INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

**SAPROXYLIC BEETLES AND DEADWOOD STRUCTURE IN MANAGED AND
NATURALLY DISTURBED SPRUCE FORESTS IN NOVA SCOTIA**

by

DeLancey J. Bishop, B.Sc.H.

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

Master of Science

Department of Biology

Carleton University

Ottawa, Ontario, Canada

28 May 1998

© DeLancey J. Bishop 1998

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-36922-6

The undersigned recommend to the
Faculty of Graduate Studies and Research
acceptance of the thesis

“SAPROXYLIC BEETLES AND DEADWOOD STRUCTURE IN MANAGED AND
NATURALLY DISTURBED SPRUCE FORESTS IN NOVA SCOTIA”

submitted by

DeLancey J. Bishop

B.Sc.H. Acadia University 1996

in partial fulfillment of the requirements for
the degree of Master of Science

Chair, Department of Biology

Thesis Supervisor

28 May 98
Date

Carleton University

ABSTRACT

Modern forestry alters invertebrate assemblages by altering the microhabitats of invertebrate species. I studied relationships between saproxylic beetles and deadwood structures in spruce forests with natural (wind and fire) and forestry (clearcut and clearcut with thinning) disturbance histories. I tested the predictions that species assemblages would differ in composition and be less diverse in managed forests due to a different and lower diversity of deadwood structures. Little evidence supported the prediction of lower species diversity, either locally or across an array of forests. However, analysis revealed different assemblage compositions between managed and naturally disturbed forests, and lower assemblage turnover between managed forests. I discerned species that may indicate different disturbance histories, species correlated with different forest structures, and the forest structures that best explain differences in species assemblages between forests of different disturbance histories. I make research and management recommendations regarding the preservation of saproxylic species in managed forests.

ACKNOWLEDGMENTS

If I have approached scientific rationality during these past two years it is largely because of my supervisor, Stewart Peck; his wisdom, patience, and kindness have allowed my time at Carleton to be a pleasant and productive learning experience. My advisors M. Forbes and F. Chapleau provided useful criticism along the way. S. Bondrup-Nielsen of Acadia University enthusiastically contributed to the study design and provided nearly all sampling materials. R. Cameron kindly and greatly assisted the forest selection process and offered laboriously-collected forest data without hesitation. K. Potter also went out of her way to provide previously collected forest data. L. Parriag, L. Maddison, and C. Bishop provided fine field and laboratory assistance. The following coleopterists kindly identified whatever form of beetle I could not: J. Cook (Carleton University), F. Andrews (USDFA Analysis and Identification, California), D. Chandler (University of New Hampshire), J. Klimaszewski (BC Research, British Columbia), Y. Bousquet, D. Bright, A. Davies, S. Laplante, and A. Smetana (all from the Agriculture Canada Biosystematics Research Center, Ottawa). Without the support of these individuals and the availability of the *invaluable* Canadian National Collection this work would be less than what it is—hundreds of species less. A scholarship from the Natural Sciences and Engineering Research Council funded this aspect of my education. The Nova Scotia Department of Natural Resources supported a summer assistant, thanks to T. Duke and J.S. Boates. Another keystone of this project is J. Kukalova-Peck, who's motherly kindness perhaps saved this oft homesick boy. And I am never without the love of Mom, Dad, Linda, and Cohen. Finally, I thank the saproxylic beetles; I hope this helps you!

TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	ix
LIST OF APPENDICES.....	x
CHAPTER ONE	
DEADWOOD DIVERSITY AND SAPROXYLIC BEETLE DIVERSITY IN MANAGED AND NATURALLY DISTURBED SPRUCE FORESTS: TESTING RELATIONSHIPS AND ASKING WHETHER ECOLOGICAL INTEGRITY IS VIOLATED BY MODERN FORESTRY PRACTICES.....	1
INTRODUCTION.....	1
METHODS.....	6
Study forests.....	6
Forest habitat structure.....	7
Saproxylic beetle sampling and identification.....	11
Statistical analyses.....	13
RESULTS.....	19
Local diversity scale.....	22
Beta diversity scale.....	26
Gamma diversity scale.....	29
DISCUSSION.....	31
The beta-scale: spatial turnover in forest composition and ecological integrity.....	33
More of fewer species? A potential sampling error with dire consequences.....	36
Future research and forest management in Nova Scotia.....	38
Summary.....	42

CHAPTER TWO

SAPROXYLIC BEETLE SPECIES AS INDICATORS OF DISTURBANCE HISTORY
AND FOREST STRUCTURE IN NOVA SCOTIA SPRUCE FORESTS.....43

INTRODUCTION.....	43
METHODS.....	46
Statistical analyses.....	46
RESULTS.....	49
Species indicators of forest disturbance history.....	49
Species~structure models.....	50
Fauna differentiating forest disturbance classes and structural correlates	51
DISCUSSION.....	55
Indicators of forest disturbance and indicators of forest structures.....	56
Observation and hypothesis testing towards confirming or rejecting species as indicators.....	58
LITERATURE CITED.....	61

LIST OF TABLES

CHAPTER 1

Table 1. Mean age of dominant canopy trees and general disturbance history of each forest.....	9
Table 2. Distribution of forests delineated by age and disturbance history classes.....	9
Table 3. Description of forest structure variables measured in each forest.....	10
Table 4. Description of calculated habitat (A) and beetle (B) diversity attributes.....	15
Table 5. Spearman's rank correlations between forest structure variables.....	20
Table 6. Mean and standard deviation of each forest structure within forest disturbance classes, and Kruskal-Wallis results for test of differences between disturbance classes....	20
Table 7. Mean and standard deviation of each forest structure diversity attribute within forest disturbance classes, and ANOVA results for test of differences between disturbance classes.....	24
Table 8. Mean and standard deviation of each beetle assemblage diversity attribute within forest disturbance classes, and ANOVA results for test of differences between disturbance classes.....	25
Table 9. Significant multiple linear regression models of beetle assemblage attributes regressed against forest structure diversity attributes.....	25
Table 10. Results of multi-response permutation procedures analysis, testing for separation of disturbance history classes based on (A) beetle assemblage and (B) forest habitat structures.....	27

CHAPTER 2

Table 1. Results of indicator species analysis.....	50
Table 2. Species with positive relationships with structures considered characteristic of wind disturbed forests and species with positive relationships with structures considered characteristic of thinned forests.....	51

LIST OF FIGURES

CHAPTER 1

Figure 1. Location of forests sampled.....	10
Figure 2. The window flight intercept trap design.....	12
Figure 3. Means of crown closure and deadwood variables for each forest within each disturbance history class.....	21
Figure 4. Habitat structure diversity measures for each forest within disturbance history classes.....	23
Figure 5. Beetle assemblage measures for each site within disturbance history classes....	24
Figure 6. Non-metric multidimensional scaling ordination diagrams of forest sites in two-dimensional space defined by (A) beetle assemblage and (B) habitat structures	28
Figure 7. Species-area curves for each forest disturbance class.....	30
Figure 8. Hypothetical species-area curves to illustrate the expected contrast of a curve derived from forests with more of fewer species relative to a control.....	30

CHAPTER 2

Figure 1. Canonical correspondence analysis ordination bi-plot of forest sites in the space of linear combinations of the forest structures best correlated with the beetle assemblage.....	54
---	----

LIST OF APPENDICES

APPENDIX 1. List of saproxylic beetle assemblage sampled, name of determiner, new collection records, and total abundance of individuals sampled.....	70
APPENDIX 2. Forest structure information matrix.....	76
APPENDIX 3. Dufrene and Legendre's (1997) method of calculating indicator values, which assumes that two or more <i>a priori</i> groups of sample units exist, and that species abundances have been recorded in each of the sample units.....	77
APPENDIX 4. Generalized linear regression models for beetle species in relation to forest structures.....	79
APPENDIX 5. Abundance of each saproxylic beetle species sampled in each forest.....	84
APPENDIX 6. Forest location information as on beetle specimen collection labels.....	93

CHAPTER ONE

DEADWOOD DIVERSITY AND SAPROXYLIC BEETLE DIVERSITY IN MANAGED AND NATURALLY DISTURBED SPRUCE FORESTS: TESTING RELATIONSHIPS AND ASKING WHETHER ECOLOGICAL INTEGRITY IS VIOLATED BY MODERN FORESTRY PRACTICES

INTRODUCTION

Along with climatic, geologic, and biogeographic factors, disturbance is one of the main determinants of ecosystem structure, composition, and function (reviewed in Pickett and White 1985 and Attiwill 1994). The concern over changing biodiversity in forest ecosystems most basically relates to the differences between historic natural disturbances and the disturbances caused by modern forestry practices (Haila and Kouki 1994, Haila *et al.* 1994). Haila *et al.* (1994) summarize three major changes to forest environments affected by modern forestry: (1) changes in the size, age, and configuration of forest stands, (2) changes in the structural features of forests and edge-effects, and (3) loss of particular microhabitats, especially those that emerge in the later stages of forest development. Concern about changes in assemblages of forest species, obviously, relates to changes in the habitats on which species depend.

Heightened scientific awareness and public concern about forest biodiversity has led to the inclusion of biodiversity values in many forest management strategies (e.g., Canadian Council of Forest Ministers 1995; National Board of Forestry, Sweden 1996). The general agreement is that 'ecological integrity' in managed forests is approximated when human behavior in forest ecosystems does not generate biodiversity patterns and processes that are

different than what would result by historical natural disturbances in those ecosystems. Thus, many strongly advocate the evaluation of management practices by their capacities to approximate the effects of natural disturbances (Attiwill 1994; Haila *et al.* 1994; Haila 1994; McCarthy and Burgman 1994). Approaching ecological integrity by this manner faces the challenges of identifying (1) what biodiversity patterns are indicative of natural disturbances, (2) how this biodiversity is different from that generated by forestry practices, and (3) how alteration of habitat elements by forestry mediate changes in biodiversity.

Clearly the above strategy requires the use of biodiversity indicators appropriate for examining the relationships between forest disturbances, forest structures, and forest species. In the current study, saproxylic beetles (Order Coleoptera) are used to examine these relationships in spruce (*Picea rubens* Sarg. or *P. mariana* Mill.) forests in Nova Scotia.

Many authors suggest that beetles in general tend to fulfill indicator criteria relatively better than other invertebrate groups (Pearson 1992; Pearson and Cassola 1992; Nilsson *et al.* 1995; Weaver 1995; Oliver and Beattie 1996). Beetles represent one of the most diverse and taxonomically well known invertebrate orders in forest ecosystems. Higher beetle taxa occupy a breadth of habitats and many species are associated with specialized niches (Warren and Key 1991). This attribute allows large samples that show high sensitivity to spatial and temporal heterogeneity in forest habitats. At temperate latitudes, beetles are relatively well known and stable taxonomically (though this is certainly more true of the Old World fauna). These facts and the fact that beetles can be easily sampled using relatively inexpensive methods contribute to the general value of beetles as an indicator of forest biodiversity.

Several reasons warrant the use of saproxylic beetles as indicators. Saproxylic beetles, by definition, depend directly or indirectly on one of the most abundant forest resources, deadwood. Deadwood is a critical component in the composition and function of forest ecosystems. Most research into the ecological importance of deadwood probably comes from Europe. Warren and Key (1991) cite literature that describes as many as 20 variables of deadwood substrates by which the microhabitats of European saproxylic insects (predominately beetles) are segregated. These variables include tree age, species, size, moisture, decay state, and microclimate. The same authors point out that as many as 20 species of saproxylic beetles once endemic to the UK are thought to have gone extinct over the last few centuries.

Deadwood is undoubtedly a key determinant of forest biodiversity. Much evidence suggests that the abundance, physical state, and quality of deadwood is often changed when natural disturbances are replaced by forestry disturbances (Gore and Patterson 1986; Hagan and Grove 1996; Sturtevant *et al.* 1997). Particular conservation issues become evident as one considers the factors that differentiate forestry practices from natural disturbances. Unlike natural disturbances which occur stochastically, forestry is deterministic (Attiwill 1994) and aimed toward specific economic ends, namely, the maximization of sustainable fiber productivity. Over recent decades, industry and government in Canada and across the globe have favored even-age management practices of clearcut-replanting or clearcut-regeneration with thinning. Natural disturbances have therefore been replaced predominately by even-age forestry, resulting in the following changes in deadwood structures: (1) loss of deadwood size structures (large diameter deadwood disappears due to short-lasting stand

rotations); (2) a decreased local array of deadwood decay structures (reduced to cohorts of single decay stages passing through even-aged stand cycles); (3) loss of standing deadwood (during clearcutting and thinning because there is no, or decreased, economic value in standing deadwood), and (4) loss of deadwood from non-economic tree species (due to removal or thinning of the undesirable species).

The trends outlined above lead to a set of predictions explaining the relationship between saproxylic beetle assemblages and habitat structures in managed and naturally disturbed forests. These are summarized below, conceptualized under the three scales of heterogeneity (alpha, beta, and gamma) as delineated by Whittaker (1972).

At the local, within-forest (alpha) scale,

- naturally disturbed forests will exhibit higher local heterogeneity in deadwood habitat structures than forests under even-age management regimes;
- local diversity of saproxylic beetle assemblages within forests is proportional to the heterogeneity of deadwood habitat structures within forests;
- local diversity of saproxylic beetle assemblages will be higher within naturally disturbed forests than within even-age managed forests.

At the regional, between forest (beta) scale,

- heterogeneity in deadwood habitat structures will be higher between naturally disturbed forests than between forests under even-age management regimes;
- turnover of saproxylic beetle assemblages between forests is proportional to the heterogeneity of deadwood habitat structures between forests;

- turnover of saproxylic beetle assemblages will be higher between naturally disturbed forests than between even-age managed forests;
- the beetle assemblage and forest structures will differ depending on disturbance history classes; this is to say that forests defined by beetle species and forests defined by deadwood structures will be more similar within disturbance classes than between disturbance classes.

Considering the overall (gamma) diversity,

- the overall (gamma) diversity will be higher in naturally disturbed forests than in evenly managed forests.

The larger goal of this study is to help understand the importance of structural heterogeneity of habitats on a scale by scale basis, and how the total saproxylic beetle assemblage in naturally-disturbed and managed forests is built-up by heterogeneity of deadwood at the alpha and beta scales. Ultimately, this paper attempts to addresses whether changes to forest management may be warranted at the local scale and/or regional scale, and what the general nature of these changes might be.

METHODS

Study forests

Thirty spruce forests with predominately natural (fire and wind) or anthropogenic (clearcutting and clearcutting followed by thinning) disturbance histories were selected for beetle sampling in central Nova Scotia. Forests were concentrated in two regions: in or adjacent to the Liscomb Game Sanctuary and in an area north of St. Margaret's Bay (Figure 1). Table 1 shows the mean age and disturbance history of each forest. Selection of forests with the desired disturbance histories was achieved by first interviewing forestry company managers and local Nova Scotia Department of Natural Resources forest technicians. Their initial suggestions were followed up by visiting each forest for closer appraisal. To limit variability related to tree species diversity, I stipulated that forest canopy trees had to be dominated by spruce (70 % minimum). Stands of this vegetation composition had to be large enough to contain a 40 x 120 m trap sampling grid with a surrounding 100 m barrier to limit edge effects from forests of different composition, riparian areas, or other non-forested areas (including recent clearcuts). Times since last intense disturbance (clearcut, fire, severe hurricane, etc.) were limited to a minimum of 30 years, as indicated by age of dominant canopy trees. Table 2 shows the distribution of the 30 forests among disturbance history and age classes. A concentration of thinned forests in the young age range reflects the recent history of thinning as a management practice. A concentration of wind disturbed forests in the older age range reflects the fact that wind disturbance in Nova Scotia is generally of low intensity, allowing trees to become much older than does short-rotation forestry disturbance. Managed forests were common and thus chosen randomly from a larger subset of forests; the

rarity of naturally disturbed spruce forests, on the other hand, allowed no room for random selection.

Mean age of dominant canopy trees in forests ranged from 30 to over 250 years. The closest two forest centers were 800 m apart while the most distant two were separated by 190 km. Coarse granite glacial till comprised the underlying substrate of all forests except for two with a slate bedrock. Red spruce (*Picea rubens* Sarg.) was the dominant canopy tree species in 27 forests. The remaining three forests were of fire origin and dominated by black spruce (*Picea mariana* Mill.), a species dependent on fire for regeneration when not in lowland or bog soils. One should note that black and red spruce are known to cross and they are often difficult or impossible to distinguish (Roland and Smith 1983). Although one might still expect beetle variation in fire origin forests solely due to the dominance by black spruce instead of red spruce, the nature of this research is to consider differences caused by different disturbance histories, and black spruce in fire origin forests is one of these differences.

Forest habitat structure

To subsample deadwood volume and crown closure in each forest, six 15 x 15 m plots were located at 40 m intervals along two parallel transects spaced 40 m apart. For each piece of deadwood, the length and diameter at each end were measured to permit calculation of volume based on the frustum of a cone. However, a slightly different method was used for 11 of the forests, where the volume of standing dead trees was calculated based on the volume of a complete cone by using basal diameter and height measurements. All deadwood measurements for these 11 forests was collected one year previously by Potter (1997). Tree

species and decay state were recorded for each piece of deadwood to allow subsequent tallying of volumes in different classes. Deadwood decay classes follow the Nova Scotia Department of Natural Resources' Forest Resource Inventory 1992-2001 Field Specifications (class boundaries stated in Table 3). To estimate percent crown closure, two methods were used. In most forests, a flat 5 x 5 cm mirror with 20 equally-spaced dots was held horizontal at chest level to determine the proportion of dots occurring in crown-covered space. In remaining forests, a bathroom-tissue tube was used as a crude scope to visually estimate proportions of crown closure. Applying both methods in one forest to test comparability returned similar results, and neither method was dominant in any one forest disturbance class (a possible source of bias). Three crown closure readings were taken at random distances (10 -20 m) from each of the six plot centers throughout late July to early August (during peak deciduous foliage). Within each plot, a healthy dominant canopy tree was cored to estimated tree age. Descriptions of all variables measured are given in Table 3. Appendix 2 presents the forest structure information.

Table 1. Mean age of dominant canopy trees and general disturbance history of each forest. PCT = pre-commercial thinning, CT = commercial thinning.

Forest No.	Age	Disturbance History	Forest No.	Age	Disturbance History	Forest No.	Age	Disturbance History
1	47	fire	11	49	wind	21	90	wind
2	70	wind	12	52	clearcut	22	72	clearcut
3	50	clearcut	13	52	clearcut, CT	23	200	wind
4	51	clearcut	14	44	clearcut, CT	24	250	wind
5	118	wind	15	69	fire	25	102	wind
6	51	clearcut	16	59	fire	26	59	wind
7	45	clearcut, PCT	17	70	fire	27	46	clearcut, PCT
8	38	clearcut, PCT	18	106	wind	28	53	clearcut
9	67	clearcut, CT	19	75	wind	29	30	clearcut, PCT
10	45	clearcut	20	35	clearcut, PCT	30	115	wind

Table 2. Distribution of forests delineated by age and disturbance history classes.

Disturbance History Classes	Class Codes for Reference Hereafter	Mean Canopy Tree Age (years)		
		30 - 49	50 - 69	70+
clearcut origin	CLEARCUT aka CC	1	6	4
clearcut and subsequently thinned	CC&THINNED aka CC&T aka THINNED	6	2	0
naturally disturbed (fire origin)	FIRE	1	2	1
naturally disturbed (wind only)	WIND	1	2	5
total		9	11	10

Figure 1. Location of forests sampled. Forests indicated by numbers 1-30.

Table 3. Description of forest structure variables measured in each forest.

