicola*, *B. terricola*, *B. vagans*). One person collected data in each summer, but observers differed between years.

Where necessary, variables were transformed to normality using Box–Cox transformations. Residuals from all model fits were checked for normality and homogeneity. Data were tabulated at the level of the compartment, census number, and year. Statistical analysis was performed using JMP 5.0 (JMP 2002). MANOVA was used to describe the impact of different logging treatments on the abundances of the 15 plant species, an impact distilled as 95% centroids (multivariate least squares means) of the first two canonical variables.



Plant Species	CV1	CV2
Lathyrus ochroleucus	-0.047	0.008
Arnica cordifolia	-0.032	0.042
Epilobium angustifolium	-0.025	0.012
Vicia americana	-0.019	-0.018
Astragalus americanus	-0.001	0.070
Aster conspicuous	0.003	0.024
Mertensia paniculata	0.005	0.024
Delphinium glaucum	0.010	0.026
Rosa spp.	0.015	0.017
Maianthermum canadense	0.021	-0.006
Trifolium hybridum	0.027	-0.002
Lonicera dioica	0.037	-0.018
Pyrola asarifolia	0.049	0.014
Solidago canadensis	0.071	-0.034

Figure 1. Multivariate description of the plant community following logging of different intensities. The first two canonical variates explain 96% of the correlation among groups in the 14 species, flower abundances. Centroids indicate 95% confidence intervals for each of the groups, whose labels indicate % trees remaining after logging. The table on the right shows the loadings of the original variables on the first two eigenvectors.

Repeated-measures ANCOVAs tested within-year effects of treatment (eventual or actual) on bumble bee abundance, flower abundance, and plant species diversity. Regressions tested for conformity of bumble bees and flowers to an IFD.

Results

I used data from the pre-logging (control) year, 1998, 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 necessary because flower abundance data were collected differently in each year, and because observers differed between years. There were no differences among compartments in bumble bee abundance (transformed by $\ln(1 + \#)$) or flower abundance (transformed by $\ln(1 + \#)$) according to their eventual logging treatment (repeated-measures ANCOVAs with time as the repeated factor, eventual treatment as the main effect, and transect length (transformed to normality by $-\text{length}^{-0.4}$) as the covariate; effect of eventual treatment; $F_{3,27} = 0.13$, $p = 0.94$ for bumble bee abundance, $F_{3,27} = 0.92$, $p = 0.44$ for flower abundance). There was a significant time by treatment interaction for number of plant species (transformed by $(1 + \#)^{0.6}$), where compartments destined to become clearcuts dropped more steeply in diversity through the season than those destined for the other treatments (time by treatment interaction $F_{6,52} = 3.12$, $p = 0.01$). This trend is unlikely to account for observed post-logging trends in plant species diversity with time (see below).

If bumble bees were equally detectable in the years before and after logging, then there was no difference in overall abundance of bumble bees from 1 year to the next (ANCOVA predicting $\ln(1 + \#\text{bees})$ from year, census and $-\text{transect length}^{-0.4}$: year effect $F_{1,310} = 0.074$, $p = 0.79$); least square means ± SE, pre-logging: 0.513 ± 0.069; post-logging: 0.536 ± 0.051). Any differences in bumble bee density detected in comparisons between logging treatments therefore reflect the relative distribution of the same number of bumble bees across differences in their floral resources.

How did logging affect the plant and bumble bee communities over the short term? Overall, it changed the species composition and abundance of the plant community (MANOVA of the ln-transformed numbers of flowers of 14 of the plant species listed in Figure 1 versus logging treatment and $-\text{transect length}^{-0.4}$: logging treatment Wilks' $\lambda_{42,487} = 0.468$, $p < 0.0001$). In particular, the plant community in the three logged treatments was distinct from that of the control treatment, as shown by their separation along CV1, which explains 78% of the correlation among groups in community composition (Figure 1). There was more *Solidago*, *Pyrola and Lonicera* in control habitats, and more *Lathyrus* and *Arnica* in logged ones. Canonical variate 2 arranges the logging treatments in order of their magnitude of tree removal (low values for clearcuts, high values for 50–75% trees remaining; Figure 1). There was more

Solidago in lightly logged habitats, and more *Lathyrus*, *Arnica* and *Astragalus* in heavily logged ones. In contrast, logging had no detectable impact on the species composition and abundance of the three most common bumble bee species (i.e., *Bombus flavifrons*, *B. terricola*, and *B. vagans*: MANCOVA of the ln-transformed numbers of bumble bees of the three species versus logging treatment and $-$transect length$^{-0.4}$; logging treatment Wilks $\lambda_{9,236} = 0.955$, $p = 0.87$).

When we reduce the taxonomic resolution by examining total densities of all bumble bees and flowers, regardless of species, and total numbers of plant species, we see an effect of logging on both bumble bees and plants. But this effect of logging is seasonally dependent, as shown by the significant treatment by time interactions (repeated-measures ANCOVAs, Figure 2). Bumble bees were more abundant in control areas in the first census, but by the third and fourth censuses later that same summer, moderately logged areas contained more bumble bees. Plant species diversity was generally highest in treatments where 50–75% and 10–20% of trees remained, but not in the second census. Note that the late-season drop in diversity detected in 1998 data from compartments scheduled to be clearcut was not observed in the year following clearcut. Flowers were most abundant in control areas in the first two censuses, but by the third and fourth censuses, they were more common in the two non-clearcut logging treatments. Overall, intermediate levels of logging appear to increase both plant and bumble bee densities, and increase plant species diversity (Figure 2).

How did logging affect the distribution of bumble bees across their floral resources? The null hypothesis is that bumble bees distribute themselves across their floral resources according to an IFD, an equilibrium where the slope of the regression of bumble bees on resources is 1. The particular form of IFD envisioned here is the continuous input model (Lessells 1995). At an IFD, each bumble bee would receive an equal rate of return, regardless of the local resource density in its current compartment. To test for an IFD, I transformed measures of bumble bee and flower abundances to percentages, such that the number of bumble bees and flowers in a compartment were expressed as a percent of total bumble bee or flower abundance during that census (in all treatments). A slope of 1 between these variables implies an IFD. In 1998 (i.e., before logging), there was indeed an IFD (Figure 3).

Following logging, the slopes of the bumble bee versus flower regressions were equal to 1 for the two intermediate treatments, but less than 1 for clearcuts and control areas (Figure 4). That is, bumble bees evenly matched resources under natural conditions, but when there was logging in the landscape they 'undermatched' (Tregenza 1995) in clearcuts and control areas, in that too few bumble bees visited compartments with many flowers, and too many bumble bees visited compartments of the same treatment with few flowers. A consequence of this undermatching is that bumble bees would on average have foraged more poorly in clearcuts and controls, relative to bumble bees in the 10–20% or 50–75% treatments. The conclusion of undermatching

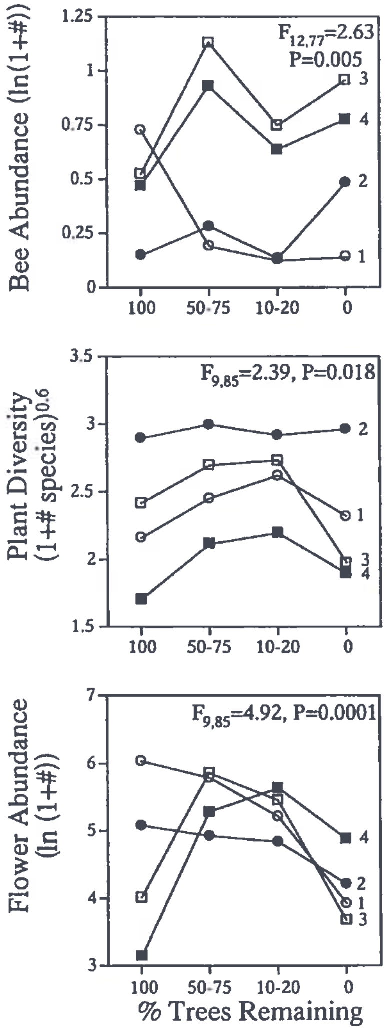


Figure 2. Treatment and seasonal trends in bumble bee abundance, plant species richness and flower abundance. Least square means from repeated-measures ANCOVAs (census is the repeated factor, treatment the main effect, and (transect length)$^{-0.4}$ the covariate) are plotted. Lines connect points for a particular census number. *F*-statistics report the census by treatment interactions.

in clearcuts is equivocal: when the two outlier points on the % flower axis (Figure 4) are excluded from the clearcut analysis, there was no relationship between bumble bees and flowers (slope $t_{19} = 1.38$, $p = 0.60$). That is, the

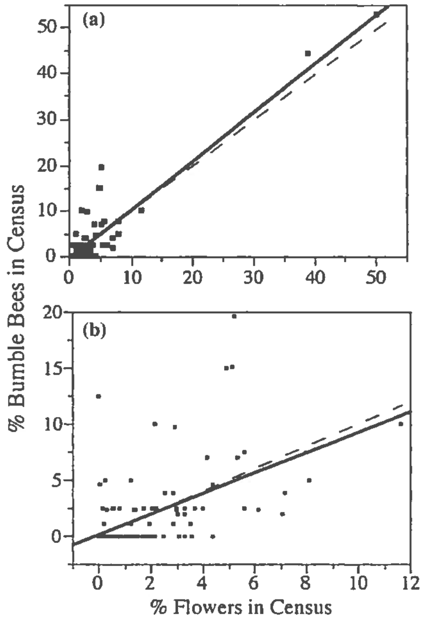


Figure 3. The distribution of bumble bees across flowers in the summer before logging. (a) All data. The regression line has a slope of 1.064 (SE = 0.043, t_{130} = 24.94, $p < 0.0001$). (b) Excluding the two largest values in (a) as potential outliers. The regression line has a slope of 0.912 (SE = 0.118, t_{130} = 7.70, $p < 0.0001$). Neither slope is different from the IFD prediction of 1 (slope ± 2 SEs overlaps 1 in both cases). The dashed lines show the IFD expectation of slope = 1 and intercept = 0.

number of bumble bees in a clearcut may actually have been independent of the number of flowers there.

A second way to use the IFD to detect the impact of logging is to express data from each compartment as a difference between % bees and % flowers. The IFD prediction is that these differences should on average be zero (i.e., % bees = % flowers). This 'difference measure' provides an indication of which treatments are over- or under-used by bumble bees, relative to their flower abundance – essentially a question of intercept, not slope, in the bumble bees versus flowers regression. The distribution of differences (Δ = % bees – % flowers) were non-normal for each treatment, so the nonparametric Wilcoxon Signed-Rank Test was used to test for departures from an expected mean of zero. In clearcuts, differences were positive, but not significantly so (mean Δ = +0.94%: Signed-rank = 36, df = 22, p = 0.28). However, given the large sample variance, the mean Δ in clearcuts would have been +2.16% or greater to have powerfully (power = 0.8) detected a true difference from zero using a one-sample t-test.

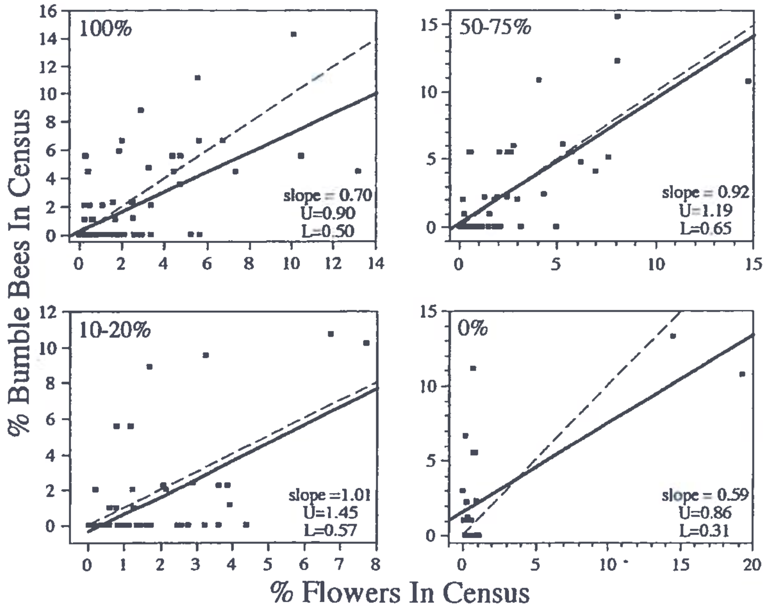


Figure 4. Regressions (solid lines) showing the distribution of bumble bees across flowers over four censuses in the summer after logging. Labels show % of trees remaining after logging. For each regression, the slope and its 95% upper (U) or lower (L) CI are shown. Regression statistics for each slope are: 100%, t_{74} = 7.05, p = 0.000; 50–75%, t_{43} = 6.79, p = 0.000; 10–20%, t_{44} = 4.63, p = 0.000; 0%, t_{21} = 4.42, p = 0.000). When the two highest values for % flowers in census are omitted from the 0% treatment, the regression is no longer statistically significant (t_{19} = 0.53, p = 0.60). The dashed lines show the IFD expectation of slope = 1 and intercept = 0.

Hence, we detect no difference from a Δ of zero in clearcuts, but have little power to detect a true difference. In the other treatments, there were significantly fewer bumble bees in the 10–20% treatment (mean, Δ = – 0.29%: Signed-rank = –220.5, df = 45, p = 0.014), an IFD number of bumble bees in the 50–75% treatment (mean Δ = +0.16%: Signed-rank = –56, df = 44, p = 0.52), and significantly fewer bumble bees in the unlogged control (mean Δ = 0.32%; Signed-rank = –377.5, df = 75, p = 0.026).

An alternative (non-IFD) means of examining the match between bumble bees and flowers is to compare the number of bumble bees among treatments after controlling for flower abundance in an ANCOVA (main effects were census, treatment, and their interaction; covariate – (number of flowers + 1)$^{-0.6}$). There were no covariate by main effect interactions. With this approach, clearcuts had more bumble bees than did the control and 10–20% treatments (Figure 5).

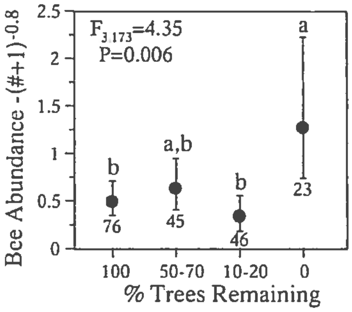


Figure 5. The abundance of bumble bees after logging, controlling for flower abundance. Least square means ± 1 SE, from an ANCOVA (see text for variables in the model) are shown. Sample size appears below each point. Letters show groups that are significantly different (Tukey–Kramer HSD). There was no census by treatment interaction ($F_{9,173} = 0.83$, $p = 0.59$), so the F value associated with the treatment effect is reported in the graph.

Discussion

Overall, this paper detects strong immediate effects of logging disturbance on the community of bumble bees, and the plants that they typically visit. The frequencies of bumble bee species did not vary among treatments, but the frequencies of plant species did, with the greatest detectable impact being that of any logging, regardless of its intensity (Figure 1). Generally, intermediate levels of logging (i.e., leaving roughly 50–75% of the original trees unlogged) produced a larger floral and bumble bee community, and a more diverse floral display, but this effect varied with time of year (Figure 2). Season had a similarly strong effect in accounting for beetle abundances relative to fragment size in Chilean temperate forests (Barbosa and Marquet 2002). It seems that moderate levels of logging, relative to clearcutting or unlogged controls, increase the opportunities for understory plants favoured by bumble bees. Analyses of bumble bee and plant abundance in the year before logging demonstrate that the effects of logging detected here were not a simple consequence of initial differences among compartments.

The bumble bee community, which thrives on the denser aggregations of flowers that follow disturbances such as fire, windthrow, or clearcut logging, appears to be slightly enhanced soon after intermediate levels of logging. In a similar vein, intermediate levels of logging (stands with small logged openings) best preserved the original assemblage of Carabid beetles in a Finnish boreal forest (Koivula 2002). 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 bumble bees (Heinrich 1978; Osborne et al. 1999) relative to the scale of logging used in the present experiment (≈9 ha per compartment). The impact of logging on plants that bumble bees visit is more dramatic: the nature of the community is fundamentally different immediately following logging (Figure 1). Given that interspecific competition among bumble bees is mediated through tongue length (Inouye 1980; Harder 1985), and given that the flower community differs between logged and unlogged communities, it is likely that the bumble bee community in logged landscapes will eventually shift to a different mix of species, reflecting a different flower-selected mix of tongue lengths. This study was a comparison across a single bumble bee generation. Any change in the bumble bee community, both in density and in constituent species, may take several generations (years) to manifest itself.

While flower abundance and diversity were generally higher in logged sites (Figure 2), there was no area-wide numerical response from the bumble bee community: the overall density of bumble bees in the summers before and after logging was similar (as found for soil macroarthropods by Siira-Pietkainen et al. 2003). What changed between years was in where the bumble bees foraged. To reiterate, bumble bees chose compartments from a range of different treatments simultaneously available to them.

Before logging, bumble bees conformed to an IFD (Figure 3), meaning that the abundance of bees matched the abundance of flowers. Bumble bee foraging success was presumably equivalent regardless of where an individual foraged. After logging, bumble bees in clearcuts and controls did not conform to an IFD: they 'undermatched' (i.e., slope < 1, Figure 4), such that compartments with more flowers contained fewer bumble bees than merited based on the quantity of resources, and compartments with fewer flowers contained more bumble bees than would be expected from the quantity of resources. A fascinating consequence of this undermatching may be that plants in low density compartments, i.e., those with the smallest population sizes, may be *less* susceptible to pollinator limitation and Allee effects than would be the case under an IFD. In this same situation, bumble bees foraging in high flower abundance compartments, would have higher fitness than bumble bees foraging in low abundance compartments, who would experience higher levels of competition for pollen and nectar.

Clearcut logging caused bumble bees to concentrate in this treatment (Figure 5), possibly without regard to the local abundance of flowers (Figure 4, lower right graph). Intermediate levels of logging (10–20% and 50–75% trees remaining) produced IFD slopes for the bumble bees using these habitats (Figure 4). But the total density of bumble bees was higher than warranted by resources in the 10–20% treatment (Δ analysis). So only the 50–75% logging treatment preserved the bumble bee–flower match observed in the summer before logging.

Perhaps the most compelling result is the match between bumble bees and floral resources in control (unlogged) compartments. Whereas this match was an IFD in the year before logging, the presence of logged areas on the landscape caused 'undermatching' (slope < 1) in control sites (Figure 4). Control sites also contained fewer bumble bees on average than expected by an IFD

(Δ analysis). In sum, control sites appear to have been negatively affected by the mere proximity and availability of logged sites.

Of all logging treatments, the moderate one (50–75% of trees remaining) appears to have the lowest negative impact on bumble bees and bumble bee-visited flowers. It generally contained the most bumble bee individuals, the most flowers, and the most flower species of all the treatments (Figure 1), and it was the only one that did not in any detectable way distort the IFD match of bumble bees and flowers (Figure 4, Δ analysis). One admittedly speculative take-home message for forest managers might therefore be: leaving 50–75% of the trees intact after logging is the best way of preserving, or even enhancing, the bumble bee and bumble bee-visited plant community in the boreal forest. Note, however, that the plant species that are thrive in such partial cuts are different from those in, control areas (Figure 1), so a forest thus 'enhanced' is different from its unlogged state.

No data were obtained on plant and bee fitness in this study. Neither have the long-term numerical responses of bumble bees and plants been presented. But the IFD results, if they persist in subsequent years, allow for some intriguing speculation. Plants in unlogged control areas could obtain diminished pollination service and therefore reduced fitness, because they are visited disproportionately less often (Figure 5), with no year to year increases in the total abundance of pollinators. Plants in low-density control areas may not suffer this diminished pollination fate, if undermatching exists (Figure 4, 100%). The proximity of logging to pristine areas may therefore act as pollinator 'attractors' that negatively impact plants in the pristine areas, particularly those in the high-density control areas. These kinds of potential edge effects between logged and pristine habitats deserve further attention.

The mechanism that accounted for the disproportionate attraction of bumble bees to clearcuts remains unresolved. It may be that bumble bees may more easily see flowers in clearcuts based on their greater visibility in this habitat, and therefore be more attracted to flowers here.

Alternatively, bumble bees may prefer to forage in clearcuts because of the warmer temperatures experienced there, making it metabolically cheaper for bumble bees to forage. Or bumble bees may be more easily detected on flowers in the more open habitat of clearcuts. None of these factors (apparency of flowers, preferred temperature, detectability of bumble bees) seems to account for the observed pattern of bumble bee densities: partially logged habitats would also be warmer, more open, and more easy to detect bees, but relative bumble bee densities were no higher in these habitats (Figure 5).

Regardless, any bumble bee density differences among logging treatments resulting from temperature, bumble bee detectability, and flower apparency cannot explain the undermatching (or no matching, if two outliers are removed) between bumble bees and flowers observed in clearcuts (Figure 4, 0%), or the departure from an IFD in the 10–20% treatment (Δ analysis). Instead, greater visibility of flowers should result in overmatching (if density of competitors is hard to assess) or an IFD (if density of competitors is easy to assess).

Flowers may be more difficult for bumble bees to encounter in unlogged forests, which are structurally more complex, which may explain the undermatching seen here. But why, then, was there no undermatching in these same control habitats before logging disturbance appeared on the landscape? There appears to be an interaction between the form of the within-habitat bumble bee versus flower relationship in unlogged habitats and the local presence of logging disturbance. Clearly, to untangle this interaction we need to account for the spatial context of movements of pollinators, within and among treatments, in a logged landscape.

Such landscape effects on bumble bee distributions are likely to be complex. For example, properties of the surrounding habitat matrix affect the likelihood of bumble bee visitation to knapweed (*Centaurea jacea*) (Hirsch et al. 2003). Similarly, the species richness of bumble bees at focal habitat patches is a function of both patch attributes and attributes of the surrounding matrix (Dauber et al. 2003). While attributes of the surrounding habitat matrix may influence animal movement (e.g., Ricketts 2001), relative to open areas, even intact forests are not necessarily the barriers to bee movement that they would appear to be (Kreyer et al. 2004).

In conclusion, the bumble bee–flower relationship is affected in the short term by clearcut logging disturbance in two distinct ways. First, clearcut logging produces greater bumble bee densities (relative to floral resources) than no logging or intermediate levels of logging (Figure 5). Second, clearcut logging distorts or eliminates the achievement of an IFD in this treatment (Figure 4), despite the fact that a pre-logging IFD existed in these sites. Most intriguingly, the pre-logging IFD that obtained in control (unlogged) sites was altered by the presence of logging in the landscape. Hence, with respect to IFD relationships, control sites in this experiment, nestled as they are among the various experimental treatments, are not true controls.

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References

Banaszak J. 1980. Studies on methods of censusing the numbers of bees (Hymenoptera, Apoidea). Polish Ecological Studies 6: 355–366.

Barbosa O. and Marquet P.A. 2002. Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. Oecologia 32: 296–306.

Dauber J., Hirsch M., Simmering D., Waldhardt R., Otte A. and Wolters V. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems and Environment 98: 321–329.

Fretwell S.D. and Lucas L.J. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16–36.

Grove S.J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33: 1–23.

Harder L.D. 1985. Morphology as a predictor of flower choice by bumble bees. Ecology 66: 198–210.

Heinrich B. 1978. Bumblebee Economics. Harvard University Press, Cambridge, Massachusetts.

Hirsch M., Pfaff S. and Wolters V. 2003. The influence of matrix type on flower visitors of *Centaurea jacea* L. Agriculture, Ecosystems and Environment 98: 331–337.

Inouye D.W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumble bees. Oecologia 45: 197–201.

JMP 2002. JMP Statistical Discovery Software. SAS Institute, Cary, North Carolina.

Koivula M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). Forest Ecology and Management. 67: 103–21.

Kreyer D., Oed A., Walther-Hellwig K. and Frankl R. 2004. Are forests potential landscape barriers for foraging bumble bees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). Biological Conservation 116: 111–118.

Lessells C.M. 1995. Putting resource dynamics into continuous input ideal free distribution models. Animal Behaviour 49: 487–494.

Niemelelä J. 1997. Invertebrates and forest management. Conserv. Biol. 11: 601–610.

Osborne J.L., Clark S.J., Morris R.J., Williams I.H., Riley J.R. and Smith A.D. et al. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36: 519–533.

Ricketts T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158: 87–99.

Siira-Pietkainen A., Haimi J. and Siitonen J. 2003. Short-term responses of soil macroarthropod community to clear felling and alternative forest regeneration methods. Forest Ecology and Management 172: 339–353.

Schneider R.R. 2002. Alternative Futures: Alberta's Boreal Forest at the Crossroads. Alberta Centre for Boreal Research, Edmonton, Alberta, Canada.

Teräs I. 1983. Estimation of bumblebee densities (*Bombus*: Hymenoptera, Apidae). Acta Entomologica Fennica 42: 103–113.

Tregenza T. 1995. Building on the ideal free distribution. Advances in Ecological Research 26: 253–307.

Forest-floor chemical properties are altered by clear-cutting in boreal mixedwood forest stands dominated by trembling aspen and white spruce

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Abstract: Alterations in the chemical properties of the forest floor following clear-cut harvesting may have implications for forest productivity in boreal stands. We used proximate analysis, carbon-13 (^{13}C) isotopic determination, and cross-polarization, magic-angle spinning (CPMAS) ^{13}C nuclear magnetic resonance (NMR) spectroscopy to examine differences in the characteristics of the forest floors from uncut stands and clear-cut stands dominated by white spruce (*Picea glauca* (Moench) Voss; SPRUCE) and trembling aspen (*Populus tremuloides* Michx.; ASPEN) in northern Alberta. Proximate analysis revealed no difference in the chemical properties of forest floors from clear-cut and uncut stands in either stand type, but the acid-insoluble residue of forest floors from clear-cut ASPEN stands was enriched in ^{13}C compared with those from uncut ASPEN stands. CPMAS ^{13}C NMR spectroscopy revealed that forest floors from clearcuts were enriched in total aromatic C, particularly in ASPEN stands, and depleted in phenolic C, particularly in SPRUCE stands. These patterns indicate that forest floors from the clearcuts have become more humified, which may reflect stand-type differences in the amount of labile C available to the forest-floor microbial community and reductions in above- and below-ground inputs to the forest floor following clear-cutting in both stand types. Changes in the chemical properties of forest floors from clear-cut SPRUCE and ASPEN stands could exacerbate C limitation in these soils and alter patterns of nutrient cycling.

Résumé : L'altération des propriétés chimiques de la couverture morte après une coupe à blanc pourrait avoir des conséquences sur la productivité de la forêt boréale. Les auteurs ont utilisé l'analyse quantitative approximative, la mesure isotopique de ^{13}C ainsi que la polarisation croisée et la rotation à l'angle magique en spectroscopie par résonance magnétique nucléaire (CPMAS ^{13}C RMN) pour examiner les différences dans les caractéristiques de la couverture morte entre des peuplements coupés à blanc et non coupés dominés par l'épinette blanche (*Picea glauca* (Moench) Voss: Epb) et le peuplier faux-tremble (*Populus tremuloides* Michx.; Pet) dans le nord de l'Alberta. L'analyse quantitative approximative n'a révélé aucune différence dans les propriétés chimiques de la couverture morte entre les peuplements coupés à blanc et les peuplements non coupés dans aucun des types de peuplements. Par contre, les résidus insolubles dans l'acide de la couverture morte des peuplements de Pet coupés à blanc étaient enrichis en ^{13}C comparativement à la couverture morte des peuplements de Pet non coupés. La spectroscopie CPMAS ^{13}C RMN a révélé que la couverture morte des coupes à blanc était enrichie en C aromatique total, particulièrement dans les peuplements de Pet et appauvrie en C phénolique, particulièrement dans les peuplements d'Epb. Ces patrons indiquent que la couverture morte dans les coupes à blanc est devenue plus humifiée, ce qui reflète possiblement les différences entre les types de peuplements dans la quantité de carbone labile disponible pour la communauté microbienne de la couverture morte, ainsi que les réductions dans les apports souterrains et aériens à la couverture morte à la suite d'une coupe à blanc dans les deux types de peuplements. Les changements dans les propriétés chimiques de la couverture morte des peuplements d'Epb et de Pet pourraient amplifier le manque de C dans ces sols et modifier les patrons de recyclage des nutriments.

