*"Nature first, then theory. Or, better, Nature and theory closely intertwined while you throw all your intellectual capital at the subject.*

*Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and the pleasure will have been enough."*

*-E. O. Wilson, Naturalist*

# University of Alberta

# Conservation of boreal moth communities in the mixedwood boreal forests of northwestern Alberta: Impacts of green tree retention and slash-burning

by

Esther W. Kamunya

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for degree of

Master of Science
in
Forest biology and management

Department of Renewable Resources

Fall 2012
Edmonton, Alberta

*To my husband, Simon, for his unconditional love*

*To my Son, Sam, for his energy, drive and inspiration*

*To my daughter, Susan, for her beautiful smile that lights even the darkest of night*

*And,*

*To my mum, Susan, for her prayers – the Amazing grace that leads me on*

# Abstract

Green tree retention (GTR), which involves leaving dispersed or clustered live trees on harvested stands, is being adopted as an alternative to clear-cutting, and to conserve biodiversity on managed forests. This thesis examines the post-harvest (7-10yrs) recovery of boreal moths following retention harvest and slash-burning in the managed mixedwood boreal of northwestern Alberta. Night-flying moths were light-trapped from coniferous (CDOM) and deciduous (DDOM) stands harvested to three retention levels (10%, 20% and 50%), stands harvested to 10% retention and burned (slash-burns), and compared to un-cut control stands that had regenerated from wildfires (~80-140 yrs ago). At the 50% level, moth communities of the DDOM cover-type did not differ from un-harvested stands, but those of the CDOM cover-type were still very different, 8-yrs post-harvest. Retentions at the 20% level were insufficient to promote the recovery of moth communities on harvested stands of both cover-types. The abundances of moths that feed on pioneer plant species in their larval stages were increased while feeding specialists were decreased at both levels of retention. Thus, higher levels of retention are likely required in order to conserve feeding and habitat specialists in the managed mixedwood boreal. Arboreal larval assemblages on trees sampled from harvested stands were not significantly different from those on un-harvested stands. Larval abundance and richness greatly varied among trees of the same species due to tree height, diameter at breast height and the

percent crown-cover around individual trees. Retaining single dispersed trees of different species, size and age classes on harvested blocks may therefore help to maintain populations of specialized feeders, albeit in low abundances, through the stand regeneration cycle. Burning slash after harvesting did not promote a recovery of moth assemblages different from that found in low (20%) retention harvest, 8-yrs post harvest, but both forms of disturbance greatly reduced moth abundances and richness compared to unharvested controls. It is likely that fire behavior and intensity is modified in stands where low retention levels have been applied. Hence, prescribed burning aimed at complementing GTR will better achieve conservation objectives as complements to high retention or unharvested forest stands.

## Acknowledgements

I would like to thank the following individuals whose great contributions to my life and career at the University of Alberta will always be cherished:

- My supervisors Drs. John Spence and Jan Volney for their guidance and encouragement throughout the program
- The examining committee, Drs. Nadir Erbilgn, Fangliang He, and Andrew Keddie
- Past and current members of the Spence Lab, Renewable Resources and Biological Sciences graduate community for their wonderful camaraderie and friendship
- Jason Edwards, Charlene Hahn, Stuart Morrison, Kimberly Stang, Xiao-Dong Yu and, the EMEND core-crew of 2005 - 2008 for their assistance with field work
- Jaime Pinzon, Richard Caners, Elisabeth Beaubien, Xianli Wang, Anayansi Cohen and, Irma Diaz, for their continuous encouragement, enlightening conversations and unending effort in reviewing drafts of my thesis
- Jason Dombroskie, Greg Phol Gary Anweiler and Chris Schmidt for their unreserved help in moth taxonomy and identification
- The RENR administrative staff for administrative and logistical support

Financial and logistical support from the following agencies/organizations and individuals made this thesis possible, and was greatly appreciated.

- Department of Renewable Resources Graduate Research and Teaching Assistantships
- EMEND project through collaboration with Alberta Sustainable Resource Development, Canadian Forest Products Ltd., Daishowa-Marubeni International Ltd., Manning and, the Canadian Forest Services (Northern Forestry Center).
- NSERC operating grant to Dr. John Spence
- Sustainable Forest Management Network operating grant to Dr. John Spence
- University of Alberta Provost Doctoral Entrance Award
- University of Alberta GSA travel Award

Many thanks to Simon, my husband, and to our lovely children, Sam and Susan, for their unfailing love and support, for believing in me and encouraging me to never give up even when the going got tough, and for patiently waiting till we all arrived to what was to come.

I thank my Abba Father, the shining light that guides my path and sets my feet on solid ground.

## List of Tables

## List of Figures

## List of Appendices

# Chapter 1: Introduction

The boreal forest is the largest terrestrial ecosystem on Earth accounting for almost one third of global forests. It constitutes the majority of intact and unmanaged forests worldwide (UNEP, 2002) and harbors a significant amount of global biodiversity (UNCED, 1992). Boreal forests perform many important functions, including carbon sequestration and the regulation of global climates (Brown, 1996). Boreal ecosystems have long provided the main economic base for human populations in northern countries (Volney and Fleming, 2000). In the past century, however, a growing interest in exploiting these forests for timber and wood fiber led to the adoption of unsustainable forestry practices, including clear-cutting, plantations, use of chemicals and short cropping cycles (Sullivan *et al*., 1996; Timoney, 2003). These approaches to forest use have detrimental effects on landscape structural complexity and are a tremendous threat to forest biodiversity (Bergeron *et al*., 1998; Bergeron *et al*., 2001; Kuuluvainen, 2009). Hence, we now search for ecologically-sound management practices that will sustain both the forest industry and biodiversity in managed landscapes (Franklin *et al*., 1997; McRae *et al*., 2001; Niemelä *et al*., 2001; Burton *et al*., 2006).

## 1.1 Natural disturbance in Boreal ecosystems

Boreal forests are disturbance adapted ecosystems. Wildfire (Angelstam, 1998; Engelmark *et al*., 2000; Bergeron *et al*., 2001; Work *et al*., 2003), insect outbreaks ( Fleming and Volney, 1995; Volney and Fleming, 2000) and natural gap dynamics (Attwill, 1994) occur over a range of spatial and temporal scales (Foster *et al*., 1998; Engelmark *et al*., 2000; Bergeron *et al*., 2002; Volney and Hirsch, 2005), creating the complex and heterogeneous habitat structures that help to maintain biodiversity.

Different forms of disturbance differ in their scale and impact on forest structure and function. On one hand, disturbance by fire promotes growth of herbaceous plants adapted to fire, thus increasing abundance, richness and diversity of some species in burned as compared to unburned sites (Huntzinger, 2003). Disturbance by insects, on the other hand, has more selective effects than fire as most insect outbreaks are host–specific and thus have more patchy effects within stands and on forest landscapes. In addition, some insects mainly attack mature stands that have passed their peak productivity (Mitchell *et al*., 1983). Such outbreaks often leave non-host and surviving host trees standing while creating light and nutrient 'gaps' that accelerate growth of remaining canopy trees and understory plants (Romme *et al*., 1986). Similarly, insect frass, falling debris of dead leaves, twigs and trees all generally increase quantity and quality of soil litter. As well, coarse woody debris affects soil nutrient dynamics and thus has implications for forest productivity. Open gaps change the amount and chemical composition of 'through-fall' (rain infiltrating through the canopy, Reynolds *et al*., 2000) which in turn affects soil moisture content, decomposition and nutrient dynamics.

Over the past several decades, forest management practices have greatly altered disturbance dynamics that characterize the boreal eco-region. Fire suppression has led to extensive change in disturbance regimes and forest community composition, reflecting increased fuel loads and dominance of fire-intolerant plant species (Ryan, 2002). Similarly, habitat changes caused by clear-cut logging strongly affect forest biota due to changes in microhabitat features and canopy openings (Niemelä *et al*., 1993; Franklin *et al*., 1997; Lindenmayer and Franklin, 1997). Furthermore, recovery of original forest habitats through regeneration can take many years (Bergeron and Harvey, 1997). There is no way to predict if the conditions of the previous forest stand will be fully restored (Spence *et al*., 1999a) or if regenerated sites will be within the reach of new colonists before they are cut again in the next rotation (Niemelä *et al*., 1992).

Attempts to develop ‘near-to-nature’ silvicultural practices that better promote structural and biological legacies normally associated with natural disturbances have increasingly become important (Hunter, 1989; 1993; Perry, 1998; Simberloff, 1999; Work *et al*., 2003; 2004). One such practice that has since gained in popularity is green tree retention (Franklin, *et al*., 1997; Rosenvald and Lõhmus 2008; Gustafsson *et al*., 2010).

## 1.2 Green tree retention and boreal biodiversity conservation

Green tree retention (GTR) is a modification of clear-cutting where live trees are left standing, singly or in groups within harvested blocks. The goal of GTR is to preserve on-site critical aspects of the pre-disturbance seral stage by ensuring that the regenerating habitat has structural features required to support continuous occupancy of species on harvested blocks (‘lifeboating’, Rosenvald and Lõhmus, 2008) and preserves habitat connectivity for dispersal of forest species (Franklin *et al*., 1997). Thus the objectives of green tree retention in broader terms is emulating (but not replicating) both the effects of fire and insect disturbances and, to some extent allowing somewhat natural gap dynamics to operate within managed stands.

Nonetheless, faunal populations and assemblage dynamics on landscapes modified by fire may differ from those in which fire is absent. For instance, fire directly kills some insects, while at the same time it creates suitable habitat for other fire-loving (pyrophilous) insect species (Schultz and Crone, 1998; Cobb *et al*., 2007; Hyvarinen *et al*., 2009). Similarly, partial and clear-cut logging differ in their immediate impacts on species diversity and assemblages for several forest groups of forest biota, including bryophytes (Caners *et al*., 2010), terrestrial plants ( Macdonald and Fenniak, 2007; Craig and Macdonald, 2009), gastropods (Abele, 2010), arthropods (Morneau, 2002; Summerville and Crist, 2002; Thomas, 2002; Jacobs *et al*., 2007)  and mammals (Mazurek and Zielinski, 2004; Sullivan *et al*., 2008). Thus, the usefulness of this new management practice in conserving biodiversity needs to be assessed for a variety of species that perform different functions and respond to ecological changes at different spatial scales. This is because the loss of individual species in managed forests, including those that are least understood, is unprecedented and can have widespread effects on whole ecosystems (Wilson, 1992). Furthermore, the impacts of any new management strategy should be monitored and compared with respect to natural processes in unmanaged ecosystems in order to assess the credibility of the new system with respect to emulating natural disturbance (Spence *et al*., 2001).

## 1.3 Study rationale

Insects have long been considered as one of the most critical components of forest biodiversity; thus, monitoring changes in their assemblages offers practical and reliable ways of understanding changes in overall ecosystem biodiversity (Summerville and Crist, 2002). Several characteristics of insects contribute to their high potential as ecological indicators (Langor and Spence, 2006). For instance, insects represent the greatest morphological and functional diversity in the animal kingdom and they play essential roles in most terrestrial ecosystems (Wilson 1987; Mattson and Addy, 1975; Samways, 1993). In addition, most insect taxa have short generation times, and coupled with environmental variation, this can drive dramatic population fluctuations. Thus changes in insect biodiversity provides the basis of an ‘early warning’ of changes in either habitat quality or in ecosystem processes important for the biota (Southwood *et al*., 1979). Despite their diversity and contribution to overall ecosystem structure and function, mechanisms driving insect assemblage patterns are poorly understood; perhaps because they are a large group and are difficult to quantify (Danks, 1989; Langor and Spence, 2006). Taxonomic complexity and lack of expertise for species level identification have made preserving biodiversity of this group difficult (Noss, 1990).

Lepidopterans (moths and butterflies) are among the ‘big four’ insect orders; along with Coleopterans, Hymenopterans and Dipterans, they make up 80% of the insects (Young, 1997). The order Lepidoptera contains about 150,000 described species, which makes up ~17% of all insect species (Gullan and Cranston, 2010). Among the lepidopterans, butterflies have received much more attention than moths because of their diurnal habits and conspicuous appearance. Nevertheless, moths are much more diverse than butterflies (constituting 88% of the order), and some can be just as colorful (e.g., some arctiids and sphingids). They perform critical functional roles as herbivorous converters, links in food chains, and detritivores (Hammond and Miller, 1998). Thus their responses to ecosystem changes resulting from human disturbance are crucial for informing wise management and biodiversity conservation decisions. Furthermore, most moth species have at least one generation per year; they respond quickly to perturbations and to the recovery of the forest from such perturbations (Thomas, 2002).

In the boreal forest, moths are among the primary insect herbivores (Volney and Mallett, 1998). Some moth species are major forces of natural disturbance and can cause extensive forest stand replacement (Volney and Fleming, 2000). Understanding their response to harvesting is crucial to the future of the boreal ecosystems. Nonetheless, studies of boreal moth assemblages, including their responses to anthropogenic disturbances, are scarce, although significant efforts have been dedicated to population dynamics of individual species (Summerville and Crist, 2008). This latter focus is often driven by interest in pests or potential pests.

A few studies comparing boreal moth assemblages based on forest stand age indicate that old stands host a higher abundance and diversity of species and that particular species unique to old forest structure are absent on young stands (Thomas, 2002;  Morneau, 2002; Pohl *et al*., 2004).  This response of forest moths to harvesting disturbances may be attributed to changes in the forest canopy structure, the understory species composition as well as the quality of plant material available as food plants for phytophagous insects (Altegrim and Sjoberg, 1996; Summerville and Crist, 2001).

Research about the conservation benefits of GTR for forest arthropods has been concentrated on epigaeic arthropods (e.g., see Gustafsson *et al*., 2010; Work *et al*., 2010; Pinzon *et al*., 2011); however, studies about other arthropod taxa, especially phytophagous lepidopterans, are lacking. Because the juveniles of most moths feed directly on plant material and many species are host-specific, (Young, 1997) they are likely to respond differently than boreal arthropod taxa previously examined, to changes in disturbance regimes that alter the plant community.

## 1.4 Thesis Objectives

In this thesis I investigate and evaluate the impacts of green tree retention and slash-burning on boreal lepidopterans. This study is part of the larger Ecosystem Management Emulating Natural disturbance (EMEND) project established in NW Alberta (see Spence *et al*., 1999b; Work *et al*., 2010 and individual chapters of this thesis for further information on EMEND objectives and experimental design).

In Chapter 2, I assess the post-harvest recovery of moth communities by comparing assemblages of stands harvested with retention and naturally regenerated for 8 years to those of un-cut control stands that were regenerated from wildfires ~80-140 yrs ago.

In Chapter 3, I address the effectiveness of single dispersed trees in 'lifeboating' boreal lepidopterans within retention stands. Here, I ask whether caterpillar assemblages inhabiting single dispersed trees are similar to those found on trees sampled within intact forest stands. Because the forest canopy influences the density and composition of understory vegetation (Roberts and Gilliam 1995; Macdonald and Fenniak 2007) and microclimatic conditions (Madigosky 2004), the roles of the canopy and understory forest strata in maintaining boreal moth diversity are further investigated.

In Chapter 4, I explore whether retention harvest, followed by burning (slash-burn), maintains similar moth assemblages as those found in the wake of a simple GTR. I seek to find out whether including fire on harvested landscapes could help to mitigate the potential impacts of harvesting on forest moths, in the short-term.

The data for both chapters 2 and 4 were collected by periodically sampling adult moths using light traps over whole summer season (June to August). I sampled dusk to dawn in order to sample the entire assembly of boreal lepidopterans that is attracted to light. Light trap catches were identified to species and assigned to feeding guilds according to their larval food preferences. I hypothesized that post-harvest recovery of moth communities would be determined by the level of harvest retention interacting with pre-harvest forest-cover.

Data for answering questions for chapter 3 were collected through whole tree sampling of canopy caterpillars and ‘beating’ understory shrubs (understory caterpillars) within a 5m radius of every tree sampled. Caterpillars were collected over a large tarp or beating sheet, respectively, and afterwards reared to obtain adults. I expected that the canopy and understory forest layers would harbor different assemblages of moth species with greater abundances expected on the canopy than the understory layer.

In the last chapter of my thesis (Chapter 5) I summarize and synthesize the major findings from the previous chapters about the impacts of retention harvest and slash-burning on the abundance, richness and composition of boreal moths. Using taxonomic and feeding guild classifications, I discuss the interactions between the level of retention harvest, the pre-harvest canopy composition and moths’ feeding preferences, in determining post-harvest recovery of moth assemblages.

## References

Abele, S., 2010. Gastropod diversity in the boreal mixedwood forest of northern Alberta - variation among forest types and response to partial harvesting. MSc Thesis, Department of Renewable Resources, University of Alberta. Edmonton, AB.

Angelstam, P.K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science,* 9(4): 593-602.

Atlegrim, O., Sjoberg, K., 1996. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management,* 87(1-3): 139-148.

Attwill, P., 1994. The disturbance of forest ecosystems - the ecological basis for conservative management. *Forest Ecology and Management,* 64: 247-300.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., Sirois, L., 1998. Key issues in disturbance dynamics in boreal forests: Introduction. *Journal of Vegetation Science,* 9: 464-468.

Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Management,* 92: 235-242.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. *Canadian Journal of Forest Research,* 31: 384-391.

Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fennica,* 36(1): 81-95.

Brown, S., 1996. Present and potential roles of forests in the global climate change debate. *Unasylva*, 47(185): 3-10.

Burton, P.J., Messier, C., Adamowicz, W.L., Kuuluvainen, T. 2006. Sustainable management of Canada's boreal forests: Progress and prospects. *Ecoscience*, 13: 234-248.

Caners, R.T., Macdonald, S.E., Belland, R.J. 2010. Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. *Botany*, 88: 315-328.

Cobb, T.P., Langor, D.W., Spence, J.R., 2007. Biodiversity and multiple disturbances: Boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forestry Research,* 37: 1310-1323.

Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Forest Ecology and Management,* 258(12): 2619-2627.

Danks, H., 1989. Insects of the boreal zone of Canada. *Canadian Entomology,* 121: 625-690.

Engelmark, O., Gauthier, S., van der Maarel, E., 2000. Disturbance dynamics in boreal and temperate forests: Introduction. *Journal of Vegetation Science,* 4(6): 730-732.

Fleming, R.A., Volney, W.J.A., 1995. Effects of Climate-Change on Insect Defoliator Population Processes in Canada Boreal Forest: Some plausible scenarios. *Water air and soil pollution,* 82(1-2): 445-454.

Foster, D.R., Knight, D.H., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. *Ecosystems*, 1(6): 497-510.

Franklin, J.F., 1993. Lessons from old-growth. *Journal of Forestry,* 91(12): 10-13.

Franklin, J.F., Rae Berg, D., Thornburgh, D.A., Trappeiner, J.C., 1997. Alternate silvicultural approaches to timber harvesting: Variable retention harvest systems. In: Franklin, J.F., Kohm, K.A., (Eds.).Creating a forest for 21st century: The science of ecosystem management. Island Press, Washington, D.C., pp. 111-139.

Gullan, P. J., Cranston, P. S., 2010. The Insects: An Outline of Entomology. Wiley-Blackwell, Oxford, UK. 565 pp.

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: A review of ecological consequences. *Scandinavian Journal of Forest Research,* 25(4): 295-308.

Hammond, P.C., Miller, J.C., 1998. Comparison of the biodiversity of Lepidoptera within three forested ecosystems. *Annals of the Entomological Society of America,* 91(3): 323-328.

Hunter, M.L., 1989. What constitutes an old-growth stand? *Journal of Forestry,* 87(8): 33-35.

Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation,* 65(2): 115-120.

Huntzinger, M., 2003. Effects of fire management practices on butterfly diversity in the forested western United States. *Biological Conservation,* 113(1): 1-12.

Hyvarinen, E., Kouki, J., Martikainen, P., 2009. Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Biodiversity,* 2(2): 93-105.

Jacobs, J.M., Spence, J.R., Langor, D.W., 2007. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. *Canadian Journal of Forest Research*, 37(9): 1631-1642.

Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. *Ambio: A Journal of the Human Environment,* 38(6): 309-315.

Langor, D.W., Spence, J.R., 2006. Arthropods as ecological indicators of sustainability in Canadian forests. *Forestry Chronicle,* 82(3): 344-350.

Lindenmayer, D.B., Franklin, J.F., 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. *Conservation Biology,* 11(5): 1053-1068.

Macdonald, S.E., Fenniak, T.E., 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. *Forest Ecology and Management,* 242(1): 34-48.

Madigosky, S.R., 2004. Tropical microclimate considerations. In: Lowman, M.D., Rinker, H.B., (Eds.), Forest canopies. *Elsevier Academic Press,* pp. 24-48.

Mattson, W., Addy, N., 1975. Phytophagous insects as regulators of forest primary production. *Science,* 190(4214): 515-522.

Mazurek, M.J., Zielinski, W.J., 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. *Forest Ecology and Management,* 193(3): 321-334.

McRae, D., Duchesne, L., Freedman, B., Lynham, T., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Reviews,* 9(4): 223-260.

Mitchell, R.G., Waring, R.H., Pitman, G.B., 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine-beetle. *Forest Science,* 29(1): 204-211.

Morneau L., 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P., 1992. Small-scale heterogeneity in the spatial-distribution of carabid beetles in the southern Finnish Taiga. *Journal of Biogeography,* 19(2): 173-181.

Niemelä, J., Langor, D., Spence, J.R., 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera, Carabidae) in western Canada. *Conservation Biology,* 7(3): 551-561.

Niemelä, J., Larsson, S., Simberloff, D., 2001. Concluding remarks - finding ways to integrate timber production and biodiversity in fennoscandian forestry. *Scandinavian Journal of Forest Research*, 16(2, Supp. 3): 119-123.

Noss, R., 1990. Indicators for monitoring biodiversity - a hierarchical approach. *Conservation Biology,* 4(4): 355-364.

Perry, D.A., 1998. The scientific basis of forestry. *Annual review of Ecology and Systematics,* 29: 435-466.

Pinzon, J., Spence, J.R., Langor, D.W., 2011. Spider assemblages in the overstory, understory, and ground layers of managed stands in the western boreal mixedwood forest of Canada. *Environmental Entomology,* 40(4): 797-808.

Pohl, G.R., Langor, D.W., Landry, J.F., Spence, J.R. 2004. Lepidopteran from boreal mixedwood forest in east-central Alberta: Comparison of assemblages from a mature and an old stand. Natural Resource Canada, Canadian Forest Service, Northern Forestry Centre. Edmonton, AB. inf. ref. NOR-X-396: 1-20.

Reynolds, B.C., Hunter, M.D., Crossley, D.A., Jr., 2000. Effects of canopy herbivory on nutrient cycling in a northern hardwood forest in western North Carolina. *Selbyana*, 21(1-2): 74-78.

Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. *Ecological Applications,* 5: 969-977.

Romme, W.H., Knight, D.H., Yavitt, J.B., 1986. Mountain pine bettle outbreaks in the Rocky-Mountains: regulators of primary productivity. *American Naturalist,* 127(4): 484-494.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management,* 255(1): 1-15.

Ryan, K.C., 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica,* 36(1): 13-39.

Samways, M., 1993. Insects in biodiversity conservation: some perspectives and directives. *Biodiversity Conservation,* 2(3): 258-282.

Schultz, C.B., Crone, E.E., 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the fender's blue. *Restoration Ecology,* 6(3): 244-252.

Simberloff, D., 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management,* 115(2-3): 101-111.

Southwood, T., Brown, V., Reader, P., 1979. Relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society,* 12(4): 327-348.

Spence, J.R., Buddle, C.M., Gandhi, K.J.K., Langor, D.W., Volney, W.J.A., Hammond, H.E.J., Pohl, G.R., 1999a. Invertebrate biodiversity, forestry and emulation of natural disturbance: A down-to-earth perspective. *In:* R. T. Meurisse, W. G. Ypsilantis & C. Seybold (Editors), *Proceedings: Pacific Northwest Forest and Rangeland Soil Organism Symposium*. USDA Forest Service, General Technical Report PNW GTR-461, Portland, pp. 80-90.

Spence J.R., Volney W.J.A., 1999b. EMEND: Ecosystem management emulating natural disturbance. Sustainable Forest Management Network report 1999-14, pp. 17. Sustainable Forest Management Network, Edmonton, Alberta.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2008. Influence of variable retention harvests on forest ecosystems: Plant and mammal responses up to 8 years post-harvest. *Forest Ecology and Management*, 254(2): 239-254.

Sullivan, T., Lautenschlager, R., Wagner, R., 1996. Influence of glyphosate on vegetation dynamics in different successional stages of sub-boreal spruce forest. *Weed Technology*, 10(2): 439-446.

Summerville, K.S., Crist, T.O., 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology,* 82(5): 1360-1370.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest lepidoptera: Community, guild, and species responses. *Ecological Applications,* 12(3): 820-835.

Summerville, K.S., Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: A review. *Canadian Entomology,* 140(4): 475-494.

Thomas A.W., 2002. Moth diversity in a northeastern North American red spruce forest II: the effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). Atlantic Forestry Centre, Fredericton, N.B.

Timoney, K.P., 2003. The changing disturbance regime of the boreal forest of the Canadian Prairie Provinces. *Forestry Chronicle,* 79(3): 502-516.

United Nations Conference on Environment and Development (UNCED), 1992. The global partnership for environment and development: A guide to agenda 21.

United Nations Environment Programme (UNEP), 2002. Global environment outlook 3: Past, present and future perspectives.

Volney, W.J.A., Mallett, K.I., 1998. Integrated pest management in western Canadian boreal forests. *Forestry Chronicle,* 74(4): 597-605.

Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. 82(1-3): 283-294.

Volney W.J.A., Spence J.R., Lefebvre E.M., 2001. Boreal Odyssey: *Proceedings: North American forest insect work conference,* May 14-18. Natural Resource Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, AB, inf. ref. NOR-X-381.

Volney, W.J.A., Hirsch, K.G., 2005. Disturbing forest disturbances. *Forestry Chronicle,* 81(5): 662-668.

Wilson, E.O., 1987. The little things that run the world. (The importance and conservation of invertebrates). *Conservation Biology,* 1(4): 344-346.

Wilson E.O., 1992. The diversity of life. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Work, T.T., Spence, J.R., Volney, W.J.A., Morgantini, L.E., Innes, J.L., 2003. Integrating biodiversity and forestry practices in western Canada. *Forestry Chronicle,* 79(5): 906-916.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, 34(2): 417-430.

Young M., 1997. The natural history of moths. T & A D Poyser, London, pp. 271.

# Chapter 2: Impacts of green tree retention on boreal lepidopterans: Community, feeding guilds and species responses

## 2.1 Introduction

Until relatively recently, boreal forestry in Canada has focused mainly on meeting market demands for forest fibre. The result has been a significant increase in the area of forest subjected to harvesting, with clear-cut logging replacing natural disturbances as a major driver of forest regeneration (Pratt and Urquhart, 1994; Volney and Hirsch, 2005). Many studies suggest that biodiversity will regenerate differently after clear-cutting or natural disturbance (e.g., Swanson and Franklin, 1992; Bengtsson *et al*., 2000; Buddle *et al*., 2006). Given resulting concerns about the future state of boreal biodiversity, forest managers and policy makers alike are compelled to re-think forest management options. Harvesting strategies that promote structural and biological legacies associated with natural disturbances are gaining in popularity (Hunter, 1993; Simberloff, 1999; Franklin *et al*., 2002), and are the predominant approach to addressing conservation concerns in Canada (Work *et al*., 2003).

Across Alberta, green tree retention (GTR) is being adopted as an alternative to clear-cut logging. GTR is a form of partial cutting where live trees of varying size and multiple canopy layers are left standing on cut-blocks as either aggregated or dispersed retention (Franklin *et al*., 1997). It is believed that such unharvested trees will preserve critical structural aspects of the pre-disturbance forest condition, but these ideas have not been rigorously tested (Spence *et al*., 2001). Retaining structural elements of old forest within cut-blocks is deemed desirable as they preserve habitats thought to act as ‘lifeboats’ (Rosenvald and Lõhmus, 2008) from which populations of some species may re-colonize harvested stands (Peet and Christensen, 1988; Gandhi *et al*., 2004).

Studies on the usefulness of GTR in lifeboating biodiversity elements have shown mixed results, and evidently, the benefits of GTR for biodiversity maintenance are taxon-specific (Haeussler *et al*., 2007; Rosenvald and Lõhmus, 2008; Gustafsson *et al*., 2010). For example, GTR shows potential for maintaining forest species in groups such as ectomycorrhizal fungi, epiphytic lichen, some carabid beetles and small mammals (Rosenvald and Lõhmus, 2008). However GTR appears to be inadequate for maintaining disturbance sensitive species like bryophytes ( Nelson and Halpern, 2005; Caners *et al*., 2010), forest interior specialists such as saproxylic beetles (Jacobs *et al*., 2007) and some epigaeic taxa that depend on advanced successional stages (Work *et al*., 2010).

Research on the conservation benefits of GTR for forest arthropods has been concentrated on epigaeic arthropods (e.g., see Gustafsson *et al*., 2010; Work et al. 2010; Pinzon *et al*., 2011), but there is comparatively little known about other arthropod taxa, especially phytophagous lepidopterans. Because the juveniles of most moths feed directly on plant material and many species are host-specific (Young, 1997), lepidopterans are likely to respond differently than epigaeic taxa to changes in disturbance regimes that alter the plant community. Lepidopteran responses are likely to be important because moths are primary herbivores in boreal ecosystems (Volney and Mallett, 1998) and provide critical trophic links in converting primary production to animal biomass (Hammond and Miller, 1998). Furthermore, some lepidopteran defoliators are a major force of natural disturbance and can drive extensive replacement of forest stands (Volney and Fleming, 2000).

I investigated the richness, composition, dominance and guild structure of a boreal lepidopteran community. My objectives were twofold: 1) to investigate the species richness and composition of moths associated, respectively, with the early- and late-successional deciduous and coniferous cover-types and 2) to assess post-harvest recovery of moth communities by comparing assemblages from stands harvested through retention harvest and naturally regenerated for 7 years with those of unharvested stands that had regenerated naturally after wildfires ~80-140 yrs ago.

## 2.2 Materials and Methods

### 2.2.1 Study site

This research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site located in the boreal region of northwestern Alberta, approximately 90 km northwest of Peace River (56˚ 44'N, 118˚ 20'W). EMEND was established in 1997 to test hypotheses about the impact of partial harvesting and prescribed burning on forest structure and function (Spence *et al*., 1999; Work *et al*., 2003, 2010). Treatments were applied to c. 10-ha harvest units (a portion of forest stand; hereafter referred to as compartments) in three replicate stands of each cover-type in the winter of 1999 (Figure 1). The present study was conducted in the summer of 2006, seven years post-harvest.

EMEND is in a region characterized by cold winters (mean temperatures = -16.6 ± 5.3 °C) and moderately warm summers (mean temperature = 16.0 ± 1.2 °C), with a total annual precipitation of 378 mm occurring mostly in June and July (Environment Canada, 2011). The area ranges in elevation between 689 and 838 m above sea level, the topography is gently rolling and soils are predominantly from fine-textured glacio-lacustrine parent materials (Kishchuk, 2004).

The forest at EMEND is characterized by early successional deciduous dominated stands, which establish after disturbance (mainly by fire and insect outbreaks). Over time these stands are replaced by late successional coniferous forests. I studied moths in EMEND treatment compartments representing the following two cover-types: 1) deciduous compartments (DDOM, mean age = 93.9 ± 16.30 yr), consisting of >70% of deciduous *Populus* species, mainly *P. tremuloides* Michx. and *P. balsamifera* L. with a small component of *Betula papyrifera* Marshall; and 2) coniferous compartments (CDOM, mean age = 127.4

± 24.82 yr) that consisted of >70% white spruce *Picea glauca* (Moench) with a significant proportion of black spruce *Picea mariana* (P. Mill.) in some stands. The understory structure of the DDOM cover-type is dense, consisting mainly alder (*Alnus crsipa* (Ait.) Pursh), willow (*Salix spp.*), low-bush cranberry [*Viburnum edule* (Michx.)], prickly rose (*Rosa acicularis* Lindl.) and buffalo-berry [*Shepherdia canadensis* (L.) Nutt.], all in relatively equal abundance (Kishchuk *et al*., 2004; Macdonald and Fenniak, 2007). CDOM stands, on the other hand, have a less dense and more heterogeneous understory, including mainly low-bush cranberry, prickly rose and feather mosses [*Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Bird.) Mitt. and *Ptilium crista-castrensis* (Hedw.) DeNot, Caners, 2010].

### 2.2.2 Moth samples

Macromoths were sampled using light traps from three replicate compartments of the CDOM and DDOM cover-types representing two levels of retention harvest (20% and 50%) and uncut forest checks, i.e., light traps were run in a total of 18 compartments. As with most insect traps, light traps provide biased samples of communities, e.g., they are biased toward collection of nocturnal insects that are attracted to light. Lepidopteran species which may be collected by baiting to sugars and pheromones, as well as those with wingless adults (e.g., females of some lymantriids and geometrids) or with poor flight ability are also generally underrepresented in light trap catches (Summerville and Crist, 2008). However, light traps yield high numbers of individuals and species that may be reasonably compared among locations, making them the most widely used technique for sampling adult moths (Southwood, 1994; 1995).

The light traps used (Bioquip #2851; CA, USA) consisted of a plastic bucket with a ‘roof’ and 12-W u-shaped UV black lights powered by a 12-V battery; a killing agent (Vapona™) was placed inside the bucket during each night of trap operation. One light trap was set on permanent light trapping stations previously established in the centre of each compartment at EMEND (Morneau, 2002). Traps were deployed consistently 2m above ground by hanging them on tripods in order to minimize the influence of ground vegetation on trap efficiency (Figure 2). In order to sample a wide range of macro moths species, I ran the light traps over five nights at c. 10-14 day intervals between June and August in 2006 (90 samples in total), which is the most active flight period for forest moths in northwestern Alberta (Morneau, 2002; Pohl *et al*., 2004b).

Trap lights were on from dusk to dawn, under control of a 12V DC digital timer, because moth species vary in nightly activity period (Scalercio *et al*., 2009). Light traps were also deployed only during nights with little to no moonlight, temperatures above $5^{o}$C and when precipitation was minimal because trap catches are influenced by such conditions (Scalercio *et al*., 2009). To maximize comparability among catches, traps were deployed during the same nights at all sites. Catches were transferred into paper bags the morning following trapping and frozen for processing.

Macro-moths (higher Dytrisia: Superfamilies Geometroidia to Noctuoidea) were sorted from the light trap samples, identified to species and thereafter classified into feeding guilds based on information in the literature about their larval host-plants (Root, 1973). A wide range of literature was used in species identification and guild classifications, including most prominently Hodges (1983), Miller (1996), Miller and Hammond (2000, 2003), Robinson (2002), Pohl *et al*., (2004b), Wagner and Wagner (2005), and Powell and Opler (2009). I also consulted online resources, including the University of Alberta E. H. Strickland Virtual Entomological Museums, the North American Moth Photographers Group and The Canadian Biodiversity Information Facility hosted website, The Moths of Canada, and museum reference collections at the University of Alberta (E. H. Strickland Museum) and the Northern Forestry Centre in Edmonton AB, Canada. A reference collection containing voucher specimens for this study was deposited at the Northern Forestry Centre.

## 2.3 Data analysis

The response of boreal moths to retention harvests and cover-types was examined both for species assemblages and feeding guilds, using permutational multivariate analysis of variance [PerMANOVA, (Anderson, 2001; Anderson, 2005)]. PerMANOVA is a distance-based technique for analyzing variance in multivariate datasets and testing hypotheses arising from planned experiments. It is appropriate for determining multivariate responses of non-independent variables such as an assemblage of species in a given sample (Anderson, 2005). Model significance is evaluated using a permutation test, and thus multivariate normality is not assumed and, furthermore, multivariate distances can be based on any distance metric. I used the Bray-Curtis measures of multivariate distance in the analyses described above.

I used a two-factor design with three levels of retention (20%, 50% and 100%) and two levels of forest cover-type (CDOM and DDOM). The analysis was performed using the PerMANOVA program (Anderson, 2005) with 9999 permutations and based on Bray-Curtis dissimilarity of log-transformed data. *A posteriori* pair-wise comparisons were made when significant effects were observed.

I used non-metric multidimensional scaling (NMS) ordination of log-transformed data using Bray-Curtis distance to examine patterns in moth assemblages between the cover-types and among harvesting treatments. These analyses were performed separately for moth species and feeding guild, using the PC-Ord statistical package (McCune and Grace, 2002). NMS makes no assumptions about normality as only the rank order of the original distances is preserved.

Indicator species analysis (ISA, Dufrene and Legendre, 1997) was used to assess associations between moth species and different levels of harvest intensity within each cover-type and, in turn, to determine which species were responsible for any differences among harvest treatments. ISA involves calculating the relative abundance (the distribution of abundances among groups for each species) and constancy (relative frequency of each species in a group) in order to obtain an indicator value (IndVal). Indicator values were calculated using the PC-Ord program (McCune and Grace, 2002). A species was considered a significant indicator when its indicator value differed significantly from random (at $\alpha < 0.05$) after a Monte Carlo test based on 999 permutations.

To determine the impact of retention harvest on the dominance structure of moth assemblages within cover-types and among harvest treatments, I calculated the species dominance value (*DV*), as described by Pinzon and Spence (2010). This metric weighs the overall proportional abundance (*AP*) of a given species against its overall proportional frequency (*w*) and provides a value of *DV* for each species in the assemblage. Species dominance values are then interpreted based on values of relative dominance (*DV'*) estimated as the proportional amount of dominance (*DV*) for each species in relation to the total sum of all *DV* values in the assemblage.

Once the *DV* is calculated for a species, its status within the assemblage is assigned based on tabulated dominance values (*DV'*) as well as its location on a four-quadrant dominance plot of *w* against *AP* values. Species are considered truly dominant (D) if they are among the most abundant and most frequently sampled; dominant species appear in the upper right quadrant. Subdominant (S) species are those that are frequently sampled but in low abundances; they fall in the lower right of the quadrant. Species that are infrequently collected, though in high abundances, appear in the upper left quadrant and are considered to be locally abundant. According to Pinzon and Spence (2010), most species are expected to be on the lower left quadrant, and should be sampled in relatively equal abundances.  This quadrant is further subdivided into two to designate common (C) and un-common (U) species that appear in the right and in the left subdivisions of this quadrant, respectively.

## 2.4 Results

A total of 4, 833 macro-moth individuals belonging to 190 species and eight families were included in my samples (Appendix 2.1). The most frequently collected families were Noctuidae and Geometridae, accounting for 54.6% and 33.4% of the total catch, respectively (Table 2.1). The most abundant species were two noctuids, *Enargia decolor* (Wlk.) with 486 individuals (10.06 % of the total catch), and *Brachylomia algens* (Grt.) with 288 individuals (5.96 % of the total catch). Over 25% of the species in the light trap samples were singletons or doubletons (18.4 % and 7.37% of the total sample, respectively).  Traps in DDOM compartments accounted for 68 % of the macro-moth abundance, with the remaining 32% collected in light traps from CDOM compartments. Catches from DDOM compartments were more diverse, containing 92% of the species collected compared with 78% from the CDOM cover-type.

Moth species were assigned to nine feeding guilds based on larval host plant and feeding preferences. Nearly 50% of the moth species caught in light traps had deciduous trees as part of their larval plant diet. Of these, 22.6% were considered oligophagous, feeding exclusively on closely related deciduous trees (DT, Table 2.1) in the Salicaceae (willows and poplars). Another 16.8% were considered polyphagous as they fed on a wide range of unrelated plant species, including deciduous trees as well as woody shrubs from several families (DWP). I classified polyphagous species as true generalist (GEN) feeders if they were known to include conifers in their larval diet in addition to a wide range of deciduous, woody and low herbaceous plants. The GEN feeding guild constituted less than 10% of the total sample.  Moth species belonging to other feeding guilds, e.g., those that feed on grasses (GR) as well as those feeding on dead leaves, lichens and fungus (DET), constituted smaller proportions (5.3 % and 3.2%, respectively) of the total catch. Interestingly, only 8 species, representing 4.2% of the total richness, were classified as true conifer (CON) specialists. Feeding associations could not be determined for 17% of the species (classified as ‘unknown’ in Table 2.1).

### 2.4.1 Moth assemblage response to harvesting treatments

In DDOM stands mean moth species richness declined with decreasing retention and fell away from the richness observed in unharvested compartments. In contrast, mean richness increased slightly but not significantly in CDOM compartments after harvesting to 50% retention, and only clearly declined in compartments harvested to 20% retention (Figure 2.3a). Mean moth abundance exhibited a similar trend in both cover-typess being highest in the unharvested stands and declining as retention level decreased, significantly so in stands harvested to 20% retention (Figure 2.3b). However, the overall decrease in abundance was more extreme in DDOM stands.

Species composition of moth assemblages differed significantly between forest cover-types and among compartments subjected to different harvest prescriptions, with a marginally significant interaction between the two factors (PerMANOVA, Table 2.2). Moth assemblages from the 20% and 50% retention treatments did not differ significantly in paired comparisons (Table 2.2); however, assemblages of stands harvested with 20% retention differed significantly from those trapped in unharvested stands. In contrast, differences between assemblages in stands harvested with 50% retention and the unharvested controls were only marginally significant seven years post-harvest (Table 2.2).

The preferred NMS ordination depicting species composition of assemblages was a two dimensional solution (final stress of 10.3; Figure 2.4a) generally consistent with the results of the PerMANOVA described above. Moth assemblages of the two retention-harvest treatments were clearly distinguished from those of control stands along axis-1 in the ordination space. Notable cover-type effects associated with the uncut control compartments were clearly evident along axis-2 and, to a smaller extent, DDOM and CDOM sites separated also along axis-1.Interestingly, however, the distinction between cover-types is blurred seven years post-harvest; i.e., moth assemblages of DDOM and CDOM retention stands group closer to each other in the ordination space than to those of their respective unharvested stands. Furthermore, post-harvest moth assemblages are grouped according to the level of retention, irrespective of their pre-harvest cover-types (Figure 2.4a).