Variable	Description
CROWN	crown closure (%)
SIZE1	volume of deadwood with diameter 0-15 cm ($\text{m}^3 / 100\text{m}^2$)
SIZE2	volume of deadwood with diameter 16-30 cm ($\text{m}^3 / 100\text{m}^2$)
SIZE3	volume of deadwood with diameter >30 cm ($\text{m}^3 / 100\text{m}^2$)
DECAY1	volume of deadwood with little or no decay ($\text{m}^3 / 100\text{m}^2$)
DECAY2	volume of deadwood with 1-5 cm decay depth ($\text{m}^3 / 100\text{m}^2$)
DECAY3	volume of deadwood with >5 cm decay depth ($\text{m}^3 / 100\text{m}^2$)
STANDING	volume of deadwood standing, > 45° from floor ($\text{m}^3 / 100\text{m}^2$)
FALLEN	volume of deadwood fallen, < 45° from floor ($\text{m}^3 / 100\text{m}^2$)
DECIDUOUS	volume of deadwood in deciduous species ($\text{m}^3 / 100\text{m}^2$)
CONIFER	volume of deadwood in coniferous species ($\text{m}^3 / 100\text{m}^2$)
ALLDWOOD	volume of all deadwood measured ($\text{m}^3 / 100\text{m}^2$)

Saproxylic beetle sampling and identification

To systematically sample saproxylic beetles in spruce forests, window flight intercept traps (FIT) were deployed (Figure 2). The FIT is passive in that it does not attract beetles, thus providing random samples of the fauna that are active in the local environment (though samples are clearly biased toward sampling flying fauna). Økland (1996) showed that window FITs were superior to other methods for providing large samples of saproxylic beetles. The current design consists of two bisecting 30 x 30 cm transparent plastic (Lexan 0.030) panes, covered with a white plastic (Styrene 0.040) conical roof for rain shelter, and attached to a Styrene collecting funnel below. Removable plastic urine sample jars attached at the base of the collecting funnel hold a killing/preserving solution of water-diluted ethylene glycol antifreeze (50:50) with a small amount of detergent. In each site, six FITs were hung from existing tree branches, with the bottom of the trapping surface approximately 1 m above the forest floor. FITs were located approximately 40 m apart along two parallel transects separated by the same distance. Traps were positioned approximately along the axis of forest structure sampling plots.

All FITs were set up during 13-19 May 1997 and run until 13-15 August 1997. Catches were collected every two weeks within 3 days of each other, and the antifreeze solution was changed during this time. This gave six two-week samples for each trap, with the collection dates on or adjacent to 3 June, 16 June, 1 July, 13 July, 30 July, and 14 August. Beetles were separated from each trap sample within one week and preserved in acetic 70% ethyl alcohol.

Figure 2. The window flight intercept trap design.

Only saproxylic beetle species were identified for this study, defined here using a modification of Speight's (1989) definition of saproxylic invertebrates: 'Species [in the order Coleoptera] that are dependent, during some part of their life cycle, on the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics.' Appendix 1 gives the full list of species selected for analysis and the total number of specimens sampled from each species. Due to a lack of information on species-specific habitat associations for North American saproxylic beetles, decisions for including species in the data analysis was based on family-level habitat information; therefore, not all species analyzed as saproxylic are necessarily so. For example, while many larvae of the family Elateridae (click beetles) are known to be

saproxyllic, many others are known to be soil dwellers, but the later fact did not lead to the exclusion of elaterid species from the analysis. On the other hand, 13 species that were sampled in low abundance and suspected to be introduced (according to Bousquet 1991) were excluded from analysis, even if known to be saproxyllic, because they were not part of the pre-Columbian fauna and thus not considered equally valuable as indicators of ecological integrity.

Beetle species were identified by beetle specialists or by myself through a combination of keys (largely Downey and Arnett 1996 but also numerous more specific references) and comparison/confirmation using specimens from the Canadian National Collection at the Biosystematics Research Center in Ottawa. Nomenclature mainly follows Bousquet (1991).

Statistical analyses

The aim of the initial analysis was to determine if the habitat structures measured in each forest were correlated with each other. For this, Spearman's rank correlation tests (Freund 1992) were used, with level of significance adjusted for multiple tests using a Bonferroni correction (Weisberg 1985).

The next objective was to test whether habitat structures differed depending on the disturbance history classes: (1) clearcut, (2) cc & thinned, (3) fire, and (4) wind. For this, distribution-free Kruskal-Wallis tests (non-parametric analogs to one way analysis of variance) were used, followed by Numenyi *a posteriori* multiple comparison tests where the initial tests suggested a significant ($p < 0.05$) difference (described in Zar 1996).

To test predictions pertaining to the local (alpha) scale, the initial procedure was to reduce the forest structure and beetle assemblage information from each forest to meaningful diversity attributes. The Shannon diversity index (Brower *et al.* 1990) was chosen to index both entities, based on the following reasons: (1) the Shannon index seems to be more statistically robust to parametric analyses relative to similar indices (Magurran 1988); (2) the measure is among the class of diversity indices that are more sensitive to the occurrence of rare species than to species evenness (Magurran 1988) (favorable here because the species data set is dominated by infrequently sampled species); and (3) the measure is also applicable to the task of quantifying habitat diversity (Brower *et al.* 1990), so the single index could serve both forest entities.

To allow deeper insight into how structural diversity compares between the four disturbance regimes, the Shannon diversity value was calculated independently for four aspects of structural diversity: diversity of (1) deadwood decay classes, (2) deadwood size classes, (3) deadwood standing/fallen classes, and (4) deadwood hardwood/softwood classes. The Shannon diversity for the beetle assemblage was calculated without refinement. Nine additional beetle assemblage attributes were calculated for each forest: total species richness, total abundance, richness:abundance ratio, and the number of species in each site with an all-sites sample total of 1, 5 or less, 10 or less, 15 or less, 30 or less, and 60 or less. Variables depicting habitat and beetle diversity are in Table 4.

The structural diversity and beetle assemblage attributes were independently tested for any differences with respect to disturbance history using parametric, one-way ANOVA, with Tukey HSD multiple comparison tests to detect the location of significant ($p < 0.05$)

differences between each disturbance history class. Taking the measures of the beetle assemblage to be the dependent variables and the forest habitat diversity variables as the independent variables, stepwise multiple linear regression analysis (Weisberg 1985) was used to test if and how aspects of the beetle assemblage were related to deadwood habitat heterogeneity. Assumptions of independence and homogeneity of variance were checked by plotting residuals. The assumption of normality of residuals was checked with histograms of residuals for each test.

Table 4. Description of calculated habitat (A) and beetle (B) diversity attributes.

Variable Name	Description
(A) SHAN-SIZE	Shannon diversity index of deadwood in 3 size classes
SHAN-DECAY	Shannon diversity index of deadwood in 3 decay classes
SHAN-POS	Shannon diversity index of deadwood in 2 position classes (standing and fallen)
SHAN-D/C	Shannon diversity index of deadwood in 2 tree type classes (deciduous or conifer)
SHAN-ALL	Shannon diversity index of all 10 deadwood classes (above)
(B) ABUNDANCE	total number of beetles from all species sampled
RICHNESS	total number of beetle species sampled
RICH/ABUN	RICHNESS / ABUNDANCE (above)
SHANNON	Shannon diversity index of all beetles in each site
RARE-1	number of species sampled at site for which the total catch was 1 individual
RARE-5	number of species sampled at site for which the total catch was 5 or fewer
RARE-10	number of species sampled at site for which the total catch was 10 or fewer
RARE-15	number of species sampled at site for which the total catch was 15 or fewer
RARE-30	number of species sampled at site for which the total catch was 30 or fewer
RARE-60	number of species sampled at site for which the total catch was 60 or fewer

The structural diversity and beetle assemblage diversity attributes were separately tested for any differences with respect to disturbance history using parametric, one-way ANOVA, with Tukey HSD multiple comparison tests to detect the location of significant ($p < 0.05$) differences between each disturbance history class. Taking the measures of the beetle assemblage to be the dependent variables and the forest habitat diversity variables as the independent variables, stepwise multiple linear regression analysis (Weisberg 1985) was used to test if and how beetle assemblage diversity attributes were related to deadwood structural diversity attributes and crown closure. Assumptions of independence and homogeneity of variance were checked with residual plots. The assumption of normality of residuals was checked with histograms of residuals for each test.

Analysis at the regional scale demanded a very different statistical approach for the objective of observing spatial turnover of the beetle communities and forest structures between forests in relation to disturbance history classes. First, the ordination technique non-metric multidimensional scaling (NMS) (see Clark 1993) was used to observe the relationship between forests of different disturbance histories with regard to the habitat structures and the beetle assemblages. The results of these ordinations are represented in two-dimensional scatter plots wherein the space between forest points represents their dissimilarity with regard to beetle assemblages and forest structures, allowing an immediate and intuitive visual evaluation.

Secondly, multi-response permutation procedures (MRPP) were used to test whether beetle- and structure-defined forests differed across disturbance history classes. This non-parametric analog to discriminant analysis circumvents assumptions of normality and

homogeneity of variance that almost certainly could not be met with the current data set. The MRPP method also returns the mean distance between sample points within each disturbance history group to determine the relative heterogeneity between forests within each class.

For the distance measure in both the NMS and MRPP, the Sørensen coefficient (also known as the Czekanowski or Bray-Curtis coefficient) was used. It measures percent dissimilarity (PD) between two samples. The distance is calculated

$$PD = 1 - 2W/A + B$$

where W is the sum of shared abundances and A and B are the sums of abundances in individual sample units. Studies illustrate that the Sørensen coefficient is indeed a linear function of the difference in composition between samples, assuming adequate sample sizes (Wolda 1981; Kohn and Riggs 1982). In simulation testing of the robustness of several distance measures, Faith *et al.* (1987) found that the Sørensen coefficient was one of the most reliable performers. In NMS and MRPP, the Sørensen coefficient is thought to de-emphasize outliers compared to the more commonly employed Euclidean distance measure (McCune and Mefford 1995).

For analysis at the gamma scale, species-sample curves were constructed with first and second order Jackknife estimates to test the prediction that total species richness of all naturally disturbed forests (fire and wind, inclusive) was higher than that of all managed forests (clearcut and clearcut plus thinned, inclusive). Species-sample curves were also constructed for each forest disturbance history class individually to allow a visual evaluation of the regional richness trends relating to these classes.

Correlation analysis, ANOVA, and multiple linear regression techniques were performed using SYSTAT Version 5.02 (Systat Inc. 1993). The ordination and species-sample curves were calculated using PC-ORD Version 3.09 (McCune and Mefford 1997).

RESULTS

The identified saproxylic beetle assemblage totaled 11569 individuals representing 286 species in 43 families (Appendix 1). The assemblage includes a high proportion of new provincial, regional, and national collection records, and species that are undescribed. More details regarding the fauna are presented in Chapter Two.

Forest structure generally showed high variation within disturbance history classes (Figure 3). Significant positive correlations existed between several of the deadwood habitat variables (Table 5), which is to be expected because the categorization of these structures were not exclusive of each other. Significant between-class differences were identified for 2 of the 12 variables tested (Table 6). Crown closure (CROWN) was significantly higher in wind disturbed forests than in fire disturbed forests. Small-diameter deadwood (SIZE1) showed significantly higher volumes in thinned forests than in either clearcut or wind disturbed forests. A marginally significant Kruskal-Wallis p-value (0.07) for the variable DECAY2 probably points towards a higher volume of moderately-decayed deadwood in wind disturbed forests.

Table 5. Spearman's rank correlations between forest structure variables. Shading denotes significant correlations ($p < 0.05$) after a Bonferroni correction.

	CROWN	SIZE1	SIZE2	SIZE3	DECAY1	DECAY2	DECAY3	STAND.	FALL.	DECID.	CON.
SIZE1	-0.31										
SIZE2	-0.07	0.20									
SIZE3	-0.05	-0.26	0.26								
DECAY1	-0.11	0.29	0.40	0.09							
DECAY2	-0.01	-0.07	0.49	0.49	0.40						
DECAY3	0.00	0.40	0.44	0.44	-0.16	0.05					
STAND.	-0.06	0.14	0.25	0.31	0.21	0.18	0.40				
FALL.	0.03	0.29	0.56	0.39	0.50	0.41	0.42	0.27			
DECID.	-0.22	0.07	0.31	0.33	0.05	0.23	0.19	0.18	0.19		
CON.	-0.05	0.40	0.53	0.33	0.25	0.37	0.61	0.24	0.51	-0.14	
ALLDW.	-0.25	0.53	0.75	0.49	0.42	0.45	0.70	0.41	0.68	0.30	0.76

Table 6. Mean and standard deviation of each forest structure within forest disturbance classes, and Kruskal-Wallis results for test of differences between disturbance classes. Shading denotes significant differences ($p < 0.05$).

Forest Structure	CLEARCUT mean±SD	CC&THINNED mean±SD	FIRE mean±SD	WIND mean±SD	Kruskal-Wallis	
					χ -square	p-value
CROWN	83.53±5.28	71.91±14.89	57.03±13.06	84.65±8.03	10.54	0.015 ^a
SIZE1	0.0755±0.0379	0.1550±0.0556	0.1463±0.0827	0.0902±0.0592	8.36	0.039 ^b
SIZE2	0.0742±0.0402	0.1055±0.0682	0.0856±0.0532	0.1585±0.1001	2.72	0.437
SIZE3	0.0562±0.0848	0.0596±0.0913	0.0387±0.0347	0.2652±0.5445	2.31	0.511
DECAY1	0.0871±0.0474	0.1171±0.1137	0.1488±0.1140	0.1279±0.1669	0.37	0.947
DECAY2	0.0471±0.0309	0.0414±0.0282	0.0624±0.0384	0.1977±0.3784	6.34	0.074
DECAY3	0.0716±0.0538	0.1617±0.1361	0.0596±0.0147	0.1883±0.1264	2.82	0.420
STANDING	0.0942±0.0738	0.1034±0.1115	0.1459±0.0725	0.1086±0.0370	2.60	0.457
FALLEN	0.1116±0.0567	0.1715±0.0563	0.1248±0.0626	0.4052±0.6555	5.13	0.162
DECIDUOUS	0.0609±0.0526	0.1115±0.1277	0.0429±0.0448	0.0450±0.0553	3.95	0.267
CONIFER	0.1710±0.0866	0.1900±0.1175	0.2278±0.1732	0.4334±0.6573	3.57	0.312
ALLDWOOD	0.2058±0.1086	0.3202±0.1542	0.2707±0.1321	0.5138±0.6412	2.14	0.543

a Numenyi multiple comparison difference: WIND>FIRE.

b Numenyi multiple comparison difference: CCT>CC, CCT>WIND.

Figure 3. Means of crown closure and deadwood variables for each forest within each disturbance history class. Wind disturbed forest # 25 is removed from presentation due to much higher volumes of deadwood in all classes. Actual variable means for all forests are presented in Appendix 2.

Alpha (local) diversity scale

The structural diversity attributes for each forest are illustrated in Figure 4. The ANOVA analysis to test whether naturally disturbed forests exhibited higher diversity of deadwood structures (Table 7) offered evidence for one of the five attributes tested. The variable SHAN-DECAY, indexing the diversity of deadwood decay classes in each forest, was significantly higher in both fire ($p=0.035$) and wind ($p=0.004$) disturbed forests than in thinned forests. The SHAN-DECAY variable also averaged higher in these classes than in clearcut forests, though not significantly.

The general linear regression models constructed to determine whether the beetle diversity could be explained by structural diversity attributes resulted in a model for seven of ten of those attempted (Table 9). The habitat variable SHAN-D/C was a positive predictor of ABUNDANCE and a negative predictor of RICH/ABUN. Thus the later relationship probably relates to ABUNDANCE being the denominator of RICH/ABUN. SHAN-POS was also a negative predictor of RICH/ABUN, as it was for two of the RARE richness measures. Negative relationships between the variable CROWN and most of the RARE richness measures suggests the presence of more infrequently sampled species in forests with lower crown closure. This result may be explained by the facts that fire disturbed forests had consistently lower crown closure and a high proportion of beetle species restricted only to this habitat (detailed in Chapter Two).

One statistically non-significant trend may further assist interpretation of the CROWN relationships. Relatively lower CROWN and higher species diversity values in thinned forests (Table 8) may suggest that the CROWN variable is negatively correlated with the

species diversity variables due to linkage through the thinned disturbance class. This is to suggest that the negative correlation between CROWN and species diversity may actually reflect a correlated factor associated with the thinned forests. For example, pre-commercial thinning inevitably leads to a lower crown closure and higher volume of small-diameter, fallen deadwood, and it is conceivable that this structure could lead to samples of higher species diversity. This scenario is further addressed in the discussion.

Figure 4. Habitat structure diversity measures for each forest within disturbance history classes. Only SHAN-DECAY significantly differed between classes.

Table 7. Mean and standard deviation of each forest structure diversity attribute within forest disturbance classes, and ANOVA results for test of differences between disturbance classes. Shading denotes significant differences ($p < 0.05$).

Forest Structure	CLEARCUT mean $\pm$ SD	CC&THINNED mean $\pm$ SD	FIRE mean $\pm$ SD	WIND mean $\pm$ SD	ANOVA	
					F	P
SHAN-SIZE	1.306 $\pm$ 0.223	1.199 $\pm$ 0.250	1.118 $\pm$ 0.424	1.279 $\pm$ 0.191	0.636	0.599
SHAN-DECAY	1.294 $\pm$ 0.249	1.044 $\pm$ 0.276	1.400 $\pm$ 0.221	1.422 $\pm$ 0.164	4.751	0.009*
SHAN-POS	0.859 $\pm$ 0.132	0.813 $\pm$ 0.187	0.970 $\pm$ 0.047	0.848 $\pm$ 0.243	0.622	0.607
SHAN-D/C	0.677 $\pm$ 0.295	0.723 $\pm$ 0.217	0.598 $\pm$ 0.455	0.485 $\pm$ 0.280	1.167	0.341
SHAN-ALL	4.136 $\pm$ 0.599	3.778 $\pm$ 0.415	4.085 $\pm$ 0.702	4.035 $\pm$ 0.591	0.589	0.628

* Tukey HSD multiple comparison differences: WIND>CCT ($p=0.004$), FIRE>CCT ($p=0.035$).

Figure 5. Beetle assemblage measures for each site within disturbance history classes. Only RICHNESS/ABUNDANCE differed significantly between classes.

Table 8. Mean and standard deviation of each beetle assemblage diversity attribute within forest disturbance classes, and ANOVA results for test of differences between disturbance classes. Shading denotes significant differences ($p < 0.05$).

Beetle Diversity Attribute	CLEARCUT mean $\pm$ SD	CC&THINNED mean $\pm$ SD	FIRE mean $\pm$ SD	WIND mean $\pm$ SD	ANOVA F P	
ABUNDANCE	299.857 $\pm$ 49.131	423.250 $\pm$ 216.176	545.750 $\pm$ 219.709	354.636 $\pm$ 321.921	1.001	0.408
RICHNESS	57.571 $\pm$ 5.442	63.750 $\pm$ 17.758	59.000 $\pm$ 11.605	58.091 $\pm$ 9.027	0.464	0.710
RICH/ABUN	0.195 $\pm$ 0.022	0.171 $\pm$ 0.051	0.116 $\pm$ 0.028	0.228 $\pm$ 0.093	3.255	0.038*
SHANNON	0.685 $\pm$ 0.044	0.679 $\pm$ 0.112	0.576 $\pm$ 0.096	0.698 $\pm$ 0.173	0.866	0.471
RARE-1	2.429 $\pm$ 1.618	3.125 $\pm$ 2.949	2.500 $\pm$ 1.000	2.182 $\pm$ 1.888	0.319	0.812
RARE-5	9.286 $\pm$ 2.984	12.250 $\pm$ 8.067	9.750 $\pm$ 2.630	10.727 $\pm$ 3.289	0.500	0.685
RARE-10	14.429 $\pm$ 2.992	18.375 $\pm$ 10.743	15.750 $\pm$ 2.872	17.000 $\pm$ 5.020	0.479	0.700
RARE-15	19.143 $\pm$ 3.078	23.750 $\pm$ 12.533	21.250 $\pm$ 4.349	21.455 $\pm$ 5.905	0.442	0.725
RARE-30	25.857 $\pm$ 4.059	31.250 $\pm$ 14.069	28.000 $\pm$ 6.782	27.818 $\pm$ 7.026	0.468	0.707
RARE-60	36.143 $\pm$ 4.776	42.750 $\pm$ 17.153	38.000 $\pm$ 9.832	37.727 $\pm$ 7.901	0.528	0.667

* Tukey HSD multiple comparison difference: WIND>FIRE ($p=0.031$).

Table 9. Significant multiple linear regression models of beetle assemblage attributes (dependent variables) regressed against forest structure diversity attributes (explanatory variables). Construction by forward and backward stepwise inclusion and exclusion of variables, based on two-tailed p-value of 0.1.