[Traduit par la Rédaction]

Introduction

Boreal mixedwood forests in North America are under increasing pressure from the timber and oil industries (Schneider et al. 2003), yet relatively little is known about the effects of timber removal on the long-term site productivity and integrity of these ecosystems (Spence 2001). The forest floor, which includes the surface organic horizons that overlie the mineral soil (Green et al. 1993), accounts for 10%–35% of the total carbon (C) found in North American boreal forests (Morrison et al. 1993; Huang and Schoenau 1996; Nalder and Wein 1999; Lee et al. 2002) and contains a significant portion of the site nutrient capital (Van Cleve et al.

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1983; Bormann and Sidle 1990; Prescott et al. 2000). Forest-floor characteristics may change following clear-cut harvesting in response to alterations in soil moisture and temperature regimes, and shifts in the quantity, quality, and timing of detrital inputs (Keenan and Kimmins 1993; Ballard 2000; Prescott et al. 2000). Given that the quality of organic matter controls the rate at which it decomposes (Fogel and Cromack 1977; Melillo et al. 1982; Scott and Binkley 1997), the size and composition of the microbial community that it supports (Vance and Chapin 2001; Webster et al. 2001; Park et al. 2002), and the concentrations of available nutrients (e.g., nitrogen) that it supplies (Stump and Binkley 1993; Hart et al. 1994; Prescott et al. 2003), changes in the properties of forest-floor organic matter could have implications for long- and short-term forest productivity (Prescott et al. 2000; Dai et al. 2001). However, few studies have compared the properties of forest-floor organic matter in clear-cut and undisturbed forests (Dai et al. 2001; Preston et al. 2002).

A number of methods have been employed to assess the properties of organic matter in forest soils. These include separation of organic matter into broad chemical fractions using wet chemistry, i.e., proximate analysis (Fogel and Cromack 1977; McClaugherty et al. 1985; Ryan et al. 1990), examination of changes in the ^{13}C-isotope composition of whole or fractionated organic matter (Nadelhoffer and Fry 1988; Melillo et al. 1989; Quideau et al. 2003), and description of the chemical environment of organic C using cross-polarization, magic-angle spinning (CPMAS) ^{13}C nuclear magnetic resonance (NMR) spectroscopy (Kögel et al. 1987; Zech et al. 1987; Baldock and Preston 1995). All of these methods are complicated by a common problem: the forest floor is a complex material that is composed of substrates ranging from very labile to highly recalcitrant forms of organic matter (Berg and McClaugherty 2003). Important changes in organic matter composition may not be detected because the materials that are the most labile, and thus the most sensitive to change, are probably the least abundant (Dai et al. 2001; Preston et al. 2002). Therefore, a combination of techniques was used in the present study, with the aim of increasing our sensitivity to changes in the properties of forest-floor organic matter (Zech et al. 1992).

The Ecosystem Management Emulating Natural Disturbance (EMEND) experiment in northwestern Alberta is a long-term research study covering 1000 ha of boreal mixedwood forest that includes stands dominated by trembling aspen (*Populus tremuloides* Michx.) or white spruce (*Picea glauca* (Moench) Voss). This controlled and replicated experiment was established, in part, to examine variation among stand types in the response of various ecosystem-level processes to logging at varying intensities. The results of previous experiments suggest that forest floors from stands dominated by trembling aspen (ASPEN) exhibit more rapid C, nitrogen (N), and phosphorus (P) cycling than forest floors from stands dominated by white spruce (SPRUCE) (Flanagan and Van Cleve 1983; Paré and Bergeron 1996; Lindo and Visser 2003). Following clear-cutting, forest floors from both SPRUCE and ASPEN stands at the EMEND site exhibited less fine root biomass, less litter input, reduced concentrations of microbial biomass C, and decreased rates of C mineralization (Lindo and Visser 2003). The aims of the present study were (*i*) to determine whether the properties of forest floor organic matter from SPRUCE and ASPEN stands were altered by clear-cutting and (*ii*) to determine whether postharvest changes in the properties of forest-floor organic matter were stronger in ASPEN or in SPRUCE stands.

Materials and methods

Study site

The EMEND site (56°46′13′′N, 118°22′28′′W) is located on the boreal mixedwood plain in the Clear Hills Upland ecoregion within the Boreal Plains ecozone (Wiken 1986; Ecoregions Working Group 1989). The area is characterized by cold winters (mean temperature –14.0 °C), warm summers (mean temperature 11.6 °C), and an average 433 mm of precipitation, two-thirds of which usually falls during the summer (Environment Canada 2004). The site is characterized by a rolling topography ranging in elevation from 677 to 880 m asl. Soils are usually Orthic Gray or Dark Gray Luvisols that have developed on fine-textured glaciolacustrine parent material (Kishchuk 2004). Harvesting of the clearcuts, which are approximately 10 ha in size, was completed in the winter of 1998–1999. Whole trees were harvested using a feller–buncher and skidded directly to the landing, where stems were delimbed. Debris from the delimbing process was piled on the landing and burned (Sidders and Luchkow 1998).

Sample collection

In June 2002, samples of forest floor were collected for assessment of bulk density, analysis using proximate fractionation, determination of ^{13}C-isotope composition and characterization using CPMAS ^{13}C NMR spectroscopy. Sampling for analysis using CPMAS ^{13}C NMR spectroscopy was repeated in June 2003. In both years, samples of forest floor were collected from three 10-ha replicates each of uncut (undisturbed) SPRUCE and ASPEN stands ranging in age from 80 to 140 years, and three 10-ha replicates each of clear-cut SPRUCE and ASPEN stands (12 experimental units in total). Uncut SPRUCE stands consist of >70% white spruce, with some trembling aspen, balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), or lodgepole pine (*Pinus contorta*). The understory of SPRUCE stands includes *Rosa acicularis*, *Shepherdia canadensis*, and a dense ground cover of moss, especially stair-step moss (*Hylocomium splendens*). Forest floors from SPRUCE stands are typically Humimors (Green et al. 1993). Selected descriptive data for the FH-layer forest floors from SPRUCE stands are provided in Table 1. Uncut ASPEN stands consist of >70% trembling aspen, with some of the tree species listed above for SPRUCE stands. The understory of ASPEN stands includes *R. acicularis*, *Viburnum edule*, and *Alnus* spp., with an herb layer of *Calamagrostis canadensis*, *Chamerion angustifolium* subsp. *angustifolium*, and *Cornus canadensis*. Forest floors from ASPEN stands are typically Mormoders (Green et al. 1993). Selected descriptive data for the FH-layer forest floors from ASPEN stands are provided in Table 1.

Six sampling sites were randomly selected within each experimental unit. Some prospective sampling sites were rejected to avoid visibly disturbed forest floors and rotten wood.

Table 1. Characteristics of FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	SPRUCE		ASPEN	
	Uncut	Clear-cut	Uncut	Clear-cut
Moisture content (%)				
2002	203.3 (66.9)	217.4 (38.8)	195.1 (23.1)	184.4 (34.1)
2003	301.8 (55.7)	307.3 (32.8)	254.4 (35.6)	238.8 (19.3)
Thickness (m)	0.14 (0.02)	0.10 (0.01)	0.08 (0.01)	0.10 (0.02)
Bulk density (kg/m^3)	59.6 (9.8)	68.5 (17.5)	80.2 (7.9)	94.5 (12.4)
Ash (g/kg)	122.5 (24.2)	144.1 (14.7)	183.9 (5.6)	187.6 (53.6)
pH*	4.5 (0.3)	4.8 (0.5)	5.1 (0.3)	5.6 (0.5)

Note: Each value is the mean of three replicates. Values in parentheses show the standard deviation.
*Determined using a 1:10 ratio of forest floor (fresh mass in grams) to 0.01 mol·L^{-1} CaCl$_2$ (millilitres).

It should be noted, therefore, that timber removal, rather than clear-cutting per se, was the actual treatment effect examined in this study. At each sampling site, the FH-layer forest floor within a 15 cm × 15 cm template that had been placed on the surface of the forest floor was excavated to the depth of the mineral-soil surface. The F and H layers of the forest floor were not separated during sample collection because the F layer was very thin in ASPEN stands and therefore difficult to separate from the H layer. In SPRUCE stands, the bulk of the forest floor was dominated by decomposing moss, which made it difficult to distinguish the boundary between the F and H layers. The thickness of the FH-layer forest floor (from the upper surface of the F layer to the surface of the mineral soil) was measured at the four corners of the 15 cm × 15 cm cavity. All of the FH-layer material removed from the cavity was placed in a plastic bag and kept on ice until it was transported to the laboratory, where it was stored at approximately 5 °C for a maximum of 30 days. Large roots and woody materials greater than 5 mm in diameter were removed and each sample was weighed. Bulk density was calculated by dividing the dry mass of the whole sample (kilograms) by the volume of the sample (cubic metres, i.e., 0.15 m × 0.15 m × thickness of the FH-layer (m)).

For two of the three replicates of SPRUCE and ASPEN clear-cut and uncut stands, the six subsamples of FH-layer forest floor collected within each replicate in 2002 were composited prior to proximate fractionation, ^{13}C-isotope determination, and ^{13}C NMR analyses. For the remaining replicate of each stand type × harvesting treatment combination, proximate fractionation, ^{13}C-isotope determination, and ^{13}C NMR analyses were performed separately on the six subsamples collected within the replicate, to examine variability among subsamples and relationships among measured variables. All six subsamples collected from each replicate in 2003 were composited prior to NMR analysis.

Proximate fractionation

Samples of FH-layer forest floor were sieved (6.3 mm mesh) to remove roots and twigs, thoroughly mixed, and dried at 65 °C for 48 h. Dried samples of the FH-layer forest floor were finely ground using a ball mill. An aliquot was heated at 500 °C overnight to determine the ash content. Nonpolar extractives were determined using extraction in a 1:2 (*v/v*) mixture of chloroform and methanol (Bligh and Dyer 1959; Suberkropp et al. 1976; Kögel-Knabner 1995); water-soluble extractives were determined using hot-water (100 °C) extraction (Technical Association of the Pulp and Paper Industry 1999); and acid-soluble (ACID) and acid-insoluble (AIR) fractions were determined using a two-stage digestion in sulfuric acid (Effland 1977). Nonpolar extractives are more commonly estimated by extraction in dichloromethane (Heng and Goh 1981; McClaugherty et al. 1985; Ryan et al. 1990) but we chose to use a chloroform:methanol extractant, which includes a range of polarities, to produce higher yields of extract (Kögel-Knabner 1995). However, it should be noted that the use of methanol in the nonpolar extraction step might have removed some materials that are water-soluble. The fraction of chloroform-soluble (CHLORO), methanol-soluble (METH), water-soluble (WATER), and ACID extractives, as well as AIR residues were calculated on an ash-free basis (Ryan et al. 1990). Because water and methanol may have extracted similar materials, statistical analyses were also performed on the sum of the two fractions. The C and N contents and ^{13}C composition of finely ground unfractionated FH-layer forest floor and the WATER (after freeze-drying) and AIR fractions were determined by combustion on a Costech C/N elemental analyzer interfaced using a Finnigan Mat Conflo III to a Finnigan Mat, Delta Plus Advantage mass spectrometer. The ^{13}C-isotope compositions were expressed as ‰ deviation from the standard reference material, Pee Dee Belemnite.

CPMAS ^{13}C NMR analyses

Solid-state CPMAS ^{13}C NMR experiments were carried out on sieved, dried, and ground forest-floor samples using a Varian Chemagnetics CMX Infinity 200 (B_0 = 4.7 T, $\nu_L(^{13}C)$ = 50.3 MHz) NMR spectrometer using a 7.5-mm double-resonance MAS probe with high-power ^{1}H decoupling. All samples were packed into 7.5 mm (o.d.) Zirconia (ZrO$_2$) sleeves with drive tips made of Kel-F and end caps and spacers made of Teflon (Dupont, Circleville, Ohio). All ^{13}C NMR spectra were acquired using cross-polarization and referenced to TMS (δ_{iso} = 0.0 ppm) by setting the high-frequency isotropic peak of solid adamantane to 38.56 ppm (Earl and VanderHart 1982; Bryce et al. 2001). The ^{1}H 90° pulse and Hartmann–Hahn matching conditions were also determined using this sample. All ^{13}C NMR spectra were acquired using a ^{1}H 90° pulse width of 4.5 µs, a pulse delay of 5.0 s, a contact time of 1.0 ms (Preston et al. 1997), an acquisition time of 17.1 ms (Preston 2001), and a spinning fre-

Table 2. Mean concentrations ($mg \cdot g^{-1}$, ash-free basis) of proximate fractions in FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	SPRUCE		ASPEN	
	Uncut	Clear-cut	Uncut	Clear-cut
CHLORO	30.9 (2.9)	29.7 (7.0)	25.0 (8.8)	19.7 (3.5)
METH + WATER	103.9 (16.6)	102.5 (4.4)	118.8 (5.5)	115.1 (5.0)
METH	4.4 (5.4)	18.2 (16.4)	7.2 (6.6)	7.6 (6.7)
WATER	99.5 (21.1)	84.2 (12.4)	111.6 (9.3)	107.5 (8.5)
ACID	448.5 (44.5)	447.8 (4.0)	493.8 (17.7)	522.6 (83.2)
AIR	416.7 (51.6)	420.0 (6.0)	362.4 (23.2)	342.6 (90.0)

Note: Each value is the mean of three replicates. Values in parentheses show the standard deviation. Differences between uncut and clear-cut forests within stand types, or between stand types within uncut forests and clearcuts were not significant. CHLORO, chloroform-extractable fraction; METH, methanol-extractable fraction; WATER, water-extractable fraction; ACID, acid-soluble fraction; AIR, acid-insoluble residue.

quency of 6.5 kHz. One thousand transients were collected for each sample of forest-floor material that was analyzed. A ^{1}H decoupling field of 56 kHz, using the two-pulse phase-modulation scheme (Bennett et al. 1995), was employed during the acquisition of all spectra. A Gaussian line broadening of 100 Hz was used to process all spectra. The contribution of the background signal to the spectra was determined by acquiring a spectrum of an empty rotor set under identical conditions as for the forest-floor material. This contribution was subtracted from all Fourier-transformed ^{13}C NMR spectra before analysis. Corrections for spinning side bands were not applied because they did not appear to have a strong effect on any of the spectra.

Bruker's WIN-NMR package (Bruker Instruments Inc., Karlsruhe, Germany) was used to estimate the relative integrated areas of various regions between 0 and 194 ppm. Many different spectral regions for the integration have been reported (e.g., Skjemstad et al. 1997; Mao et al. 2000; Preston et al. 2000). In this study the spectral divisions were assigned on the basis of local minima of the spectra. The following regions were used for integration: ~0 to ~45 ppm attributed to alkyl C (ALK); ~45 to ~112 ppm attributed to *O*-alkyl C (O-ALK); ~112 to ~166 ppm attributed to aromatic C (AROM), and ~166 to ~194 ppm attributed to carbonyl C (CARB). AROM includes regions associated with both *C*-aryl C (~112 to ~140 ppm) and *O*-aryl, or phenolic, C (~140 to ~160 ppm).

Dipolar dephasing (DD) ^{13}C NMR spectra of FH-layer forest floor material from SPRUCE and ASPEN stands were produced by inserting a delay period of 40 µs (in the absence of ^{1}H decoupling) between the cross-polarization and acquisition portions of the CPMAS pulse sequence (Hatcher 1987). Peaks in spectra generated by DD generally correspond either to quaternary C or to C capable of significant motion in the solid state (e.g., methyl C; Lorenz et al. 2000). As a consequence, features of lignins and tannins can be more easily distinguished using DD than using CPMAS pulse sequence (Hatcher 1987; Wilson and Hatcher 1988; Lorenz et al. 2000). Peaks in CPMAS and DD spectra were compared to determine the relative importance of lignins and tannins in the FH-layer forest-floor material from uncut and clear-cut SPRUCE and ASPEN stands.

Statistical analyses

Data collected using solid-state CPMAS ^{13}C NMR experiments are considered "semi-quantitative", primarily because of variability in ^{1}H–^{13}C cross-polarization efficiencies (Preston et al. 1997; Smernik and Oades 2003; Ussiri and Johnson 2003). Thus, CPMAS ^{13}C NMR spectroscopy cannot be used to determine the quantities of different C types within a sample, but can be used to compare the relative abundances of different C types among similar samples, provided that they are analyzed under identical conditions (Kinchesh et al. 1995; Preston et al. 1997; Peuravuori et al. 2003).

Data obtained by proximate fractionation and determination of ^{13}C-isotope composition were analyzed using two-by-two (harvesting treatment × stand type) factorial analysis of variance (ANOVA) for a completely randomized design. Data obtained by CPMAS ^{13}C NMR spectroscopy were analyzed using a two-by-two (harvesting treatment × stand type) factorial ANOVA for a completely randomized design with year as a split effect. When significant interactions were detected between stand type and harvesting treatments, one-way ANOVA was used to examine harvesting effects within stand types. Differences were considered statistically significant if $p < 0.05$. To determine the relationships between the results of the proximate analyses, ^{13}C-composition analyses, and CPMAS ^{13}C NMR analyses, Pearson's correlations were calculated using the data for the six subsamples that had been collected in June 2002 from a SPRUCE clearcut, a SPRUCE uncut stand, an ASPEN clearcut, and an ASPEN uncut stand and not composited prior to chemical analysis. Correlations were considered statistically significant if $p < 0.05$. Bonferroni corrections were used to test for overall significance of the correlation matrix (Legendre and Legendre 1998). Data did not require transformation to meet the assumptions of the analyses. All statistical analyses were performed using SAS® version 8.01 (SAS Institute Inc. 1999–2000).

Results

Proximate fractionation

ACID and AIR were the most abundant fractions in FH-layer forest floors, together accounting for approximately

Table 3. Carbon (C) concentrations, C:N ratios, and ^{13}C-isotope composition of unfractionated FH-layer forest floors and selected proximate fractions of FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	SPRUCE		ASPEN	
	Uncut	Clear-cut	Uncut	Clear-cut
Unfractionated forest floor				
C ($mg \cdot g^{-1}$)	468.1 (9.0)	467.5 (12.2)	428.1 (17.7)	442.3 (28.3)
C:N ratio	26.0 (3.1)	24.0 (0.5)	19.1 (0.8)	19.0 (1.3)
^{13}C composition	–26.7 (0.4)	–26.8 (0.3)	–27.8 (0.2)	–27.5 (0.2)
WATER				
C ($mg \cdot g^{-1}$)	360.0 (24.5)	357.7 (12.7)	356.7 (5.5)	352.0 (7.0)
C:N ratio	19.8 (2.0)	19.1 (2.4)	15.2 (0.3)	15.2 (0.2)
^{13}C composition	–25.9 (0.2)	–26.1 (0.2)	–26.9 (0.3)	–26.9 (0.7)
AIR				
C ($mg \cdot g^{-1}$)	538.2 (14.8)	529.3 (12.2)	499.7 (20.6)	511.8 (44.3)
C:N ratio	32.0 (1.2)	29.3 (1.7)	23.6 (1.0)	24.0 (1.7)
^{13}C composition	–28.0 (0.4)	–28.4 (0.2)	–29.7 (0.1)a	–29.3 (0.2)b

Note: Each value is the mean of three replicates. Values in parentheses show the standard deviation. Within each row, values followed by a different letter are significantly different at $p < 0.05$, based on a one-way ANOVA. WATER, water-extractable fraction; AIR, acid-insoluble residue.

85% of total forest-floor mass (Table 2). WATER was the next most abundant fraction, making up about 10% of the total forest-floor mass, with CHLORO and METH each accounting for less than 3%. Two-way ANOVA revealed no significant effects of clear-cut harvesting or stand type on the distribution of organic matter among proximate fractions in FH-layer forest floors (data not shown).

Regardless of the source of the sample, unfractionated forest floors had greater C concentrations (mg/g) and higher C:N ratios than the WATER fraction, and smaller C concentrations and lower C:N ratios than the AIR fraction (Table 3). In addition, unfractionated forest floors were depleted in ^{13}C relative to the WATER fraction and enriched in ^{13}C relative to the AIR fraction. The C:N ratio and abundance of ^{13}C in unfractionated forest floors and in the WATER fraction and AIR fraction from SPRUCE stands were consistently greater than in those from ASPEN stands (Table 4). Unfractionated FH-layer forest floors from SPRUCE stands also had a higher C concentration than those from ASPEN stands. The ^{13}C composition of the AIR fraction showed a significant interaction between stand type and harvesting treatment. One-way ANOVA indicated that the AIR fraction of FH-layer forest floors from clear-cut ASPEN stands was significantly enriched in ^{13}C relative to FH-layer forest floors from uncut ASPEN stands (Table 3; $p = 0.049$). In contrast, the ^{13}C composition of the AIR fraction of SPRUCE forest floors did not differ significantly (at $p < 0.05$) in clearcuts and uncut stands.

NMR spectroscopy

The major peaks in the ^{13}C NMR spectra of FH-layer forest floors from uncut SPRUCE and ASPEN stands, which have been described elsewhere (Hannam et al. 2004), were similar to those of FH-layer forest floors from clearcuts (Fig. 1). Briefly, the peaks at 30 ppm in the ALK region indicate that alkyl C in these forest floors was mainly of polymethylene origin (Keeler and Maciel 2000), while the shoulders at 56 ppm, which were stronger in FH-layer forest floors from clear-cut and uncut ASPEN stands, indicate the presence of methoxyl C from lignin. The O-ALK region was dominated by a peak at 73 ppm, with a shoulder at 63 ppm, characteristic of C in carbohydrates such as cellulose and hemicelluloses (Preston et al. 2000). In the AROM region, the small peaks at 104, 117, and 130–131 ppm probably originate from aromatic C in guaiacyl, syringyl, and *p*-hydroxyphenyl lignin monomers and from tannins or tannin-like structures (Preston et al. 2000). A single peak, probably originating from the methoxylated aromatic carbons of guaiacyl and syringyl lignin monomers, was apparent around 151–154 ppm in all spectra of FH-layer forest floors from ASPEN stands. Spectra of FH-layer forest floors from SPRUCE stands showed two peaks, one at 145–148 ppm and the other at 151–154 ppm, that are considered indicative of the presence of condensed tannins (Landucci et al. 1998; Lorenz et al. 2000; Preston et al. 2000). Finally, the CARB region was dominated by a peak at 175 ppm, indicative of the carbonyl C in acetyl and ester moieties (Skjemstad et al. 1997).

DD ^{13}C NMR spectra of FH-layer forest floors from SPRUCE stands showed a strong peak at 130 ppm and two overlapping peaks centered at 145 and 152 ppm, while DD ^{13}C NMR spectra of FH-layer forest floors from ASPEN stands showed a clear peak at 56 ppm and a single peak at 151 ppm. Such a pattern indicates that FH-layer forest floors from uncut and clear-cut SPRUCE stands were relatively depleted in lignin and enriched in condensed tannins compared with FH-layer forest floors from uncut and clear-cut ASPEN stands (Preston et al. 1997; Lorenz et al. 2000).

Qualitative differences in the NMR spectra of FH-layer forest floors from uncut and clear-cut stands of either stand type were not immediately obvious, apart from a general broadening of peaks in the spectra of FH-layer forest floors from the clearcuts. However, the abundance of *O*-aryl C (~140 to ~160 ppm) was relatively lower than that of *C*-aryl C (~112 to ~140 ppm) in FH-layer forest floors from the clearcuts of both stand types, although the pattern was most

Table 4. Results of two-way ANOVA of carbon (C) concentrations, C:N ratios, and ^{13}C-isotope compositions of unfractionated FH-layer forest floors and selected proximate fractions of FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	Source of varation	df	SS	p
Unfractionated forest floor				
C concentration	H	1	1.38	0.54
	S	1	31.92	**0.015**
	H × S	1	1.64	0.51
	Error	8	26.96	
C:N ratio	H	1	3.17	0.33
	S	1	108.04	**0.0003**
	H × S	1	2.78	0.36
	Error	8	23.90	
^{13}C composition	H	1	0.046	0.49
	S	1	2.39	**0.0007**
	H × S	1	0.068	0.40
	Error	8	0.69	
WATER				
C concentration	H	1	0.37	0.69
	S	1	0.61	0.61
	H × S	1	0.043	0.89
	Error	8	16.83	
C:N ratio	H	1	0.29	0.74
	S	1	54.97	**0.0015**
	H × S	1	0.33	0.73
	Error	8	19.66	
^{13}C composition	H	1	0.082	0.49
	S	1	2.55	**0.0037**
	H × S	1	0.033	0.66
	Error	8	1.25	
AIR				
C concentration	H	1	0.075	0.92
	S	1	23.42	0.10
	H × S	1	3.31	0.51
	Error	8	55.12	
C:N ratio	H	1	4.09	0.20
	S	1	138.71	**<0.0001**
	H × S	1	7.27	0.097
	Error	8	16.50	
^{13}C composition	H	1	0.00090	0.91
	S	1	5.10	**<0.0001**
	H × S	1	0.42	**0.023**
	Error	8	0.43	

Note: Values in boldface type denote a significant effect at $p < 0.05$. WATER, water-extractable fraction; AIR, acid-insoluble residue; H, harvesting treatment; S, stand type; SS, sum of squares.

obvious in the DD ^{13}C NMR spectra of forest floors from SPRUCE stands (Fig. 1).

^{13}C NMR spectra of FH-layer forest-floor samples collected in 2002 and 2003 from uncut and clear-cut SPRUCE and ASPEN stands were dominated by the O-ALK region, followed by the ALK, the AROM, and finally the CARB region (Table 5). The year of sample collection had a strong effect on the distribution of C within all NMR regions (Table 6). Samples collected in 2002 exhibited consistently lower relative concentrations of alkyl and O-alkyl C and consistently higher relative concentrations of aromatic and carbonyl C than samples collected in 2003. This pattern may reflect year-to-year differences in moisture content (Table 1) and, thus, the degree of microbial processing of organic matter in the 2 years, or small differences in the type of forest-floor material collected for analysis in 2002 and 2003. Nonetheless, there were no significant interactions between year and harvesting treatment or between year and stand type, indicating that the effects of harvesting treatment and stand type on the organic matter composition of these forest floors did not change with sampling date. Thus, O-ALK was significantly more abundant in FH-layer forest floor from SPRUCE stands, while CARB was significantly more abundant in FH-layer forest floor from ASPEN stands (Table 6). Furthermore, there were significant interactions between stand type and harvesting treatment in the abundance of AROM and in the AROM:OALK ratio in these forest floors. One-way ANOVA indicated that the AROM:O-ALK ratio, an index of the extent of organic matter decomposition (Baldock and Preston 1995), was significantly greater in FH-layer forest floors from clear-cut ASPEN stands than from uncut ASPEN stands in 2003 ($p = 0.019$; Table 5). There was also a strong trend toward greater AROM in FH-layer forest floors from clear-cut ASPEN stands than from uncut ASPEN stands in 2003 ($p = 0.071$).