### 2.4.2 Response of moth feeding guilds to harvest treatments

Feeding guilds responded to harvested compartments in a pattern consistent with that observed for data about species composition. Moth guilds of the retention compartments differed significantly in relative importance from those of the unharvested controls; however, the harvested compartments showed no significant differences in guild structure (PerMANOVA, Table 2.2). The analysis, however, showed a significant statistical interaction between the effects of retention harvest and cover-type. Among DDOM stands, *a posteriori* pair-wise comparisons revealed a significant difference in guild structure from unharvested compartments only in those harvested to 20% retention (Table 2.2). On the other hand, both 20% and 50% retention had a significant impact on the structure of feeding guilds in the CDOM cover-type (Table 2.2).

Further analysis using NMS ordination showed that DDOM guild structure in both the 20% and 50% retention compartments remained somewhat similar to that of unharvested controls. In contrast, however, guild structure in the harvested CDOM compartments differed markedly from that of the respective controls. In fact, seven years post-harvest CDOM assemblages appeared to be more similar to the harvested stands of the DDOM cover-type (Figure 2.4b).

Responses of different moth feeding guilds to harvest treatments followed two general patterns: 1) richness and abundance decreased with increasing retention, irrespective of pre-harvest cover-type, and 2) responses of moths belonging to the same feeding guild differed, apparently depending on interactions between retention level and pre-harvest cover-type.

The first pattern of response was seen for five of the nine feeding guilds in the sample (Figure 2.5 and 2.6, a-i). These five guilds included species with larvae that feed on canopy trees or a combination of deciduous trees, woody and low herbaceous plants, as well as species dependent on fungi, lichens and dead leaves (Figure 2.5 and 2.6, a-i). The response of these feeding guilds to harvesting is partly responsible for the effects on moth abundance in both cover-types and for the disproportionate effects on species richness seen in DDOM compartments (refer to Figure 2a and b).

The second pattern of response is in the general lack of impact on moth abundance and richness in compartments harvested to 50% retention, especially in the CDOM cover-type. Moths that depend on grasses (Graminaeae) were, in fact, more abundantly collected in the 50% retention treatments of both cover-types, with increases in richness being statistically significant in CDOM compartments (Figure 2.5f and 2.6f). Likewise, lepidopteran species feeding on low herbaceous plants were more abundant and speciose in the 50% CDOM compartments, while their abundance and richness decreased with increasing harvest intensity in the DDOM stands (Figure 2.6f & 2.6f). For conifer specialists the response was greatly reduced abundance in harvested DDOM and 20% CDOM compartments (Figure 2.6e). However, for this guild there was no significant impact on species richness in the 50% retention CDOM compartments.

### 2.4.3 Dominance patterns and species responses to harvesting

Of the 190 moth species captured in light traps, 27 had significant indictor values. A large proportion of this indicator group, 23 out of the 27 species, was significantly associated with the unharvested stands. Of these, 19 were significant indicators of the unharvested DDOM stands (Table 2.3), and were either deciduous specialists or generalist feeders in their larval stages. Not surprisingly, the four macro-moth species that were indicative of the unharvested CDOM stands included two conifer feeders in the family Noctuidae: *Idia aemula* and *Xestia perquiritata* (Morr.): (Table 2.4). Only 4 species, two geometrids [*Plemyria georgii* Hulst and *Epirrita autumnata* (Bkh.)], and two noctuids [*Leucania insueta* Gn. and *Platypolia anceps* (Steph.)], were significant indicators of the 50% retention treatments and only for the DDOM cover-type. No significant indicator species were associated with stands harvested to 20% retention in either cover-type.

The light trap samples comprised a few dominant species, but many sub-dominant and common species (Table 2.4). Interestingly, dominance structure differed greatly between even unharvested compartments of the two cover-types. A total of seven species could be considered as dominant in unharvested CDOM stands, as compared to only three in the DDOM stands. The two cover-types shared two dominant species: *E. decolor* (CDOM *DV'*: 10.69 and DDOM *DV'*: 15.04), the larvae of which feeds on trembling aspen, and *V. cambrica* Curt. (CDOM *DV'*: 5.17 and DDOM *DV'*: 8.02), with larvae that feed more generally non woody plants (WP) in the understory (Table 2.5). All three species that were dominant in unharvested DDOM compartments were also significant indicators of this treatment. In CDOM stands, the five other dominant species were also indicator species for the unharvested stands of this cover-type. Of these, two species [*I. aemula* (*DV'*: 6.03), and *X. perquiritata* (*DV'*: 8.79)] feed on conifers in their larval stages, two [*Polia nimbosa* (Gn.), *DV'*: 6.38 and *X. mixta* (Wlk.), *DV'*:

6.38] are polyphagous on woody and low herbaceous plants (WLP) while the host plant associations for the fourth species [*Perizoma basaliata* (Wlk.)*,* (*DV'*: 7.07)] are largely unknown.

Even seven years post-harvest, the dominance structure of CDOM compartments which had been harvested with retention differed markedly with those that remained unharvested. Conifer specialists that dominated unharvested CDOM stands were mostly replaced by species belonging to other feeding guilds in the retention treatments. Only *E. decolor*, the deciduous specialist that was dominant in CDOM compartments before harvest, remained dominant seven years post-harvest, despite being much less abundant in compartments harvested to 20% and 50% retention in both cover-types (Figure 2.7a). In addition, the noctuid, *Protodeltote albidula* (Gn.), the larvae of which feeds on grasses, exhibited high dominance values in CDOM stands harvested with retention (Table 2.5f, Figure 2.7 d). Other species that became dominant in harvested CDOM compartments included two generalists, *B. algens* (Noctuidae) and *Dysstroma walkerata* (Pears.) (Geometridae), in the 20% retentions, and low herbaceous plants feeders such as *Virbia ferruginosa* (Wlk.); Erebidae, *Lacinopolia lorea* (Gn.); Noctuidae, and *Sparginia luctuata* (D & S); Geometridae, in the 50% retention treatments (Table 2.4).

In contrast, the 50% retention harvest treatment caused little apparent impact on dominance structure in DDOM compartments harvested to 50%

retention. Specifically, two of the species that were dominant in the unharvested compartments remained so, while *V. cambrica* was replaced by *Platypolia anceps* (Steph.) as a dominant species. The larvae of *P. anceps* feed on low herbaceous plants (LP). This species was also a significant indicator for the 50% DDOM stands (Tables 2.3 and 2.4). Seven years post-harvest, however, the moth dominance structure of DDOM compartments harvested to 20% retention differed significantly from that seen in unharvested compartments. *P. albidula* and *Sicya macularia* (Harr.), a deciduous and woody plant feeder, were the dominant species after this harvesting treatment.

It is important to note that although harvesting generally decreased the abundance of the dominant species in both cover-types, this increase was only significant in the 20% retention compartments (Figure 2.7 a, b & c).

## 2.5 Discussion

### 2.5.1 Cover-type effects on moth assemblages

Moth species richness and composition differed greatly between the DDOM and CDOM cover-types that are generally held to respectively represent the early and late stages of local forest canopy succession in the boreal mixedwoods (Chen and Popadiouk, 2002). This result is consistent with studies of other taxa at EMEND, including understory vascular plants (Craig and Macdonald, 2009; Macdonald and Fenniak, 2007), arthropods (Work *et al.*, 2004) and gastropod species (Abele, 2010).

Despite differences in moth assemblages between the cover-types, they shared many species. As revealed by the guild classifications presented here, the moth community at EMEND exploits a wide range of broad-leaved trees, shrubs and herbaceous plants in the understory; conifer specialists are relatively few. The understory plant community composition at EMEND varies with canopy composition, being less dense and relatively patchy in conifer compared to deciduous stands (Macdonald and Fenniak, 2007), and this may explain why moth richness and abundance was higher in deciduous stands.

Perhaps the most interesting inference to be drawn from these data is that, in general, boreal macro-moths treat the mixedwood as a single cover-type, rather than as a strict mosaic of different habitats. Cover-type effects mainly alter the relative abundance of species, in response to differences in stand characteristics. For example, early successional deciduous stands are likely to have more habitats for insects adapted to feeding on broad-leaved plants, as compared with the late successional stands that are dominated by a few conifer specialists. Conifer components (~30%) in stands classified as DDOM at EMEND, and a similar broadleaf component in conifer stands, diversifies local moth communities. Thus, retaining live trees of both species at the stand level thus can contribute to maintaining a continuum of pre-harvest cover-type characteristics through the forest regeneration cycle.  In the boreal mixedwood system, which is set back to earlier DDOM stages through harvest (e.g., Work et al. 2010), this may retain local populations of many conifer specialists during stand recovery.

### 2.5.2 Lepidopterans response to green tree retention

A significant question facing applied forest ecologists today is whether recovery of forest biotas is better under new management practices such as green tree retention. Previous studies at EMEND revealed that both understory plant (Macdonald and Fenniak, 2007) and moth communities (Morneau, 2002) initially differed between compartments harvested to 20% retention and unharvested controls, two years post-harvest. Higher retention levels (≥ 50%), on the other hand, appeared to maintain communities of both taxa similar to unharvested controls. Seven years post-harvest, plant communities showed evidence of recovery starting in the 20% retention compartments (Craig and Macdonald, 2009). Although logical to expect phytophagous insects to recover synchronously with their hostplants, I found that moth communities flying in the 20% retention compartments still differed significantly from unharvested controls seven years post-harvest. Other studies (e.g., Thomas 2002) have documented loss of moth species immediately after low retention harvesting and, as underscored in the present study, the effects of these disturbances are likely to persist even after plant communities start to show signs of recovery (see also Summerville and Crist, 2002; Summerville *et al.*, 2009).

A somewhat complex response to retention harvest is suggested by moth response in the 50% retention compartments, especially when pre-harvest cover-type and moth feeding guilds are taken into account. Two years post-harvest, light-trapped moth assemblages of compartments harvested to 50% retention in either cover-type did not differ from those of unharvested compartments (Morneau 2002). However, data presented here reveal significant differences between moth assemblages of the CDOM stands harvested to 50% retention and unharvested controls. Thus, it seems that moth responses to retention harvest will depend on pre-harvest canopy composition in the mid-term. This finding underscores both the general problem of generalizing long-term impacts of harvesting from short-term data and the need for long-term experiments like EMEND.

Responses of moth communities following a 50% retention harvest seem to be slower in the CDOM cover-type than in the DDOM. In fact, from work with other taxa logging appears to set the boreal mixedwood forest back to the earlier DDOM seral stages (e.g., Work et al. 2010). My work is consistent with this idea, showing that moth assemblages recovering from harvested stands are dominated by guilds that feed on early regeneration deciduous, herbaceous and graminoid species. Studies of the invertebrate fauna at EMEND (Abele 2009; Work *et al*., 2010; Pinzon *et al*., 2012) suggest that low retentions are insufficient to support faunal recovery. Unlike what has been observed with understory plant communities, only levels of dispersed retention higher than commercially feasible (≥ 50%) are likely to conserve the full range of arthropod biodiversity of unharvested stands, especially in the CDOM cover-type. Instead, a combination of aggregated and distributed retention seems to be the most promising conservation solution (Pinzon *et al*., 2012).

My study suggests that species groups (e.g., feeding guilds) within taxa will exhibit similar responses to post-harvest forest regeneration only if they use the habitat in similar ways. The abundance and richness of moth species that depend on grasses (e.g., *P. albidula*), for instance, increased in the 50% retention stands of both cover-types, in parallel to increases in graminoid cover observed in these same stands (Craig and Macdonald, 2010). Thus phytophagous lepidopterans feeding on early successional plants respond to changes in resource availability following disturbance.

Morneau (2002) reported similar response of moth guilds to harvesting at EMEND, 1-2 years post harvest, and Schmidt and Roland (2006) observed an increase in species dependent on grasses and non-woody plants in forest sites in central Alberta that had experienced ≥ 50% fragmentation. However, despite an obvious influx of grass feeders into the harvested sites in the present study, there was no significant increase in the overall species richness in disturbed sites (Figure 2.5f). Grass feeders are not a well developed guild in the boreal eco-region (Pohl *et al*., 2004b; Powell, 1980) and increases in this guild will not compensate for losses of other forest moths in a way that conserves boreal moth diversity.

Moth response to retention harvest applied in different forest cover-types may differ, even among species that belong to the same feeding guild. For instance, the abundance and richness of moths dependent on low herbaceous plants (e.g., *Virbia ferruginosa* and *Lacinopolia lorea*) decreased with retention in the DDOM stands, but retaining 50% of the forest cover actually was associated with somewhat higher numbers of individuals and species of this guild in the CDOM stands (Figure 2.5d). This likely reflects the increase in plant diversity associated with high retention levels (Craig and Macdonald, 2010). As demonstrated here, lepidopterans feeding on a wide range of hosts will respond positively to changes in the understory plant community in canopy gaps created by harvesting, thus mimicking natural gap dynamics (Chavez and Macdonald, 2010).

Unlike generalists, specialized feeders were greatly reduced in compartments that had been harvested to low (20%) levels of retention, even 7-yrs post-harvest. However, 50% retention supported some lepidopteran species groups, e.g., those dependent on deciduous and coniferous canopy trees (DT and CON feeding guilds, respectively), especially in the CDOM cover-type. The significant loss of species in these two feeding guilds following the 20% retention harvest is likely a response to a reduction in canopy feeding habitats for these species. For example, *E. decolor*, a deciduous specialist, was greatly reduced in abundance following harvesting, even though it remained dominant after harvesting. In general, the abundance of moths feeding on trees and woody plants declined. The response of these specialists shows that night flying moths are sensitive to local habitat changes on the scale of the EMEND compartments, and that, in general, moths don't fly far from sites where they feed as larvae (Monkkonen and Mutanen, 2003).

Harvesting modifies the vertical structure and micro-climatic conditions provided by the forest canopy. Low retention harvests, such as the 20% level investigated here, are likely to have a greater impact on understory plant species and micro-habitats utilized by some moth species (see also Atlegrim and Sjoberg, 1996). In fact, Ober and Hayes (2010) concluded that percent canopy cover was the single most important factor in determining lepidopteran diversity and community structure in a conifer dominated forest, due principally to its impact on the understory plant community. As shown in Chapter 3 of this thesis, some lepidopterans migrate between the canopy and understory forest strata at different life-stages making them even more vulnerable to canopy removal by harvesting.

## 2.6 Conclusion and management implications

Forest harvesting, even with retention, drives complex changes in moth species assemblages at the community, guild and species levels. This study shows that 1) significant changes in community composition of moths follow retention harvest, 2) the degree of change depends on both pre-harvest cover-type and level of retention, and 3) these changes persist even after plant communities start to show some signs of recovery from disturbance. Thus, I argue that low (20%) levels of dispersed retention are inadequate to promote quick recovery of boreal lepidopteran diversity after harvest.

Retention harvesting regimes that promote a continuum of stand development across seral stages and conserve the full range of cover-types of the boreal mixedwoods should maintain a diverse lepidopteran community through the post-harvest regeneration cycle. Here, I show that higher (50%) retention levels are associated with more moderate impact as they support persistence of some specialized species on harvested landscapes, albeit in low abundances. Because retention levels high enough to provide conservation value are unlikely to be commercially feasible, retention patches should be considered as better and effective instruments of promoting the recovery of disturbance-sensitive lepidopterans at the stand level, especially in coniferous stands. In fact, patches embedded within a harvested matrix and acting as surrogates for fire-skips have been found to hold forest species on the landscape after harvest for other forest taxa (e.g., Gandhi *et al*., 2004). Additionally, a combination of aggregated and dispersed variable retention may provide a more effective approach to conserving a wide range of boreal arthropod diversity (Pinzon, *et al*., 2012)

Usually, ecological pressures act similarly on particular species that interact with their environment in fairly similar ways. This is particularly important for small-bodied arthropod species, including phytophagous lepidopterans, for which environmental perception is at scales finer and more intricate than humans are able to decode without serious investigation (Spence *et al*., 2008). Thus, it is best to approach effective conservation of boreal moths by maintaining an array of intact habitat elements on harvested landscapes.

# References

Abele, S., 2010. Gastropod diversity in the boreal mixedwood forest of northern Alberta - variation among forest types and response to partial harvesting. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26(1): 32-46.

Anderson, M.J., 2005. PerMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance, version 1. Department of Statistics, University of Auckland, New Zealand.

Atlegrim, O., Sjoberg, K., 1996. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management,* 87(1-3): 139-148.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management,* 132(1): 39-50.

Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R., 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation,* 128(3): 346-357.

Butler, L., Strazanac, J., 2000. Occurrence of Lepidoptera on selected host trees in two Central Appalachian national forests. *Annals of the Entomological Society of America,* 93(3): 500-511.

Caners, R.T., Macdonald, S.E., Belland, R.J. 2010. Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. *Botany,* 88: 315-328.

(CBIF) Canadian Biodiversity Information Facility (2003). The moths of Canada. http://www.cbif.gc.ca/spp_pages/misc_moths/phps/mothindex_e.php [accessed 2006-2008].

Chavez, V., Macdonald, S.E., 2010. The influence of canopy patch mosaics on understory plant community composition in boreal mixedwood forest. *Forest Ecology and Management,* 259(6): 1067-1075.

Chen, H., Popadiouk, R., 2002. Dynamics of North American boreal mixedwoods. *Environmental Reviews*, 10: 137-166.

Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Forest Ecology and Management,* 258(12): 2619-2627.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs,* 67(3): 345-366.

Environment Canada, 2011. National climate data and information archive: Peace River, Alberta. http://climate.weatheroffice.gc.ca/climateData/canada_e.html [accessed January 2011].

Franklin, J.F., Rae Berg, D., Thornburgh, D.A., Trappeiner, J.C., 1997. Alternate silvicultural approaches to timber harvesting: Variable retention harvest systems. In: Franklin, J.F., Kohm, K.A., (Eds.). Creating a forest for 21st century: The science of ecosystem management. Island Press, Washington, D.C., pp. 111-139.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management,* 155(1-3): 399-423.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., Morgantini, L.E., Cryer, K.J., 2004. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. *Canadian Journal of Forest Research,* 34(6): 1319-1331.

Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A., 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: A review of ecological consequences. *Scandinavian Journal of Forest Research,* 25(4): 295-308.

Haeussler, S., Macdonald, S.E., Gachet, S., Bergeron, Y., 2007. Understory and epiphytic vegetation as indicators of the ecological integrity of managed forests: A synthesis of the special issue. *Forest Ecology and Management,* 242(1): 1-4.

Hammond, P.C., Miller, J.C., 1998. Comparison of the biodiversity of Lepidoptera within three forested ecosystems. *Annals of the Entomological Society of America,* 91(3): 323-328.

Hodges, R.W., 1983. Check list of the Lepidoptera of America North of Mexico, including Greenland. In: E.W. Classey and the Wedge Entomological Research Foundation, London, pp. 284.

Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation,* 65(2): 115-120.

Jacobs, J.M., Spence, J.R., Langor, D.W., 2007. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. *Canadian Journal of Forest Research*, 37(9): 1631-1642.

Kishchuk B.E., Northern Forestry Centre, 2004. Soils of the ecosystem management emulating natural disturbance (EMEND) experimental area, northwestern Alberta. Northern Forestry Centre, Edmonton.

Macdonald, S.E., Fenniak, T.E., 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. *Forest Ecology and Management,* 242(1): 34-48.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities, version 5, MjM Software Design, Oregon State University, Oregon.

Miller J.C., 1996. Caterpillars of pacific northwest forests and woodlands. National Center of Forest Health Management, U.S. Department of Agriculture, Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2000. Macromoths of northwest forests and woodlands. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2003. Lepidoptera of the Pacific Northwest: Caterpillars and adults. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Monkkonen, M., Mutanen, M., 2003. Occurrence of moths in boreal forest corridors. *Conservation Biology,* 17(2): 468-475.

Morneau L., 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

Museums and Collections Services, University of Alberta, E.H. Strickland Entomological Museum, Virtual Museum. http://www.entomology.ualberta.ca/ [Accessed 2006-2008]

Nelson, C.R., Halpern, C.B., 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. *Canadian Journal of Botany,* 83(6): 610-620.

Niemelä, J. 1997. Invertebrates and boreal forest management. *Conservation Biology,* 11(3): 601-610.

North American Moth Photographers Group. http://mothphotographersgroup.msstate.edu/MainMenu.shtml. [Accessed: 2006-2010].

Ober, H.K., Hayes, J.P., 2010. Determinants of nocturnal lepidopteran diversity and community structure in a conifer-dominated forest. *Biodiversity and Conservation,* 19(3): 761-774.

Peet, R.K., Christensen, N.L., 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. In: During, H.J., Werner, M.J.A., Willems, H.J., (Eds.). Diversity and pattern in plant communities. SPB Academic Publishing, The Hague, The Netherlands.

Pinzon, J., Spence, J.R., 2010. Bark-dwelling spider assemblages (Araneae) in the boreal forest: Dominance, diversity, composition and life-histories. *Journal of Insect Conservation,* 14(5): 439-458.

Pinzon, J., Spence, J.R., Langor, D.W., 2011. Spider assemblages in the overstory, understory, and ground layers of managed stands in the western boreal mixedwood forest of Canada. *Environmental Entomology,* 40(4): 797-808.

Pinzon, J., Spence, J.R., Langor, D.W., 2012. Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. *Forest Ecology and Management*, 266: 42–53.

Pohl, G.R., Langor, D.W., Landry, J.F., Landry, J.F., 2004a. Moths and butterflies (Lepidoptera) of the boreal mixedwood forest near Lac La Biche, Alberta, including new provincial records. *Canadian Field-Naturalist,* 118(4): 530-549.

Pohl, G.R., Langor, D.W., Landry, J.F., Spence, J.R. 2004b. Lepidopteran from boreal mixedwood forest in east-central Alberta: Comparison of assemblages from a mature and an old stand. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre. Edmonton, AB. inf. ref. NOR-X-396: 1-20.

Powell, J.A., 1980. Evolution of larval food preferences in microlepidoptera. *Annual Review of Entomology,* 25: 133-159.

Powell J.A., Opler P.A., 2009. Moths of Western North America [electronic resource]. University of California Press, Berkeley.

Pratt L., Urquhart I.T., 1994. The last great forest: Japanese multinationals and Alberta's northern forests. NeWest Press, Edmonton, AB.

Robinson G.S., 2002. Hostplants of the moth and butterfly caterpillars of America North of Mexico. American Entomological Institute, Gainesville, FL.

Root, R., 1973. Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs,* 43(1): 95-120.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management,* 255(1): 1-15.

Scalercio, S., Infusino, M., Woiwod, I.P., 2009. Optimizing the sampling window for moth indicator communities. *Journal of Insect Conservation,* 13(6): 583-591.

Schmidt, B. C., Roland J., 2006. Moth Diversity in a Fragmented Habitat: Importance of Functional Groups and Landscape Scale in the Boreal Forest. *Annals of Entomological Society of America,* 99(6): 1110-1120.

Simberloff, D., 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management,* 115(2-3): 101-111.

Southwood, T.R.E., 1994. The Importance of Long-Term Experimentation, In: Leigh, R.A., Johnston, A.E., (Eds.), Conference on insight from foresight - the role of long-term experiments and databases in agricultural and ecological science, celebrating the 150th anniversary of Rothamsted experimental-station; CY: JUL 14-17, 1993; CL: Rothamsted Experiment, Harpenden, England; TC: 6, 3-8.

Southwood T.R.E., 1995. Ecological methods: With particular reference to the study of insect populations (2nd Edition). Chapman and Hall, London, Eng, pp. 524.

Spence J.R., Volney W.J.A., 1999. EMEND: Ecosystem management emulating natural disturbance. Sustainable Forest Management Network report 1999-14, Sustainable Forest Management Network, Edmonton, pp. 17.

Spence, J.R., Langor, D.W., Jacobs, J.M., Work, T.T., Volney, W.J.A., 2008. Conservation of forest-dwelling arthropod species: Simultaneous management of many small and heterogeneous risks. *Canadian Entomologist,* 140(4): 510-525.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest Lepidoptera: Community, guild, and species responses. *Ecological Applications,* 12(3): 820-835.

Summerville, K.S., Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: A review. *Canadian Entomology,* 140(4): 475-494.

Summerville, K.S., Courard-Hauri, D., Dupont, M.M., 2009. The legacy of timber harvest: Do patterns of species dominance suggest recovery of lepidopteran communities in managed hardwood stands? *Forest Ecology and Management,* 259(8): 8-13.

Swanson, F.J., Franklin, J.F., 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications,* 2(3): 262-274.

Thomas A.W., 2002. Moth diversity in a northeastern North American red spruce forest II: the effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). Canadian Forest Service. Atlantic Forestry Centre, Fredericton, NB.

Troubridge, J.T., Lafontaine, J.D., The moths of Canada. http://www.cbif.gc.ca/spp_pages/misc_moths/phps/mothindex_e.php. 2004. 2006-2010.

Volney, W.J.A., Mallett, K.I., 1998. Integrated pest management in western Canadian boreal forests. *Forestry Chronicle,* 74(4): 597-605.

Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. 82(1-3): 283-294.

Volney W.J.A., Spence J.R., Lefebvre E.M., 2001. Boreal Odyssey: *Proceedings: North American forest insect work conference,* May 14-18. Natural Resource Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, AB. inf. ref. NOR-X-381.

Volney, W.J.A., Hirsch, K.G., 2005. Disturbing forest disturbances. *Forestry Chronicle,* 81(5): 662-668.

Wagner, D.L., Wagner, D.L., 2005. Caterpillars of eastern North America: A guide to identification and natural history. Princeton University Press, pp. 496.

Work, T.T., Spence, J.R., Volney, W.J.A., Morgantini, L.E., Innes, J.L., 2003. Integrating biodiversity and forestry practices in western Canada. *Forest Chronicle,* 79(5): 906-916.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, 34(2): 417-430.

Work, T.T., Jacobs, J.M., Spence, J.R., Volney, W.J., 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications,* 20(3): 741-751.

Young M., 1997. The natural history of moths. T & A D Poyser, London, pp. 271.

Zenner, E.K., Krueger, J.A., 2006. Understory and overstory growth responses to structural retention of mature eastern white pine (*Pinus strobus* L.). *Journal of the Torrey Botanical Society,* 133(4): 585-592.

**Table 2.1** Total number of individuals and species richness by family and feeding guilds of moths sampled using light traps at EMEND. Feeding guilds are according to larval host-plant species/feeding preferences (See materials and methods section).

| **Family** | Species richness | % Richness | Trap Catch | % catch | **Guild** | Species richness | % richness | Trap Catch | % catch |
|---|---|---|---|---|---|---|---|---|---|
| Cossidae* | 1 | 0.53 | 10 | 0.21 | CON | 8 | 4.21 | 138 | 2.86 |
| Drepanidae | 4 | 2.11 | 73 | 1.51 | DET | 6 | 3.16 | 56 | 1.16 |
| Erebidae | 21 | 11.05 | 260 | 5.38 | DT | 43 | 22.63 | 1081 | 22.37 |
| Geometridae | 60 | 31.58 | 1613 | 33.37 | DWP | 32 | 16.84 | 670 | 13.86 |
| Hepialidae* | 1 | 0.53 | 1 | 0.02 | GEN | 17 | 8.95 | 759 | 15.70 |
| Lasiocampidae | 2 | 1.05 | 31 | 0.64 | GR | 10 | 5.26 | 299 | 6.19 |
| Noctuidae | 89 | 46.84 | 2640 | 54.62 | LP | 28 | 14.21 | 484 | 10.01 |
| Notodontidae | 8 | 4.21 | 134 | 2.77 | WLP | 10 | 8.95 | 110 | 13.26 |
| Sphingidae | 2 | 1.05 | 37 | 0.77 | WP | 20 | 5.26 | 595 | 2.28 |
| Uraniidae | 1 | 0.53 | 34 | 0.70 | UKN | 16 | 10.53 | 641 | 12.31 |
| **Total** | 190 | 100 | 4833 | 100 | Total | 190 | 100 | 4833 | 100 |

*Notes:* Guild designations are as follows: conifers (CON), Dead leaves, lichens, and fungi (DET), deciduous trees only (DT), deciduous trees and woody shrubs (DWP), generalists on deciduous and conifer trees, shrubs and low herbaceous plants (GEN), Graminae (GR), low herbaceous plants only (LP), Woody shrubs and low herbaceous species (WLP), Woody plants only (WP), unknown host plant (UKN).

*Micromoth families-excluded from statistical analyses

**Table 2.2** Results of PerMANOVA based on Bray-Curtis distance for taxonomic species and feeding guilds of moths sampled using light traps from two forest cover-types (coniferous and deciduous) and three harvesting treatments (50% , 20% and unharvested controls treatments at EMEND.

| **Taxonomic Species** | **Source** | **df** | ***F*** | ***P*** |
|---|---|---|---|---|
| | Cover-type | 1 | 2.80 | 0.006 |
| | % retention | 2 | 2.42 | 0.003 |
| | Cover-type*% retention | 2 | 1.62 | 0.06 |
| | Residual | 12 | | |
| | Total | 17 | | |

| | **Pair-wise** *a posteriori* **comparisons** | *t* | *P* |
|---|---|---|---|
| | Unharvested vs. 50% | 1.46 | 0.06 |
| | Unharvested vs. 20% | 1.62 | 0.02 |
| | 20% vs. 50% | 1.14 | 0.25 |

| **Feeding guilds** | **Source** | **df** | ***F*** | ***P*** |
|---|---|---|---|---|
| | Cover-type | 1 | 7.01 | 0.002 |
| | % retention | 2 | 6.12 | 0.001 |
| | Cover-type*% retention | 2 | 2.46 | 0.04 |
| | Residual | 12 | | |
| | Total | 17 | | |

| | **Pair-wise** *a posteriori* **comparisons** | CDOM | | DDOM | |
|---|---|---|---|---|---|
| | | *t* | *P* | *t* | *P* |
| | Unharvested vs. 50% | 2.70 | 0.02 | 1.68 | 0.11 |
| | Unharvested vs. 20% | 2.20 | 0.04 | 2.98 | 0.01 |
| | 20% vs. 50% | 1.29 | 0.23 | 1.53 | 0.14 |

**Table 2.3** Results of the Indicator Species Analysis for the coniferous (CDOM) and deciduous (DDOM) unharvested (100%), 20% and, 50% retention treatments at EMEND.

| Species | Cover-type by % retention | Indicator Value (IndVal) | Mean | S.Dev | *p*-value * |
|---|---|---|---|---|---|
| *Acronicta grisea* Wlk. | DDOM_100% | 40 | 27.4 | 5.63 | 0.023 |
| *Apamea cogitata* (Sm.) | DDOM_100% | 95.2 | 26.4 | 15.6 | 0.006 |
| *Brachylomia algens* (Grt.) | DDOM_100% | 52.8 | 33.7 | 9.03 | 0.02 |
| *Campaea perlata* (Gn.) | DDOM_100% | 89.7 | 30 | 13.85 | 0.006 |
| *Clostera albosigma* Fitch | DDOM_100% | 81.8 | 36.8 | 12.67 | 0.005 |
| *Cyclophora pendulinaria* (Gn.) | DDOM_100% | 45.7 | 31.4 | 6.24 | 0.006 |
| *Diachrysia aereoides* (Grt.) | DDOM_100% | 85.2 | 30.6 | 13.52 | 0.006 |
| *Drepana bilineata* (Pack.) | DDOM_100% | 92 | 29.5 | 14.87 | 0.006 |
| *Dysstroma walkerata* (Pears.) | DDOM_100% | 46.4 | 30.8 | 5.12 | 0.02 |
| *Enargia decolor* (Wlk.) | DDOM_100% | 73.3 | 29.1 | 13.3 | 0.01 |
| *Epirrita autumnata* (Bkh.) | DDOM_50% | 49.4 | 34.9 | 6.55 | 0.03 |
| *Eueretagrotis perattentus* (Grt.) | DDOM_100% | 74.3 | 30.5 | 12.07 | 0.006 |
| *Idia aemula* (Hbn) | CDOM_100% | 66 | 33.3 | 12.77 | 0.05 |
| *Leucania insueta* Gn. | DDOM_50% | 84.6 | 27.3 | 13.9 | 0.007 |
| *Macaria notata* (Pears.) | DDOM_100% | 92.3 | 26.4 | 15.11 | 0.006 |
| *Malacosoma disstria* Hbn. | DDOM_100% | 65 | 28.4 | 11.46 | 0.01 |
| *Perizoma basaliata* (Wlk.) | CDOM_100% | 52.3 | 33.1 | 8.72 | 0.01 |
| *Platypolia anceps* (Steph.) | DDOM_50% | 91.1 | 29.7 | 14.26 | 0.006 |
| *Plemyria georgii* (Hulst) | DDOM_50% | 90.9 | 26.6 | 14.75 | 0.006 |
| *Polia nimbosa* (Gn.) | DDOM_100% | 70.6 | 30 | 11.85 | 0.007 |
| *Polychrysia esmeralda* (Oberth.) | DDOM_100% | 58.7 | 29.2 | 10.27 | 0.007 |
| *Protitame virginalis* (Hulst) | DDOM_100% | 75 | 31.4 | 11.77 | 0.006 |
| *Spargania luctuata* (D. & S.) | DDOM_100% | 44.1 | 28.3 | 4.98 | 0.006 |
| *Sutyna privata* (Wlk.) | DDOM_100% | 86.1 | 30 | 13.97 | 0.006 |
| *Venusia cambrica* Curt. | DDOM_100% | 50 | 32.6 | 9.12 | 0.05 |
| *Xestia mixta* (Wlk.) | CDOM_100% | 80.4 | 34.2 | 15.06 | 0.03 |
| *Xestia perquiritata* (Morr.) | CDOM_100% | 86.4 | 35 | 13.15 | 0.007 |

**Table 2.4** Relative dominance values (*DV'*) for the dominant (D), sub-dominant (S), and common (C) moth species light trapped IN coniferous (CDOM) and deciduous (DDOM) unharvested (100%), 20% and, 50% retention treatments at EMEND.

| | | CDOM | | | DDOM | | |
|---|---|---|---|---|---|---|---|
| **Guild** | **Species** | **100%** | **50%** | **20%** | **100%** | **50%** | **20%** |
| CON | *Xestia perquiritata* (Morr.) | 8.79 D | 0.56 S | | | | |
| | *Aplectoides condita* (Gn.) | 0.46 C | | | 0.38 S | | |
| | *Idia sp. nr. Aemula* (Hbn) | 6.03 D | 1.40 S | 0.46 S | 0.42 S | | |
| | *Idia americalis et. al.* (Gn.) | | | | 0.08 C | | |
| | *Macaria signaria* (Hbn) | 0.17 C | | | | | |
| DET | *Eilema bicolor* (Grt.) | 0.80 C | 0.37 S | | 0.25 S | 0.16 S | |
| | *Phalaenophana pyramusalis* (Wlk.) | | | | 0.25 S | 0.41 S | 0.55 S |
| | *Zanclognatha lutalba* (Sm.) | | | | 0.21 S | | 1.32 S |
| DT | *Andropolia contacta* (Wlk.) | | 0.75 S | | 1.25 S | 0.57 S | 2.65 S |
| | *Acronicta grisea* Wlk. | | | | 1.25 S | | |
| | *Acossus populi (*Wlk.*)* | | | | 0.13 C | | |
| | *Anathix puta* (G. & R.) | | | | 0.17 S | 0.41 S | |
| | *Brachylomia populi* (Stkr.) | | | | 0.29 S | 1.64 S | |
| | *Cabera variolaria* Gn. | 0.86 C | 2.53 S | 1.53 S | 1.88 S | 1.15 S | 3.75 S |
| | *Digrammia rippertaria (*Duponchel) | 0.69 C | | | 0.17 S | 0.12 S | |
| | *Enargia decolor (*Wlk.*)* | 10.69 D | 7.58 D | 19.24 D | 15.04 D | 12.04 D | 3.75 S |
| | *Eulithis flavibrunneata* (McD.) | | | | 0.06 C | | |
| | *Eulithis testata* (L.) | | | 0.13 C | 0.25 S | 0.88 S | |
| | *Antepirrhoe semiatrata* (Hulst) | 0.46 C | | | 0.13 C | 0.25 S | |
| | *Gluphisia septentrionis* Wlk. | 1.84 S | 0.84 S | | 0.10 C | 1.72 S | 0.33 S |
| | *Hydriomena ruberata* Freyer | 0.17 C | | | | 0.41 S | |
| | *Iridopsis larvaria* (Gn.) | | | | 0.13 C | | |
| | *Ipimorpha pleonectusa* Grt. | | 1.68 S | 1.22 S | 0.50 S | 1.47 S | 0.66 S |
| | *Lithomoia germana* (Morr.) | | | 0.46 S | 0.38 S | | |
| | *Metanema determinata* Wlk. | | | 0.92 S | | | |
| | *Malacosoma disstria* Hbn. | | | | 1.50 S | | |
| | *Metanema inatomaria* Gn. | | 0.84 S | | 0.21 S | | |
| | *Speranza loricaria* (Hulst) | 0.52 C | 0.56 S | 0.46 S | 0.44 S | 0.41 S | 0.88 S |
| | *Nycteola cinereana* N. & D. | | | | 0.08 C | | |
| | *Paradiarsia littoralis* (Pack.) | | | 1.53 S | | | |
| | *Pheosia rimosa* (Pack.) | 1.38 S | | | 0.94 S | 0.41 S | |
| | *Parastichtis suspecta (*Hbn.*)* | | | 1.37 S | 0.25 S | 0.12 S | 0.66 S |
| | *Protitame virginalis* (Hulst) | | | | 2.26 S | 0.61 S | 0.55 S |
| | *Smerinthus cerisyi* Kby | 0.92 C | | | 0.56 S | 0.37 S | 0.33 S |
| | *Xestia oblate* (Morr.) | | 0.94 S | | | | |
| | *Xanthia tatago* Laf. | | | 3.21 S | 0.29 S | 0.25 S | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| DWP | *Autographa ampla* (Wlk.) | | | | | | |
| | *Abagrotis placida* (Grt.) | | | | | 0.12 S | |
| | *Clostera albosigma* Fitch | 0.34 C | | | 2.19 S | | |
| | *Cabera erythemaria* Gn. | 0.17 C | 1.12 S | | | | |
| | *Cabera exanthemata* (Scopoli) | 2.59 S | 0.75 S | 2.14 D | 1.19 S | | 1.10 S |
| | *Drepana bilineata* (Pack.) | | | | 1.44 S | | |
| | *Eurois astricta* (Morr.) | 0.80 C | 0.75 S | 2.14 S | 2.69 S | 2.87 S | 6.95 S |
| | *Enargia infumata* (Grt.) | 0.34 C | 0.94 S | | | 0.12 S | |
| | *Ennomos magnaria* Gn. | | | | 0.17S | 0.90 S | |
| | *Eulithis xylina* (Hulst) | 0.86 C | 0.75 S | | 0.63 S | | 0.44 S |
| | *Graphiphora augur F.* | 0.80 C | | | 0.31 S | | 1.32 S |
| | *Lophocampa maculata* Harr. | | | | 0.17 S | 0.37 S | |
| | *Oligia illocata* (Wlk.) | | | | 0.96 S | 4.30 S | 1.21 S |
| | *Orthosia hibisci* (Gn.) | | | | | 0.06 C | |
| | *Phyllodesma americana* (Harr.) | | | | | 0.33 S | |
| | *Papestra cristifera* (Wlk.) | | | | | 0.33 S | |
| | *Plemyria georgii* (Hulst) | | | | 0.29 S | 2.95 S | |
| | *Platarctia parthenos* (Harr.). | 0.92 C | 0.56 S | | 0.25 S | | |
| | *Phlogophora periculosa* | | | | 0.25 S | | |
| | *Protolampra rufipectus* (Morr.) | | 0.28 S | | 0.13 C | 0.74 S | |
| | *Smerinthus jamaicensis* (Drury) | | | 0.92 S | 0.21 S | 0.25 S | |
| | *Sicya macularia* (Harr.) | 0.80 C | 4.49 D | 1.53 S | 1.00 S | 2.46 S | 9.93 D |
| | *Xanthorhoe lacustrata* Gn. | 0.34 C | 0.75 S | | 0.25 S | 1.31 S | 1.32 S |
| GEN | *Anaplectoides pressus* (Grt.) | 0.29 C | | | 0.17 S | | |
| | *Brachylomia algens* (Grt.) | | 3.55 S | 6.87 D | 9.52 D | 11.06 D | 2.43 S |
| | *Campaea perlata* (Gn.) | 2.76 S | 3.65 S | 3.05 S | 4.01 S | 2.58 S | 3.53 S |
| | *Dysstroma walkerata* (Pears.) | 2.24 S | 3.93 S | 8.70 D | 4.01 S | 2.33 S | 2.98 S |
| | *Epirrita autumnata* (Bkh.) | | 0.47 S | | | 2.70 S | |
| | *Eurois occulta* (L.) | 2.64 S | 1.96 S | 3.66 S | 0.17 S | 0.57 S | |
| | *Eueretagrotis perattentus* (Grt.) | | | | 1.63 S | 0.49 S | |
| | *Hydriomena furcata* (Thunb.) | | 0.84 S | | 0.63 S | 0.25 S | |
| | *Hydriomena perfrecta* Swett | 0.17 C | | | 0.13 C | 1.23 S | 0.88 S |
| | *Lobophora nivigerata* Wlk. | 0.46 C | | | | | |
| GR | *Amphipoea americana* (Speyer) | 0.34 C | | | 0.06 C | 0.33 S | |
| | *Apamea cogitata* (Sm.) | 0.70 C | 1.12 S | 0.46 S | 0.75 S | | 0.66 S |
| | *Protodeltote albidula* (Gn.) | | 9.26 D | 8.24 D | 1.69 S | 3.69 S | 9.05 D |
| | *Leucania insueta* Gn. | | 0.75 S | | | 2.70 S | |
| | *Rivula propinqualis* Gn. | 0.34 C | 2.25 S | 0.76 S | 0.63 S | 0.25 S | 2.87 S |
| LP | *Autographa mappa* (G. & R.) | | | | 0.13 C | | |
| | *Callizzia amorata* Pack. | 1.21 S | 1.40 S | | 0.63 S | 0.33 S | 0.88 S |
| | *Epirrhoe alternata* (Mull.) | | | | 0.25 S | | |
| | *Ecliptopera silaceata* (D. & S.) | | | | 0.13 C | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Grammia virgo* (L.) | | 0.56 S | | | | |
| | *Virbia ferruginosa* (Wlk.) | | 6.45 D | 3.97 S | 0.33 S | 0.78 S | 2.87 S |
| | *Lacinipolia lorea* (Gn.) | 0.57 C | 5.05 D | | 1.25 S | 1.06 S | 1.77 S |
| | *Oligia mactata* (Gn.) | | 1.12 S | | 0.71 S | 2.21 S | |
| | *Platypolia anceps* (Steph.) | 3.22 S | 1.96 S | 2.75 S | 3.82 S | 13.76 D | |
| | *Caradrina montana* (Bremer) | | | 0.46 S | 0.19 S | | |
| | *Spargania luctuata* (D. & S.) | 2.07 S | 4.49 D | 3.05 S | 2.82 S | 1.72 S | 1.10 S |
| | *Spargania magnoliata* Gn. | 0.57 C | | | | | |
| | *Sutyna privata* (Wlk.) | | | | 1.94 S | 0.12 S | |
| | *Xanthorhoe abrasaria* (H.-S.) | 0.34 C | 1.68 S | 2.14 S | 0.69 S | 0.20 S | |
| WLP | *Diachrysia aereoides (*Grt.*)* | | | | 1.44 S | | |
| | *Polia nimbosa* (Gn.) | 6.38 D | | | 0.81 S | 0.12 S | 0.88 S |
| | *Polia purpurissata (*Grt.*)* | | | 1.22 S | | | |
| WP | *Cryptocala acadiensis* (Bethune) | | | | | 0.16 S | 1.10 S |
| | *Clostera brucei* (Hy. Edw.) | | | | 0.17 S | | |
| | *Cyclophora pendulinaria* (Gn.) | 0.69 C | | | 3.38 S | 0.25 S | 0.88 S |
| | *Drepana arcuata* (Wlk.) | | | | 0.50 S | 0.41 S | |
| | *Dysstroma brunneata* (Pack.) | 0.17 C | | | | | |
| | *Dysstroma hersiliata* (Gn.) | | 0.28 S | | | | |
| | *Euphyia intermediata* (Haw.) | | | | 0.29 S | | |
| | *Hypena humuli* Harr. | 0.57 C | | | 0.21 S | | |
| | *Speranza bitactata* (Wlk.) | | | | 0.17 S | | |
| | *Macaria notata* (Pears.) | | | | 0.81 S | | 1.66 S |
| | *Oreta rosea* (Wlk.). | | | 0.76 S | 0.58 S | | 0.55 S |
| | *Sunira verberata* (Sm.) | | | 0.76 S | 0.06 C | | |
| | *Venusia cambrica* Curt. | 5.17 D | 2.81 S | | 8.02 D | 3.81 S | 11.48 D |
| | *Xylotype arcadia* B. & Benj. | 1.03 C | | | | 0.57 S | |
| | *Xestia mixta* (Wlk.) | 6.38 D | 0.28 S | | 0.17 S | | |
| | *Xestia smithii* (Snell.) | 0.69 C | 3.55 S | 3.66 S | 0.38 S | 2.33 S | 1.32 S |
| UKN | *Acronicta impressa* Wlk. | 0.92 S | | | | | |
| | *Brachylomia discinigra* (Wlk.) | | | 0.25 S | | | |
| | *Diarsia dislocata* (Sm.) | 3.45 S | 2.81 S | 5.04 S | 0.69 S | 1.35 S | 3.31 S |
| | *Eupithecea spp* | 3.28 S | 2.53 S | | 1.25 S | 0.33 S | |
| | *Hypena atomaria* Smith | 1.09 C | | | 0.25 S | | |
| | *Lacanobia radix* (Wlk.) | 0.46 C | | | | | |
| | *Perizoma basaliata* (Wlk.) | 7.07 D | | | | | |
| | *Polychrysia esmeralda* (Oberth.) | | 1.25 S | | | | |
| | *Scopula spp.* | 2.59 S | 3.37 S | 2.75 S | 0.63 S | 0.66 S | 4.97 S |
| | *Zenophleps alpinata* Cass. | 0.23 C | 0.94 S | | 0.10 C | 0.12 S | |
| | *Zanclognatha sp.* | 1.03 C | 4.49 D | 3.66 S | 0.63 S | 1.47 S | 6.18 S |

*Notes:* Blank spaces indicate that a given row (species) was either absent or uncommon (UC) in a given column (cover-type by harvest treatment).