Dependent Variable	Explanatory Variable(s)	Coefficient $\pm$ SE	T / P (2-tailed)	F-Statistic	Model P-value	Adjusted Multiple R ²
ABUNDANCE	Intercept	215.687 $\pm$ 97.556	2.211 / 0.035	3.735	0.063	0.086
	SHAN-D/C	279.363 $\pm$ 144.555	1.933 / 0.063			
RICH/ABUN	Intercept	0.358 $\pm$ 0.060	5.989 / 0.000	4.533	0.020	0.196
	SHAN-POS	-0.143 $\pm$ 0.065	-2.211 / 0.036			
	SHAN-D/C	-0.074 $\pm$ 0.041	-1.816 / 0.080			
RARE-1	Intercept	9.305 $\pm$ 2.262	4.113 / 0.000	4.583	0.019	0.198
	CROWN	-5.192 $\pm$ 2.439	-2.128 / 0.043			
	SHAN-POS	-3.260 $\pm$ 1.830	-1.781 / 0.086			
RARE-5	Intercept	17.446 $\pm$ 4.071	4.285 / 0.000	2.900	0.100	0.061
	SHAN-POS	-7.907 $\pm$ 4.644	-1.703 / 0.100			
RARE-15	Intercept	34.810 $\pm$ 7.468	4.661 / 0.000	3.279	0.081	0.073
	CROWN	-17.374 $\pm$ 9.594	-1.811 / 0.081			
RARE-30	Intercept	45.203 $\pm$ 8.609	5.250 / 0.000	3.979	0.056	0.093
	CROWN	-22.063 $\pm$ 11.060	-1.995 / 0.056			
RARE-60	Intercept	56.547 $\pm$ 10.656	5.307 / 0.000	2.885	0.100	0.061
	CROWN	-23.253 $\pm$ 13.689	-1.699 / 0.100			

Beta diversity scale

Analysis at the beta diversity scale tended to offer more support for the original predictions. Figure 6 shows the NMS ordination scatter plots of forest sites in a two-dimensional space defined by (A) the beetle assemblage and (B) forest structure. Table 10 presents the MRPP results. The forest sites plotted in the space of the beetle assemblage show two important patterns: differences in the between-site distances within disturbance classes and actual segregation of forest disturbance classes. Clearcut forests show the tightest aggregation (mean distance = 0.4532), followed by thinned forests (0.5822), and then fire disturbed forests (0.5912), with wind disturbed forests showing the greatest heterogeneity (0.6356). Thus the prediction of lower heterogeneity in managed forests at the beta scale is supported. If one were to subdivide the thinned forest class, the average between-forest distances would dramatically decrease again due to close aggregations of commercially thinned forests (sites 9, 13, and 14) and pre-commercially thinned forests (sites 7, 8, 20, 27, and 29). Interestingly, the MRPP tests of separation of disturbance classes from each other were all found to be at least marginally significant. Thus, strong evidence supports the prediction that the beetle assemblages in each forest differ depending on the disturbance history classes.

Less significant and somewhat different patterns were observed in the space of forests defined by forest structures. Figure 6B shows that, unlike the species-defined plot, fire disturbed forests show the greatest heterogeneity (0.3534), followed by thinned forests (0.2963), followed by clearcut forests (0.2168), and wind disturbed forests with the lowest heterogeneity (0.1750). However, one must note that the outlying wind disturbed forest number 25 had an extremely high volume of deadwood and was removed due to the difficulty

in otherwise interpreting the NMS diagram. The MRPP average distance for wind disturbed forests when the outlier was included ranked the wind disturbed class as second most heterogeneous, behind fire disturbed forests. Evaluated in this manner, one again finds support for the predicted forest heterogeneity pattern: managed forests have lower structural heterogeneity. The only group separation observed in the structure-defined plot occurred between the wind disturbed and thinned classes, and between the wind disturbed and fire disturbed classes, though these comparisons were only marginally significant (Table 10 B). Careful comparison of the two ordination plots reveals that forests in both plots fall approximately in the same positions relative to one another, supporting the prediction that the forest habitat structures measured in the study have a deterministic effect on the beetle assemblage sampled.

Table 10. Results of multi-response permutation procedures (MRPP) analysis, testing for separation of disturbance history classes based on (A) beetle assemblage and (B) forest habitat structures. Mean distance within class can be read as a relative measure of beta heterogeneity within disturbance history classes. P-values associated with multiple comparisons identify separation between groups. Adjusted multiple comparison α level for p-value significance at $0.05 = 0.009$, and for significance at $0.10 = 0.017$, based on adjusted $\alpha = 1 - (1 - \alpha)^{1/\text{number of comparisons}}$.

	CLEARCUT	CC-THINNED	FIRE	WIND	All-groups
(A) mean distance within class	0.4532	0.5822	0.5912	0.6356	p-value
CC&THINNED	0.0143				
FIRE	0.0009	0.0313			0.0002
WIND	0.0023	0.0591	0.0228		
(B) mean distance within class	0.2168	0.2963	0.3534	0.1750	
CC&THINNED	0.2189				
FIRE	0.2464	0.7535			0.0970
WIND	0.1472	0.0600	0.0777

Figure 6. Non-metric multidimensional scaling ordination diagrams of forest sites in two-dimensional space defined by (A) beetle assemblage and (B) forest structures. Symbols signify disturbance history class of forests: X = CLEARCUT, * = THINNED, ◇ = FIRE, and ● = WIND. Numbers identify the specific forest. Forest number 25 was excluded as an outlier in (B) due to much higher deadwood volumes than all other forests.

Gamma diversity scale

Of the 286 saproxylic species sampled, 218 (76.8%) were sampled amid naturally disturbed forests and 220 (77.4%) were sampled amid the managed forests. The first and second order Jackknife estimates of total species richness were 288.0 and 320.8 for naturally disturbed forests and 294.7 and 336.6 for managed forests. This does not support the prediction that the total fauna richness would be higher in naturally disturbed forests; in fact, the opposite appears more likely to be true. The species-sample curves constructed for the four disturbance classes (Figure 7) suggest the following relationship of species richness across disturbance history classes: thinned>wind>fire>clearcut. However, limited by a small number of samples in each forest class, it is difficult to say whether, given more samples, the final leveling of species number may differ from this pattern. For example, the higher curve of thinned compared to wind disturbed forests may actually be approaching peak faster.

Figure 7. Species-sample curves for each forest disturbance class.

Figure 8. Hypothetical species-sample curves to illustrate the expected contrast of a curve derived from forests with more individuals of fewer species relative to a control.

DISCUSSION

The current study is limited to forests of a few different disturbance histories, ages, and tree compositions; therefore, the results offer limited insight into these sources of variation. Factors pertaining to the landscape scale or to temporal forest continuity were also not accessible. The saproxylic beetle fauna sampled, though rich in species, can be considered only a proportion of the total in Nova Scotia spruce forests. These facts should accompany interpretation of this discussion and suggest the breadth of research remaining to be done.

Predictions pertaining to the beta scale were generally better supported than those pertaining to the alpha or gamma scales. However, some evidence did suggest that forestry can decrease deadwood diversity: the finding of lower decay-class diversity in thinned forests compared to wind and fire disturbed forests. Interpretation demands an understanding of the thinning practice. Both pre-commercial and commercial thinning treatments were represented in the thinned forest class (five and three forests, respectively). Pre-commercial thinning is applied to young regenerating or replanted forests to increase productivity through removal of non-desirable tree species and spacing of remaining trees to reduce competition. Commercial thinning or 'partial harvest', is applied in more mature stands and removes a portion of the marketable fiber (typically 30-70%), often felling and leaving trees that are dead, moribund, or otherwise non-desirable. While thinning treatments may be applied at different times to different stands, the results are usually an immediate increase in the volume of similar-diameter downed deadwood, which leads to local homogeneity of deadwood structure. Homogeneity in any single thinned stand is magnified by the fact that this deadwood senesces as a cohort, representing little decay variation in space; this is probably

the best explanation for lower decay-class diversity in thinned forests. The significant pattern of higher small-diameter deadwood volume in thinned forests probably reflects the dominance of pre-commercial thinning in the thinned class, because of the fact that pre-commercial treatments are applied in forests with young, small trees. Lower diversity and increased volumes of deadwood may thus be generally associated with the thinning practice.

One explanation for the lack of support for alpha-level deadwood diversity predictions is well worth considering: the lingering existence of harvest and pre-harvest deadwood in managed forests. Nearly all managed forests in this study were in their first or second even-age management rotation. Hence most managed forests likely contained large amounts of residual deadwood from deciduous species and large trees. For a notion of how long larger deadwood can endure, one forest in this study that was severely disturbed by a hurricane in 1956 (forest number 25) was dominated by deadwood over 30 cm in diameter, and still in the first and second decay states (0-5 cm decay depths). The occurrence of residual deadwood undoubtedly could have complicated the current study, in that deadwood patterns in managed forests simply had not yet had enough time to become altered in the way predicted. I suggest that the loss of structural diversity of deadwood in many of Nova Scotia's second-growth forests has not yet occurred. But while the old-forest residual deadwood decomposes in second growth forests during a time of unprecedented even-age harvesting, one can only anticipate the loss of these structures with no subsequent replacement—and hence the loss of any species that depend on these structures.

An explanation for the weak correlation between beetle diversity and deadwood diversity at the alpha scale may simply be that deadwood was measured over an area inadequate to

reflect its deterministic influence on the local beetle assemblage. One cannot necessarily assume that a sampled array of flying beetles will reflect only the microhabitats available within a few hundred meters. The deadwood sampling area ideal for discerning relationships, in theory, emerges from the conglomeration of 'best' areas for individual species and individual forests. In recognizing this quandary of FIT sampling, Økland (1996) tested the habitat relationships for individual beetle species in Norway and found that habitat measurements collected over an area of 32 hectares produced the strongest and highest number of significant relationships. To assume that the forest measurements in this study represented the surrounding forest environment over this large an area would probably necessitate assumptions of forest homogeneity that are beyond reason. Thus it is plausible to attribute poor alpha relationships to poor quantification of deadwood variables.

The beta-scale: spatial turnover in forest composition and ecological integrity

While the alpha- and gamma-scale predictions focus on absolute diversities of habitat and beetle assemblages within forests and within disturbance classes, the beta-scale predictions figure highly on relative composition of the beetle assemblage. Although the beetle assemblage diversity did not correlate with diversity of deadwood structures nor differ between forest classes, the actual compositions of the communities were different among classes, and higher turnover between naturally disturbed forests was evident. Similar observations of high turnover of saproxylic beetle species without change in species richness have been made in central Finland by Kaila *et al.* (1997) when comparing recent clearcuts with mature forests, and by Väisänen *et al.* (1993) when comparing the fauna of birch trunks

in old-growth forests with that in managed forests. Thus, while the current study does not support the prediction of reduced species diversity related to reduced deadwood habitat diversity in managed forests, the results do support the claim that managed forests support different species assemblages (Niemelä 1997).

The general pattern of similar species diversity but different species compositions between disturbance classes leads one to ask whether forestry in Nova Scotia violates ecological integrity. The answer rests on how one values the preservation of particular species assemblages relative to the preservation of absolute numbers of species. Thus it is important to consider the range of management goals that relate to these values.

Some researchers have approached the ‘enhancement’ of biodiversity as though it depended merely on the increase of species numbers. By extension of this philosophy, some managers seem to have judged modern forestry as being even better than natural disturbance because it tends to increase species numbers locally (e.g., Duelli *et al.* 1997). Several arguments oppose the use of this criterion. Niemelä (1997) points out that while practices like clearcutting may increase local diversity, when applied on a large scale the same practices can lead to decreased regional diversity due to loss of old-forest dependents and due to general landscape homogenization. Not only this, but it is questionable whether higher numbers of species are favorable to begin with. The idea is based on a notion that increased diversity leads to increased stability and functioning, which has little scientific support. Another misguided assumption is that all species are equally valuable in a system, whether they are introduced clearcut-loving “weeds”, community keystones, or endangered dependents of hollow deciduous trees from the forest primeval. Furthermore, the idea says

nothing about the value of minimizing the anthropogenic alteration of ecosystems and species assemblages—the basic issue from which biodiversity conservation arose.

At the other extreme, there are those who advocate maintaining or restoring the exact composition of ‘natural’, pre-Columbian ecosystems. Sprugel (1991) and Budianski (1995) both take issue with this approach on the grounds that they are equilibrium-centered ideas that ignore inherent ecosystem variability driven by natural disturbances. Ehrlich (1996) augments this rationale with the facts that science can never really know exactly what pre-Columbian ecosystems were and that humans have already affected all ecosystems on Earth to some degree. Ehrlich thus dissuades biologists from “worrying about exactly what previous state ecosystems should be managed to resemble,” and suggests instead that management should aim to maximize the preservation of the species diversity of native organisms.

A similar rationale is implicit in a modern and widely accepted management strategy: to model forestry practices on natural disturbances (Hunter 1993; Haila *et al.* 1994; Bondrup-Nielsen 1995; Niemelä 1997). The idea is that if native species could survive natural disturbances, then the same species should be able to survive forestry practices that present similar environmental challenges and opportunities. Ecological integrity, according to this goal, is violated when managed forests differ with respect to forests with natural disturbance histories. The indication offered here by saproxylic beetles in spruce forests is that species compositions are indeed different between natural and managed disturbance history classes and thus, defined in this way, ecological integrity appears to be violated by spruce forest management in the studied ecosystems.

To contrast this conclusion, consider the same patterns interpreted under the premise that highest absolute species richness is the desirable biodiversity end. Observing similar alpha diversity across classes one would conclude no apparent problem associated with even-age forest management. Or, after observing higher species numbers in thinned forests at the regional scale, thinning might be advocated as a method to ‘enhance’ biodiversity. Native species that cannot reside under current forestry conditions would be otherwise ignored—and perhaps destined to run out of habitat in managed forests.

More of fewer species? A potential sampling error with dire consequences

The final prediction of lower saproxylic beetle species diversity in managed forest compared to naturally disturbed forests was not supported. This prediction was partly underpinned by an assumption that forest habitat structures differed between forest classes at the alpha scale which, as noted above, was not necessarily the case. If anything, the higher species-sample curve depicting species richness in thinned forests seems to suggest that thinning disturbance generates more species than either of the two natural disturbance classes tested. Otherwise, clearcut forests seemed to have a lower diversity of species than both wind and fire origin forests. This pattern would support the prediction of lower regional diversity due to forestry.

These mixed results at the regional scale are inconclusive. But before dismissing the prediction of species depletion in managed forests, it is important to acknowledge another phenomenon that may have impeded the capacity to accumulate evidence toward the predictions of this study. The phenomenon deals with a potential beetle sampling error linked to thinned forests. It assumes, as alluded to above, that thinning tends to decrease

structural diversity of deadwood and concentrate volume among a few size, decay, position, and species classes. With thinning treatments, one might still predict a habitat-related decrease in the diversity of saproxylic associates but, simultaneously, a flourishing of the species suited to the particular habitats that have increased. Essentially, more of fewer kinds of habitats leads to more individuals of fewer saproxylic species in thinned forests compared to naturally disturbed forests.

This becomes an issue as one considers an obvious though oft-forgotten fact of trap sampling: the assemblage sampled by traps will not be the entire targeted fauna but rather a reflection of the fauna that depends not only on the presence of each species but also on the probability of sampling each species. Where all other factors of sampling probability for a given species remains constant, an increase in the abundance of that species will tend to increase the probability of it being sampled. Thus, the fauna sampled in a thinned forest that has more of fewer species should represent a higher proportion of the actual faunal richness compared to a sample from a site with fewer individuals of more species. Ultimately, compared to other forests, thinned forests could produce samples of similar or even higher species richness when in fact the opposite could be the case.

In summary, increased deadwood volume, when representing a lower diversity of deadwood habitats, should lead to a higher proportion of the actual saproxylic species sampled. Comprehensively testing this prediction was beyond the scope of the current project. However, given its plausibility, it probably should not be ruled out as a factor that may have impeded evidence to support predictions of this study. In retrospect, several lines of evidence may suggest that this scenario affected the current study. From the alpha

analysis, a lower (though not significantly lower) mean RICHNESS:ABUNDANCE ratio in thinned forests (0.171) compared to wind disturbed forests (0.228) suggests more individuals per species in thinned forests. Secondly, if one envisions the projection of the species-sample curves in Figure 7, the possibility of the thinned class curve being surpassed by the wind class curve seems probable. Figure 8 illustrates the expected relationship between two species-sample curves where one has more individuals of fewer species, showing a faster but lower leveling-out of a sample where more individuals of fewer species are present. At lower numbers of samples, one would mistakenly conclude more species in the habitat that actually had more of fewer species. The truth becomes more evident as samples are increased toward the point of leveling, where all potential species are sampled. Thus one can see the increased importance of adequate sample effort when comparing communities that may have disproportionate richness:abundance ratios.

It is not known whether samples in this study were affected by a pattern of more individuals of fewer species in thinned forests. The situation should nevertheless be acknowledged for its potential to undermine the conclusions of biodiversity studies that attempt to link diversity of habitats to the diversity of organisms dependent on them.

Future research and forest management in Nova Scotia

In recent decades the management of temperate forest ecosystems has shifted from a paradigm of mainly economic interests to one that must accommodate diverse human values. Preserving biodiversity amid these values in working forest landscapes is undoubtedly the most challenging. Most agree that facing this challenge successfully will require the

collaboration of government, industry, and science (Hautaluoma and Woodmansee 1994; Niemelä 1997). The descriptive complexity of biodiversity and the rapid rate at which it is being altered has led several people to emphasize the need to immediately change existing management practices based on available knowledge, and continually modify practices as new information becomes available (Haila 1994; Franklyn 1995; Ehrlich 1996; Niemelä 1997). It is a working experiment, in which ecological integrity is approached by successive adaptation in response to the best available biodiversity knowledge. The need herein for integration of all interests is even more obvious. Hence now I discuss implications for research and forest management in the manner that they will have to be addressed: hand in hand.

Acknowledging Nova Scotia's historical and current forestry trends gives context to the importance of invertebrate microhabitat conservation in the province. While forests in Nova Scotia have experienced hundreds of years less of intensive forestry than have forests in the Old World, the province has the longest running tradition of forestry in North America (McMahon 1989). For this reason, Nova Scotia's forests currently exhibit a very young age-class distribution with no more than 0.6 percent of forest land currently considered "old forests" (greater than 100 years) (McMahon 1989).

The general claim that modern forestry in northern forests has altered invertebrates by altering forest habitat structure is well supported in the literature (Niemelä 1997 gives a good overview). Conclusions from the current study help extend this claim to the case of saproxylic beetles in Nova Scotia forests: that managed and naturally-disturbed forests differ with respect to the composition of their beetle assemblage, that the beetle assemblages are

less variable between naturally disturbed forests, and that forest structure composition correlates with the composition of the saproxylic beetle assemblage. If management is to decrease the altering effect of forestry practices, the next requirement is to identify or confirm the particular aspects of forest structure that are being altered and in turn are altering biodiversity (Essen *et al.* 1992; Swanson and Franklin 1992; Noss and Cooperrider 1994; Franklin 1995; Lubchenco 1995; Niemelä 1997).

Research from countries with longer histories of intensive forestry has revealed several cases of invertebrate endangerment due to loss of microhabitats found in deadwood or moribund trees. Some of these microhabitats are lost because they are found within tree species that are not economically desirable, like aspen (Siitonen and Martikainen 1994) and beech (Nilsson and Baranowski 1997). Other microhabitats are threatened because they are within trees with large diameters, which are not maintained amid short-lasting even-age stand rotations (Økland *et al.* 1994; Nilsson *et al.* 1995). These and other factors have led to concern about the diversity of deadwood microhabitats in general, as defined by decay, size, and tree species (Økland *et al.* 1994).

Ensuring the survival of saproxylic invertebrates in North American temperate forests will likely reach conclusions and implicate actions similar to those in the Old World. The work done in European countries has greatly advanced the capacity to make decisions for adaptive management with which to approach ecological integrity. Following Europe's exemplary strides, like identifying threatened microhabitats and deriving red-lists of their dependent organisms, will require much basic investigation in the New World. A general approach might begin with the identification of broad habitat associations for large groups of

species, and be followed by subsequent refinement through well planned observation and stringent hypothesis testing (addressed in Chapter Two).

The possible venues for linking management objectives with preservation objectives must be considered. As concern about fiber sustainability in Northern forests escalates, pressure continues to be placed on increasing productivity. Thinning is strongly being encouraged throughout North America as a method to shorten stand rotation times. Therefore, it may be wise to consider the potential to approach conservation initiatives of maintaining species in working landscapes by working with the thinning practice. Because thinning is already labor-intensive, the practice could serve as one venue to accommodate straight forward recommendations regarding deadwood retention. At the stand scale, important questions need to be addressed. For example, could currently threatened classes of deadwood be accommodated through selections for particular tree species and sizes? Or, at a larger scale, could even-age management accommodate vulnerable species through planning regional stand mosaics wherein all microhabitats are continuously available within relevant dispersal ranges of species? These are examples of the many questions that should be addressed if forest managers are to accommodate biodiversity values amid pressing economic interests.