Correlations between proximate fractions, ^{13}C-isotope composition, and NMR regions

There were a number of significant relationships between the results of proximate fractionation, determination of ^{13}C-isotopic composition, and analysis using CPMAS ^{13}C NMR spectroscopy. For example, there was a negative relationship between ACID and CARB and between AIR and O-ALK, but a positive relationship between AIR and CARB (Table 7). The ^{13}C composition of the acid-insoluble residue (^{13}C-AIR) was negatively correlated with ALK and CARB and positively correlated with AROM and WATER + METH.

Discussion

Despite the relatively short time since harvest, there was considerable evidence that the organic matter composition of FH-layer forest floors from ASPEN and SPRUCE stands had been altered by timber removal: (*i*) the acid-insoluble residue of forest floors from clear-cut ASPEN stands was enriched in ^{13}C relative to the acid-insoluble residue of forest floors from uncut ASPEN stands; (*ii*) aromatic C concentrations were higher in forest floors from clearcuts, particularly in ASPEN stands; and (*iii*) phenolic C concentrations were lower in forest floors from clearcuts, particularly in SPRUCE stands. Such changes are probably related to reductions in above- and below-ground inputs of fresh organic material after clear-cut harvesting and to continued decomposition of the organic matter in the forest floors of these clear-cut stands.

Following clear-cutting, forest floors from both SPRUCE and ASPEN stands at the EMEND site exhibited less fine-root biomass and lower quantities of litter input. However, fine-root biomass and litter-input rates remained higher in forest

Fig. 1. Representative cross-polarization magic-angle spinning and dipolar-dephased ^{13}C nuclear magnetic resonance spectra of FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN).

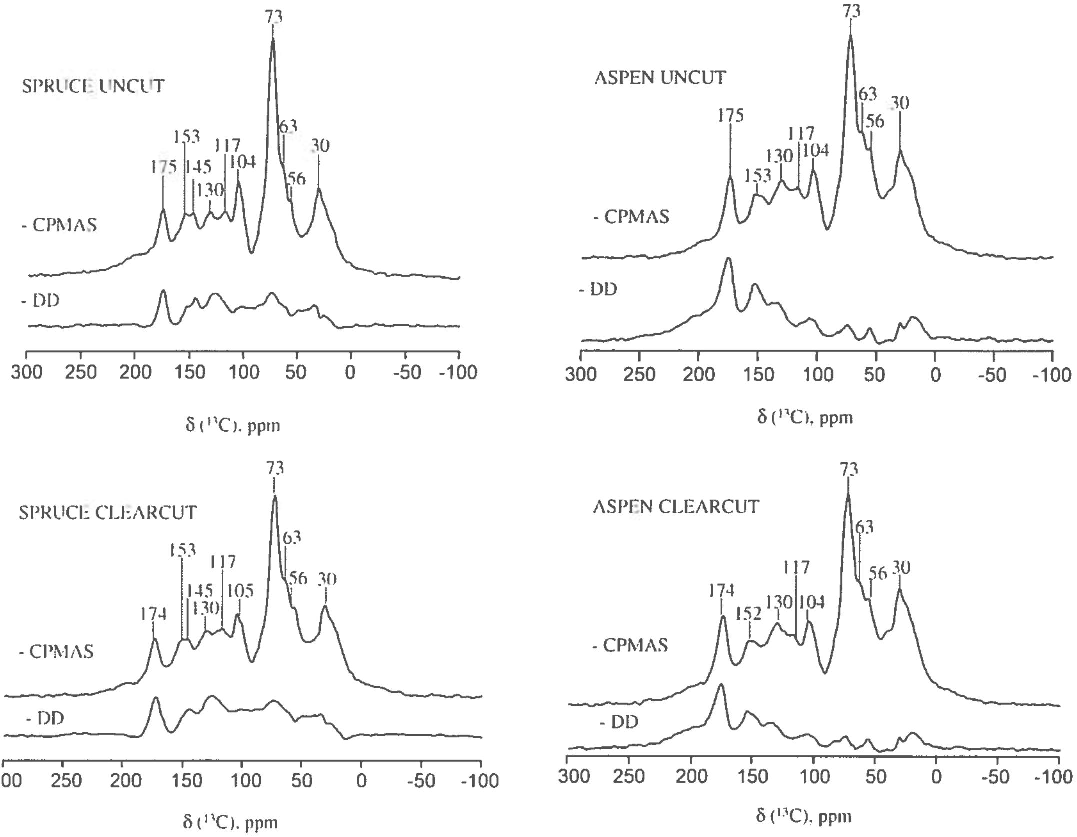

Table 5. Distribution of carbon (C: % of total peak area) in ALK, O-ALK, AROM, and CARB regions of CPMAS ^{13}C NMR spectra obtained from the FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	SPRUCE		ASPEN	
	Uncut	Clear-cut	Uncut	Clear-cut
2002				
ALK	21.4 (1.8)	22.7 (2.1)	22.8 (1.6)	22.5 (1.6)
O-ALK	52.9 (2.1)	54.6 (2.8)	52.1 (2.0)	50.6 (2.5)
AROM	17.4 (0.2)	14.9 (2.8)	14.5 (1.5)	16.2 (1.8)
CARB	8.3 (0.4)	7.7 (1.5)	10.6 (0.4)	10.8 (0.06)
ALK:O-ALK	0.41 (0.05)	0.42 (0.03)	0.44 (0.05)	0.45 (0.05)
AROM:O-ALK	0.33 (0.02)	0.27 (0.07)	0.28 (0.04)	0.32 (0.05)
2003				
ALK	25.3 (2.1)	24.1 (0.1)	25.8 (2.0)	25.7 (1.4)
O-ALK	58.6 (2.0)	58.4 (2.4)	56.8 (1.0)	54.6 (1.4)
AROM	11.9 (0.4)	12.7 (1.2)	11.5 (0.6)	13.1 (1.0)
CARB	4.1 (0.2)	4.7 (1.2)	6.0 (0.5)	6.6 (0.7)
ALK:O-ALK	0.43 (0.05)	0.41 (0.02)	0.45 (0.04)	0.47 (0.04)
AROM:O-ALK	0.20 (0.01)	0.22 (0.03)	0.20 (0.01)a	0.24 (0.02)b

Note: Each value is the mean of three replicates. Values in parentheses show the standard deviation. Within each row, values followed by a different letter are significantly different at $p < 0.05$, based on a one-way ANOVA. ALK, alkyl C; O-ALK, *O*-alkyl C; AROM, aromatic C; CARB, carbonyl C.

Table 6. Results of two-way ANOVA (with year as a split effect) of the distribution of C (% of total peak area) in ALK, O-ALK, AROM, and CARB regions of CPMAS ^{13}C NMR spectra obtained from FH-layer forest floors from uncut and clear-cut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site.

	Source of variation	df	SS	*p*
ALK	S	1	3.77	0.28
	H	1	0.013	0.95
	S × H	1	0.18	0.81
	Error 1	8	22.13	0.54
	Y	1	49.30	**0.0035**
	Y × S	1	0.24	0.78
	Y × H	1	2.09	0.43
	Y × S × H	1	3.03	0.34
	Error 2	8	22.13	
O-ALK	S	1	42.21	**0.0048**
	H	1	1.65	0.47
	S × H	1	10.10	0.96
	Error 1	8	22.73	0.84
	Y	1	123.87	**0.0018**
	Y × S	1	0.19	0.86
	Y × H	1	2.30	0.55
	Y × S × H	1	0.57	0.76
	Error 2	8	46.97	
AROM	S	1	1.03	0.40
	H	1	0.69	0.49
	S × H	1	9.51	**0.028**
	Error 1	8	10.57	0.83
	Y	1	71.11	**0.0009**
	Y × S	1	0.85	0.59
	Y × H	1	3.87	0.26
	Y × S × H	1	4.24	0.24
	Error 2	8	21.52	
CARB	S	1	31.00	**<0.0001**
	H	1	0.33	0.29
	S × H	1	0.26	0.34
	Error 1	8	2.03	0.96
	Y	1	94.40	**<0.0001**
	Y × S	1	0.97	0.34
	Y × H	1	0.99	0.33
	Y × S × H	1	0.19	0.67
	Error 2	8	7.50	
ALK:O-ALK	S	1	0.0076	0.070
	H	1	0.000083	0.83
	S × H	1	0.0036	0.66
	Error 1	8	0.0014	0.54
	Y	1	0.0015	0.40
	Y × S	1	0.000081	0.84
	Y × H	1	0.00018	0.77
	Y × S × H	1	0.00062	0.58
	Error 2	8	0.015	
AROM:O-ALK	S	1	0.00011	0.72
	H	1	0.00048	0.45
	S × H	1	0.0054	**0.030**
	Error 1	8	0.0062	0.83
	Y	1	0.044	**0.0007**
	Y × S	1	0.00019	0.74
	Y × H	1	0.0016	0.35
	Y × S × H	1	0.0020	0.29
	Error 2	8	0.013	

Table 6 (*concluded*).

Note: Values in boldface type denote a significant effect at $p < 0.05$. ALK, alkyl C; O-ALK, *O*-alkyl C; AROM, aromatic C; CARB, carbonyl C; S, stand type; H, harvesting treatment; Y, year; SS, sum of squares.

floors from ASPEN clearcuts than in those from SPRUCE clearcuts (Lindo and Visser 2003). Given that dissolved organic C leached from senesced foliage and exudates from fine roots are important sources of microbially available C (Clein and Schimel 1995; Grayston et al. 1996; Magill and Aber 2000; Park et al. 2002), stronger quantitative changes in the composition of FH-layer forest floors from clear-cut ASPEN stands than in those from clear-cut SPRUCE stands may be due to differences in the rates of microbial activity and, thus, organic matter processing in these forest floors. Indeed, microbial C concentrations and C mineralization rates were greater in forest floors from clear-cut ASPEN stands than in those from clear-cut SPRUCE stands 2.5 years after harvesting at the EMEND site (Lindo and Visser 2003), which suggests that microbial activity was probably greater in the FH-layer of clear-cut ASPEN stands.

Stand-type differences in the susceptibility of forest-floor organic matter to decomposition may also have contributed to differences in the pattern of change observed in the forest floors from ASPEN and SPRUCE stands after clear-cut harvesting. Although relative concentrations of O-ALK (associated with carbohydrates) were greater in FH-layer forest floors from SPRUCE stands than in those from ASPEN stands (Table 5), there was a stronger trend in ASPEN stands toward reduced O-ALK in forest floors from the clearcuts, particularly in 2003 ($p = 0.10$). Given that a large fraction of carbohydrates in forest soil may be physically protected and therefore less susceptible to decomposition (Zech et al. 1992), the stronger treatment difference in O-ALK in FH-layer forest floors from ASPEN stands suggests that a larger fraction of the carbohydrates in these forest floors was available for microbial degradation than that in SPRUCE forest floors. If this is the case, carbohydrates in FH-layer forest floors from ASPEN stands may have more strongly stimulated microbial decomposition of the AIR fraction, leading to a greater change in the ^{13}C composition of the AIR fraction in forest floors from ASPEN stands than in those from SPRUCE stands.

The increased abundance of ^{13}C in the AIR fraction of FH-layer forest floors from ASPEN stands was unexpected because AIR is generally the fraction that is considered most resistant to microbial decay (McClaugherty et al. 1985; Melillo et al. 1989; Ryan et al. 1990). As a result, the AIR fraction was not expected to show significant changes in composition in the short time that had elapsed since harvesting. Enrichment in ^{13}C during aerobic decomposition is widely believed to be caused by discrimination against ^{13}C during the catabolic breakdown of organic substrates by soil microbes and (or) accumulation of ^{13}C in the microbial biomass and in humic materials of microbial origin (Melillo et al. 1989; Ehleringer et al. 2000; Quideau et al. 2003). This pattern

Table 7. Selected correlation coefficients (Pearson's *r*) describing the relationships between the results of proximate fractionation, ^{13}C-isotope determination, and CPMAS ^{13}C NMR spectroscopy of FH-layer forest floors from clear-cut and uncut stands dominated by white spruce (SPRUCE) and trembling aspen (ASPEN) at the Ecosystem Management Emulating Natural Disturbance site (n = 24).

	CHLORO		METH + WATER		ACID		AIR		^{13}C-AIR	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
ALK	–0.28	0.18	–0.37	0.084	0.00064	0.99	0.37	0.072	**–0.42**	0.040
O-ALK	–0.040	0.85	0.22	0.32	0.35	0.095	**–0.53**	0.0082	0.22	0.31
AROM	0.30	0.15	0.39	0.064	–0.038	0.86	–0.21	0.32	**0.62**	0.0011
CARB	0.075	0.72	–0.29	0.17	**–0.45**	0.027	**0.45**	0.026	**–0.52**	0.010
^{13}C-AIR	–0.57	0.79	**0.51**	0.014	0.22	0.30	–0.37	0.075		

Note: Values in boldface type denote a significant relationship at $p < 0.05$. The adjusted *p* value using a Bonferroni correction is 0.0021. ALK, alkyl C; O-ALK, *O*-alkyl C; AROM, aromatic C; CARB, carbonyl C; CHLORO, chloroform-extractable fraction; METH + WATER, methanol-plus-water-extractable fractions; ACID, acid-soluble fraction; AIR, acid-insoluble residue; ^{13}C-AIR, ^{13}C composition of the acid-insoluble residue.

may have been absent in SPRUCE forest floors because guiacyl monomers that are present in conifer lignin are more depleted in ^{13}C and less susceptible to mineralization than the syringyl monomers that dominate lignin of deciduous origin (Hedges et al. 1985; Goñi and Eglinton 1996). Regardless of the specific mechanisms involved, the ^{13}C enrichment of the AIR fraction in ASPEN stands is probably due to the continued decomposition and humification of organic C in the FH-layer forest floors of these stands after clear-cutting.

Decomposition and humification of organic matter have been associated with an increased abundance of aromatic C following clear-cut harvesting in previous work using ^{13}C NMR. Higher aromatic C concentrations were detected in soil solution collected from a 14-year-old clearcut in New Hampshire compared with soil solution from an uncut hardwood stand nearby (Dai et al. 2001). However, no differences in aromatic C concentration were detected in the organic matter of forest floors from different seral stages of coastal forest on Vancouver Island, which may have been due to the fact that these forest floors were dominated by slowly decomposing, woody material (Preston et al. 2002). In the present study, woody material was avoided during forest-floor sampling, which may have made it easier to detect harvesting effects on the characteristics of forest-floor organic matter, particularly aromatic C.

Despite stronger quantitative differences in the relative abundance of AROM in FH-layer forest floors from clear-cut and uncut ASPEN stands, there is evidence for more advanced microbial processing of aromatic C in forest floors from clearcuts than in those from uncut stands of both stand types. DD ^{13}C NMR spectra of forest floors from clear-cut SPRUCE and ASPEN stands revealed a shift in the aromatic region toward a greater abundance of *C*-aryl C, indicating that less aromatic C in forest floors from the clearcuts had originated directly from plant material (Zech et al. 1992). Instead, this material had been more thoroughly processed and modified by forest-floor microbes. In fact, the trend appeared to be stronger in forest floors from SPRUCE clearcuts. Thus, quantitative changes in the organic matter composition of FH-layer forest floors were stronger in clear-cut ASPEN stands, but important qualitative changes had also occurred in FH-layer forest floors from clear-cut SPRUCE stands.

Although higher soil temperatures and moisture contents are widely believed to increase rates of decomposition following clear-cut harvesting (Bormann et al. 1974), such an effect does not appear to be a contributing factor in this study. As mentioned above, Lindo and Visser (2003) found that microbial biomass and microbial respiration rates were reduced in forest floors from clearcuts relative to those from uncut stands of both stand types 2.5 years after harvest. Furthermore, forest-floor moisture contents were not strongly enhanced in the clearcuts of either stand type when samples were collected in 2002 and 2003, and a litter-bag study revealed no evidence for more rapid decomposition in the clearcuts at the EMEND site (L. Jerabkova, The University of British Columbia, personal communication). Therefore, the changes in composition of forest-floor organic matter that occurred following clear-cutting at the EMEND site do not appear to be the result of enhanced rates of decomposition.

Despite the fact that boreal forest floors have high C:N ratios (Huang and Schoenau 1996; Schwendenmann 2000; Vance and Chapin 2001; Ekblad and Nordgren 2002), low organic matter quality is believed to limit the availability of C to the forest-floor microbial community (Flanagan and Van Cleve 1983; Vance and Chapin 2001; Ekblad and Nordgren 2002). Our results suggest that timber removal altered the properties of the organic matter in forest floors from both SPRUCE and ASPEN stands at the EMEND site. In other forested ecosystems, postharvest changes in the nature of the forest floor appear not only to lower the microbial activity of forest soils but also to modify nutrient cycling patterns (Hart et al. 1994; Bradley et al. 2000; Prescott et al. 2003). Data from previous studies at the EMEND site indicate that mineral N and P cycles in the forest floors from SPRUCE and ASPEN stands have been altered by clear-cutting, but the pattern and timing of these changes appear to be stand-type specific, with forest floors from ASPEN stands generally responding more strongly and more rapidly than those from SPRUCE stands (Kishchuk 2002; Lindo and Visser 2003). Such a pattern is consistent with the observation that the organic matter of FH-layer forest floors from ASPEN stands is also more sensitive to clear-cutting than that from SPRUCE stands. The relationship between the properties of forest-floor organic matter and patterns of nutrient cycling remains unclear but is currently being examined at the EMEND site using pool-dilution techniques and enzyme assays (L. Jerabkova, The University of British Columbia, personal communication).

Summary

In summary, 3.5 and 4.5 years after harvesting, the organic matter composition of FH-layer forest floors from clear-cut ASPEN and SPRUCE stands differed from that of uncut stands. The AIR fraction of FH-layer forest floors from ASPEN stands was significantly enriched in ^{13}C, probably as a result of microbial processing. Differences in organic matter composition, as revealed by CPMAS ^{13}C NMR spectroscopy, indicated that forest floors from clear-cut SPRUCE and ASPEN stands had become more enriched in aromatic C. This trend was stronger in FH-layer forest floors from ASPEN stands. Furthermore, aromatic C in FH-layer forest floors from the clearcuts of both stand types showed a shift toward a greater abundance of *C*-aryl C, suggesting that these forest floors had become more humified. This pattern tended to be stronger in forest floors from SPRUCE stands. Taken together, these results indicate that the organic matter of FH-layer forest floors from both clear-cut SPRUCE and ASPEN stands has been modified, but the changes appear to be stronger in ASPEN stands. Previous studies suggest a link between postharvest changes in the nature of forest-soil organic matter and altered patterns of nutrient cycling, a hypothesis that is under investigation.

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References

Baldock, J.A., and Preston, C.M. 1995. Chemistry of carbon decomposition processes in forests as revealed by solid-state carbon-13 nuclear magnetic resonance. *In* Carbon forms and functions in forest soils. *Edited by* J.M. Kelly and W.W. McFee. Soil Science Society of America, Madison, Wis. pp. 89–117.

Ballard, T.M. 2000. Impacts of forest management on northern forest soils. For. Ecol. Manage. **133**: 37–42.

Bennett, A.E., Rienstra, C.M., Auger, M., Lakshmi, K.V., and Griffin, R.G. 1995. Heteronuclear decoupling in rotating solids. J. Chem. Phys. **103**: 6951–6958.

Berg, B., and McClaugherty, C. (*Editors*). 2003. Decomposition as a process. *In* Plant litter: decomposition, humus formation, C sequestration. Springer-Verlag, Berlin. pp. 11–29, 84.

Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. **37**: 911–917.

Bormann, B.T., and Sidle, R.C. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. J. Ecol. **78**: 561–578.

Bormann, F.H., Likens, G.E., Siccam, T.G. Pierce, R.S., and Eaton, J.S. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecol. Monogr. **44**: 255–277.

Bradley, R.L., Titus, B.D., Hogg, K., Preston, C., Prescott, C.E., and Kimmins, J.P. 2000. Assessing the controls on soil mineral-N cycling rates in managed coastal western hemlock ecosystems of British Columbia. J. Sustain. For. **10**: 213–219.

Bryce, D.L., Bernard, G.M., Gee, M., Lumsden, M.D., Eichele, K., and Wasylishen, R.E. 2001. Practical aspects of modern routine solid-state multinuclear magnetic resonance spectroscopy: one-dimensional experiments. Can. J. Anal. Sci. Spectrosc. **46**: 46–82.

Clein, J.S., and Schimel, J.P. 1995. Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. Soil Biol. Biochem. **27**: 743–752.

Dai, K.H., Johnson, C.E., and Driscoll, C.T. 2001. Organic matter chemistry and dynamics in clear-cut and unmanaged hardwood forest ecosystems. Biogeochemistry, **54**: 51–83.

Earl, W.L., and VanderHart, D.L. 1982. Measurement of ^{13}C chemical shifts in solids. J. Magn. Reson. **48**: 35–54.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada, first approximation. Ecological Land Classification Series 23. Ecoregions Working Group of the Canada Committee on Ecological Land Classification, Sustainable Development Branch, Canadian Wildlife Service, Environment Canada, Ottawa, Ont.

Effland, M.J. 1977. Modified procedure to determine acid soluble lignin in wood and pulp. TAPPI, **60**: 143–144.

Ehleringer, J.R., Buchmann, N., and Flanagan, L.B. 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecol. Appl. **10**: 412–422.

Ekblad, A., and Nordgren, A. 2002. Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? Plant Soil, **242**: 115–122.

Environment Canada. 2004. Canadian climate normals or averages 1971–2002: Eureka River, Alberta [online]. Available from http://climate.weatheroffice.ec.gc.ca/climate_normals [cited 1 December 2004].

Flanagan, P.W., and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Can. J. For. Res. **13**: 795–817.

Fogel, R., and Cromack, K., Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. **55**: 1632–1640.

Goñi, M.A., and Eglinton, T.I. 1996. Stable carbon isotopic analyses of lignin-derived CuO oxidation products by isotope ratio monitoring – gas chromatography – mass spectrometry (irm-GC-MS). Org. Geochem. **24**: 601–615.

Grayston, S.J., Vaughan, D., and Jones, D. 1996. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol. **5**: 29–56.

Green, R.N., Trowbridge, R.L., and Klinka, K. 1993. Towards a taxonomic classification of humus forms. For. Sci. Monogr. 29 (For. Sci. Suppl. 39).

Hannam, K.D., Quideau, S.A., Oh, S.-W., Kishchuk, B.E., and Wasylishen, R.E. 2004. Forest floor composition in aspen- and spruce-dominated stands of the boreal mixedwood forest. Soil Sci. Soc. Am. J. **68**: 1735–1743.

Hart, S.C., Nason, G.E., Myrold, D.D., and Perry, D.A. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology, **75**: 880–891.

Hatcher, P.G. 1987. Chemical structural studies of natural lignin by dipolar dephasing solid-state ^{13}C nuclear magnetic resonance. Org. Geochem. **11**: 31–39.

Hedges, J., Cowie, G.L., Ertel, J.R., Barbour, R.J., and Hatcher, P.G. 1985. Degradation of carbohydrates and lignins in buried wood. Geochim. Cosmochim. Acta, **49**: 701–711.

Heng, S., and Goh, K.M. 1981. A rapid method for extracting lipid components from forest litter especially adapted for ecological studies. Commun. Soil Sci. Plant Anal. **12**: 1283–1292.

Huang, W.Z., and Schoenau, J.J. 1996. Forms, amounts and distribution of carbon, nitrogen, phosphorus and sulfur in a boreal aspen forest soil. Can. J. Soil Sci. **76**: 373–385.

Keeler, C., and Maciel, G.E. 2000. ^{13}C NMR spectral editing of humic material. J. Mol. Struct. **550–551**: 297–305.

Keenan, R.J., and Kimmins, J.P. 1993. The ecological effects of clear-cutting. Environ. Rev. **1**: 121–144.

Kinchesh, P., Powlson, D.S., and Randall, E.W. 1995. ^{13}C NMR studies of organic matter in whole soils: II. A case study of some Rothamsted soils. Eur. J. Soil Sci. **46**: 139–146.

Kishchuk, B.E. 2002. Nutritional responses to harvesting and burning in the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment. Final report for soil and nutritional research in the EMEND experiment 1999–2000 under collaborative research agreement with Weyerhaeuser Canada Ltd. Northern Forestry Centre, Canadian Forest Service, Edmonton, Alta.

Kishchuk, B.E. 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-397.

Kögel, I., Hempfling, R., Hatcher, P.G., and Schulten, H.R. 1987. Decomposition in forest humus layers studies by CPMAS 13C NMR, pyrolysis – field ionization – mass spectroscopy and CuO oxidation. Sci. Total Environ. **622**: 111–113.

Kögel-Knabner, I. 1995. Composition of soil organic matter — extractable lipids. *In* Methods in applied soil microbiology and biochemistry. *Edited by* K. Alef and P. Nannipieri. Academic Press, London. pp. 72–73.

Landucci, L.L., Ralph, S.A., and Hammel, K.E. 1998. ^{13}C NMR characterization of guaiacyl, guaiacyl/syringyl and syringyl dehydrogenation polymers. Holzforschung, **52**: 160–170.

Lee, J., Morrison, I.K., Leblanc, J.-D., Dumas, M.T., and Cameron, D.A. 2002. Carbon sequestration in trees and regrowth vegetation as affected by clearcut and partial cut harvesting in a second-growth boreal mixedwood. For. Ecol. Manage. **169**: 83–101.

Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd ed. Elsevier Science, Amsterdam.

Lindo, Z., and Visser, S. 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. Can. J. For. Res. **33**: 1610–1620.

Lorenz, K., Preston, C.M., Raspe, S., Morrison, I.K., and Feger, K.-H. 2000. Litter decomposition and humus characteristics in Canadian and German spruce ecosystems: information from tannin analysis and ^{13}C CPMAS NMR. Soil Biol. Biochem. **32**: 779–792.

Magill, A.H., Aber, J.D. 2000. Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. Soil Biol. Biochem. **32**: 603–613.

Mao, J.-D., Hu, W.-G., Schmidt-Rohr, K., Davies, G., Ghabbour, E.A., and Xing, B. 2000. Quantitative characterization of humic substances by solid-state carbon-13 nuclear magnetic resonance. Soil Sci. Soc. Am. J. **64**: 873–884.

McClaugherty, C.A., Pastor, J., Aber, J.D., and Melillo, J.M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology, **66**: 266–275.

Melillo, J.M., Aber, J.D., and Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology, **63**: 621–626.

Melillo, J.M., Aber, J.D., Linkins, A.E., Ricca, A., Fry, B., and Nadelhoffer, K.J. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *In* Ecology of arable land. *Edited by* M. Clarholm and L. Bergström. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 53–62.

Morrison, I.K., Foster, N.W., and Hazlett, P.W. 1993. Carbon reserves, carbon cycling and harvesting effects in three mature forest types in Canada. N.Z. J. For. Sci. **23**: 403–412.

Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. **52**: 1633–1640.

Nalder, I.A., and Wein, R.W. 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochem. Cycles, **13**: 951–968.

Paré, D., and Bergeron, Y. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can J. For. Res. **26**: 1022–1031.

Park, J.-H., Kalbitz, K., and Matzner, M. 2002. Resource control on the production of dissolved organic carbon and nitrogen in a deciduous forest floor. Soil Biol. Biochem. **34**: 813–822.

Peuravuori, J., Ingman, P., and Pihlaja, K. 2003. Critical comments on accuracy of quantitative determination of natural humic matter by solid state ^{13}C NMR spectroscopy. Talanta, **59**: 177–189.