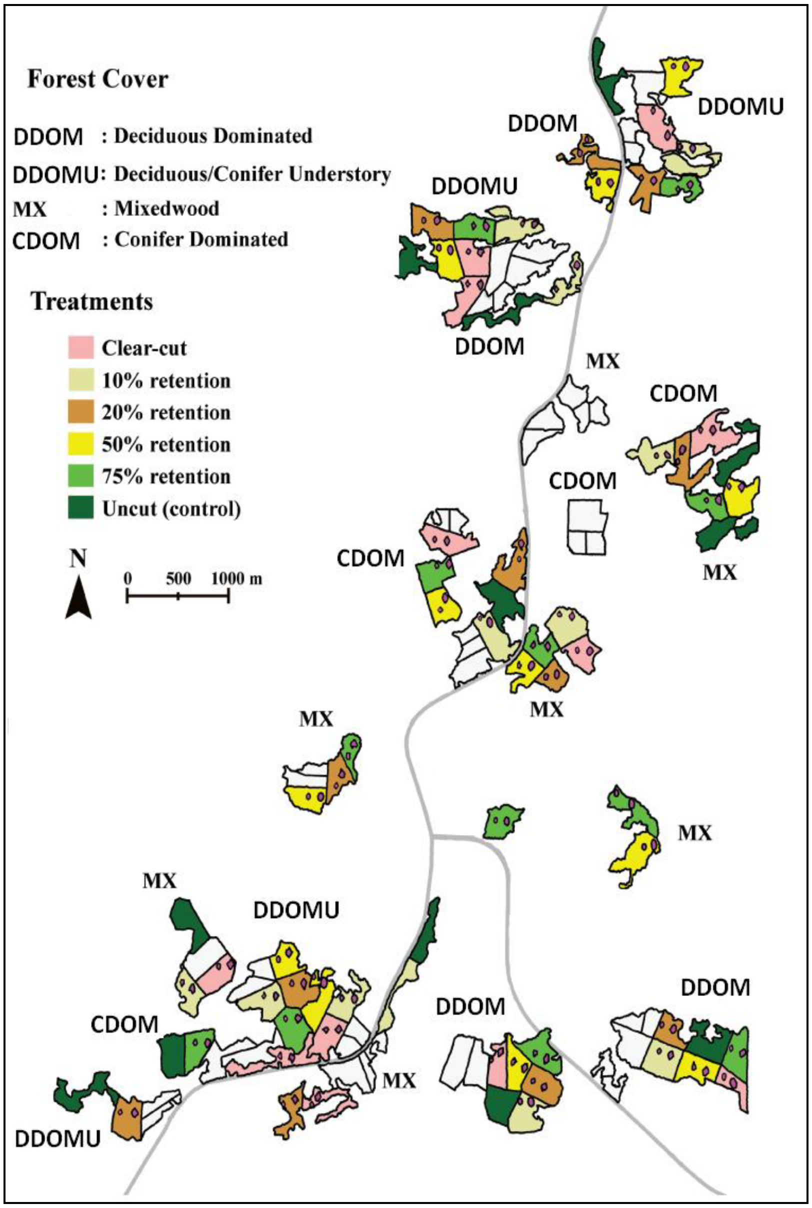

**Figure 2.1** A map of EMEND showing the different forest cover-types that characterize the mixedwoods. Treatments were applied to c. 10-ha compartments (colored polygons). Data for this chapter were collected from only two cover-types (DDOM and CDOM) with two levels of retention harvest (50%, and 20%), and the uncut controls.

**Figure 2.2** Light trap design used to collect night-flying moths

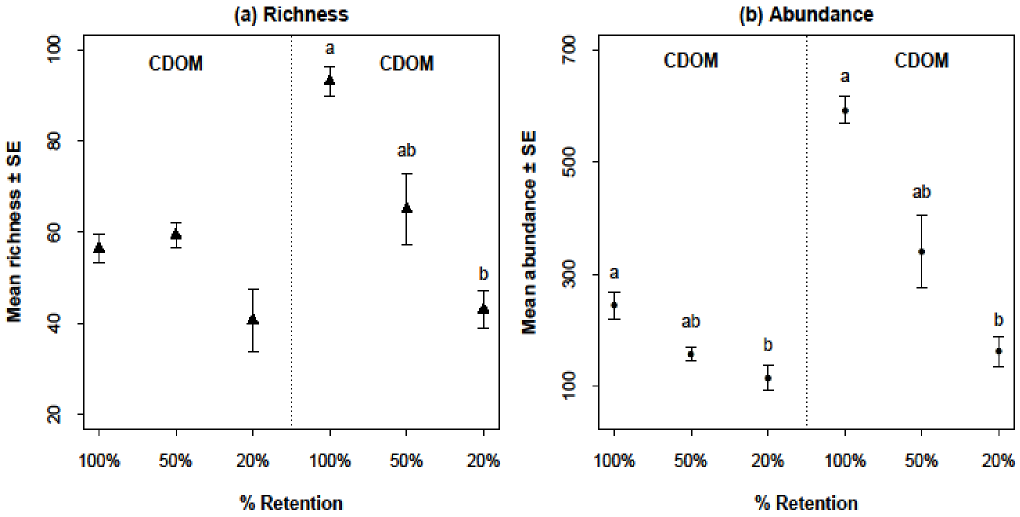

**Figure 2.3** Mean richness ± SE (a) and abundance ± SE (b), of moths sampled using light traps from coniferous (CDOM) and deciduous (DDOM) unharvested (100%), 50% and 20% retention harvest treatments at EMEND. Treatment means with the same letter above denote no significant differences ($\alpha$ = 0.05); comparisons only shown within each forest cover-type.

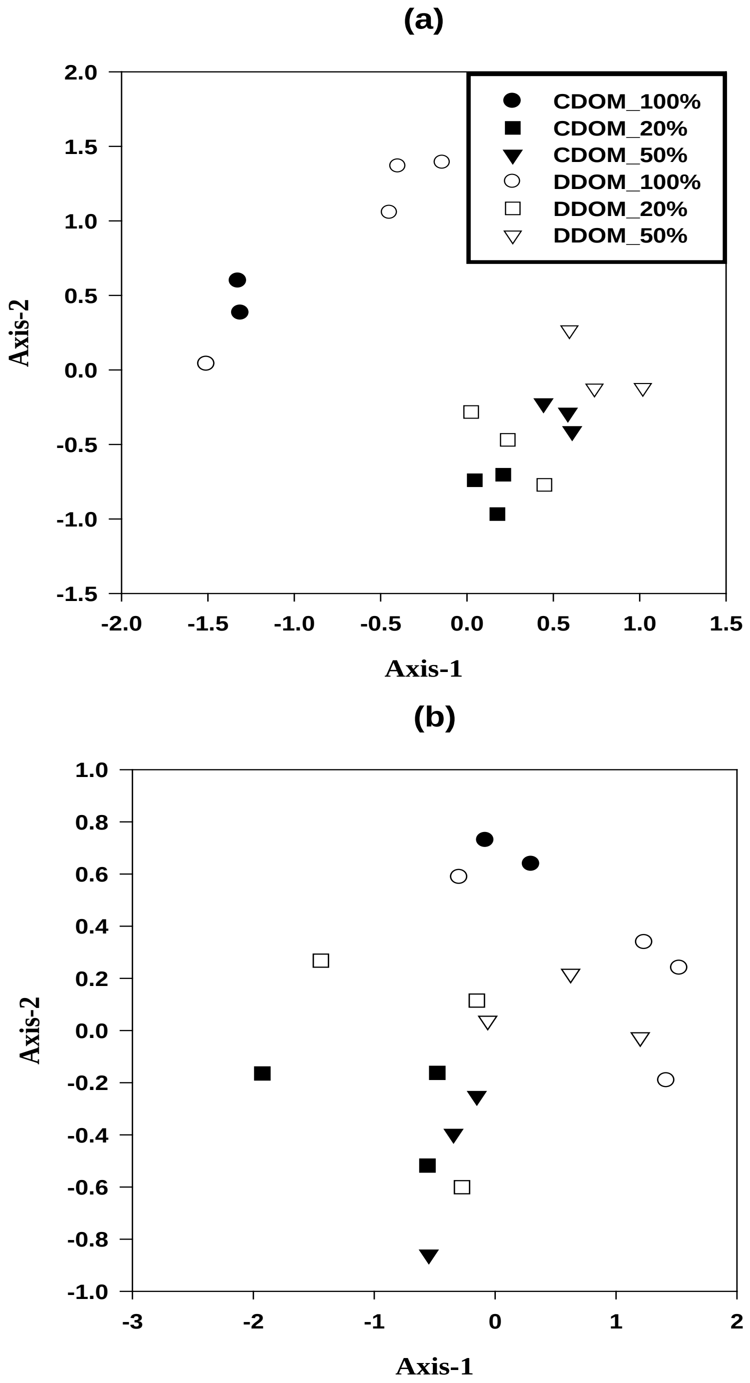

**Figure 2.4** Two-dimentional NMS ordination analyses based on Bray-Curtis distances of (a) the community assemblages (final stress = 10.3), and (b) feeding guilds of moths (final stress = 9.8)light trapped from the coniferous and deciduous unharvested (100%) and harvested 20% and 50% retention treatments at EMEND.

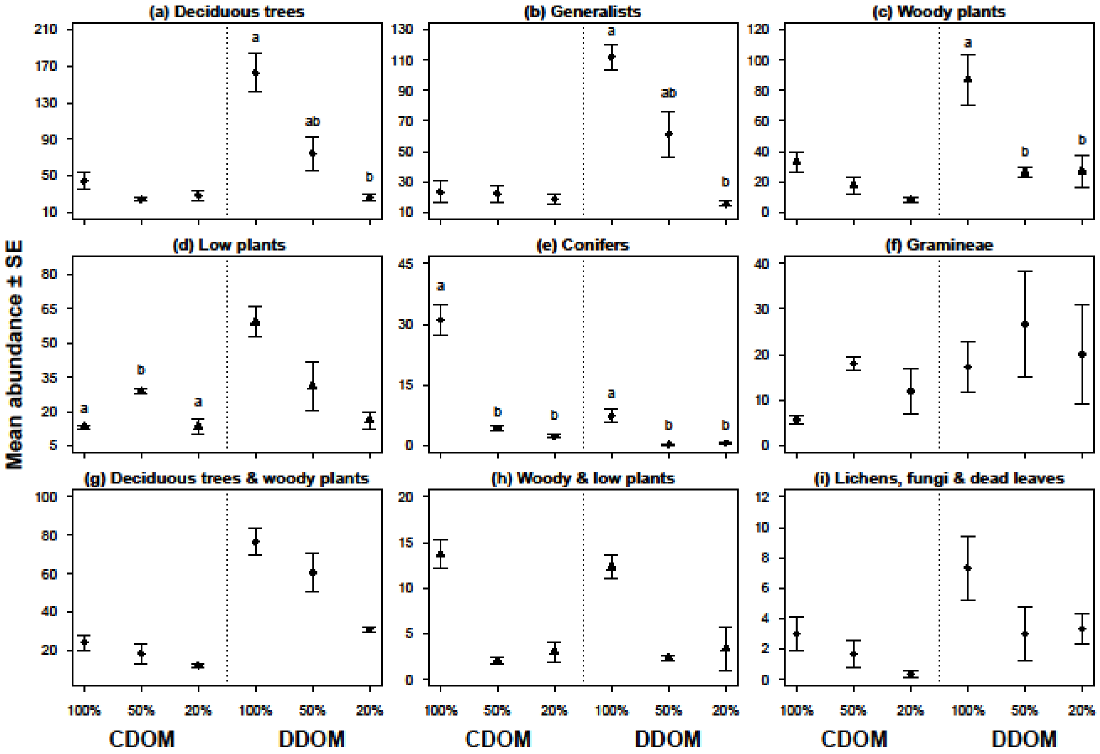

**Figure 2.5** Mean abundance ± SE of moths belonging to nine feeding guilds sampled using light traps from coniferous (CDOM) and deciduous (DDOM) unharvested (100%), 50% and 20% harvest treatments at EMEND. Treatment means with the same letter above denote no significant differences (α = 0.05); comparisons only shown within each forest cover-type.

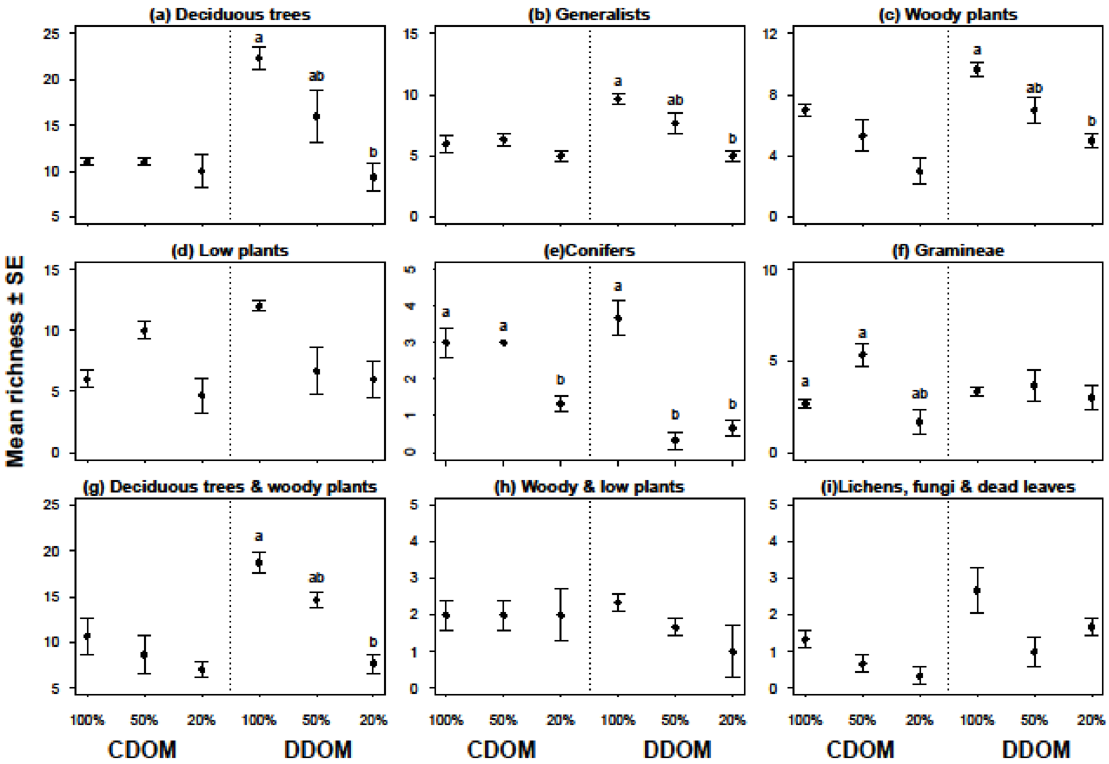

**Figure 2.6** Mean richness ± SE of moths belonging to nine feeding guilds sampled using light traps from coniferous (CDOM) and deciduous (DDOM) unharvested (100%), 50% and 20% harvest treatments at EMEND. Treatment means with the same letter above denote no significant differences ($\alpha = 0.05$); comparisons only shown within each forest cover-type.

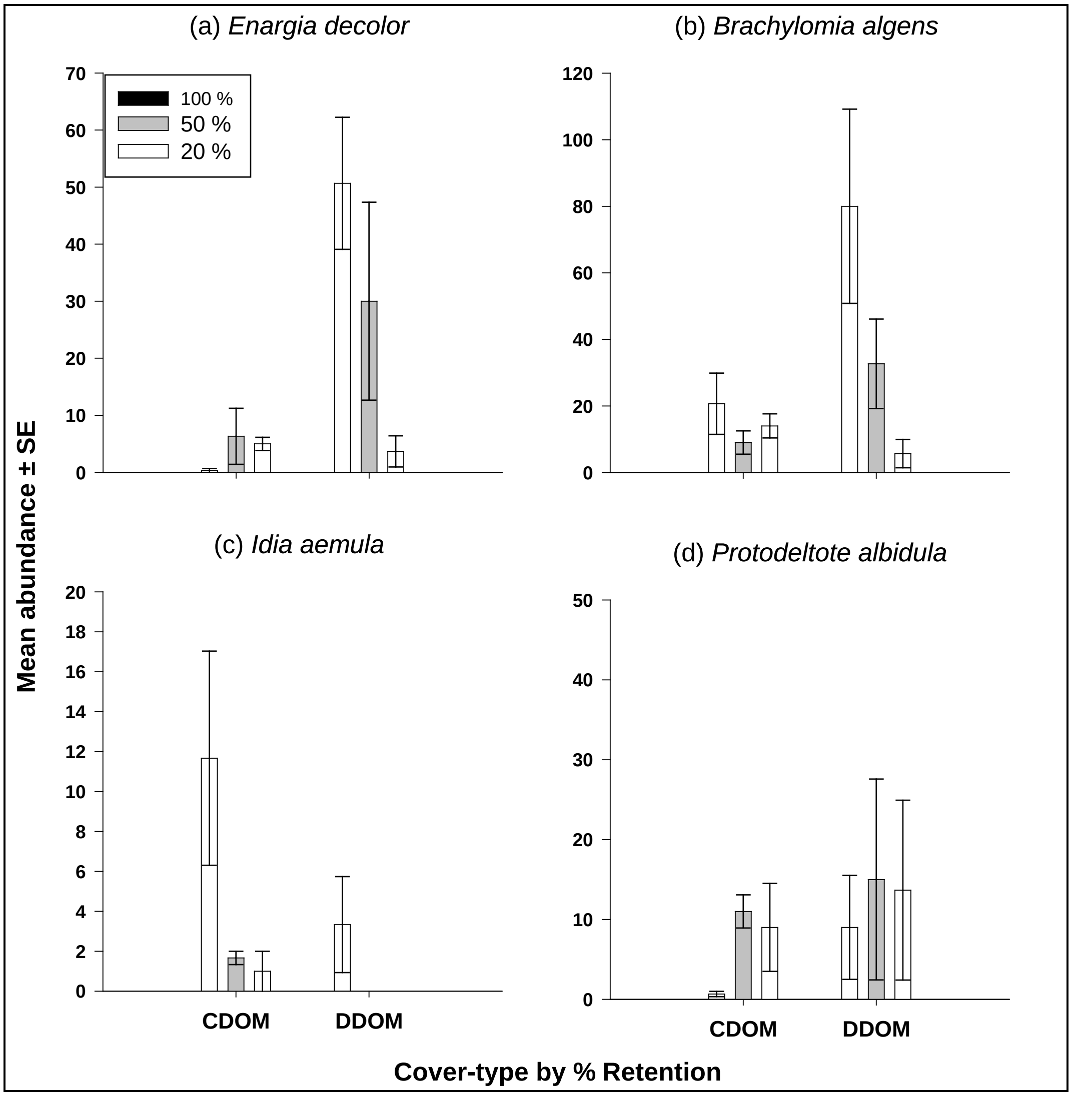

**Figure 2.7** Mean abundance ± SE of two of the most dominant species (a, and b), a dominant species in CDOM control compartments (c), and most dominant grass feeding species in harvested stands (d).

**Appendix 2.1** Lepidopteran species sampled using light traps from coniferous and deciduous un-cut, 20% and 50% retention treatments at EMEND. Feeding guilds are according to larval host plant species: conifer (CON), dead leaves, lichens and fungi (DET), deciduous trees only (DT), deciduous trees and woody shrubs (DWP), generalists on deciduous and conifer trees, shrubs and herbaceous species (GEN), Graminae (GR), low herbaceous plants only (LP), Woody shrubs and low herbaceous species (WLP), Woody plants only (WP), unknown host plant (UKN).

| Family | ZooKeys[1] | Species | Guild | Trap catch |
|---|---|---|---|---|
| Cossidae | 392 | *Acossus populi* (Wlk.) | DT**** | 9 |
| Crambidae | 1033 | *Pyrausta scurralis* (Hulst) | UKN | 1 |
| Drepanidae | 1236 | *Drepana arcuata* (Wlk.) | WP | 19 |
| | 1237 | *Drepana bilineata* (Pack.) | DWP | 25 |
| | 1231 | *Habrosyne scripta Gosse* | WP | 2 |
| | 1239 | *Oreta rosea* (Wlk.). | WP | 27 |
| Erebidae | 1711 | *Catocala briseis Edw.* | DT | 3 |
| | 1705 | *Catocala relicta* Wlk. | DT | 1 |
| | 1713 | *Catocala semirelicta* Grt. | DT | 1 |
| | 1663 | *Chytolita petrealis* Grt. | DET | 1 |
| | 1652 | *Ctenucha virginica (Esp.)* | GR | 1 |
| | 1645 | *Dodia albertae Dyar.* | UKN | 1 |
| | 1609 | *Eilema bicolor (*Grt.*).* | DET | 21 |
| | 1698 | *Euclidia cuspidea (H*Gn.*)* | GR | 1 |
| | 1648 | *Gnophaela vermiculata (*Grt.*)* | LP | 1 |
| | 1620 | *Grammia parthenice (W.* Kby .*).* | LP | 3 |
| | 1621 | *Grammia virguncula (Kirby)* | LP | 1 |
| | 1675 | *Hypena atomaria* Smith | UKN | 26 |
| | 1677 | *Hypena humuli* Harr. | WP | 14 |
| | 1654 | *Idia americalis et. al.* (Gn.) | DET | 5 |
| | 1649 | *Lophocampa maculata* Harr. | DWP | 9 |
| | 1660 | *Phalaenophana pyramusalis* (Wlk.) | DET | 18 |
| | 1631 | *Platarctia parthenos (*Harr.*).* | DWP | 18 |
| | 1671 | *Rivula propinqualis* Gn. | GR | 48 |
| | 1680 | *Scoliopteryx libatrix* (L.) | DT | 1 |
| | 1613 | *Virbia ferruginosa* (Wlk.) | LP | 77 |
| | 1662 | *Zanclognatha lutalba* (Sm.) | DET | 9 |

| | | | | |
|---|---|---|---|---|
| Geometridae | 1450 | *Aethalura intertexta* (Wlk.) | WP | 3 |
| | 1258 | *Antepirrhoe semiatrata* (Hulst) | DT | 13 |
| | 1517 | *Besma quercivoraria* (Gn.) | WP | 1 |
| | 1472 | *Cabera erythemaria* Gn. | DWP | 9 |
| | 1471 | *Cabera exanthemata* (Scopoli) | DWP | 51 |
| | 1473 | *Cabera variolaria* Gn. | DT | 80 |
| | 1494 | *Campaea perlata* (Gn.) | GEN | 140 |
| | 1380 | *Cyclophora pendulinaria* (Gn.) | WP | 66 |
| | 1436 | *Digrammia rippertaria* (Duponchel) | DT** | 15 |
| | 1250 | *Dysstroma brunneata* (Pack.) | WP | 4 |
| | 1247 | *Dysstroma hersiliata* (Gn.) | WP | 3 |
| | 1245 | *Dysstroma walkerata* (Pears.) | GEN | 138 |
| | 1260 | *Ecliptopera silaceata* (D. & S.) | LP | 7 |
| | 1495 | *Ennomos magnaria* Gn. | DWP | 17 |
| | 1308 | *Epirrhoe alternata* (Mull.) | LP | 10 |
| | 1322 | *Epirrita autumnata* (Bkh.) | GEN | 30 |
| | 1256 | *Eulithis explanata* (Wlk.) | WLP | 3 |
| | 1255 | *Eulithis flavibrunneata* (McD.) | DT | 4 |
| | 1252 | *Eulithis propulsata* (Wlk.) | DT | 1 |
| | 1253 | *Eulithis testata* (L.) | DT | 13 |
| | 1257 | *Eulithis xylina* (Hulst) | DWP | 26 |
| | 1311 | *Euphyia intermediata* (Haw.) | WP | 10 |
| | | *Eupithecea spp* | UKN | 54 |
| | 1273 | *Hydriomena furcata* (Thunb.) | GEN | 23 |
| | 1267 | *Hydriomena perfrecta* Swett | GEN | 22 |
| | 1271 | *Hydriomena ruberata* Freyer | DT** | 12 |
| | 1453 | *Iridopsis larvaria* (Gn.) | DT | 3 |
| | 1376 | *Lobophora nivigerata* Wlk. | GEN | 11 |
| | 1424 | *Macaria notata* (Pears.) | WP | 20 |
| | 1429 | *Macaria signaria (Hbn)* | CON | 5 |
| | 1504 | *Metanema determinata* Wlk. | DT | 6 |
| | 1504 | *Metanema inatomaria* Gn. | DT | 7 |
| | 1405 | *Nematocampa resistaria (Haw.)* | GEN | 1 |
| | 1722 | *Nycteola frigidana* (Wlk.) | DT** | 1 |
| | 1287 | *Perizoma basaliata* (Wlk.) | UKN | 45 |
| | 1490 | *Pero morrisonaria (Hy Edw.)* | GEN | 1 |
| | 1510 | *Plagodis phlogosaria* (Gn.) | DWP | 1 |
| | 1509 | *Plagodis pulveraria* (Linn) | GEN | 4 |
| | 1262 | *Plemyria georgii* (Hulst) | DWP | 34 |
| | 1507 | *Probole alienaria (H,-S.)* | GEN | 1 |
| | 1406 | *Protitame virginalis* (Hulst) | DT | 48 |

|  |  |  |  |  |
|---|---|---|---|---|
|  | 1456 | *Protoboarmia porcelaria* (Gn.) | CON | 2 |
|  |  | *Scopula spp.* | UKN | 66 |
|  | 1522 | *Sicya macularia* (Harr.) | DWP | 94 |
|  | 1286 | *Spargania luctuata* (D. & S.) | LP | 102 |
|  | 1285 | *Spargania magnoliata* Gn. | LP | 7 |
|  | 1414 | *Speranza bitactata* (Wlk.) | WP | 9 |
|  | 1409 | *Speranza brunneata* (Thunb.) | DWP | 4 |
|  | 1421 | *Speranza loricaria* (Hulst) | DT* | 25 |
|  | 1416 | *Speranza occiduaria (Packard)* | DWP | 1 |
|  | 1497 | *Spodolepis substriataria* (Hulst) | CON | 1 |
|  | 1524 | *Tetracis jubararia* (Hulst) | DWP | 2 |
|  | 1317 | *Venusia cambrica* Curt. | WP | 256 |
|  | 1302 | *Xanthorhoe algidata* (Moschler) | UKN | 3 |
|  | 1295 | *Xanthorhoe abrasaria* (H.-S.) | LP | 34 |
|  | 1306 | *Xanthorhoe ferrugata (Cl.)* | LP | 5 |
|  | 1296 | *Xanthorhoe iduata* (Gn.) | LP | 3 |
|  | 1293 | *Xanthorhoe labradorensis* (Pack.) | DWP | 2 |
|  | 1307 | *Xanthorhoe lacustrata* Gn. | DWP | 35 |
|  | 1312 | *Zenophleps alpinata* Cass. | UKN | 19 |
| Hepialidae | 8 | *Sthenopis purpurascens* (Pack.) | DT*** | 1 |
| Lasiocampidae | 1537 | *Malacosoma disstria* Hbn. | DT* | 26 |
| Lasiocampidae | 1536 | *Phyllodesma americana* (Harr.) | DWP | 5 |
| Noctuidae | 2357 | *Abagrotis placida* (Grt.) | DWP | 7 |
|  | 1725 | *Abrostola urentis* Gn. | WLP | 5 |
|  | 1787 | *Acronicta grisea* Wlk. | DT | 21 |
|  | 1796 | *Acronicta impressa* Wlk. | UKN | 6 |
|  | 2335 | *Agnorisma bugrai Kocak* | WLP | 2 |
|  | 1962 | *Amphipoea americana* (Speyer) | GR | 10 |
|  | 2309 | *Anaplectoides pressus* (Grt.) | GEN | 11 |
|  | 2003 | *Anathix puta* (G. & R.) | DT | 9 |
|  | 2022 | *Andropolia contacta* (Wlk.) | DT | 41 |
|  | 1931 | *Apamea cogitata* (Sm.) | GR | 30 |
|  | 1924 | *Apamea commoda* (Wlk.) | DT* | 2 |
|  | 2310 | *Aplectoides condita* (Gn.) | CON | 11 |
|  | 1744 | *Autographa ampla* (Wlk.) | DWP | 4 |
|  | 1737 | *Autographa bimaculata* (Steph.) | LP | 1 |
|  | 1738 | *Autographa mappa* (G. & R.) | LP | 5 |
|  | 1739 | *Autographa pseudogamma* (Grt.) | LP | 3 |

| | | | |
|---|---|---|---|
| 2009 | *Brachylomia algens (*Grt.*)* | GEN | 288 |
| 2010 | *Brachylomia discinigra* (Wlk.) | UKN | 5 |
| 2008 | *Brachylomia populi* (Stkr.) | DT | 27 |
| 1905 | *Caradrina montana* (Bremer) | LP | 8 |
| 2040 | *Chytonix palliatricula (Gn)* | DET | 2 |
| 2301 | *Cryptocala acadiensis* (Bethune) | WP | 14 |
| 1727 | *Diachrysia aereoides (*Grt.*)* | WLP | 27 |
| 2291 | *Diarsia dislocata* (Sm.) | UKN | 73 |
| 2293 | *Diarsia rosaria (*Grt.*)* | LP | 3 |
| 2292 | *Diarsia rubifera (*Grt.*)* | LP | 1 |
| 2019 | *Enargia decolor* (Wlk.) | DT* | 486 |
| 2020 | *Enargia infumata (*Grt.*)* | DWP | 14 |
| 2312 | *Eueretagrotis perattentus (*Grt.*)* | GEN | 35 |
| 2305 | *Eurois astricta* (Morr.) | DWP | 117 |
| 2304 | *Eurois occulta* (L.) | GEN | 50 |
| 2216 | *Euxoa campestris (*Grt.*)* | WP | 1 |
| 2195 | *Euxoa divergens* (Wlk.) | LP | 2 |
| 1619 | *Grammia virgo* (L.) | LP | 6 |
| 2307 | *Graphiphora augur F.* | DWP | 21 |
| 2007 | *Hillia iris (Zett.)* | DT** | 7 |
| 1981 | *Homoglaea hircina* (Morr.) | DT | 1 |
| 1954 | *Hypocoena inquinata* (Gn.) | GR | 1 |
| 1972 | *Hyppa contrasta McD* | DT | 3 |
| 1656 | *Idia aemula (Hbn)* | CON | 53 |
| 2021 | *Ipimorpha pleonectusa* Grt. | DT | 33 |
| 2082 | *Lacanobia atlantica ((*Grt.*)* | DWP | 5 |
| 2083 | *Lacanobia radix* (Wlk.) | UKN | 8 |
| 2152 | *Lacinipolia lorea* (Gn.) | LP | 76 |
| 2153 | *Lacinipolia olivacea* (Morr.) | LP | 2 |
| 2150 | *Lacinopolia renigera* (Steph.) | LP | 5 |
| 2123 | *Lasionycta secedens* (Wlk.) | WLP | 1 |
| 2120 | *Leucania insueta* Gn. | GR | 26 |
| 1983 | *Litholomia napaea* (Morr.) | GEN | 2 |
| 1980 | *Lithomoia germana* (Morr.) | DT | 12 |
| 1994 | *Lithophane thaxteri* (Grt.) | GEN | 1 |
| 2085 | *Melanchra adjuncta* (Gn.) | WLP | 1 |
| 2035 | *Mniotype ducta* (Grt.) | WLP | 1 |
| 2114 | *Mythemna oxygala (*Lesser Waiscot) | GR | 4 |
| 1722 | *Nycteola cinereana* N. & D. | DT | 8 |
| 1945 | *Oligia illocata* (Wlk.) | DWP | 71 |
| 1944 | *Oligia mactata* (Gn.) | LP | 50 |

|  |  |  |  |  |
|---|---|---|---|---|
|  | 2046 | *Orthosia hibisci* (Gn.) | DWP | 4 |
|  | 2045 | *Orthosia segregata* (Sm.) | WLP | 2 |
|  | 1669 | *Palthis angulalis (*Hbn.*)* | CON | 6 |
|  | 2099 | *Papestra cristifera* (Wlk.) | DWP | 7 |
|  | 2097 | *Papestra quadrata* (Sm.) | GEN | 1 |
|  | 2295 | *Paradiarsia littoralis* (Pack.) | DT | 8 |
|  | 2012 | *Parastichtis suspecta (*Hbn.*)* | DT | 17 |
|  | 1910 | *Phlogophora periculosa* | DWP | 8 |
|  | 2030 | *Platypolia anceps* (Steph.) | LP | 214 |
|  | 1763 | *Plusia putnami* Grt. | GR | 3 |
|  | 2074 | *Polia nimbosa* (Gn.) | WLP | 63 |
|  | 2079 | *Polia purpurissata (*Grt.*)* | WLP | 5 |
|  | 1731 | *Polychrysia esmeralda* (Oberth.) | UKN | 22 |
|  | 1767 | *Protodeltote albidula* (Gn.) | GR | 175 |
|  | 2344 | *Protolampra rufipectus* (Morr.) | DWP | 16 |
|  | 2162 | *Protorthodes oviduca* (Gn.) | LP | 1 |
|  | 1873 | *Pyrrhia exprimens* (Wlk.) | DWP | 2 |
|  | 2002 | *Sunira verberata* (Sm.) | WP | 9 |
|  | 2037 | *Sutyna privata* (Wlk.) | LP | 36 |
|  | 1837 | *Sympistis badistriga (*Grt.*)* | LP | 1 |
|  | 1755 | *Syngrapha alias (Otto)* | CON | 1 |
|  | 1752 | *Syngrapha diasema (Bdv.)* | WP | 7 |
|  | 2005 | *Xanthia tatago* Laf. | DT** | 18 |
|  | 2331 | *Xestia conditoides* (Ben.) | UKN | 3 |
|  | 2326 | *Xestia imperita (*Hbn.*)* | UKN | 2 |
|  | 2325 | *Xestia mixta* (Wlk.) | WP | 46 |
|  | 2315 | *Xestia oblata*(Morr.) | DT** | 7 |
|  | 2329 | *Xestia perquiritata* (Morr.) | CON | 59 |
|  | 2313 | *Xestia smithii* (Snell.) | WP | 67 |
|  | 1977 | *Xylena thoracica (Put.-Cram.)* | DT | 1 |
|  | 2033 | *Xylotype arcadia* B. & Benj. | WP | 17 |
|  |  | *Zanclognatha sp* | UKN | 93 |
| Notodontidae | 1572 | *Clostera albosigma* Fitch | DWP | 39 |
|  | 1575 | *Clostera apicalis* (Wlk.) | DWP | 4 |
|  | 1574 | *Clostera brucei* (Hy. Edw.) | WP | 7 |
|  | 1585 | *Furcula occidentalis (Lint.).* | DT | 2 |
|  | 1586 | *Furcula scolopendrina Bdv.* | DT | 1 |
|  | 1580 | *Gluphisia septentrionis* Wlk. | DT* | 43 |
|  | 1576 | *Pheosia rimosa* (Pack.) | DT | 34 |
|  | 1591 | *Schizura unicornis (J.E. Smith).* | DWP | 4 |

| | | | | |
|---|---|---|---|---|
| Sphingidae | 1554 | *Smerinthus cerisyi* Kby | DT | 23 |
| Sphingidae | 1553 | *Smerinthus jamaicensis* (Drury) | DWP | 14 |
| Uraniidae | 1240 | *Callizzia amorata* Pack. | LP | 34 |

[1] Taxonomic reference numbers are according to Pohl *et al*., 2010. An annotated list of the Lepidoptera of Alberta, Canada. ZooKeys 38: 1–549.

*Specific to trembling aspen (*Populus spp*.), **Specific to *Salix* spp., ***Root borer and ****Wood borer.

**Appendix 2.2** Results of PerMANOVA for the taxonomic assemblage. Due to the small sample size (n = 3), Monte-Carlo (MC) *p-values* ($\alpha < 0.05$) were used in tests of significance in the PerMANOVA model and pair-wise comparisons.

```
PERMANOVA v.1.6
 -----------------
 A program for analysing multivariate data on the basis of any distance measure,
 according to any linear ANOVA model, using permutations.

 by M.J. Anderson
 Department of Statistics
 University of Auckland (2005)


 Input file of design information: Moths2006_design.txt
 Input file of data: Moth2006_data.txt

 --- Experimental Design ---
  Factor 1 is Forest   with  2 levels and is fixed
  Factor 2 is Treat    with  3 levels and is fixed
  The sample size (n)         =    3
  The total no. of observations =   18
  The total no. of variables    =  191

 --- Results ---
  Permutational Multivariate Analysis of Variance (Table 2.2)

  Source          df       SS          MS         F     P(perm) P(MC)
 ----------------------------------------------------------------------------
  Fo              1     3777.2098    3777.2098    2.7997  0.0001  0.0062
  Tr              2     6517.3832    3258.6916    2.4153  0.0001  0.0026
  FoxTr           2      4374.6580    2187.3290    1.6212  0.0134  0.0641
  Residual        12     16190.0574    1349.1715
  Total           17    30859.3085
 ----------------------------------------------------------------------------
  Data were transformed to log10(x+1)
  No standardisation
  Analysis based on Bray-Curtis dissimilarities
  Unrestricted permutation of raw data using correct permutable units
  Integer used as seed     =    2
  No. of permutations used = 9999

  --- Details of the expected mean squares (EMS) for the model ---

  Source                          Terms included in the EMS
 ----------------------------------------------------------------------------
  Fo                   = 1          R + 1
```

```
 Tr                  = 2         R + 2
 FoxTr                 = 12        R + 12
 Res                  = R         R
----------------------------------------------------------------------------


                     #permutable  #unique vals   Term used for
 Source                  units     in perm dist  denom MS in F-ratio
----------------------------------------------------------------------------
 Fo                     18         9911      Res
 Tr                     18         9892      Res
 FoxTr                    18         9903      Res
----------------------------------------------------------------------------

Tests among levels of the factor Treat (Table 2.2)
-----------------------------------------------------------
   Groups       t       P_perm    P_MC   #unique vals
-----------------------------------------------------------
  ( 1, 2)     1.6208    0.0025   0.0202    462
  ( 1, 3)     1.4595    0.0120   0.0554    461
  ( 2, 3)     1.1390    0.1944   0.2520    461
-----------------------------------------------------------

 Average dissimilarities within/between groups
      1      2      3
   1  51.815
   2  65.820  63.772
   3  57.332  60.003  52.762
```

**Appendix 2.3** Results of PerMANOVA for the guild assemblage. Due to the small sample size (n = 3), Monte-Carlo (MC) *p-values* ($\alpha < 0.05$) were used in tests of significance in the PerMANOVA model and pair-wise comparisons.

```
PERMANOVA v.1.6
 -----------------
 A program for analyzing multivariate data on the basis of any distance measure
 according to any linear ANOVA model, using permutations.

 By M.J. Anderson
 Department of Statistics
 University of Auckland (2005)

 Input file of design information: Moths2006_design.txt
 Input file of data: Guild_data.txt

 --- Experimental Design ---
  Factor 1 is Forest   with  2 levels and is fixed
  Factor 2 is Treat    with  3 levels and is fixed
```

```
 The sample size (n)          =    3
 The total no. of observations =   18
 The total no. of variables    =   9

--- Results ---
 Permutational Multivariate Analysis of Variance: Table 2.2)

 Source          df       SS          MS         F     P(perm) P(MC)
---------------------------------------------------------------------------
 Fo             1     3687.0825    3687.0825    7.0107  0.0007  0.0015
 Tr            2     6437.4133    3218.7067    6.1202  0.0002  0.0005
 FoxTr           2      2590.5846    1295.2923    2.4629  0.0412  0.0427
 Residual         12      6311.0320     525.9193
 Total           17     19026.1124
---------------------------------------------------------------------------
 No standardisation
 Analysis based on Bray-Curtis dissimilarities
 Unrestricted permutation of raw data using correct permutable units
 Integer used as seed    =    2
 No. of permutations used = 9999

 --- Details of the expected mean squares (EMS) for the model ---

 Source                          Terms included in the EMS
---------------------------------------------------------------------------
 Fo                   = 1          R + 1
 Tr                  = 2          R + 2
 FoxTr                  = 12         R + 12
 Res                   = R          R
---------------------------------------------------------------------------


                  #permutable  #unique vals   Term used for
 Source                 units      in perm dist  denom MS in F-ratio
---------------------------------------------------------------------------
 Fo                       18          9943       Res
 Tr                      18          9951       Res
 FoxTr                     18          9931       Res
---------------------------------------------------------------------------

Tests among levels of the factor Treat
 within: (Table 2.2)
 level   1 of the factor Forest
 ------------------------------------------------------------
   Groups        t       P_perm     P_MC    #unique vals
 ------------------------------------------------------------
  ( 1, 2)     2.2034    0.1043    0.0375       10
  ( 1, 3)     2.6882    0.1021    0.0181       10
```

```
 ( 2, 3)      1.2861     0.1024     0.2314       10
-------------------------------------------------------------

 Average dissimilarities within/between groups
      1       2       3
  1  23.623
  2  47.868  37.397
  3  42.788  34.212  24.482


Tests among levels of the factor Treat
 within: (Table 2.2)
 level   2 of the factor Forest
-------------------------------------------------------------
  Groups        t       P_perm     P_MC    #unique vals
-------------------------------------------------------------
 ( 1, 2)      2.9767     0.1023     0.0113       10
 ( 1, 3)      1.6787     0.0989     0.1132       10
 ( 2, 3)      1.5321     0.1998     0.1399       10
-------------------------------------------------------------

 Average dissimilarities within/between groups
      1       2       3
  1  20.533
  2  61.068  40.171
2      36.127  44.693  35.723
```

**Appendix 2.4** PCORD output of the non-metric multidimensional analysis (NMS) based on Bray-Curtis distances of (a) the community matrix and (b) feeding guild matrix of moths light trapped from the coniferous and deciduous unharvested (100%) and harvested 20% and 50% retention treatments at EMEND.

### (a) Community matrix (Figure 2.4 a)

```
STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)
------------------------------------------------------------------
       Stress in real data        Stress in randomized data
         250 run(s)            Monte Carlo test,    249 runs
    ------------------------  ----------------------------------
Axes  Minimum     Mean  Maximum  Minimum     Mean  Maximum     p
------------------------------------------------------------------
  1   18.962   44.479   54.435
  2   10.298   13.360   37.197
------------------------------------------------------------------
p = proportion of randomized runs with stress < or = observed stress
i.e., p  = (1 + no. permutations <= observed)/(1 + no. permutations)


Conclusion:  a 2-dimensional solution is recommended.

Selected file CONFIG2.GPH  for the starting configuration for
  the final run.
```

| | | |
|---|---|---|
| CDOM_100 | -1.5075 | 0.03943 |
| CDOM_100 | -1.31015 | 0.38235 |
| CDOM_100 | -1.32451 | 0.59771 |
| CDOM_20 | 0.17616 | -0.96725 |
| CDOM_20 | 0.21097 | -0.70305 |
| CDOM_20 | 0.04509 | -0.74037 |
| CDOM_50 | 0.58403 | -0.28763 |
| CDOM_50 | 0.44366 | -0.22421 |
| CDOM_50 | 0.60976 | -0.41156 |
| DDOM_100 | -0.14143 | 1.39141 |
| DDOM_100 | -0.39803 | 1.36626 |
| DDOM_100 | -0.44797 | 1.05533 |
| DDOM_20 | 0.02456 | -0.2822 |
| DDOM_20 | 0.44849 | -0.77173 |
| DDOM_20 | 0.23681 | -0.46909 |
| DDOM_50 | 1.01822 | -0.1194 |
| DDOM_50 | 0.73857 | -0.12359 |

```
DDOM_50       0.59324       0.2676


Ordination of Samples  in Species  space.      18 Samples     191 species

        The following options were selected:
ANALYSIS OPTIONS
        1.  SORENSEN = Distance measure
        2.        2 = Number of axes (max. = 6)
        3.      250 = Maximum number of iterations
        4.  FROM FILE = Starting coordinates (random or from file)
        5.        2 = Reduction in dimensionality at each cycle
        6.     0.20 = Step length (rate of movement toward minimum stress)
        7.  USE TIME = Random number seeds (use time vs. user-supplied)
        8.        1 = Number of runs with real data
        9.        249 = Number of runs with randomized data
       10.       NO = Autopilot
       11.  0.000010 = Stability criterion, standard deviations in stress
                   over last  15 iterations.
OUTPUT OPTIONS
       13.      YES = Write distance matrix?
       14.       NO = Write starting coordinates?
       15.       NO = List stress, etc. for each iteration?
       18.      YES = Plot stress vs. iteration?
       17.       NO = Plot distance vs. dissimilarity?
       16.      YES = Write final configuration?
       19.  UNROTATED = Write varimax-rotated or unrotated scores for graph?
       20.       NO = Write run log?
       21.       NO = Write weighted-average scores for Species
```

**(b) <u>Guild matrix (Figure 2.4 b)</u>**

```
PC-ORD 5.10
6/28/2011, 10:41 PM

STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)
---------------------------------------------------------------------
        Stress in real data        Stress in randomized data
          250 run(s)             Monte Carlo test,  249 runs
     -------------------------  -----------------------------------
Axes  Minimum    Mean  Maximum  Minimum    Mean  Maximum     p
---------------------------------------------------------------------
```

```
  2   9.831   10.244   36.778   13.601   21.834   35.991    0.0040
------------------------------------------------------------------
p = proportion of randomized runs with stress < or = observed stress
i.e., p  = (1 + no. permutations <= observed)/(1 + no. permutations)

Conclusion:  a 2-dimensional solution is recommended.

Selected file CONFIG2.GPH  for the starting configuration for
  the final run.
  Guild_        Matrix
         18     points
  C1001        -0.29548     0.58772
  C1002        -0.07917     0.72945
  C1003         0.29985     0.63812
  C201         -1.92435    -0.16495
  C202         -0.55907    -0.51802
  C203         -0.47796    -0.16241
  C501         -0.15016    -0.25093
  C502         -0.34403    -0.39648
  C503         -0.54788    -0.85935
  D1001         1.52431     0.23971
  D1002         1.23444     0.33783
  D1003         1.41795    -0.19149
  D201          -0.1501     0.11459
  D202         -1.44005     0.26746
  D203          -0.2731    -0.60069
  D501          0.62473      0.2177
  D502         -0.06006     0.03761
  D503          1.20011    -0.02587

Guild_Matrix
Ordination of Samples  in Variable space.        18 Samples        10 Variables

        The following options were selected:
ANALYSIS OPTIONS
        1.   SORENSEN = Distance measure
        2.          2 = Number of axes (max. = 6)
        3.         50 = Maximum number of iterations
        4.  FROM FILE = Starting coordinates (random or from file)
        5.          2 = Reduction in dimensionality at each cycle
        6.       0.20 = Step length (rate of movement toward minimum stress)
        7.   USE TIME = Random number seeds (use time vs. user-supplied)
        8.          1 = Number of runs with real data
```

```
      9.     0 = Number of runs with randomized data
     10.    NO = Autopilot
     11.  0.000010 = Stability criterion, standard deviations in stress
                  over last  15 iterations.
OUTPUT OPTIONS
     13.   YES = Write distance matrix?
     14.   YES = Write starting coordinates?
     15.    NO = List stress, etc. for each iteration?
     18.   YES = Plot stress vs. iteration?
     17.   YES = Plot distance vs. dissimilarity?
     16.   YES = Write final configuration?
     19.  ROTATED = Write varimax-rotated or unrotated scores for graph?
     20.    NO = Write run log?
     21.   YES = Write weighted-average scores for Variable?
------------------------------------------------------------------------------
```

**Variance explained**

```
Coefficients of determination for the correlations between ordination
distances and distances in the original n-dimensional space:

        R Squared
Axis  Increment  Cumulative
 1     .842      .842
 2     .096      .938

Increment and cumulative R-squared were adjusted for any lack
of orthogonality of axes.

Axis pair    r    Orthogonality,% = 100(1-r^2)
 1 vs 2   0.240   94.2

Number of entities = 18
Number of entity pairs used in correlation = 153
Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)
```

**Appendix 2.5** Indicator species analysis output. Data are sorted according to the p*-column. The 27 species that were significant indicators ($\alpha < 0.05$) are highlighted in bold on the first column. Full names for the species codes (First letter = genus and subsequent letters = species name) are according to Table 2.3 and Appendix 2.1.

| Column | Species | Maxgrp | Observed Indicator Value (IndVal) | Mean | S.Dev | p * |
|---|---|---|---|---|---|---|
| **18** | Cpenduli | 12 | 81.8 | 36.8 | 12.67 | 0.0054 |
| **4** | Cperlata | 12 | 45.7 | 31.4 | 6.24 | 0.0056 |
| **9** | Sluctuat | 12 | 44.1 | 28.3 | 4.98 | 0.006 |
| **21** | Pvirgina | 12 | 75 | 31.4 | 11.77 | 0.006 |
| **32** | Daereoid | 12 | 85.2 | 30.6 | 13.52 | 0.006 |
| **34** | Calbosig | 12 | 89.7 | 30 | 13.85 | 0.006 |
| **35** | Sprofund | 12 | 86.1 | 30 | 13.97 | 0.006 |
| **36** | Eperatte | 12 | 74.3 | 30.5 | 12.07 | 0.006 |
| **50** | Mdisstri | 12 | 92.3 | 26.4 | 15.11 | 0.006 |
| **51** | Dbilinea | 12 | 92 | 29.5 | 14.87 | 0.006 |
| **56** | Pesmeral | 12 | 90.9 | 26.6 | 14.75 | 0.006 |
| **57** | Agrisea | 12 | 95.2 | 26.4 | 15.6 | 0.006 |
| **30** | Pbasalia | 11 | 91.1 | 29.7 | 14.26 | 0.0064 |
| **20** | Pnimbosa | 11 | 58.7 | 29.2 | 10.27 | 0.0068 |
| **39** | Pgeorgii | 32 | 70.6 | 30 | 11.85 | 0.0068 |
| **49** | Linsueta | 32 | 84.6 | 27.3 | 13.9 | 0.0068 |
| **22** | Xperquir | 11 | 86.4 | 35 | 13.15 | 0.0074 |
| **44** | Eautumna | 32 | 73.3 | 29.1 | 13.3 | 0.011 |
| **6** | Panceps | 32 | 52.3 | 33.1 | 8.72 | 0.0122 |
| **60** | Mulstera | 12 | 65 | 28.4 | 11.46 | 0.0132 |
| **7** | Dwalkera | 12 | 46.4 | 30.8 | 5.12 | 0.0164 |
| **2** | Balgens | 12 | 52.8 | 33.7 | 9.03 | 0.0204 |
| **1** | Edecolor | 12 | 49.4 | 34.9 | 6.55 | 0.0272 |
| **43** | Acogitat | 12 | 40 | 27.4 | 5.63 | 0.028 |
| **29** | Xmixta | 11 | 80.4 | 34.2 | 15.06 | 0.033 |
| **24** | Iaemula | 11 | 66 | 33.3 | 12.77 | 0.0502 |
| **3** | Vcambric | 12 | 50 | 32.6 | 9.12 | 0.0516 |
| 90 | Zlutalba | 22 | 44.4 | 27.3 | 12.84 | 0.0672 |
| 79 | Acondita | 12 | 54.5 | 27.8 | 11.79 | 0.0732 |
| 16 | Oillocat | 32 | 49.3 | 28 | 10.95 | 0.077 |
| 101 | Minatoma | 31 | 42.9 | 28.8 | 14.12 | 0.08 |
| 78 | Lgermana | 12 | 50 | 29.6 | 12.66 | 0.1146 |
| 145 | Ediverge | 32 | 66.7 | 22.4 | 15.96 | 0.1152 |
| 152 | Pexprime | 32 | 66.7 | 22.4 | 15.96 | 0.1152 |
| 87 | Cerythem | 31 | 44.4 | 28.1 | 12.22 | 0.1172 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 137 | Ilarvari | 12 | 66.7 | 27.5 | 14.36 | 0.1184 |
| 118 | Ppurpuri | 21 | 53.3 | 24.3 | 16.22 | 0.1196 |
| 53 | Hfurcata | 12 | 43.5 | 33.4 | 10.87 | 0.127 |
| 45 | Bpopuli | 32 | 49.4 | 27.5 | 14.91 | 0.1308 |
| 105 | Xoblata | 31 | 47.6 | 27.1 | 14.29 | 0.1316 |
| 40 | Premosa | 12 | 44.1 | 29.2 | 11.03 | 0.1478 |
| 55 | Hperfect | 32 | 45.5 | 30.9 | 10.48 | 0.1486 |
| 94 | Pmontana | 12 | 37.5 | 28.5 | 13.05 | 0.1512 |
| 8 | Eastrict | 12 | 36.8 | 29.1 | 6.36 | 0.1584 |
| 47 | Exylina | 12 | 38.5 | 29.4 | 8.04 | 0.1656 |
| 84 | Eunangul | 12 | 46.7 | 28.7 | 14.7 | 0.1708 |
| 65 | Xtatago | 21 | 38.9 | 30 | 11.73 | 0.1772 |
| 95 | Ppericul | 12 | 50 | 31.5 | 15.8 | 0.1924 |
| 33 | Acontact | 12 | 48.8 | 35 | 11.25 | 0.2106 |
| 88 | Lmaculat | 32 | 33.3 | 27.9 | 12.04 | 0.2112 |
| 54 | Scerisyi | 12 | 39.1 | 28.6 | 9.88 | 0.2186 |
| 42 | Ipleonec | 32 | 36.4 | 28.8 | 6.89 | 0.2186 |
| 120 | Aampla | 11 | 50 | 26.3 | 15.1 | 0.222 |
| 104 | Smagnoli | 11 | 47.6 | 28.2 | 15.24 | 0.2278 |
| 117 | Pamerica | 32 | 53.3 | 28.6 | 14.8 | 0.2286 |
| 69 | Prufipec | 32 | 37.5 | 27.6 | 8.54 | 0.2348 |
| 23 | Eupethec | 12 | 37 | 30 | 8.32 | 0.2372 |
| 61 | Darcuata | 12 | 42.1 | 34.9 | 16.75 | 0.2454 |
| 66 | Emagnari | 32 | 43.1 | 32.9 | 16.11 | 0.2503 |
| 25 | Cexanthe | 12 | 37.3 | 29.8 | 7.77 | 0.2605 |
| 68 | Xarcadia | 11 | 35.3 | 28.5 | 14.02 | 0.2893 |
| 100 | Mbictata | 12 | 38.1 | 28.5 | 14.02 | 0.2899 |
| 83 | Ealterna | 12 | 40 | 29.7 | 15.01 | 0.2909 |
| 97 | Cbrucei | 12 | 38.1 | 28.7 | 13.87 | 0.3023 |
| 93 | Plittora | 21 | 41.7 | 28.2 | 14.85 | 0.3315 |
| 86 | Aputa | 32 | 37 | 25.9 | 15.25 | 0.3323 |
| 110 | Amappa | 12 | 40 | 26.8 | 13.99 | 0.3329 |
| 134 | Eexplana | 31 | 44.4 | 22.8 | 17.11 | 0.3375 |
| 112 | Bdiscini | 32 | 40 | 24.4 | 16.28 | 0.3437 |
| 140 | Xhomogen | 31 | 44.4 | 23 | 16.86 | 0.3455 |
| 27 | Omactata | 32 | 36 | 34.4 | 13.65 | 0.3523 |
| 46 | Orosea | 12 | 34.6 | 29.5 | 13.79 | 0.3621 |
| 91 | Lradix | 11 | 33.3 | 26.7 | 12.71 | 0.3631 |
| 12 | Cvariola | 12 | 37.5 | 34.9 | 8.7 | 0.3735 |
| 63 | Pparthen | 11 | 29.6 | 29.7 | 9.81 | 0.3887 |
| 41 | Xabrasar | 12 | 32.4 | 28.6 | 7.04 | 0.3987 |
| 77 | Hruberat | 32 | 27.8 | 28 | 11.08 | 0.4439 |
| 13 | Hferrugi | 31 | 29.9 | 29.5 | 8.77 | 0.4455 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 15 | Ddisloca | 11 | 27.4 | 26.3 | 3.2 | 0.4493 |
| 102 | Pcristif | 32 | 38.1 | 28.8 | 13.98 | 0.4613 |
| 107 | Gvirgo | 31 | 33.3 | 27.5 | 12.47 | 0.4635 |
| 10 | Smacular | 22 | 31.9 | 30.2 | 5.92 | 0.4675 |
| 38 | Camorata | 12 | 29.4 | 29.3 | 8.06 | 0.4839 |
| 52 | Mloricar | 12 | 28 | 26.7 | 5.06 | 0.4931 |
| 31 | Gseptent | 32 | 32.6 | 34.1 | 10.66 | 0.5119 |
| 108 | Mdetermi | 21 | 33.3 | 26.1 | 14.65 | 0.5239 |
| 70 | Dhebatat | 11 | 26.7 | 28.2 | 11.17 | 0.5261 |
| 26 | Eocculta | 11 | 30.7 | 33.3 | 9.48 | 0.5465 |
| 89 | Sverbera | 21 | 18.5 | 27.4 | 14.92 | 0.5623 |
| 37 | Xlacustr | 32 | 30.5 | 35.5 | 11.31 | 0.5707 |
| 19 | Scopula | 11 | 22.7 | 24.1 | 2.79 | 0.5915 |
| 121 | Aoccidua | 12 | 33.3 | 24.4 | 15.12 | 0.5929 |
| 114 | Latlanti | 32 | 26.7 | 26.8 | 13.95 | 0.5969 |
| 122 | Aoxygala | 11 | 33.3 | 24.5 | 14.61 | 0.6047 |
| 115 | Lreniger | 21 | 26.7 | 27.2 | 14.12 | 0.6115 |
| 96 | Aplacida | 12 | 19 | 27.5 | 14.49 | 0.6119 |
| 128 | Sunicorn | 11 | 33.3 | 24.9 | 14.94 | 0.6123 |
| 17 | Xsmithii | 32 | 28.4 | 30.2 | 7.27 | 0.6329 |
| 74 | Sjamaice | 12 | 23.8 | 27.6 | 9.2 | 0.6439 |
| 80 | Apressus | 12 | 24.2 | 29.3 | 14.62 | 0.6477 |
| 98 | Esilacea | 12 | 28.6 | 27.2 | 12.9 | 0.6627 |
| 75 | Esemiatr | 11 | 20.5 | 27.8 | 9.28 | 0.6635 |
| 59 | Gaugur | 12 | 23.8 | 30.9 | 10.32 | 0.6853 |
| 103 | Sdiasema | 31 | 19 | 26.6 | 12.47 | 0.6933 |
| 58 | Ebicolor | 11 | 22.2 | 28.3 | 12.3 | 0.7187 |
| 67 | Psuspect | 12 | 23.5 | 28 | 8.78 | 0.7345 |
| 81 | Lniviger | 11 | 24.2 | 28.3 | 10.39 | 0.7357 |
| 72 | Einfumat | 31 | 23.8 | 28.2 | 11.21 | 0.759 |
| 82 | Aamerica | 32 | 26.7 | 27.9 | 12.49 | 0.7728 |
| 64 | Ppyramus | 12 | 22.2 | 29.6 | 12.59 | 0.8176 |
| 109 | Pangulal | 31 | 22.2 | 27.2 | 12.49 | 0.8216 |
| 14 | Llorea | 12 | 26.3 | 37.7 | 11.5 | 0.8246 |
| 119 | Xferruga | 12 | 26.7 | 25.8 | 12.37 | 0.8292 |
| 73 | Hhumuli | 11 | 23.8 | 29.1 | 12.32 | 0.854 |
| 71 | Cacadien | 22 | 23.8 | 29.3 | 12.24 | 0.8606 |
| 62 | Zalpinat | 31 | 17.5 | 28.4 | 11.2 | 0.8608 |
| 28 | Rpropinq | 12 | 20.8 | 29.6 | 8.8 | 0.875 |
| 76 | Etestata | 22 | 20.5 | 28 | 9.28 | 0.8974 |
| 11 | Zanclog | 22 | 20.1 | 27.7 | 5.48 | 0.9302 |
| 99 | Hiris | 21 | 19 | 27.2 | 10.85 | 0.9666 |
| 5 | Lalbidul | 31 | 18.9 | 32 | 7.98 | 0.972 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 48 | Hatomari | 11 | 24.4 | 34.9 | 16.18 | 1 |
| 111 | Aurentis | 11 | 13.3 | 27 | 14.16 | 1 |
| 116 | Msignari | 11 | 20 | 28.8 | 15.05 | 1 |
| 123 | Capicali | 11 | 8.3 | 24.4 | 14.85 | 1 |
| 124 | Dbrunnea | 11 | 25 | 30 | 13.54 | 1 |
| 129 | Ainterte | 11 | 11.1 | 22.5 | 16.9 | 1 |
| 133 | Drosaria | 11 | 11.1 | 23.1 | 17.29 | 1 |
| 136 | Hcontras | 11 | 11.1 | 22.9 | 17.15 | 1 |
| 138 | Pputnami | 11 | 11.1 | 23 | 17.22 | 1 |
| 141 | Xiduata | 11 | 11.1 | 22.8 | 17.01 | 1 |
| 144 | Cpalliat | 11 | 16.7 | 22.8 | 16.43 | 1 |
| 151 | Osegrega | 11 | 16.7 | 22.5 | 16.1 | 1 |
| 156 | Xlabrado | 11 | 16.7 | 22.4 | 15.93 | 1 |
| 180 | Nresista | 11 | 33.3 | 33.3 | 0.47 | 1 |
| 188 | Slibatri | 11 | 33.3 | 33.3 | 0.47 | 1 |
| 85 | Apopuli | 12 | 22.2 | 30.2 | 15.37 | 1 |
| 92 | Ncinerea | 12 | 16.7 | 28.5 | 14.94 | 1 |
| 113 | Iamerica | 12 | 26.7 | 31.4 | 12.88 | 1 |
| 125 | Eflavibr | 12 | 25 | 29.9 | 13.47 | 1 |
| 127 | Ohibisci | 12 | 25 | 29.9 | 13.42 | 1 |
| 146 | Focciden | 12 | 16.7 | 21.8 | 15.22 | 1 |
| 147 | Hscripta | 12 | 16.7 | 22.5 | 16.09 | 1 |
| 148 | Lnapaea | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 149 | Lolivace | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 150 | Mbitacta | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 159 | Bquerciv | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 161 | Cpetreal | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 169 | Epropuls | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 170 | Fscolope | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 173 | Hbadistr | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 178 | Moccidua | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 181 | Palienar | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 182 | Pmorriso | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 184 | Pphlogos | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 186 | Pscurral | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 187 | Salias | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 190 | Ssubstri | 12 | 33.3 | 33.3 | 0.47 | 1 |
| 106 | Aimpress | 21 | 33.3 | 33.3 | 0.47 | 1 |
| 126 | Mbrunnea | 21 | 8.3 | 24.9 | 15.04 | 1 |
| 131 | Cbriseis | 21 | 11.1 | 22.8 | 17.12 | 1 |
| 139 | Xfossari | 21 | 22.2 | 27.5 | 14.37 | 1 |
| 142 | Abugrai | 21 | 16.7 | 22.1 | 15.6 | 1 |
| 154 | Sjubarar | 21 | 16.7 | 22.6 | 16.23 | 1 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 155 | Ximperit | 21 | 16.7 | 22.4 | 15.91 | 1 |
| 165 | Dalberta | 21 | 33.3 | 33.3 | 0.47 | 1 |
| 175 | Lthaxter | 21 | 33.3 | 33.3 | 0.47 | 1 |
| 191 | Xthoraci | 21 | 33.3 | 33.3 | 0.47 | 1 |
| 130 | Apseudos | 22 | 22.2 | 27.5 | 14.37 | 1 |
| 157 | Abimacul | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 162 | Crelicta | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 168 | Ecuspide | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 183 | Poviduca | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 185 | Pquadrat | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 189 | Spurpura | 22 | 33.3 | 33.3 | 0.47 | 1 |
| 132 | Dhersili | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 135 | Gparthen | 31 | 11.1 | 23 | 17.15 | 1 |
| 143 | Acommoda | 31 | 16.7 | 22.8 | 16.39 | 1 |
| 153 | Pporcela | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 158 | Aseceden | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 160 | Cinquina | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 166 | Drubifer | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 171 | Gvermicu | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 174 | Hhircina | 31 | 33.3 | 33.3 | 0.47 | 1 |
| 163 | Csemirel | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 164 | Cvirgini | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 167 | Ecampest | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 172 | Gvirgunc | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 176 | Madjunct | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 177 | Minotype | 32 | 33.3 | 33.3 | 0.47 | 1 |
| 179 | Nfrigida | 32 | 33.3 | 33.3 | 0.47 | 1 |

**Appendix 2.6** R-models and outputs for the Analysis of variance (ANOVA) for the total number of individuals and species night flying moths (Figure 2.3) and the total number of individuals and species within each of the nine feeding guilds, (Figure 2.5 & ad 2.6). *P-values* are highlighted bold, significant values are marked with asterisks.

```
>  ##########################Import data
> data.cdom=dat.guild[1:9, ]
> fix(data.cdom)
> data.ddom = dat.guild[10:18, ]
> fix(data.ddom)

>#Total abundance and species richness
> rich.cc=aov(rich~treat,data=data.cdom)
> summary(rich.cc)
          Df Sum Sq Mean Sq F value Pr(>F)
treat       2 602.89  301.44  2.3674 0.1746
Residuals    6 764.00  127.33
> #TukeyHSD(rich.cc)
> abund.cc=aov(abund~treat,data=data.cdom)
> summary(abund.cc)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2  26318   13159  5.4264 0.04513 *
Residuals    6  14550    2425
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.cc)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = abund ~ treat, data = data.cdom)

$treat
    diff       lwr       upr     p adj
b-a  -87 -210.3685 36.368545 0.1567623
c-a -130 -253.3685 -6.631455 0.0408723
c-b  -43 -166.3685 80.368545 0.5649809
> rich.dd=aov(rich~treat,data=data.ddom)
> summary(rich.dd)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2   3768    1884  10.644 0.01063 *
Residuals    6   1062     177
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(rich.dd)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = rich ~ treat, data = data.ddom)
```

```
$treat
    diff       lwr        upr     p adj
b-a  -28 -61.32999   5.329992 0.0924793
c-a  -50 -83.32999 -16.670008 0.0087660
c-b  -22 -55.32999  11.329992 0.1868921

> abund.dd=aov(abund~treat,data=data.ddom)
> summary(abund.dd)
            Df Sum Sq Mean Sq F value   Pr(>F)
treat        2 280088  140044   12.51 0.007236 **
Residuals    6  67166   11194
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.dd)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = abund ~ treat, data = data.ddom)

$treat
    diff       lwr        upr     p adj
b-a -252 -517.0621   13.06213 0.0603009
c-a -430 -695.0621 -164.93787 0.0060081
c-b -178 -443.0621   87.06213 0.1787459

> Guilds Assemblages
> dat.guild=read.csv("C:/work/Point plots/Guild abund&rich.csv")
> fix(dat.guild)
> data.cdom = dat.guild[1:9, ]
> fix(data.cdom)
> data.ddom = dat.guild[10:18, ]
> fix(data.ddom)

> #########################CON
> abund.ccCON=aov(CON_abun~treat,data=data.cdom)
> summary(abund.ccCON)
            Df  Sum Sq Mean Sq F value    Pr(>F)
treat        2 1536.89  768.44  28.229 0.0008866 ***
Residuals    6  163.33   27.22
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ccCON)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = CON_abun ~ treat, data = data.cdom)
```

```
$treat
         diff       lwr       upr     p adj
b-a -26.66667 -39.73771 -13.59562 0.0018729
c-a -28.66667 -41.73771 -15.59562 0.0012767
c-b  -2.00000 -15.07105  11.07105 0.8877622

> rich.ccCON=aov(CON_rich~treat,data=data.cdom)
> summary(rich.ccCON)
            Df Sum Sq Mean Sq F value  Pr(>F)
treat        2 5.5556 2.77778    6.25 0.03411 *
Residuals    6 2.6667 0.44444
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(rich.ccCON)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = CON_rich ~ treat, data = data.cdom)

$treat
         diff       lwr         upr     p adj
b-a  0.000000 -1.670157 1.670157055 1.0000000
c-a -1.666667 -3.336824 0.003490388 0.0503964
c-b -1.666667 -3.336824 0.003490388 0.0503964

> abund.ddCON=aov(CON_abun~treat,data=data.ddom)
> summary(abund.ddCON)
            Df Sum Sq Mean Sq F value  Pr(>F)
treat        2 93.556  46.778  8.2549 0.01894 *
Residuals    6 34.000   5.667
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ddCON)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = CON_abun ~ treat, data = data.ddom)

$treat
          diff       lwr        upr     p adj
b-a -7.0000000 -12.96365 -1.0363465 0.0263670
c-a -6.6666667 -12.63032 -0.7030131 0.0322698
c-b  0.3333333  -5.63032  6.2969869 0.9839595

> rich.ddCON=aov(CON_rich~treat,data=data.ddom)
> summary(rich.ddCON)
            Df Sum Sq Mean Sq F value   Pr(>F)
treat        2 20.222 10.1111  15.167 0.004503 **
```

```
Residuals    6  4.000  0.6667
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(rich.ddCON)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = CON_rich ~ treat, data = data.ddom)

$treat
          diff       lwr        upr     p adj
b-a -3.3333333 -5.378850 -1.2878170 0.0058769
c-a -3.0000000 -5.045516 -0.9544837 0.0097552
c-b  0.3333333 -1.712183  2.3788496 0.8740031

> ############################DET
> abund.ccDET=aov(DET_abun~treat,data=data.cdom)
> summary(abund.ccDET)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 10.667  5.3333  1.3714 0.3232
Residuals    6 23.333  3.8889
> #TukeyHSD(abund.ccDET)
> rich.ccDET=aov(DET_rich~treat,data=data.cdom)
> summary(rich.ccDET)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 1.5556 0.77778  2.3333  0.178
Residuals    6 2.0000 0.33333
> #TukeyHSD(rich.ccDET)
> abund.ddDET=aov(DET_abun~treat,data=data.ddom)
> summary(abund.ddDET)
            Df  Sum Sq Mean Sq F value Pr(>F)
treat        2  34.889  17.444  1.0329 0.4116
Residuals    6 101.333  16.889
> #TukeyHSD(abund.ddDET)
> rich.ddDET=aov(DET_rich~treat,data=data.ddom)
> summary(rich.ddDET)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 4.2222  2.1111  1.7273 0.2556
Residuals    6 7.3333  1.2222
> #TukeyHSD(rich.ddDET)

> ############################DT
> abund.ccDT=aov(DT_abun~treat,data=data.cdom)
> summary(abund.ccDT)
            Df  Sum Sq Mean Sq F value Pr(>F)
treat        2  680.67  340.33  1.3062 0.3381
Residuals    6 1563.33  260.56
> #TukeyHSD(abund.ccDT)
```

```
> rich.ccDT=aov(DT_rich~treat,data=data.cdom)
> summary(rich.ccDT)
          Df Sum Sq Mean Sq F value Pr(>F)
treat       2      2       1  0.1429 0.8697
Residuals    6     42       7
> #TukeyHSD(rich.ccDT)
> abund.ddDT=aov(DT_abun~treat,data=data.ddom)
> summary(abund.ddDT)
          Df  Sum Sq Mean Sq F value Pr(>F)
treat       2 28966.9 14483.4  8.7139 0.0168 *
Residuals    6  9972.7  1662.1
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ddDT)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = DT_abun ~ treat, data = data.ddom)

$treat
          diff       lwr       upr     p adj
b-a  -88.66667 -190.8026  13.46928 0.0829180
c-a -137.00000 -239.1359 -34.86406 0.0147288
c-b  -48.33333 -150.4693  53.80261 0.3757170

> rich.ddDT=aov(DT_rich~treat,data=data.ddom)
> summary(rich.ddDT)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2 253.56 126.778  5.3821 0.04585 *
Residuals    6 141.33  23.556
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(rich.ddDT)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = DT_rich ~ treat, data = data.ddom)

$treat
          diff       lwr        upr     p adj
b-a  -6.333333 -18.49226  5.8255936 0.3166222
c-a -13.000000 -25.15893 -0.8410731 0.0385980
c-b  -6.666667 -18.82559  5.4922602 0.2861672

> ##########################GEN
> abund.ccGEN=aov(GEN_abun~treat,data=data.cdom)
> summary(abund.ccGEN)
          Df  Sum Sq Mean Sq F value Pr(>F)
```

```
treat       2   34.67  17.333   0.098 0.9081
Residuals    6 1061.33 176.889
> #TukeyHSD(abund.ccGEN)
> rich.ccGEN=aov(GEN_rich~treat,data=data.cdom)
> summary(rich.ccGEN)
          Df  Sum Sq Mean Sq F value Pr(>F)
treat       2  2.8889  1.4444  0.8125 0.4872
Residuals    6 10.6667  1.7778
> #TukeyHSD(rich.ccGEN)
> abund.ddGEN=aov(GEN_abun~treat,data=data.ddom)
> summary(abund.ddGEN )
          Df Sum Sq Mean Sq F value   Pr(>F)
treat       2  14126  7063.0  11.765 0.008388 **
Residuals    6   3602   600.3
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> TukeyHSD(abund.ddGEN)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = GEN_abun ~ treat, data = data.ddom)

$treat
    diff       lwr       upr     p adj
b-a  -51 -112.3825  10.38253 0.0958695
c-a  -97 -158.3825 -35.61747 0.0068280
c-b  -46 -107.3825  15.38253 0.1318643

> rich.ddGEN=aov(GEN_rich~treat,data=data.ddom)
> summary(rich.ddGEN)
          Df Sum Sq Mean Sq F value Pr(>F)
treat       2 32.889 16.4444     7.4  0.024 *
Residuals    6 13.333  2.2222
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> TukeyHSD(rich.ddGEN)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = GEN_rich ~ treat, data = data.ddom)

$treat
         diff       lwr       upr     p adj
b-a -2.000000 -5.734585  1.734585 0.3000234
c-a -4.666667 -8.401251 -0.932082 0.0201719
c-b -2.666667 -6.401251  1.067918 0.1514369

> #############################GR
```

```
> abund.ccGR=aov(GR_abun~treat,data=data.cdom)
> summary(abund.ccGR )
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 228.22 114.111  2.1219 0.2009
Residuals    6 322.67  53.778
> #TukeyHSD(abund.ccGR )
> rich.ccGR=aov(GR_rich~treat,data=data.cdom)
> summary(rich.ccGR )
            Df Sum Sq Mean Sq F value  Pr(>F)
treat        2 21.556 10.7778  6.4667 0.03183 *
Residuals    6 10.000  1.6667
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> TukeyHSD(rich.ccGR )
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = GR_rich ~ treat, data = data.cdom)

$treat
         diff        lwr        upr     p adj
b-a  2.666667 -0.5675786  5.9009119 0.0982743
c-a -1.000000 -4.2342452  2.2342452 0.6323720
c-b -3.666667 -6.9009119 -0.4324214 0.0304650

> abund.ddGR=aov(GR_abun~treat,data=data.ddom)
> summary(abund.ddGR )
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2  138.7   69.33  0.1249 0.8848
Residuals    6 3331.3  555.22
> #TukeyHSD(abund.ddGR )
> rich.ddGR=aov(GR_rich~treat,data=data.ddom)
> summary(rich.ddGR )
            Df  Sum Sq Mean Sq F value Pr(>F)
treat        2  0.6667 0.33333  0.1304 0.8801
Residuals    6 15.3333 2.55556
> #TukeyHSD(rich.ddGR )
> ##############################LP
> abund.ccLP=aov(LP_abun~treat,data=data.cdom)
> summary(abund.ccLP)
            Df Sum Sq Mean Sq F value  Pr(>F)
treat        2 480.67 240.333  8.5157 0.01768 *
Residuals    6 169.33  28.222
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> TukeyHSD(abund.ccLP)
  Tukey multiple comparisons of means
    95% family-wise confidence level
```

```
Fit: aov(formula = LP_abun ~ treat, data = data.cdom)

$treat
         diff       lwr       upr     p adj
b-a  15.6666667   2.357705 28.975628 0.0260505
c-a   0.3333333 -12.975628 13.642295 0.9967512
c-b -15.3333333 -28.642295 -2.024372 0.0285024

> rich.ccLP=aov(LP_rich~treat,data=data.cdom)
> summary(rich.ccLP)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2 46.222 23.1111  3.7818 0.08656 .
Residuals    6 36.667  6.1111
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> #TukeyHSD(rich.ccLP)
> abund.ddLP=aov(LP_abun~treat,data=data.ddom)
> summary(abund.ddLP)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2 2905.6 1452.78  4.1733 0.07315 .
Residuals    6 2088.7  348.11
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> #TukeyHSD(abund.ddLP)
> rich.ddLP=aov(LP_rich~treat,data=data.ddom)
> summary(rich.ddLP)
          Df Sum Sq Mean Sq F value Pr(>F)
treat       2 64.889  32.444  2.7547 0.1417
Residuals    6 70.667  11.778
> #TukeyHSD(rich.ddLP)
> ##############################WLP
> abund.ccWLP =aov(WLP_abun~treat,data=data.cdom)
> summary(abund.ccWLP)
          Df  Sum Sq Mean Sq F value   Pr(>F)
treat       2 250.889 125.444  16.851 0.003452 **
Residuals    6  44.667   7.444
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ccWLP)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = WLP_abun ~ treat, data = data.cdom)

$treat
        diff       lwr       upr     p adj
b-a -11.66667 -18.502079 -4.831254 0.0046737
```

```
c-a -10.66667 -17.502079 -3.831254 0.0072567
c-b   1.00000  -5.835412  7.835412 0.8967099

> rich.ccWLP=aov(WLP_rich~treat,data=data.cdom)
> summary(rich.ccWLP)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2      0  0.0000       0      1
Residuals    6     10  1.6667
> #TukeyHSD(rich.ccWLP)
> abund.ddWLP=aov(WLP_abun~treat,data=data.ddom)
> summary(abund.ddWLP)
            Df Sum Sq Mean Sq F value  Pr(>F)
treat        2    182  91.000  6.3488 0.03304 *
Residuals    6     86  14.333
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ddWLP)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = WLP_abun ~ treat, data = data.ddom)

$treat
    diff        lwr        upr     p adj
b-a  -10 -19.484669 -0.5153312 0.0407842
c-a   -9 -18.484669  0.4846688 0.0607223
c-b    1  -8.484669 10.4846688 0.9444684

> rich.ddWLP=aov(WLP_rich~treat,data=data.ddom)
> summary(rich.ddWLP)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 2.6667  1.3333  1.0909 0.3944
Residuals    6 7.3333  1.2222
> #TukeyHSD(rich.ddWLP)
> ########################################WP
> abund.ccWP =aov(WP_abun~treat,data=data.cdom)
> summary(abund.ccWP)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 957.56  478.78  3.2181 0.1123
Residuals    6 892.67  148.78
> #TukeyHSD(abund.ccWP)
> rich.ccWP=aov(WP_rich~treat,data=data.cdom)
> summary(rich.ccWP)
            Df Sum Sq Mean Sq F value Pr(>F)
treat        2 24.222 12.1111  3.2059  0.113
Residuals    6 22.667  3.7778
> #TukeyHSD(rich.ccWP)
> abund.ddWP=aov(WP_abun~treat,data=data.ddom)
```

```
> summary(abund.ddWP)
          Df Sum Sq Mean Sq F value  Pr(>F)
treat       2   7322  3661.0   4.794 0.05703 .
Residuals    6   4582   763.7
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(abund.ddWP)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = WP_abun ~ treat, data = data.ddom)

$treat
    diff        lwr       upr     p adj
b-a  -61 -130.23098  8.230981 0.0788435
c-a  -60 -129.23098  9.230981 0.0833897
c-b    1  -68.23098 70.230981 0.9989179

> rich.ddWP=aov(WP_rich~treat,data=data.ddom)
> summary(rich.ddWP)
          Df Sum Sq Mean Sq F value Pr(>F)
treat       2 32.889 16.4444  7.7895 0.0215 *
Residuals    6 12.667  2.1111
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> TukeyHSD(rich.ddWP)
  Tukey multiple comparisons of means
    95% family-wise confidence level

Fit: aov(formula = WP_rich ~ treat, data = data.ddom)

$treat
         diff       lwr        upr     p adj
b-a -2.666667 -6.306690  0.9733562 0.1408342
c-a -4.666667 -8.306690 -1.0266438 0.0180261
c-b -2.000000 -5.640023  1.6400229 0.2849420
```

# Chapter 3: Does green tree retention 'life-boat' moths through post-harvest forest recovery in the extensively managed boreal mixedwoods?

## 3.1 Introduction

Forest canopies are among the most species rich of terrestrial habitats, an assertion supported by decades of arthropod research in the tropics (Stork, 1988; Erwin, 1982; Basset *et al*., 2003c). Despite a growing appreciation of the importance of forest canopies for the maintenance of arthropod biodiversity, the bulk of canopy research has been concentrated in the tropics, and only recently extended to European (see Floren and Schimdl, 2008 and references therein) and North American temperate forests (Wagner, *et al*., 1995; Winchester and Ring, 1996; Summerville *et al*., 2003; Buddle *et al*., 2000). We have very little understanding of the diversity, structure and community composition of arthropods in the boreal canopies, e.g., studies about canopy lepidopterans have mainly been focused on population dynamics of economically important species (Summerville and Crist, 2008). Notwithstanding the lack of information about potential biodiversity impacts, large-scale harvesting activities driven by market demands continue to alter the structure of boreal canopies, and the ecosystems to which they contribute.

Traditional forest harvesting techniques such as clear-cut logging have been linked to loss of biodiversity (Niemelä, 1997; Monkkonen, 1999; Lindenmayer and Franklin, 2002). In order to avert these loses and to balance between ecological and economical aspects of forestry, new silvicultural practices that are modeled after natural disturbance dynamics are being adopted (Franklin *et al*., 1997). In the boreal mixedwoods of northwestern Alberta green tree retention (GTR) is being applied as an alternative to clear-cut logging. Most of what we know about the ecological impacts of retention harvest on forest arthropods has come from ground-level research, mainly on epigaeic arthropods (Monkkonen and Mutanen, 2003; Work *et al*., 2004; Rosenvald and Lõhmus, 2008) and saproxylic beetles (Jacobs *et al*., 2007). It has been argued, for example, that retention trees act as 'life-boats' for saproxylic species and their associated biological communities by providing a supply of dead wood habitat through the regeneration cycle (Rosenvald and Lõhmus, 2008). Nonetheless, the functional connection between this new approach and the abundance and composition of canopy arthropods, especially the phytophagous species, remains unclear.

In forested ecosystems, the greatest diversity of phytophagous assemblages is concentrated in the order Lepidoptera (Ober and Hayes, 2010). Given their trophic roles as herbivores, detritivores and prey items for predatory species, the activities of lepidopteran caterpillars are integral to ecosystem function and forest health (Scoble, 1992). Some moth species are significant pests and drivers of forest regeneration (Volney and Mallett, 1998). A majority of lepidopteran species are characterized by seasonal and temporal dynamics in which different larval and adult stages migrate between the canopy and understory strata for feeding, pupation, mating or finding refuge in enemy free spaces (Basset *et al*., 2003a). Thus, understanding interactions between the canopy and understory in structuring insect herbivores is crucial for designing management practices that maintain their diversity on managed boreal landscapes.

Most studies of moth diversity, including those about vertical stratification, have employed light traps as the main sampling technique, mainly due to the high abundance and species diversity associated with trap catches (Schulze *et al*., 2001; Hacker *et al*., 2008; Bolz *et al*., 2008). Nonetheless, light trap samples are biased towards sampling moth species that are attracted to light and the resulting data do not support conclusions about specific species-habitat associations. Sampling caterpillars directly, on the other hand, though not likely to yield large numbers of species, may provide critical information about lepidopteran natural history by directly linking specific moth species to their host plants or to the habitats from which they were sampled (Wagner and Wagner, 2005).

To provide a view different from light trap samples and to assess the role played by retention trees in maintaining boreal moths, I collected, reared and compared caterpillar assemblages from stands of trembling aspen (*Populus tremuloides* Michx.) and white spruce [*Picea glauca* (Moench)] in the boreal mixedwoods of northwestern Alberta. I sought to: 1) compare caterpillar assemblages between the two dominant overstory tree species, 2) compare caterpillar assemblages among trees in retention and unharvested stands and 3) compare over- and understory caterpillar assemblages within coniferous dominated stands in the managed boreal mixedwoods.

## 3.2 Materials and Methods

### 3.2.1 Study site

This research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site located in the boreal region of northwestern Alberta, approximately 90 km northwest of Peace River (56˚ 44'N, 118˚ 20'W). EMEND was established in 1997 with the aim of testing hypotheses about the impacts of variable retention on boreal forest structure and function (Spence *et al*., 1999; Work *et al*., 2003). Harvesting treatments employing a range of retention levels were randomly applied to ~10-ha compartments within each of the distinct forest cover-types along the successional gradient of the boreal mixedwoods (Rowe, 1971).

Two cover-types; coniferous dominated (CDOM) and deciduous dominated (DDOM), and two harvest retention treatments; 20% retention and the unharvested controls (100% retention) were chosen for this study. The two cover-types, respectively, represent early and late successional stages of the boreal mixedwoods in this area (Lieffers *et al*., 2008). The deciduous composition of DDOM stands varies but mainly consisted of ≈ 50% balsam poplar (*Populus balsamifera* L.), 40% trembling aspen (*Populus tremuloides* Michx.), and 10% paper birch (*Betula papyrifera* Marsh.) with a small proportion of conifers, mainly white spruce [*Picea glauca* (Moench)]. The understory structure of this cover-type is dense, consisting mainly alder (*Alnus crsipa* (Ait.) Pursh), willow (*Salix spp.*), low-bush cranberry [*Viburnum edule* (Michx.)], prickly rose (*Rosa acicularis* Lindl.) and buffalo-berry [*Shepherdia canadensis* (L.) Nutt.], all in relatively equal abundances (Kishchuk *et al*., 2004; Macdonald and Fenniak, 2007). CDOM stands, on the other hand, are primarily white spruce but some blocks have significant amounts of black spruce [*Picea mariana* (Mill.)] with a less dense and more heterogeneous understory composition of mainly low-bush cranberry, prickly rose and feather mosses [*Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Bird.) Mitt., and *Ptilium crista-castrensis* (Hedw.) DeNot, Caners 2010].

To achieve 20% retention, which is within the range of industrially feasible levels of harvesting, 5m wide strips that were 15m apart were harvested using feller-buncher machines. Harvests were deployed in the compartments studied here in 1999, by systematically cutting stems (DBH > 5cm) from the vegetation strips between machine corridors at the ratio of 3:1 in the order at which trees, regardless of species, were encountered by machine operators.

### 3.2.2 Sampling caterpillars

In 2007 (10-22 June), caterpillars were sampled from 12 compartments, including three replicates each of unharvested and 20% retention treatments from both DDOM and CDOM cover-types. Two trees of the dominant tree species, trembling aspen (*Populus tremuloides*) in DDOM and white spruce (*Picea glauca*) in CDOM stands, were selected for sampling in each compartment. Each tree was felled onto a large tarp spread out the ground. The tree was then thoroughly searched for caterpillars (macro and micro-moth species) by a team of 8-10 people per tree. Additional variables including tree height, crown height (the length from the first branch near the ground to the crown of the tree) and diameter at breast height (DBH) were measured and recorded (Table 1). Percent crown cover above each tree selected for sampling was estimated using a standard convex densiometer (Lemmon, 1956).

In 2008 (11-21 June), I sampled caterpillars from both spruce canopies and understory shrub layer from 3 replicates of unharvested conifer compartments. First, understory caterpillars were collected by beating throughout a circular plot (5m radius) around each tree selected for sampling in each stand. Canopy caterpillars were collected by climbing and clipping tree branches at different heights from the same trees in each stand. Branches were dropped onto a large tarp spread out on the ground and were subsequently searched for caterpillars by a team of 4 people. In addition, tree variables (height, crown height and DBH) and % canopy cover were estimated, as in 2007, and all woody plants (DBH < 5cm) and shrubs within the circular plots from which understory caterpillars were counted and identified to species (Table 1).

Caterpillars collected in both years were sorted and grouped into morpho-species based on relevant literature (Ives and Wong, 1988; Wagner and Wagner, 2005; Duncan, 2006). Individuals were then reared in small plastic cups singly or in groups of 2-4 individuals. They were fed with young fresh foliage of the host from which they were collected that was obtained from or in close proximity to the sampled stands. Adult moths that emerged after rearing and images of caterpillars that either died before pupation or whose adults failed to emerge were later identified to species based on relevant literature and identification guides (Hodges, 1983; Miller, 1996; Miller and Hammond, 2000; 2003) or online resources available through the E. H. Strickland Entomological Museum and The Moths of Canada. Identifications were checked against reference collections at the University of Alberta (E. H. Strickland Entomological Museum) and the Northern Forestry Centre of the Canadian Forest Service located in Edmonton, AB. Identifications were further confirmed and difficult specimens identified with the help of Jason Dombroskie (moth specialist, Alberta Lepidopterist Guild, Edmonton, AB). Reference collections containing voucher specimens for this study have been deposited at the Northern Forestry Centre.

### 3.2.3 Data analysis

As with most canopy studies, caterpillar samples in this study were a snap-shot in time (Basset *et al*., 2003b), and therefore, most of the species actually present in the compartments may be under-represented or entirely absent from the sample. As well, the distribution of species frequencies was very much skewed towards a few dominant pest species. In order to exclude the influence of these dominant species, only presence-absence data were used in the community level analysis. Comparisons between the under- and over-story caterpillar assemblages were also based on presence-absence data to minimize the effects of differences in sampling the two strata.

The assemblage pattern of arboreal caterpillars was analyzed using non-metric multidimensional scaling (NMS) ordination in the PC-Ord statistical package Version 5 (McCune *et al*., 2002). The goal of this analysis is to compress the information in a data set into a final plot with minimum dimensionality (number of axes) while at the same time minimizing stress (influence of noise). The NMS software iteratively selects the best solution, which maximizes the correspondence between actual community dissimilarities and distances in the ordination space. Ordinations were performed on Bray-Curtis dissimilarity because it is sensitive to heterogeneous data sets and it gives less weight to outliers (McCune *et al*., 2002).

To statistically evaluate the multivariate response of caterpillar assemblages to harvesting treatments and forest cover-types, I used permutational multivariate analysis of variance (PerMANOVA, (Anderson, 2001; 2005). The model used was similar to a typical two-way analysis of variance that partitioned the variance due to forest cover-type, harvesting treatment and the residual. Two levels of treatment effects (20% harvested and unharvested controls) and two levels of cover-type (CDOM and DDOM) with three replicates were analyzed in a single model. The PerMANOVA technique is most appropriate for determining multivariate responses of non-independent variables such as an assemblage of species in a given sample (Anderson, 2001) based on any dissimilarity index. The PerMANOVA program (Anderson, 2005) with Bray-Curtis dissimilarity for this analysis. Due to the small sample size, 9999 unrestricted permutations of presence-absence data were performed for the PerMANOVA tests and Monte-Carlo *p-values* were used to interpret significant differences ($\alpha<0.05$).

### ***Responses to environmental variables***

I used classification and regression trees (CART; herein referred to as regression trees, (De'ath and Fabricius, 2000) to relate the overall abundance and species richness of caterpillar assemblages to the environmental variables (tree height, crown height, DBH and % crown cover) measured at each site. This analysis was restricted to the 2007 dataset in which sampling included the 20% residual and the unharvested control compartments. As such, larval responses to the environmental variables measured could be explored in light of retention harvest.

Regression tree analysis is a non-parametric procedure that is best suited for the analysis of complex ecological data with multiple interactions. This analysis can incorporate nominal, ordinal and continuous data, and is robust to non-linearity, heteroscedasticity, and multicollinearity in the data (De’ath and Fabricius, 2000). For this analysis, I used log-transformed abundance data and species richness in each sample as numerical input. Regression trees were then constructed by splitting the data into more homogenous groups based on four numerical exploratory variables: tree height, crown height, DBH and % crown cover. The optimal tree size was then determined using the recommended 10-fold cross validation of errors and “1-SE rule” (De’ath and Fabricius, 2000). This analysis was implemented using the ‘rpart’ package in R-Software 2.1.11 (R Development Core Team). Because all but one (% crown cover) of the explored variables were related to individual tree characteristics, the role of individual tree attributes in maintaining arboreal caterpillars could be determined.

## 3.3 Results

### 3.3.1 Caterpillar assemblages among cover-types and harvesting treatments

***Larval abundance:***

In total, 3,648 individual caterpillars and 46 species were collected and reared from white spruce and trembling aspen of unharvested and 20% retention compartments in 2007 (Appendix 3.1). Only 31.8% of the reared caterpillars emerged as adults; 48.8% remained as pupae, presumably requiring diapause before emergence. The remaining caterpillars (c. 20%) died of parasitism (15.5%) or unknown causes (6.8%).

Caterpillar samples were dominated by species with known outbreak potential. The most dominant species, *Operophtera bruceata* (Geometridae), which constituted over 67% of the total caterpillar abundance, is a common out-breaking species in deciduous dominated forests. The next most abundant species were potential pests of spruce trees, *Zeiraphera canadensis* and *Z. unfortunana* (Tortricidae) both of which constituted, respectively, 15.8% and 6.3% of the total caterpillar sample. Only three of the remaining 43 species contributed > 1% of the sample. These included two species collected from spruce trees: *Acleris variana* (1.3%) and *Coleotechnites blastovora* (1.5%) and one species, *Epinotia nisella* (2.5%), collected from aspen trees.

The number of caterpillars observed varied greatly between the two tree species, as well as among individual trees of the same species. Overall, larger numbers of caterpillars were collected from trembling aspen (71.6% of the sample abundance) compared to only 28.4% individuals collected from white spruce compartments (Figure 3.1A). Likewise, more caterpillars were collected on single trees in unharvested than in 20% retention compartments of both forest types. This difference was much more pronounced among trembling aspen, with trees sampled from retention compartments accounting for only a third of the overall abundance in that cover-type.

***Species richness:***

Of the 46 caterpillar species present in the sample, 23 were encountered on aspen and 30 on spruce trees. Three species collected from white spruce could not be classified as spruce feeders. They included two well known deciduous feeders: *Enargia decolor* (2 specimens) and *O. bruceata* (1 specimen), also present on aspen trees; their occurrences on spruce were excluded from further analyses (see Table 3.1). The third is the larvae of *Gnophaela vermiculata* which were observed ascending and afterwards collected from the top most tips of white spruce trees. None of the 21 individuals, which successfully pupated and emerged as adults, were observed feeding on spruce; larvae of this species are only known to feed on lung-wart (*Mertensia paniculata*). Likewise larvae of *Eupethecia spp.* and *Orygia sp.* were collected on both aspen and spruce trees; they could not be classified as aspen feeders and were therefore excluded from further analysis for this host tree species. Lepidopteran larvae that feed on both conifer and deciduous trees are rare; no caterpillar species were confirmed to be feeding on both host tree species in this study.

More caterpillar species were collected on white spruce (mean species richness = 13.7 ± 5.1) and aspen (12.0 ± 1.3) trees sampled from unharvested compartments compared to the 20% retention treatments of both cover-types (11.0 ± 1.0 and 7.0 ± 3.6 respectively, Figure 3.1B). Generally, caterpillar species sampled from aspen trees were absent or collected in lower abundances in the compartments harvested to 20% retention (Appendix 3.1).

### ***Community composition:***

Caterpillar assemblages found on white spruce and trembling aspen differed significantly. On one hand, spruce canopies were dominated by two tortricids in the genus *Zeiraphera, Z. canadensis* and *Z. unfortunana*, and these accounted for

75.98 % of the total number of caterpillars collected on spruce. On the other hand, *O. bruceata* accounted for >90% of all lepidopteran larvae sampled from aspen trees. Caterpillars of macro-moth species sampled from white spruce were mostly conifer-specialists while those collected from trembling aspen were mainly polyphagous feeders on deciduous trees and woody plants.

PerMANOVA revealed significant differences in larval assemblages based on cover-type (F = 26.2, df $_{1,11}$ P = 0.0001). However, no statistical differences could be demonstrated between assemblages of unharvested and 20% retention compartments of either cover-type (F = 0.69, df $_{1,11}$ P = 0.50). Caterpillar assemblages' response to cover-type and harvest treatments as visualized in a two-dimentional NMS ordination with a final stress of 9.2 (Figure 3.2) paint a picture slightly different from the PerMANOVA results. Assemblages from each of the four treatment combinations grouped distinctly.

Notably, assemblages from control compartments of both cover-types are separated from each other on Axis 1. Likewise, the 20% retention assemblages group are separated from their unharvested control counterparts along Axis 2, with assemblages from harvested aspen compartments grouping out the furthest from their control compartments. Interestingly, assemblages from the harvested compartments, although clustered in two separate groups, appeared to be much closer to each other than they were to the control compartments of their pre-harvest cover-type. This ordination result suggests a harvesting impact that could not be statistically verified in the PerMANOVA model described above; an observation attributed to within stand variation in the abundance, richness and composition of lepidopteran species inhabiting the canopy trees.

### 3.3.2 Caterpillar assemblages within stands

The local variation observed in both the number of individual caterpillars and species richness (Figure 3.1) warranted further analysis with respect to the role of individual tree traits (tree height, crown height and DBH) and habitat quality (measured as % crown cover, Table 3.1) in structuring caterpillar assemblages. Classification and regression tree analyses revealed that arboreal caterpillar abundance was most influenced by the % crown cover around each tree sampled in addition to (DBH) and tree height on spruce and aspen trees, respectively (Figure 3.3 and 3.4). Tree attributes of DBH and height also influenced the species richness of arboreal caterpillars on white spruce trees, while crown cover % alone most strongly influenced variations in caterpillar richness among aspen trees (Figure 3.5 and 3.6).

The most parsimonious regression tree based on the total number of caterpillars collected on white spruce had two splits with 3 terminal nodes. The first spilt separated the variation in caterpillar abundance according to % crown cover (<84.79≥ %), with the second split separating larger trees from smaller ones (DBH <30.85≥ inches). Taken together these two splits explained 86 % of the variance in larval abundance (Figure 3.3). Larval abundance was the highest on 2 spruce trees with a DBH < 30 inches, both of which were embedded in crown cover ≥ 84.79%. These two trees were sampled from the control compartments of the coniferous dominated cover-type.

As in white spruce, a 3-split regression tree indicated that % crown cover, with tree height, other than DBH, were the best predictors of variation in larval abundance on trembling aspen. The first split, separated the variation in larval abundances according to % crown cover (<53.59≥ %), and explained 39 % of the variation in larval abundance (Figure 3.4). Together, the two variables of % crown cover and tree height explained up to 56 % of the total variance in caterpillar abundance on trembling aspen. The highest number of caterpillars was collected on 3 trees, all of which were taller than 22.8m and were associated with crown cover ≥ 53.59 %. All 3 trees were sampled from the unharvested control compartments.

Tree attributes of DBH and height were also important in explaining variations in species richness on white spruce (Figure 3.5). The lowest number of species on this tree species was found on a single tree (DBH < 22.5 inch), which separated out from all others at the first split. This split explained 54 % of the total variance explained by the regression. Interestingly, this tree was sampled from an unharvested control stand. The second split, which accounted for only 16% of the total variance in larval species richness, separated shorter trees from taller ones (<22.35≥ m); 6 of the taller trees recorded the highest number of species.

Crown cover (%) alone most strongly influenced the species richness of caterpillars collected on trembling aspen, and explained 57 % of the total variance in the regression (Figure 3.6). The highest number of species were recorded on 7 trees which were surrounded by a crown cover ≥ 66.33 %; all, but one, of these trees were sampled from unharvested control compartments of this cover-type. This is in comparison to only an average of 3.6 species collected on the remaining 5 trees in the 20% retention compartments.

### 3.3.3 Caterpillar assemblages among forest layers

A total of 33 species representing 1378 individuals were collected from white spruce and 8 understory plant species of unharvested coniferous compartments in 2008. Assemblages of caterpillars inhabiting the overstory differed significantly (PerMANOVA: F = 10.5, df $_{1,5}$ P = 0.01) from those found on understory plant species. This result is visualized in a 3-dimensional NMS ordination with a final stress of 8.00. This ordination shows a clear separation between the canopy and understory larval assemblages (Figure 3.7). These differences between assemblages of the two forest strata were driven by micro lepidopterans of the family Torticidae, including mainly the genera *Zeiraphera*, *Acleris* and *Epinotia,* and the gelechiid species, *Coleotechnites blastovora*. *C. blastovora* dominated the overstory larval community, while the understory samples were dominated by macro-lepidopterans of the families Geometridae, Noctuidae and Arctiidae. Only one micromoth species, *Clepsis persicana,* was sampled and successfully reared from both the white spruce needles as well as the understory shrub species, *Alnus crispus*.

## 3.4 Discussion

### 3.4.1 Patterns of larval abundance and richness among tree species and forest layers

There were differences in the overall number of caterpillar species feeding on trembling aspen and white spruce. The two host trees also harbored highly distinct larval assemblages. Although host specialization in temperate and boreal forests is now believed to be lower than previously thought (Summerville *et al.*, 2003; Ober and Hayes, 2010), caterpillars that include both conifers and broad leaved plants in their larval host-plant range are rare, perhaps a reflection of the differences in basic leaf chemistry between the two host species (Young, 1997). A progressive approach to forest harvesting should therefore attempt to preserve the distinct associations between the biota and the canopy tree species that characterize the different cover-types of the boreal mixedwoods.

Like Summerville *et al.*, (2003) I found that larval abundance and richness greatly varied between trees of the same species, a finding that was attributed to within stand variation in tree traits (mainly DBH and height) as well as the stand structure and quality (measured as % crown cover). Species turnover is likely a function of rare species, rather than resource abundance (Summerville *et al.*, 2003), with common species exhibiting a high intra-specific aggregation while rare species occur on very few host trees as single dispersed individuals, a pattern that was evident in the present study.

Retention harvest should therefore help to maintain moth richness within harvested stands if retained trees are within the range of the variation expected in unharvested stands. Additionally, the spatial distribution of retained trees is important as trees that were within a % crown cover ≥ 50% harbored more caterpillars than trees in isolation (% crown cover ≤ 20%). This is important as it is likely to allow dispersal and therefore maintenance (life-boating) of rare and sparsely distributed species through the regeneration cylce.

Caterpillar abundance, composition and dominance patterns differed markedly between the canopy and the understory layers, a result consistent with observations made for caterpillars and other arthropods in forested habitats (Wagner *et al*., 1995; Shaw, 2004; Schowalter and Zhang, 2005; Larrivee and Buddle, 2009; Sobek *et al*., 2009). Only larvae of one generalist moth species, *Clepsis persicana* (Robinson, 2002), were successfully reared on spruce foliage as well as on a broad-leafed understory shrub, *Alnus crispus*. The dominance of a few potential out-breaking species on the canopy trees in the present study is consistent with the moth community structure observed in forest canopies in northwestern North America (Summerville and Crist, 2008). This pattern is to be expected in the single-species dominated canopies of the boreal mixedwoods; in which larval densities will tend to concentrate on a few dominant species coupled with a decrease in overall species diversity (Root, 1973).

Compared to canopy trees, understory plant communities may in fact contribute the most to the boreal plant biodiversity (Legare *et al*., 2002). The understory plant community under coniferous stands at EMEND are species rich but the vegetation is sparsely distributed (Chavez and Macdonald, 2010), explaining, in part, why a handful of individual caterpillars collected from the understory plants contained relatively large number of species (~50% of the total sample) compared with the overstory layer of this cover-type.

Determinants of patterns of caterpillar assemblages have scarcely been studied, but Ober and Hayes (2010) showed that understory plant richness drives species turnover of adult moths in coniferous dominated forests, a pattern that is also likely to be manifested by larval communities. In addition the extreme micro-climatic conditions associated with forest canopies (Ozanne *et al*., 2003) may favor smaller defoliators and internal feeders (e.g., most micro-moth species), but deter the much larger external feeders that constitute the macro-lepidopteran community. A comprehensive retention harvest strategy, therefore, should seek to preserve both the over-story trees and the understory plant community in order to conserve the distinct lepidopteran fauna inhabiting the two forest layers.

### 3.4.2 Retention trees as important habitats for moths in harvested compartments

Although more individual caterpillars and species were collected on trees sampled from unharvested than harvested compartments, these differences were not significant. Species that were commonly sampled were represented in the canopies of both unharvested and harvested compartments. Thus, retention harvest may help to maintain populations of larval communities following disturbance, thus life-boating moth species that would not persist in clear cuts through the regeneration cycle. However, whether species persist on retained trees in logged sites will depend on the feeding preferences and habitat requirements of the different species. For example, larvae that feed on or inhabit the canopy are likely to benefit the most from retention harvest. These include macro-moth species sampled from white spruce, which are well known conifer specialists that also tend to be sparsely distributed on boreal landscapes (Morneau, 2002; Pohl, 2004). Given that there are fewer species adapted to feeding on conifers than on deciduous broad-leaved trees (Young, 1997) retention harvest that allows the persistence of a considerable proportion of the coniferous canopy trees will help to maintain these moth specialists on the boreal landscapes. This is especially important because early successional stands tend to regenerate as deciduous irrespective of the pre-harvest cover-type.

Still, there are lepidopteran species that, though not feeding directly on canopy trees, depend on habitats closely associated with mature trees present in old-growth forests. For example, *Eilema bicolor* (Grt.), which feeds on lichens, was collected on the canopy of both harvested and unharvested white spruce compartments. Moth species belonging to this feeding guild are also rare on the landscape (Pohl, 2004), and retention harvest will help to maintain their presence on harvested landscapes. Indeed, retention harvests of 30% and 70% have been found to maintain a similar loading and richness of most lichen groups found in unharvested controls (Coxson and Stevenson, 2005), but low retention levels of a few scattered trees (an average of 20 live trees ha$^{-1}$) were detrimental, especially to the vitality of epiphytic species on harvested stands (Lõhmus *et al*., 2006).

Some species of lepidopterans have larvae that feed on both the canopy and the understory layers during different larval instars. For instance, 1st instar larvae of *C. persicana* feeds in the understory layer while the late in-star ascends to complete feeding on a wide range of canopy foliage, including conifers, before pupating under tree bark. This species, originally thought to feed only on *A. crispus* in Alberta (Greg Phol, personal communication), has been previously reared on conifers in other forest types (Robinson, 2002; Duncan, 2006), and in fact was successfully reared on both white spruce needles and *A. crispus* in this study. This observation supports the idea of retaining trees on harvested blocks in order to provide habitat requirements for species whose larvae feed from both the canopy and the understory forest layers.

Different life-stages of moths may require different micro-climatic conditions as well as host plant species (Young, 1997). The canopy and understory layers complement each other in providing the diversity of habitats for moth populations. This study presents, for the first time, observations on the pupation habitats for at least two boreal species: 1) the last instar larvae of *G. vermiculata* was observed migrating vertically and later collected at the top-most tips of white spruce trees and 2) the larvae of *Virbia ferruginosa* (Wlk.), which feeds on low plants, were encountered and later observed to pupate on white spruce trees. The larvae of *G. vermiculata* feed on *Mertensia paniculata* while the adults mostly forage on the flowers of golden rod (*Solidago spp*., Miller, 1996), but also on other plants, e.g., cow parsnip (*Heracleum maximum*). Similarly, *V. ferruginosa* larvae feed on low herbaceous plants possibly associated with coniferous canopies and its presence on the canopy points to this forest layer as its preferred pupation habitat. Retention harvest, by preserving some form of the vertical structure on harvested landscape, therefore provides diverse habitats for species that move up or down the canopy during various life stages.

While leaving live trees on harvested landscapes may preserve habitats for species that use the canopy at certain life-stages, the detrimental effects of harvesting on herbaceous plants used by these same species during other life-stages may compromise any biodiversity management gains obtained from retention harvest. For instance, Intense harvesting has been shown to reduce the density of *Mertensia paniculata*, the host-plant of *G. vermiculata* larvae, and in fact, only retentions of at least 75% will apparently preserve this understory plant species (Craig and Macdonald, 2009). Not surprisingly, all the 21 specimens of *G. vermiculata* larvae were only encountered on trees sampled from the unharvested compartments.

Because larval assemblages are generally patchy in their distribution, with many species being rare even on un-disturbed forested landscapes (Summerville and Crist, 2003; Summerville *et al*., 2008), higher levels of retention may be required in order to maintain populations of lepidopteran species whose understory host-plants are greatly impacted by low retention harvest (e.g., see Atlegrim, 1996). Canopy reduction at low retention levels most likely significantly alters availability of food resources, micro-environment conditions as well as oviposition and enemy free habitats found in the understory forest layer.

Besides the forest cover-type and the level of retention harvesting, tree physical attributes of height and DBH, also clearly influenced the structure of caterpillar assemblages. Thus, the success of green tree retention in maintaining moth diversity will depend on the extent with which retained trees represent the structural heterogeneity (e.g., DBH, height, age and health) of unharvested compartments. The high number and richness of caterpillars species encountered on larger but shorter white spruce trees, for example, indicate that larval populations are more likely to thrive on trees located below the canopy. Tree height and DBH are indicators of a tree’s age, thus older trees that are better chemically defended against herbivore attacks either due to chemical concentration or repeated attacks (Herms and Mattson, 1992) may experience low herbivore loads. Similarly, larger and older trees undergoing senescence are less well defended while trees that are already attacked by wood boring insects are not preferred by herbivorous species as indicated by the absence of caterpillars on one of the white spruce trees sampled from a control white spruce stand in 2008. This tree was later discovered to be infested with bark boring beetles.

Whether larval populations persist on harvested blocks long enough through regeneration will depend on the rate of blow-downs within these retention compartments, as low retention harvests are likely to experience the greatest amount of blow-down over time. As well the rate at which the forest regenerates back to a white spruce dominated stand will determine how long conifer specialists will persist on harvested boreal landscapes. Solarik *et al*., (2010) showed that spruce regeneration after harvesting depended on the density of retained trees and the availability of seed trees on harvested blocks.

## 3.5 Conclusion

This study provides baseline information on the natural variation and structure of arboreal and understory caterpillar assemblages of the boreal mixedwoods. As demonstrated here, and elsewhere (Young, 1997), habitat requirements for lepidopterans greatly differ among species as well as between different developmental stages of the same species, yet many of these requirements remain unknown for a majority of boreal lepidopterans. Green tree retention at the level studied here may help to preserve the vertical structure of the forest canopy and the varieties of habitats associated with them. This is especially critical for lepidopteran species that depend on conifers as post-harvest early regeneration stands in the boreal mixedwoods are typically deciduous dominated. The success of retention harvest in maintaining and promoting the recovery of moth communities on harvested landscapes will therefore depend on the extent with which retained trees represent the structural and compositional heterogeneity of the pre-harvest forest cover. The life-span of retained trees is also crucial in facilitating the persistence of arboreal caterpillar assemblages, as the number of downed trees is likely to increase with decreasing levels of retention.

Conserving some phytophagous lepidopterans, e.g., those that feed on understory plants that are adversely affected by low retention harvest, on harvested landscapes will likely require higher retentions that preserve the understory plant species utilized by caterpillar species. The design of any retention harvesting regime should therefore seek to maintain a wide range of vertical and horizontal habitat variations, in the long-term, to act as a ‘life-boat’ for lepidopterans on harvested landscapes.

## References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26(1): 32-46.

Anderson, M.J., 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance, version 1. Department of Statistics, University of Auckland, New Zealand.

Atlegrim, O., Sjoberg, K., 1996. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management,* 87(1-3): 139-148.

Basset, Y., Hammond, P.A., Barrios, H., Holloway, J.D., Miller, S.E., 2003a. Vertical stratification of arthropod assemblages. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., Novotny, V., Miller, S.E., Kitching, R.L., 2003 (Eds). Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, UK., pp. 17-27.

Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., 2003b. Methodological advances and limitations in canopy entomology. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., Novotny, V., Miller, S.E., Kitching, R.L., 2003 (Eds). Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, UK., pp. 7-16.

Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., 2003c. Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, UK., pp. 474.

Bolz, R., Floren, A., Schmidl, J., 2008. Diversity of moth communities (Insecta: Lepidoptera) in differently-structured oak-hornbeam forests: A comparison of different phases of succession in coppice with standards and forests with high standard trees. In: Floren, A., Schmidl, J., 2008(Eds). Canopy arthropod research in Europe: Basic and applied studies from the high frontier. Nuremberg, Germany, pp. 427-443.

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

Caners, R.T., 2010. Conservation and ecology of bryophytes in partially harvested boreal mixed-wood forests of west-central Canada. PhD Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

(CBIF) Canadian Biodiversity Information Facility (2003). The moths of Canada. http://www.cbif.gc.ca/spp_pages/misc_moths/phps/mothindex_e.php [accessed 2006-2008].

Chavez, V., Macdonald, S.E., 2010. Understory species interactions in mature boreal understory plant communities. *Botany*, 88(10): 912-922.

Coxson, D.S., Stevenson, S.K., 2005. Retention of canopy lichens after partial-cut harvesting in wet-belt interior cedar–hemlock forests, British Columbia, Canada. *Forest Ecology and Management,* 204(1): 99-114.

Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Forest Ecology and Management,* 258(12): 2619-2627..

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, 81(11): 3178-3192.

Duncan, R.W. 2006. Conifer defoliators of British Columbia. Natural Resource Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, pp. 359.

Erwin, T.L. 1982. Tropical forests their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin,* 36(1): 74-75.

Floren, A., Schmidl, J., 2008. Canopy arthropod research in Europe: Basic and applied studies from the high frontier. Nuremberg, Germany. pp. 576.

Franklin, J.F., Rae Berg, D., Thornburgh, D.A., Trappeiner, J.C., 1997. Alternate silvicultural approaches to timber harvesting: Variable retention harvest systems. In: Franklin, J.F., Kohm, K.A., (Eds.). Creating a forest for 21st century: The science of ecosystem management. Island Press, Washington, D.C., pp. 111-139.

Hacker, H., Mueller, J., Floren, A., Schmidl, J., 2008. Stratification of 'macrolepidoptera' (Insecta) in northern Bavarian forest stands dominated by different tree species. In Floren, A., Schmidl, J., 2008 (Eds). Canopy arthropod research in Europe: Basic and applied studies from the high frontier. Nuremberg, Germany. pp. 355-382.

Herms, D., Mattson, W., 1992. The dilemma of plants - to grow or defend. *Quarterly Review Of Biology,* 6(3):, 283-335.

Hodges, R.W., 1983. Check list of the Lepidoptera of America North of Mexico, including Greenland. In: E.W. Classey and the Wedge Entomological Research Foundation, London, pp. 284.

Ives, W.G.H., Wong, H.R., 1988. Tree and shrub insects of the Prairie Provinces. Natural Resource Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, AB. NOR-X-292, pp. 327.

Jacobs, J.M., Spence, J.R., Langor, D.W., 2007. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. *Canadian Journal of Forest Research*, 37(9): 1631-1642.

Kishchuk B.E., Northern Forestry Centre, 2004. Soils of the ecosystem management emulating natural disturbance (EMEND) experimental area, northwestern Alberta. Northern Forestry Centre, Edmonton.

Larrivee, M., Buddle, C.M., 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. *Agricultural and Forest Entomology,* 11(2): 225-237.

Legare, S., Bergeron, Y., Pare, D., 2002. Influence of forest composition on understory cover in boreal mixedwood forests of western Quebec. *Silva Fennica,* 36: 353-366.

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science,* 2(4): 314-320.

Lieffers, V.J., Armstrong, G.W., Stadt, K.J. and Marenholtz, E. H. 2008. Forest regeneration standards: are they limiting management options for Alberta’s boreal mixedwoods? *Forestry Chronicle,* 84(1): 76-82.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving forest biodiversity: A comprehensive multiscaled approach. Island Press, Washington, DC., pp. 351.

Lõhmus, P., Rosenvald, R., Lõhmus, A., 2006. Effectiveness of solitary retention trees for conserving epiphytes: Differential short-term responses of bryophytes and lichens. *Canadian Journal of Forestry Research,* 36(5): 1319-1330.

Macdonald, S.E., Fenniak, T.E., 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. *Forest Ecology and Management,* 242(1): 34-48.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities, version 5, MjM Software Design, Oregon State University, Oregon.

Miller J.C., 1996. Caterpillars of pacific northwest forests and woodlands. National Center of Forest Health Management, U.S. Department of Agriculture, Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2000. Macromoths of northwest forests and woodlands. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2003. Lepidoptera of the Pacific Northwest: Caterpillars and adults. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Monkkonen, M., Mutanen, M., 2003. Occurrence of moths in boreal forest corridors. *Conservation Biology,* 17(2): 468-475.

Monkkonen, M., 1999. Managing Nordic boreal forest landscapes for biodiversity: Ecological and economic perspectives. *Biodiversity and Conservation,* 8(1): 85-99.

Morneau L., 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

Museums and Collections Services (2001–2008) University of Alberta, E.H. Strickland Entomological Museum, Virtual Museum. http://www.entomology.ualberta.ca/ [accessed 2006-2008]

Niemelä, J., 1997. Invertebrates and boreal forest management. *Conservation Biology,* 11(3): 601-610.

Ober, H.K., Hayes, J.P., 2010. Determinants of nocturnal lepidopteran diversity and community structure in a conifer-dominated forest. *Biodiversity and Conservation,* 19(3): 761-774.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Korner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Dias, P.L.S., Stork, N.E., Wright, S.J., Yoshimura, M., 2003. Biodiversity meets the atmosphere: A global view of forest canopies. *Science*, 301(5630): 183-186.

Pohl, G.R., Langor, D.W., Landry, J.F., Spence, J.R. 2004b. Lepidopteran from boreal mixedwood forest in east-central Alberta: Comparison of assemblages from a mature and an old stand. Natural Resource Canada, Canadian Forest Service. Northern Forest Centre, Edmonton, AB. inf. ref. NOR-X-396: 1-20.

Powell, J.A., 1980. Evolution of larval food preferences in microlepidoptera. *Annual Review of Entomology,* 25: 133-159.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Robinson G.S., 2002. Hostplants of the moth and butterfly caterpillars of America North of Mexico. American Entomological Institute, Gainesville, FL.

Root, R., 1973. Organization of a plant-arthropod association in simple and diverse habitats - fauna of collards (*Brassica oleracea*). *Ecological Monographs,* 43(1): 95-120.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management,* 255(1): 1-15.

Rowe, J., 1971. Why classify forest land. *Forestry Chronicle,* 47(3): 144-&.

Schowalter, T.D., Zhang, Y.L., 2005. Canopy arthropod assemblages in four overstory and three understory plant species in a mixed-conifer old-growth forest in California. *Forest Science,* 51(3): 233-242.

Schulze, C.H., Linsenmair, K.E., Fiedler, K., 2001. Understory versus canopy: Patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecology,* 153(1-2): 133-152.

Scoble M.J., 1992. The Lepidoptera: Form, function and diversity. Oxford University Press, Oxford, pp. 404.

Shaw, D., 2004. Vertical organization of canopy biota. In: Lowman, M.D., Rinker, H.B., (Eds.). Forest canopies. Elsevier Academic Press, pp. 3-23.

Sobek, S., Tscharntke, T., Scherber, C., Schiele, S., Steffan-Dewenter, I., 2009. Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecology and Management,* 258(5): 609-615.

Solarik, K.A. Lieffers V.J., Volney, W.J.A, Pelletier, R. and Spence, J.R., 2010. Seed tree density, variable retention and stand composition influence recruitment of white spruce in boreal mixedwood forests. *Canadian Journal of Forest Research,* 40(9): 1821–1832.

Spence J.R., Volney W.J.A., 1999. EMEND: Ecosystem management emulating natural disturbance. Sustainable Forest Management Network report 1999-14, pp. 17. Sustainable Forest Management Network, Edmonton.

Stork, N.E., 1988. Insect diversity - facts, fiction and speculation. *Biological Journal of the Linnean Society,* 35(4): 321-337.

Summerville, K.S., Crist, T.O., 2003. Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region and patch size. *Oikos*, 100(1): 134-148.

Summerville, K.S., Crist, T.O., Kahn, J.K., Gering, J.C., 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. *Ecological Entomology,* 28(6): 747-757.

Summerville, K.S., Steichen, R.M., Lewis, M.N., 2005. Restoring lepidopteran communities to oak savannas: Contrasting influences of habitat quantity and quality. *Restoration Ecology,* 13(1): 120-128.

Summerville, K.S., Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: A review. *Canadian Entomology,* 140(4): 475-494.

Summerville, K.S., Dupont, M.M., Johnson, A.V., Krehbiel, R.L., 2008. Spatial structure of forest lepidopteran communities in oak hickory forests of Indiana. *Environmental Entomology,* 3(5): 1224-1230.

Sutton S.L., 1983. The spatial distribution of flying insects in tropical rain forests.

Volney, W.J.A., Mallett, K.I., 1998. Integrated pest management in western Canadian boreal forests. *Forestry Chronicle,* 74(4): 597-605.

Wagner, D.L., Peacock, J.W., Carter, J.L., Talley, S.E., 1995. Spring caterpillar fauna of oak and blueberry in a Virginia deciduous forest. *Annals of the Entomological Society of America,* 88(4): 416-426.

Wagner, D.L., Wagner, D.L., 2005. Caterpillars of eastern North America: A guide to identification and natural history. Princeton University Press, Princeton, NJ., pp. 496.

Winchester, N.N., Ring, R.A., 1996. Northern temperate coastal Sitka spruce forests with special emphasis on canopies: Studying arthropods in an unexplored frontier. *Northwest Science,* 70: 94-103.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, 34(2): 417-430.

Work, T.T., Spence, J.R., Volney, W.J.A., Morgantini, L.E., Innes, J.L., 2003. Integrating biodiversity and forestry practices in western Canada. *Forest Chronicle,* 79(5): 906-916.

Young M., 1997. The natural history of moths. T & A D Poyser, London, pp. 271.

**Table 3.1** Means (SE) of environmental variables, canopy caterpillar abundance and richness observed in deciduous dominated (DDOM) and coniferous dominated (CDOM) compartments at EMEND in 2007.

|  | **DDOM** |  | **CDOM** |  |
|---|---|---|---|---|
| **Environmental variable** | **100%** Mean(SE) | **20%** Mean(SE) | **100%** Mean(SE) | **20%** Mean(SE) |
| Crown cover (%) | 85.27(2.09) | 56.63(4.66) | 83.98(3.94) | 36.56(8.35) |
| DBH (in) | 33.67(1.09) | 32.48(1.90) | 28.40(2.17) | 30.80(4.04) |
| Tree height (m) | 23.23(0.85) | 21.72(0.84) | 22.24(1.85) | 22.30(2.43) |
| Crown height(m) | 9.42(0.90) | 7.10(0.67) | 15.40(1.16) | 14.94(1.72) |

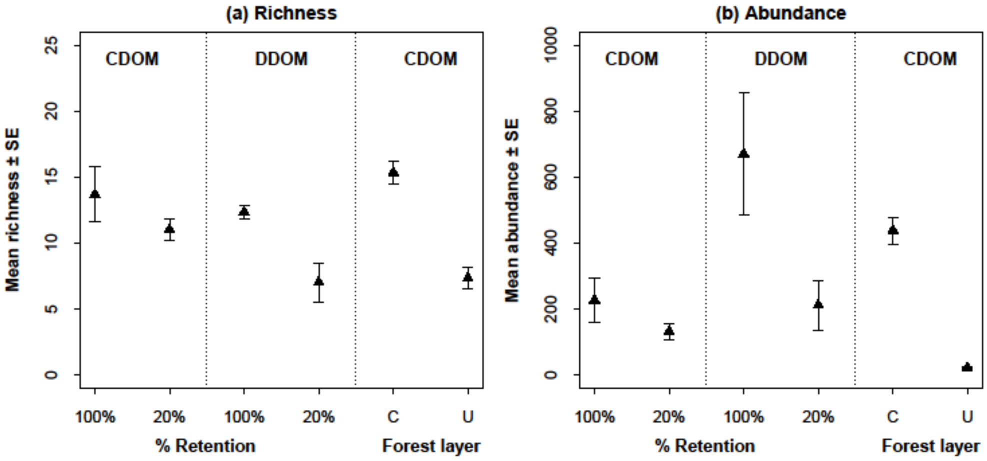

**Figure 3.1** Mean number of individuals (a) and species richness (b) of caterpillars collected on white spruce (CDOM) and trembling aspen (DDOM) in unharvested (100%) and 20% retention compartments, and the canopy (C) and understory (U) forest layers at EMEND. CDOM and DDOM canopy trees were sampled in 2007. The canopy and understory layers were sampled in 2008, and only in CDOM compartments.

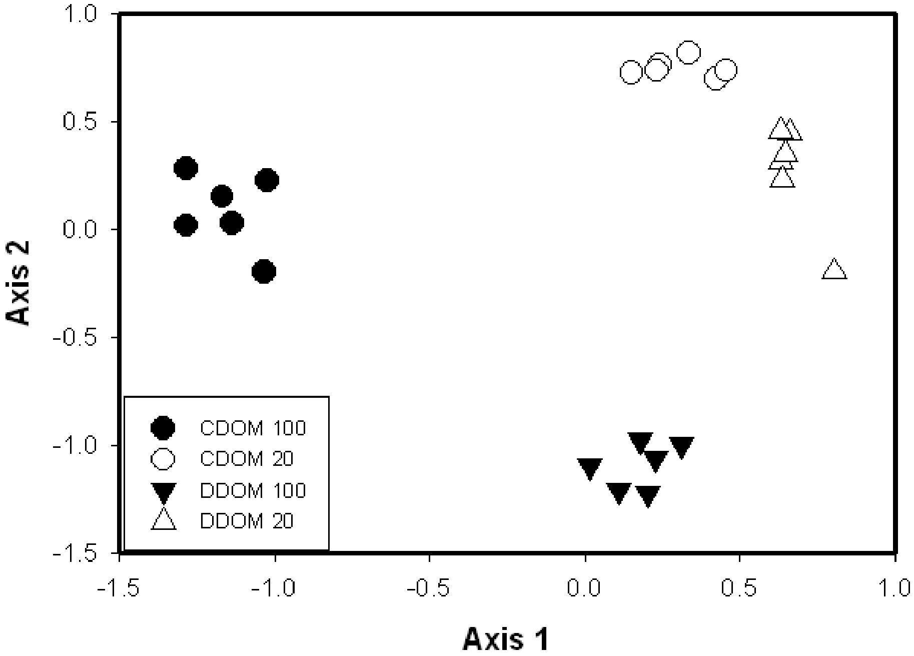

**Figure 3.2** NMDS ordination based on 24 samples and 46 caterpillar species collected from white spruce and trembling aspen of coniferous (CDOM) and deciduous (DDOM) unharvested and 20% retention compartments at EMEND in 2007. Final stress = 9.2. R-squared: Axis 1; 33.8%, Axis 2; 53.9%.

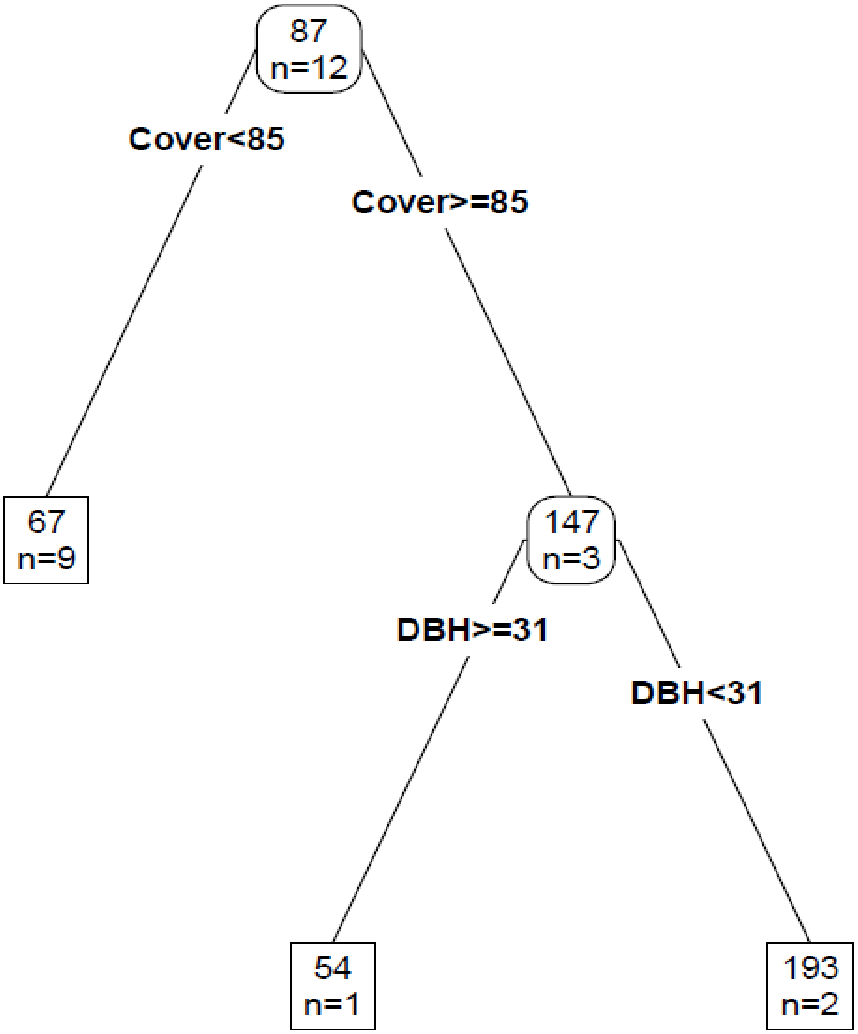

**Figure 3.3** Results of regression tree analyses of the total number of caterpillars (abundance) collected from white spruce in coniferous dominated (CDOM) compartments at EMEND. The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). Each node is labeled with the average rating (mean) and the number of observations (n) in each group. The regression tree had two splits and explained 86 % of the total variance, with 61 % and 25 % explained by the first (% crown cover) and second (DBH) splits, respectively.

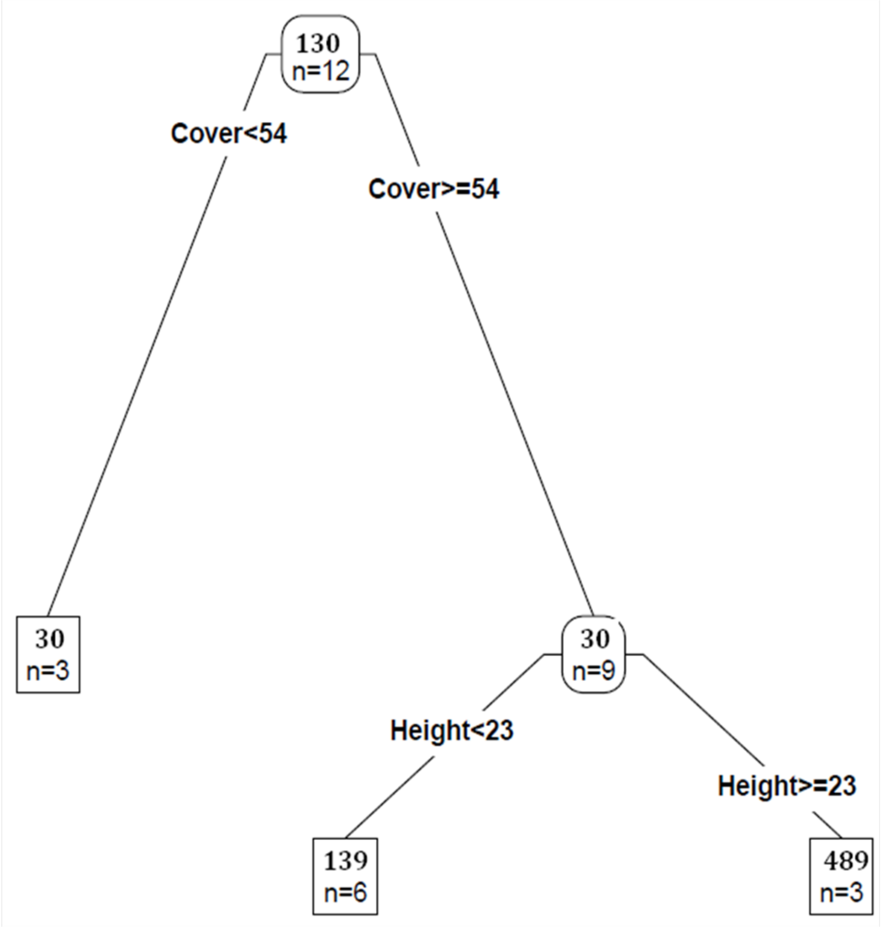

**Figure 3.4** Results of regression tree analyses of the total number of individual caterpillars (abundance) collected from trembling aspen in deciduous dominated (DDOM) compartments at EMEND. The exploratory variables were % crown cover, crown size, tree height and diameter at breast height (DBH). Each node is labeled with the average rating (mean) and the number of observations (n) in each group. The regression tree had two splits and explained 56 % of the total variance, with 39 % and 17 % explained by the first (% crown cover) and second (Height) splits, respectively.

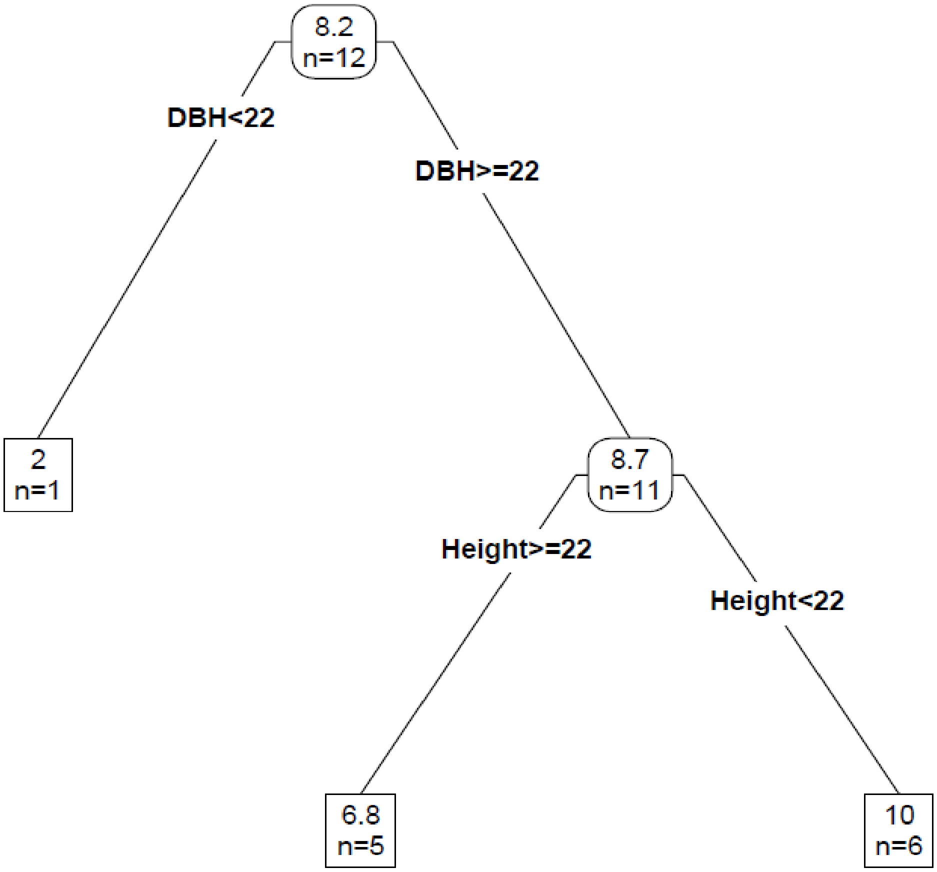

**Figure 3.5** Results of regression tree analyses of the total number of caterpillar species (richness) collected from white spruce in coniferous dominated (CDOM) compartments at EMEND. The exploratory variables were % crown cover, crown size, tree height and diameter at breast height (DBH). Each node is labeled with the average rating (mean) and the number of observations (n) in each group. The relative lengths of vertical lines within each tree represent the proportion of the total variance explained by each split. The regression tree had two splits and explained 70 % of the total variance, with 54 % and 16 % explained by the first (DBH) and second (Height) splits, respectively.

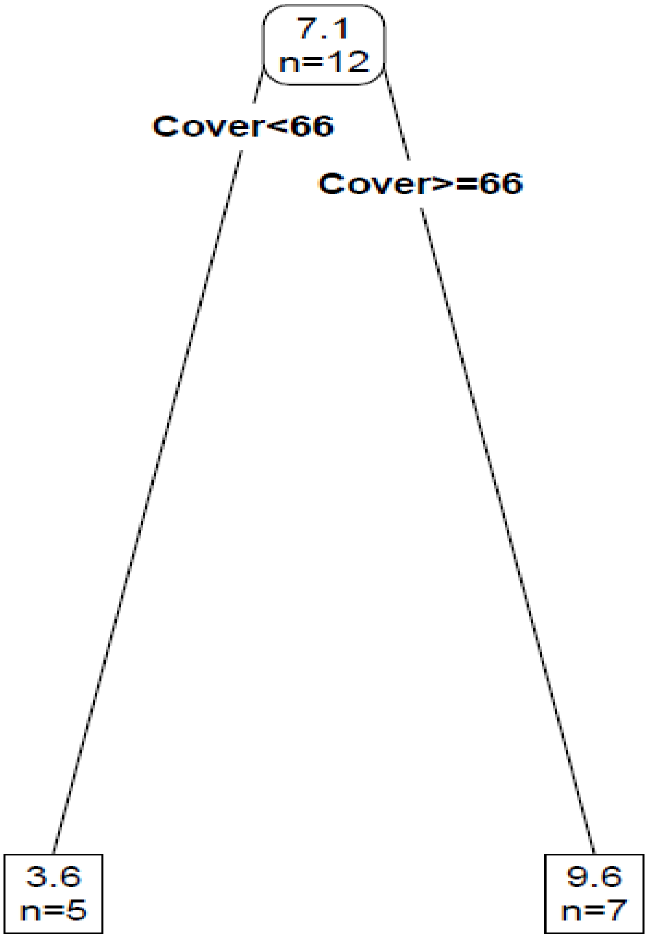

**Figure 3.6** Results of regression tree analyses of the total number of caterpillar species (richness) collected from trembling aspen in deciduous dominated (DDOM) compartments at EMEND. The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). Each node is labeled with the average rating (mean) and the number of observations (n) in each group. The regression tree had only one split with % crown cover explaining 57 % of the total variance.

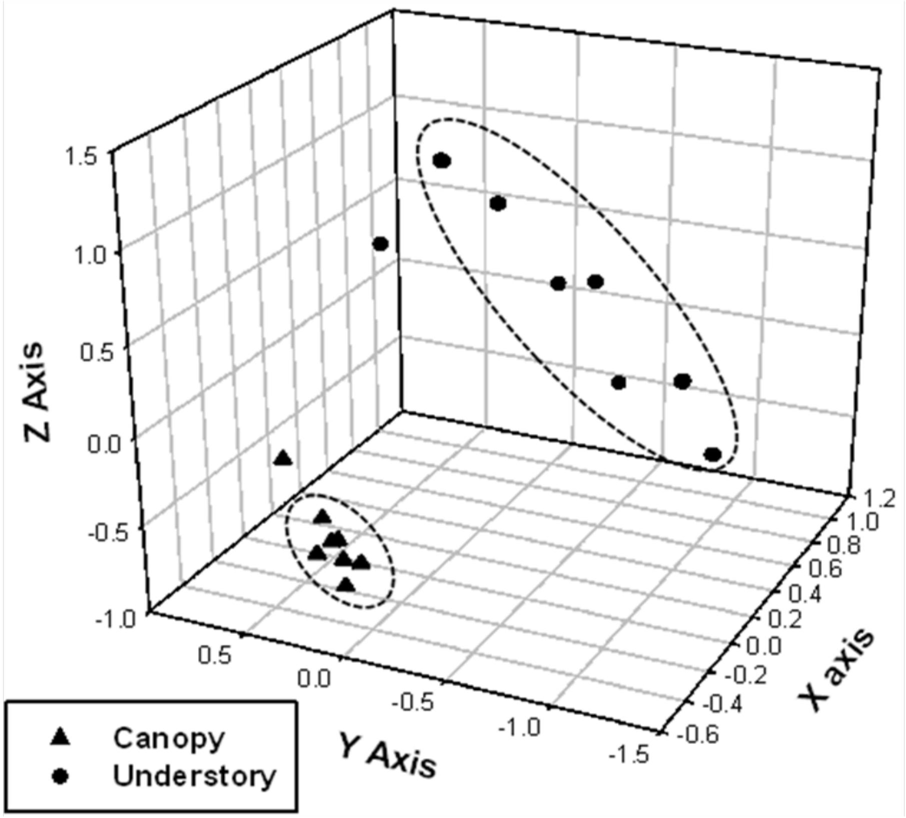

**Figure 3.7.** NMDS ordination based on 16 samples and 31 caterpillar species collected from the under- and overstory strata of coniferous dominated compartments at EMEND in 2008: Black and White symbols represent the overstory and understory samples, respectively. Final stress = 9.8. R-squared: X Axis: 41.1%, Y Axis: 23.7% and Z Axis: 27.4.

**Appendix 3.1** Abundance of macro and micro-lepidopteran larvae collected from trembling aspen and white spruce of unharvested and 20% treatment compartments at EMEND in 2007.

| **Species name** | **CDOM 100%** | **CDOM 20%** | **DDOM 100%** | **DDOM 20%** |
|---|---|---|---|---|
| *Archepandemis conferana* Mutuura | 0 | 2 | 0 | 0 |
| *Acronicta sp* | 0 | 0 | 0 | 1 |
| *Anacampsis niveopulvella* (Cham.) | 1 | 0 | 17 | 7 |
| *Archips parckardiana* (Fern.) | 3 | 1 | 0 | 0 |
| *Archips striana* (Fern.) | 3 | 1 | 0 | 0 |
| *Acleris variana* (Fern.) | 77 | 13 | 0 | 0 |
| *Anacampsis sp.* | 0 | 0 | 0 | 1 |
| *Apotomis sp.* | 0 | 1 | 0 | 0 |
| *Archips sp.* | 0 | 1 | 0 | 0 |
| Unknown Noctuidae 1 | 0 | 0 | 11 | 6 |
| Unknown Noctuidae 2 | 0 | 0 | 2 | 0 |
| Unknown Tortricidae | 0 | 0 | 1 | 0 |
| *Coleotechnites blastovora* (McLeod) | 27 | 30 | 0 | 0 |
| *Choristoneura fumiferana* (Clem.) | 3 | 4 | 0 | 0 |
| *Campaea perlata* (Gn.) | 0 | 0 | 7 | 0 |
| *Clepsis persicana* Fitch | 0 | 3 | 0 | 0 |
| *Catacola sp.* | 0 | 0 | 3 | 1 |
| *Cyclophora sp.* | 0 | 0 | 5 | 0 |
| *Dysstroma sp.* | 1 | 0 | 0 | 0 |

| | | | | |
|---|---|---|---|---|
| *Eilema bicolor* (Grt.) | 5 | 1 | 0 | 0 |
| *Epinotia criddleana* (Kft.) | 0 | 0 | 8 | 2 |
| *Enargia decolor* (Wlk.)** | 2 | 0 | 11 | 5 |
| *Epinotia nisella* (Cl.) | 0 | 0 | 32 | 17 |
| *Epinotia Solandriana* (L.) | 2 | 0 | 0 | 0 |
| *Egira sp.* | 0 | 0 | 3 | 0 |
| *Epinotia sp.* | 0 | 1 | 0 | 0 |
| *Eupethecia spp.* | 9 | 9 | 1 | 0 |
| *Gypsonoma adjuncta* Heinrich | 0 | 0 | 1 | 0 |
| *Griselda radicana* (Heinrich) | 1 | 2 | 0 | 0 |
| *Gnophaela vermiculata* (Grote)* | 21 | 0 | 0 | 0 |
| *Ipimorpha pleonectusa* Grt. | 0 | 0 | 3 | 1 |
| Unknown Noctuidae 3 | 0 | 1 | 0 | 0 |
| *Malacosoma disstria* Hbn. | 0 | 0 | 0 | 2 |
| *Operophtera bruceata* Hulst** | 1 | 0 | 1901 | 575 |
| Unknown Olethreutinae | 2 | 0 | 0 | 0 |
| *Orygia sp.* | 4 | 3 | 0 | 1 |
| *Pandemis limitata* (Rob.) | 0 | 0 | 1 | 0 |
| *Syngrapha alias* (Ottol.) | 7 | 2 | 0 | 0 |
| *Speranza loricaria* (Hulst.) | 0 | 0 | 7 | 0 |
| *Syngrapha viridisgma* (Grt.) | 5 | 1 | 0 | 0 |
| *Scopula junctaria* (Wlk.r) | 2 | 0 | 0 | 0 |

| | | | | |
|---|---|---|---|---|
| *Macaria sp.* | 1 | 0 | 0 | 0 |
| *Gluphisia septentrionis* Wlk. | 0 | 0 | 1 | 0 |
| *Zeiraphera sp.* | 1 | 0 | 0 | 0 |
| *Virbia ferruginosa* (Wlk.) | 3 | 1 | 0 | 0 |
| *Zale sp* | 0 | 0 | 2 | 0 |
| *Zeiraphera canadensis* | 49 | 182 | 0 | 0 |
| *Zeiraphera unfortunana* Ferris & Kruse. | 454 | 131 | 0 | 0 |

*.Excluded from statistical analyses-Larvae feeds on *Mertensia paniculata* but caterpillars ascend to the tree top where they pupate.

**I individuals collected on non-host tree species not included in the analysis

**Appendix 3.2:** Abundance of macro and micro-lepidopteran larvae collected from white spruce and 8 understory plant species of unharvested coniferous compartments at EMEND in 2008.

| **Species name** | **CDOM 100% (Canopy trees)** | **CDOM 100% (Understory plants)** |
|---|---|---|
| *Archepandemis conferana* Mutuura | 5 | 0 |
| *Anacampsis sp.* | 0 | 1 |
| *Archips parckardiana* (Fern.) | 20 | 0 |
| *Apotomis removana* | 0 | 2 |
| Unknown Noctuidae 1 | 0 | 13 |
| *Archips striana* (Fern.) | 4 | 0 |
| *Acleris variana* (Fern.) | 77 | 0 |
| *Coleotechnites blastovora* (McLeod) | 15 | 0 |
| *Choristoneura fumiferana* (Clem.) | 9 | 0 |
| *Campaea perlata* (Gn.) | 2 | 5 |
| *Clepsis persicana* Fitch | 0 | 3 |
| *Dysstroma walkerata* (Pears.) | 0 | 7 |
| *Eilema bicolor* (Grt.) | 1 | 0 |
| *Epinotia Solandriana* (L.) | 0 | 1 |
| *Euchlaena sp* | 11 | 0 |
| *Eupethecia spp.* | 15 | 5 |
| *Griselda radicana* (Heinrich) | 1 | 0 |
| *Idia aemula* | 12 | 0 |
| *Macaria signaria* (Hbn) | 7 | 0 |
| *Speranza sp*1 | 0 | 6 |
| Unkown Noctuidae 3 | 0 | 1 |
| Unkown Noctuidae 4 | 0 | 1 |
| *Operophtera bruceata* Hulst. | 0 | 6 |
| *Pandemis limitata* (Rob.) | 0 | 5 |
| *Protoboarmia porcelaria* | 1 | 0 |
| *Syngrapha alias* (Ottol.) | 7 | 0 |
| *Scopula junctaria* (Wlk) | 0 | 8 |
| *Speranza loricaria* (Hulst.) | 3 | 0 |
| *Syngrapha viridisgma* (Grt.) | 4 | 0 |
| *Virbia ferruginosa* (Wlk.) | 9 | 0 |
| *Xestia sp.* | 2 | 0 |
| *Zeiraphera canadensis* | 686 | 0 |
| *Zeiraphera unfortunana* Powell | 423 | 0 |

**Appendix 3.3:** Results of PerMANOVA. Due to the small sample size (n = 3), Monte-Carlo (MC) *p-values* ($\alpha < 0.05$) were used in tests of significance in the PerMANOVA model and pair-wise comparisons.

```
 PERMANOVA v.1.6
-----------------
 A program for analyzing multivariate data on the basis of any distance measure,
 according to any linear ANOVA model, using permutations.

 by M.J. Anderson
 Department of Statistics
 University of Auckland (2005)

--- Experimental Design ---
  Factor 1 is Forest   with  2 levels and is fixed
  Factor 2 is Treat    with  2 levels and is fixed
  The sample size (n)          =   3
  The total no. of observations =   12
  The total no. of variables    =   46

 --- Results ---
  Permutational Multivariate Analysis of Variance (PerMANOVA statistics in the table
below are included as text in section 3.3.1. community composition)

  Source          df      SS         MS         F      P(perm) P(MC)
 ----------------------------------------------------------------------------
  Fo              1    24247.4374   24247.4374   26.1789  0.0012  0.0001
  Tr              1      639.7512     639.7512    0.6907  0.5745  0.4946
  FoxTr           1     1185.1360    1185.1360    1.2795  0.2493  0.2809
  Residual        8     7409.7606     926.2201
  Total          11    33482.0852
 ----------------------------------------------------------------------------
  Data were transformed to pres/abs
  No standardisation
  Analysis based on Bray-Curtis dissimilarities
  Unrestricted permutation of raw data using correct permutable units
  Integer used as seed    =   2
  No. of permutations used = 9999
```

**Appendix 3.4:** NMS Ordination output for the analysis of caterpillars sampled from the spruce and aspen canopy trees in 2007 (figure 3.2). A final configuration (ordination scores) with stress = 9.2 was selected (Highlighted in **bold** on the NMS output)

The following options were selected:

ANALYSIS OPTIONS

1. SORENSEN = Distance measure

```
     2.        2 = Number of axes (max. = 6)
     3.      100 = Maximum number of iterations
     4.  FROM FILE = Starting coordinates (random or from file)
     5.        2 = Reduction in dimensionality at each cycle
     6.     0.20 = Step length (rate of movement toward minimum stress)
     7.   USE TIME = Random number seeds (use time vs. user-supplied)
     8.        1 = Number of runs with real data
     9.        0 = Number of runs with randomized data
    10.       NO = Autopilot
    11.   0.000010 = Stability criterion, standard deviations in stress
                over last  15 iterations.
OUTPUT OPTIONS
    13.      YES = Write distance matrix?
    14.      YES = Write starting coordinates?
    15.      YES = List stress, etc. for each iteration?
    18.      YES = Plot stress vs. iteration?
    17.      YES = Plot distance vs. dissimilarity?
    16.      YES = Write final configuration?
    19.   ROTATED = Write varimax-rotated or unrotated scores for graph?
    20.       NO = Write run log?
    21.      YES = Write weighted-average scores for species ?

------------------------------------------------------------------------------
STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)
--------------------------------------------------------------------
        Stress in real data        Stress in randomized data
           250 run(s)            Monte Carlo test,  249 runs
     -------------------------  -----------------------------------
Axes  Minimum    Mean  Maximum  Minimum    Mean  Maximum     p
--------------------------------------------------------------------
  2    9.217   10.804   36.860   11.465   21.041   44.406    0.0040
--------------------------------------------------------------------
p = proportion of randomized runs with stress < or = observed stress
i.e., p  = (1 + no. permutations <= observed)/(1 + no. permutations)


Conclusion:  a 2-dimensional solution is recommended.

NMS_MothsCats2007_Ord

Coefficients of determination for the correlations between ordination
distances and distances in the original n-dimensional space:

         R Squared: Axis variance
explained
Axis   Increment   Cumulative
```

```
 1     .338     .338
 2     .539     .878

Increment and cumulative R-squared were adjusted for any lack
of orthogonality of axes.

Axis pair    r    Orthogonality,% = 100(1-r^2)
  1 vs 2    0.052    99.7

Number of entities = 24
Number of entity pairs used in correlation = 276
Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)
```

**Final configuration (ordination scores) for this run**

```
NMS_MothsCats2007_Ord
24 po        ints
C1001T1      -1.28445    0.01685
C1001T2      -1.16845    0.15112
C1002T1      -1.13689    0.02975
C1002T2      -1.28536    0.28177
C1003T1      -1.02311    0.22428
C1003T2      -1.03332   -0.19544
C201T1        0.24494    0.76033
C201T2         0.3351    0.81681
C202T1         0.4251    0.69837
C202T2        0.45746    0.73462
C203T1        0.15184    0.72253
C203T2        0.23485    0.73449
D1001T1       0.20508   -1.22442
D1001T2       0.31167   -0.99959
D1002T1       0.01917   -1.09671
D1002T2       0.23085   -1.06211
D1003T1       0.11094   -1.20602
D1003T2       0.18079   -0.97429
D201T1        0.63424    0.30879
D201T2        0.66278    0.44666
D202T1        0.80516     -0.1978
D202T2        0.63831    0.23085
```

| | | |
|---|---|---|
| D203T1 | 0.63485 | 0.45333 |
| D203T2 | 0.64847 | 0.34584 |

C; CDOM, D; DDOM, 100; Unharvested controls, 20; 20% retention harvest, T1 and T2; tree 1 and 2, respectively.

**Appendix 3.5:** Regression tree analysis output of the total number of caterpillars (abundance) collected from white spruce in coniferous dominated (CDOM) compartments at EMEND (figure 3.3). The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). The table of cp values used for cross validation of errors (un-pruned tree) and for interpreting variance explained by the final tree (pruned tree) are highlighted in bold.

```
R version 2.13.2 (2011-09-30)
Copyright (C) 2011 The R Foundation for Statistical Computing
ISBN 3-900051-07-0
Platform: i386-pc-mingw32/i386 (32-bit)

> #Import data
> library(rpart)
> library(rpart.plot)
> CDOM=read.csv("CDOM_pos.csv")
> #fix(CDOM)
> #attach(CDOM)
> CDOM1=CDOM[, c(1:5, 32,34)]
> fix(CDOM1)
> #attach(CDOM1)
> #Import data
> library(rpart)
> library(rpart.plot)
> CDOM=read.csv("CDOM_pos.csv")
> #fix(CDOM)
> #attach(CDOM)
> CDOM1=CDOM[, c(1:5, 32,34)]
> #fix(CDOM1)
> #attach(CDOM1)
> #
> #Regression tree using rpart package
> #
> #Regression tree for CDOM abundance
> #fit1=unpruned tree for CDOM abundance
> fit1=rpart(abund~Cover+DBH+Height+Crown, method="anova", data=CDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0))
> printcp(fit1)# print the complexity parameter (cp) table for the rpart object

Regression tree:
```

```
rpart(formula = abund ~ Cover + DBH + Height + Crown, data = CDOM1,
    method = "anova", control = rpart.control(minsplit = 3, xval = 10,
        cp = 0))

Variables actually used in tree construction:
[1] Cover  Crown  DBH    Height

Root node error: 36299/12 = 3024.9

n= 12

         CP nsplit rel error xerror    xstd
1 0.3912154      0  1.000000 1.1478 0.43048
2 0.3548499      1  0.608785 2.8342 0.91182
3 0.1045796      2  0.253935 2.8342 0.91182
4 0.0290955      4  0.044775 2.6398 0.85028
5 0.0011754      5  0.015680 2.8996 0.83483
6 0.0000000      6  0.014505 2.8630 0.83220

> tree1=rpart(abund~Cover+DBH+Height+Crown, method="anova", data=CDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0.2))
> summary(tree1)
Call:
rpart(formula = abund ~ Cover + DBH + Height + Crown, data = CDOM1,
    method = "anova", control = rpart.control(minsplit = 3, xval = 10,
        cp = 0.2))
  n= 12

         CP nsplit rel error   xerror      xstd
1 0.3912154      0 1.0000000 1.205483 0.4455143
2 0.3548499      1 0.6087846 2.889958 0.9193728
3 0.2000000      2 0.2539347 2.889958 0.9193728

Node number 1: 12 observations,    complexity param=0.3912154
  mean=87.08333, MSE=3024.91
  left son=2 (9 obs) right son=3 (3 obs)
  Primary splits:
      Cover  < 84.79 to the left,  improve=0.3912154, (0 missing)
      Crown  < 19.3  to the left,  improve=0.3245378, (0 missing)
      Height < 17.65 to the right, improve=0.2872818, (0 missing)
      DBH    < 25.7  to the right, improve=0.2015223, (0 missing)

Node number 2: 9 observations
  mean=67.22222, MSE=1023.284

Node number 3: 3 observations,    complexity param=0.3548499
  mean=146.6667, MSE=4296.222
  left son=6 (1 obs) right son=7 (2 obs)
```

```
  Primary splits:
      DBH    < 30.85 to the right, improve=0.9993793, (0 missing)
      Height < 25.3  to the right, improve=0.9993793, (0 missing)
      Cover  < 86.74 to the right, improve=0.2718797, (0 missing)
      Crown  < 16.7  to the left,  improve=0.2287410, (0 missing)

Node number 6: 1 observations
  mean=54, MSE=0

Node number 7: 2 observations
  mean=193, MSE=4

> printcp(tree1)
```

**Appendix 3.6:** Regression tree analysis output of the total number of caterpillars (abundance) collected from trembling aspen in deciduous dominated (DDOM) compartments at EMEND (figure 3.4). The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). The table of cp values used for cross validation of errors (un-pruned tree) and for interpreting variance explained by the final tree (pruned tree) are highlighted in bold.

**Regression tree for CDOM richness**

```
rpart(formula = rich ~ Cover + DBH + Height + Crown, data = CDOM1,
    method = "anova", control = rpart.control(minsplit = 3, xval = 10,
        cp = 0))

Variables actually used in tree construction:
[1] Cover  DBH    Height

Root node error: 89.667/12 = 7.4722

n= 12

         CP nsplit rel error xerror    xstd
1 0.4626563      0  1.000000 1.1554 0.48115
2 0.3797229      1  0.537344 1.2138 0.44243
3 0.1189591      2  0.157621 1.3181 0.71860
4 0.0237918      3  0.038662 1.6330 0.98614
5 0.0074349      4  0.014870 1.5855 0.98494
6 0.0000000      6  0.000000 1.7230 1.05736

> tree2=rpart(rich~Cover+DBH+Height+Crown, method="anova", data=CDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0.2))
> printcp(tree2)

Regression tree:
rpart(formula = rich ~ Cover + DBH + Height + Crown, data = CDOM1,
    method = "anova", control = rpart.control(minsplit = 3, xval = 10,
```

```
        cp = 0.2))

Variables actually used in tree construction:
[1] DBH    Height

Root node error: 89.667/12 = 7.4722

n= 12

       CP nsplit rel error xerror    xstd
1 0.46266      0   1.00000 1.1869 0.48277
2 0.37972      1   0.53734 1.2591 0.44416
3 0.20000      2   0.15762 1.3502 0.71526

> prp(tree2, type=4, extra=1,clip.right.labs=FALSE, leaf.round=0)
> prp(tree2, type=4, extra=1,clip.right.labs=FALSE, uniform = FALSE, leaf.round=0)
>  prp(tree2, type=4, extra=1,clip.right.labs=FALSE, uniform = FALSE, leaf.round=0)
>
```

**Appendix 3.7:** Regression tree analysis output of the total number of caterpillar species (richness) collected from white spruce in coniferous dominated (CDOM) compartments at EMEND (figure 3.5). The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). The table of cp values used for cross validation of errors (un-pruned tree) and for interpreting variance explained by the final tree (pruned tree) are highlighted in bold.

```
R version 2.13.2 (2011-09-30)
Copyright (C) 2011 The R Foundation for Statistical Computing
ISBN 3-900051-07-0
Platform: i386-pc-mingw32/i386 (32-bit)

> #Import data
> library(rpart)
> library(rpart.plot)
> DDOM=read.csv("DDOM.csv")
> #fix(DDOM)
> attach(DDOM)
> DDOM1=DDOM[, c(1:5, 30,33)]
> #fix(DDOM1)
> attach(DDOM1)

> #Regression tree using rpart package
> #
> Regression tree for DDOM abundance
> fit1=rpart(abund~Cover+DBH+Height+Crown, method="anova", data=DDOM1,
+ control=rpart.control(minsplit=3, xval=50, cp=0))
> printcp(fit1)# print the complexity parameter (cp) table for the rpart object
```

```
Regression tree:
rpart(formula = abund ~ Cover + DBH + Height + Crown, data = DDOM1,
   method = "anova", control = rpart.control(minsplit = 3, xval = 50,
      cp = 0))

Variables actually used in tree construction:
[1] Cover  Height

Root node error: 2.6607/12 = 0.22173

n= 12

        CP nsplit rel error  xerror    xstd
1 0.60591210      0  1.000000 1.19008 0.42883
2 0.22393101      1  0.394088 0.71685 0.25071
3 0.05294681      2  0.170157 0.59888 0.19899
4 0.04584977      3  0.117210 0.49522 0.14209
5 0.04104404      4  0.071360 0.43377 0.11508
6 0.01065733      5  0.030316 0.37982 0.12218
7 0.00081513      6  0.019659 0.41447 0.14102
8 0.00000000      7  0.018844 0.41447 0.14102

> plotcp(fit1, minline = TRUE, lty = 3, col = 1)
> tree1=rpart(abund~Cover+DBH+Height+Crown, method="anova", data=DDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0.2))
> summary(tree1)
Call:

rpart(formula = abund ~ Cover + DBH + Height + Crown, data = DDOM1,
   method = "anova", control = rpart.control(minsplit = 3, xval = 10,
      cp = 0.2))
  n= 12

        CP nsplit rel error    xerror      xstd
1 0.6059121      0 1.0000000 1.1579436 0.4263899
2 0.2239310      1 0.3940879 0.6590677 0.2331847
3 0.2000000      2 0.1701569 0.8048942 0.2351781

Node number 1: 12 observations,    complexity param=0.6059121
  mean=2.113725, MSE=0.2217274
  left son=2 (3 obs) right son=3 (9 obs)
  Primary splits:
      Cover  < 53.59 to the left,  improve=0.6059121, (0 missing)
      Crown  < 8     to the left,  improve=0.5276916, (0 missing)
      DBH    < 32.45 to the left,  improve=0.4327846, (0 missing)
      Height < 20.75 to the left,  improve=0.3283766, (0 missing)
  Surrogate splits:
```

```
     DBH    < 31.2  to the left,  agree=0.833, adj=0.333, (0 split)
     Height < 20.75 to the left,  agree=0.833, adj=0.333, (0 split)

Node number 2: 3 observations
  mean=1.478869, MSE=0.05680362

Node number 3: 9 observations,    complexity param=0.223931
  mean=2.325344, MSE=0.09757225
  left son=6 (6 obs) right son=7 (3 obs)
  Primary splits:
     Height < 22.8  to the left,  improve=0.6784941, (0 missing)
     Crown  < 8.85  to the left,  improve=0.6784941, (0 missing)
     DBH    < 36.45 to the right, improve=0.2734683, (0 missing)
     Cover  < 88.17 to the left,  improve=0.2265719, (0 missing)
  Surrogate splits:
     Crown < 8.85  to the left,  agree=1, adj=1, (0 split)

Node number 6: 6 observations
  mean=2.143407, MSE=0.02565649

Node number 7: 3 observations
  mean=2.689218, MSE=0.0427972

> printcp(tree1)

Regression tree:
rpart(formula = abund ~ Cover + DBH + Height + Crown, data = DDOM1,
    method = "anova", control = rpart.control(minsplit = 3, xval = 10,
        cp = 0.2))

Variables actually used in tree construction:
[1] Cover  Height

Root node error: 2.6607/12 = 0.22173

n= 12

       CP nsplit rel error  xerror    xstd
1 0.60591      0   1.00000 1.15794 0.42639
2 0.22393      1   0.39409 0.65907 0.23318
3 0.20000      2   0.17016 0.80489 0.23518

> prp(tree1, type=4, extra=1,clip.right.labs=FALSE,uniform = FALSE,leaf.round=0)
> fit2=unpruned tree for DDOM richness
> fit2=rpart(rich~Cover+DBH+Height+Crown, method="anova", data=DDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0.2))
> printcp(fit2)# print the complexity parameter (cp) table for the rpart object
```

**Appendix 3.8:** Regression tree analysis output of the total number of caterpillar species (richness) collected from trembling aspen in deciduous dominated (DDOM) compartments at EMEND (figure 3.6). The exploratory variables were % crown cover (cover), crown size, tree height and diameter at breast height (DBH). The table of cp values used for cross validation of errors (un-pruned tree) and for interpreting variance explained by the final tree (pruned tree) are highlighted in bold.

## Regression tree for DDOM richness

```
rpart(formula = rich ~ Cover + DBH + Height + Crown, data = DDOM1,
   method = "anova", control = rpart.control(minsplit = 3, xval = 10,
      cp = 0))

Variables actually used in tree construction:
[1] Cover  Crown  Height

Root node error: 142.92/12 = 11.91

n= 12

        CP nsplit rel error  xerror    xstd
1 0.7277135      0  1.000000 1.20947 0.34569
2 0.0841983      1  0.272287 0.70294 0.25780
3 0.0643065      2  0.188088 1.11397 0.35839
4 0.0186589      4  0.059475 1.26145 0.37521
5 0.0046647      5  0.040816 1.14500 0.36245
6 0.0011662      6  0.036152 1.18698 0.36206
7 0.0000000      7  0.034985 1.21749 0.39472


> plotcp(fit2, minline = TRUE, lty = 3, col = 1)
> tree2=rpart(rich~Cover+DBH+Height+Crown, method="anova", data=DDOM1,
+ control=rpart.control(minsplit=3, xval=10, cp=0.1))
> summary(tree2)
Call:
rpart(formula = rich ~ Cover + DBH + Height + Crown, data = DDOM1,
   method = "anova", control = rpart.control(minsplit = 3, xval = 10,
      cp = 0.1))
  n= 12

Regression tree:
rpart(formula = rich ~ Cover + DBH + Height + Crown, data = DDOM1,
   method = "anova", control = rpart.control(minsplit = 3, xval = 10,
      cp = 0.1))

Variables actually used in tree construction:
[1] Cover
```

```
Root node error: 142.92/12 = 11.91

n= 12

       CP nsplit rel error  xerror    xstd
1 0.72771      0   1.00000 1.24135 0.35190
2 0.10000      1   0.57229 0.72842 0.25596

> prp(tree2, type=4, extra=1,clip.right.labs=FALSE,uniform = FALSE, leaf.round=0)
> prp(tree2, type=4, extra=1,clip.right.labs=FALSE,leaf.round=0)
> prp(tree2, type=4, extra=1,clip.right.labs=FALSE,unifrom = FALSE,leaf.round=0)
Error: prp: illegal argument "unifrom"
> prp(tree2, type=4, extra=1,clip.right.labs=FALSE,uniform = FALSE,leaf.round=0)
>

Node number 1: 12 observations,    complexity param=0.7277135
  mean=7.083333, MSE=11.90972
  left son=2 (5 obs) right son=3 (7 obs)
  Primary splits:
      Cover  < 66.33 to the left,  improve=0.7277135, (0 missing)
      DBH    < 31.2  to the left,  improve=0.4986089, (0 missing)
      Height < 20.75 to the left,  improve=0.3267250, (0 missing)
      Crown  < 8     to the left,  improve=0.2451895, (0 missing)
  Surrogate splits:
      DBH    < 31.2  to the left,  agree=0.833, adj=0.6, (0 split)
      Height < 20.75 to the left,  agree=0.833, adj=0.6, (0 split)
      Crown  < 8     to the left,  agree=0.750, adj=0.4, (0 split)

Node number 2: 5 observations
  mean=3.6, MSE=3.44

Node number 3: 7 observations
  mean=9.571429, MSE=3.102041

> printcp(tree2)
```

**Appendix 3.9:** NMS Ordination output for the analysis of caterpillars sampled from the spruce canopy trees and the understory layer of the CDOM cover-type in 2008 (figure 3.7). A final configuration (ordination scores) with stress = 9.8 was selected (Highlighted in **bold** on the NMS output)

```
STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)
--------------------------------------------------------------------
        Stress in real data        Stress in randomized data
           250 run(s)            Monte Carlo test,  249 runs
     -------------------------  -----------------------------------
Axes  Minimum     Mean  Maximum  Minimum     Mean  Maximum      p
--------------------------------------------------------------------
  3    9.769   31.645   62.193   11.820   18.383   39.684    0.0040
--------------------------------------------------------------------
p = proportion of randomized runs with stress < or = observed stress
i.e., p  = (1 + no. permutations <= observed)/(1 + no. permutations)


Conclusion:  a 3-dimensional solution is recommended.
```

**Final configuration (ordination scores) for this run**

```
NMS_                                  Cats2008_Ord_18
                                      Axis1     Axis2     Axis3
C1T1C                                -0.37653  -0.31386  -0.62349
C1T2C                                -0.16566  -0.17276  -0.69535
C1T3C                                -0.15078  -0.44728  -0.65143
C2T1C                                -0.55949  -0.29622  -0.17832
C2T2C                                -0.01311  -0.21181  -0.82764
C2T3C                                -0.45955  -0.48218  -0.49875
C3T1C                                -0.33601  -0.15355  -0.65136
C3T2C                                  -0.253   -0.1759  -0.72218
C3T3C                                 -0.2475   0.00933  -0.62315
C1T1U                                -0.15787   0.76071   0.57585
C1T2U                                 0.33032   0.26455   0.86484
C1T3U                                 1.08346  -0.25758   0.48326
C2T1U                                -0.72547   0.45197   0.63947
C2T2U                                 1.24727   0.37743   0.01195
C2T3U                                -0.09384   0.19049   1.06173
C3T1U                                 0.15325     1.365  -0.05821
C3T2U                                 0.32948   -0.3205   0.98661
C3T3U                                 0.39504  -0.58784   0.90619
```

```
************************** Output from Graph **************************
PC-ORD 5.10
1/14/2011, 3:28 PM

NMS_Cats2008_Ord

Coefficients of determination for the correlations between ordination
distances and distances in the original n-dimensional space:

          R Squared: Axis variance explained
Axis   Increment   Cumulative
 1      .312        .312
 2      .254        .566
 3      .349        .915

Increment and cumulative R-squared were adjusted for any lack
of orthogonality of axes.

Axis pair     r     Orthogonality,% = 100(1-r^2)
  1 vs 2    0.087    99.2
  1 vs 3    0.354    87.5
  2 vs 3    0.240    94.2

Number of entities = 18
Number of entity pairs used in correlation = 153
Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)
```

# Chapter 4 : Slash-burning as a biodiversity management tool in forestry: Is green tree retention sufficient to conserve boreal moths?

## 4.1 Introduction

Natural disturbances play an important role in maintaining forest ecosystem function (Roberts and Gilliam, 1995). Thus, understanding of the relationships between biotic diversity and disturbance may be applied to indicate whether management is affecting forest systems in ways similar to common natural disturbance regimes (Spence *et al*., 2008). In boreal forests, disturbance events such as fire (Angelstam, 1998; Bergeron, *et al*., 2001; Work *et al*., 2003) and insect outbreaks (Volney and Fleming, 2000) are particularly important in shaping the forest biota through their influences on plant species composition and structure (Price *et al*., 1999). These disturbances often create more heterogeneous plant communities (Summerville *et al*., 2001), which in turn influence composition of forest arthropod, bird and mammal assemblages. Comparisons of natural and anthropogenic disturbances can usefully contribute to development of ecologically sensitive forest management.

Over the past five decades, forestry activities in the boreal zone have supplanted and altered natural disturbance dynamics. On one hand, clear-cut logging has replaced wildfire as the predominant form of disturbance on boreal landscapes (Pratt and Urquhart, 1994; Timoney, 2003). In some cases, considerable success in modern fire suppression has dramatically altered disturbance regimes and left us with extensive tracts of old-growth forests that are long overdue for a major disturbance (Ryan, 2002). Forest managers are faced with increasing public pressure to reassess current management practices. Attempts to model natural disturbance dynamics and to reflect this understanding in improving logging and regeneration techniques have increased. Consequently silvicultural practices that better promote structural and biological legacies normally associated with natural disturbances have increasingly become important (Hunter, 1989; 1993; Perry, 1998; Simberloff, 1999; Work *et al.*, 2003; 2004).

Green tree retention (GTR), which involves leaving a range of living trees in multiple canopy layers on cut blocks, either in clustered or dispersed retention (Franklin *et al*., 1997), continues to gain in popularity as an approach to emulating natural disturbance. GTR is currently the major strategy being applied to conserve biodiversity in the Canadian boreal (Work *et al*., 2003). It is widely supposed that GTR will preserve critical on-site aspects of pre-disturbance seral stages, thus facilitating the recovery of forest biota to pre-disturbed conditions.

Although retention harvest may well maintain structural and compositional components usually absent in clear-cuts, such cut-blocks may not act as surrogates for fire residuals of naturally burned forest. For example, some plant and arthropod species are uniquely present in fire skips while being reduced or completely absent in harvest residuals (e.g., Gandhi *et al*., 2004). Furthermore, the structure and composition of plant communities that regenerate after logging differ profoundly from those that regenerate in naturally disturbed forests (Purdon *et al*., 2004). Clearly, human-initiated changes dramatically alter other forest assemblages and affect biodiversity patterns (Schultz and Crone, 1998; Bengtsson *et al*., 2000; Huntzinger, 2003).

Ecological impacts of GTR on forest structure and composition unmistakably deviate from those of wildfire (McRae *et al*., 2001). Hence, additional techniques are required to complement GTR in order to effectively conserve biodiversity. Prescribed burning offers some potential for conservation of fire dependent habitats and their associated biota, such as forest arthropods, on harvested landscapes. Arthropods are an important component of forest biodiversity that generally respond to disturbance in ways that are taxon specific (Langor and Spence, 2006). Thus, development of ecologically suitable management regimes are required in order to conserve the significant structural and functional roles performed by forest arthropods on the landscape (e.g., Cobb *et al*., 2010).

The potential use of fire in managing habitats for conservation of arthropod diversity is relatively well studied for butterflies in grasslands (Schultz and Dlugosch, 1999) and for carabid, staphylinid and saproxylic beetles in boreal ecosystems (Koivula and Spence, 2006; Koivula *et al*., 2006; Hyvarinen *et al*., 2009). Re-introduction of fire in fire-suppressed managed forests increases richness, enhances heterogeneity, and maintains a larger proportion of landscape and regional butterfly diversity (Huntzinger, 2003). In another study, prescribed burning of unharvested forest stands increased the abundance of rare and red listed saproxylic species in the Fennoscandian boreal forests (Hyvarinen *et al*., 2005). However, comparable studies on the impact of prescribed burning on boreal lepidopterans are lacking.

Forest moths are among the primary insect herbivores of boreal ecosystems (Volney and Mallett, 1998), and are therefore highly relevant to forest biodiversity and trophic function (Summerville *et al*., 2004). Most moths feed directly on plant material, and many are host specific in their larval stages; they are therefore likely to respond differently to changes in disturbance regimes than boreal taxa examined previously. Also, many boreal moth species use understory plants that re-establish quickly on burned sites. Growing evidence that moth assemblages can be negatively impacted by anthropogenic reductions in natural disturbances (Summerville and Crist, 2002; 2008) prompts concern about their diversity on landscapes modified by humans.

In this study, I examined whether burning slash after harvest (hereafter, ‘slash-burn’, or SB) sustains boreal moth communities that differ from those associated with simple GTR harvesting without fire (hereafter, ‘retention harvest’, or RH). This study had the following two main objectives: 1) to compare the impact of RH and SB treatments on moth communities in relation to unharvested stands; and 2) to determine whether slash-burned stands maintain a moth community which differs from that supported by a simple GTR. This study provides important baseline data for future monitoring of GTR harvest treatments at EMEND and information about possible ecological benefits of prescribed burning as a complement to GTR harvesting.

## 4.2 Materials and Methods

### 4.2.1 Study site

This study was conducted at the Ecosystem Management Emulating Natural disturbance (EMEND) experimental site established in 1997 in the boreal forest of NW Alberta, Canada, (56˚ 44'N, 118˚ 20'W). The project is focused on how various GTR levels and prescribed burns influence conservation and recovery of the forest biota [detailed site description and experimental design are available in (Spence *et al.*, 1999)]. The forest at EMEND is typical of the boreal mixedwood and exists as a mosaic of deciduous and coniferous canopies in pure or locally mixed stands, hereafter referred to as cover-types (Work *et al*., 2004).

Two of four EMEND cover-types were chosen for the present study: deciduous dominated (DDOM) and coniferous dominated (CDOM) stands, which in certain circumstances have been considered to represent early and late seral stages of forest succession in the northwestern boreal respectively (Chen & Popadiouk 2002). The deciduous composition of stands classified as DDOM varies but mainly consists of ≈ 50% balsam poplar (*Populous balsamifera* L.), 40%

trembling aspen (*Populus tremuloides* Michx.), and 10% paper birch (*Betula papyrifera* Marsh.). In addition, there is a small proportion of conifers, mainly white spruce. Understory vegetation of this cover-type is dense, mainly consisting of alder [*Alnus crsipa* (Ait.) Pursh], willow (*Salix spp.*), low-bush cranberry [*Vibrurnum edule* (Michx.)], prickly rose (*Rosa acicularis* Lindl.) and buffalo-berry [*Shepherdia canadensis* (L.) Nutt.], all in relatively equal abundances (Kishchuk, 2004). CDOM stands, on the other hand, are primarily white spruce but some blocks have black spruce [*Picea mariana* (Mill.)] with a less dense and more variable understory composition of mainly low-bush cranberry, prickly rose and feather mosses [*Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Bird.) Mitt., and *Ptilium crista-castrensis* (Hedw.) DeNot].

### 4.2.2 Moth sampling

Slash-burning treatments consisted of ~10-ha compartments that had been harvested with 10% retention (GTR) during the winter of 2003 after which the slash was evenly distributed. Each harvested compartment was then divided into two approximately equal sizes of c. 5-ha each; one half was burned (SB) and the other was not further treated to provide the harvest treatment (RH). Slash-burn compartments of CDOM and DDOM cover-types were burned in the fall of 2003 and the spring of 2005, respectively. Moths light trapped from unharvested compartments (c. 10-ha) of both cover-types provided a basis for comparison of samples from disturbed sites with unharvested controls. These unharvested stands represent mature forests that have regenerated from historical natural disturbance (~80-140 yrs), mainly by fire and insects. Three replicates of each treatment by cover-type combination were included in this study for a total of 18 samples.

In the summers of 2006 (unharvested compartments) and 2007 (SB and RH compartments), I sampled adult moths by light trapping, a passive sampling technique that has been widely used for studying adult moths (Southwood, 1995). Although light trap samples do not usually represent the full complement of moth species in an area, the high number of species and individuals sampled argue in the favor of their use (Southwood, 1994; 1995). Light trapping is also biased towards the collection of nocturnal insects that are attracted to light, while species which may be collected using baits (e.g. sugars or pheromones), as well as wingless adults (e.g. females of some lymantriids and geometrids) and those with poor flight ability, are generally underrepresented in light trap catches (Summerville and Crist, 2008).

The light traps used (Bioquip #2851; CA, USA) consisted of a plastic bucket with a ‘roof’ and 12-W u-shaped UV black lights powered by a 12-V battery; a killing agent (Vapona™) was placed inside the bucket during each collection night. One light trap was established on permanent light trapping stations previously established in the centre of each compartment at EMEND (Morneau, 2002). Traps were deployed 2m above ground by hanging them on tripods in order to minimize the influence of ground vegetation on trap efficiency.

Because different moth species are most active at different times of the night (Scalercio *et al*., 2009), trap lights were on from dusk to dawn. Light traps were also deployed only on days with little to no moonlight, night temperatures above 5°C and when precipitation was minimal because trap catches are influenced by moonlight and weather conditions (Scalercio *et al.*, 2009). To allow for comparisons between sites and to minimize differential effects of weather conditions on trap efficiency, traps were deployed during the same night at all sites; a 12V DC digital timer attached on the trap-roof was used to control lights being on or off simultaneously at all sites.

Overnight (including dusk and dawn) trap catches were transferred into paper bags the morning following trapping and frozen for subsequent processing. All macro moths were identified to species using relevant literature sources (Hodges, 1983; Miller, 1996; Miller and Hammond, 2000; 2003). I also consulted online resources including the University Of Alberta E. H. Strickland Virtual Entomological Museums, the North American Moth Photographers Group, and The Canadian Biodiversity Information Facility hosted website, The Moths of Canada), and museum reference collections at the University of Alberta the E. H. Strickland Entomological Museum and the Northern forestry Centre, both located in Edmonton AB, Canada. Voucher specimens have been deposited in the moth reference collection at the Northern Forestry Centre.

Although the unharvested compartments were twice as large (~10 ha) as disturbed compartments (~5 ha) and the unharvested and the two treated compartment types (SB and SH) were sampled in different years, comparisons are reasonable for two main reasons. First, temporal variation in abundance and species composition of boreal moths is generally insignificant compared to spatial variations, being mainly taxon-specific in relation to population levels, especially during outbreaks (Thomas, 1991, Leps *et al*., 1998). No species appeared to be in outbreak during our sampling period. Second, light traps attract moths mainly from the area defined by a 20-25m radius around the trap (Morneau, 2002; Muirhead-Thomson, 1991), and therefore, each compartment irrespective of size was sampled at roughly the same spatial scale. In addition, light interception by surrounding vegetation (invisibility) increases with distance especially in undisturbed forest (Morneau, 2002). Thus, in this study effects of sampling bias based on compartment size would be important only if traps collected more moths from disturbed than from intact forest. This is not usually the case (Thomas, 2002) and the opposite pattern certainly occurred in this study (Section 4.4: Results).

## 4.3 Data analysis

I used non-metric multidimensional scaling (NMS) with Bray-Curtis distance as implemented by PC-Ord (McCune and Grace, 2002) to visualize patterns in moth assemblages that could be related to the various cover-types by treatment. The goal of NMS is to produce a graphic-plot in which objects that differ significantly are placed far apart in the ordination space, while similar objects are placed close together (Gotelli and Ellison, 2004). This technique reduces stress (e.g., dissimilarity) among sites by preserving only the rank ordering of distances and can be used with any dissimilarity index. NMS does not assume linear relationships among variables making it suitable for analysis of often complex and non-dependent arthropod communities (Clarke, 1993).

Differences in composition of the moth assemblages among treatments were analyzed using permutational multivariate analysis of variance (Anderson, 2001), using a model that included cover-type x treatment interactions. This analysis is especially well suited for testing hypotheses about responses of many potentially non-independent variables, such as abundances of species in an assemblage. The method partitions variation directly among individual terms in a multi-factorial ANOVA based on any distance measure and does not require that data conform to a multivariate normal distribution (Anderson, 2001). I did this analysis using Bray-Curtis distances calculated on non-standardized data and 9999 permutations using the PerMANOVA software (Anderson, 2005). Monte-Carlo *p-values* were used in the interpretation of the significance tests as they are much more reliable for small sample sizes; *p-values* <0.05 were considered statistically significant. PerMANOVA was followed by *a posteriori* pair-wise comparisons when significant differences were found.

## 4.4 Results

A total of 2565 macrolepidopterans belonging to 166 species were captured and identified in this study (Table 4.1). This constitutes >92% of species richness previously recorded from EMEND (Morneau, 2002; Chapter 2 of this thesis). Noctuids and geometrids, which are among the most diverse lepidopterans (Summerville and Crist, 2008) in North American forested habitats, were the most abundant and species rich groups in the sample (Table 4.1). Together these two families contributed 87% of the species richness and comprised >93% of the total abundance in the light trap samples. The remaining 22 moth species from nine families (Arctiidae, Drepanidae, Lasiocampidae, Notodontidae, Sphingidae, Thyatiridae and Uraniidae), together contributed ~7% and ~14% of the total moth abundance and species richness, respectively.

The four most abundant species were *Enargia decolor* (Wlk.), 9% of total catch; *Brachylomia algens* (Grt.), 6%; *Venusia cambrica* Curt., 6% and *Xestia smithii* (Snell), 5%; the first three of these are noctuids while the fourth is a geometrid. None of the remaining 163 species accounted for more than 3% of the total moth abundance.

Moth abundance and species richness in disturbed sites of both cover-types was significantly lower than found in the unharvested stands (Table 4.2 and Figure 4.1a). In fact, the number of individuals collected from unharvested stands of both cover-types accounted for 74% of the overall catch. Similarly, traps placed in unharvested stands of both cover-types had the highest mean species richness, with over 17% (29 species) of the 166 species being uniquely collected from DDOM unharvested stands. At the other end of the spectrum, the lowest mean abundance and species richness was recorded from CDOM-RH and CDOM-SB compartments (Table 4.2 and Figure 4.1a and b). Each of these CDOM treatments contributed less than 5% of the total number of individual moths collected in light traps and, in combination, included only 25% of the species sampled in this study.

The best two-dimensional NMS ordination of light trap catches had a final stress of 10.5 and explained up to 88% of the total variation in moth assemblages.  In this ordination, axis 1 and 2 explained 57% and 31% of the total variance, respectively (Figure 4.2). Moth assemblages were predominately distinguished between unharvested and disturbed stands along axis 1. Moth assemblages from the unharvested DDOM and CDOM compartments were further separated into two distinct groups by the ordination along axis 2. Assemblages from treated compartments were clustered by cover-type in ordination space along axis 2, without clear separation of moth assemblages from the SB and RH treatments. Clearly, however, assemblages from both treatments in CDOM were much more dispersed in ordination space, than were those of DDOM compartments.

PerMANOVA indicated significant differences between moth assemblages of the two cover-types and between treatments with no significant interaction between cover-type and treatment (Table 4.3). Pair-wise *a posteriori* comparisons showed that moth communities differed significantly between unharvested and both SB and RH compartments while assemblages from the SB and RH  treatments did not differ from each other (Table 4.3).

A closer look at individual species' responses to disturbance treatments revealed a range of responses. First, a significant decrease in light trap catches in disturbed compared to unharvested controls, irrespective of pre-disturbance cover-type. This was the pattern exhibited by most species including two of the most abundant species in light trap samples, *E. decolor* and *V. cambrica*, which were significantly more abundant in unharvested compartment than in the RH and SB compartments of both cover-types, and were virtually absent from CDOM disturbed sites (Figure 4.4a and b).

There were a few exceptions to the general pattern described above. For instance, *X. smithii* and *P. rufipectus* were more abundant in disturbed sites of both DDOM and CDOM than in unharvested stands, with no evident differences between disturbance types (Figure 4.4c and d). On the other hand, *D. dislocata* catches increased in DDOM-SB and RH but decreased equally in disturbed CDOM compartments (Figure 4.4e). Finally, one relatively uncommon species, *Hydriomena furcata* (Thunb.), which was more frequently encountered in DDOM than CDOM stands, was more abundantly collected in burned than in un-burned stands (Figure 4.4f). This species was also more abundant in DDOM-SB and RH compartments than in treatments of this cover-type that were unharvested. H. furcata was captured in very low numbers to allow further investigations for a positive response to fire disturbance.

## 4.5 Discussion

### 4.5.1 Slash-burning as a forest management tool

Forest management using fire has previously been linked to conservation of moth communities (Rudolph and Ely, 2000), but the possible direct and immediate benefits of using fire has not been demonstrated for lepidopterans, as for other arthropod species. The role of fire in maintaining other arthropod species is related to the creation of favorable habitats for certain species including some saproxylic beetles (Lindenmayer and Franklin, 1997) or fire pyrophilous beetles that are specifically associated with burned stands (Koivula *et al*., 2006; Wikars and Schimmel, 2001).

Reductions in insect abundance after fire have been reported elsewhere and attributed to fire-induced mortality (McCullough *et al*., 1998; Swengel, 1998; Wikars and Schimmel, 2001). This immediate negative impact is usually short-term for arthropod species favored by fire. For instance, Hyvarinen *et al*., (2005) reported actual increases in the abundances of rare and red-listed saproxylic species in harvested stands that had been burned as compared to un-burned harvested stands. In my study, it is unlikely that fire-induced mortality could explain the decrease in moth abundance and richness observed in the SB compartments. This is because sampling occurred 2-4 years post fire which is beyond the time range within which fire-induced mortality has been observed. Instead, the low amount of retention (10%) likely explains my observation as fire behavior and intensity is most likely modified in cut-blocks compared to unharvested forest stands (Wikars and Schimmel, 2001). Therefore, the success of using fire as a complementary management tool to green tree retention will likely depend on the amount and distribution of post-harvest retention.

The significant reduction in moth abundance and richness in the disturbed treatments of both cover-types suggest, in part, that moth assemblages vary with the extent of canopy development, as the treated compartments had only 10% of the canopy retained following harvesting. Previous studies on the impact of low retention harvest on moths at EMEND showed that moth assemblages of compartments harvested to a 20% retention prescription changed significantly 1-2 years post-harvest while those harvested to a 50% retention prescription did not (Morneau, 2002). Additionally, the high occurrence of singletons and doubletons in collections from disturbed sites in my study is consistent with the findings of Thomas (2002). Generally, intensive harvest resets the successional trajectory of a stand, and early seral communities are typically impoverished for Lepidoptera (Summerville and Crist, 2002).

The absence of most boreal moths observed in stands harvested with low retention prescriptions is remarkable, given the fact that most species are understory feeders. It appears, therefore, that GTRs of 10% are insufficient to conserve moth assemblages characteristic of either unharvested deciduous or conifer dominated stands in unharvested blocks. Notably, some generalist species such as *V. cambrica,* whose larvae feed on a wide range of woody plants (Miller and Hammond, 2000; Robinson, 2002), were consistently absent in disturbed sites. However, *E. decolor*, whose larvae are commonly associated with aspen (Miller and Hammond, 2000; Robinson, 2002), were similarly present in only unharvested stands of both cover types, despite a dense regeneration of aspen by suckering on disturbed sites. Thus, host plant distribution alone cannot adequately explain the presence of some moth species, including those with a wide range of food choices (Leps *et al*., 1998). Instead, overall habitat quality is important in structuring moth assemblages (see Summerville and Crist, 2001). The high abundance and richness of moths associated with unharvested stands is therefore most likely a reflection of habitat quality, other than the abundance of host plants alone, resulting from a fully developed post disturbance canopy. Hence, higher retention levels that preserve habitat quality other than quality alone should be more favorable for local conservation of boreal moths.

### 4.5.2 Comparisons between harvesting and slash burning treatments

My study showed that moth assemblages following slash-burning (SB) did not necessarily differ from those of low retention harvest without burn (RH), at least in the medium-term. Instead, a slight decrease in moth abundance and richness was observed in slash-burn treatments, and this was more evident in the DDOM cover-type. Thus, multiple disturbances at a site seem to increase the impact on boreal moth assemblages as has been observed for boreal beetles (Cobb *et al*., 2007).

Overall similarities in moth abundance and richness between harvested sites that were burned and un-burned suggest that moth responses to fire and harvesting are most likely driven by similar short term mechanisms operating at low retention levels. Reduction in canopy trees after harvesting seems to have more impact on moth communities than does the addition of a burning treatment and differences in regeneration after fire and harvesting may not be evident, perhaps not until the canopy fully recovers from disturbance.

Whether moth assemblages of burned and un-burned sites will eventually differentiate depends possibly on factors related to fire behavior and the subsequent interactions between early successional communities and site-specific physical characteristics. For example, Johnstone and Kasischke, (2005) showed that burn severity had both immediate and lasting impacts in structuring post-fire plant biomass and canopy species composition. Although specific data for the SB treatments at EMEND was not available, all SB burn treatments in DDOM compartments were considered to be low intensity while those of CDOM stands were low to moderate intensity (Jason Edwards, personal communication). The impacts of fire on the landscape may last up to a decade (Weber *et al*., 1987) and persist to influence the structure and composition of mature stands, and through such impacts affect moth communities. Since fire can be patchy even at the stand level, stands regenerating after SB treatments will in the long run become more heterogeneous than those regenerating from harvesting alone and such differences may lead to differences in moth assemblages.

A closer look at individual species' responses to disturbance revealed patterns consistent with the overall moth community response to low retention harvest, with or without burning. The few exceptions observed are readily attributed to specific habitat requirements of the species in question. For example, *P. rufipectus* and *X. smithii* are generalists, feeding on herbaceous and woody plants species (Miller and Hammond, 2000; Robinson, 2002). Both of these species were, on average, more commonly collected in disturbed as compared to unharvested sites, likely reflecting post-disturbance changes in the understory vegetation (McRae *et al*., 2001). *H. furcata*, also a generalist feeder, was more abundantly collected in burned than un-burned DDOM compartments. This species was however captured in very low numbers to allow further investigations for a positive response to fire disturbance.

## 4.6 Management implications

This study documents medium-term (8-yrs post–harvest and 2-4 years post-fire treatments) impacts of retention harvest and slash-burning on lepidopterans in the managed boreal mixedwoods. Slash-burning in stands harvested to 10% retention did not alter boreal moth assemblages compared to retention harvest without burning. Fire behavior and intensity are likely modified in harvested stands, especially where low retention levels are applied, compared to unharvested. Hence, prescribed burning aimed at complementing GTR will better achieve conservation objectives as complements to high retention harvest or unharvested stands.

Although fire is a major form of disturbance in the boreal ecosystems, there are site-specific differences that determine whether disturbance by fire will naturally occur or not (Johnstone and Kasischke, 2005), and these ought to be considered and incorporated into boreal management plans. Fire resistant deciduous forests may be better managed with dispersed retention, a practice that is likely to mimic the impact of selective herbivory during insect outbreaks and the absence fire (Kemball *et al.*, 2005). On the other hand, clumped retention of sizable patches seems desirable in conifer stands as a way to emulate landscape renewal and gap dynamics created by fire, although more research is required to determine the range of patch sizes appropriate for conservation of boreal lepidopterans.

Because the impacts of fire on the landscape persist and influence the structure and composition of mature stands for a long time, harvested and burned sites will likely follow different regeneration trajectories and these differences only become apparent over an extended period of time (Buddle *et al*., 2006). Determining whether burning slash in stands harvested with retention enhance the recovery of boreal lepidopterans in managed forests will require long-term commitments to monitoring and experimentation. Without such work, suggestions about complementing green tree retention harvests with prescribed burns will only be guesses (Langor and Spence, 2008).

## References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology,* 26(1): 32-46.

Anderson, M.J., 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance, version 1. Department of Statistics, University of Auckland, New Zealand.

Angelstam, P.K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science,* 9(4): 593-602.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management,* 132(1): 39-50.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. *Canadian Journal of Forest Research,* 31: 384-391.

Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fennica,* 36(1): 81-95.

Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R., 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation,* 128(3): 346-357.

(CBIF) Canadian Biodiversity Information Facility (2003). The moths of Canada. http://www.cbif.gc.ca/spp_pages/misc_moths/phps/mothindex_e.php [accessed 2007-2008].

Clarke, K.R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology,* 18(1): 117-143.

Cobb, T.P., Langor, D.W., Spence, J.R., 2007. Biodiversity and multiple disturbances: Boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forestry Research,* 37: 1310-1323.

Cobb, T.P., Hannam, K.D., Kishchuk, B.E., Langor, D.W., Quideau, S.A., Spence, J.R., 2010. Wood-feeding beetles and soil nutrient cycling in burned forests: Implications of post-fire salvage logging. *Agricultural and Forest Entomology,* 12(1): 9-18.

Craig, A., Macdonald, S.E., 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Forest Ecology and Management,* 258(12): 2619-2627.

Franklin, J.F., Rae Berg, D., Thornburgh, D.A., Trappeiner, J.C., 1997. Alternate silvicultural approaches to timber harvesting: Variable retention harvest systems. In: Franklin, J.F., Kohm, K.A., (Eds.).Creating a forest for 21st century: The science of ecosystem management. Island Press, Washington, D.C., pp. 111-139.

Gandhi, K.J.K., Spence, J.R., Langor, D.W., Morgantini, L.E., Cryer, K.J., 2004. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. *Canadian Journal of Forest Research,* 34(6): 1319-1331.

Gotelli N.J., Ellison A.M., 2004. A primer of ecological statistics. Sinauer Associates Publishers, Sunderland, Mass, pp. 510.

Hodges, R.W., 1983. Check list of the Lepidoptera of America North of Mexico, including Greenland. In: E.W. Classey and the Wedge Entomological Research Foundation, London, pp. 284.

Hornberg, G., Zackrisson, O., Segerstrom, U., Svensson, B.W., Ohlson, M., Bradshaw, R.H.W., 1998. Boreal swamp forests. *Bioscience,* 48(10): 795-802.

Hunter, M.L., 1989. What constitutes an old-growth stand? *Journal of Forestry,* 87(8): 33-35.

Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation,* 65(2): 115-120.

Huntzinger, M., 2003. Effects of fire management practices on butterfly diversity in the forested western United States. *Biological Conservation,* 113(1): 1-12.

Hyvarinen, E., Kouki, J., Martikainen, P., Lappalainen, H., 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management,* 212(1-3): 315-332.

Hyvarinen, E., Kouki, J., Martikainen, P., 2009. Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Biodiversity,* 2(2): 93-105.

Jacobs, J.M., Spence, J.R., Langor, D.W., 2007. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. *Canadian Journal of Forest Research*, 37(9): 1631-1642.

Johnstone, J.F., Kasischke, E.S., 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research,* 35(9): 2151-2163.

Johnstone, J., Chapin, F., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems,* 9(1): 14-31.

Kemball, K.J., Wang, G.G., Dang, Q.L., 2005. Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Canadian Journal of Forest Research,* 83(12): 1550-1560.

Kishchuk B.E., Northern Forestry Centre, 2004. Soils of the ecosystem management emulating natural disturbance (EMEND) experimental area, northwestern Alberta. Northern Forestry Centre, Edmonton.

Koivula, M., Cobb, T., Dechene, A.D., Jacobs, J., Spence, J.R., 2006. Responses of two *Sericoda kirby*, 1837 (Coleoptera: Carabidae) species to forest harvesting, wildfire, and burn severity. *Entomologica Fennica,* 17(3): 315-324.

Koivula, M., Spence, J.R., 2006. Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *Forest Ecology and Management,* 236(1): 102-112.

Langor, D.W., Spence, J.R., 2006. Arthropods as ecological indicators of sustainability in Canadian forests. *Forestry Chronicle,* 82(3): 344-350.

Langor, D., Spence, J., 2008. Maintaining arthropods in northern forest ecosystems: Symposium proceedings. *Canadian Entomologist,* 140: 453-474.

Leps, J., Spitzer, K., Jaros, J., 1998. Food plants, species composition and variability of the moth community in undisturbed forest. *Oikos,* 81(3): 538-548.

Lindenmayer, D.B., Franklin, J.F., 1997. Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. *Conservation Biology,* 11(5): 1053-1068.

McCullough, D.G., Werner, R.A., Neumann, D., 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology,* 43: 107-127.

McCune, B., Grace, J.B., 2002. Analysis of ecological communities, version 5, MjM Software Design, Oregon State University, Oregon.

McRae, D., Duchesne, L., Freedman, B., Lynham, T., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Reviews,* 9: 223-260.

Miller J.C., 1996. Caterpillars of Pacific Northwest forests and woodlands. National Center of Forest Health Management, U.S. Department of Agriculture, Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2000. Macromoths of northwest forests and woodlands. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Miller J.C., Hammond P.C., 2003. Lepidoptera of the Pacific Northwest: Caterpillars and adults. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Morneau L., Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Museums and Collections Services (2001–2008) University of Alberta, E.H. Strickland Entomological Museum, Virtual Museum. http://www.entomology.ualberta.ca/ [Accessed 2006-2008]

Muirhead-Thomson R.C., 1991. Trap responses of flying insects: The influence of trap design on capture efficiency. Academic Press, London; San Diego, pp. 304.

Niemelä, J., Haila, Y., Punttila, P., 1996. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography,* 19(3): 352-368.

North American moth photographers group. http://mothphotographersgroup.msstate.edu/MainMenu.shtml. [Accessed 2006-2010].

Perry, D.A., 1998. The scientific basis of forestry. *Annual review of Ecology and Systematics,* 29: 435-466.

Pratt L., Urquhart I.T., 1994. The last great forest: Japanese multinationals and Alberta's northern forests. NeWest Press, Edmonton, AB

Price, D.T., Halliwell, D.H., Apps, M.J., Peng, C.H., 1999. Adapting a patch model to simulate the sensitivity of central-Canadian boreal ecosystems to climate variability. *Journal of Biogeography,* 26(26): 1101-1113.

Purdon, M., Brais, S., Bergeron, Y., 2004. Initial response of understory vegetation to fire severity and salvage-logging in the southern boreal forest of Quebec. *Applied Vegetation Science,* 7(1): 49-60.

Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. *Ecological Application,* 5(4): 969-977.

Robinson G.S., 2002. Hostplants of the moth and butterfly caterpillars of America North of Mexico. American Entomological Institute, Gainesville, FL.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management,* 255(1): 1-15.

Rudolph, D.C., Ely, C.A., 2000. The influence of fire on lepidopteran abundance and community structure in forested habitats of eastern Texas. *Texas Journal of Science,* 52(4): 127-138.

Scalercio, S., Infusino, M., Woiwod, I.P., 2009. Optimizing the sampling window for moth indicator communities. *Journal of Insect Conservation,* 13(6): 583-591.

Schultz, C.B., Crone, E.E., 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the fender's blue. *Restoration Ecology,* 6(3): 244-252.

Schultz, C.B., Dlugosch, K.M., 1999. Nectar and host plant scarcity limit populations of an endangered Oregon butterfly. *Oecologia,* 119(2): 231-238.

Simberloff, D., 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management,* 115(2-3): 101-111.

Southwood, T.R.E., 1994. The Importance of Long-Term Experimentation, In: Leigh, R.A., Johnston, A.E., (Eds.), Conference on insight from foresight - the role of long-term experiments and databases in agricultural and ecological science, celebrating the 150th anniversary of Rothamsted experimental-station; CY: JUL 14-17, 1993; CL: Rothamsted Experiment, Harpenden, England; TC: 6, 3-8.

Southwood T.R.E., 1995. Ecological methods: With particular reference to the study of insect populations ($2^{nd}$ Edition). Chapman and Hall, London, Eng, pp. 524.

Spence J.R., Volney W.J.A., 1999. EMEND: Ecosystem management emulating natural disturbance. Sustainable Forest Management Network report 1999-14, Sustainable Forest Management Network, Edmonton, pp. 17.

Summerville, K.S., Crist, T.O., 2001. The species richness of Lepidoptera in a fragmented landscape: A supplement to the checklist of moths of Butler County, Ohio. *Great Lakes Entomologist,* 34(1): 93-110.

Summerville, K.S., Metzler, E.H., Crist, T.O., 2001. Diversity of Lepidoptera in Ohio forests at local and regional scales: How heterogeneous is the fauna? *Annals of Entomological Society of America,* 94(4): 583-591.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest Lepidoptera: Community, guild, and species responses. *Ecological Applications,* 12(3): 820-835.

Summerville, K.S., Ritter, L.M., Crist, T.O., 2004. Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: A preliminary assessment. *Biological Conservation,* 116(1): 9-18.

Summerville, K.S., Crist, T.O., 2008. Structure and conservation of lepidopteran communities in managed forests of northeastern North America: A review. *Canadian Entomology,* 140(4): 475-494.

Swengel, A.B. 1998. Effects of management on butterfly abundance in Tallgrass prairie and Pine Barrens. *Biological Conservation,* 83(1): 77-89.

Swengel, A.B., Swengel, S.R., 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire-managed sites. *Journal of Insect Conservation,* 11(3): 263-279.

Thomas A.W., 2002. Moth diversity in a northeastern North American red spruce forest II: the effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). Canadian Forest Service. Atlantic Forestry Centre, Fredericton, NB.

Thomas, C.D., 1991. Spatial and temporal variability in a butterfly population. *Oecologia,* 87(4): 577-580.

Timoney, K.P., 2003. The changing disturbance regime of the boreal forest of the Canadian Prairie Provinces. *Forestry Chronicle,* 79(3): 502-516.

Troubridge, J.T., Lafontaine, J.D., The moths of Canada. http://www.cbif.gc.ca/spp_pages/misc_moths/phps/mothindex_e.php. 2004. 2006-2010.

Volney, W.J.A., Mallett, K.I., 1998. Integrated pest management in western Canadian boreal forests. *Forestry Chronicle,* 74(4): 597-605.

Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. 82(1-3): 283-294.

Volney W.J.A., Spence J.R., Lefebvre E.M., 2001. Boreal Odyssey: *Proceedings: North American forest insect work conference,*, May 14-18. 2001, Edmonton, Alberta. Canadian forest Service, Northern Forestry Center, Edmonton, Alberta, inf. ref. NOR-X-381.

Weber, M.G., Hummel, M., Vanwagner, C.E., 1987. Selected parameters of fire behavior and *Pinus banksiana* Lamb. regeneration in eastern Ontario. *Forestry Chronicle,* 63: 340-346.

Wikars, L.O., Schimmel, J., 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *Forest Ecology and Management,* 141(3): 189-200.

Work, T.T., Spence, J.R., Volney, W.J.A., Morgantini, L.E., Innes, J.L., 2003. Integrating biodiversity and forestry practices in western Canada. *Forest Chronicle,* 79(5): 906-916.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, 34(2): 417-430.

Young M., 1997. The natural history of moths. T & A D Poyser, London, pp. 271.

**Table 4.1** Total number of individuals and species richness by family of moths sampled using light traps at EMEND. Unharvested compartments were sampled in 2006 and disturbed sites sampled in 2007

| **Family** | **Richness** | **% richness** | **Abundance** | **% abundance** |
|---|---|---|---|---|
| Arctiidae | 6 | 3.61 | 42 | 1.36 |
| Drepanidae | 3 | 1.81 | 38 | 1.48 |
| Geometridae | 58 | 33.73 | 827 | 32.09 |
| Lasiocampidae | 1 | 0.6 | 8 | 0.31 |
| Noctuidae | 86 | 53.01 | 1565 | 61.44 |
| Notodontidae | 8 | 4.82 | 52 | 2.03 |
| Sphingidae | 2 | 1.2 | 17 | 0.66 |
| Uraniidae | 1 | 0.6 | 15 | 0.58 |
| Thyatiridae | 1 | 0.6 | 1 | 0.034 |
| **Total** | **166** | **100%** | **2565** | **100%** |

**Table 4.2** Mean abundance (± SE) and richness (± SE) of moths sampled by cover-type and treatment EMEND. Unharvested compartments were sampled in 2006 and disturbed sites sampled in 2007

| **Treatment** | **Mean abundance ± SE** | **Mean richness ± SE** |
|---|---|---|
| DDOM-unharvested | 443.3 ± 39.0 | 87.3 ± 5.4 |
| CDOM-unharvested | 190.3 ± 52.6 | 47.3 ±9.4 |
| DDOM-SB | 66.3 ± 7.3 | 24.7 ± 3.1 |
| DDOM-RH | 86.0 ± 7.0 | 32.0 ± 3.5 |
| CDOM-SB | 33.7 ± 17.3 | 19.0 ± 7.2 |
| CDOM-RH | 35.3 ± 2.4 | 19.3 ± 1.3 |

**Table 4.3** Results from two-way Permutational Multivariate Analysis of Variance (PERMANOVA) testing the effect of forest type, slash and slash-burn treatments and their interactions in structuring boreal moth communities at EMEND.

| **Source** | **df** | ***F*** | ***P*** |
|---|---|---|---|
| Cover-type | 1 | 2.95 | 0.008 |
| Treatment | 2 | 4.11 | 0.0004 |
| Cover-type*treatment | 2 | 1.43 | 0.15 |
| Residual | 12 | | |
| Total | 17 | | |
| **Pair-wise** *a posteriori* **comparisons** | | ***t*** | ***P*** |
| Unharvested vs. SB | | 2.19 | 0.0008 |
| Unharvested vs. RH | | 2.30 | 0.002 |
| SB vs. RH | | 0.72 | 0.80 |

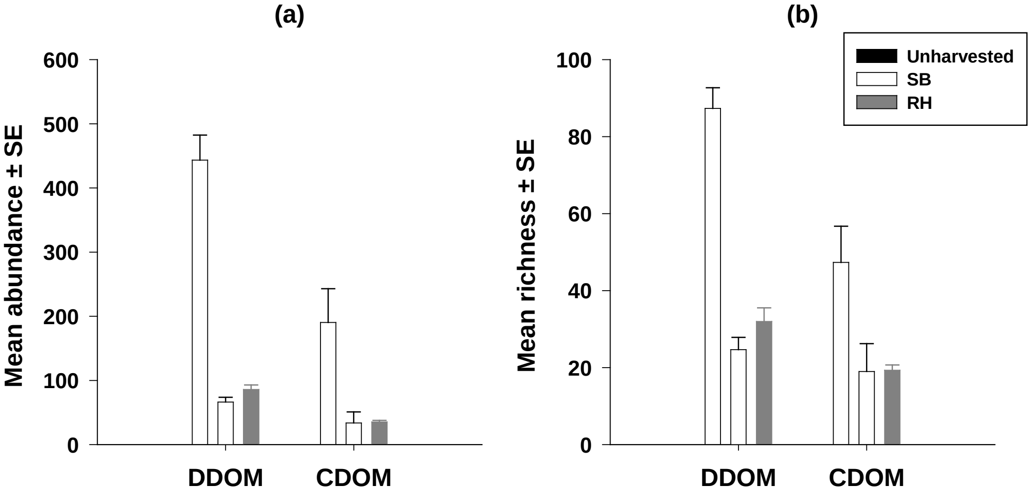

**Figure 4.1** Mean abundance ± SE (a) and richness ± SE (b) of moths sampled from the coniferous **(**CDOM**)** and deciduous **(**DDOM**)** unharvested, slash-burn (SH) and harvested (RH) treatment stands at EMEND.

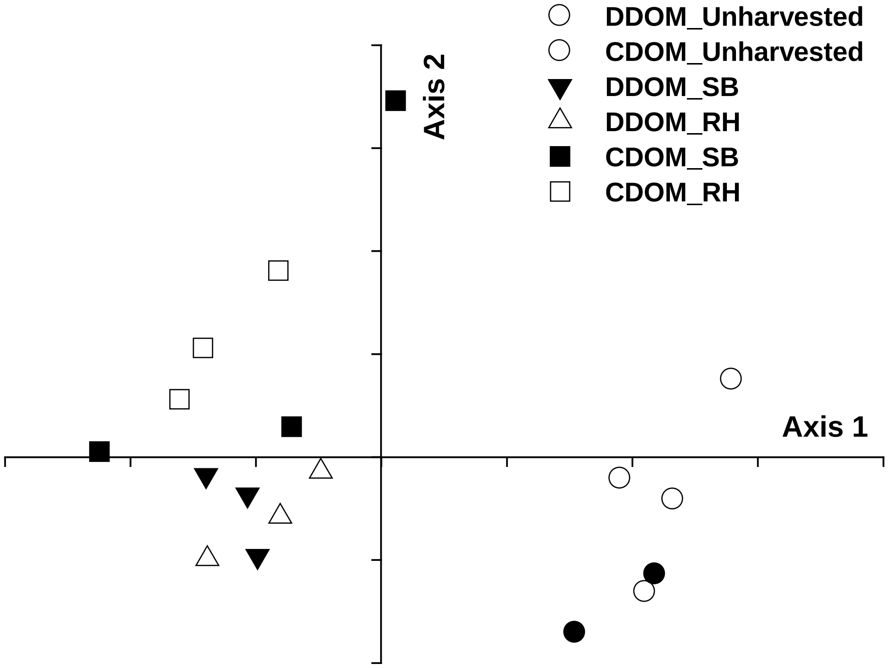

**Figure 4.2** NMDS of moth species sampled using light traps from the coniferous (CDOM) and deciduous (DDOM) unharvested, slash-burn (SB) and harvested (RH) treatment stands at EMEND. Axis 1 = 57%; Axis 2 = 31%; Final stress = 10.5.

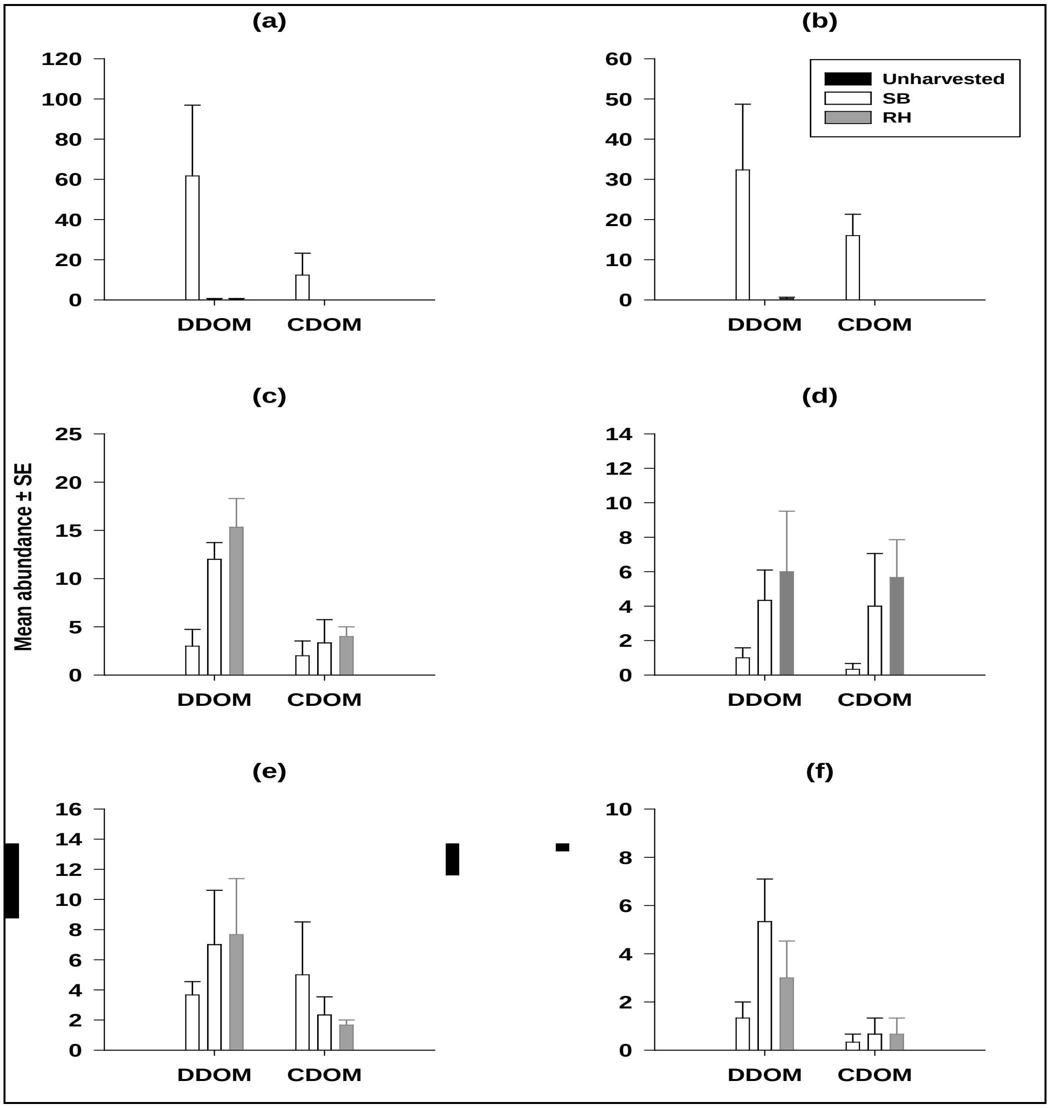

**Figure 4.3** Mean abundance ± SE of select species sampled in unharvested, harvested and slash-burn of deciduous (DDOM) and conifer (CDOM) dominated stands, illustrating the different responses observed: Decreased abundance: (a) *Enargia decolor* (Wlk.) and (b) *Venusia cambrica* Curt, increase in abundance (c) *Xestia smithii* (Snell.) and (d) *Protolampra rufipectus* (Morr.), Differential response due to pre-disturbance cover-type: (e) *Diarsia dislocata* (Sm.) and, increased abundance in burned sites: (f) *Hydriomena furcata* (Thunb.)

**Appendix 4.1:** NMS Ordination output. A final configuration (ordination scores) with stress = 10.5 was selected (Highlighted in bold on the NMS output)

```
******************** Nonmetric Multidimensional Scaling ********************
PC-ORD, 5.10
27 May 2010, 17:31


Slashburn
Ordination of plots    in species  space.        18 plots        168 species

        The following options were selected:
ANALYSIS OPTIONS
        1.   SORENSEN = Distance measure
        2.         2 = Number of axes (max. = 6)
        3.       100 = Maximum number of iterations
        4.     RANDOM = Starting coordinates (random or from file)
        5.         1 = Reduction in dimensionality at each cycle
        6.      0.20 = Step length (rate of movement toward minimum stress)
        7.   USE TIME = Random number seeds (use time vs. user-supplied)
        8.        50 = Number of runs with real data
        9.       500 = Number of runs with randomized data
       10.        NO = Autopilot
       11.   0.000010 = Stability criterion, standard deviations in stress
                      over last  15 iterations.
OUTPUT OPTIONS
       13.       YES = Write distance matrix?
       14.       YES = Write starting coordinates?
       15.       YES = List stress, etc. for each iteration?
       18.       YES = Plot stress vs. iteration?
       17.       YES = Plot distance vs. dissimilarity?
       16.       YES = Write final configuration?
       19.   ROTATED = Write varimax-rotated or unrotated scores for graph?
       20.       YES = Write run log?
       21.       YES = Write weighted-average scores for species ?
------------------------------------------------------------------------------


--------------------------------------------------------------------
Random data: 0 = not randomized, 1 = randomized
Start file: 0 = random starting coordinates, 1 = read from file
Seeds: initial seeds for random number generator
* Stability criterion not met.
**To run a single NMS ordination that repeats the best result,
  specify this file as the starting configuration,
  rather than using a random start.  It is best to
  save this file under a new name, to avoid its being
  overwritten by the next NMS run.  To do this, open the
  file using File | Open | Graph Row file, then
  File | Save as | Graph Row file (then specify new name).
```

```
STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)
-------------------------------------------------------------------
        Stress in real data        Stress in randomized data
            50 run(s)            Monte Carlo test,  500 runs
     -------------------------  -----------------------------------
Axes  Minimum     Mean  Maximum  Minimum     Mean  Maximum      p
-------------------------------------------------------------------
   1   21.126   38.704   54.433   32.384   49.526   54.462   0.0020
   2   10.515   11.786   14.840   19.504   25.279   37.194   0.0020
-------------------------------------------------------------------
p = proportion of randomized runs with stress < or = observed stress
i.e., p  = (1 + no. permutations <= observed)/(1 + no. permutations)


Conclusion:  a 2-dimensional solution is recommended.

Selected file CONFIG2.GPH  for the starting configuration for
   the final run.


Slashburn
Ordination of plots    in species  space.        18 plots        168 species

       The following options were selected:
ANALYSIS OPTIONS
       1.   SORENSEN = Distance measure
       2.          2 = Number of axes (max. = 6)
       3.        100 = Maximum number of iterations
       4.  FROM FILE = Starting coordinates (random or from file)
       5.          2 = Reduction in dimensionality at each cycle
       6.       0.20 = Step length (rate of movement toward minimum stress)
       7.   USE TIME = Random number seeds (use time vs. user-supplied)
       8.          1 = Number of runs with real data
       9.          0 = Number of runs with randomized data
      10.         NO = Autopilot
      11.   0.000010 = Stability criterion, standard deviations in stress
                     over last  15 iterations.
OUTPUT OPTIONS
      13.        YES = Write distance matrix?
      14.        YES = Write starting coordinates?
      15.        YES = List stress, etc. for each iteration?
      18.        YES = Plot stress vs. iteration?
      17.        YES = Plot distance vs. dissimilarity?
      16.        YES = Write final configuration?
      19.    ROTATED = Write varimax-rotated or unrotated scores for graph?
      20.         NO = Write run log?
      21.        YES = Write weighted-average scores for species ?
-------------------------------------------------------------------------------

 Coordinates of starting configuration
   plots         Axis
  No.  Name        1         2
    1 AD_852     61.9838    44.2895
```

```
    2 AD_862      17.3730    84.0630
    3 AD_940      85.6601    60.9204
    4 CD_889      50.7016    62.7523
    5 CD_915      14.8228    47.6576
    6 CD_918       2.5278   42.0083
    7 AD_8561     16.7359    87.0514
    8 AD_8562     54.1441    43.3556
    9 AD_8581     49.5788     6.4627
   10 AD_8582     71.9930    38.3930
   11 AD_9421     88.7808    19.9632
   12 AD_9422     86.6018     2.3709
   13 CD_8971     54.8949    17.9138
   14 CD_8972     70.0849    77.6496
   15 CD_9161      5.3073    55.8531
   16 CD_9162     88.2260     1.9570
   17 CD_9251      1.6729    31.2123
   18 CD_9252     59.4927    27.6904
```

```
     10.51515 = final stress for 2-dimensional solution
      0.00000 = final instability
           69 = number of iterations

Final configuration (ordination scores) for this run
   plots           Axis
Number Name           1         2
    1 AD_852     -0.5220    1.1216
    2 AD_862     -0.6020    1.0719
    3 AD_940     -0.1809    1.1356
    4 CD_889     -1.3744    0.4464
    5 CD_915     -0.8612    0.8067
    6 CD_918     -0.7400    0.6067
    7 AD_8561     0.5471   -0.1379
    8 AD_8562     0.4962    0.0225
    9 AD_8581     0.6763    0.1330
   10 AD_8582     0.8515    0.0363
   11 AD_9421     0.6336   -0.3076
   12 AD_9422     0.2413   -0.0719
   13 CD_8971    -0.9917   -1.4190
   14 CD_8972     0.3070   -0.8323
   15 CD_9161     0.9274   -0.6357
   16 CD_9162     0.5220   -0.6742
   17 CD_9251     0.2195   -0.3193
   18 CD_9252    -0.1496   -0.9828
```

Slashburn

```
Simultaneous VARIMAX rotation of 2-dimensional solution.
Adapted from program by P. M. Mather.
```

```
Eigenanalysis for varimax rotation reached
tolerance after   10 iterations.

Configuration after varimax rotation is listed below.

Final configuration (ordination scores) for this run
   plots          Axis
Number Name           1         2
    1 AD_852     -1.0496    0.6548
    2 AD_862     -1.0895    0.5695
    3 AD_940     -0.7715    0.8528
    4 CD_889     -1.3953   -0.3762
    5 CD_915     -1.1619    0.2059
    6 CD_918     -0.9512    0.1044
    7 AD_8561     0.5337    0.1831
    8 AD_8562     0.4035    0.2897
    9 AD_8581     0.4940    0.4806
   10 AD_8582     0.6936    0.4952
   11 AD_9421     0.6988    0.0881
   12 AD_9422     0.2414    0.0714
   13 CD_8971    -0.0564   -1.7303
   14 CD_8972     0.7115   -0.5298
   15 CD_9161     1.1240   -0.0264
   16 CD_9162     0.8054   -0.2800
   17 CD_9251     0.3582   -0.1477
   18 CD_9252     0.4111   -0.9052

Writing weighted average scores on 2 axes for   168 species
  into file for graphing.
      0.65 minutes elapsed time.

**************************** Calculations finished ****************************


Slashburn
   18 points
AD_852     -1.04960    0.65484
AD_862     -1.08947    0.56954
AD_940     -0.77146    0.85280
CD_889     -1.39526   -0.37617
CD_915     -1.16191    0.20588
CD_918     -0.95115    0.10443
AD_8561     0.53369    0.18306
AD_8562     0.40347    0.28966
AD_8581     0.49402    0.48060
AD_8582     0.69362    0.49522
AD_9421     0.69882    0.08808
AD_9422     0.24142    0.07143
CD_8971    -0.05638   -1.73030
CD_8972     0.71149   -0.52979
CD_9161     1.12400   -0.02643
CD_9162     0.80538   -0.27996
CD_9251     0.35823   -0.14769
CD_9252     0.41110   -0.90519
```

## NMS Ordination axis variance explained

```
************************* Output from Graph *************************
PC-ORD 5.10
5/27/2010, 5:49 PM

Slashburn_var

Coefficients of determination for the correlations between ordination
distances and distances in the original n-dimensional space:

          R Squared
Axis   Increment   Cumulative
 1     .574       .574
 2     .307       .880

Increment and cumulative R-squared were adjusted for any lack
of orthogonality of axes.

Axis pair     r     Orthogonality,% = 100(1-r^2)
  1 vs 2    -0.216     95.3

Number of entities = 18
Number of entity pairs used in correlation = 153
Distance measure for ORIGINAL distance: Sorensen (Bray-Curtis)
```

**Appendix 4.2: Results of PerMANOVA.** Due to the small sample size (n = 3), Monte-Carlo (MC) *p-values* ($\alpha < 0.05$) were used in tests of significance in the PerMANOVA model and pair-wise comparisons.

```
 PERMANOVA v.1.6
-----------------
A program for analyzing multivariate data on the basis of any distance measure,
according to any linear ANOVA model, using permutations.
 by M.J. Anderson
Department of Statistics
University of Auckland (2005)
 --- Experimental Design ---
 Factor 1 is Forest   with  2 levels and is fixed
 Factor 2 is Treat    with  3 levels and is fixed
 The sample size (n)          =    3
 The total no. of observations =   18
 The total no. of variables    =  168
```

```
--- Results ---
 Permutational Multivariate Analysis of Variance

 Source         df      SS          MS          F      P(perm) P(MC)
-------------------------------------------------------------------------
 Fo              1    6092.6396   6092.6396   2.9453  0.0076  0.0114
 Tr              2   17021.0035   8510.5018   4.1142  0.0004  0.0006
 FoxTr           2    5922.6801   2961.3400   1.4316  0.1080  0.1464
 Residual       12   24822.8080   2068.5673
 Total          17   53859.1313
-------------------------------------------------------------------------
 No transformation
 No standardisation
 Analysis based on Bray-Curtis dissimilarities
 Unrestricted permutation of raw data using correct permutable units
 Integer used as seed     =   2
 No. of permutations used = 4999

--- Results ---
 Pair-wise a posteriori comparisons
---------------------------------------------------------
 Term chosen: Tr
 Name of the factor being tested: Treat
 No. of sets of pairwise comparisons =       1
 No. of groups compared within each set =    3
 Total no. of tests done =                 3
 No. of raw observations per group =        6
 No. of permutable units per group =        6
 No. of permutations done =             4999
 Integer chosen for the random seed =       2
 Permutation of raw data using appropriate permutable units
---------------------------------------------------------


 Tests among levels of the factor Treat
---------------------------------------------------------
  Groups        t      P_perm     P_MC   #unique vals
---------------------------------------------------------
  ( 1, 2)    2.1865   0.0016   0.0008     462
  ( 1, 3)    2.3038   0.0024   0.0016     462
  ( 2, 3)    0.7204   0.9444   0.7996     462
---------------------------------------------------------
  Average dissimilarities within/between groups
      1      2      3
  1  66.283
```

|  |  |  |  |
|---|---|---|---|
| 2 | 90.236 | 72.363 |  |
| 3 | 88.851 | 67.066 | 68.189 |

I; Undisturbed, 2; Slash –burn (SB) and 3; Harvest (RH)

# Chapter 5: Conclusion and management implications

It is now widely recognised that conserving a significant proportion of forest biodiversity will require a far more comprehensive and multi-scaled approach than simply partitioning forest lands into reserves and production areas (Lindenmayer and Franklin, 2002). In fact, conservation strategies for managed landscapes have become an integral part of policies governing resource utilization. These new policies reflect movement toward practices that attempt to recreate as much as possible the structural and biological legacies normally associated with natural forest stands.

Central among such ‘near to nature’ strategies in Canada are a suite of harvesting techniques under the umbrella of green tree retention (Work *et al.*, 2004). A wealth of data is now available about how forest flora and fauna respond to harvesting with retention (Rosenvald and Lõhmus, 2008). From this we understand that the amount and quality of habitat maintained within the harvested matrix is important in promoting post-harvest recovery for populations of most species.

However, information about recovery of various taxa after GTR harvests is still too spotty for wide-sweeping generalization. My thesis is only the second study (see Morneau, 2002) to assess the potential of GTR in promoting post-harvest recovery of forest lepidopterans, perhaps the most ecologically important group of phytophagous species in the boreal ecosystems. Results presented in my thesis corroborate with findings about other forest arthropods (e.g., Pinzon *et al*., 2012; Work *et al*., 2010), in suggesting that responses to harvesting disturbance are determined by the level of retention, the pre-harvest cover-type as well as species-specific habitat requirements (Chapter 2). Clearly, the responses of forest lepidopterans to harvest impacts depended on cover-type differences, and differences in post-disturbance stand recovery reflect differences between the early and late successional stages (Chapter 2). Late succession coniferous forests are reset furthest from their pre-harvest conditions, and so are the biotas associated with this cover-type in the mixedwood.

For boreal moths, different levels of retention harvest determine the composition of post-harvest moth assemblages, and these changes are expressed differently in the deciduous and coniferous forests. Moth assemblages of the CDOM cover-type were characterized by grass and low plant feeders as opposed to the coniferous specialists that dominated these stands before harvesting disturbance (Chapter 2, section 2.4.3 & Table 2.4). Deciduous stands, on the other hand, did not show significant differences in moth assemblages of unharvested compartments, especially when 50% retention was applied. This observation can be attributed to the differential changes in the vegetation structure of the coniferous and deciduous dominated forest cover-types, post-harvest. Indeed, coniferous stands experience the greatest change in plant structure following harvesting as regenerating stands in sites studied herein are dominated by deciduous saplings, graminoids, woody and herbaceous plants (Craig and Macdonald, 2010). It is no wonder that the moth assemblages of the CDOM stands at EMEND differed from unharvested stands more than did those of DDOM stands.

My work demonstrates some conservation benefits for leaving at least 50% of the trees in deciduous dominated stands (Chapter 2). Specifically, retention harvest at this level supported a boreal moth community that was similar to that of the intact forest, e.g., species that are dependent on deciduous canopy trees (Chapter 2). At the same time, these retention harvests were characterized by an increase in species that feed on plants associated with early regeneration communities. Lower retention levels of 20%, however, did not promote such influxes in early successional species; neither did they maintain the community of canopy dependent species (Chapter 2).

Even though there was an overall reduction in moth populations in low retention (20 %) harvest compartments (Chapter 2), single dispersed trees in stands with such low retention showed potential for conserving moth species by maintaining populations of canopy specialists on harvested landscapes, albeit in low abundances (Chapter 3). The complete life-histories of many of these species are largely unknown. It is uncertain as to whether these presumably canopy specialists would use regenerating tree saplings as alternate hosts when the forest is cleared as no studies have examined the effect of clear-cutting on boreal canopy specialists. Thus leaving even a few single dispersed trees may be critical for ‘lifeboating’ these habitat specialists. This is especially true for moth species that are specifically associated with the coniferous stands as the density of conifers on harvested landscapes is greatly reduced by commercial forestry, and regeneration of similar areas back to the coniferous cover-type may take decades.

Despite the expected benefits of green tree retention, we must acknowledge that harvesting occurs at different spatial and temporal scales than does wildfire. In addition, factors that determine natural disturbance frequency, intensity and size, e.g., of fire, are hardly considered in the new harvesting approaches and are difficult to emulate in designing harvesting prescriptions. Most importantly, the specific impacts of natural disturbance are variable, and depend on a combination of stand structure, prevailing weather conditions and, to some extent, *bon chance*. For instance normal weather conditions may minimize the likelihood of insect outbreak, while a summer drought, especially in the context of steadily warming climate, can increase the chance of a large scale fire. Harvests are generally not designed to encompass this sort of variation. Perhaps stand and weather conditions should guide formulation of particular harvesting prescriptions so that overall landscape structure may more closely reflect the sort of variation expected to result from natural disturbance. In addition, fire does more than simply drive stand regeneration in relation to environmental conditions and the tree species being regenerated. For instance, a timely fire may kill insect populations and diseases that have reached outbreak densities (Volney and Fleming, 2000) and modify soil characteristics and nutrient dynamics (Kuuluvainen, 2002) in ways that are not comparable to post-harvest recovery.

Thus, on the whole the impacts of harvesting, even with retention, on forest structure and composition notably deviate from those of natural disturbance (McRae et al, 2001). This raises the question of whether green tree retention alone can adequately model natural disturbance. Techniques have been suggested to complement retention harvest; however we lack clearly outlined procedures and understanding of potential challenges to meet long-term goals for biodiversity conservation and forest sustainability. Incorporating fire as a management tool on harvested blocks might offer desirable results. However, harvesting regimes including green tree retention do not normally include fire in their prescriptions.

Burning slash left behind on harvested blocks is one option that might be considered to meet biodiversity management objectives. This will help to ensure that at least some harvested blocks maintain legacies associated with fire, and avoid their consistent loss and long-term exclusion on landscapes managed by humans. From the perspective of disturbance ecology this would contribute to increasing structural and biological heterogeneity on managed landscapes (Weber and Taylor, 1992).

Prescribed burning is increasingly becoming a popular tool in other aspects of forestry, promoted to manage 1) fuel loads (Moghaddas and Stephens. 2007; Kiil, 1969), 2) regeneration of fire dependent tree ecosystems [e.g., pine (Hatten, *et al*., 2008; Mcrae, *et al*., 1994,) or oak (Brose and Van Lear, 1998; Brose *et al*.,, 1999), 3) nutrient cycling (Driscoll et. al., 1998), and in general 4) to restore fire's ecological functions of structuring and maintaining forest biodiversity (Hyvarinen, *et al*., 2009). Data about the potential conservation benefits of burning following GTR harvest prescriptions for herbivorous insects are however lacking. Because the juveniles of most moths feed directly on plant material and many species are host-specific (Young, 1997), they are likely to respond differently than epigaeic taxa to changes in disturbance regimes that alter the plant community. Understanding how phytophagous lepidopterans respond to multiple disturbances of harvesting and burning will greatly contribute to the efforts of conserving boreal biodiversity.

My study is an initial attempt to assess the recovery of boreal moths following prescribed fire subsequent to retention harvest (Chapter 4). Moth responses to multiple disturbances did not depend on pre-disturbance cover-type as both forms of disturbance significantly altered the abundance, richness and composition of moth assemblages compared to those that characterized unharvested stands (Chapter 4). It is likely that long-term effects will emerge following differences in fire-created regeneration trajectories between the two cover-types (e.g., see Buddle *et al.*, 2006). Without much anthropogenic intervention, and even here we have been notably unsuccessful in the boreal mixedwood, coniferous stands that have been harvested will not automatically regenerate back to conifer. Thus, harvesting disturbances will generally increase the dominance of hardwood species (Timoney *et al*.,, 1997) on managed landscapes, without adoption of strategies to circumvent this. And, clearly this will have associated impacts on biodiversity, both for Lepidoptera (Chapter 2, 3 $ 4) and other taxa (Work *et al*., 2004; 2010; Pinzon *et al.*, 2012). It seems that low to moderate burns such as was observed in the CDOM cover-type of this study, will favor conifer regeneration much more than harvesting (Johnstone and Chapin, 2006). Thus, moth community structure of burnt than un-burnt sites may eventually differentiate in response to plant structure emerging from harvested or burnt sites, as harvesting and fire have been shown to affect biodiversity in different ways both in the short- and long-terms (McRae et. al., 2001).

Despite the fact that wildfire is recognised as a major 'natural disturbance' driver of boreal ecosystems, variations in temporal and spatial dynamics exist (Cumming, 2001; Bergeron *et al.*, 2002; Johnstone and Kasischke, 2005), and might well be considered in boreal management plans that attempt to follow a natural disturbance framework. Cumming (2001), for instance, showed that aspen dominated stands of NW Alberta are unlikely to burn, at least not until they have developed a significant amount of spruce canopy. In such stands, other forms of disturbance such as insect and disease outbreaks may be particularly important, and this should be considered especially if stands are to be left to regenerate naturally (Kemball *et al*., 2005). In contrast, fire dependent conifer stands will likely benefit the most from management plans that include prescribed burning, but spatial variation in the probability of natural fires occurring within these stands should be considered e.g., swamp forests and north facing slopes are important fire-free refugia (Hornberg *et al.*, 1998).

### ***Sampling forest moths***

A small proportion of macro-moth species previously collected using light traps in studies at EMEND (Chapter 2; Morneau, 2002) were represented in my rearing samples (Chapter 3). These species included *Enargia decolor, Ipipmorpha pleonectusa,* and *Speranza loricaria* from trembling aspen, and *Syngrapha alias*, *Macaria signaria, Idia aemula, Protoboramia porcilaria,* and *Virbia ferruginosa* from white spruce. In addition, *Scopula junctaria* (Wlk) and *Dysstroma walkerata* (Pears.) were collected from the understory of coniferous canopies. It is important to note that the fore mentioned five caterpillar species collected on white spruce are among the eight conifer feeders sampled by light traps (Chapter 2). This result is an assurance that single dispersed tress may serve as important refugia for habitat and feeding specialists, thus lifeboating these species through the regeneration cycle, especially in cases where young saplings are not used as alternate hosts after mature trees have been removed thorough harvesting.

The fact that many species collected by light traps were missing from caterpillar samples supports the idea that light trap samples better characterize whole moth communities. Light trap samples include a high number of individuals and species; lepidopteran larvae, in contrast, are challenging to sample, even though they *must* be out there. Nonetheless, key findings from caterpillar samples (Chapter 3) highlight the importance of supplementing light traps with caterpillar samples to achieve more complete inventories. For instance moths with flight periods that do not coincide with the ideal temperature conditions for light trapping available in the summer were notably absent from light trap samples. For instance, the geometrid species, *Operothoptera bruceata,* has a fall flight period and the females are flightless (Wagner, 2005). Fall night temperatures are at times too low ($< 5^0$C) for light trapping, making caterpillar sampling the best sampling method for this species. Indeed, *O. bruceata* was the most abundant caterpillar species collected on trembling aspen.  Likewise, larvae of *Gnophaela vermiculata,* a day flying moth and therefore not usually represented in light traps, were also well represented in samples collected on white spruce.

Additionally, study of larval assemblages offers important insights about lepidopteran natural history not likely to be revealed from light trap catches.

Two examples from the present study are worth noting: 1) additional information was discovered about habitat requirements for two understory species, *G. vermiculata* and *V. ferruginosa*, observed to move into the canopy for pupation; and 2) expansion of the known host-plant range for *C. persicana* in Alberta. Host plant-larval relationships have accumulated fairly slowly over the years because larvae are difficult to collect and identify. Thus, the habitat requirements of many moth species are still not yet known. Studies like mine contribute to the fuller understanding of boreal moth communities required to connect management prescriptions for biodiversity protection to relevant detail of natural history. Larval sampling also reveals that forest stratification into canopy and understory is important for understanding lepidopteran biodiversity, even though this will not be evident from light trap samples alone. Although there are some linkages, moth communities associated with the canopy are quite distinct from those found in the understory plant layer and vice versa.

Lepidopterists speculate that the understory in the boreal forest harbors more moth species in low abundances compared with the canopy (Greg Pohl, personal communication), but such a hypothesis has proved difficult to examine. My study does provide some support for this hypothesis (Chapter 3, Figure 3.1, and Appendix 3.2). My work also highlights the importance of both the canopy and understory forest layers in maintaining the diverse assemblage of caterpillars that characterize the boreal mixedwoods (Chapter 3).

Harvesting techniques aimed at improving conservation of biodiversity in the spirit of sustainable forest management must therefore seek to preserve both these structural elements on harvested landscapes. As stands are harvested, even with GTR prescriptions, there will be inevitable effects on the biodiversity of groups like forest moths that depend on the vegetation that is removed or affected. Thus, management cannot focus strictly on on-site preservation of taxa, but wise conservation initiatives will also consider how to best promote full forest recovery. Such broad management goals can only be achieved through a combination of management prescriptions, including retentions at different levels, unharvested patches and prescribed burning on harvested blocks. The benefits maybe slow in coming and quite likely will be hard to recognize in the short term or in the absence of baseline information. This thesis, together with that of Morneau (2002), provides baseline data about boreal moths which are required for recognizing and understanding the extent of recovery of the boreal moth fauna on landscapes managed for commercial forestry. Thus, the full significance of my results can only be appreciated in the future.

### *Future work*

In this thesis, I show that single dispersed trees, even at low levels of retention, can play an important role in maintaining canopy dependent species. The conservation of the whole range of the boreal lepidopteran community, including species that utilize the understory layer will however require higher retention levels than those that are currently applied in commercial forestry.

Thus, the future of boreal moth research should perhaps focus on establishing thresholds for optimal patch size required for their conservation on harvested landscapes. Retention patches have shown conservation benefits for other forest taxa, especially when applied together with dispersed retention (Pinzon *et al*., 2012). The size and spatial distribution of retention patches are important for achieving conservation benefits, and have been investigated for other boreal taxa (e.g., Pyper, 2009). Understanding the size and distribution of retention patches required for achieving meaningful conservation of forest biodiversity, and especially disturbance sensitive species such as lepidopterans, is crucial. This is because numerous studies confirm that over 50% of dispersed retention is required to achieve conservation goals, a prescription that may not be economically viable for logging companies to apply (Pinzon *et al*., 2012).

Information on how boreal biodiversity is partitioned along the vertical gradient remains elusive, and sampling the canopy is tedious and cost-ineffective. Among the handful of studies that have investigated harvesting disturbance effects on boreal moths (Morneau, 2002; Thomas, 2002 and this thesis) have mostly focused on boreal macromoths, and only the last two (both from the EMEND experiment) included sampling the canopy layer for lepidopterans. Both Morneau (2002) and this thesis show that the boreal canopy, especially in the coniferous cover-type, is characterized by a larger number of microlepidopterans (primitive moths, Monotrysian, and the lower Ditrysian superfamilies sensu). Thus, understanding how microplepidopteran species respond to canopy removal through harvesting may be more important for determining in full the ecological benefits of single dispersed trees in facilitating post-harvest recovery of forest lepidopterans. Microplepidopterans are especially vulnerable to harvesting disturbances as most are highly host-specific and are generally not strong fliers (Scoble, 1992). Some are relatively rare and for most, very little is known in terms of their natural history, feeding preferences or habitat requirements (Pohl *et al.*, 2005). Knowledge about the natural history of specific moths as well as an in depth analysis of their response to forest management practices will go a long way in developing tools for indicator species and long-term monitoring of managed boreal ecosystems.

## References

Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fennica,* 36(1): 81-95.

Brose, P.H., Van Lear, D.H., Cooper, R., 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *Forest Ecology and Management,* 113(2-3): 125-141.

Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Ecology,* 28(3): 331-339.

Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R., 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. *Biological Conservation,* 128(3): 346-357.

Cumming, S.G., 2001. Forest type and wildfire in the Alberta boreal mixedwood: What do fires burn? *Ecological Applications,* 11(1): 97-110.

Driscoll, K.G., Arocena, J.M., Massicotte, H.B. 1998. Post-fire soil nitrogen content and vegetation composition in Sub-Boreal spruce forests of British Columbia's central interior, Canada. Fort Ecol. and Manage. 121 (3): 227-237

Hatten, J.A., Zabowski, D., Ogden, A. and Thies, W., 2008. Soil organic matter in a ponderosa pine forest with varying seasons and intervals of prescribed burn. *Forest Ecology and Management,* 255(7): 2555-2565.

Hornberg, G., Zackrisson, O., Segerstrom, U., Svensson, B.W., Ohlson, M., Bradshaw, R.H.W., 1998. Boreal swamp forests. *Bioscience,* 48(10): 795-802.

Hyvarinen, E., Kouki, J., Martikainen, P., 2009. Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Biodiversity,* 2(2): 93-105.

Johnstone, J.F., Kasischke, E.S., 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research,* 35(9): 2151-2163.

Kemball, K.J., Wang, G.G., Dang, Q.L., 2005. Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Canadian Journal of Forest Research,* 83(12): 1550-1560.

Kiil, A.D., 1969. Fuel Consumption by a Prescribed Burn in Spruce-Fir Logging Slash in Alberta. *Forestry Chronicle,* 45(2): 100-102.

Kuuluvainen T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica,* 36(1):97-125.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving forest biodiversity: A comprehensive multiscaled approach. Island Press, Washington, DC., pp. 351.

McRae, D., Duchesne, L., Freedman, B., Lynham, T., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Reviews,* 9(4): 223-260.

McRae, D.J., Lynham, T.J. and Frech, R.J., 1994. Understory Prescribed Burning in Red Pine and White-Pine. *Forestry Chronicle,* 70(4): 395-401.

Moghaddas, E.E.Y., Stephens, S.L., 2007. Thinning, burning, and thin-burn fuel treatment effects on soil properties in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management,* 250(3): 156-166.

Morneau L., 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Pinzon, J., Spence, J.R., Langor, D.W., 2012. Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. *Forest Ecology and Management*, 266: 42–53.

Pohl, G.R., Langor, D.W., Landry, J.F., Spence, J.R. 2004b. Lepidopteran from boreal mixedwood forest in east-central Alberta: Comparison of assemblages from a mature and an old stand. Canadian Forest Service. Northern Forestry Centre. NOR-X-396: pp. 1-20.

Pyper, M. P. 2009. Retention patch characteristics and ground dwelling beetle diversity: Implications for natural disturbance-based management. MSc Thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alberta.

Scoble M.J., 1992. The Lepidoptera: Form, function and diversity. Oxford University Press, Oxford, pp. 404.

Thomas A.W., 2002. Moth diversity in a northeastern North American red spruce forest II: the effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). Atlantic Forestry Centre, Fredericton, N.B.

Timoney, K.P., Peterson, G., Wein, R., 1997. Vegetation development of boreal riparian plant communities after flooding, fire, and logging, Peace River, Canada. *Forest Ecology and Management,* 93(1-2): 101-120.

Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. 82(1-3): 283-294.

Wagner D.L., Ferguson D.C., McCabe T.L., Reardon R.C., 2001. Geometrid caterpillars of northeastern and Appalachian forests. Forest Health Technology Enterprise Team, U.S. Department of Agriculture Forest Service, Morgantown, WV.

Weber, M. G. Taylor, S. W., 1992. The use of prescribed fire in the management of Canada's forested lands. *Forestry Chronicle,* 68(3): 324-334.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Canadian Journal of Forest Research*, 34(2): 417-430.

Work, T.T., Jacobs, J.M., Spence, J.R., Volney, W.J., 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications,* 20(3): 741-751.