Summary

If society's goal for preserving biodiversity in managed forests is to maintain patterns of heterogeneity similar to those maintained by the natural disturbances which operated in pre-Columbian ecosystems, the indication offered here by saproxylic beetles is that the goal is not being met. Nova Scotia forestry practices are thus violating ecological integrity if defined by this goal. If the province has not yet suffered biodepletion to the extent of Old World forests, this may only reflect the fact that not enough time has passed for residual deadwood lingering from old-forests to turn to soil.

If attention is paid now to the fate of forest structures and the assemblages of species dependent on them, the restoration of pre-Columbian forest biodiversity seems an attainable goal, demanding relatively few costs—biological or otherwise. If, however, we are to wait-out predictable species extirpations and a more informed and 'caring' society, the required procedures at that time will have to be more elaborate. Such procedures might include impractical, expensive, and unpredictable invertebrate rearing and habitat translocations such as have been resorted to in Europe. Ball and Key (1996) suggest that these measures should only be considered as last alternatives after preventive approaches have failed. While we hesitate, critical microhabitats are decaying in managed forests—and with them the opportunities and hopes for preserving many saproxylic species. The needs are immediate for forestry modification based on available knowledge and new knowledge including species and habitat vulnerability.

CHAPTER TWO

SAPROXYLIC BEETLE SPECIES AS INDICATORS OF DISTURBANCE HISTORY AND FOREST STRUCTURE IN NOVA SCOTIA SPRUCE FORESTS

INTRODUCTION

Lists of threatened species and a basic knowledge of their habitat associations are quintessential for delineating forest conservation values and for developing strategies for preserving ecological integrity. Compared to European efforts, North America lags decades behind in documenting the vulnerability of invertebrates, one of the most functionally important, diverse, and threatened components of forest ecosystems.

Niemelä (1997) offers a simple view of how invertebrate communities are altered by even-age forestry practices: the species adapted to open, dry conditions following forestry disturbances will flourish (Muona and Rutanen 1994; Kaila *et al.* 1997) while species dependent on old-forest features will decline (Väisänen *et al.* 1993; Samuelsson *et al.* 1994). The fate of each species depends on the fate of its habitat resources. As resources change, through forestry or otherwise, the assemblage of species dependent on those resources changes. Thus, several studies have observed high dissimilarity of invertebrate assemblages between managed and naturally-disturbed forests (Väisänen *et al.* 1993; Buse and Good 1993; Butterfield *et al.* 1995; Martikainen *et al.* 1996; Atlegrim *et al.* 1997; Kaila *et al.* 1997).

The adoption of new biodiversity strategies with goals to maintain or restore historical species assemblages in working forest landscapes makes it highly important to know what species tend to benefit from or suffer from the effects of forestry disturbance. Knowing what species suffer from forestry disturbance is even more important when species extinction is a concern. Thus, the establishment of species lists is a pre-requisite to effective invertebrate conservation (Speight 1997). For an example, the observation of fewer red-listed invertebrate species in managed forests in Finland (Väisänen *et al.* 1993; Kaila *et al.* 1997) can assist in making informed conservation decisions, but such observations are not possible until the conservation value of the species is known.

Thousands of years of deforestation in Europe have undoubtedly had greater effects on the organisms that inhabited naturally-disturbed forests than would be expected in North America. It is not surprising, then, that the issue of forest invertebrate conservation in North America has lagged behind that in the Old World, especially given the longer and more intense history of taxonomic and ecological study on invertebrates in the Old World. As Hammond (1997) points out, most work in the Canadian context on saproxylic invertebrates has focused on the taxonomy and biology of economic pests, and on the and the fauna of economically important tree species. Little effort has been made to discern species that are threatened due to loss of particular deadwood microhabitats.

If action is taken now, the later commencement of deforestation in North America may lead to better results per conservation effort than in forests with longer forestry histories. Large-scale deforestation commenced in Nova Scotia earlier than in any other part of North America (McMahon 1989) so this province seems an important starting place in the task of

learning how the North American fauna have been and stand to be affected by forestry.

Acquiring basic knowledge on species' habitat associations and related species' vulnerability in the context of North American forests is clearly a pre-requisite to conservation of this continent's invertebrate species.

Probably the highest concern about alteration of structures important as invertebrate microhabitats pertains to moribund and dead trees. Among invertebrates associated with these habitats, saproxylic beetles are among the best-known, both taxonomically and ecologically (Speight 1989). This study takes some initial steps to discover saproxylic beetle species that may indicate managed (clearcut and clearcut-thinned) and natural (wind and fire) forest disturbance histories, and to reveal species-structure relationships that may help explain these associations. Toward this end, I put forward a list of species whose abundances may be altered by forestry practices along with some habitat-related explanations. The list is intended to promote further research involving detailed observation and stringent hypothesis-testing.

METHODS

This work focuses on the same list of saproxylic beetle species (Appendix 1) and environmental variables (Appendix 2) described in the previous chapter. The field sampling and beetle identification methods are also described therein.

Statistical analyses

Indicator species analysis (ISA) in PC-ORD (McCune and Mefford 1997) was used to reveal the value of individual species as indicators of particular disturbance classes. This technique employs Dufrene and Legendre's (1997) method for calculating an indicator value (IV) for each species in each disturbance class based on (1) the concentration of abundance and (2) the faithfulness of occurrence of each species in each class (Appendix 3). The maximum IV for each species ranges from 0 (no indication) to 100 (perfect indication), where perfect indication means that presence of a species points entirely to one particular class. A Monte Carlo test evaluates whether the maximum IV is significantly larger than would be expected by chance, whereby the probability of Type I error is the proportion of times that the maximum IV from the randomized data set equals or exceeds that of the actual data set (summarized from McCune and Mefford 1997). One thousand randomization runs were chosen for the Monte Carlo procedure. All species were subjected to the ISA.

Generalized linear regression models were constructed to explore if and how individual species were related to particular forest structures. Two structure variables were excluded from this analysis to avoid complications associated with interpreting their biological or conservation significance; these were SIZE2 and DECAY2 (volume of deadwood in

intermediate diameter and decay classes). The actual abundances of widespread species (sampled in at least 25 of 30 forests) were taken as the dependent variables to build models by classical multiple linear regression analysis (Weisberg 1985). Assumptions of independence and homogeneity of variance were checked using plots of residuals against predicted values and against significant predictor values, while normality of residuals was evaluated using histograms. For species that occurred at a moderate distribution (fewer than 25 but more than 19 forests), the classical method was rejected due to inability to assume normality of residuals. To model the abundance of these species, Poisson regression was used (McCullagh and Nelder 1983), which assumes a variance proportional to μ and a Poisson distribution of the residuals (here caused by many zero abundance values). For species occurring in fewer than 20 but more than 3 forests, abundances were reduced to presence or absence, and logistic regression (Hosmer and Lemeshow 1989) was used to model the probability of presence of each species. This technique assumes a binomial distribution of residuals and a variance proportional to $\mu(1-\mu)$. Classical models were constructed by backward step-wise deletion of terms followed by forward addition. Poisson and logistic models were constructed by forward addition with subsequent deletion. Term acceptance and deletion was based on a model improvement p -value < 0.05 . Standardized deviance residuals were plotted against each significant model term and against predicted values to assess assumptions of the non-classical models. While assumptions were somewhat relaxed due to the exploratory nature of an already labor-demanding analysis, all models were considered to have adequate integrity with no further transformations. Classical linear

regression models were constructed using SYSTAT (Systat 1993) while S-PLUS (Mathsoft 1995) was employed to build the Poisson and logistic models.

Canonical correspondence analysis (CCA) was used to help identify the structural variables that best explain the disturbance history associations for all the species that were simultaneously disturbance class indicators and correlated with at least one forest structure. Forest scores were based on linear combinations of forest structures, and re-scaling of forest scores with a mean of zero and a variance of one.

RESULTS

The identified saproxylic beetle assemblage chosen for analysis totaled 11569 individuals representing 286 species from 43 families (Appendix 1). This assemblage is a high proportion of the entire beetle fauna trapped in the study, for which the total richness is estimated to be 370 to 400 species. Approximately 87% of the saproxylic species were identified to the species level. According to the data in Bousquet (1991), my sample includes 95 species as new records for Nova Scotia, including 47 species which are new records for Atlantic Canada and 3 species as records new for Canada. A further 7 species are considered by taxonomic specialists to be undescribed.

Species as indicators of forest disturbance history

The indicator species analysis returned 28 species with Monte Carlo test p-values <0.01 (Table 1). The highest indicator values for half of these species was in fire disturbed forests, suggesting that they are most abundant in this disturbance class of forests. Six species were indicators of thinned forests, five species were indicators of clearcut forests, and three species were indicators of wind disturbed forests. Of this group, 17 species were indicators at a more significant p-value <0.05 . Higher or lower representation of particular families or genera was not apparent among the indicators.

Table 1. Results of indicator species analysis. Species are sorted by the disturbance class that their abundances indicate and then by significance of indication (for all species with $p < 0.10$). Shading highlights significance at $p < 0.05$. The 15 species for which significant species-structure models were also built are denoted by asterisks.

Species			Max. IV	Mean IV	St.dev	P- value	Dist. class indicated
Cephaloidea	<i>Cephaloon</i>	<i>ungulare*</i>	53.3	29.4	6.9	0.003	cc
Eucnemidae	<i>Hylis</i>	<i>terminalis</i>	28.6	14.1	7.3	0.056	cc
Leiodidae	<i>Agathidium</i>	<i>depressum*</i>	42.4	33.1	5.3	0.060	cc
Staphylinidae	<i>Erichsonius</i>	<i>patella</i>	28.6	14.2	7.8	0.061	cc
Scydmaenidae	<i>Euconnus</i>	<i>sp.*</i>	30.1	17.4	9.6	0.093	cc
Ciidae	<i>Orthocis</i>	<i>punctatus*</i>	60.9	23.0	10.2	0.002	cc&t
Elateridae	<i>Denticollis</i>	<i>denticornis*</i>	62.8	37.4	7.8	0.002	cc&t
Elateridae	<i>Limoni</i>	<i>aeger*</i>	48.6	31.1	6.9	0.022	cc&t
Scaptiidae	<i>Anaspis</i>	<i>flavipennis</i>	44.6	33.2	5.4	0.035	cc&t
Staphylinidae	<i>Bryoporus</i>	<i>sp.</i>	37.5	15.4	8.9	0.071	cc&t
Pythidae	<i>Priognathus</i>	<i>monilicornis</i>	35.4	21.1	8.8	0.088	cc&t
Latridiidae	<i>Melanophthalma</i>	<i>pumila*</i>	65.8	39.9	7.5	0.000	fire
Latridiidae	<i>Melanophthalma</i>	<i>americana</i>	80.9	28.1	11.1	0.000	fire
Elateridae	<i>Ampedus</i>	<i>mixtus*</i>	64.8	21.9	10.9	0.006	fire
Scolytidae	<i>Pityophthorus</i>	<i>opaculus</i>	45.8	15.4	8.6	0.006	fire
Cerambycidae	<i>Leptura</i>	<i>subhamata*</i>	57.0	24.1	10.9	0.009	fire
Latridiidae	<i>Cartodere</i>	<i>constricta</i>	50.0	14.2	7.5	0.011	fire
Scolytidae	<i>Pityophthorus</i>	<i>puberulus</i>	41.1	16.3	9.0	0.011	fire
Scolytidae	<i>Cryphalus</i>	<i>ruficollis</i>	59.4	28.8	9.7	0.012	fire
Scaptiidae	<i>Canifa</i>	<i>pusilla*</i>	53.8	33.8	7.5	0.014	fire
Nitidulidae	<i>Glischrochilus</i>	<i>siepmanni</i>	50.0	14.3	8.0	0.017	fire
Elateridae	<i>Dalopius</i>	<i>cognatus</i>	48.7	27.8	8.6	0.027	fire
Staphylinidae	<i>Phloeonomus</i>	<i>pusillus</i>	31.0	17.1	9.0	0.049	fire
Elateridae	<i>Ampedus</i>	<i>luctuosus*</i>	38.4	22.7	9.6	0.068	fire
Scolytidae	<i>Polygraphus</i>	<i>rufipennis*</i>	41.9	25.6	10.0	0.078	fire
Staphylinidae	<i>Leptusa</i>	<i>smetanaiella*</i>	40.0	27.1	7.3	0.057	wind
Staphylinidae	<i>Leptusa</i>	<i>~cribratula*</i>	41.2	27.4	8.6	0.064	wind
Elateridae	<i>Ctenicera</i>	<i>p.propola*</i>	31.2	18.7	9.8	0.096	wind

Species-structure models

The species-structure regression analysis yielded models for 66 species (Appendix 4). It is not surprising that a higher number of significant indicators resulted via this method, given that species abundances should reflect habitat availability and given that the habitat structures showed little variation between forest disturbance classes (Chapter One). Table 2 presents

species that are positively correlated with structures considered to be characteristic of wind disturbance or with structures considered to be characteristic of thinned forests.

Table 2. Species with positive relationships with structures considered characteristic of wind disturbed forests (crown closure or large diameter deadwood) and species with positive relationships with structures considered characteristic of thinned forests (small diameter deadwood or fallen deadwood).

Species		CROWN	Lg.dia. DW	Sm.dia. DW	FALLEN DW	Disturbance history
Elateridae	<i>Athous rufifrons</i>	*				wind
Staphylinidae	<i>Leptusa smetanaiella</i> *	*				wind
Chrysomelidae	<i>Syneta ferruginea</i>	*				wind
Staphylinidae	<i>Leptusa-cribratula</i> *	*				wind
Scolytidae	<i>Dryocoetes betulae</i>	*				wind
Chrysomelidae	<i>Syneta extorris borealis</i>	*				wind
Scolytidae	<i>Xyloterinus politus</i>		*			wind
Scaphididae	<i>Scaphisoma sp.</i>		*			wind
Anobiidae	<i>Dorcatoma falli</i>		*			wind
Elateridae	<i>Ctenicera p.propola</i> *		*			wind
Carabidae	<i>Bradycellus semipubescens</i>		*			wind
Scolytidae	<i>Xylechinus americanus</i>		*			wind
Cerambycidae	<i>Evodinus m.monticola</i>			*		thinned
Melandryidae	<i>Serropalpus substriatus</i>			*		thinned
Staphylinidae	<i>Mycetoporus consors</i>				*	thinned
Elateridae	<i>Denticollis denticornis</i> *				*	thinned
Cerambycidae	<i>Strangalepta abbreviata</i>				*	thinned

Fauna differentiating forest disturbance classes and their structural correlates

Fifteen species in total were simultaneously indicators of a disturbance history class and significantly correlated with at least one forest structure variable; this overlap is indicated by asterisks in Tables 1 and 2. This refined species array comprised the fauna subjected to the CCA. The resulting CCA direct ordination biplot (Figure 1) suggests that the two structure variables CROWN (percentage of crown closure) and DECIDUOUS (volume of deadwood from deciduous tree species) correlate with the refined species array to explain much of the forest class separation. As indicated by the slightly longer CROWN axis in the biplot,

CROWN exhibits a stronger correlation than DECIDUOUS. One also can observe the nature of forest class separation relating to these two variables. In relation to CROWN, wind disturbed forests and their indicator species all fall clearly toward the tip of the axis (away from the centroid) suggesting the correlation of these forests and species with higher crown closure. The fire disturbed forests and their indicator species show the opposite extreme, falling entirely on the other side of and distant from the centroid, reflecting the lower crown closure in these forests and negative correlations of these indicators with crown closure. The clearcut and thinned forests are arranged intermediately between the two CROWN extremes. Clearcut forests and their indicators tend to fall along the higher than average CROWN range while the thinned forests and their indicators fall along the lower than average CROWN range. Thus the association of the forest disturbances and their indicator species relative to crown closure can be summarized as wind > clearcut > thinned > fire.

The only discernible associations relating forest disturbance classes and class indicators to DECIDUOUS exist for the thinned and fire classes. Thinned forests and their indicators generally fall in the above-average DECIDUOUS range, while the fire forests and their indicators are all in the below-average DECIDUOUS range. Thus, high deciduous deadwood volumes seem to be a factor explaining indicators of thinned forests; this may relate to higher volumes of deciduous deadwood resulting from the thinning practice of felling the non-desirable deciduous trees. The fact that lower volumes of the same forest element are generally associated with fire indicator species is more difficult to interpret.

Having extracted the most general and consistent forest-species-structure patterns from the CCA, it may be useful to emphasize some other species-structure relationships (from

Appendix 4) to lend further insight to the biological meaning of the disturbance class indicators. All indicators of wind disturbed forests showed positive correlations with the CROWN variable while, not surprisingly, the fire disturbance indicators all showed a negative correlations with CROWN. One wind disturbed forest indicator showed a positive correlation with the variable SIZE3 (large diameter deadwood), considered here to be an old-forest characteristic. A single fire disturbed forest indicator correlated with this variable, though negatively. The volume of conifer deadwood was a positive indicator for two of the wind disturbed forest indicator species, a pattern not observed elsewhere in the regression models for disturbance class indicators. Models for indicators of the clearcut disturbance class contained three species correlating negatively with the variable SIZE1 (small diameter deadwood) and two species with positive relationships with STAND (standing deadwood). This finding may relate more to the low abundance of these species in the thinned forests, where SIZE 1 is relatively abundant and STAND is relatively non-abundant.

Figure 1. Canonical correspondence analysis ordination bi-plot of forest sites in the space of linear combinations of the forest structures best correlated with the beetle assemblage. Symbols signify forest disturbance history classes: X = CLEARCUT, * = THINNED, $\diamond$ = FIRE, and $\bullet$ = WIND. Abbreviated names denote beetle species used in the analysis; full names are given in Table 1 marked by asterisks. Numbers identify the actual forest.

DISCUSSION

The high number of new collection records coming from this research is an indication of the paucity of information about the distribution of invertebrate species in this part of Canada. Given the fact that beetles are among the most frequently collected invertebrate orders only emphasizes this fact. The several species collected here that are yet undescribed makes real the possibility that species could be endangered by human disturbances before they are even known to science.

Bousquet (1991) recognized 1320 beetle species known to occur in Nova Scotia. Knowing that 41% of the species identified in the present study were new provincial records allows an opportunity to calculate a crude estimate of the number of species that might be revealed with a similar sampling effort if one used a variety of methods and applied these across a broad range of habitats in Nova Scotia. Assuming that the ratio of known to new records from the current samples approximates the ratio of total known to sampleable new records, one could calculate the sampleable number of species in the province to be in the vicinity of 1860 species. However, the representation of rarely-sampled species would undoubtedly continue to increase with sampling effort, and probably reveal many more undescribed species among these. The total number of species is probably much higher.

Three factors probably contribute to the high proportion of new collection records in this study. First, with the exception of recent related studies (Kehler *et al.* 1996; Potter 1997), the method, intensity, and duration of trapping is new for the region. Second, some of the forest disturbance classes in this study were probably not sampled by past collectors, and obviously contained distinct forest structures and fauna. For example, a high proportion of the new

records from fire origin and thinned forests correlates with their structural uniqueness, such as lower crown closure in fire origin forests and very high volumes of small, well-decayed deadwood in pre-commercially thinned forests. Third, the effort devoted toward species-level identification was high compared to typical research and thus many new records do not necessarily represent previously uncollected species, but simply species that were previously not identified.

Indicators of forest disturbance and indicators of forest structures

The information presented in Table 1 and Table 2 serves as species-specific evidence of forest organisms that differ in abundance depending on forest disturbance history and in relation to forest structures. These ‘indicator species’ do not directly support the notion that species are endangered by modern forestry, *per se*; such a conclusion would demand a much broader understanding of the distribution and natural history of each species. Further, it is probable that most threatened species in the current study system occur in abundances too low to sample with the methods and effort employed here. Clearly, however, the findings illustrate the capacity of different disturbances to alter species populations, and they are consistent with the claim that variability in forest structures is a medium through which disturbance alters forest species assemblages.