Prescott, C.E., Maynard, D.G., and Laiho, R. 2000. Humus in northern forests: friend or foe? For. Ecol. Manage. **133**: 23–36.

Prescott, C.E., Hope, G.D., and Blevins, L.L. 2003. Effect of gap size on litter decomposition and soil nitrate concentrations in a high-elevation spruce–fir forest. Can. J. For. Res. **33**: 2210–2220.

Preston, C.M. 2001. Carbon-13 solid-state NMR of soil organic matter — using the technique effectively. Can. J. Soil Sci. **81**: 255–270.

Preston, C.M., Trofymow, J.A., Sayer, B.G., and Niu, J. 1997. ^{13}C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning investigation of the proximate-analysis fractions used to assess litter quality in decomposition studies. Can. J. Bot. **75**: 1601–1613.

Preston, C.M., Trofymow, J.A., and the Canadian Intersite Decomposition Experiment Working Group. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Can. J. Bot. **78**: 1269–1287.

Preston, C.M., Trofymow, J.A., Niu, J., and Fyfe, C.A. 2002. Harvesting and climate effects on organic matter characteristics in British Columbia coastal forests. J. Environ. Qual. **31**: 402–413.

Quideau, S.A., Graham, R.C., Feng, X., and Chadwick, O.A. 2003. Natural isotopic distribution in soil surface horizons differentiated by vegetation. Soil Sci. Soc. Am. J. **67**: 1544–1550.

Ryan, M.G., Melillo, J.M., and Ricca, A. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. Can. J. For. Res. **20**: 166–171.

SAS Institute Inc. SAS® version 8.01 [computer program]. SAS Institute Inc., Cary, N.C.

Schneider, R.R., Stelfox, J.B., Boutin, S., and Wasel, S. 2003. Managing the cumulative impacts of land-uses in the Western Canadian sedimentary basin: a modeling approach. Conserv. Ecol. [online], **7**: 1–14. Available from http://www.ecologyandsociety.org/vol7/iss1/art8/main.html.

Schwendenmann, L. 2000. Soil properties of boreal riparian plant communities in relation to natural succession and clearcutting, Peace River lowlands, Wood Buffalo National Park, Canada. Water Air Soil Pollut. **122**: 449–467.

Scott, N.A., and Binkley, D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia, **111**: 151–159.

Sidders, D.M., and Luchkow, S. 1998. EMEND final harvest layout and extraction pattern [online]. Available from http://www.biology.ualberta.ca/old_site/emend//treatments/ harvest_e.html [cited 1 December 2004].

Skjemstad, J.O., Clarke, P., Golchin, A., and Oades, J.M. 1997. Characterization of soil organic matter by solid-state ^{13}C NMR spectroscopy. *In* Driven by Nature — plant litter quality and decomposition. *Edited by* G. Cadisch and K.E. Giller. CAB International, Wallingford, UK. pp. 253–271.

Smernik, R.J., and Oades, J.M. 2003. Spin accounting and RESTORE — two new methods to improve quantitation in solid-state ^{13}C NMR analysis of soil organic matter. Eur. J. Soil Sci. **54**: 103–116.

Spence, J.R. 2001. The new boreal forestry: adjusting timber management to accommodate biodiversity. Trends Ecol. Evol. **160**: 591–593.

Stump, L.M., and Binkley, D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. **23**: 492–502.

Suberkropp, K., Godshalk, G.L., and Klug, M.J. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology, **57**: 720–727.

Technical Association of the Pulp and Paper Industry (TAPPI). 1999. Water solubility of wood and pulp. Pulp Properties Committee of the Process and Product Quality Division, TAPPI, Atlanta, Ga. T207 cm-99.

Ussiri, D.A.N., and Johnson, C.E. 2003. Characterization of organic matter in northern hardwood forest soil by ^{13}C NMR spectroscopy and chemical methods. Geoderma, **111**: 123–149.

Vance, E.D., and Chapin, F.S., III. 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biol. Biochem. **33**: 173–188.

Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. **13**: 747–766.

Webster, E.A., Hopkins, D.W., Chudek, J.A., Haslam, S.F.I., Šimek, M., and Pîcek, T. 2001. The relationship between microbial carbon and the resource quality of soil carbon. J. Environ. Qual. **30**: 147–150.

Wiken, E.B. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series 19. Environment Canada, Ottawa, Ont.

Wilson, M.A., and Hatcher, P.G. 1988. Detection of tannins in modern and fossil barks and in plant residues by high-resolution solid-state ^{13}C nuclear magnetic resonance. Org. Geochem. **12**: 539–546.

Zech, W., Johansson, M.-B., Haumaier, L., and Malcolm, R.L. 1987. CPMAS ^{13}C NMR and IR spectra of spruce and pine litter and of the Klason lignin fraction at different stages of decomposition. Z. Pflanzenernaehr. Bodenkd. **150**: 262–265.

Zech, W., Ziegler, F., Kogel-Knabner, I., and Haumaier, L. 1992. Humic substance distribution and transformation in forest soils. Sci. Total Environ. **117–118**: 155–174.

Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types

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Abstract: We investigated whether impacts on boreal forest songbird communities in northwestern Alberta could be mitigated through a harvesting system that attempts to emulate the local natural disturbance regime. The EMEND (Ecosystem Management by Emulating Natural Disturbance) project is a multidisciplinary experiment to compare clearcuts and partial-retention cuts in four upland cover types with uncut forest and with experimentally burned stands. We studied breeding birds at EMEND between 1998 (pretreatment) and 2000, focusing on their responses to partial harvesting. Partial cuts were generally intermediate (and varied in a linear fashion) between clearcuts and undisturbed forest for community and species measures. Species that declined in abundance in partial cuts were typically dependent on shrubs and trees, whereas species that benefited were typically ground nesters. While partial cutting offered some advantages over clear-cutting in conserving short-term avian diversity, we suggest that low retention levels (i.e., 10%, 20%) cannot be justified from this perspective. The benefits that accrued in these treatments were relatively small, and species that declined or disappeared were typically characteristic of mature forest habitats. Higher retention levels (i.e., 50%, 75%) may conserve some species of concern, but the extent to which these treatments offer productivity advantages over lower residuals requires further study.

Résumé : Les auteurs ont voulu vérifier si les impacts sur les communautés de passereaux forestiers dans le nord-ouest de l'Alberta pouvaient être atténués par un système de récolte qui tente d'émuler le régime local de perturbations naturelles. Le projet EMEND (« Ecosystem Management by Emulating Natural Disturbance », c.-à-d. aménagement écosystémique par l'émulation des perturbations naturelles) est une expérimentation multidisciplinaire visant à comparer les coupes à blanc et les coupes partielles à rétention avec des forêts non coupées et des peuplements issus d'un brûlage expérimental dans quatre types de couverts mésiques. Ils ont étudié les oiseaux nicheurs à EMEND entre 1998 (prétraitement) et 2000 en ciblant leurs réponses à la récolte partielle. Les coupes partielles étaient en général intermédiaires (et variaient selon un profil linéaire) entre les coupes à blanc et la forêt non perturbée en ce qui a trait aux mesures de communauté et d'espèce. Les espèces dont l'abondance diminuait dans les coupes partielles étaient typiquement dépendantes des arbres et arbustes, tandis que celles qui en bénéficiaient étaient des nicheurs au sol. Bien que la coupe partielle offre certains avantages par rapport à la coupe à blanc en conservant à court terme la diversité aviaire, ils ne croyent pas que de faibles niveaux de rétention (c.-à-d. 10 %, 20 %) soient justifiables de ce point de vue. Les bénéfices obtenus par ces traitements sont relativement faibles et les espèces qui ont diminué ou sont disparues étaient typiquement caractéristiques des forêts matures. Des niveaux plus élevés de rétention c.-à-d. 50 %, 75 %) peuvent conserver certaines espèces visées, mais il faudra d'autres études pour déterminer dans quelle mesure ces traitements offrent des avantages en termes de productivité par rapport aux niveaux plus faibles de rétention.

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Introduction

The response of forest birds to harvesting has been the subject of considerable research over the past few decades. At the stand level, forest harvesting creates conditions amenable to species favouring early-successional habitats (i.e., Crawford et al. 1981; Thompson et al. 1992) and generally leads to a decrease in the number of habitat dimensions available to birds (DesGranges and Rondeau 1993). In other words, the forest characteristics that create ecological niches for birds are those that are reduced by harvesting: vegetation composition and layering (MacArthur and MacArthur 1961; Franzreb and Ohmart 1978), snags and coarse woody debris (Niemi and Hanowski 1984; Hansen et al. 1991; Westworth and Telfer 1993), and stand age (Schieck and Nietfeld 1995; Kirk et al. 1996).

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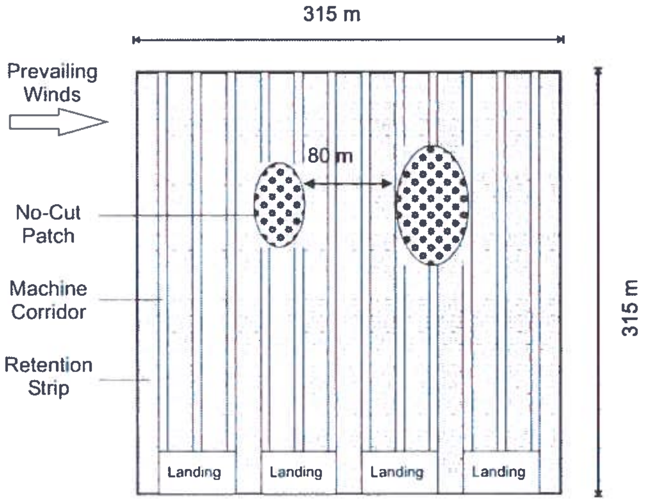
Recently, efforts have been made to mitigate harvesting impacts on ecological integrity through a natural disturbance paradigm, which suggests that critical processes inherent in forest systems might be maintained by emulating natural disturbance patterns (Hunter 1993*a*; Haila 1994; Brawn et al. 2001), for instance, via partial cutting. Natural disturbances such as fire (the major agent of stand replacement in the western boreal forest) typically leave structural legacies of live and dead woody material, reducing the contrast between disturbed and undisturbed stands (Hansen et al. 1991). If partial cutting can leave behind similar legacies, harvesting might better approximate natural patterns (Lee et al. 1997), and the impact of tree removal may be lessened (Merrill et al. 1998; Schieck and Hobson 2000).

The usefulness of the natural disturbance approach at present lacks substantial empirical support. There is debate as to whether logging can effectively mimic fire (DesGranges and Rondeau 1993; Hutto 1995) in terms of site disturbance, soil fertility, and residual snags and woody debris. Comparisons of fire- and logging-origin stands indicate convergence over time for spider communities (Buddle et al. 2000), but only partial convergence in terms of vegetation (Crites 1999) and bird communities (Schulte and Niemi 1998; Hobson and Schieck 1999; Schieck and Hobson 2000; Simon et al. 2002). More specifically, the effects of partial cutting on bird communities have been studied throughout western North America, including areas in the western United States (Franzreb and Ohmart 1978; Medin and Booth 1989; Anderson and Crompton 2002), the Pacific Northwest (Hansen et al. 1995; Beese and Bryant 1999; Hayes et al. 2003), and the British Columbia Interior (Steventon et al. 1998; Lance and Phinney 2001; Leupin et al. 2004). In the boreal mixedwood forest of western Canada, Norton and Hannon (1997), Tittler (1998), and Tittler et al. (2001) examined the effects of group retention harvesting in deciduous-dominated forest in northeastern Alberta. In general, these studies have indicated that partially harvested stands initially retain a portion of the mature forest bird community not found in clearcuts, while still allowing the incursion of some early-successional species.

The EMEND (Ecosystem Management by Emulating Natural Disturbance) project is a multidisciplinary research project initiated in 1995 in northwestern Alberta, Canada. EMEND is an attempt to model harvest and regeneration of upland mixedwood forests on natural disturbance regimes via a comparison of partial-retention cuts (human-caused disturbances) with stands burned at a variety of intensities (natural disturbances). Unharvested controls were also maintained. EMEND represented a good opportunity to test whether traditional logging practices in the boreal mixedwood forest could be modified at the stand level to better accommodate nontimber values, such as avian biodiversity.

In this paper we detail 3 years of field study (1998–2000) of the effects of partial cutting on songbird communities at EMEND, as detected by point count sampling. Six levels of tree retention were examined in four cover types. Based, in part, on trends found in other partial-cut studies in western North America, we predicted that partial cuts would be intermediate between clearcuts and unharvested controls for all community measures, in all forest cover types, and that measures would vary linearly with level of tree retention. We also predicted that guilds and species dependent on shrub or tree cover for nesting and foraging would be most negatively impacted by harvesting and that their abundance would also vary linearly with level of retention.

Fig. 1. Schematic representation of compartmental layout at EMEND, Alberta, Canada.



Materials and methods

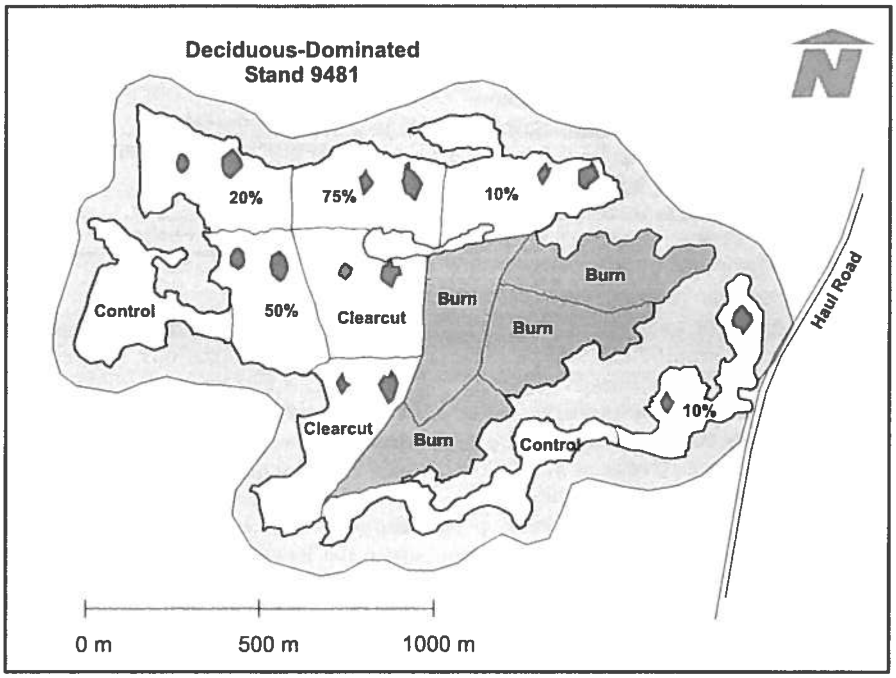
Study area

The EMEND project is located in an area of upland boreal mixedwood forest near Peace River in northwestern Alberta (56°44′N, 118°20′W). Dominant tree species in this region include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). Older stands are characterized by white spruce (*Picea glauca* (Moench) Voss), and wet areas of black spruce (*Picea mariana* (Mill.) B.S.P.) are interspersed throughout the landscape. Understory vegetation on mesic sites is commonly composed of wild rose (*Rosa* spp.), low-bush cranberry (*Viburnum edule* (Michx.) Raf.), and alder (*Alnus crispa* (Ait.) Pursh, *Alnus rugosa* (Du Rois) Spreng.). The topography is generally low and rolling, with some plateaus, and soils are typically luvisolic (Strong and Leggat 1981).

Experimental design

EMEND is a large-scale experiment (>1000 ha) designed to systematically study combinations of two driving variables: forest canopy composition and amount of residual structure left after harvest. Four mature forest cover types were represented: (1) deciduous dominated (80%–95%); (2) deciduous dominated with coniferous understory (extensive and at least 50% of canopy height); (3) mixed (conifer and deciduous composition each 35%–65%); (4) conifer dominated (80%–95%). Deciduous trees were primarily trembling aspen, with a secondary balsam poplar component; coniferous trees were almost exclusively white spruce. Within each cover type, six levels of tree retention were chosen: 0% (clearcut), 10%, 20%, 50%, 75%, and 100% (control). Three replicates of each treatment were selected for

Fig. 2. Example of spatial arrangement of treatment and control compartments in one block at EMEND, Alberta, Canada. Dark polygons within treatment compartments represent retention ellipses. Burn treatments were part of EMEND experimental design, but had not been carried out at the time of this study.



each forest type. Here, we use "retention" and "residual" synonymously.

Site selection occurred in 1997; baseline data were collected in the spring–summer of 1998, and harvesting treatments were implemented in the winter of 1998–1999 in cutblocks or "compartments", each approximately 8–10 ha in size. Harvesting was in a uniform shelterwood strip pattern (Fig. 1), with 15 m wide retention strips separated by 5 m wide machine corridors, oriented in a north–south direction (perpendicular to prevailing winds). Different levels of tree retention were attained by varying the degree of tree extraction from retention strips. Two additional elliptical patches (0.25 and 0.5 ha) of trees were retained in most of the harvested compartments for use as intrastand controls for other studies. Compartments were arranged in a partially blocked design, with constrained allocation of treatment types, and were separated from the surrounding landscape by 50–100 m forested buffers. Typically, blocks were at least 500 m apart, and controls were at least 1000 m apart. Within blocks, treated compartments were usually adjacent to two or more treatments, whereas controls were usually adjacent to only one treatment and surrounded on three sides by undisturbed forest (Fig. 2). Posttreatment bird sampling was conducted in 1999 and 2000. Harvesting implications have been interpreted in relation to preharvest conditions and uncut control stands.

Vegetation surveys

The composition and structure of the vegetation surrounding each bird sampling station was measured in August 1998 using a protocol modified from Martin (1992*a*). Circular plots of 0.04 ha were centered on the station. Ground cover in seven categories was estimated to the nearest 5%, in four nested 1-m^2 quadrats. Stems of shrubs between 50 and 140 cm high were also counted within these quadrats. Saplings (dbh <2.5 cm) and poles (dbh 2.5–8 cm) were counted by species in a 0.008-ha nested subplot, and trees in four diameter classes (8–15, 15–23, 23–38, and >38 cm) were tallied by species for the entire plot. We also recorded the number of snags in five diameter classes (8–12, 12–15, 15–23, 23–38, and >38 cm). Posttreatment vegetation was surveyed in 2000 using the same methodology in the same compartments. Plots that overlapped retention ellipses were moved outside the ellipse in a randomly chosen direction to better represent treatment-related changes.

Bird surveys

We used a fixed-radius point count method (Hutto et al. 1986) to estimate relative abundance within compartments. Every combination of cover type and treatment was sampled, and each compartment contained one or two randomly situated points, depending on its configuration. We visited each point three times in 1998 and five times in both 1999 and 2000 during the breeding season (mid-May to early July). During each visit, observers recorded all birds seen and heard within a given radius around the point, over a 5-min sampling interval. Approximately half the point count stations were 100 m radius counts, where observations were noted within two concentric circles: one at 50 m and one at 100 m. At the remaining points, observations were limited to one 50 m radius circle because of compartment size constraints. Birds observed flying over the point were recorded in the field but excluded from all analyses. The methodology was standardized to reduce possible sources of seasonal, diurnal, and environmental bias, within and between years (Verner 1985), and observers were trained in detection and counting

Fig. 3. Mean changes in bird species richness per sampling station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to cubic regression in coniferous sites and linear regression in all others. Line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 6.7 (4.3–8.9); mixed = 4.5 (0.6–7.7).

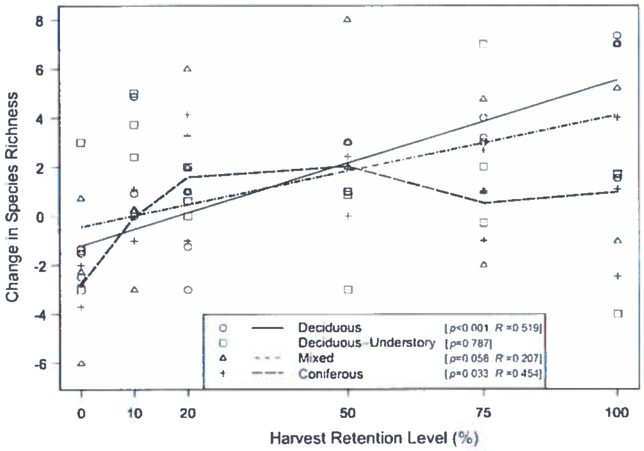
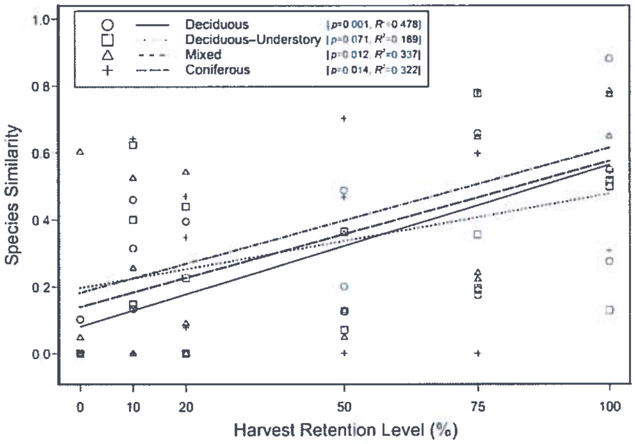


Fig. 4. Mean species similarity per compartment between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to linear regression in all sites. Line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 0.47 (0.25–0.73); deciduous–understory = 0.27 (0.02–0.49); mixed = 0.43 (0.15–0.68); coniferous = 0.42 (0.26–0.61).



residual level increased in all four cover types (Fig. 4), due in part to the low similarity (or complete turnover) of bird communities in clearcuts between years. An overall increase in similarity across treatments between the first and second postharvest year was detected for MIX sites ($p = 0.032$).

Of the 71 forest bird species detected between 1998 and 2000, foraging guilds consisted of aerial foragers (16 species = 23%), bark gleaners (9 species = 13%), foliage gleaners (23 species = 32%), and ground gleaners (23 species = 32%). Nesting guilds consisted of cavity nesters (15 species = 21%), ground nesters (22 species = 31%), and shrub–tree nesters (34 species = 48%). For some guilds (aerial foragers, bark gleaners, and cavity nesters), per-station bird abundances were low because of a paucity of species and the relatively small sampling area, and therefore data were not analyzed.

Among foraging guilds between 1998 and 2000 (Fig. 5), foliage gleaner abundance increased linearly as residual level increased in three cover types. The remaining cover type (DEC–UND) exhibited a significant cubic relationship for the same period, although a linear trend similar to that for the other cover types was observed between 1998 and 1999 ($p = 0.017$, $R^2 = 0.309$). Conversely, ground forager abundance declined linearly as residual level increased in three cover types. Among nesting guilds (Fig. 6), the abundance of shrub–tree nesters increased linearly as residual level increased in three cover types, and in the fourth type (DEC–UND), a similar linear trend was observed between 1998 and 1999 ($p = 0.088$, $R^2 = 0.172$). Ground nester abundance declined linearly in MIX and CON sites.

An overall increase in abundance across treatments between the first and second postharvest year was detected for foliage gleaners in three cover types (DEC: $p = 0.023$; DEC–UND: $p = 0.099$; MIX: $p = 0.008$), ground foragers in three cover types (DEC: $p = 0.038$; MIX: $p = 0.014$; CON: $p = 0.001$), ground nesters in all cover types (DEC: $p = 0.002$; DEC–UND: $p = 0.007$; MIX: $p = 0.015$; CON: $p = 0.001$), and shrub–tree nesters in one cover type (MIX: $p = 0.008$).

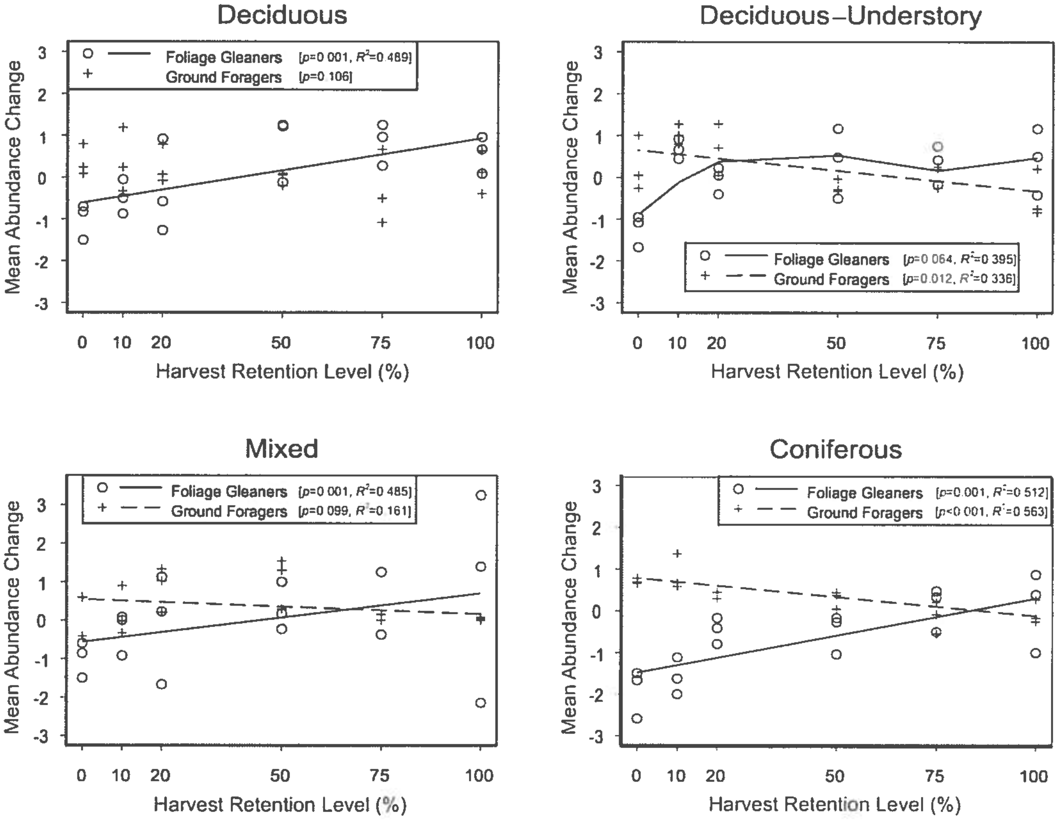
Changes in annual abundances were analyzed for the 15–20 most abundant species in each cover type, or those detected in at least 5 of the 18 compartments, to ensure each analyzed species was represented in two or more compartments in at least two treatments (Appendix A). Only a few species in each cover type exhibited statistically significant mean abundance changes relative to the controls, or significant linear regression trends (Table 3). Small samples resulted in generally low power for these tests. In qualitative terms, among species with enough observations to be analyzed, the 10% and 20% residual treatments exhibited slightly fewer local "extinctions", or species losses, than the clearcuts, where almost all declines were extinctions, and slightly more extinctions than the 50% and 75% residuals (Table 4). Controls experienced almost no extinctions in any cover type.