The idea that even-age management generates forest structures that differ from the structures generated by natural disturbances is supported by the current findings. The ordination analysis revealed that the percent of crown closure and the volume of deadwood from deciduous trees correspond best with a differentiation of the beetle communities

between disturbance history classes. These findings, in combination with the preponderance of the same two variables in the species-structure models, suggest two factors that should demand high attention in any attempts to modify forestry practices based on natural disturbance as a model. Applied research might seek to determine, for example, how forestry practices could be modified to better approximate the high percentage of crown closure indicative of wind disturbance.

An even more interesting observation from this research, however, is that deadwood structures characteristic of old-forests may exist residually in many managed forests in Nova Scotia. The direct findings of no significant differences between structures such as the volume of large-diameter deadwood or deadwood from deciduous trees (Chapter One) supports this point. Indirectly, evidence also exists in the fact that more species showed relationships with structures (66) than to particular disturbance histories (28); the idea here being that if beetles are indeed related to structures and structures showed little variation between disturbance histories, then one would expect fewer indicators of forest disturbance histories than indicators of forest structures. The implication, depending on the degree to which this is true, is that alteration of deadwood structures and deadwood-dependent organisms by forest management is probably in its early and dissuadable stages in Nova Scotia spruce forests, and forests with similar management histories. Therefore, forestry management recommendations are delivered in a hopeful context, with the suggestion that a high potential exists for maintaining species populations in these managed forests provided that effort is taken immediately to accommodate critical habitat structures.

Observations and hypothesis testing towards confirming or rejecting species as indicators

In considering future research, one should first acknowledge that the species treated in this study are a biased representation of the saproxylic beetle fauna of Nova Scotia spruce forests. This has mostly to do with the flight intercept trapping method. Obviously, the method is biased against sampling species that do not fly. Thus many saproxylic species, even abundant species, had little chance of being considered in this research due only to the particular methodology. This fact raises an important issue as one acknowledges the conservation concern related to the *continuity* of forest habitats. While it is important for old-forest habitats to be available for the organisms that depend on those habitats, it is equally important for many species that these habitats are available continuously and abundantly through time. Continuity seems to be particularly important for species with limited dispersal and recolonization capacities. In Sweden, for example, Nilsson and Baranowski (1997) implicated lack of habitat continuity and poor dispersal ability as factors that have threatened a high proportion of the beetles that live in hollow beech trees.

Species that were sampled in my work are among the best beetle dispersers. Because species vulnerability increases as their dispersal ability decreases, and because dispersal ability is proportional to flight ability, the methodology used here is suspected to ‘miss’ much of fauna that is in most need of attention—species that do not fly. One should anticipate that conclusions from this research may provide relatively little insight into the very big problem of habitat continuity hiatuses. Continuity is strongly recommended as an issue for future research.

Speight (1989; 1997) and Good (1997) both emphasize the basic necessity of deriving species lists for conservation tools. Speight (1989) details the process of developing a list of saproxylic invertebrate indicators in Europe. Good (1997) offers convincing insights as to why selection and monitoring of primeval forests for biodiversity conservation is better if based on indicator assemblages of invertebrates rather than single indicator species. Speight (1997) uses a case study to exemplify how invertebrate species lists may be used to indicate forest conservation priorities and for monitoring the success of conservation actions. When the basic knowledge of saproxylic invertebrate ecology in North America is at an appropriate level, following the examples of these pioneers, and learning from their mistakes, may prove to be the most efficient approach.

This research is intended to commence the task of discerning species that are native in Nova Scotia spruce forests and that are particularly susceptible to loss of microhabitats due to modern forestry practices replacing natural disturbance. The lists of indicators I offer here suggests first that such species probably do exist, and serves as a starting point upon which to base testable hypotheses and plan observational studies. This early approach resembles the initial stages of the European process (Speight 1989; Good 1997). Ultimately, one looks forward to management tools such as Europe's 'red list' of threatened and endangered species or, more precisely, the recognition, if it is appropriate, of saproxylic invertebrate species under Canada's Act to Protect Endangered and Threatened Species. Achieving this end would not only allow for intelligent recommendations on measures of protection, but would establish the legislative capacities to ensure that recommendations are addressed.

I suggest that reaching the preferred ends will first demand that the information offered here as lists of indicator species be regarded as preliminary working hypotheses. To be able to consider the information reliable and replicable, these hypotheses must be subjected to stringent testing and observational studies on the basic ecology of each species. As Ball and Key (1997) suggest, autecological research must subsequently determine whether any particular associations between a species and a microhabitat (e.g., large, standing, well-decayed spruce) is also dependent on other ecological parameters (e.g., nectar, a lichen species, or moisture). Ultimately, factors at the larger spatial scale of landscape and at the temporal scale (continuity) will have to be part of any attempts to approximate the effects of natural disturbances by modifying the management of fiber resources.

LITERATURE CITED

- Atlegrim, O., K. Sjöerg, and J.P. Ball. 1997. Forestry effects on a ground beetle community in spring: selective logging and clear-cutting compared. *Entomologica Fennica* **8**:19-26.
- Attiwell, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* **63**:247-300.
- Ball, S.G. and R.S. Key. 1997. The management of ancient trees for the benefit of saproxylic invertebrate fauna: the British Experience. In *Conservation, management, and restoration of habitats for invertebrates: enhancing biological diversity*. Proceedings of a conference held in Killarney, Ireland, 26-29 May 1996. Council of Europe, Strasbourg.
- Bondrup-Nielsen, S. 1995. Forestry and the boreal forest: maintaining inherent landscape patterns. *Water, Air, and Soil Pollution* **82**:71-76.
- Bousquet, Y. (editor). 1991. *Checklist of beetles of Canada and Alaska*. Agriculture Canada Research Branch Publication **1861/E**.
- Brower, J.E., J.H. Zar, and C.N. von Ende. 1990. *Field and laboratory methods for general ecology*. 3rd ed. W.C. Brown Publishers, Dubuque, IA.
- Budianski, S. 1995. *Nature's keepers: the new science of nature conservation*. Free Press, New York.
- Buse, A. and J.E.G. Good. 1993. The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. *Biological Conservation* **64**:67-76.

- Butterfield, J., M.L. Luff, M. Bains, and M.D. Eyre. 1995. Carabid beetle communities as indicators of conservation potential in upland forests. *Forest Ecology and Management* 79:63-77.
- Canadian Council of Forest Ministers. 1995. *Defining sustainable forest management: a Canadian approach to criteria and indicators*. Canadian Forest Service, Natural Resources Canada.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143.
- Ehrlich, P.R. 1996. Conservation in temperate forests—what do we need to do? *Forest Ecology and Management* 85:9-19.
- Essen, P.-A., B. Ehnström, L. Ericson, and K. Sjöberg. 1992. Boreal forests-the focal habitat of Fennoscandia. Pages 252-325 in L. Hansson, editor, *Ecological principals of nature conservation*. Elsevier Applied Science, London.
- Downie, N.M. and R.H. Arnett Jr. 1996. *The beetles of Northeastern North America*. In 2 volumes. The Sandhill Crane Press, Gainesville, FL.
- Duelli, P., P. Flückiger, and M. Obrist. 1997. *To enhance biodiversity: managing forests-or edges and gaps?* Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland.
- Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366.
- Faith, D.P., P.R. Minchin, and L. Belbin. 1987. Composition dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57-68.

- Franklin, J.F. 1995. Why link species conservation, environmental protection, and resource management? Pages 326-335 in C.G. Jones and J.H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York.
- Franklin, J.F., K. Cromack Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, G. Juday. 1981. *Ecological characteristics of old-growth Portland, OR. Douglas-fir forests*. USDA Forest Service General technical report PNW-118,
- Freund, J.E. 1992. *Mathematical statistics*. Prentice-Hall, London.
- Good, J.A. 1997. The use of macroinvertebrate indicator assemblages for Pan-European habitat conservation of saproxylic communities. In *Conservation, management, and restoration of habitats for invertebrates: enhancing biological diversity*. Proceedings of a conference held in Killarney, Ireland, 26-29 May 1996. Council of Europe, Strasbourg.
- Gore, J.A. and W.A. Patterson III. 1985. Mass downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. *Canadian Journal of Forest Research* 16:335-339.
- Hagan, J.M. and S.L. Grove. 1996. *1995 Report: Selection cutting, old-growth, birds, and forest structure in Maine*. Manomet Observatory Report MODCF-96002.
- Hafernik, J.E. 1992. Threats to invertebrate biodiversity: implications for conservation strategies. Pages 171-196 in P.L. Fiedler and S.K. Jain, editors. *Conservation Biology*. Chapman and Hall, New York.
- Haila, Y., I.K. Hanski, J. Niemelä, P. Punttila, S. Raivio, and H. Tukia. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. *Annales Zooligici Fennici* 31:187-202.

- Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Annales Zooligici Fennici* **31**:203-217.
- Haila, Y. and J. Kouki. 1994. The phenomenon of biodiversity in conservation biology. *Annales Zooligici Fennici* **31**:5-18.
- Hammond, H.E.J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. *The Canadian Entomologist* **129**:1009-1033.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133-302.
- Hautaluoma, J. and R. Woodmansee. 1994. New roles in ecological research and policy making. *Ecological International Bulletin* **21**:1-10.
- Hosmer, D.W. and S. Lemeshow. 1989. *Applied Logistic Regression*. John Wiley & Sons, New York.
- Hunter, M. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* **65**:115-120.
- Kaila, L., P. Martikainen, and P. Punttila. 1997. Dead trees left in clearcuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation* **6**:1-18.
- Kehler, D., C. Corkum, and S. Bondrup-Nielsen. 1996. *Habitat associations and species diversity of forest beetle communities of Nova Scotia*. Results of two summers of

- research by the Center for Wildlife and Conservation Biology, Acadia University, Wolfville, Nova Scotia, Canada.
- Kohn, A.J. and A.C Riggs. 1982. Sample size dependence in measures of proportional similarity. *Marine Ecological Progress Series* 9:147-151.
- Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, and M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: Their use as indicators in conservation planning. *Conservation Biology* 7:796-808.
- Kremen, C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecological Applications* 4:407-422.
- Lubchenco, J. 1995. The role of science in formulating a biodiversity strategy. *BioScience* 45:s7-s9.
- Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey.
- Mathsoft Inc. 1995. S-Plus for Windows, Version 3.3, Release 1.
- Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non epidemic conditions: a comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120:257-264.
- McCarthy, M.A. and M.A. Burgman. 1995. Coping with uncertainty in forest wildlife planning. *Forest Ecology and Management* 74:23-36.
- McCullagh, P. and Nelder, J.A. 1983. *Generalized Linear Models*. Chapman and Hall, London.

- McCune, B. and M.J. Mefford. 1997. *PC-ORD for Windows: multivariate analysis of ecological data, Version 3.09*. MJM Software, Glenden Beach, Oregon, USA.
- McMahon, J. 1989. The new forest in Nova Scotia. Pages 159-162 in A. Schneider, editor, *Deforestation and "development" in Canada and the tropics*. University College of Cape Breton.
- Muona, J., and I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zooligici Fennici* **31**:109–121.
- National Board of Forestry, Sweden. 1996. *Action plan for biological diversity and sustainable forestry*. National Board of Forestry, Jönköping.
- Niemelä, J. 1997. Invertebrates and boreal forest management. *Conservation Biology* **11**:601–610.
- Nilsson, S.G., U. Arup, R. Baranowski, and S. Ekman. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* **5**:1208-1215.
- Nilsson, S.G. and R. Baranowski. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* **20**:491-498.
- Noss, R.F. and A.Y. Cooperrider. 1994. *Saving nature's legacy. Protecting and restoring biodiversity*. Island Press, Washington, D.C.
- Oliver, I. and A.J. Beattie. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* **6**:594-607.
- Pearson, D.L. 1992. Tiger beetles as indicators for biodiversity patterns in Amazonia. *National Geographic Research and Exploration* **8**:116-117.

- Pearson, D.L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6:376-391.
- Pickett, S.T.A. and P.S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL, 472 pp..
- Pimentel, D., U. Stachow, D.A. Takacs, H.W. Brubaker, A.R. Dumas, J.J. Meaney, J.A.S. O'Neil, D.E. Onsi, and D.B. Corzilius. 1992. Conserving biodiversity in agricultural/forestry systems. *BioScience* 42:383-392.
- Potter, K.M. 1997. *Beetle communities of managed softwood forests in Nova Scotia*. B.Sc. Honors thesis. Department of Environmental Science, Acadia University, Nova Scotia.
- Roland, A.E. and E.C. Smith. 1969. *The Flora of Nova Scotia*. The Nova Scotia Museum, Halifax, Nova Scotia.
- Samuelsson, J., L. Gustafsson, and T. Ingelög. 1994. *Dying and dead trees-a review of their importance for biodiversity*. Swedish threatened species unit, Uppsala.
- Siitonen, J. and P. Martikainen. 1994. Occurrence of rare and threatened insects on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research* 9:185-191.
- Speight, M.C.D. 1997. Invertebrate species lists as management tools: an example using databased information about Syrphidae (Diptera). In *Conservation, management, and restoration of habitats for invertebrates: enhancing biological diversity*. Proceedings of a conference held in Killarney, Ireland, 26-29 May 1996. Council of Europe, Strasbourg.

- Speight, M.C.D. 1989. *Saproxyllic invertebrates and their conservation*. Nature and Environment Series, no. 42. Council of Europe, Strasbourg.
- Sprugel, D.G. 1991. Disturbance, equilibrium and environmental variability: what is 'natural' vegetation in a changing environment. *Biological Conservation* 58:1-18.
- Sturtevant, B.R., J.A. Bissonette, J.N. Long, and D.W. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecological Applications* 7:702-712.
- Swanson, F.J., and J.F. Franklin. 1992. New forestry principals from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* 2:262-274.
- Systat Inc. 1993. *Systat 5.02 for Windows*.
- Väisänen, R., O. Biström, and K. Heliövaara. 1993. Subcortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? *Biodiversity and Conservation* 2:95-113.
- Warren, M.S. and R.S. Key. 1991. Woodlands: past present and potential for insects. Chapter 8 in Collins, N.M. and J.A. Thomas, editors, *The Conservation of Insects and their Habitats. 15th Symposium of the Royal Entomological Society of London*. 14-15 September 1989. College, London. Academic Press Limited, San Diego, CA.
- Weaver, J.C. 1995. Indicator species and scale of observation. *Conservation Biology* 9:939-942.
- Weisberg, S. 1985. *Applied Linear Regression*, 2nd edition. New York, Wiley.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21:213-251.

- Wolda, H. 1981. Similarity indices, sample size, and diversity. *Oecologia* **50**:296-302.
- Zar, J.H. 1996. Biostatistical analysis. 3rd edition. Prentice-Hall, New Jersey. 662 pp.

APPENDIX 1

List of saproxylic beetle assemblage sampled, name of determiner, new collection records, and total abundance of individuals sampled. New records are based on Bousquet (1991). New record codes indicate the following: NS = new to Nova Scotia, AC = new to Atlantic Canada, CAN = new to Canada, Und. = an undescribed species.

Family	Species	Determined By	New Records	Abun.
Aderidae	<i>Vanonus wickhami</i> Casey	D.J. Bishop '98		4
Anobiidae	<i>Caenocara oculatum</i> (Say)	D.J. Bishop '98		2
Anobiidae	<i>Dorcatoma falli</i> R.E. White	D.J. Bishop '98	AC	11
Anobiidae	<i>Dorcatoma pallicornis</i> LeConte	D.J. Bishop '98	NS	12
Anobiidae	<i>Hadrobergmus notatus</i> (Say)	D.J. Bishop '98		31
Anobiidae	<i>Hemicoelus carinatus</i> (Say)	D.J. Bishop '98	NS	1
Anobiidae	<i>Platybergmus canadensis</i> Fisher	D.J. Bishop '98		1
Anobiidae	<i>Ptilinus ruficornis</i> Say	D.J. Bishop '98		3
Anobiidae	<i>Sculptotheca puberula</i> (LeConte)	D.J. Bishop '98	AC	3
Buprestidae	<i>Melanophila d. drummundi</i> (Kirby)	D.J. Bishop '98	NS	1
Carabidae	<i>Bembidion minus</i> Hayward	Y. Bousquet '98		1
Carabidae	<i>Bradycellus nigriceps</i> LeConte	Y. Bousquet '98	AC	1
Carabidae	<i>Bradycellus nigrinus</i> (Dejean)	Y. Bousquet '98		3
Carabidae	<i>Bradycellus semipubescens</i> (Dejean)	Y. Bousquet '98	NS	5
Carabidae	<i>Cymindis limbata</i> Dejean	Y. Bousquet '98		1
Carabidae	<i>Dromius piceus</i> Lindroth	Y. Bousquet '98		9
Carabidae	<i>Syntomus americanus</i> (Dejean)	Y. Bousquet '98		1
Cephaloidea	<i>Cephaloon lepturoides</i> Newman	D.J. Bishop '98	AC	1
Cephaloidea	<i>Cephaloon unguare</i> LeConte	D.J. Bishop '98	NS	90
Cerambycidae	<i>Acmaeops p. proteus</i> (Kirby)	D.J. Bishop '98	NS	1
Cerambycidae	<i>Acmaeopsoides rufulus</i> (Haldeman)	D.J. Bishop '98		1
Cerambycidae	<i>Anthophylax attenuatus</i> (Haldeman)	D.J. Bishop '98		2
Cerambycidae	<i>Anthophylax cyaneus</i> (Haldeman)	D.J. Bishop '98	NS	2
Cerambycidae	<i>Anthophylax viridis</i> LeConte	D.J. Bishop '98		10
Cerambycidae	<i>Asemum striatum</i> (Linnaeus)	D.J. Bishop '98	NS	2
Cerambycidae	<i>Charisalia americana</i> (Haldeman)	D.J. Bishop '98	AC	1
Cerambycidae	<i>Cosmosalia chrysocoma</i> (Kirby)	D.J. Bishop '98		7
Cerambycidae	<i>Evodinus m. monticola</i> (Randall)	D.J. Bishop '98		46
Cerambycidae	<i>Hyperplatys maculata</i> Haldeman	D.J. Bishop '98		1
Cerambycidae	<i>Idiopidonia pedalis</i> (LeConte)	D.J. Bishop '98		39
Cerambycidae	<i>Judolia m. montivagens</i> (Couper)	D.J. Bishop '98		7
Cerambycidae	<i>Leptura subhamata</i> Randall	D.J. Bishop '98		17
Cerambycidae	<i>Molorchus b. bimaculatus</i> Say	D.J. Bishop '98	AC	1
Cerambycidae	<i>Monochamus s. scutellatus</i> (Say)	D.J. Bishop '98		1
Cerambycidae	<i>Nealosterna capitata</i> (Newman)	D.J. Bishop '98		1
Cerambycidae	<i>Pidonia rufficollis</i> (Say)	D.J. Bishop '98		358
Cerambycidae	<i>Pogonocherus penicillatus</i> LeConte	D.J. Bishop '98		3
Cerambycidae	<i>Stictoleptura c. canadensis</i> (Olivier)	D.J. Bishop '98		2
Cerambycidae	<i>Strangalepta abbreviata</i> (Germar)	D.J. Bishop '98		98
Cerambycidae	<i>Tetropium c. cinnamopterum</i> (Kirby)	D.J. Bishop '98		1
Cerambycidae	<i>Trachysida aspera brevifrons</i> (Howden)	D.J. Bishop '98		2
Cerambycidae	<i>Trachysida mutabilis</i> (Newman)	D.J. Bishop '98		2
Cerambycidae	<i>Xestoleptura tibialis</i> (LeConte)	D.J. Bishop '98		1
Cerylonidae	<i>Cerylon castaneum</i> Say	D.J. Bishop '98		84
Chrysomelidae	<i>Syneta extorris borealis</i> Brown	D.J. Bishop '98		9

Chrysomelidae	<i>Syneta ferruginea</i> (Germar)	D.J. Bishop '98		34
Chrysomelidae	<i>Syneta pilosa</i> Brown	D.J. Bishop '98		2
Ciidae	<i>Ceracis sallei</i> (Mellié)	D.J. Bishop '98	AC	2
Ciidae	<i>Ceracis thoracicornis</i> (Ziegler)	D.J. Bishop '98	AC	1
Ciidae	<i>Cis fuscipes</i> Mellié	D.J. Bishop '98		1
Ciidae	<i>Cis horridulus</i> Casey	D.J. Bishop '98		1
Ciidae	<i>Orthocis punctatus</i> (Mellié)	D.J. Bishop '98	NS	22
Clambidae	<i>Clambus</i> sp.	D.J. Bishop '98		64
Cleridae	<i>Phlogistosternus dislocatus</i> (Say)	D.J. Bishop '98	NS	1
Cleridae	<i>Thanasimus undatulus</i> (Say)	D.J. Bishop '98		4
Cucujidae	<i>Cucujus c. clavipes</i> Fabricius	D.J. Bishop '98		1
Cucujidae	<i>Dendrophagus cygnaei</i> Mannerheim	D.J. Bishop '98	NS	3
Cucujidae	<i>Laemophloeus fasciatus</i> Melsheimer	D.J. Bishop '98	AC	1
Elateridae	<i>Agriotes collaris</i> (LeConte)	D.J. Bishop '98		34
Elateridae	<i>Agriotes limosus</i> (LeConte)	D.J. Bishop '98		17
Elateridae	<i>Agriotes stabilis</i> (LeConte)	D.J. Bishop '98	NS	3
Elateridae	<i>Ampedus deletus</i> (LeConte)	S. Laplante '98		70
Elateridae	<i>Ampedus fuscus</i> (LeConte)	S. Laplante '98	NS	1
Elateridae	<i>Ampedus longibursa</i> Ramberg(mn)	D.J. Bishop '98	NS	2
Elateridae	<i>Ampedus luctuosus</i> (LeConte)	D.J. Bishop '98		13
Elateridae	<i>Ampedus mixtus</i> (Herbst)	S. Laplante '98		13
Elateridae	<i>Ampedus</i> n.sp. undescribed	D.J. Bishop '98	Und.	1
Elateridae	<i>Ampedus protervus</i> (LeConte)	D.J. Bishop '98		2
Elateridae	<i>Ampedus pullus</i> Germar	D.J. Bishop '98		2
Elateridae	<i>Ampedus semicinctus</i> (Randall)	D.J. Bishop '98		1
Elateridae	<i>Athous brightwelli</i> (Kirby)	D.J. Bishop '98		4
Elateridae	<i>Athous orvus</i> Becker	D.J. Bishop '98		4
Elateridae	<i>Athous rufifrons</i> (Randall)	D.J. Bishop '98		96
Elateridae	<i>Athous scapularis</i> (Say)	D.J. Bishop '98	AC	1
Elateridae	<i>Ctenicera appressa</i> (Randall)	D.J. Bishop '98	NS	1
Elateridae	<i>Ctenicera cylindricornis</i> (Herbst)	D.J. Bishop '98		1
Elateridae	<i>Ctenicera falsifica</i> (LeConte)	D.J. Bishop '98		87
Elateridae	<i>Ctenicera hamata</i> (Say)	D.J. Bishop '98		2
Elateridae	<i>Ctenicera insidiosa</i> (LeConte)	D.J. Bishop '98		56
Elateridae	<i>Ctenicera nitidula</i> (LeConte)	D.J. Bishop '98		12
Elateridae	<i>Ctenicera p. propola</i> (LeConte)	D.J. Bishop '98		7
Elateridae	<i>Ctenicera pulchra</i> (LeConte)	D.J. Bishop '98		4
Elateridae	<i>Ctenicera resplendens aeraria</i> (Randall)	D.J. Bishop '98		5
Elateridae	<i>Ctenicera rufopluralis</i> (Fall)	D.J. Bishop '98		2
Elateridae	<i>Ctenicera spinosa</i> (LeConte)	D.J. Bishop '98		112
Elateridae	<i>Ctenicera sulcicollis</i> (Say)	D.J. Bishop '98	AC	1
Elateridae	<i>Ctenicera triundulata</i> (Randall)	D.J. Bishop '98		188
Elateridae	<i>Ctenicera vulnerata</i> (LeConte)	D.J. Bishop '98		7
Elateridae	<i>Dalopius cognatus</i> Brown	D.J. Bishop '98		128
Elateridae	<i>Dalopius fuscipes</i> Brown	D.J. Bishop '98		4
Elateridae	<i>Dalopius gentilis</i> Brown	D.J. Bishop '98	AC	69
Elateridae	<i>Dalopius</i> n.sp. undescribed	E. Becker '98	Und.	1
Elateridae	<i>Dalopius vagus</i> Brown	D.J. Bishop '98		79
Elateridae	<i>Denticollis denticornis</i> (Kirby)	D.J. Bishop '98		112
Elateridae	<i>Drasterius debilis</i> LeConte	D.J. Bishop '98		10
Elateridae	<i>Eanus maculipennis</i> (LeConte)	D.J. Bishop '98	NS	6
Elateridae	<i>Limonius aeger</i> LeConte	J. Cook '98		60
Elateridae	<i>Limonius confusus</i> LeConte	D.J. Bishop '98		1
Elateridae	<i>Oxygonus montanus</i> Schaeffer	D.J. Bishop '98		32
Elateridae	<i>Sericus honestus</i> (Randall)	D.J. Bishop '98	NS	48

Elateridae	<i>Sericus incongruus</i> (LeConte)	D.J. Bishop '98		31
Elateridae	<i>Sericus viridanus</i> (Say)	D.J. Bishop '98		7
Endomychidae	<i>Mycetina perpulchra</i> (Newman)	D.J. Bishop '98		11
Endomychidae	<i>n.g n.sp.</i> undescribed	Y. Bousquet '98	Und.	2
Endomychidae	<i>Phymaphora pulchella</i> Newman	D.J. Bishop '98		7
Erotylidae	<i>Triplax dissimulator</i> (Crotch)	D.J. Bishop '98	AC	2
Erotylidae	<i>Triplax flavicollis</i> Lacordaire	D.J. Bishop '98	AC	1
Erotylidae	<i>Tritoma pulchra</i> Say	D.J. Bishop '98		34
Eucinetidae	<i>Eucinetus morio</i> LeConte	D.J. Bishop '98		2
Eucnemidae	<i>Dirhagus pectinatus</i> (LeConte)	D.J. Bishop '98	NS	3
Eucnemidae	<i>Epiphanis cornutus</i> Eschscholtz	D.J. Bishop '98	NS	16
Eucnemidae	<i>Hylis terminalis</i> (LeConte)	D.J. Bishop '98	AC	3
Eucnemidae	<i>Isorhipis obliqua</i> (Say)	D.J. Bishop '98		3
Histeridae	<i>Hister curtatus</i> J.E.LeConte	Y. Bousquet '98		1
Histeridae	<i>Paromalus teres</i> LeConte	S. Laplante '98	NS	4
Cryptophagidae	<i>Anchicera sp.1</i>	D.J. Bishop '98		33
Cryptophagidae	<i>Atomaria sp.1</i>	D.J. Bishop '98		12
Cryptophagidae	<i>Atomaria sp.2</i>	D.J. Bishop '98		2
Cryptophagidae	<i>Caenoscelis basalis</i> Casey	D.J. Bishop '98	AC	1
Cryptophagidae	<i>Cryptophagus sp.</i>	D.J. Bishop '98		3
Cryptophagidae	<i>Henoticus serratus</i> (Gyllenhal)	D.J. Bishop '98	AC	1
Cryptophagidae	<i>Henotiderus obesulus</i> (Casey)	D.J. Bishop '98		13
Lagriidae	<i>Paratenetus fuscus</i> LeConte	D.J. Bishop '98	AC	32
Lampyridae	<i>Ellychnia corrusca</i> (Linnaeus)	D.J. Bishop '98		98
Lampyridae	<i>Lucidota atra</i> (Olivier)	D.J. Bishop '98		2
Lampyridae	<i>Photinus consanguineus</i> LeConte	D.J. Bishop '98		8
Latridiidae	<i>Cartodere constricta</i> (Gyllenhal)	F.G. Andrews '98	NS	2
Latridiidae	<i>Corticaria n.sp.1. & Corticaria n.sp.2</i>	F.G. Andrews '98	2 Und.	9
Latridiidae	<i>Enicmus tenuicornis</i> LeConte	F.G. Andrews '98	AC	51
Latridiidae	<i>Latridius sp.</i> Mannerheim	F.G. Andrews '98	AC	5
Latridiidae	<i>Melanophthalma americana</i> Mannerheim	F.G. Andrews '98	AC	48
Latridiidae	<i>Melanophthalma n.sp.</i>	F.G. Andrews '98	Und.	10
Latridiidae	<i>Melanophthalma pumila</i> (LeConte)	F.G. Andrews '98	AC	757
Latridiidae	<i>Stephostethus litratus</i> (LeConte)	F.G. Andrews '98		7
Leiodidae	<i>Agathidium depressum</i> Fall	D.J. Bishop '98	AC	137
Leiodidae	<i>Agathidium difforme</i> (LeConte)	D.J. Bishop '98	AC	2
Leiodidae	<i>Agathidium sp.1</i>	D.J. Bishop '98		1
Leiodidae	<i>Agathidium sp.2</i>	D.J. Bishop '98		3
Leiodidae	<i>Anisotoma basalis</i> (LeConte)	D.J. Bishop '98		3
Leiodidae	<i>Anisotoma blanchardi</i> (Horn)	D.J. Bishop '98	AC	2
Leiodidae	<i>Anisotoma horni</i> Wheeler	D.J. Bishop '98	NS	3
Leiodidae	<i>Anisotoma inops</i> Brown	D.J. Bishop '98	NS	127
Leiodidae	<i>Leiodes assimilis</i> (LeConte)	D.J. Bishop '98		1
Lucanidae	<i>Ceruchus piceus</i> (Weber)	D.J. Bishop '98		6
Lycidae	<i>Celetes basalis</i> LeConte	D.J. Bishop '98		7
Lycidae	<i>Dictyopterus aurora</i> (Herbst)	D.J. Bishop '98		74
Lycidae	<i>Eros humeralis</i> (Fabricius)	D.J. Bishop '98	AC	11
Lycidae	<i>Plateros ?subfurcatus</i> Green	J. Cook '98	AC	1
Lycidae	<i>Plateros lictor</i> (Newman)	D.J. Bishop '98		13
Melandryidae	<i>Dircaea liturata</i> (LeConte)	D.J. Bishop '98	NS	20
Melandryidae	<i>Emmesa connectans</i> Newman	D.J. Bishop '98		15
Melandryidae	<i>Eustrophus tomentosus</i> Say	D.J. Bishop '98	AC	1
Melandryidae	<i>Mystaxus simulator</i> (Newman)	D.J. Bishop '98		1
Melandryidae	<i>Orchesia castanea</i> (Melsheimer)	D.J. Bishop '98		12
Melandryidae	<i>Prothalia undata</i> LeConte	D.J. Bishop '98		6

Melandryidae	<i>Scotochroa atra</i> LeConte	D.J. Bishop '98	NS	2
Melandryidae	<i>Scotochroa buprestoides</i> (Kirby)	D.J. Bishop '98	NS	3
Melandryidae	<i>Scotochroides antennatus</i> Mank	D.J. Bishop '98	AC	20
Melandryidae	<i>Serropalpus substriatus</i> Haldeman	D.J. Bishop '98	NS	20
Melandryidae	<i>Spilotus quadripustulatus</i> (Melsheimer)	D.J. Bishop '98	AC	1
Melandryidae	<i>Symphora flavicollis</i> (Haldeman)	D.J. Bishop '98		3
Melandryidae	<i>Xylita laevigata</i> (Hellenius)	D.J. Bishop '98	NS	2
Melandryidae	<i>Xylita livida</i> (C.R.Sahlberg)	D.J. Bishop '98		2
Mycetophagidae	<i>Mycetophagus pluripunctatus</i> LeConte	D.J. Bishop '98	AC	1
Nitidulidae	<i>Glischrochilus fasciatus</i> (Olivier)	D.J. Bishop '98		4
Nitidulidae	<i>Glischrochilus sanguinolentus</i> (Olivier)	D.J. Bishop '98		54
Nitidulidae	<i>Glischrochilus siepmanni</i> Brown	D.J. Bishop '98	NS	2
Oedemeridae	<i>Calopus angustus</i> LeConte	D.J. Bishop '98	AC	2
Pselaphidae	<i>Batrisodes globosus</i> (LeConte)	D.S. Chandler '98		14
Pselaphidae	<i>Biblopectus integer</i> (LeConte)	D.S. Chandler '98		2
Pselaphidae	<i>Bibloporus bicanalis</i> (Casey)	D.S. Chandler '98	CAN	32
Pselaphidae	<i>Euplectus duryi</i> Casey	D.S. Chandler '98		1
Pselaphidae	<i>Euplectus elongatus</i> Brendel	D.S. Chandler '98	AC	3
Pselaphidae	<i>Reichenbachia spatulifer</i> Casey	D.S. Chandler '98	NS	1
Pyrochroidae	<i>Dendroides canadensis</i> Latreille	D.J. Bishop '98		3
Pyrochroidae	<i>Dendroides concolor</i> (Newman)	D.J. Bishop '98		7
Pyrochroidae	<i>Schizotus cervicalis</i> Newman	D.J. Bishop '98		2
Pythidae	<i>Priognathus monilicornis</i> (Randall)	J. Cook '98		10
Rhizophagidae	<i>Rhizophagus dimidiatus</i> Mannerheim	D.J. Bishop '98		7
Salpingidae	<i>Rhinosimus viridiaeneus</i> Randall	J. Cook '98		2
Scaphidiidae	<i>Baeocera</i> sp.1	D.J. Bishop '98		1
Scaphidiidae	<i>Baeocera</i> sp.2	D.J. Bishop '98		1
Scaphidiidae	<i>Scaphidium quadriguttatum</i> Say	D.J. Bishop '98	AC	1
Scaphidiidae	<i>Scaphisoma</i> sp.	D.J. Bishop '98		7
Scolytidae	<i>Conophthorus coniperda</i> (Schwarz)	D.E. Bright '98		1
Scolytidae	<i>Cryphalus ruficollis</i> Hopkins	D.E. Bright '98		30
Scolytidae	<i>Crypturgus borealis</i> Swaine	D.E. Bright '98		28
Scolytidae	<i>Dendroctonus rufipennis</i> (Kirby)	D.E. Bright '98		4
Scolytidae	<i>Dryocoetes affabber</i> (Mannerheim)	D.E. Bright '98		2
Scolytidae	<i>Dryocoetes autographus</i> (Ratzeburg)	D.E. Bright '98		19
Scolytidae	<i>Dryocoetes betulae</i> Hopkins	D.E. Bright '98		15
Scolytidae	<i>Hylurgops pinifex</i> (Fitch)	D.E. Bright '98		2
Scolytidae	<i>Monarthrum mali</i> (Fitch)	D.E. Bright '98	NS	2
Scolytidae	<i>Pityogenes hopkinsi</i> Swaine	D.E. Bright '98		8
Scolytidae	<i>Pityokteines sparsus</i> (LeConte)	D.E. Bright '98		4
Scolytidae	<i>Pityophthorus balsameus</i> Blackman	D.E. Bright '98		5
Scolytidae	<i>Pityophthorus biovalis</i> Blackman	D.E. Bright '98		3
Scolytidae	<i>Pityophthorus dentifrons</i> Blackman	D.E. Bright '98		5
Scolytidae	<i>Pityophthorus opaculus</i> LeConte	D.E. Bright '98		5
Scolytidae	<i>Pityophthorus puberulus</i> (LeConte)	D.E. Bright '98		6
Scolytidae	<i>Pityophthorus</i> sp.	D.E. Bright '98		1
Scolytidae	<i>Polygraphus rufipennis</i> (Kirby)	D.E. Bright '98		35
Scolytidae	<i>Trypodendron betulae</i> Swaine	D.E. Bright '98		9
Scolytidae	<i>Trypodendron lineatum</i> (Olivier)	D.E. Bright '98		36
Scolytidae	<i>Trypodendron rufitarsus</i> (Kirby)	D.E. Bright '98		29
Scolytidae	<i>Xyleborus sayi</i> (Hopkins)	D.E. Bright '98	AC	6
Scolytidae	<i>Xylechinus americanus</i> Blackman	D.E. Bright '98		4
Scolytidae	<i>Xyloterinus politus</i> (Say)	D.E. Bright '98		15
Scraptiidae	<i>Anaspis flavipennis</i> Haldeman	D.J. Bishop '98	NS	307
Scraptiidae	<i>Anaspis nigrina</i> Csiki	D.J. Bishop '98	NS	7

Scraptiidae	<i>Anaspis rufa</i> Say	D.J. Bishop '98		3880
Scraptiidae	<i>Canifa pusilla</i> (Haldeman)	D.J. Bishop '98	NS	125
Scydmaenidae	<i>Euconnus</i> sp.	D.J. Bishop '98		5
Scydmaenidae	<i>Stenichmus</i> sp.	D.J. Bishop '98		17
Sphindidae	<i>Eurysphindus hirtus</i> LeConte	D.J. Bishop '98	AC	1
Sphindidae	<i>Odontosphindus denticollis</i> LeConte	D.J. Bishop '98	AC	3
Sphindidae	<i>Sphindus trinifer</i> Casey	D.J. Bishop '98	AC	5
Staphylinidae	<i>Acidota crenata</i> (Fabricius)	A. Davies '98		1
Staphylinidae	<i>Acrotona</i> sp.	J. Klimaszewski '98		1
Staphylinidae	<i>Amischa</i> sp.	J. Klimaszewski '98		2
Staphylinidae	<i>Atheta</i> sp.1	J. Klimaszewski '98		10
Staphylinidae	<i>Atheta</i> sp.2	J. Klimaszewski '98		14
Staphylinidae	<i>Atheta</i> sp.3	J. Klimaszewski '98		1
Staphylinidae	<i>Atheta</i> sp.4	J. Klimaszewski '98		1
Staphylinidae	<i>Atheta</i> sp.5	J. Klimaszewski '98		2
Staphylinidae	<i>Atheta</i> sp.6	J. Klimaszewski '98		1
Staphylinidae	<i>Brachida</i> sp.	J. Klimaszewski '98		1
Staphylinidae	<i>Bryoporus rufescens</i> LeConte	A. Davies '98	NS	18
Staphylinidae	<i>Bryoporus</i> sp. LeConte	A. Davies '98		3
Staphylinidae	<i>Charyphus picipennis</i> (LeConte)	A. Davies '98		5
Staphylinidae	<i>Deinopsis</i> sp.	A. Davies '98		1
Staphylinidae	<i>Erichsonius patella</i> (Horn)	A. Smetana '98	AC	2
Staphylinidae	<i>Eusphalerum convexum</i> (Fauvel)	D.J. Bishop '98		276
Staphylinidae	<i>Eusphalerum fenyessi</i> (Bernhauer)	D.J. Bishop '98		744
Staphylinidae	<i>Eusphalerum pothos</i> (Mannerheim)	A. Davies '98		3
Staphylinidae	<i>Gabrieus microphthalmus</i> (Horn)	A. Smetana '98	AC	6
Staphylinidae	<i>Gyrophana</i> sp.	J. Klimaszewski '98		2
Staphylinidae	<i>Hapalareae hamata</i> (Fauvel)	A. Davies '98		8
Staphylinidae	<i>Hapalareae</i> n.sp.	A. Davies '98	Und.	3
Staphylinidae	<i>Leptusa ~cribratula</i> Casey	J. Klimaszewski '98		23
Staphylinidae	<i>Leptusa opaca</i> Casey	J. Klimaszewski '98	CAN	16
Staphylinidae	<i>Leptusa smetanaiella</i> Pace	J. Klimaszewski '98	CAN	32
Staphylinidae	<i>Leptusa</i> sp.1	J. Klimaszewski '98		2
Staphylinidae	<i>Leptusa</i> sp.2	J. Klimaszewski '98		2
Staphylinidae	<i>Lithocharis thoracica</i> (Casey)	A. Davies '98	NS	1
Staphylinidae	<i>Lordithon quaesitor</i> (Horn)	A. Davies '98		1
Staphylinidae	<i>Meotica</i> sp.	J. Klimaszewski '98		2
Staphylinidae	<i>Mycetoporus consors</i> LEConte	A. Davies '98		204
Staphylinidae	<i>Myllaena</i> sp.	A. Davies '98		1
Staphylinidae	<i>Ontholestes cingulatus</i> (Gravenhorst)	D.J. Bishop '98		1
Staphylinidae	<i>Oxyopoda</i> sp.	J. Klimaszewski '98		1
Staphylinidae	<i>Palaminus</i> sp.	A. Davies '98		1
Staphylinidae	<i>Philhygra</i> sp.1	J. Klimaszewski '98		2
Staphylinidae	<i>Philhygra</i> sp.2	J. Klimaszewski '98		2
Staphylinidae	<i>Phloeonomus pusillus</i> (Gravenhorst)	A. Davies '98		5
Staphylinidae	<i>Phloeonomus</i> sp.	J. Klimaszewski '98		1
Staphylinidae	<i>Phloeopora</i> sp.	J. Klimaszewski '98		2
Staphylinidae	<i>Platydracus violaceus</i> (Gravenhorst)	A. Smetana '98		1
Staphylinidae	<i>Platydracus viridanus</i> Horn	A. Smetana '98		1
Staphylinidae	<i>Quedius canadensis</i> (Casey)	A. Smetana '98	NS	2
Staphylinidae	<i>Quedius capucinus</i> (Gravenhorst)	A. Smetana '98	AC	3
Staphylinidae	<i>Quedius peregrinus</i> (Gravenhorst)	A. Smetana '98		1
Staphylinidae	<i>Quedius plagiatu</i> Mannerheim	A. Smetana '98	NS	3
Staphylinidae	<i>Quedius rusticus</i> Smetana	A. Smetana '98	NS	24
Staphylinidae	<i>Scopaeus</i> sp.	A. Davies '98		1