Discussion

Bird community response

Our prediction that community measures in partial cuts would vary linearly with level of retention was generally supported. In DEC and MIX sites, less retention resulted in lower species richness. In CON sites, a cubic relationship was observed, indicating that the "midrange" retention levels retained species to a greater degree than in other cover types. In DEC–UND sites, no pattern was evident, but the extensive coniferous understory and more complex vegetative structure may have "buffered" species loss in harvest treatments. Interestingly, the number of species postharvest actually increased in the higher residuals (50%, 75%, 100%) in most cover types, partly because of an overall rise in richness observed across all treatments in 2000 (as compared to 1999). The reasons for this trend (and the increases in overall abundance exhibited by guilds in 2000 relative to 1999) are unclear, but may be related to regional population fluctuations and a slightly more intensive sampling regime. We do not

Fig. 5. Mean changes in foraging guild abundances per station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to cubic regression for deciduous–understory foliage gleaners and linear regression for all others. Foliage gleaner line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 1.56 (0.90–2.00); mixed = 2.17 (0.98–3.35); coniferous = 1.80 (0.83–2.55). Ground forager line slopes for significant relationships are as follows: deciduous–understory = –1.02 (–1.52 to –0.29); mixed = –0.33 (–0.72 to 0.07); coniferous = –0.91 (–1.29 to –0.56).

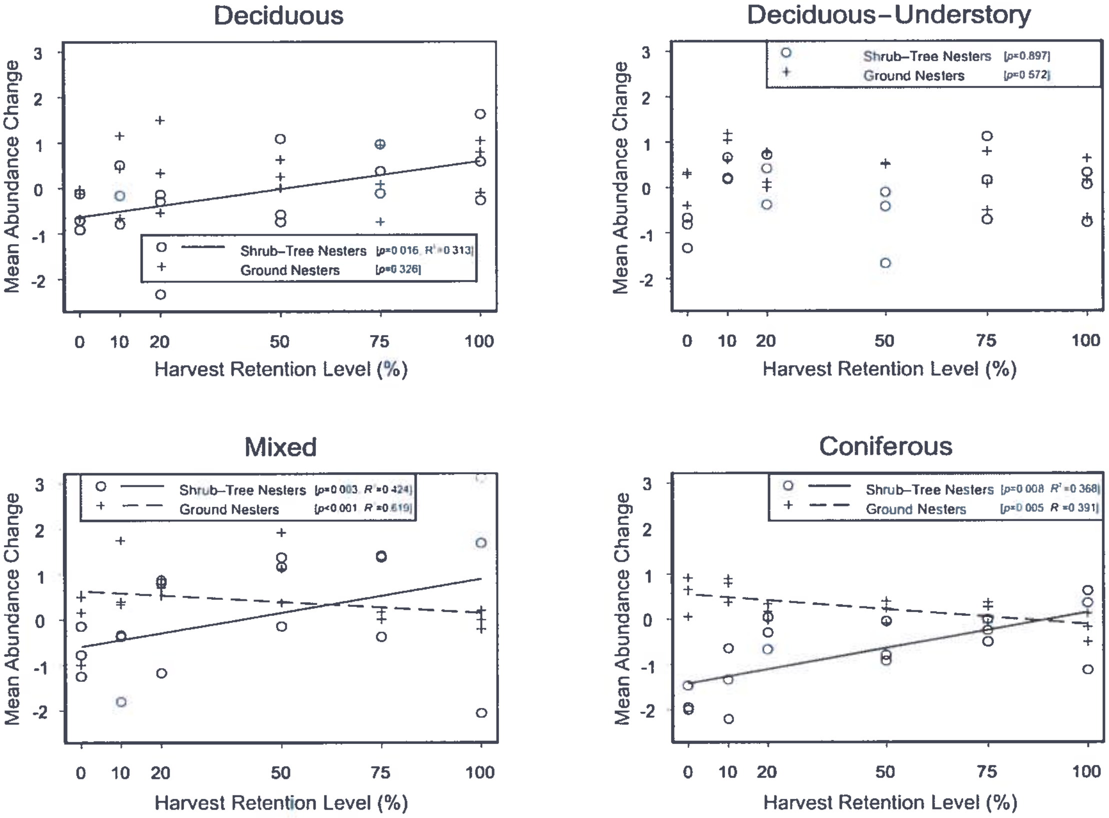


believe increases in the uncut stands reflect posttreatment crowding effects, as controls were typically separated from treatments by a forest buffer on three sides. Additionally, most of the data were collected in the second postharvest year, and studies in similar forests in northeastern Alberta have shown crowding to be relatively ephemeral in these systems (see Schmiegelow et al. 1997; Schmiegelow and Hannon 1999). Patterns of community similarity followed a similar trend in all four cover types: the lower the retention level, the lower the similarity between pre- and post-harvest communities.

Bird response by guild and species

Our second prediction, that guilds and species dependent on shrub or tree cover would be most negatively impacted by partial cutting, was also supported. Guild trends were linear: less retention resulted in lower foliage gleaner and shrub–tree nester abundance (three cover types), but higher ground forager abundance (three cover types) and ground nester abundance (two cover types). Species data were more variable, and many comparisons lacked statistical power, but a distinct pattern emerged. In all cover types, most declines relative to controls occurred in the lower residual treatments (0%, 10%, 20%), by species typically dependent on shrubs or trees for nesting and foraging (i.e., Golden-crowned Kinglet (*Regulus satrapa*), Red-eyed Vireo (*Vireo olivaceus*), Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*)). The Ovenbird (*Seiurus aurocapilla*), which also declined in lower residual treatments, is a ground nester and forager, but requires the presence of canopy trees: Schieck and Nietfeld (1995) classify it as most abundant in mature aspen mixedwood forests in Alberta. Even at higher residual treatments, some species declined in abundance (i.e., Golden-crowned Kinglet, Ovenbird, Swainson's Thrush), and while most declines were not statistically significant, we believe they indicate generally lower habitat quality for these species. Losses typically persisted through both years in all cover types. Most increases relative to the controls were also exhibited in the lower residuals, by ground nesting and foraging species (i.e., Dark-eyed Junco (*Junco hyemalis*), Lincoln's Sparrow (*Melospiza lincolnii*), White-throated Sparrow (*Zonotrichia albicollis*)). An exception to this pattern in all cover types was the Chipping Sparrow (*Spizella passerina*), a ground forager that is generally considered a shrub–tree nester. However, we observed this species nesting on the ground on several occasions in 2000. Mourning Warbler (*Oporornis Philadelphia*) and Tennessee Warbler (*Vermivora peregrina*), both ground nesters, exhibited the same colonization tendency: increases were not observed until the second

Fig. 6. Mean changes in nesting guild abundances per station between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada. Probability and goodness-of-fit measures correspond to linear regression in all sites. Shrub–tree nester line slopes for significant relationships (with 95% confidence interval) are as follows: deciduous = 1.24 (0.41–2.17); mixed = 2.27 (0.87–3.68); coniferous = 1.58 (0.58–2.26). Ground nester line slopes for significant relationships are as follows: mixed = –1.00 (–1.41 to –0.58); coniferous = –0.65 (–1.09 to –0.23).



year postharvest, by which time shrub and sapling regrowth may have been sufficient to satisfy their foraging needs.

In northeastern Alberta, partial cuts in hardwood stands (~10%, 30%, 40%) were also intermediate to clearcuts and controls in most measures after 1 year (Norton and Hannon 1997). Forest dwellers (dependent on trees and shrubs) benefited from increasing residual tree retention, but ground dwellers were generally unaffected. Three years postlogging, species that benefited from the partial cuts tended to be habitat generalists; most forest dwellers had abandoned the partial cuts (Tittler et al. 2001). Accordingly, community similarity was found to be lower between year 0 (preharvest) and year 3 than between year 0 and year 1 (Tittler 1998), perhaps resulting from an initial failure of some species to breed successfully or from competition between forest-dwelling and early-successional species (i.e., ecological lags in response). Tittler et al. (2001) also observed a shift towards species characteristic of open habitats in the third year postharvest, hypothesizing that lags in vegetation regeneration and dispersal resulted in delayed colonization. We detected a similar pattern at EMEND: ground nesters increased between the first and second years postharvest in low-retention treatments in all cover types, and ground foragers increased in all but DEC–UND sites, with most increases attributable to species classified by Tittler et al. as open-habitat birds.

Other forest ecosystems across North America exhibit similar patterns: as a rule, partially harvested stands retain a portion of the mature forest bird community not found in clearcuts, although at lower numbers, while supporting some early-successional species (i.e., Franzreb and Ohmart 1978; Hansen et al. 1995; Costello et al. 2000; Hayes et al. 2003). Bird abundances and species richness are generally proportional to degree of retention, although some studies have detected greater species diversity and (or) abundance in partial cuts compared to that on uncut sites (i.e., Annand and Thompson 1997; Simon et al. 2000; Lance and Phinney 2001; Anderson and Crompton 2002). Whether this effect is observed may depend on regional bird community composition and duration of study. At EMEND, few early-successional colonist species were present in the regional species pool because of the relatively intact condition of the forest; thus, we expected that short-term gains in partial cuts would be outnumbered by losses of mature forest species. This expectation was generally not borne out, as species richness rose across most partial-cut treatments in 2000; however, richness still increased linearly with retention level because of a contemporaneous rise in the uncut controls. All studies report loss of some mature forest-dependent species, typically from groups that nest or forage in the canopy (i.e., Franzreb and Ohmart 1978; Hayes et al. 2003) or which glean bark and nest in cavities (i.e., Medin and Booth 1989; Anderson and Crompton 2002). Species benefiting from partial cuts typically belong to ground-foraging or ground-nesting guilds (i.e., Beese and

Table 3. Significant mean species abundance changes (relative to controls) and regressions observed between 1998 and 2000, as a result of partial harvest of different forest cover types at EMEND, Alberta, Canada.

			Harvest retention level%[c]					Linear regression[d]			
Cover type	Species[a]	Foraging guild, nest guild[b]	0	10	20	50	75	p	R^2	Slope	95% CI
DEC	DEJU	G, G	+					ns			
	WTSP	G, G		+				(0.077)	0.183	–0.26	–0.55 to –0.03
	CAWA	A, G					–	ns			
	REVI	A, ST	–		–			(<0.001)	0.595	0.36	0.20 to 0.52
	TEWA	F, G	–					(0.001)	0.492	0.40	0.18 to 0.61
	GCKI	F, ST			–			ns			
	YRWA	F, ST		–	–			0.059	0.206	0.44	0.20 to 0.63
	RBNU	B, C	–					ns			
	YBSA	B, C					–	ns			
DEC–UND	DEJU	G, G		+				0.039	0.241	–0.28	–0.46 to –0.06
	LISP	G, G		+				ns			
	OVEN	G, G						0.033	0.253	0.39	0.12 to 0.76
	CHSP	G, ST			+			0.028	0.266	–0.47	–0.77 to –0.20
	YRWA	F, ST	–					ns			
MIX	DEJU	G, G			+	+		ns			
	OVEN	G, G		–				ns			
	WTSP	G, G		+				ns			
	CHSP	G, ST				+		ns			
	MOWA	F, G		+				ns			
	SWTH	F, ST	–	–		–		0.021	0.290	0.21	0.07 to 0.38
	YRWA	F, ST				+		ns			
CON	DEJU	G, G	+					0.026	0.275	–0.35	–0.55 to –0.19
	LISP	G, G						(0.086)	0.173	–0.15	–0.32 to 0.02
	GRJA	G, ST				+		ns			
	BTNW	F, ST		–				ns			
	GCKI	F, ST	–		–	–		(0.015)	0.315	0.49	0.11 to 0.88
	WETA	F, ST		–				ns			
	WWCR	F, ST					+	ns			
	YRWA	F, ST	–	–	–			(<0.001)	0.803	1.05	0.77 to 1.32
	RBNU	B, C					+	ns			

[a] BTNW, Black-throated Green Warbler; CAWA, Canada Warbler; CHSP, Chipping Sparrow; DEJU, Dark-eyed Junco; GCKI, Golden-crowned Kinglet; GRJA, Gray Jay; LISP, Lincoln's Sparrow; MOWA, Mourning Warbler; OVEN, Ovenbird; RBNU, Red-breasted Nuthatch; REVI, Red-eyed Vireo; SWTH, Swainson's Thrush; TEWA, Tennessee Warbler; WETA, Western Tanager; WTSP, White-throated Sparrow; WWCR, White-winged Crossbill; YBSA, Yellow-bellied Sapsucker; YRWA, Yellow-rumped Warbler.

[b] Foraging guilds: A, aerial; B, bark; F, foliage; G, ground. Nesting guilds: C, cavity; G, ground; ST, shrub or tree.

[c] Changes compared to control values using independent sample Student's t tests, $\alpha = 0.10$.

[d] p values in parentheses were determined by weight estimation regression; ns, not significant; positive slope indicates an increase in abundance with increasing retention; negative slope indicates a decrease in abundance with increasing retention; CI denotes confidence interval.

Bryant 1999; Simon et al. 2000). Finally, most studies agree that partial cutting cannot accommodate all native bird species. Addressing this objective requires a variety of management approaches across multiple spatial scales, including the retention of unharvested areas (i.e., landscape-level retention) to accommodate the needs of sensitive species.

None of the species observed at EMEND are on the national list of species at risk prepared by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2004), nor are any designated as threatened or endangered provincially in Alberta. However, several species are designated as "sensitive" provincially, indicating that special attention may be required to prevent them from becoming at risk (Alberta Sustainable Resource Development 2003). Two of these, the Black-throated Green Warbler (*Dendroica virens*; in CON sites) and the Canada Warbler (*Wilsonia canadensis*; in DEC sites), exhibited significant decreases in harvest treatments. Most of the other species were observed too infrequently for resultant data to be analyzed, yet several are considered sensitive to forestry activities in boreal mixedwood forests (Hannon et al. 2004). Resident species, as a group, are of particular conservation concern in boreal forests (Schmiegelow and Mönkkönen 2002) and are often not well sampled during conventional point count survey periods because of the earlier onset of breeding activities. Alternate survey techniques are thus required to evaluate responses of these species to partial cutting.

Caveats

Short temporal scale

While this study had the advantage of a strong pre- and post-harvest design, we monitored only short-term responses;

Table 4. Mean species abundance changes observed between 1998 and 2000, as a result of partial harvest (categories represent 0%–100% harvest retention levels) of different forest cover types at EMEND, Alberta, Canada.

	DEC[b]						DEC–UND[b]						MIX[b]						CON[b]					
Species[a]	0	10	20	50	75	100	0	10	20	50	75	100	0	10	20	50	75	100	0	10	20	50	75	100
AMRE		+			+	c		e		c	e													
BCCH	c	c	c	c	c	c	e	c			c	c												
BOCH														c	–	e		–	e			–	c	c
BTNW													e	e		–	+	–	e	e*	–	c	e	–
CAWA	c	e	e	e	–*	+																		
CHSP	c	+	c		c		c	c	c*	+	+	–	+	+	c	c*	c	c	c	+	c	–	+	c
CMWA																				e		e	e	–
COWA	e	–	e	–		+																		
DEJU	c*	c	c	c	c		c	c*	+	c	c		nc	+	c*	c*	c	+	c*	c	nc	+	+	–
GCKI	e	e	e*		–		e		e	–	e	–	e	e	e	–	e	–	e*	–	–*	–*	–	–
GRJA								+	–	e	c	e	–	e	–	–	e	–	e	+	–	c*	–	–
LEFL	e	c		e		–																		
LISP	c	c		c			c	c*			c								c	c	c			
MOWA	c	c	c	c	c	c							c	+*		c	c							
OVEN	e	e	e	e	–	+	e	e	e	–	–	–		e*	e	e	e	e						
PISI																c		–	e		e	e	e	e
RBGR					c	c																		
RBNU	e*	c	+	e	–			c	e	e		+	e	–	e	–	e	+	e	–	+	–	+*	–
REVI	e*	–	e*	nc	c	c																		
SWTH	c	e	c	–	+	–	e	–	–	c	e	–	e*	e*	c	e*	–	+	e	e	e	e		nc
TEWA	c*	+	+	c	+	+	c	+	c	c	+	+	e	+	c	e	–	+	e	–	+		c	–
WAVI	e	e	e		+	+	e	e	c	–	–	–												
WETA																				e*	e		c	c
WIWR																			e		+	+	–	+
WTSP	+	+*	+	–	+	nc	c	+	c	+	+		c	+*	c	c	c		c	c	–	c	c	–
WWCR															c			–	e	c		+	+*	–
YBSA	0	+	0	c	e*	c																		
YRWA	e	–*	–*	+	+	+	e*	+	–	+	–	+	–	+	–	+*	+	+	e*	–*	–*	+	+	+

Note: Changes marked with an asterisk are significant relative to changes in controls during same period.

[a] AMRE, American Redstart; BCCH, Black-capped Chickadee; BOCH, Boreal Chickadee; BTNW, Black-throated Green Warbler; CAWA, Canada Warbler; CHSP, Chipping Sparrow; CMWA, Cape May Warbler; COWA, Connecticut Warbler; DEJU, Dark-eyed Junco; GCKI, Golden-crowned Kinglet; GRJA, Gray Jay; LEFL, Least Flycatcher; LISP, Lincoln's Sparrow; MOWA, Mourning Warbler; OVEN, Ovenbird; PISI, Pine Siskin; RBGR, Rose-breasted Grosbeak; RBNU, Red-breasted Nuthatch; REVI, Red-eyed Vireo; SWTH, Swainson's Thrush; TEWA, Tennessee Warbler; WAVI, Warbling Vireo; WETA, Western Tanager; WIWR, Winter Wren; WTSP, White-throated Sparrow; WWCR, White-winged Crossbill; YBSA, Yellow-bellied Sapsucker; YRWA, Yellow-rumped Warbler.

[b] Changes were compared to control values using independent sample Student's t tests, $\alpha = 0.10$; "–" indicates species decreased in abundance in that retention level between 1998 and 2000; "+" indicates species increased in abundance between 1998 and 2000; "e" denotes a local extinction, where species disappeared between 1998 and 2000; "c" denotes a local colonization, where species was detected in 2000 but not in 1998; "nc" indicates species did not change in abundance between 1998 and 2000.

how these may relate to longer-term patterns is unclear. For example, retaining mature trees in deciduous-dominated stands may promote the growth of shade-tolerant white spruce (Bella and Gál 1996) over aspen and may consequently be reflected in future bird communities by favouring species associated with coniferous trees. Regrowth may result in increased similarity between low- and high-retention stands within cover types. Schieck and Hobson (2000) detected partial convergence of bird communities over 15–30 years between small and large retention patches in boreal mixedwood forests, probably due to growth of trees in surrounding cutover areas. Alternatively, while higher retention stands are initially more structurally complex (Sullivan et al. 2001; Lee et al. 1997.), there may be convergence over time within residual patches if, for example, snag loss outweighs snag recruitment. Clearly, longer term monitoring at EMEND is necessary to accurately assess response and provide reliable management recommendations.

Assumption of link between abundance and productivity

Abundance data, such as that derived from point counts, are frequently used to infer habitat quality, under the assumption that individuals will occur at greater densities in better quality habitats (with associated higher survival and reproduction rates). However, density alone can be misleading (see van Horne 1983; Vickery et al. 1992*a*). For example, song output can be a deceptive indicator of pairing status, since unpaired males may sing more frequently than paired males (Gibbs and Wenny 1993). To test this assumption, Harrison (2002) concurrently studied breeding behaviours of Swainson's Thrush (*Catharus ustulatus*) at EMEND and found that populations in partial cuts appeared to consist almost entirely of nonreproducing birds. This suggests the results presented here should be considered optimistic, at best.

Compartment size considerations

A maximum of two point count stations could be situated within each 10-ha compartment at EMEND. This resulted in small sample sizes for many species, and the concomitant high variability compromised our ability to detect changes postharvest. Furthermore, 10 ha may be too small a patch for some species in western forests (Hannon 1993). For example, the Ovenbird has been classified as an "area-sensitive species" because of its reliance on large patches of homogeneous mature forest habitat (Freemark and Collins 1992; Thompson et al. 1993), and pairing success among Ovenbirds has been positively correlated to forest patch size and distance from edge (Van Horn et al. 1995; Burke and Nol 1998). It is possible that in-block retention strategies over a large expanse might be suitable for Ovenbirds and possibly other area-sensitive species, but we could not detect this at EMEND.

Landscape context

The EMEND Project was designed to address questions at the level of the stand, and resultant data must be supplemented by broader scale information. The distribution of birds may depend on factors such as patch area, degree of fragmentation, and connectivity (Walters 1998; Villard et al. 1999; Brotons et al. 2003); hence, species presence and abundance may depend upon landscape context. In addition, metapopulation theory suggests that low-quality or "sink" bird populations may be sustained through immigration from neighboring subpopulations (i.e., Pulliam 1988; Martin 1992*b*), and therefore local assemblages may be as much a reflection of neighboring habitats as of local habitat conditions (McGarigal and McComb 1995; Drapeau et al. 2000). Consequently, caution should be exercised in both the interpretation of stand-level responses and in extrapolating these to evaluate habitat disturbance at a larger scale.

Management implications

In-block retention of live trees through partial cutting represents one facet of an ecosystem-based approach to forest management modeled after a natural disturbance regime. It is apparent that the needs of all forest species will not be met by partial cutting, as evidenced by the species lost from even the high-retention partial cuts at EMEND. However, consistent with other partial-retention studies in western North America, a portion of the mature forest bird community at EMEND did not disappear from partial cuts, suggesting some advantages over clear-cutting for conservation of avian diversity. Nevertheless, concurrent behaviour monitoring at EMEND (Harrison 2002) cautions against naive interpretation of these result: the presence of mature forest species in partial cuts was not reflected in reproductive activity, a measure of the quality of these habitats. We suggest that lower retention treatments (10%, 20%) cannot, therefore, be justified from a short-term avian diversity perspective. Higher retention levels (50%, 75%) may confer greater biodiversity advantages, but monitoring of reproductive activity should be undertaken to assess whether these treatments offer productivity advantages over lower retention levels, particular for species with known sensitivities to forest harvesting (i.e., Black-throated Green Warbler and Canada Warbler).

EMEND consists of a wider range of harvest retention levels than most other partial-cut studies in western North America. This permitted simultaneous evaluation of the operational feasibility and ecological benefit of varying retention levels. Based on expected increased economic costs, and associated logistical challenges, it is likely that in the absence of a significant shift in policy, at best 10% or 20% retention levels will be implemented on a widespread basis within existing forest tenures in Alberta. These levels are generally consistent with the amounts of live residual patches that typically remain after wildfires in western (Lee et al. 2002) and eastern boreal forests (Bergeron et al. 2002). Such patches are large enough to have been detected historically using relatively coarse-scale remotely sensed data (i.e., aerial photography). Clearly, a large proportion of the forest bird community was lost when low levels of retained trees were left dispersed throughout harvested blocks. In northeastern Alberta, Schieck et al. (2000) and Schieck and Hobson (2000) found that retaining trees in a clumped rather than a scattered pattern resulted in bird communities that were more similar to those in old-growth forest, a strategy consistent with site-level patch retention based on natural disturbance. There nevertheless remains a paucity of information regarding variation in live-stem retention resulting from variation in severity within burns, which is arguably the more appropriate basis for establishing in-block retention levels of residual live material following harvest.

Management questions regarding retention are usually posed as binary choices for fixed levels of retention at a stand level (i.e., At 10% retention, is an aggregated or dispersed strategy more advantageous?) or formulated as a trade-off across spatial scales (i.e., Given that 10% of the merchantable volume will not be harvested, is it better to retain this as structure within harvested stands or as larger patches distributed across a given land base?). However, these are artificial dichotomies from the perspective of a natural disturbance regime, which operates at multiple scales. Under a given fire regime, characterized by a particular fire frequency, fire size, and fire severity, some areas will escape burning altogether, and thus a portion of a region will consist of stands considerably older than the fire cycle. Within burned areas, unburned patches (often referred to as fire skips) will persist. Finally, variation in fire severity will result in variation in the number of live stems remaining within a burned stands. There exist few data on this latter attribute of fire regimes, but recent figures from central Alberta (Stepnisky 2003) and western Quebec (Bergeron et al. 2002) suggest that values of 50% and greater are not uncommon, dependent, in part, on forest type. Furthermore, Stambaugh (2003) found that lightly to moderately burned areas (i.e., those with naturally high retention of live trees) supported breeding songbird populations equivalent to those in old, unburned stands. Thus, from an ecological perspective, high levels of in-block retention may be justified in some cases. While this has obvious implications for timber supply, it must also be considered in the broader context of ecosystem management based on an understanding of natural system dynamics.

EMEND attempts to address the question of "How much residual is enough?" in a natural disturbance approach to forest management at the stand level. This is a vital question, but is not the only challenge faced by planners. In order for biodiversity to coexist with industrial forestry, management must also understand the effects of natural disturbances in terms of spatial patterns (i.e., size and configuration of openings) and temporal scale (i.e., frequency of harvest) (Hunter 1993*b*; Lee et al. 2002). This requires managing for spatial and temporal heterogeneity on many scales simultaneously (Hunter 1990). Haila et al. (1994) suggest identifying critical scales for a set of taxa and using these as guidelines for planning forest operations over a large area. Our study has provided some information for one vertebrate taxon; nonetheless, we caution against applying these results to other taxonomic groups, which may respond to disturbance in very different ways, on much smaller or larger scales. We also emphasize that our recommendations are based on short-term research only, and any management action based on them should be accompanied by a longer term monitoring scheme (i.e., an adaptive management approach).

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References

Alberta Sustainable Resource Development. 2003. The general status of Alberta wild species 2000 [online]. Available from http://www3.gov.ab.ca/srd/fw/speciesatrisk/aws.htm [updated 20 August 2003; cited 10 November 2004].

Anderson, S.H., and Crompton, B.J. 2002. The effects of shelterwood logging on bird community composition in the Black Hills, Wyoming. For. Sci. **48**(2): 365–372.

Annand, E.M., and Thompson, F.R. 1997. Forest bird response to regeneration practices in central hardwood forests. J. Wildl. Manage. **61**(1): 159–171.

Beese, W.J., and Bryant, A.A. 1999. Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. For. Ecol. Manage. **115**: 231–242.

Bella, I.E., and Gál, J. 1996. Growth, development, and yield of mixed-wood stands in Alberta following partial-cutting of white spruce. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-346.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fenn. **36**: 81–95.

Brawn, J.D., Robinson, S.K., and Thompson, F.R., III. 2001. The role of disturbance in the ecology and conservation of birds. Annu. Rev. Ecol. Syst. **32**: 251–276.

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A., and Rajasärkkä, A. 2003. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. Landsc. Ecol. **18**: 377–393.

Buddle, C.M., Spence, J.R., and Langor, D.W. 2000. Succession of boreal forest spider assemblages following wildlfire and harvesting. Ecography, **23**(4): 424–436.

Burke, D.M., and Nol, E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk, **115**(1): 96–104.

Conover, W.J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley & Sons, New York.

COSEWIC 2004. Canadian species at risk, May 2004 [online]. Available from http://www.cosewic.gc.ca/eng/sct0/sar_2004_05_e.cfm [updated 27 July 2004; cited 10 November 2004].

Costello, C.A., Yamasaki, M., Pekins, P.J., Leak, W.B., and Neefus, C.D. 2000. Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest. For. Ecol. Manage. **127**: 41–54.

Crawford, H.S., Hooper, R.G., and Titterington, R.W. 1981. Songbird population response to silvicultural practices in Central Appalachian hardwoods. J. Wildl. Manage. **45**(3): 680–692.

Crites, S. 1999. A test case for the natural disturbance model: understory vegetation communities following fire and harvesting in aspen mixedwood stands. *In* Science and Practice: Sustaining the Boreal Forest: Proceedings from the Sustainable Forest Managment Network, Edmonton, Alta., 14–17 February 1999. *Edited by* T.S. Veeman, D.W. Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin. Sustainable Forest Management Network, Edmonton, Alta. pp. 607–610.

DesGranges, J., and Rondeau, G. 1993. Forest bird response to natural perturbations and silvicultural practices: Does logging mimic nature? *In* Birds in the Boreal Forest. Proceedings of a workshop. Prince Albert, Sask., 10–12 March 1992. *Edited by* D.H. Kuhnke. Northern Forestry Centre. Edmonton. Alta. pp. 80–92.