Staphylinidae	<i>Sepedophilus cinctulus</i> (Erichson)	A. Davies '98	AC	1
Staphylinidae	<i>Sepedophilus crassus</i> (Gravenhorst)	A. Davies '98	AC	3
Staphylinidae	<i>Stenus angustus</i> Casey	A. Davies '98		1
Staphylinidae	<i>Stenus immarginatus</i> Maklin	A. Davies '98		1
Staphylinidae	<i>Tachinus fumipennis</i> (Say)	A. Davies '98		2
Staphylinidae	<i>Tachinus luridus</i> Erichson	A. Davies '98		1
Staphylinidae	<i>Tachyporus chrysomelinus</i> (Paykull)	A. Davies '98		1
Staphylinidae	<i>Tachyporus nitidulus</i> (Fabricius)	A. Davies '98	NS	3
Staphylinidae	<i>Tinotus</i> sp.	J. Klimaszewski '98		1
Staphylinidae	<i>Tympanophorus puncticollis</i> (Erichson)	A. Smetana '98	NS	5
Tenebrionidae	<i>Bolitophagus corticola</i> Say	D.J. Bishop '98	AC	1
Tenebrionidae	<i>Capnochora fuliginosa</i> (Melsheimer)	D.J. Bishop '98	NS	2
Tenebrionidae	<i>Hymenorus niger</i> (Melsheimer)	D.J. Bishop '98	NS	8
Tenebrionidae	<i>Isomira quadristriata</i> (Couper)	D.J. Bishop '98		1129
Tenebrionidae	<i>Mycetochara analis</i> (LEConte)	D.J. Bishop '98	AC	3
Tenebrionidae	<i>Mycetochara bicolor</i> (Couper)	D.J. Bishop '98	AC	2
Tetratomidae	<i>Abstrulia tessellata</i> (Melsheimer)	D.J. Bishop '98	AC	3
Tetratomidae	<i>Penthe pimelia</i> (Fabricius)	D.J. Bishop '98	NS	4
Throscidae	<i>Aulonothroscus constrictor</i> (Say)	D.J. Bishop '98		133
Throscidae	<i>Trixagus carinicollis</i> (Schaeffer)	D.J. Bishop '98	NS	8

APPENDIX 2

Forest structure information matrix. Description of each variable is in Chapter One, Table 3.

forest	DH	age	CROWN	SIZE1	SIZE2	SIZE3	DECAY1	DECAY2	DECAY3	STAND.	FALL.	DECID.	CONIFER	ALLDW
1	fire	47	75.0	0.0642	0.0000	0.0107	0.0250	0.0146	0.0353	0.0513	0.0236	0.0413	0.0336	0.0749
2	wind	70	87.2	0.1728	0.0922	0.0099	0.1159	0.0801	0.0789	0.1357	0.1392	0.0079	0.2670	0.2749
3	cc	50	84.6	0.0716	0.0985	0.2659	0.1817	0.0825	0.1718	0.2372	0.1989	0.1265	0.3095	0.4360
4	cc	51	81.3	0.0347	0.1249	0.0750	0.0262	0.0135	0.1949	0.1206	0.1140	0.1075	0.1271	0.2346
5	wind	118	89.4	0.0380	0.1372	0.0825	0.0926	0.0997	0.0653	0.0893	0.1683	0.0664	0.1913	0.2577
6	cc	51	74.4	0.0707	0.0747	0.0879	0.0533	0.1019	0.0781	0.1621	0.0711	0.1145	0.1188	0.2333
7	cc&t	45	81.7	0.1670	0.0528	0.0385	0.0442	0.0183	0.1958	0.0878	0.1705	0.0442	0.2141	0.2583
8	cc&t	38	80.8	0.1565	0.1605	0.1426	0.2106	0.0437	0.2053	0.2326	0.2270	0.4144	0.0452	0.4596
9	cc&t	67	89.4	0.1442	0.1073	0.0000	0.1590	0.0563	0.0362	0.0681	0.1834	0.1029	0.1486	0.2515
10	cc	45	85.6	0.1002	0.1023	0.0063	0.1272	0.0123	0.0692	0.1376	0.0712	0.0319	0.1768	0.2087
11	wind	49	77.7	0.0497	0.1709	0.1035	0.0625	0.0484	0.2132	0.1414	0.1827	0.0496	0.2745	0.3241
12	cc	52	76.9	0.0304	0.0404	0.0608	0.0856	0.0271	0.0189	0.0233	0.1083	0.0211	0.1105	0.1316
13	cc&t	52	42.5	0.1030	0.1703	0.0465	0.2111	0.0873	0.0214	0.0373	0.2826	0.1169	0.2029	0.3198
14	cc&t	44	55.6	0.1059	0.0348	0.0066	0.0993	0.0336	0.0143	0.0207	0.1235	0.0515	0.0957	0.1472
15	fire	69	42.5	0.2798	0.1072	0.0597	0.3310	0.0424	0.0733	0.2523	0.1943	0.0045	0.4422	0.4467
16	fire	59	46.9	0.1478	0.1446	0.0000	0.1489	0.0746	0.0689	0.1581	0.1343	0.0196	0.2728	0.2924
17	fire	70	63.8	0.0935	0.0907	0.0846	0.0901	0.1178	0.0609	0.1217	0.1471	0.1061	0.1627	0.2688
18	wind	106	91.9	0.0486	0.1093	0.2394	0.0277	0.0786	0.2910	0.1278	0.2695	0.0246	0.3727	0.3973
19	wind	75	86.3	0.0405	0.0931	0.0246	0.0297	0.0679	0.0606	0.0773	0.0810	0.0049	0.1533	0.1582
20	cc&t	35	76.4	0.2063	0.2240	0.0164	0.0180	0.0761	0.3526	0.0223	0.0942	0.1042	0.3425	0.4467
21	wind	90	70.3	0.2063	0.2240	0.0093	0.0854	0.0766	0.2776	0.1722	0.2674	0.2030	0.2366	0.4396
22	cc	72	82.5	0.0402	0.0470	0.0000	0.0567	0.0180	0.0125	0.0166	0.0706	0.0035	0.0837	0.0872
23	wind	200	75.0	0.0471	0.1356	0.1058	0.1037	0.1117	0.0731	0.1010	0.1876	0.0404	0.2482	0.2886
24	wind	250	93.8	0.0573	0.0991	0.1158	0.0978	0.1053	0.0690	0.0953	0.1769	0.0272	0.2450	0.2722
25	wind	102	75.6	0.1098	0.4302	1.8874	0.6203	1.3294	0.4777	0.0605	2.3669	0.0205	2.4069	2.4274
26	wind	59	92.3	0.0990	0.0987	0.0018	0.0997	0.0519	0.0479	0.0479	0.1516	0.0299	0.1696	0.1995
27	cc&t	46	82.5	0.0903	0.0208	0.0020	0.0147	0.0079	0.0904	0.1378	0.1540	0.0136	0.0994	0.1130
28	cc	53	85.6	0.1514	0.1366	0.0038	0.1124	0.0416	0.1378	0.0759	0.2159	0.0216	0.2702	0.2918
29	cc&t	30	66.4	0.2671	0.0739	0.0745	0.0300	0.0082	0.3773	0.0709	0.1369	0.0440	0.3715	0.4155
30	wind	115	84.4	0.1374	0.0611	0.0234	0.0466	0.0333	0.1420	0.0422	0.1797	0.0200	0.2019	0.2219

APPENDIX 3

Dufrene and Legendre's (1997) method of calculating indicator values, which assumes that two or more *a priori* groups of sample units exist, and that species abundances have been recorded in each of the sample units.

For each species, the following steps are made in the implementation in PC-ORD:

1. Calculate the proportional abundance of a particular species in a particular group relative to the abundance of that species in all groups. Also express as a percentage and display the intermediate result.

Let A = sample unit x species matrix

a_{ijk} = abundance of species j in sample unit i of group k

n_k = number of sample units in group k

g = total number of groups

First calculate the mean abundance x_{kj} of species j in group k :

$$x_{kj} = \frac{\sum_{i=1}^{n_k} a_{ijk}}{n_k}$$

Then calculate the relative abundance RA_{kj} of species j in group k

$$RA_{kj} = \frac{x_{kj}}{\sum_{k=1}^g x_{kj}}$$

2. Calculate the proportional frequency of the species in each group, i.e. the percentage of sample units in each group that contain that species. Also express as a percentage and display the intermediate result.

First transform A to a matrix of presence-absence, B :

Then calculate relative frequency RF_{kj} of species j in group k :

$$RF_{kj} = \frac{\sum_{i=1}^{n_k} b_{ijk}}{n_k}$$

3. Combine the two proportions calculated in steps 1 and 2 by multiplying them. Express the result as a percentage, yielding an indicator value IV_{kj} for each species j in each group k .

$$IV_{kj} = RA_{kj} * RF_{kj} * 100$$

4. The highest indicator value (IVmax) for a given species across groups is saved as a summary of the overall indicator value of that species.

5. Evaluate statistical significance of IVmax by a Monte Carlo method. Randomly reassign SU's to groups a large number of times (default=1000). Each time, calculate IVmax. The probability of type I error is the proportion of times that the IVmax from the randomized data set equals or exceeds the IVmax from the actual data set. The null hypothesis is that IVmax is no larger than would be expected by chance (i.e. that the species has no indicator value).

From McCune and Mefford (1997).

APPENDIX 4

Generalized linear regression models for beetle species in relation to forest structures.

CLASSICAL MODELS	Species	Explanatory Variable(s)	Coeff. $\pm$ SE	T values	Model F	Model P	Multiple R ² (adjusted)
Tenebrionidae	<i>Isomira quadristriata</i>	Intercept DECIDUOUS	25.694 $\pm$ 5.668 180.522 $\pm$ 54.672	4.533 3.302	10.902	0.003	0.255
Staphylinidae	<i>Mycetoporus consors</i>	Intercept SIZE3 DECAY1 FALLEN	7.065 $\pm$ 1.742 -32.759 $\pm$ 15.496 -39.821 $\pm$ 15.672 35.569 $\pm$ 13.904	4.056 -2.114 -2.541 2.558	3.288	0.036	0.191
Lampyridae	<i>Ellychnia corrusca</i>	Intercept DECAY3 DECIDUOUS	3.094 $\pm$ 0.543 -7.948 $\pm$ 2.874 18.672 $\pm$ 4.241	5.702 -2.765 4.403	11.582	<0.001	0.422
Latridiidae	<i>Melanophthalma pumila</i>	Intercept CROWN	104.281 $\pm$ 34.596 -103.182 $\pm$ 44.445	3.014 -2.322	5.39	0.028	0.131
Leiodidae	<i>Agathidium depressum</i>	Intercept SIZE1 STANDING	5.277 $\pm$ 1.49 -30.661 $\pm$ 9.876 25.867 $\pm$ 10.36	3.542 -3.105 2.497	6.471	0.005	0.274
Elateridae	<i>Ctenicera spinosa</i>	Intercept DECIDUOUS	1.885 $\pm$ 0.79 27.95 $\pm$ 7.617	2.387 3.67	13.465	0.001	0.301
Elateridae	<i>Denticollis denticornis</i>	Intercept FALLEN	1.816 $\pm$ 1.279 35.92 $\pm$ 13.29	1.42 2.703	3.878	0.033	0.166

POISSON MODELS	Species	Explanatory Variables	Coeff. $\pm$ SE	T value	Model G	Model P
Cerylonidae	<i>Cerylon castaneum</i>	Intercept DECIDUOUS DECAY3	1.006 $\pm$ 0.176 4.383 $\pm$ 0.976 -2.714 $\pm$ 1.228	5.728 4.489 -2.21	17.97	0.0001
Cerambycidae	<i>Strangalepta abbreviata</i>	Intercept SIZE3 FALLEN DECAY3	0.684 $\pm$ 0.235 -9.776 $\pm$ 1.729 7.411 $\pm$ 1.414 -2.257 $\pm$ 1.185	2.91 -5.655 5.24 -1.905	43.385	<0.0001
Elateridae	<i>Ampedus deletus</i>	Intercept DECAY3 CROWN SIZE1	4.543 $\pm$ 0.739 -4.884 $\pm$ 1.977 -3.604 $\pm$ 0.894 -5.831 $\pm$ 2.660	6.146 -2.47 -4.034 -2.192	46.382	<0.0001

Elateridae	<i>Athous rufifrons</i>	Intercept	-0.954 ± 0.778	-1.227	17.532	0.0002
		DECIDUOUS	3.247 ± 0.862	3.768		
		CROWN	2.372 ± 0.951	2.495		
Cerambycidae	<i>Evodinus m. monticola</i>	Intercept	-0.239 ± 0.307	-0.778	7.072	0.0078
		SIZE1	5.364 ± 1.944	2.759		
Elateridae	<i>Limonius aeger</i>	Intercept	4.032 ± 0.606	6.659	32.578	<0.0001
		CROWN	-4.345 ± 0.859	-5.06		
		STANDING	-5.586 ± 2.058	-2.715		
		DECAY3	2.351 ± 0.893	2.631		
Clambidae	<i>Clambus sp.</i>	Intercept	-3.047 ± 1.497	-2.035	35.786	<0.0001
		DECAY1	-10.471 ± 2.791	-3.751		
		FALLEN	6.590 ± 1.901	3.466		
		SIZE1	9.074 ± 2.284	3.972		
		CONIFER	-4.213 ± 1.514	-2.783		
		CROWN	4.274 ± 1.653	2.585		
Lycidae	<i>Dictyopterus aurora</i>	Intercept	-0.418 ± 1.024	-0.408	28.762	<0.0001
		DECAY3	7.721 ± 1.810	4.267		
		CROWN	1.386 ± 1.218	1.137		
		CONIFER	-8.545 ± 2.389	-3.577		
		FALLEN	7.335 ± 2.169	3.382		
		DECIDUOUS	-4.385 ± 2.015	-2.176		
Cephaloidea	<i>Cephaloon unguare</i>	Intercept	1.978 ± 0.253	7.819	26.061	<0.0001
		CONIFER	-3.745 ± 1.327	-2.821		
		SIZE1	-6.175 ± 2.036	-3.034		
		DECAY3	3.943 ± 1.409	2.799		
Scraptiidae	<i>Canifa pusilla</i>	Intercept	2.992 ± 0.423	7.079	15.615	0.0004
		CROWN	-1.809 ± 0.553	-3.272		
		DECIDUOUS	-3.703 ± 1.633	-2.268		
Throscidae	<i>Aulonothroscus constrictor</i>	Intercept	-6.037 ± 1.076	-5.611	86.63	<0.0001
		CROWN	7.503 ± 1.129	6.648		
		SIZE1	12.205 ± 1.650	7.396		

LOGISTIC MODELS	Species	Explanatory Variables	Coeff. ± SE	T value	Model G	Model P
Scolytidae	<i>Trypodendron lineatum</i>	Intercept	-0.506 ± 0.715	-0.708	7.831	0.0199
		SIZE3	-7.547 ± 3.610	-2.091		
		DECAY1	19.258 ± 9.746	1.976		
Kryptophagidae	<i>Anchicera sp.1</i>	Intercept	1.751 ± 0.984	1.78	4.108	0.0427
		CONIFER	-5.923 ± 4.145	-1.429		
Staphylinidae	<i>Leptusa smetanaiella</i>	Intercept	-4.768 ± 2.801	-1.702	13.094	0.0014
		SIZE3	-19.303 ± 8.705	-2.217		
		CROWN	8.296 ± 3.824	2.17		

Chrysomelidae	<i>Syneta ferruginea</i>	Intercept CROWN DECIDUOUS	-9.303 ± 4.337 10.620 ± 5.059 21.128 ± 12.126	-2.145 2.099 1.742	10.861	0.0044
Staphylinidae	<i>Leptusa ~cribratula</i>	Intercept CONIFER CROWN	-7.608 ± 3.458 12.557 ± 5.264 6.641 ± 3.665	-2.2 2.385 1.812	10.714	0.0047
Erotylidae	<i>Tritoma pulchra</i>	Intercept CROWN	-5.928 ± 3.142 7.630 ± 3.936	-1.887 1.939	5.53	0.0187
Staphylinidae	<i>Eusphalerum convexum</i>	Intercept STANDING DECAY3	-0.797 ± 0.902 24.593 ± 1.935 -14.805 ± 7.356	-0.884 2.249 -2.013	12.201	0.0022
Elateridae	<i>Sericus incongruus</i>	Intercept DECIDUOUS	-0.955 ± 0.601 13.890 ± 8.659	-1.588 1.604	4.198	0.0405
Scolytidae	<i>Dryocoetes autographus</i>	Intercept SIZE1 DECAY1	0.936 ± 0.913 -31.562 ± 13.394 18.451 ± 10.490	1.025 -2.356 1.759	12.557	0.0019
Staphylinidae	<i>Bryoporus rufescens</i>	Intercept DECAY3	-1.487 ± 0.667 9.335 ± 4.312	-2.231 2.165	6.428	0.0112
Melandryidae	<i>Serropalpus substriatus</i>	Intercept SIZE1	-1.980 ± 0.873 13.876 ± 6.815	-2.27 2.036	5.139	0.0234
Scolytidae	<i>Polygraphus rufipennis</i>	Intercept SIZE3 CROWN	6.466 ± 3.383 -20.122 ± 11.986 -7.690 ± 4.111	1.911 -1.679 -1.871	10.786	0.0045
Scolytidae	<i>Xyloterinus politus</i>	Intercept SIZE3	-0.992 ± 0.543 8.260 ± 6.192	-1.825 1.334	3.868	0.0492
Cerambycidae	<i>Leptura subhamata</i>	Intercept CROWN	4.560 ± 2.573 -6.952 ± 3.355	1.772 -2.072	5.42	0.0199
Elateridae	<i>Ampedus luctuosus</i>	Intercept CROWN	4.840 ± 2.637 -7.322 ± 3.437	1.835 -2.131	5.873	0.0154
Elateridae	<i>Sericus honestus</i>	Intercept CROWN STANDING SIZE3	13.114 ± 6.469 -22.066 ± 9.463 49.394 ± 2.635 -44.277 ± 22.154	2.027 -2.332 2.394 -1.999	23.195	0.0004
Melandryidae	<i>Orchesia castanea</i>	Intercept CONIFER FALLEN	0.306 ± 0.648 -29.089 ± 12.125 28.243 ± 12.325	0.473 -2.399 2.292	14.035	0.0009
Anobiidae	<i>Dorcatoma pallicornis</i>	Intercept DECAY1	-2.214 ± 0.839 11.947 ± 6.512	-2.639 1.835	6.271	0.0123