Drapeau, P., Leduc, A., Giroux, J., Savard, J.L., Bergeron, Y., and Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. **70**(3): 423–444.

Efron, B., and Tibshirani, R. 1998. An introduction to the bootstrap. CRC Press, New York.

Ehrlich, P.R., Dobkin, D.S., and Wheye, D. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon & Shuster, New York.

Franzreb, K.E., and Ohmart, R.D. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor, **80**: 431–441.

Freemark, K., and Collins, B. 1992. Landscape ecology of birds breeding in temperate forest fragments. *In* Ecology and Conservation of Neotropical Migrant Landbirds. Proceedings of a Symposium. Woods Hole, Mass., 6–9 December 1989. *Edited by* J.M Hagan and D.W. Johnston. Manomet Bird Observatory, Manomet, Mass. pp. 443–454.

Gibbs, J.P., and Wenny, D.G. 1993. Song output as a population estimator: effect of male pairing status. J. Field Ornithol. **64**(3): 316–322.

Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research and management. Ann. Zool. Fenn. **31**: 203–217.

Haila, Y., Hanski, I.K., Niemela, J., Punttila, P., Raivio, S., and Tukia, H. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Ann. Zool. Fenn. **31**: 187–202.

Hannon, S.J. 1993. Nest predation and forest bird communities in fragmented aspen forests in Alberta. *In* Birds in the Boreal Forest, Proceedings of a workshop, Prince Albert, Sask., 10–12 March 1992. *Edited by* D.H. Kuhnke. Northern Forestry Centre, Edmonton, Alta. pp. 127–136.

Hannon, S.J., Cotterill, S.E., and Schmiegelow, F.K.A. 2004. Identifying rare species of songbirds in managed forests: Application of a regional template to a boreal mixedwood system. For. Ecol. Manage. **191**: 157–170.

Hansen, A.J., Spies, T.A., Swanson, F.J., and Ohmann, J.L. 1991. Conserving biodiversity in managed forests: lessons from natural forests. Bioscience, **41**: 382–392.

Hansen, A.J., McComb, W.C., Vega, R., Raphael, M.G., and Hunter, M. 1995. Bird habitat relationships in natural and managed forests in the West Cascades of Oregon. Ecol. Appl. **5**(3): 555–569.

Harrison, R.B. 2002. Stand-level response of boreal forest songbirds to experimental partial-cut harvest in Northwestern Alberta. M.Sc. thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alta.

Hayes, J.P., Weikel, J.M., and Huso, M.M.P. 2003. Response of birds to thinning young Douglas -fir forests. Ecol. Appl. **13**(5): 1222–1232.

Hobson, K.A., and Schieck, J. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. **9**(3): 849–863.

Hunter, M.L. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Prentice Hall, Upper Saddle River, N.J.

Hunter, M.L. 1993*a*. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. **65**: 115–120.

Hunter, M.L. 1993*b*. Managing biodiversity in forest at large spatial and temporal scales. *In* Birds in the Boreal Forest, Proceedings of a workshop, Prince Albert, Sask., 10–12 March 1992. *Edited by* D.H. Kuhnke. Northern Forestry Centre, Edmonton, Alberta. pp. 102–112.

Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conserv. Biol. **9**(5): 1041–1058.

Hutto, R.L., Pletschet, S.M., and Hendricks, P. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk, **103**: 593–602.

James, F.C., and Wamer, N.O. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology, **63**(1): 159–171.

Kirk, D.A., Diamond, A.W., Hobson, K.A., and Smith, A.R. 1996. Breeding bird communities of western and northern Canadian boreal forest: relationship to forest type. Can. J. Zool. **74**: 1749–1770.

Lance, A.N., and Phinney, M. 2001. Bird responses to partial retention timber harvesting in central interior British Columbia. For. Ecol. Manage. **142**: 267–280.

Lee, P., Smyth, C., and Boutin, S. 2002. Large-scale planning of live treed residuals based on a natural disturbance-succession template for landscapes. *In* Ecological basis for stand management: a summary and synthesis of ecological responses to wildfire and harvesting in boreal forests. *Edited by* S. Song. Alberta Research Council, Vegreville, Alta. pp. 13.1–13.21.

Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. **7**(2): 691–701.

Leupin, E.E., Dickinson, T.E., and Martin, K. 2004. Resistance of forest songbirds to habitat perforation in high-elevation conifer forest. Can. J. For. Res. **34**: 1919–1928.

MacArthur, R.H., and MacArthur, J.M. 1961. On bird species diversity. Ecology, **42**: 594–598.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, N.J.

Martin, T.E. 1992*a*. Breeding Biology Research database (BBIRD) program: general overview and standardized protocols. US Department of the Interior. US Fish and Wildlife Service, Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas, Arkansas.

Martin, T.E. 1992*b*. Breeding productivity considerations: What are the appropriate habitat features for management? *In* Ecology and Conservation of Neotropical Migrant Landbirds. Proceedings of a Symposium, Woods Hole, Mass., 6–9 December 1989. *Edited by* J.M Hagan and D.W. Johnston. Manomet Bird Observatory, Manomet, Mass. pp. 455–473.

Marzluff, J.M., and Sallabanks, R. 1998. Past approaches and future directions for avian conservation biology. *In* Avian conservation. *Edited by* J.M. Marzlluff and R. Sallabanks. Island Press, Washington, D.C. pp. 5–14.

McGarigal, K., and McComb, W.C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. **65**(3): 235–260.

Medin, D.E., and Booth, G.D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. USDA For. Serv. Res. Pap. INT-408.

Merrill, S.B., Cuthbert, F.J., and Oehlert, G. 1998. Residual patches and their contribution to forest-bird diversity on northern Minnesota aspen clearcuts. Conserv. Biol. **12**(1): 190–199.

Neter, J., Wasserman, W., and Kutner, M.H. 1985. Applied linear statistical models. 2nd ed. Irwin, Ill.

Niemi, G.J., and Hanowski, J.M. 1984. Relationships of breeding birds to habitat characteristics in logged areas. J. Wildl. Manage. **48**(2): 438–443.

Norton, M.R., and Hannon, S.J. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Can. J. For. Res. **27**: 44–53.

Pulliam, H.R. 1988. Sources, sinks and population regulation. Am. Nat. **132**(5): 652–661.

Rice, W.R. 1990. A consensus combined *p*-value test and the family-wide significance of component tests. Biometrics, **46**(2): 303–308.

Scheiner, S.M. 1993. MANOVA: multiple response variables and multispecies interactions. *In* Design and analysis of ecological experiments. *Edited by* S.M. Sheiner and J. Gurevitch. Chapman and Hall, New York. pp. 94–112.

Schieck, J. 1999. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor, **99**: 179–190.

Schieck, J., and Hobson, K.A. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. Can. J. For. Res. **30**: 1281–1295.

Schieck, J., and Nietfeld, M. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forest in Alberta. *Edited by* B. Stelfox. Alberta Environmental Centre, Vegreville, Alta., and Canadian Forest Service, Edmonton, Alta. pp. 115–157.

Schieck, J., Stuart-Smith, K., and Norton, M. 2000. Bird communities are affected by amount and dispersion of vegetation retained in mixedwood boreal forest harvest areas. For. Ecol. Manage. **126**: 239–254.

Schmiegelow, F.K.A., and Hannon, S.J. 1999. Forest-level effects of fragmentation on boreal songbirds: the Calling Lake fragmentation studies. *In* Forest fragmentation: wildlife and management implications. *Edited by* J.A. Rochelle, L.A. Lehmann and J. Wisniewski. Brill, Leiden. pp. 201–221.

Schmiegelow, F.K.A., and Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol. Appl. **12**(2): 375–389.

Schmiegelow, F.K.A., Machtans, C.S., and Hannon, S.J. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology, **78**(6): 1914–1932.

Schulte, L.A., and Niemi, G.J. 1998. Bird communities of early-successional burned and logged forest. J. Wildl. Manage. **62**(4): 1418–1429.

Simon, N.P.P., Schwab, F.E., and Diamond, A.W. 2000. Patterns of breeding bird abundance in relation to logging in western Labrador. Can. J. For. Res. **30**: 257–263.

Simon, N.P.P., Schwab, F.E., and Otto, R.D. 2002. Songbird abundance in clear-cut and burned stands: A comparison of natural disturbance and forest management. Can. J. For. Res. **32**: 1343–1350.

SPSS Inc. 1999. SPSS Base 10.0 for windows user's guide [computer manual]. SPSS Inc., Chicago.

Stambaugh, C.A. 2003. Community-level response of birds to burned and salvage-logged forests. M.Sc. thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alta.

Steidl, R.J., Hayes, J.P., and Schauber, E. 1997. Statistical power analysis in wildlife research. J. Wildl. Manage. **61**(2): 270–279.

Stepnisky, D.P. 2003. Response of Picoides woodpeckers to salvage harvesting of burned, mixedwood boreal forest: exploration of pattern and process. M.Sc. thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alta.

Steventon, J.D., Mackenzie, K.L., and Mahon, T.E. 1998. Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia. For. Chron. **74**(5): 703–713.

Strong, W.L., and Leggat, K.R. 1981. Ecoregions of Alberta. Alberta Energy and Natural Resources, Resource Evaluation and Planning Division, Tech. Rep. T/4.

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

Thompson, F.R., and Schwalbach, M.J. 1995. Analysis of sample size, counting time, and plot size from an avian point count survey on Hoosier National Forest, Indiana. *In* Monitoring bird populations by point counts. *Edited by* C.J. Ralph, J.R. Sauer, and S. Droege. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-149. pp. 45–48.

Thompson, F.R., Dijak, W.D., Kulowiec, T.G., and Hamilton, D.A. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. J. Wildl. Manage. **56**: 23–30.

Thompson, F.R., Probst, J.R., and Raphael, M.G. 1993. Silvicultural options for neotropical migratory birds. *In* Status and Management of Neotropical Migratory Birds: Proceedings of a workshop, Estes Park, Colo., 21–25 September 1992. *Edited by* D.M. Finch and P.W. Stangel. USDA For. Serv. Gen. Tech. Rep. RM-229. pp. 353–362.

Tittler, R. 1998. Effects of residual tree retention on breeding songbirds in Alberta's boreal mixed-wood forest. M.Sc. thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alta.

Tittler, R., Hannon, S.J., and Norton, M.R. 2001. Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. Ecol. Appl. **11**(6): 1656–1666.

Van Horn, M.A., Gentry, R.M., and Faaborg, J. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. Auk, **112**(1): 98–106.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. **47**(4): 893–901.

Verner, J. 1985. Assessment of counting techniques. Curr. Ornithol. **2**: 247–302.

Vickery, P.D., Hunter, M.L., Jr., and Wells, J.V. 1992. Is density an indicator of breeding success? Auk, **109**(4): 706–710.

Villard, M., Trzcinski, M.K., and Merriam, G. 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. **13**(4): 774–783.

Walters, J.R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. *In* Avian conservation. *Edited by* J.M. Marzlluff and R. Sallabanks. Island Press, Washington, D.C. pp. 181–192.

Westworth, D.A., and Telfer, E.S. 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Can. J. For. Res. **23**: 1830–1836.

Wolf, A.T., Howe, R.W., and Davis, G.J. 1995. Detectability of forest birds from stationary points in northern Wisconsin. *In* Monitoring bird populations by point counts. *Edited by* C.J. Ralph, J.R. Sauer, and S. Droege. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-149. pp. 19–23.

Appendix A

Appendix appears on the following page.

Table A1. Species codes, common names, and scientific names for bird species detected at EMEND in at least 5 of 18 compartments, in at least one cover type.

Species code	Common name	Scientific name	Foraging guild[a]	Nesting guild[b]
AMRE	American Redstart	*Setophaga ruticilla*	A	ST
BCCH	Black-capped Chickadee	*Parus atricapillus*	F	C
BOCH	Boreal Chickadee	*Parus hudsonicus*	F	C
BTNW	Black-throated Green Warbler	*Dendroica virens*	F	ST
CAWA	Canada Warbler	*Wilsonia canadensis*	A	G
CHSP	Chipping Sparrow	*Spizella passerina*	G	ST
CMWA	Cape May Warbler	*Dendroica tigrina*	F	ST
COWA	Connecticut Warbler	*Oporornis philadelphia*	G	G
DEJU	Dark-eyed Junco	*Junco hyemalis*	G	G
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	F	ST
GRJA	Gray Jay	*Perisoreus canadensis*	G	ST
LEFL	Least Flycatcher	*Empidonax minimus*	A	ST
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	G	G
MOWA	Mourning Warbler	*Oporornis philadelphia*	F	G
OVEN	Ovenbird	*Seiurus aurocapilla*	G	G
PISI	Pine Siskin	*Carduelis pinus*	F	ST
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	F	ST
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	B	C
REVI	Red-eyed Vireo	*Vireo olivaceus*	A	ST
SWTH	Swainson's Thrush	*Catharus ustulatus*	F	ST
TEWA	Tennessee Warbler	*Vermivora peregrina*	F	G
WAVI	Warbling Vireo	*Vireo gilvus*	F	ST
WETA	Western Tanager	*Piranga ludoviciana*	F	ST
WIWR	Winter Wren	*Troglodytes troglodytes*	G	C
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	G	G
WWCR	White-winged Crossbill	*Loxia leucoptera*	F	ST
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	B	C
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	F	ST

[a] Foraging guilds: A, aerial foragers; B, bark gleaners; F, foliage gleaners; G, ground foragers.
[b] Nesting guilds: C, cavity nesters; G, ground nesters; ST, shrub or tree nesters.

Effects of partial cutting on the ectomycorrhizae of *Picea glauca* forests in northwestern Alberta

Lance W. Lazaruk, Gavin Kernaghan, S. Ellen Macdonald, and Damase Khasa

Abstract: This study assessed the impact of various harvesting practices (including those designed to emulate natural disturbances) on ectomycorrhizae (ECM) associated with white spruce (*Picea glauca* (Moench) Voss) in northwestern Alberta, Canada. Treatments included clearcuts, partial cuts (dispersed green-tree retention with 20%, 50%, and 75% residual live trees, and aggregated green-tree retention), unharvested control sites, and a burned stand. The percentage of active white spruce root tips and ECM richness and diversity, as observed in soil cores collected throughout the study site, all decreased with increasing disturbance intensity. Effects were particularly pronounced in clearcuts, machine corridors used for access by harvesting equipment in the dispersed green-tree retention stands, and in burned areas. Reductions in ECM biodiversity could be attributed to the sensitivity of late-stage ectomycorrhizae (e.g., *Cortinarius* spp., *Lactarius* spp., and *Russula* spp.) to soil disturbances and changes in microclimate associated with harvesting or burning. Areas of dispersed and aggregated green-tree retention were not dramatically different than unharvested forest in terms of root tip density and ECM richness, diversity, and composition. Harvesting practices that retain a percentage of residual live trees, either dispersed throughout the cutting unit or in aggregated patches, could be an effective means of maintaining ectomycorrhizal biodiversity at the stand level.

Résumé : Cette étude évalue l'impact de diverses pratiques de récolte (incluant celles qui sont conçues dans le but d'imiter les perturbations naturelles) sur les ectomycorhizes (ECM) associées à l'épinette blanche (*Picea glauca* (Moench) Voss) dans le nord-ouest de l'Alberta, au Canada. Les traitements incluaient la coupe à blanc, la coupe partielle (dispersée avec réserves constituées de 20, 50 et 75 % de tiges résiduelles ou avec des réserves regroupen îlots), des sites témoins non récoltés et un peuplement brûlé. Le pourcentage d'apex racinaires actifs d'épinette blanche, ainsi que la richesse et la diversité des ECM, tels qu'ils ont été observés dans les carottes de sol prélevées partout dans la zone d'étude, diminuaient tous avec l'augmentation de l'intensité des perturbations. Les effets étaient particulièrement marqués dans les coupes à blanc, les corridors d'accès utilisés par les équipements de récolte dans les peuplements où étaient conservées des tiges résiduelles dispersées et dans les zones brûlées. La baisse dans la diversité des ECM pouvait être attribuée à la sensibilité des ectomycorhizes de fin de succession (p. ex. *Cortinarius* spp., *Lactarius* spp. et *Russula* spp.) aux perturbations du sol et aux variations du microclimat associées à la récolte ou au feu. Les zones avec rétention de tiges résiduelles, dispersées ou en îlots, n'étaient pas dramatiquement différentes de la forêt non récoltée en termes de densité des apex racinaires, de richesse, diversité et composition des ECM. Les pratiques de récolte qui conservent un certain pourcentage de tiges résiduelles, soit dispersées un peu partout dans l'unité de coupe, soit regroupées en îlots, pourraient constituer un moyen efficace de maintenir la biodiversité ectomycorhizienne à l'échelle du peuplement.

[Traduit par la Rédaction]

Introduction

In recent decades forestry companies have shown increased interest in ecologically sustainable management practices in an attempt to conserve forest biodiversity. By conserving forest biodiversity it is argued that the ecological processes that the organisms govern will also remain intact, and thus, the integrity of the forest will not be compromised (Galindo-Leal and Bunnell 1995). The natural disturbance paradigm of forest management (landscape management and silvicultural practices that aim to emulate natural disturbances such as fire) is an example of one approach towards sustainable practices (Bergeron et al. 1999).

In northwestern Alberta, wildfire has historically been responsible for shaping the forest landscape. As opposed to traditional forestry practices, which uniformly remove the majority of trees in a harvesting area, forest landscapes created by wildfire tend to be a heterogeneous mosaic of burned and unburned patches (Eberhart and Woodard 1987; Johnson 1992). Thus, even within stand-replacing wildfires, patches of live trees will remain. These unburned patches, or fire residuals, are believed to be important ecosystem structures that can act as refugia and serve as a source of colonization for weakly dispersing species (Rowe and Scotter 1973).

Colonization of plant roots by ectomycorrhizal (ECM) fungi improves plant water and nutrient uptake (Duddridge

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et al. 1980; Smith and Read 1997), as well as resistance to disease (Duchesne et al. 1988; Morin et al. 1999) and tolerance to temperature fluctuations (Marx et al. 1970). At the same time, ECM fungi depend on carbon fixed by the host plant and receive from 10% to 20% of the plant's net primary productivity (Smith and Read 1997; Vogt et al. 1982). This high level of dependency makes ECM fungi vulnerable to factors that disturb their associated plant symbionts. For example, both traditional forest harvesting practices such as clear-cutting (Bradbury et al. 1998; Byrd et al. 1999; Durall et al. 1999; Hagerman et al. 1999*a*, 1999*b*; Harvey et al. 1980*a*) and stand-replacing wildfires (Stendell et al. 1999; Visser 1995) have been shown to decrease the biodiversity of ectomycorrhizae.

Given the ecological importance of ECM fungi and the high degree of physiological variation among ECM fungal species (Cairney 1999; Newton 1992; Zak and Visser 1996), it seems that maintaining ECM diversity would be important for preserving critical ecosystem processes. Although the impacts of some alternative harvesting practices on ECM communities have been investigated in northwestern British Columbia, Canada (Durall et al. 1999; Kranabetter and Wylie 1998), the pattern of natural disturbance in these forests (small gap formations caused by single-tree mortality) contrasts significantly with the natural disturbance processes inherent to much of the boreal forest. Moreover, our current knowledge of forest ecosystem structure and function (especially with regard to belowground components) is still inadequate for forest managers to formulate sound practices and policies for natural disturbance management (Maini 1998).

The objectives of this study were to assess the effectiveness of forestry practices designed to emulate natural disturbance in maintaining *Picea glauca* (Moench) Voss ECM communities. Two complementary studies were undertaken: (1) assessment of composition and diversity of ECM morphotypes associated with different levels of dispersed green-tree retention and with burning; and (2) assessment of changes in ECM morphotype diversity across the edges of two patch sizes of aggregated green-tree retention left within clearcuts.

Materials and methods

Study site

This research is one of numerous studies undertaken at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site (Work et al. 2004), which is located in the Boreal Mixedwood ecoregion (Strong and Leggat 1992) of northwestern Alberta, Canada (56°44′N, 118°20′W). The dominant tree species are white spruce (*Picea glauca*) (ranging from 114 to 131 years old), trembling aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.). Black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and paper birch (*Betula papyrifera* Marsh.) are also found scattered throughout the site. The understory is dominated by *Alnus* spp., *Calamagrostis canadensis*, *Cornus canadensis*, *Epilobium angustifolium*, *Ribes triste*, *Rosa acicularis*, *Rubus pubescens*, *Shepherdia canadensis*, and *Viburnum edule* (Fenniak 2001). Forests in this region receive an average precipitation of 464 mm·year^{-1} (nearly two thirds during the summer months) and have an average summer temperature of 12.8 °C (Strong and Leggat 1992). The parent material was glaciolacustrine, and soil types varied from imperfectly drained Luvisols (Dark Gray Luvisol, Orthic Gray Luvisol) to a well-drained Orthic Luvic Gleysol. The organic layer pH ranged from 4.41 to 4.74 (for further details see Kishchuk 2004).

The study site was harvested during the winter of 1998–1999 in a randomized block design. Our work focused on unharvested controls, clearcuts, and three levels of dispersed green-tree retention (DGTR; 20%, 50%, and 75% residual live trees). Three replicate stands for each treatment were positioned throughout the EMEND site. The DGTR stands were strip harvested, resulting in a striped pattern where 20 m wide residual strips (containing the retained live trees) alternated with 5 m wide machine corridors. In the 75% retention level trees were only removed along the machine corridor. All of the harvesting treatments were applied to areas of approximately 10 ha. Originally, a series of controlled burns was planned for the experiment as well; however, only one conifer-dominated burned stand was available at the time of this study. It was burned in July 1999 with ignition by an aerial drip torch. In the stand the fire had a medium rate of spread and burned relatively hot but patchily (EMEND 2004). Residual trees were also left in the partially harvested and clearcut stands in the form of two elliptical patches (approximately 0.25 and 0.75 ha; aggregated green-tree retention). These ellipses were designed to emulate "fire skips", which are common features inherent to wildfire-dominated forest landscapes.

Field sampling

Sampling locations

For the assessment of dispersed green-tree retention and burning we had a total of 150 sample locations, with five sample location in each of three replicate stands for each of 10 treatments: (1) clearcut, (2) unharvested control, (3) 20% DGTR, partially cut residual strip, (4) 20% DGTR, machine corridor, (5) 50% DGTR, partially cut residual strip, (6) 50% DGTR, machine corridor, (7) 75% DGTR, residual strip, (8) 75% DGTR, machine corridor, (9) unburnt control, and (10) burned stand. Replicate stands of each treatment were grouped in blocks (except the burned stand and unburnt control). For the unharvested control and clearcut stands samples were taken from five random locations (at least 20 m apart) in each of the three replicate stands. For each of three replicate stands for the DGTR treatment, we took samples from five random locations along machine corridors and five random locations within the residual strips.

Although there was only one burned stand, it was highly heterogeneous (burnt to mineral soil in some areas with other areas unburnt (EMEND 2004)). We therefore divided the stand into three burned blocks and three unburnt control blocks, which were subsequently considered to be independent replicates of the burn and unburnt control treatments. Again, we took five samples from each of the three replicates of these two treatments, samples were taken 6 m apart along a single 30-m transect that was at least 30 m from a burnt–unburnt edge. Portions of the stand characterized as burned were void of an organic soil horizon and standing live trees. Unburned portions of the stand were untouched by fire and, thus, were visually similar to the unharvested control stands. In subsequent statistical analysis, stands were considered independent replicates of each treatment, while samples were treated as subsamples.

For the evaluation of aggregated green-tree retention we utilized a further 96 sampling locations, which were established in association with a total of six residual ellipses (0.25- and 0.75-ha ellipses in each of the three clearcut stands). At each ellipse we took a total of 16 samples from four transects situated perpendicular to the edge and at right angles to one another. Samples were taken along each transect at the center of the ellipse, at the edge of the ellipse, and at 10 and 20 m from the edge into the clearcut. The four samples from the centre of the ellipse were taken approximately 1 m apart. In subsequent statistical analysis the individual ellipses were considered independent replicates, and the two ellipse sizes were treated as the main effect and the sampling position as a subplot factor in a split-plot ANOVA (see below).

Fine root tip density

The density of white spruce fine roots was determined by obtaining a soil core (2 cm diameter by 15 cm deep) in June 2000 (two growing seasons post disturbance) from each of the 135 sampling locations in the clearcut, unharvested control, dispersed green-tree retention, and burned stands (but not the unburnt control or ellipses). For the control and partially cut sites the cores only included the organic layer. For the clearcuts and, to some extent, the machine corridors in the partially cut stands, the organic and mineral horizons were somewhat mixed, and the organic layer was compacted such that some mineral soil was often included in the cores. In the burned sites consumption of the LFH by the fire was such that cores typically included a substantial portion of mineral soil.

The soil cores were placed in a plastic Ziplock® bag and stored at 4 °C for up to 3 months until processing was completed. Processing involved placing the soil cores in two nested soil sieves (32 and 115 mesh per inch) and isolating the root tips by gently rinsing off the adhering soil and organic debris. The fine roots from both sieves were subsequently characterized as inactive or active, using a stereomicroscope, based on morphological criteria outlined by Harvey et al. (1976). Inactive root tips were characterized by a wrinkled texture and a dark apex. In contrast, the majority of active root tips were smooth and turgid and had a pale or creamy white apex. Ectomycorrhizae formed by *Cenococcum geophilum* and *Tomentella* spp., however, were exceptions. The mantles formed by these species are hard and darkly pigmented; thus, root tips associated with these fungi are uniformly smooth and dark. For this reason root tips associated with these two morphotypes were carefully examined during the characterization process. Only white spruce fine root tips were examined. White spruce roots can be readily distinguished from those of poplar, pine, and ECM shrubs but roots of black spruce or balsam fir could be mistaken for white spruce (Kernaghan 2003). Since pine, fir, and black spruce were all very infrequent in the areas we sampled, we are confident that the vast majority of the roots we examined were white spruce. All root tips lacking a distinguishable apex were disregarded.

Ectomycorrhizal community

The white spruce ECM community at each of the 246 sampling locations was characterized by obtaining a soil core (3.5 cm diameter by 15 cm deep). The clearcut, dispersed green-tree retention, unharvested control, burn, and unburnt control treatments (5 samples × 10 treatments × 3 replicates) were sampled in August 2000 (end of second postdisturbance growing season), while the samples from the aggregated green-tree retention (4 samples × 4 transects per ellipse × 2 sizes of ellipse × 3 replicates) were obtained in May 2001 (start of third postdisturbance growing season). The soil cores were stored in PVC pipe (to maintain the integrity of the core during transport) for up to 4 months at 4 °C prior to processing. The isolation of the fine roots was as described above. Once isolated, all active root tips were further classified as ectomycorrhizal or nonectomycorrhizal. ECM root tips were examined with both stereo (Zeiss Stemi 2000-C, 7–40×) and compound (Leitz Labrolux K, 500–1000×) microscopes and subsequently grouped based on their morphological and anatomical characteristics according to the protocol outlined by Goodman et al. (1996). Morphological features included shape, color, and texture of the ECM system and emanating elements (hyphae and mycelial strands). Some examples of anatomical features include mantle patterning; the size, color, ornamentation, and contents of hyphal cells; the type and frequency of septa; and reactions to specific chemical compounds (e.g., KOH, sulphovanillin). Active root tips lacking distinguishable mantle features were designated "undetermined" according to Kranabetter and Wylie (1998). This included root tips with an immature or poorly developed mantle.

When possible, 50 ECM root tips per core were morphotyped; however, because of the limited number of active root tips observed in some of the cores this was not always possible. In this instance, all of the active root tips encountered in the soil core were characterized. The distinct groups, or "morphotypes", were then identified to the genus level by comparing them with published ectomycorrhizal descriptions (Agerer 1987–1998; Ingelby et al. 1990; Goodman et al. 1996; Kernaghan 2001; see Lazaruk 2002 for further details). No attempt was made to identify the morphotypes past the genus level (but some genera had only one known species) because of the morphological similarities among species within genera. In recent years there has been increasing use of molecular techniques for studies of mycorrhizal richness and community composition, often as a supplement to morphotyping (Sakakibara et al. 2002). Such an approach would have allowed us to confirm the identity of taxa and, perhaps, to identify species within genera. Thus, molecular analysis would have likely resulted in higher mycorrhizal richness. For example, Smith et al. (2004) detected a total of 140 mycorrhizal "restriction fragment length polymorphism (RFLP) species" (17 identified genera) in a study of prescribed burning in ponderosa pine (*Pinus ponderosa*) forest (compared with our 19 morphotypes). However, a recent comparison of morphotyping versus molecular analysis of mycorrhizae (Sakakibara et al. 2002) has shown that a single RFLP pattern strongly predominates for many morphotypes, including several found in our study (*Cenococcum*, E-strain, *Mycelium radicis atrovirens* (MRA), *Thelephora*); indeed, *Lactarius* and *Russula* morphotypes each showed only a single RFLP pattern. Two morphotypes found in our study showed more than one common RFLP patterns (*Amphina*: two; *Piloderma*: five) (Sakakibara et al. 2002). Overall, for our purpose of detecting treatment effects on the ECM community, morphotyping was deemed sufficient.

Data analysis

Prior to analysis, all data were tested for normality and homoscedasticity with a Kolmogorov–Smirnov test. All ANOVAs were performed using SPSS version 10.0 (SPSS Inc. 1999).

Fine root tip density

The percentage of active fine root tips was calculated, for each soil core, as a proportion based on the total number of white spruce fine root tips observed. An analysis of variance (ANOVA) was used to test the treatment effects on the total number of fine root tips and the percentage of active fine root tips (the main effects were treatment (fixed), block (random), and treatment × block (random)). The stands (grouped by blocks) were considered the true replicates of treatment type, while the soil cores collected within the various treatments were treated as subsamples. The percentage data were log transformed prior to the analysis to meet the assumption of normality.

Ectomycorrhizal community

For the clearcut, dispersed green-tree retention, unharvested control, burn, and unburnt control treatments, the relative abundance of each morphotype was calculated as a proportion based on the total number of active root tips characterized. The frequency of occurrence for each morphotype was calculated according to the percentage of soil cores and stands in which each particular morphotype was observed. ECM richness was determined for each stand within treatment based on the total number of morphotypes observed in the five soil cores collected. Lastly, ECM diversity was calculated at the stand level (according to the average relative abundance of morphotypes from the five soil cores sampled per stand for each treatment) with the Shannon–Wiener diversity index (Shannon and Weaver 1949). Active fine root tips classified as nonmycorrhizal or undetermined (see Kranabetter and Wylie 1998) were excluded from the calculation of both morphotype richness and diversity.

For the residual ellipse treatments we calculated the following values for each position for each replicate ellipse: relative abundance of each morphotype (calculated as a proportion of the total number of ECM root tips characterized in each soil core) and ECM richness and diversity (per four soil cores). We also calculated frequency of occurrence of each morphotype per position based on the number of soil cores in which the morphotype was observed. Again, root tips characterized as undetermined were not included in the morphotype richness and diversity calculations.

An ANOVA was used to test for differences in ECM richness and diversity among the 10 treatments, with the following main effects: treatment (fixed), block (random). Treatment × block could not be included in the model because richness and diversity were calculated at the stand (within-block) level. The stands were considered the true replicates of treatment type. Significant ANOVA results ($p < 0.05$) were followed by Tukey–Kramer honestly significant difference test to further distinguish differences among treatments. Following initial analysis by correspondence analysis, a detrended correspondence analysis (DCA) was chosen to examine the treatment effects on the ECM community. Only common morphotypes, those observed in more than 5% of the soil cores, were included in the analysis, which was performed using CANOCO version 4.0 (ter Braak and Šmilauer 1998).

Table 1. Results of the ANOVA model testing for treatment effects on the percentage of active fine root tips and ectomycorrhizal richness and diversity, and the split-plot ANOVA model testing for effects of patch (ellipse) size (main plot) and sampling position (subplot) on ectomycorrhizae richness and diversity associated with the aggregated green-tree retention patches located within clearcuts.

Source	df	F	p >F
ANOVA*			
Percentage of active root tips†			
Treatment	8	13.630	<0.001
Block	2	0.813	0.461
Treatment × block	16	1.659	0.066
Error	109		
Richness			
Treatment	9	8.309	<0.001
Block	2	0.245	0.785
Error	18		
Diversity			
Treatment	9	9.614	<0.001
Block	2	1.357	0.283
Error	18		
Split-plot ANOVA‡			
Richness			
Block	2	1.00	0.500
Ellipse size	1	0.04	0.868
Ellipse size × block	2	0.42	0.666
Position	3	19.90	<0.001
Ellipse size × position	3	0.86	0.491
Error	12		
Diversity			
Block	2	14.33	0.065
Ellipse size	1	3.10	0.220
Ellipse size × block	2	0.08	0.928
Position	3	17.97	<0.001
Ellipse size × position	3	0.58	0.665
Error	12		

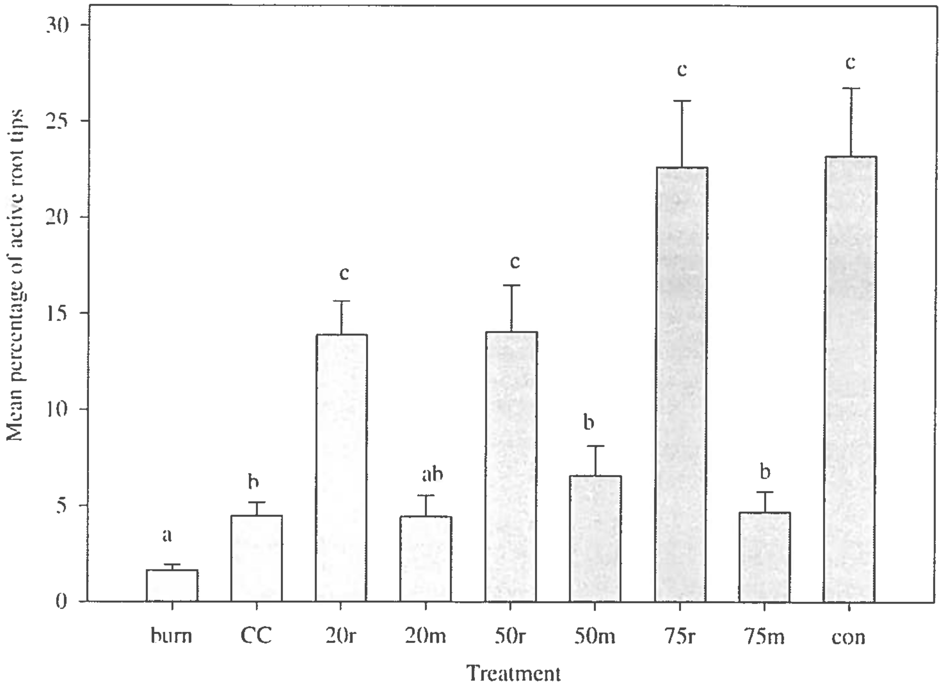
*Treatments were as follows: clearcut, dispersed green-tree retention (20%, 50%, and 75% retention including both residual strips and machine corridors), unharvested control, and burn.

†Tests performed using log-transformed data.

‡Sampling positions were as follows: within the patch, at the edge, and 10 and 20 m into the clearcut.

The effect of increasing distance from the edge and residual ellipse size on the ECM community was tested with an ANOVA using a split-plot design with ellipse size as the main plot factor and sampling position as the subplot factor. The test was performed using the ECM richness and diversity values for each position at each replicate ellipse. Significant ANOVA results ($p < 0.05$) were followed by a Tukey–Kramer honestly significant difference test to further distin-

Fig. 1. The mean percentage of active white spruce fine root tips in soil cores collected from burn (burn), clearcut (CC), dispersed green-tree retention cut (with 20%, 50%, and 75% residual live trees and sampled in both machine corridors (m) and residual strips (r)), and unharvested control stands (con) in conifer-dominated boreal forest two growing seasons after harvesting. Treatment means with different letters are significantly different (Tukey–Kramer honestly significant difference test, $p \leq 0.05$, after ANOVA with $p < 0.001$)). Analyses were performed with log-transformed data. Error bars represent 1 SE (based on the 15 soil cores per treatment).



guish differences among sampling positions. Further analysis was required to determine if differences in the ECM richness between the clearcut and residual ellipse sampling positions were due to genuine positional effects on the community or were simply due to the lower number of active root tips encountered in clearcut soil cores (see Table 3). To examine this we plotted morphotype richness against number of root tips. An average richness (for a given number of root tips) was calculated based on data from 10 repeats of random selections of 1 to 20 root tips from either residual ellipse or clearcut soil cores.

Results

Dispersed green-tree retention and fire

White spruce fine root tip density

Nearly 107 000 white spruce fine root tips were characterized as inactive or active throughout the clearcut, dispersed green-tree retention (DGTR), unharvested control, and burn treatments. The percentage of active fine root tips differed significantly among the treatments ($p < 0.001$) and appeared to be correlated with the level of disturbance (Table 1, Fig. 1). Similar, but less dramatic, trends were seen for the total number of active fine root tips (not shown). In areas with a high level of disturbance, such as the burned and clearcut stands and the machine corridors within the DGTR stands, there was a significantly lower percentage of active fine root tips than in the control stands. For the machine corridors there were no significant differences among the different retention levels, and the percentage of active fine root tips was just as low as in the clearcut stands. The lowest percentage of active root tips was found in the burn treatment. Within the residual strips of the DGTR stands, the percentage of active fine root tips increased from the 20% to the 50% and 75% retention levels, and in each case it was significantly greater than in the machine corridors with the same retention level. The percentage of active root tips did not differ between the residual strips and the unharvested control stands.

Ectomycorrhizal community

A total of 4431 white spruce fine root tips were classified as active, and of these tips, an overwhelming majority was also characterized as ectomycorrhizal (99.4%). Throughout the clearcut, DGTR, unharvested control, and burn treatments a total of 19 distinct morphotypes were described (Table 2). The most common morphotype was *Tomentella* spp. followed by *Cortinarius* spp., *Amphinema byssoides*, *Lactarius* spp., E-strain (*Wilcoxina* spp.), MRA, and *Hebeloma* spp., respectively. These seven morphotypes formed the majority of the ectomycorrhizae (nearly 72% of the root tips), while none of the remaining 12 morphotypes were observed on more than 5% of the root tips. The most ubiquitous morphotype was *Tomentella* spp., which was observed in nearly 57% of the soil cores and was the only morphotype found in every stand. Only nine root tips were classified as undetermined.

ECM richness and diversity (Table 1, Fig. 2) differed significantly among the treatments according to the level of disturbance. The values were significantly greater in the control stands than in the burned and clearcut stands. Within the residual strips of the DGTR stands, richness and diversity in-

Table 2. The total number of active root tips colonized by a given ectomycorrhizae morphotype, relative abundance (precentage of root tips), and frequency of occurrence (percentage of soil cores or stands in which the morphotype occurred) based on sampling of 10 treatments throughout the EMEND research site (n = 150) two growing seasons after harvesting.

Morphotype	No. of tips	Abundance (%)*	Frequency (%)†	
			Cores	Stands
Tomentella spp.	822	18.6	56.7	100.0
Cortinarius spp.	820	18.5	25.3	56.7
Amphinema byssoides	508	11.5	26.7	70.0
Lactarius spp.	368	8.3	13.3	40.0
E-strain	233	5.3	13.3	46.7
Mycelium radicis atrovirens	224	5.1	24.7	66.7
Hebeloma spp.	221	5.0	14.0	53.3
Cenococcum geophilum	199	4.5	28.0	76.7
Piloderma spp.	170	3.8	10.7	33.3
Russula spp.	163	3.7	7.3	36.7
cf. *Tricholoma*	156	3.5	8.7	26.7
Tuber spp.	118	2.7	4.0	20.0
Unknown A	87	2.0	4.0	20.0
Basidiomycete 1	81	1.8	2.0	10.0
Thelephora spp.	67	1.5	5.3	23.3
Unknown D	58	1.3	1.3	6.7
Unknown B	50	1.1	0.7	3.3
Dermocybe spp.	31	0.7	2.7	13.3
Nonmycorrhizal	29	0.7	4.0	20.0
cf. *Paxillus involutus*	17	0.4	0.7	3.3
Undetermined	9	0.2	1.3	6.7
Total no. of tips	4431			

Note: Treatments were as follows: clearcut; 20%, 50%, and 75% dispersed green-tree retention (including both residual strips and machine corridors); unharvested control; burn; and unburnt control.

*Relative abundance for each morphotype was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled) × 100.

†Frequency of occurrence for each morphotype was calculated as follows: (number of soil cores or sites in which morphotype was observed) / (total number of soil cores or sites) × 100.

creased slightly from the 20% to the 50% and 75% retention levels. For the machine corridors of the DGTR, stands with 50% retention had greater richness and diversity than stands with 20% or 75% retention. Overall, ECM richness and diversity tended to be greater in the residual strips than in the machine corridors for each of the levels of retention; however, this difference was not statistically significant. Furthermore, the residual strips had richness and diversity values similar to those of the control stands. The burn treatment resulted in the lowest values for both ECM richness and diversity.

The results from the ordination provided insight into the treatment effects on the ECM community (Fig. 3). The clustering of the stands along the first ordination axis ($\lambda = 0.4787$) implies a correlation with disturbance intensity. The site scores for the DGTR stands were intermediate between the heavily disturbed burned stands and clearcut stands, which were positioned on the left of the first DCA axis, and the undisturbed control stands, which were positioned on the right end of first DCA axis. Morphotypes such as MRA and *Tomentella* spp. were associated with the burned and clearcut stands, while morphotypes such as *Amphinema byssoides*, *Cortinarius* spp., E-strain, *Piloderma* spp., and *Lactarius* spp. were associated with the control stands. Furthermore, *Cenococcum geophilum*, *Hebeloma* spp., *Russula* spp., and *Thelephora terrestris* were positioned among the DGTR stands.

Aggregated green-tree retention (ellipses)

Ectomycorrhizal community

A total of 2083 active white spruce root tips were characterized and 16 different morphotypes were described from the samples taken in association with the aggregated green-tree retention patches (ellipses) (Table 3). The most common morphotype was *Cortinarius* spp. followed by *Amphinema byssoides*, *Tomentella* spp., *Cenococcum geophilum*, E-strain (*Wilcoxina* spp.), MRA, *Lactarius* spp., and *Piloderma* spp., respectively. These eight morphotypes formed the majority of the ectomycorrhizae (nearly 85%), while the other eight morphotypes were observed in less than 5% of the soil cores. Only 15 root tips were classified as undetermined.

The relative abundance of individual morphotypes varied among sampling positions (Table 3). *Lactarius* spp., *Piloderma* spp., *Tuber* spp., and "cf. *Tricholoma*" were only found within and at the edge of the residual ellipses. While no morphotypes were exclusive to the clearcut sampling positions, the relative abundance of *A. byssoides*, E-strain, and *Tomentella* spp. was greater in soil cores collected from the clearcut than in soil cores collected from the center and at the edge of the residual ellipses. *Cenococcum geophilum* and *Tomentella* spp. were the only morphotypes observed at all sampling positions; *Amphinema byssoides* was absent from only the 10 m sampling position of the 0.75-ha ellipse. In addition, the average number of root tips observed, and thus characterized, in the soil cores was much lower in the clearcut sampling positions.

The richness of ECM morphotypes also differed among sampling positions (Fig. 4*a*). ECM richness and diversity were nearly four times greater in the center and at the edge of the residual ellipse than in the clearcut (Fig. 4). No relationship was observed between the size of the residual ellipse and ECM richness or diversity (Table 1, Fig. 4).

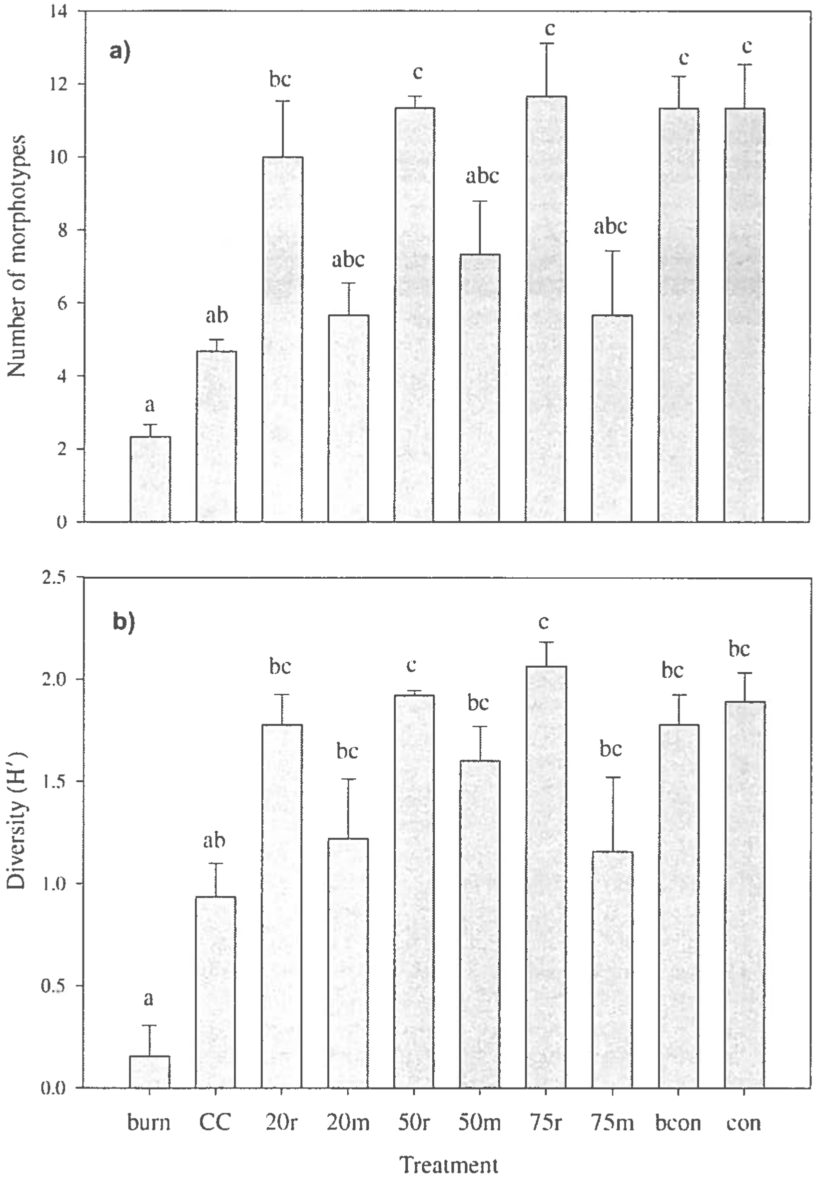
The relationship between morphotype richness and number of root tips examined differed between the clearcut and the residual ellipse soil cores (Fig. 5). In the clearcut soil cores the maximum number of morphotypes was encountered after approximately 14 root tips, while in the residual ellipse soil cores the number of morphotypes encountered continued to increase even after 20 root tips. This suggests that the ECM biodiversity in the clearcut soil cores would not have been higher even if more root tips had been encountered, and thus the clearcut ECM community is different for reasons other than just a limitation in host availability.

Discussion

Dispersed green-tree retention

Clear-cut harvesting and fire were associated with dramatic reductions in abundance and diversity of ECM and changes in community composition. Effects of dispersed green-tree retention (DGTR) were heterogeneous, however.

Fig. 2. Richness (*a*) and diversity (*b*) of ectomycorrhizal morphotypes (averaged over three replicate stands per treatment based on five soil cores (subsamples) per replicate stand) observed in burn (burn), unburnt control (bcon), clearcut (CC), dispersed green-tree retention cut (with 20%, 50%, and 75% retained live residual and sampled in both machine corridors (m) and residual strips (r)), and unharvested control stands (con) two growing seasons after harvesting. Treatment means with different letters are significantly different (Tukey–Kramer honestly significant difference test, $p \leq 0.05$). Error bars represent 1 SE (based on the three replicate stands per treatment).

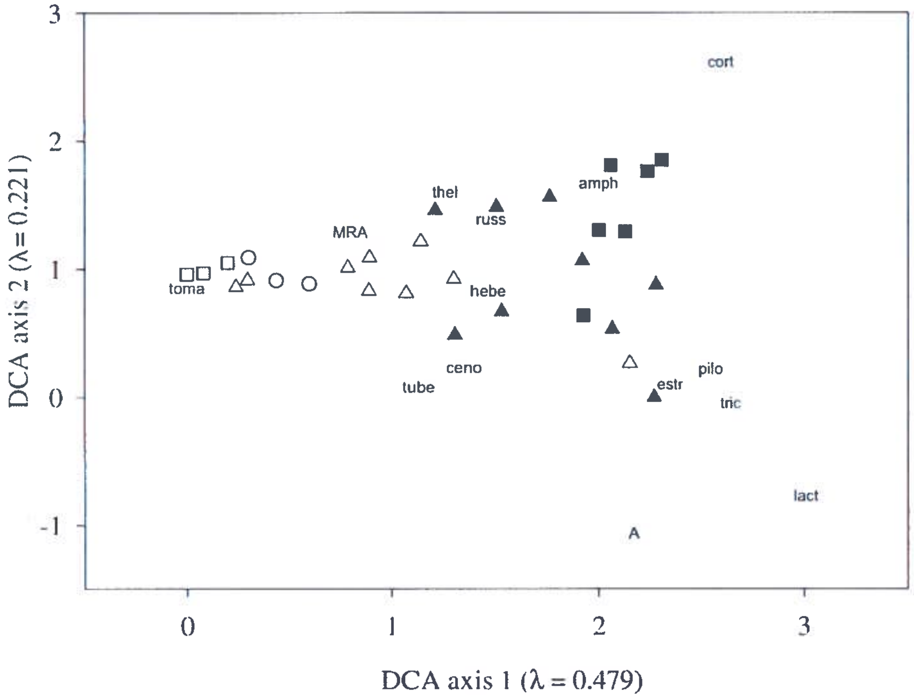


such that the machine corridors were similar to clearcuts, while the residual strips were similar to unharvested forest.

Clear-cut harvesting significantly reduced the overall density of active fine root tips. Previous studies have also reported a substantial reduction (to 4%, Hagerman et al. 1999*a*) or complete elimination (Harvey et al. 1980*a*; Parsons et al. 1994) of active root tips 2 years after clear-cutting. Not surprisingly, the burn treatment resulted in the lowest percentage of active root tips. Since white spruce has a shallow rooting system, the majority of the root tips were likely consumed along with the organic horizon.

The persistence of a small proportion of root tips in clearcuts and burned areas may be attributed to (1) the use of carbon reserves present in excised roots (Ferrier and Alexander 1985); (2) a supply of the root tips with carbon, via hyphal linkages, by ectomycorrhizae associated with refuge plants (Kranabetter 1999; Hagerman et al. 2001); and (3) physical protection against desiccation provided by the fungal mantle itself (Smith and Read 1997), enabling certain root tips to persist, at least temporarily, without a host. This may have been the case for *Cenococcum geophilum* and *Tomentella* spp., which form thick, hard mantles. In fact, the majority of active root tips encountered in the burn and clearcut soil cores in this study were morphologically similar to these ectomycorrhizae. This may also explain the increased abundance of both *Cenococcum* (Byrd et al. 1999; Hagerman et

Fig. 3. Results of detrended correspondence analysis (DCA) based on the relative abundance of ectomycorrhizal (ECM) morphotypes encountered in the sampling of unharvested, clearcut, dispersed green-tree retention, and burn treatments in conifer-dominated boreal forest. See text for details of treatments. Each point represents the location in ordination space of a stand for a given treatment. Morphotype abbreviations indicate the location of the morphotype in ordination space. Points close to one another were more similar in terms of the composition of the ECM community and were characterized by higher abundance of the morphotypes placed close to them. Abbreviations are as follows: A, unknown A; amph, *Amphinema byssoides*; ceno, *Cenococcum geophilum*; cort, *Cortinarius* spp.; estr, E-strain; hebe, *Hebeloma* spp.; lact, *Lactarius* spp.; MRA, *Mycelium radicis atrovirens*; pilo, *Piloderma* spp.; russ, *Russula* spp.; thel, *Thelephora terrestris*; toma, *Tomentella* spp.; tric, cf. *Tricholoma*; tube, *Tuber* spp. Symbols are as follows: ■, control and unburnt control; ▲, residual strips; △, machine corridors; ○, clearcut; □, burn.



al. 1999*a*; Schoenberger and Perry 1982) and *Tomentella* (Bradbury et al. 1998; Purdy et al. 2002) morphotypes in disturbed sites.

Fine root tip density was also drastically reduced in the machine corridors of the DGTR stands, although they were only 5 m wide and thus well within the rooting zone of adjacent trees. Others have also found reductions in active root tip density within 2–6 m of a forest edge (Parsons et al. 1994; Hagerman 1997). Thus some factor, such as soil compaction or microclimatic effects, other than an absence of host tree roots must thus be involved in the reduced root tip density in the machine corridors. Compaction caused by harvesting equipment can increase the bulk density of soil, in turn reducing the hydraulic conductance and infiltration rate (Startsev and McNabb 2001; Williamson and Neilson 2000). Thus, compaction caused by machine traffic could physically imped root growth and also restrict it indirectly by anoxia (Startsev and McNabb 2001).

Other than in the machine corridors there was little effect of DGTR harvesting on density of active fine root tips. In the residual strips the percentage of active fine root tips was lower (but not significant) in the 20% and 50% retention levels than in the 75% retention level (where trees were only removed in the machine corridors) or the control stands. Not surprisingly, the latter two treatments had similar percentages of active fine roots. In a previous study Harvey et al. (1980*b*) found no effect of partial cutting (~50% retention) on active root tip density in a Douglas-fir – larch forest stand.

The burn treatment had the most substantial impact on ECM biodiversity. Stand-replacing wildfires differ from harvesting in that in addition to the removal of trees, the organic layer of soil is often consumed (Johnson 1992). Since most (up to 95%) of ectomycorrhizae are found in the organic layer (Goodman and Trofymow 1998; Harvey et al. 1976), a dramatic reduction in diversity, followed by slow recovery, is expected. Young, fire-origin jack pine stands (6 years old) had significantly lower ECM abundance and diversity than did stands 41 to 122 years post fire (Visser 1995). Prescribed fire has also been shown to dramatically reduce ECM biomass of a ponderosa pine stand (Stendell et al. 1999) and mycorrhizal richness of a ponderosa pine forest (following fall underburning, Smith et al. 2004).

Of the harvesting treatments, clear-cutting had the greatest effect on ECM biodiversity. Significant reductions in ECM biodiversity have been previously reported in clearcuts for lodgepole pine (Bradbury et al. 1998; Byrd et al. 1999), Douglas-fir – larch (Harvey et al. 1980*a*), subalpine fir – Engelmann spruce (Hagerman et al. 1999*a*), and interior cedar–hemlock forests (Durall et al. 1999). The DGTR harvesting also lowered ECM richness and diversity. However, as for active root tip density, this was primarily due to ef-

Table 3. The total number of root tips sampled, overall relative abundance (percentage of root tips), frequency of occurrence (percentage of soil cores), and the average relative abundance for ectomycorrhizae morphotypes at the different sampling positions associated with the aggregated green-tree retention patches (n = 96 soil cores) at the start of the third postharvest growing season.

				Relative abundance (%)‡							
				0.25 ha				0.75 ha			
Morphotype	No. of tips	Overall relative abundance (%)*	Frequency (%)†	Center	Edge	10 m	20 m	Center	Edge	10 m	20 m
Cortinarius spp.	376	18.1	21.9	13.3	15.1	16.7	—	33.8	12.5	—	3.0
Amphinema byssoides	275	13.2	26.0	10.8	7.1	28.6	6.0	10.4	19.0	—	30.3
Cenococcum geophilum	256	12.3	31.3	15.1	13.9	50.0	16.7	14.4	1.9	9.1	5.4
Tomentella spp.	269	12.9	25.0	6.0	12.6	4.8	22.7	12.8	12.6	90.9	5.4
E-strain	177	8.5	11.5	4.7	5.6	—	—	4.9	13.9	—	21.5
Mycelium radicis atrovirens	166	8.0	11.5	14.9	6.5	—	21.4	6.7	—	—	—
Lactarius spp.	127	6.1	6.3	9.0	—	—	—	5.2	14.1	—	—
Russula spp.	126	6.1	12.5	7.4	26.2	—	—	3.2	2.4	—	1.1
Piloderma spp.	113	5.4	5.2	7.9	1.8	—	—	8.5	10.0	—	—
cf. *Tricholoma*	64	3.1	5.2	2.3	4.5	—	—	—	4.6	—	—
Unknown A	40	1.9	1.0	6.3	—	—	—	—	—	—	—
Tuber spp.	35	1.7	4.2	—	6.7	—	—	0.2	1.6	—	—
Thelephora terrestris	15	0.7	2.1	—	—	—	—	—	2.4	—	—
Undetermined	15	0.7	2.1								
Hebeloma spp.	12	0.6	1.0	—	—	—	—	—	4.0	—	—
Unknown B	13	0.6	1.0	2.4	—	—	—	—	—	—	—
Basidiomycete 1	4	0.2	1.0	—	—	—	—	—	1.1	—	—
Total no. of tips	2083			552	409	50	59	496	432	43	42

Note: Sampling positions were as follows: in the center, at the edge, and at 10 and 20 m from the edge of 0.25- and 0.75-ha residual ellipses.

*Relative abundance for each morphotype was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled) × 100.

†Frequency of occurrence for each morphotype was calculated as follows: (number of soil cores in which morphotype was observed) / (total number of soil cores) × 100.

‡Relative abundance for each morphotype at a given position was calculated as follows: (number of root tips on which morphotype was observed) / (total number of root tips sampled at that position) × 100.

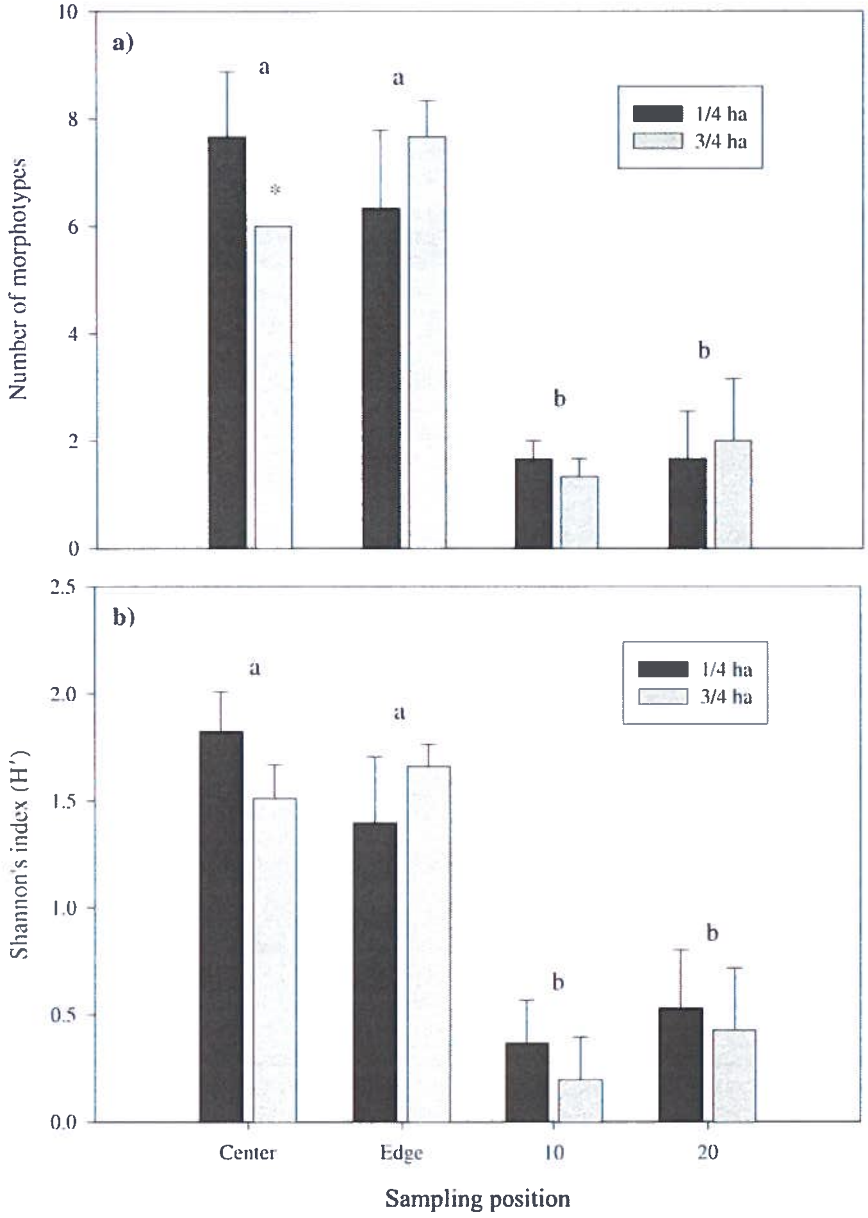
fects in the machine corridor and not in the residual strips of the DGTR stands. Indeed, richness and diversity were only marginally greater in the machine corridors than in clearcuts. As described above, this may be attributed to soil compaction and (or) microclimatic effects. Soil compaction has been previously found to be related to reduced ECM morphotype richness on outplanted seedlings (Page-Dumroese et al. 1998) and to negate any positive effects of ECM inoculation of seedlings prior to outplanting (Teste et al. 2004).

The residual strips of the DGTR stands had richness and diversity similar to those of control stands. Similarly, previous studies failed to observe a relationship between basal area retained in thinned forest stands and sporocarp production (Kranabetter and Kroger 2001; Waters et al. 1994). Waters et al. (1994) did observe, however, an association between thinning and the relative frequency of the most common genera of ECM fungi.

Differences in ECM community composition among treatments mirror those observed for diversity and were similar to those of previous studies on harvested (Hagerman et al. 1999*a*; Bradbury et al. 1998; Byrd et al. 1999) and wildfire sites (Visser 1995). Previous studies have classified ectomycorrhizae as "early stage", "late stage", or "multistage" on the basis of their association with different ages or successional stages of forest (Last et al. 1987; Deacon and Fleming 1992; Visser 1995), and we have used these classifications in the interpretation of treatment effects on the composition of the ECM community. While none of the common morphotypes were exclusive to the disturbed sites, the relative abundance of multistage ectomycorrhizae (e.g., *Hebeloma* spp., *Thelephora terrestris*, *Cenococcum geophilum* as per Visser 1995) was greater on harvested, burned, and machine corridors sites. Furthermore, fungi that have been characteristically associated with older forest (e.g., *Cortinarius* spp., *Piloderma fallax*, *Lactarius* spp., cf. *Tricholoma*; late-stage ectomycorrhizae as per Deacon and Fleming 1992; Visser 1995) were associated with the undisturbed sites (Fig. 3). Thus, the reduction in ECM richness and diversity in the disturbed sites was, in large part, due to the exclusion of late-stage ectomycorrhizae. As such, the ECM community observed in both the clearcut and burned stands was strikingly similar. The position of *Tomentella* spp. among the disturbed stands in the ordination diagram suggests that they may be characterized as early-stage ectomycorrhizal fungi; however, it was the only morphotype observed in every stand at the EMEND site, suggesting that it may have been the only broad generalist. The presence of *Amphinema byssoides* and *Cenococcum geophilum* in every treatment supports their characterization as multistage fungi (Visser 1995), which may be capable of colonizing root tips irrespective of the successional status of the site.

E-strain (*Wilcoxina* spp.) possesses early-stage characteristics (Deacon et al. 1983; Mason et al. 1983) and has been found on seedlings grown in clearcuts (Bradbury 1998;

Fig. 4. The mean ectomycorrhizal morphotype richness (*a*) and diversity (*b*) (per four soil cores) based on samples collected from the center, at the edge, and 10 and 20 m into the clearcut from two different sizes of residual ellipse in the aggregated green-tree retention harvesting. Samples were taken at the start of the third growing season post harvest. Treatment means with different letters are significantly different ($p < 0.05$; Tukey–Kramer honestly significant difference test). Error bars represent 1 SE (based on the three ellipses per position). * denotes SE = 0.

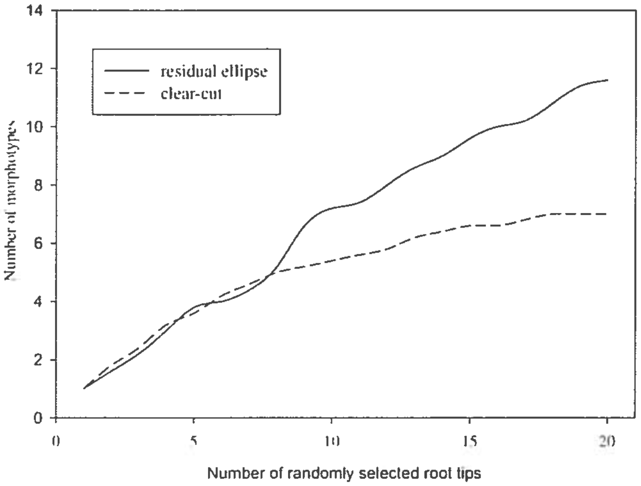


Hagerman et al. 1999*b*), but we observed E-strain in only 20 soil cores, only three of which were from disturbed (e.g., machine corridors) habitats. Hagerman et al. (1999*a*) noted that E-strain was rarely observed in soil cores collected from subalpine clearcuts in British Columbia, despite its presence on seedlings collected from the same sampling locations (Hagerman et al. 1999*b*). This discrepancy may be due to the fact that the root tips of planted seedlings represent a new, uncolonized resource for ruderal ECM fungi present in the soil, whereas mycorrhizae on the root tips of overstory trees (as found in soil cores) are formed in intimate contact with the fungi already colonizing the previous cohort of fine roots. Use of a seedling bioassay, rather than soil cores, might have revealed higher abundances of early-stage ECM fungi, particularly in disturbed sites.

Aggregated green-tree retention

Our results suggest that aggregated green-tree retention in small patches can maintain ECM biodiversity within clearcuts but its role in facilitating recolonization of the surrounding harvested area is less certain. Both ECM richness and diversity were significantly greater in and at the edge of the residual ellipse than in the surrounding clearcut. Hagerman et al. (1999*a*) reported a significant reduction in morphotype rich-

Fig. 5. The relationship between the number of randomly selected root tips examined and the total number ectomycorrhizal morphotypes observed in soil cores collected from residual ellipses and clearcut sampling positions associated with the aggregated green-tree retention harvesting. The lines are based on the average of 10 randomized samples.



ness and diversity in soil cores 16 m from the edge of intact forest. Kranabetter (1999) examined the effect of refuge trees on ECM communities and found that within clearcuts, seedlings growing within 5 m of a single mature birch tree were associated with significantly more morphotypes than seedlings collected 25–50 m from mature birch trees. This suggests that even single trees left within clearcuts may be capable of providing refuge for ECM communities. A study by Simard et al. (1997) illustrates the influence of connection to roots of mature trees on mycorrhizal richness and composition on seedlings. Trenching (removal of contact with roots of mature trees) reduced mycorrhizal (morphotype) richness on Douglas-fir seedlings by about 50% and also changed the composition (Simard et al. 1997).

While, to our knowledge, no other study has investigated the ability of retention patches to act as a refuge for ectomycorrhizae, Durall et al. (1999) and Kranabetter and Wylie (1998) have examined the effects of different sized stand openings on the ECM communities of seedlings in northwestern British Columbia. In effect, this represents the inverse situation of our residual ellipses. Both studies reported a decrease in the number of ECM morphotypes with increasing distance from the forest edge. Thus, ECM communities appear to be strongly correlated with, or dependent upon, connections to intact forest. The change in community composition between the forest and clearcut sampling positions in our study provides further evidence for this.

Lactarius spp., *Piloderma* spp., *Russula* spp., cf. *Tricholoma*, and the three undetermined morphotypes ("unknown A", "unknown B", and "basidiomycete 1") were more abundant in soil cores collected from the center and at the edge of the residual ellipse than in the clearcut. Ectomycorrhizae formed by species of *Lactarius*, *Piloderma*, and *Russula* possess late-stage characteristics (Last et al. 1987; Newton 1992; Deacon and Fleming 1992; Visser 1995). *Lactarius* and *Russula* ECM produce extracellular phenoloxidases (Agerer 2000) and have an affinity for leaf litter. *Piloderma* is a resupinate basidiomycete that fruits on decomposing plant litter and decaying wood (Goodman and Trofymow 1998) and may be an indicator of old-growth forests (Smith et al. 2000). It is not surprising therefore that these fungi were observed in association with the residual ellipses. Ectomycorrhizae with multistage characteristics, such as *Hebeloma* and *Thelephora* (Visser 1995), were only observed at the edge of the residual ellipses.

Despite their early-stage characteristics, MRA and E-strain (Deacon et al. 1983; Mason et al. 1983) were only slightly more abundant in the clearcut sampling positions. As these fungi are capable of colonizing root tips via spores, excised root tips, and hyphal fragments, it is unlikely that inoculum sources were limiting in the clearcut. However, it is possible that these species are unable to compete effectively with persisting preharvest ECM species. A lack of root tips for colonization also could have influenced the ECM community in clearcuts, since samples were collected at 10 and 20 m from the edge of the residual ellipse, and there were few white spruce seedlings in the clearcuts (L. Lazaruk, personal observation). Thus, as mentioned above, a seedling bioassay might have resulted in higher abundance of the early-stage ECM. As mentioned above, however, it is clear that direct connection to roots of mature trees is important for mycorrhizal richness and composition of seedlings. Also, Fig. 5 clearly shows that lack of available root tips cannot explain the reduced ECM richness of the clearcuts, as compared with the residual ellipses.

The relationship between morphotype richness and number of root tips clearly indicates that the low ECM richness in the clearcuts was not due only to a lack of available root tips. In this study, the ECM community in the clearcuts likely consisted largely of root tips that had persisted in the soil since harvesting. Ferrier and Alexander (1985) noted that excised ECM root tips were capable of remaining metabolically active for up to 9 months after being disconnected from their host, and Hagerman et al. (1999*a*) suggested that some root tips can survive up to three growing seasons in a clearcut in the absence of a host.

Conclusions

The results of this study suggest that partial cutting, either in the form of dispersed or aggregated green-tree retention (GTR) can be an effective means of maintaining ECM biodiversity. At the stand level, the dispersed GTR appeared to emulate the heterogeneity inherent to burned stands. However, both burning and clear-cutting significantly decreased ECM richness and diversity, suggesting that emulating natural disturbance is not synonymous with maintaining biodiversity, at least in the short term. Future research is required to determine the ability of the ectomycorrhizae associated with aggregated GTR patches to recolonize the surrounding clearcut and, in turn, their role in reforestation. While this study was capable of addressing the immediate impacts of these harvesting practices on ECM communities, further research is required to assess the long-term impacts.

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References

Agerer, R. 1987–1998. Color atlas of ectomycorrhizae. Einhorn-Verlag Eduard Dietenberger, Schwabisch Gmund, Germany.

Agerer, R., Schloter, M., and Hahn, C. 2000. Fungal enzymatic activity in fruitbodies. Nova Hedwigia Kryptogamenkd. **71**: 315–336.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. **75**: 49–54.

Bradbury, S.M. 1998. Ectomycorrhizas of lodgepole pine (*Pinus contorta*) seedlings originating from seed in southwestern Alberta cut blocks. Can. J. Bot. **76**: 213–217.

Bradbury, S.M., Danielson, R.M., and Visser, S. 1998. Ectomycorrhizas of regenerating stands of lodgepole pine (*Pinus contorta*). Can. J. Bot. **76**: 218–227.

Byrd, K.B., Parker, V.T., Vogler, D.R., and Cullings, K.W. 1999. The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming and Gallatin National Forest, Montana. Can. J. Bot. **78**: 149–156.

Cairney, J.W.D. 1999. Intraspecific physiological variation: implications for understanding functional diversity in ectomycorrhizal fungi. Mycorrhiza, **9**: 125–135.

Deacon, J.W., Donaldson, S.D., and Last, F.T. 1983. Sequences and interactions of mycorrhizal fungi on birch. Plant Soil, **71**: 257–262.

Deacon, J.W., and Fleming, L.V. 1992. Interactions of ectomycorrhizal fungi. *In* Mycorrhizal functioning, an integrative plant-fungal process. *Edited by* M.F. Allen. Chapman and Hall Inc., New York. pp. 249–300.

Duddridge, J.A., Malibari, A., and Read, D.J. 1980. Structure and function of mycorrhizal rhizomorphs with special reference to water transport. Nature (London), **287**: 834–836.

Duchesne, L.C., Peterson, R.L., and Ellis, B.E. 1988. Interaction between the ectomycorrhizal fungus *Paxillus involutus* and *Pinus resinosa* induces resistance to *Fusarium oxysporum*. Can. J. Bot. **66**: 558–562.

Durall, D.M., Jones, M.D., Wright, E.F., Kroeger, P., and Coates, K.D. 1999. Species richness of ectomycorrhizae of different sizes in the Interior Cedar–Hemlock forest of northwestern British Columbia: sporocarps and ectomycorrhizae. Can. J. For. Res. **29**: 1322–1332.

Eberhart, K.E., and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. **17**: 1207–1212.

EMEND. 2004. Prescribed burn treatments. Available from http://www.biology.ualberta.ca/old_site/emend//treatments/burns_e.html [accessed 14 July 2004].

Ferrier, R.C., and Alexander, I.J. 1985. Persistence under field conditions of excised fine roots and mycorrhizas of spruce. *In* Ecological interactions in soil. *Edited by* A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher. Blackwell Scientific Publications, Oxford, UK. pp. 175–179.

Fenniak, T. 2001. Pattern and process of understory redevelopment following partial-cut harvesting in the boreal forest. M.Sc. thesis, University of Alberta, Edmonton, Alta.

Galindo-Leal, C., and Bunnell, F.L. 1995. Ecosystem management: implications and opportunities of a new paradigm. For. Chron. **71**: 601–606.

Goodman, D.M., and Trofymow, J.A. 1998. Distribution of ectomycorrhiza in micro-habitats in mature and old-growth stands of Douglas-fir on southeastern Vancouver Island. Soil Biol. Biochem. **30**: 2127–2138.

Goodman, D.M., Durall, D.M., and Trofymow, J.A. 1996. Describing ectomycorrhizae. *In* A manual of concise descriptions of North American ectomycorrhizae. *Edited by* D.M. Goodman, D.M. Durall, J.A. Trofymow, and S.M. Berch. Mycologue Publications, Sidney, B.C.

Hagerman, S.M. 1997. Quantifying the effects of different clear-cut sizes on ectomycorrhizal fungi at a subalpine forest: persistence and diversity. M.Sc. thesis, The University of British Columbia, Vancouver, B.C.

Hagerman, S.M., Jones, M.D., Bradfield, G.E., Gillespie, M., and Durall, D.M. 1999*a*. Effects of clear-cut logging on the diversity and persistence of ectomycorrhizae at a subalpine forest. Can. J. For. Res. **29**: 124–134.

Hagerman, S.M., Jones, M.D., Bradfield, G.E., and Sakakibara, S.M. 1999*b*. Ectomycorrhizal colonization of *Picea engelmannii* × *Picea glauca* seedlings planted across cut blocks of different sizes. Can. J. For. Res. **29**: 1856–1870.

Hagerman, S.M., Sakakibara, S.M., and Durall, D.M. 2001. The potential for woody understory plants to provide refuge for ectomycorrhizal inoculum at an interior Douglas-fir forest after clear-cut logging. Can. J. For. Res. **31**: 711–721.

Harvey, A.E., Larsen, M.J., and Jurgensen, M.F. 1976. Distribution of ectomycorrhizae in a mature Douglas-fir/larch forest soil in western Montana. For. Sci. **22**: 393–398.

Harvey, A.E., Jurgensen, M.F., and Larsen, M.J. 1980*a*. Clearcut harvesting and ectomycorrhizae: survival of activity on residual roots and influence on a bordering forest stand in western Montana. Can. J. For. Res. **10**: 300–303.

Harvey, A.E., Larsen, M.J., and Jurgensen, M.F. 1980*b*. Partial cut harvesting and ectomycorrhizae: early effects in Douglas-fir – larch forests of western Montana. Can. J. For. Res. **10**: 436–440.

Ingelby, K., Mason, P.A., Last, F.T., and Fleming, L.V. 1990. Identification of ectomycorrhizas. ITE research publication No. 5. Her Majesty's Stationary Office, London.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, UK.

Kernaghan, G. 2001. Ectomycorrhizal fungi at tree line in the Canadian Rockies II. Identification of ectomycorrhizae by anatomy and PCR. Mycorrhiza, **10**: 217–229.

Kernaghan, G., Widden, P., Bergeron, Y., Légaré, S., and Paré, D. 2003. Biotic and abiotic factors affecting ectomycorrhizal diversity in boreal mixed-woods. Oikos, **102**: 497–504.

Kishchuk, B.E. 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northerwestern Alberta. Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-397.

Kranabetter, J.M. 1999. The effect of refuge trees on a paper birch ectomycorrhizal community. Can. J. Bot. **77**: 1523–1528.

Kranabetter, J.M., and Kroger, P. 2001. Ectomycorrhizal mushroom response to partial cutting in a western hemlock – western redcedar forest. Can. J. For. Res. **31**: 978–987.

Kranabetter, J.M., and Wylie, T. 1998. Ectomycorrhizal community structure across forest openings on naturally regenerated western hemlock seedlings. Can. J. Bot. **76**: 189–196.

Last, F.T., Dighton, J., and Mason, P.A. 1987. Successions of sheathing mycorrhizal fungi. Tree. **2**: 157–161.

Lazaruk, L.W. 2002. The impact of harvesting practices on the biodiversity of *Picea glauca* ectomycorrhizae. M.Sc. thesis, University of Alberta, Edmonton, Alta.

Maini, J.S. 1998. Forest policy, management, and biodiversity. *In* Policy and practices for biodiversity in managed forests: the living dance. *Edited by* F.L. Bunnell and F. Johnson. UBC Press, Vancouver, B.C. pp. 19–29.

Marx, D.H., Bryan, C.W., and Davey, C.B. 1970. Influence of temperature on aseptic synthesis of ectomycorrhizae by *Thelephora terrestris* and *Pisolithus tinctorius* on loblolly pine. For. Sci. **16**: 424–431.

Mason, P.A., Wilson, J., Last, F.T., and Walker, C. 1983. The concept of succession in relation to the spread of sheathing ectomycorrhizal fungi on inoculated tree seedlings growing in unsterile soils. Plant Soil. **71**: 247–256.

Morin, C., Samson, J., and Dessureault, M. 1999. Protection of black spruce seedlings against Cylindrocladium root rot with ectomycorrhizal fungi. Can. J. Bot. **77**: 169–174.

Newton, A.C. 1992. Towards a functional classification of ectomycorrhizal fungi. Mycorrhiza. **2**: 75–79.

Page-Dumroese, D.S., Harvey, A.E., Jurgensen, M.F., and Amaranthus, M.P. 1998. Impacts of soil compaction and tree stump removal on soil properties and outplanted seedlings in northern Idaho, USA. Can. J. Soil Sci. **78**: 29–34.

Parsons, W.F.J., Miller, S.L., and Knight, D.H. 1994. Root-gap dynamics in a lodgepole pine forest: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap formation. Can. J. For. Res. **24**: 1531–1538.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**: 289–306.

Rowe, J.S., and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. **22**: 37–45.

Sakakibara, S.M., Jones, M.D., Gillespie, M., Hagerman, S.M., Forrest, M.E., Simard, S.W., and Durall, D.M. 2002. A comparison of ectomycorrhiza identification based on morphotyping and PCR–RFLP analysis. Mycol. Res. **106**: 868–878.

Shannon, C.E., and Weaver, W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, Ill.

Shoenberger, M.M., and Perry, D.A. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings: a greenhouse bioassay. Can. J. For. Res. **12**: 343–353.

Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R. 1997. Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. **136**: 327–340.

Smith, S.E., and Read, D.J. 1997. Mycorrhizal symbiosis. 2nd ed. Academic Press, New York.

Smith, J.E., Molina, R., Huso, M.M.P., and Larsen, M.J. 2000. Occurrence of *Piloderma fallax* in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade range of Oregon, U.S.A. Can. J. Bot. **78**: 995–1001.

Smith, J.E., McKay, D., Niwa, C.G., Thies, W.G., Brenner, G., and Spatafora, J.W. 2004. Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. Can. J. For. Res. **34**: 2477–2491.

SPSS Inc. 1999. SPSS for windows release version 10.0. SPSS Inc., Chicago, Ill.

Startsev, A.D., and McNabb, D.H. 2001. Skidder traffic effects on water retention, pore-size distribution, and van Genuchen parameters of boreal forest soils. Soil Sci. Soc. Am. J. **65**: 224–231.

Stendell, E.R., Horton, T.R., and Bruns, T.D. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycol. Res. **103**: 1353–1359.

Strong, W.L., and Leggat, K.R. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Land Information Services Division, Edmonton, Alta.

ter Braak, C.J.F., and Šmilauer, P. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version IV). Microcomputer Power, Ithaca, N.Y.

Teste, F.P., Schmidt, M.G., Berch, S.M., Bulmer, C., and Egger, K.N. 2004. Effects of ectomycorrhizal inoculants on survival and growth of interior Douglas-fir seedlings on reforestation sites and partially rehabilitated landings. Can. J. For. Res. **34**: 2074–2088.

Visser, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. **129**: 389–401.

Vogt, K.A., Grier, C.C., Meier, C.E., and Edmonds, R.L. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology. **63**: 370–380.

Waters, J.R., McKelvey, K.S., Zabel, C.J., and Oliver, W.W. 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. Can. J. For. Res. **24**: 1516–1522.

Williamson, J.R., and Neilson, W.A. 2000. The influence of forest site on rate and extent of soil compaction and profile disturbance of skid trails during ground based harvesting. Can. J. For. Res. **30**: 1196–1205.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., and Langor, D. 2004. Stand composition and structure of the boreal mixedwood and apigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Can. J. For. Res. **34**: 417–430.

Zak, J.C., and Visser, S. 1996. An appraisal of soil fungal biodiversity: the functional crossroads between taxonomic and functional biodiversity. Biodivers. Conserv. **5**: 169–183.