Ciidae	<i>Orthocis punctatus</i>	Intercept DECIDUOUS	-1.772 ± 0.682 13.611 ± 8.147	-2.598 1.671	4.773	0.0289
Elateridae	<i>Ctenicera nitidula</i>	Intercept CROWN	4.744 ± 2.595 -7.452 ± 3.418	1.828 -2.18	6.027	0.0141
Endomychidae	<i>Mycetina perpulchra</i>	Intercept CONIFER DECIDUOUS	0.418 ± 1.305 -15.198 ± 7.513 23.463 ± 11.251	0.321 -2.023 2.085	13.382	0.0012
Elateridae	<i>Dalopius vagus</i>	Intercept STANDING	0.540 ± 0.856 -17.440 ± 9.522	0.631 -1.832	4.57	0.0325
Elateridae	<i>Drasterius debilis</i>	Intercept DECIDUOUS	-1.913 ± 0.695 12.782 ± 7.829	-2.751 1.633	4.514	0.0336
Scolytidae	<i>Dryocoetes betulae</i>	Intercept CROWN	-13.596 ± 6.470 15.443 ± 7.685	-2.102 2.01	7.714	0.0055
Elateridae	<i>Dalopius gentilis</i>	Intercept DECIDUOUS	-0.166 ± 0.691 -23.246 ± 15.743	-0.239 -1.477	3.858	0.0495
Scaphidiidae	<i>Scaphisoma sp.</i>	Intercept SIZE3	-2.152 ± 0.714 11.431 ± 6.682	-3.013 1.711	6.242	0.0125
Tenebrionidae	<i>Hymenorus niger</i>	Intercept CROWN SIZE1	-20.572 ± 9.421 20.596 ± 9.974 21.794 ± 11.477	-2.184 2.065 1.899	10.134	0.0063
Anobiidae	<i>Dorcatoma falli</i>	Intercept SIZE3	-2.608 ± 0.825 13.748 ± 7.250	-3.16 1.896	7.556	0.006
Chrysomelidae	<i>Syneta extorris borealis</i>	Intercept CROWN	-11.165 ± 6.234 12.009 ± 7.381	-1.791 1.627	4.604	0.0319
Elateridae	<i>Ampedus mixtus</i>	Intercept DECIDUOUS CROWN	3.619 ± 2.681 14.163 ± 8.022 -8.541 ± 3.990	1.35 1.766 -2.141	10.31	0.0058
Elateridae	<i>Ctenicera p.propola</i>	Intercept SIZE3	-2.492 ± 0.790 12.398 ± 0.925	-3.153 1.79	6.859	0.0088
Endomychidae	<i>Phymaphora pulchella</i>	Intercept SIZE3	-0.105 ± 0.632 -43.479 ± 25.327	-0.165 -1.717	7.695	0.0055
Latridiidae	<i>Stephostethus litratus</i>	Intercept SIZE1	0.654 ± 1.055 -23.579 ± 13.319	0.619 -1.77	5.227	0.0222
Lucanidae	<i>Ceruchus piceus</i>	Intercept STANDING	0.335 ± 0.930 -20.679 ± 11.645	0.36 -1.776	4.617	0.0317

Staphylinidae	<i>Gabrius microphthalmus</i>	Intercept STANDING	0.252 ± 0.921 -19.469 ± 11.300	0.274 -1.723	4.248	0.0393
Throscidae	<i>Trixagus carinicollis</i>	Intercept SIZE3	-3.452 ± 1.115 23.609 ± 10.881	-3.097 2.17	12.275	0.0005
Carabidae	<i>Bradycellus semipubescens</i>	Intercept CROWN STANDING SIZE3	22.147 ± 14.981 -29.286 ± 18.549 -46.891 ± 3.887 3.325 ± 3.217	1.478 -1.579 -1.384 1.034	18.941	0.0003
Scolytidae	<i>Pityophthorus balsameus</i>	Intercept DECAY3 DECAY1	-1.858 ± 1.365 -33.482 ± 17.724 21.705 ± 12.191	-1.362 -1.889 1.78	11.823	0.0027
Scydmaenidae	<i>Euconnus sp.</i>	Intercept SIZE1	0.472 ± 1.128 -24.773 ± 14.951	0.418 -1.657	4.684	0.0304
Histeridae	<i>Paromalus teres</i>	Intercept DECIDUOUS	-2.910 ± 0.877 12.054 ± 7.163	-3.317 1.683	4.273	0.0387
Pyrochroidae	<i>Dendroides concolor</i>	Intercept CROWN	3.195 ± 2.498 -7.076 ± 3.604	1.279 -1.963	4.102	0.0428
Scolytidae	<i>Dendroctonus rufipennis</i>	Intercept DECIDUOUS	-3.096 ± 0.951 14.161 ± 8.251	-3.255 1.716	5.185	0.0228
Scolytidae	<i>Pityokteines sparsus</i>	Intercept CROWN CONIFER	18.999 ± 10.338 -24.951 ± 12.750 -22.422 ± 13.856	1.838 -1.957 -1.618	15.379	0.0005
Scolytidae	<i>Pityophthorus dentifrons</i>	Intercept DECAY3	0.174 ± 1.119 -29.226 ± 19.995	0.156 -1.462	5.51	0.0189
Scolytidae	<i>Xylechinus americanus</i>	Intercept SIZE3	-2.351 ± 0.659 3.130 ± 2.874	-3.567 1.089	4.043	0.0444
Staphylinidae	<i>Tympanophorus puncticollis</i>	Intercept CONIFER	0.722 ± 1.290 -15.834 ± 8.768	0.56 -1.806	5.109	0.0238
Scraptiidae	<i>Anaspis nigrina</i>	Intercept STANDING	0.163 ± 1.074 -27.199 ± 16.108	0.151 -1.689	4.608	0.0318

APPENDIX 5

Abundance of each saproxylic beetle species sampled in each forest. Species arranged in same order as Appendix 1, alphabetical by family, then genus, then species.

Species	Forests																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Vanonus wickhami</i> Casey	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Caenocara oculatum</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
<i>Dorcatoma falli</i> R.E. White	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	3	3	0	0	0	1	0	
<i>Dorcatoma pallicornis</i> LeConte	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	3	0	0	1	2	1	0	0	0	0	
<i>Hadrobergmus notatus</i> (Say)	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	6	0	0	0	12	0	1	1	0	0	1	4	0	1	
<i>Hemicoelus carinatus</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Platybergmus canadensis</i> Fisher	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ptilinus ruficornis</i> Say	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Sculptotheca puberula</i> (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	
<i>Melanophila d. drummundi</i> (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bembidion minus</i> Hayward	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bradycellus nigriceps</i> LeConte	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bradycellus nigrinus</i> (Dejean)	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	
<i>Bradycellus semipubescentis</i> (Dejean)	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
<i>Cymindis limbata</i> Dejean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
<i>Dromius piceus</i> Lindroth	0	3	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0
<i>Syntomus americanus</i> (Dejean)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cephaloon lepturoides</i> Newman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cephaloon unguilare</i> LeConte	0	1	4	11	4	8	5	3	0	8	7	6	5	0	0	0	1	0	3	0	6	2	0	1	0	6	2	2	0	5	0
<i>Acmaeops p. proteus</i> (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acmaeopsoides rufulus</i> (Haldeman)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anthophylax attenuatus</i> (Haldeman)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Anthophylax cyaneus</i> (Haldeman)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Anthophylax viridis</i> LeConte	0	2	0	0	0	0	0	1	0	0	1	1	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Asemum striatum</i> (Linnaeus)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Charisalia americana</i> (Haldeman)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Cosmosalia chrysocoma</i> (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Evodinus m. monticola</i> (Randall)	0	3	3	1	2	0	2	1	2	1	0	0	5	0	7	0	1	1	1	1	2	3	1	2	1	3	0	1	2	0	1

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30				
<i>Hyperplatys maculata</i> Haldeman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0				
<i>Idiopidonia pedalis</i> (LeConte)	0	0	0	0	0	3	8	1	1	0	1	1	0	0	0	0	3	1	1	1	0	1	0	0	0	0	0	6	10	0	1			
<i>Judolia m. montivagens</i> (Couper)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0				
<i>Leptura subhamata</i> Randall	0	0	0	0	0	0	1	0	0	0	0	0	1	1	2	6	2	0	1	0	0	0	0	0	1	0	0	0	1	0	1			
<i>Molorechus b. bimaculatus</i> Say	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Monochamus s. scutellatus</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Neocalosterna capitata</i> (Newman)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0			
<i>Pidonia rufficollis</i> (Say)	8	16	20	13	14	0	3	4	204	4	0	3	7	11	2	0	1	12	0	0	0	0	0	0	3	0	0	0	0	0	33			
<i>Pogonocherus penicillatus</i> LeConte	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0			
<i>Stictoleptura c. canadensis</i> (Olivier)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Strangalepta abbreviata</i> (Germar)	0	12	0	0	3	1	3	4	8	2	1	2	11	9	3	3	2	4	8	0	8	1	0	1	0	1	0	0	4	6	1	1		
<i>Tetropium c. cinnamopterum</i> (Kirby)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Trachysida aspera brevifrons</i> (Howden)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0		
<i>Trachysida mutabilis</i> (Newman)	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Xestoleptura tibialis</i> (LeConte)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cerylon castaneum</i> Say	1	3	2	0	4	3	6	11	2	2	4	1	5	2	0	7	5	1	0	0	2	1	1	0	1	0	1	9	3	3	0	5		
<i>Syneta extorris borealis</i> Brown	0	0	0	0	1	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0		
<i>Syneta ferruginea</i> (Germar)	0	1	4	1	0	1	4	7	1	0	2	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	3	0	4	0	0		
<i>Syneta pilosa</i> Brown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1			
<i>Ceracis sallei</i> (Mellié)	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ceracis thoracicornis</i> (Ziegler)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cis fuscipes</i> Mellié	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cis horridulus</i> Casey	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Orthocis punctatus</i> (Mellié)	0	0	1	2	0	0	0	2	2	0	1	0	9	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0		
<i>Clambus</i> sp.	0	0	2	3	0	2	4	3	1	2	1	0	1	1	0	1	0	2	0	5	4	1	1	4	1	0	1	1	0	1	0	23		
<i>Phlogistosternus dislocatus</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Thanasimus undatulus</i> (Say)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cucujus c. clavipes</i> Fabricius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Dendrophagus cygnaei</i> Mannerheim	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Laemophloeus fasciatus</i> Melsheimer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Agriotes collaris</i> (LeConte)	3	2	0	0	1	0	0	6	0	1	0	0	2	1	1	1	0	2	2	0	0	0	0	0	0	0	0	0	0	5	4	1		
<i>Agriotes limosus</i> (LeConte)	0	0	1	0	1	1	0	0	0	1	0	0	6	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	0	3	
<i>Agriotes stabilis</i> (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ampedus deletus</i> (LeConte)	5	3	1	0	1	1	1	0	0	1	1	1	17	1	2	5	3	1	5	1	0	8	0	0	4	1	0	4	1	0	4	1	0	2

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30				
<i>Ampedus fuscus</i> (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Ampedus longibursa</i> Rambert (mn)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Ampedus luctuosus</i> (LeConte)	0	0	0	0	1	0	0	0	1	0	0	0	2	0	1	1	2	0	0	0	1	0	2	1	0	0	0	0	0	1	0			
<i>Ampedus mixtus</i> (Herbst)	8	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Ampedus</i> n.sp. undescribed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0			
<i>Ampedus protervus</i> (LeConte)	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Ampedus pulhus</i> Germar	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0			
<i>Ampedus semicinctus</i> (Randall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Athous brightwelli</i> (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0		
<i>Athous orvus</i> Becker	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0		
<i>Athous rufifrons</i> (Randall)	0	0	5	7	0	3	9	12	0	0	1	7	2	1	1	0	1	2	1	1	3	3	0	2	4	5	15	6	2	3				
<i>Athous scapularis</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ctenicera appressa</i> (Randall)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ctenicera cylindricornis</i> (Herbst)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ctenicera falsifica</i> (LeConte)	4	0	1	2	1	1	4	1	2	4	2	1	3	0	0	4	7	0	2	2	5	6	2	3	0	8	3	5	7	7				
<i>Ctenicera hamata</i> (Say)	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ctenicera insidiosa</i> (LeConte)	0	0	6	1	1	0	19	3	1	0	4	2	1	1	3	0	2	0	0	0	1	2	0	0	0	0	3	2	1	0	3			
<i>Ctenicera nitidula</i> (LeConte)	0	0	0	1	0	0	0	0	0	1	0	0	3	0	1	2	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0		
<i>Ctenicera p. propola</i> (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	2	1	0	0	0	0	0	0	0		
<i>Ctenicera pulchra</i> (LeConte)	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0		
<i>Ctenicera resplendens aeraria</i> (Randall)	0	0	0	3	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ctenicera rufopluralis</i> (Fall)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0		
<i>Ctenicera spinosa</i> (LeConte)	3	2	4	7	4	1	1	11	7	1	0	6	1	5	4	5	16	1	1	1	14	4	1	0	0	3	4	3	1	1				
<i>Ctenicera sulcicollis</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ctenicera triundulata</i> (Randall)	4	3	4	6	15	0	17	0	5	9	7	1	22	2	2	9	7	6	4	11	6	8	7	2	3	7	7	6	1	7				
<i>Ctenicera vulnerata</i> (LeConte)	0	1	0	0	0	0	1	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
<i>Dalopius cognatus</i> Brown	11	0	0	8	1	2	0	0	0	7	0	0	20	0	17	1	10	6	12	4	2	9	1	17	0	0	0	0	0	0	0	0	0	
<i>Dalopius fuscipes</i> Brown	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Dalopius gentilis</i> Brown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	13	27	1	0	5	0	21	0	0	0	0	0	0	0	0	0	
<i>Dalopius</i> n.sp. undescribed	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Dalopius vagus</i> Brown	12	0	0	17	0	0	1	0	1	0	0	0	29	0	0	0	0	1	0	3	0	15	0	0	0	0	0	0	0	0	0	0	0	0
<i>Denticollis denticornis</i> (Kirby)	1	1	2	5	0	1	25	13	1	0	2	7	5	1	2	0	1	0	2	4	7	1	2	1	2	2	16	1	6	1				
<i>Drasterius debilis</i> LeConte	0	0	0	0	0	0	1	3	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Eamus maculipennis</i> (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0		

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Limonius aeger</i> LeConte	1	0	0	3	1	1	3	1	3	2	0	1	9	5	1	4	2	0	0	3	3	0	0	1	5	0	3	1	5	2
<i>Limonius confusus</i> LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Oxygonus montanus</i> Schaeffer	0	0	0	2	0	0	0	7	1	1	0	0	0	1	0	0	0	3	1	0	9	0	0	0	0	1	0	1	0	5
<i>Sericus honestus</i> (Randall)	0	0	0	2	3	0	0	1	5	1	2	7	13	4	4	0	2	1	0	0	1	0	0	0	0	0	0	2	0	0
<i>Sericus incongruus</i> (LeConte)	0	1	0	0	0	0	1	2	0	0	0	0	13	4	1	2	5	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>Sericus viridanus</i> (Say)	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0
<i>Mycetina perpulchra</i> (Newman)	1	0	1	1	0	0	0	1	3	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
<i>n.g n.sp.</i> undescribed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
<i>Phymaphora pulchella</i> Newman	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1
<i>Triplax dissimulator</i> (Crotch)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Triplax flavicollis</i> Lacordaire	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tritoma pulchra</i> Say	0	2	0	3	0	2	0	9	4	1	0	1	0	0	0	0	2	1	1	0	1	0	0	0	0	1	4	1	0	1
<i>Eucinetus morio</i> LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
<i>Dirhagus pectinatus</i> (LeConte)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Epiphanius cornutus</i> Eschscholtz	0	0	0	0	0	1	5	2	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	0	1	2	1	0	0	0
<i>Hyllis terminalis</i> (LeConte)	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Isorhipis obliqua</i> (Say)	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hister curtatus</i> J.E.LeConte	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Paromalus teres</i> LeConte	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anchicera sp.1</i>	0	1	3	5	0	0	2	2	3	1	1	4	1	2	0	2	1	0	1	0	1	1	1	0	0	0	0	0	0	0
<i>Atomaria sp.1</i>	0	0	1	0	1	0	0	0	2	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1
<i>Atomaria sp.2</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
<i>Caenoscelis basalis</i> Casey	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cryptophagus sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
<i>Henoticus serratus</i> (Gyllenhal)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Henotiderus obesulus</i> (Casey)	0	0	1	0	0	1	0	1	0	0	0	1	4	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1
<i>Paratenetus fuscus</i> LeConte	1	1	1	1	4	1	1	0	2	1	0	1	4	1	0	1	1	1	0	1	0	2	2	0	0	0	1	0	3	1
<i>Ellychnia corrusca</i> (Linnaeus)	2	5	6	3	6	4	3	9	9	2	3	3	7	4	2	6	1	3	1	1	3	1	5	2	0	2	1	2	1	1
<i>Lucidota atra</i> (Olivier)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Photinus consanguineus</i> LeConte	0	0	0	0	0	0	0	0	0	1	0	0	4	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cartodere constricta</i> (Gyllenhal)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Corticaria n.sp.1. & Corticaria n.sp.2</i>	0	2	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
<i>Enicmus tenuicornis</i> LeConte	2	10	1	0	3	0	0	3	1	1	1	2	4	2	2	1	0	3	1	0	2	1	0	2	1	3	2	1	1	1
<i>Latridius sp.</i> Mannerheim	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Stenus angustus</i> Casey	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stenus immarginatus</i> * Maklin	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tachinus fumipennis</i> (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Tachinus luridus</i> Erichson	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tachyporus chrysomelinus</i> (Paykull)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tachyporus nitidulus</i> * (Fabricius)	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Tinotus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Tympanophorus puncticollis</i> (Erichson)	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Bolitophagus corticola</i> Say	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Capnochora fuliginosa</i> (Melsheimer)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
<i>Hymenorus niger</i> (Melsheimer)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	2	0	1
<i>Isomira quadristriata</i> (Couper)	37	13	26	44	16	32	95	101	26	45	15	38	5	47	11	38	28	13	22	113	85	58	44	21	25	25	20	35	42	9
<i>Mycetochara analis</i> (LEConte)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Mycetochara bicolor</i> (Couper)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Abstrilia tessellata</i> (Melsheimer)	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Penthe pimelia</i> (Fabricius)	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Autonothrus constrictor</i> (Say)	3	4	2	2	0	0	42	7	16	1	1	0	0	1	0	1	5	5	4	0	5	1	1	1	3	4	2	16	3	3
<i>Trixagus carinicollis</i> (Schaeffer)	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0

APPENDIX 6

Forest location information as on beetle specimen collection labels.

Forest	Location
1	CAN: NS: Hants Co: 9 Mile River 45yr fire blk spruce forest
2	CAN: NS: Pictou Co: Lorne mature red spru/hemlock for
3	CAN: NS: Guys Co: Dayspring Lake red spruce forest
4	CAN: NS: Halifax Co: Grassy Lake wind dist. red spru forest
5	CAN: NS: Halifax Co: Abrahams Lake old growth red spruce for
6	CAN: NS: Halifax Co: Lake Little regen red spruce forest
7	CAN: NS: Halifax Co: Ten Mile Lake pre-com.thin. red spruce
8	CAN: NS: Halifax Co: Moser Lake pre-com.thin. red spruce
9	CAN: NS: Guys Co: Seloam Lake com.thin. red spruce for
10	CAN: NS: Guys Co: Melopseketch Lake young red spruce for
11	CAN: NS: Guys Co: George Lak wind dist young red spruce for
12	CAN: NS: Guys Co: Malay Lake mature red spruce forest
13	CAN: NS: Guys Co: Malay Lake com.thin.mat. red spruce for
14	CAN: NS: Guys Co: Malay Lake com.thin.young red spruce for
15	CAN: NS: Halifax Co: Anti Dam Lake 90 yr fire origin bl spruce
16	CAN: NS: Hants Co: Armstrong Lake 75 yr fire origin red spruc
17	CAN: NS: HantsCo: Little Armstrong Lake 75 yr fire redspruce
18	CAN: NS: Lunenburg Co: Card Lake old growth red spr/hemlo
19	CAN: NS: Hants Co: Leminister mat. red spr/hemlock forest
20	CAN: NS: Halifax Co: Pogwa Lak pre-com.thin.red spruce forest
21	CAN: NS: Halifax Co: Big St. Margarets Bay old red spr for
22	CAN: NS: Halifax Co: Big St. Margarets Bay mat. red spruc
23	CAN: NS: Halifax Co: Big St. Margarets Bay oldgrowth r.spr
24	CAN: NS: Hants Co: Panuke Lak For Res oldgrowth redspr/hem
25	CAN: NS: Hants Co: Panuke Lak ForRes 45yr wind dist rd spru
26	CAN: NS: Halifax Co: Pockwock Lake mature red spruce forest
27	CAN: NS: Halifax Co: Pockwock Lake pre-com.thin.red spru for
28	CAN: NS: Halifax Co: Campbell Hill mature red spruce forest
29	CAN: NS: Halifax Co: Campbell Hill pre-com.thin. red spruce
30	CAN: NS: Halifax Co: Sandy Lake old red spr for (>120yrs)

IMAGE EVALUATION TEST TARGET (QA-3)

APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved