MAINTAINING SAPROXYLIC INSECTS IN CANADA'S EXTENSIVELY MANAGED BOREAL FORESTS: A REVIEW

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Abstract—Recent work on saproxylic insect assemblages in western Canadian boreal forests has demonstrated high faunal diversity and variability, and that adequate assessment of these insects involves significant sampling and taxonomic challenges. Some major determinants of assemblage structure include tree species, degree of decay, stand age and cause of tree death. Experiments have revealed differential impacts of wildfire and harvesting on saproxylic insect assemblages in post-disturbance boreal stands. Exploration of saproxylic insect responses to variable retention harvesting and experimental burns is contributing to development of optimal management prescriptions for boreal forests. Understanding of processes determining saproxylic insect diversity patterns and responses would benefit from increased attention to natural history. Such work would lead to a biologically meaningful classification system for dead wood and better identify habitats (and associated species) at risk due to forest management. This tool could also be used to improve strategies to better maintain saproxylic organisms and their central nutrient cycling functions in managed boreal forests.

BOREAL FORESTS AND SAPROXYLIC INSECTS

Canada is a country with abundant natural resources, including 10 percent of the world's forests spread over 417.6 million ha of forest land (Natural Resources Canada 2003). Of the 15 terrestrial ecozones in Canada, the boreal forest is the most extensive, covering ca. 340 million ha of land, and stretching from the Yukon Territory and northern British Columbia in the west to the east coast. Canada is home to about 30 percent of the world's boreal forests. Canada's boreal forests are dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), with stands of black spruce (*Picea mariana* [Mill.] B.S.P.) developing on wetter or north-facing slopes. Other minor canopy elements include paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* [L.] Miller). Canada's forests are a reservoir for biodiversity as they are home to about two-thirds of the nation's estimated 140,000 species, most of which (~70 percent) are arthropods.

The Canadian boreal forest alone harbors a diverse but poorly-studied northern fauna of arthropods. Danks and Foottit (1989) estimated that ca. 22,000 species of insects inhabit Canada's boreal forests. Over half of these do not have strictly boreal distributions, but appear to be forest habitat generalists found in other forest types as well. Although detailed biological information is available for a few species, mainly pests or highly-conspicuous groups such as butterflies, we know little more than names and general habitat affinity for the vast majority. Furthermore, an estimated 45 percent of insects inhabiting the boreal forest remain undescribed (Danks 1979, Danks and Foottit 1989). In summary, our understanding of boreal forest insect assemblages, in terms of ecological significance, natural history and spatial/temporal variation, is rudimentary.

Among the most diverse and characteristic assemblages of boreal forest arthropods are saproxylic species, that are associated with microhabitats found in or on dead and dying wood during some part of their life cycle (Speight 1989). For example, Hammond (1997) collected ca. 39,000 specimens of 5 classes, 13 orders, at least 113 families and over 2,000 species over 2 years in one relatively small-scale study of saproxylic arthropods associated with trembling aspen in two localities in the province of Alberta. Saproxylic species have a high diversity of trophic roles, including bark- and wood-feeders, predators, parasitoids, fungivores and scavengers. The bark- and wood-feeding groups are best known as they contain many conspicuous pests of trees. Boreal saproxylic assemblages exhibit high spatial variability within stands because microhabitats vary among pieces of dead wood depending on tree species, amount of decay, presence of fungal fruiting bodies, size of the wood, orientation of wood (standing or fallen), etc. (Hammond and others 2004, Siitonen 2001). There is also a temporal succession of species as the physical, chemical and biological characteristics of wood change (Hammond and others 2001).

Obviously, wood, especially dead wood, provides a unique structural characteristic of forests, and is an essential ecological element in forest ecosystems. Dead wood plays important roles in nutrient cycling and as habitat for species ranging from micro-organisms to vertebrates (Franklin and others 1987). Thus, it is increasingly accepted that dead wood management must be incorporated into forest ecosystem management (Franklin and others 1997, Hagan and Grove 1999, Lee and others 1997). This stems from the fact that the large decrease in dead wood volume, especially coarse woody debris (CWD), in managed forests in northern Europe is cited as a major factor leading to a decrease in abundance and diversity of

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invertebrate groups (Siitonen and Martikainen 1994, Heliövaara and Väisänen 1984) and cryptograms (Anderson and Hytteborn 1991, Bader and others 1995).

Fires contribute to the complexity of boreal forest communities by creating niches for organisms specialized to colonize burned areas (Granström 2001, Saint-Germain and others 2004, Wikars 1992), and by regularly defining the size, composition and structure of stands in a successional context (Hunter 1993). Low intensity forest fires, self-thinning in immature stands, and the actions of insects and fungi create large volumes of dead and dying trees (Harmon and others 1986). In addition, harvesting practices produce dead wood; however, there are many obvious physical and ecological differences between fire (and other natural disturbances) and harvesting as disturbances and in terms of the qualities and quantities of dead wood produced. As harvesting is quickly replacing natural disturbances, especially fire, as the major disturbance in boreal forests in western Canada (Pratt and Urquhart 1994), widespread discussion and some experimentation is occurring to assess how harvesting practices may be adapted to better preserve the structural and habitat complexity created by natural disturbances.

The emergence of a natural disturbance paradigm in forest management, molded by emulation of natural disturbance patterns and ecological effects, requires multidisciplinary scientific input that examines a range of ecological, economic and social response parameters (values). Over the last 10 years, we have examined saproxylic insect assemblages in western boreal forests of Canada to understand natural determinants of faunal structure and succession, and to assess faunal responses to natural and anthropogenic disturbances. Our goal is to provide input on how operational forest practices may be adapted to minimize impacts on biodiversity. This paper provides a brief summary of some of the challenges of this work, lessons learned thus far, and a research agenda for the future. Work on saproxylic assemblages in other parts of Canada is very limited but is referred to where appropriate.

THE CHALLENGES OF WORKING WITH SAPROXYLIC ARTHROPODS

Taxonomy

The single greatest limitation to the study of saproxylic arthropod biodiversity in Canadian forests is the difficulty in identifying many groups (Huber and Langor 2004). Adequate keys exist for only a small fraction of the approximately 55 percent of Canadian terrestrial arthropods known and described. For example, of the 176 identified genera of saproxylic beetles collected by Hammond (1997) from aspen CWD, at least 56 are in need of revision, and the situation is worse for Diptera, Hymenoptera and Acari. Thus, the quality of arthropod biodiversity work is strongly limited by the taxonomic soundness and stability of groups studied, and the availability of resources (keys, collections, expertise) to facilitate reliable identification. The use of higher level taxa (e.g., genus) or morphospecies (apparent species) have been advocated as a solution where taxonomic expertise is too expensive or unavailable (Oliver and Beattie 1996); however, use of such surrogates is risky. Although higher-level taxa may indicate biodiversity hot spots or areas of high conservation value, they will not serve generally to assess impacts of disturbances or to identify optimum treatments, as different species in the same genus often have different habitat requirements and, therefore, often exhibit different responses to disturbances. The usefulness of morphospecies designation in groups that are poorly known depends greatly on the skill and experience of the designator. Ideally, the designator should be a taxonomist expert in related groups to minimize the risk of poor morphospecies definition and resultant misidentifications. Furthermore, to satisfy the essential scientific criterion of repeatability, extensive voucher collections should be retained.

Alternatives to authoritative species-level identifications are rarely acceptable in meaningful arthropod biodiversity work, and research teams require considerable taxonomic expertise. This expertise may be obtained through partnership with expert taxonomists elsewhere, but often the prospect of being inundated with thousands of specimens for identification generates reluctance for taxonomists to become involved. Furthermore, the large recent declines in biosystematics expertise and training in Canada has left a shortage of qualified taxonomists (Huber and Langor 2004). Our own solution has been to provide taxonomic training for members of the team or to hire taxonomic expertise dedicated to the project. Training provides a good solution to the taxonomic impediment in both the short and long term, but often it requires a considerable investment of time before the trainee is sufficiently skilled. Unfortunately, those charged with regulating university graduate programs rarely see this extra time in program as meritorious, and even willing students are discouraged from taking the taxonomy seriously by mechanical application of program time limits. Even those interested in developing ecological indicators in Canada have not yet accepted this as a cost of doing business. The usual end result of the taxonomic challenges presented by arthropods is that the selection of study taxa is strongly biased towards taxa that are taxonomically well-known and for which identification skills and tools are readily available or fairly easily learned. If our goal is to respond to unwanted change by altering management, it is relatively useless and certainly economically dubious to monitor taxa that are not relatively easily dealt with taxonomically.

Sampling

Sampling of saproxylic insect fauna is necessary for faunistic work and for experimental designs focusing on impacts and mitigation. Saproxylic insects may be sampled in several ways: flight-intercept traps, emergence traps, rearing from wood, and hand-collecting, and each method has biases and strengths (Hammond 1997). Most work on saproxylic beetles in western Canada and northern Europe has employed flight-intercept traps attached to the boles of snags (Hammond 1997, Kaila 1993), and these may be adapted to be attached to the sides of logs and stumps (Tyler Cobb. Unpublished data. Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2E3). The benefits of these inexpensive traps are that they may be deployed quickly in large numbers distributed in standardized arrays, checked easily and are non-destructive. The major disadvantages are that not all species collected in a trap utilize the CWD to which the trap is attached, nor can we be sure that all saproxylic species using a particular substrate will be collected. For example, of the 21 bark beetle species collected by Jacobs (2004) using flight-intercept traps in mixedwood boreal forest, 14 species were collected on a host in which they do not feed and breed. Our

knowledge of the natural history of bark beetles enabled us to identify such 'false positive' captures, but similar knowledge is unavailable for most other groups. Rearing of insects from CWD can overcome these uncertainties because only species utilizing CWD will be collected. One disadvantage of rearing is that the collection of CWD from the field and transportation to cages is disruptive, resulting in escape of highly vagile species and altering of the properties of CWD (moisture, fungal growth, physical damage) that may cause high mortality of some taxa (Hammond 1997). Also, rearings are labor intensive and the cost of infrastructure (cages) limits the extent of sampling. Emergence traps attached to CWD in the field provide another view of the fauna and will sample only species emerging from CWD. Even though larger 'sleeve-style' traps may sample large areas of CWD, these traps can be inexpensive to construct and deploy. As a result, in Canada, emergence traps have not been utilized broadly for sampling saproxylic fauna, except for some groups of bark- and wood-boring insects (e.g., Langor and Raske 1987). Hand-collecting by destructively dismantling CWD not only allows sampling of the contents of CWD, but also allows the collector to make natural history observations regarding specific micro-habitats, food, etc. Such value-added observations are greatly needed for most of Canada's saproxylic fauna and can allow better interpretation of observed patterns of faunal responses. However, hand collection is extremely time-consuming, requires excellent natural history skills and is destructive. Finally, a new trapping technique for logs that deploys pitfall traps on CWD can be useful for sampling taxa that roam the surfaces of fallen CWD (Buddle 2001); however, it is probably not efficient for collecting species deeper in the wood or on snags.

The objectives and scope of a study will dictate the sampling method(s) employed. The researcher should be aware of the inherent biases associated with the chosen collecting method because such understanding is necessary for correct interpretation of data. In theory, the problems of trapping biases are minimized as long as the same approach is used across treatments and replicates, but this assumption merits debate and examination. If resources permit, it is desirable to utilize more than one collecting method within a study, especially for faunistic inventories (Hammond 1997).

Range of Natural Variation (RNV)

Baseline information about distribution and abundance of species and assemblage composition under conditions deemed to be 'normal' provides a model against which to compare responses to anthropogenic disturbances. As well, understanding of the RNV and its determinants allows for improved pre-stratified sampling and replication within experimental designs. We remain at the early stages of such work in Canada because our fauna is relatively poorly known. Although the importance of such faunistic work is frequently underestimated, it results in a treasure of information about composition of assemblages and species distribution in relation to habitat (e.g., Hammond 1997). Numbers of a species in an area can vary by several orders of magnitude over a short time because arthropods are highly sensitive to specific habitat characteristics and exhibit seasonality. Thus, the RNV can be large, so reliance on the RNV to establish response thresholds for arthropod ecological indicators is not promising without understanding how abundance and diversity are affected by environmental conditions. The indicator value of arthropods can, therefore, only be realized by examining numerical trends over larger spatial and temporal scales in the context of adequate meteorological records and biological understanding.

Paucity of Research

Canada is a huge country with about 180 native tree species and many forest ecotypes. In a recent survey of ongoing forest arthropod biodiversity projects in Canada 54 projects were listed (Biological Survey of Canada 2004), 14 of which had some current focus on saproxylic fauna, in all cases focusing on Coleoptera. Of the saproxylic studies, 8 focused only on 2-3 groups of bark- and wood-boring beetles (Curculionidae: Scolytinae, Buprestidae, Cerambycidae), that contain many native and exotic pest species, and that are taxonomically relatively well-studied. Of the six comprehensive studies that include the full order of Coleoptera, five were focused on two tree species, trembling aspen and white spruce, at a few locations in Alberta and the sixth was a new project commencing in the province of Quebec. The seemingly low interest of the Canadian research community to pursue work on saproxylic faunas is enigmatic as the interest among forest managers in CWD management for biodiversity conservation is very high. The reluctance of entomologists to delve into work on saproxylic assemblage structure may reflect a general inability to deal with the taxonomic challenges offered by this assemblage, other than some of the bark- and wood-boring groups. There is far more activity (32 current projects) on epigaeic assemblages in forests (e.g., carabid and staphylinid beetles and spiders) because these groups are more easy to deal with taxonomically. Furthermore, it is interesting that there is no serious focus on saproxylic groups other than Coleoptera, largely reflecting the fact that taxonomic challenges associated with these groups (e.g., Diptera) are worse than those associated with beetles. However, work in Europe on flies in the family Mycetophilidae has shown this to be a particularly sensitive group (Økland 1996).

MAINTAINING SAPROXYLIC ASSEMBLAGES— ADVANCES IN UNDERSTANDING

In Canada, harvesting now rivals natural agents such as fires, insects and diseases, as the major disturbance and stand initiator in boreal and other forest types (Pratt and Urquart 1994). Although harvesting has been occurring for many decades, science aimed at understanding and mitigating ecological consequences has generally not kept pace. Consequently, the forest science community is scrambling to assess ecological effects and to find ways to maintain ecological processes in managed forests as a necessary requirement of sustainable forest management. As many ecological processes are poorly understood and difficult to measure, one approach to dealing with these issues has been to focus on conserving biodiversity with the assumption that if the component biotic parts of ecosystems are present at natural levels, the stability of ecosystem processes will also be maintained. Although this theory has been heavily debated (e.g., McCann 2000) and remains largely untested, there is a growing consensus that ecosystem processes at least in part, are maintained by the plant, animal and microbial species living within a community (Naeem 2002, Naeem and others 1999).

Certain types of data and knowledge are required to assess whether biodiversity (including diversity of saproxylic arthropods) is being maintained in forested ecosystems and to design ecologically-friendly management practices. First, it is important to know what species are present in the ecosystem and how assemblages are structured. Second, it is necessary to understand the ecological and environmental drivers of assemblage structure and natural variation. Third, understanding the direction and degree to which assemblages and species respond to natural and anthropogenic disturbances at various spatial and temporal scales is necessary to assess long term impacts and to identify threats that require attention. Finally, an experimental approach is required to identify alternative practices and strategies that minimize impacts on biodiversity and which are adaptable as the knowledge base improves. In Canada, all of these areas are under investigation and some advances have been made in our understanding of how saproxylic arthropod assemblages are structured and how they may be better maintained in managed forests.

Faunistic Inventories and Assemblage Composition

The saproxylic arthropod fauna of Canada is so poorly known that it takes very little effort to discover new provincial or national records and undescribed species. Efforts over the last 10 years have greatly added to our knowledge of the composition of saproxylic insect assemblages. In particular, the Coleoptera have been the focus of nearly all studies, so our knowledge of this order has received a substantial boost. Also, most work completed to date has focused on fauna of *Populus* in north-central Alberta, and this cumulative faunistics work provides a good baseline inventory, albeit for one order on one genus of trees in a small part of one province of Canada.

In the first comprehensive study of saproxylic beetles associated with *Populus* in Alberta, a total of 257 species (excluding the highly-diverse staphylinid subfamily Aleocharinae) were identified from samples in two localities over three years (Hammond 1997). Of these, 46 species were new provincial records and an estimated 6-10 species were undescribed. Two subsequent studies on saproxylic beetle fauna associated with *Populus* in other locations in north-central Alberta have yielded an additional 12 species, 10 of which are new provincial records (Jacobs 2004) and an additional 47 species, 13 of which are new provincial records (Jim Hammond and David Langor. Unpublished data. Natural Resources Canada - Canadian Forest Service, 5320 - 122 Street, Edmonton, Alberta, Canada T6H 3S5). As each new study (locality) adds new species to the provincial inventory, it is anticipated that further work will continue to turn up large numbers of additional species. Of the 59 new saproxylic species on *Populus* found since Hammond (1997), the greatest number of new species were fungivores (21 species), followed by predators (17 spp.), bark- and wood-borers (12 spp.) and scavengers (4 spp.). The trophic role is unknown for 5 species. Hammond and others (2004) found only 142 of the total of 257 collected species to be shared between the two localities studied. With such a low level of similarity (60 percent) among localities, it is expected that the existing provincial inventory of saproxylic beetles on *Populus* is still largely incomplete. Furthermore, work on the saproxylic fauna associated with other tree species is less complete.

Although most families or subfamilies of saproxylic beetles can be easily dealt with taxonomically, a few still present major problems. The most notable is the Aleocharinae (Staphylinidae) which is hyper-diverse and relatively poorly studied in Canada. It is estimated that in Canadian forests about 40 percent of the species of Staphylinidae are Aleocharinae. Thus, if we extrapolate from the 78 species of non-aleocharine staphylinids collected by Hammond (1997), we estimate that about 50 species of Aleocharinae were not identified. Interestingly, our estimate is very similar to the 49 species Palm (1959) collected from *Populus tremula* L. in southern Sweden (out of a total fauna of 342 beetle species). Rapid advances in the taxonomy of this subfamily now allows the possibility of species level determinations for many genera, but the fact that most specimens require genitalia dissections to permit identification, and that taxonomic skills reside in only a small handful of experts still renders this subfamily relatively inaccessible for most studies given limited budgets. Thus, most researchers still tend to overlook this subfamily. Other families in dire need of revision are Lathridiidae, Cryptophagidae, Ptiliidae, as well as genera of several other families. Many of these are among the most species-rich families of beetles in dead wood. As these families become better studied, our faunistic knowledge of saproxylic assemblages (as well as other assemblages) will greatly increase. If voucher specimens are preserved for each study, the advent of new taxonomic knowledge and tools will allow old data sets to be revisited and updated.

The availability of inventories of saproxylic fauna associated with *Populus* in Canada (Hammond 1997) (James Hammond. Unpublished data. Natural Resources Canada - Canadian Forest Service, 5320 - 122 Street, Edmonton, Alberta, Canada T6H 3S5) and southern Sweden (Palm 1959) allows for an intercontinental comparison of species richness and faunal composition (table 1). Both studies sampled at roughly the same latitudes (54-59° N) and area. Palm (1959) collected 342 beetle species, including 49 species of Aleocharinae, from *P. tremula* L., of which 12 were restricted to that species, and 17 only overwintered in the CWD. Although Staphylinidae, Lathridiidae and Leiodidae were among the most species-rich families in both Alberta and Sweden, the distribution of species among families is significantly different (χ^2= 91.8, df = 38, P<0.0001) as is trophic structure (χ^2= 25.1, df = 4, P<0.0001) (table 2). Predators and fungivores dominated the faunas in Alberta and Sweden; however, predators were dominant in Alberta and fungivores were dominant in Sweden. The higher richness of predators in Alberta may be somewhat artificial as many epigaeic carabid and staphylinid beetles collected from CWD may not have any affinity for dead wood, but merely perceive it as part of the forest floor. If carabids and staphylinids are eliminated from analyses, the distribution of species among families and trophic groups do not differ significantly among Sweden and Alberta (χ^2= 35.5, df = 36, P = 0.49). The high rate of species accumulation with every new sampling effort on *Populus* in Alberta suggests that once an inventory is completed, species richness will far exceed that in Sweden. This raises interesting questions about possible long-term effects of forestry practices on the fauna of *Populus* in the Holarctic.

Table 1—Number of beetle species collected, by family, from *Populus* CWD in boreal mixed wood forests in north-central Alberta, and from 16 sites in central and southern Sweden (Palm 1959)

Family[a]	Species	
	Alberta	Sweden
	number	
Aderidae	1	2
Anobiidae	10	4
Anthribidae[b]	3	0
Aspidophoridae[b]	0	1
Bostrichidae[b]	1	0
Buprestidae	6	3
Cantharidae[b]	2	0
Carabidae[b]	18	5
Cerambycidae	7	15
Ciidae	10	13
Cleridae	1	4
Coccinellidae	4	2
Colydiidae	0	7
Corylophidae	3	3
Cryptophagidae	14	19
Cucujidae (incl. Laemophloeidae)	5	5
Curculionidae	6	7
Dermestidae	4	3
Elateridae	11	14
Endomychidae	3	4
Erotylidae	3	6
Eucnemidae	4	2
Histeridae	4	10
Latridiidae	18	22
Leiodidae	14	12
Lucanidae	1	2
Lycidae[b]	1	1
Lymexylidae[b]	1	1
Melandryidae	9	9
Melyridae (= Dasytetidae)	0	3
Mordellidae	0	3
Mycetophagidae	2	4
Nitidulidae	10	14
Pselaphidae	4	14
Ptiliidae	3	6
Ptinidae	0	3
Pyrochroidae	2	2
Rhipiphoridae[b]	1	0
Rhizophagidae	4	5
Salpingidae	2	2
Scaphidiidae	2	5
Scarabaeidae[b]	0	2
Scolytidae	2	5
Scraptiidae[b]	2	0
Scydmaenidae	1	6
Silphidae[b]	0	1
Sphindidae[b]	2	0
Staphylinidae[c]	100	30
Tenebrionidae	5	7
Trogossitidae	4	5
Total	310	293

CWD = coarse woody debris.
[a] Designation of families is according to Bousquet (1991).
[b] Species not included in chi-square test because expected values were < 1.
[c] Excludes Aleocharinae.

Table 2—A comparison of trophic structure of beetle species collected (excluding Aleocharinae and Ptiliidae) from *Populus* CWD in boreal mixed wood forests in northcentral Alberta, and from 16 sites in central and southern Sweden (Palm 1959)

Trophic role	Species	
	Alberta	Sweden
	number	
Unknown	19	0
Fungivore	92	103
Predator	126	96
Scavenger	35	45
Wood borer	35	43
Total	307	287

CWD = coarse woody debris.

Determinants of Assemblage Structure

It does not take long to realize the immense variability of CWD in terms of easily observed qualities (e.g., species, degree of decay, size), let alone more subtle differences in qualities that humans are not attuned to (e.g., species of fungi present, moisture content), but that greatly influence saproxylic insect composition and abundance. Furthermore, it is also obvious that the RNV in saproxylic assemblage composition and abundance is enormous. As an example of this variability, Hammond and others (2004) placed two flight-intercept traps on the bole of each *Populus* snag, separated by 1.5 m in vertical height. The percent similarity among fauna captured in the two traps on each snag averaged only 38 percent and ranged from 0 to 68 percent. Such high variability, also evident at other spatial scales, greatly increases the challenge of designing good experiments to adequately sample saproxylic faunas in a way that allows for meaningful comparisons and, ultimately, improves management for biodiversity on landscapes subject to industrial forestry. However, despite the high RNV, some progress has been made in understanding the major determinants of saproxylic assemblage structure in western Canada.

In a comprehensive review of knowledge of saproxylic organisms in Fennoscandian forests, Siitonen (2001) stated that the main factors determining species composition in dead wood are: tree species; stage of decay; fungal species composition; diameter and quality (snag, log, stump) of the trunk; and environmental conditions. These factors and others are also the major determinants of saproxylic insects assemblage structure in Canada where investigated.

Regional variation—Regional variation in faunal composition is evident. Hammond and others (2001, 2004) sampled saproxylic beetle assemblages in boreal *Populus* at two locations in northern Alberta. Of the 257 species collected, only 142 were shared between localities. The two localities, separated by 500 km and 1.5° latitude, belong to the Boreal Plains Ecozone, but were in two different ecoregions. The faunal differences between these two sites were interpreted as a function of differences in biophysical characteristics tempered by dispersal. Difference between the localities in terms of

climate, topography, latitude, structural characteristics and proximity to different ecozones and ecoregions may influence the availability of microhabitats and niche assembly as well as sources of immigration (Hammond and others 2004). Furthermore, Palm (1951, 1959) found that species richness and composition of saproxylic beetles on *Populus* varied greatly from northern to southern Sweden. In Canada, trembling aspen and balsam poplar are distributed from coast to coast and from the far south to tree-line in the north and occurs in almost all of Canada's ecozones and ecoregions. The large geographic variation in the saproxylic beetle assemblage associated with these tree species in Alberta suggests that the variation in assemblage structure across the range of these species in Canada will be enormous. If incorporation of biodiversity objectives into forest management is to be sensitive to all taxa, regional variation must be understood, represented in indicators, and embraced in monitoring programs.

Host species—Assessment of variability of saproxylic faunas associated with different tree species in Canada is relatively recent. To date, the best information is available on bark and wood-boring species as these groups have been well studied because of their occasional economic impact. For example, of the 213 species of Scolytinae and 171 species of Buprestidae known to occur on trees in Canada (Bright 1976, 1987), almost half (182 spp.) are known from only one tree genus (fig. 1A), and many of those from only one species. The most polyphagous species, i.e., those breeding in more than three genera of hosts, are mainly on deciduous trees. Only 5 species are known to breed in both coniferous and deciduous hosts (fig 1B). However, many other trophic groups of saproxylic insects can have less host specificity than those requiring fresh phloem or sapwood.

We assessed variation of the total saproxylic beetle fauna among white spruce and aspen snags at one site in northwestern Alberta. This work was conducted at the Ecosystem Management by Emulating Natural Disturbance (EMEND)

research site. EMEND is located in the Clear Hills Upland, Lower Foothills ecoregion of northern Alberta, approximately 90 km north-west of Peace River (56º 46' 13"N, 118º 22' 28"W, 677-880-m elevation) (Spence and others 1999). Four stand cover types were sampled: early successional deciduous dominated (DDOM) sites consisting of >70 percent deciduous species, mainly aspen; early mid-successional stands that were deciduous-dominated with a developing coniferous understory (DDOMU); late mid-successional stands that were mixedwood stands (MX) composed of 35 to 65 percent of both deciduous and coniferous species in the canopy; and late successional coniferous stands (CDOM) with >70 percent coniferous species, mainly white spruce, in the canopy. Each cover type was replicated thrice and each replicate stand covered at least 10-ha. Sampling utilized flight-intercept traps placed on 36 white spruce and 54 aspen snags that were dead for 1-7 years.

In total, 236 species were collected, 128 from both hosts, while 83 were collected only on white spruce and 25 on only aspen (Jacobs 2004). Species richness and composition of saproxylic beetle assemblages in both aspen and spruce were also influenced by stand cover type. Species richness estimated by rarefaction was much higher for white spruce assemblages in MX stands than in CDOM stands, but for species on aspen DDOMU stands had higher species richness than MX and DDOM stands (fig. 2).

Nonmetric multidimensional scaling (NMS) ordination demonstrated that there was a strong influence of cover type on the composition of spruce-associated beetle assemblages as CDOM and MX stands formed distinct clusters in ordination space (fig. 3). Furthermore, indicator species analysis showed 9 species (2 bark beetle, 3 bark beetle predators and 4 fungivores) were significantly indicative of spruce snags in CDOM stands, but none were indicative of spruce in MX stands. Although total CWD quantity differed little between CDOM and MX stands, the largest proportion of CWD in MX-spruce stands was deciduous and the largest proportion in CDOM
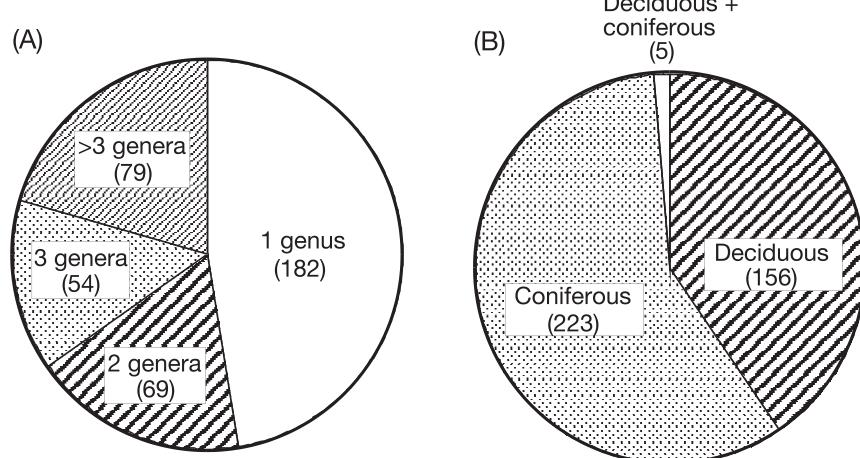

Figure 1—Host specificity of species of Scolytidae and Buprestidae in trees in Canada. (A) Proportion of beetle species utilizing 1, 2, 3, or > 3 host genera. (B) Proportion of beetle species utilizing deciduous hosts, coniferous hosts, or both. Numbers in parentheses indicate the number of species of each category.
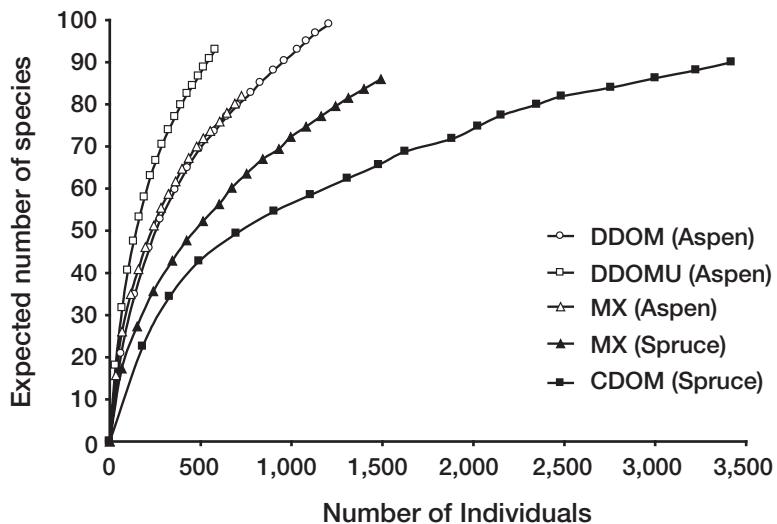
Figure 2—Rarefaction estimates of saproxylic beetle species collected using flight-intercept traps on white spruce and trembling aspen snags in each stand cover type at the Ecosystem Management by Emulating Natural Disturbance experimental site, Alberta.
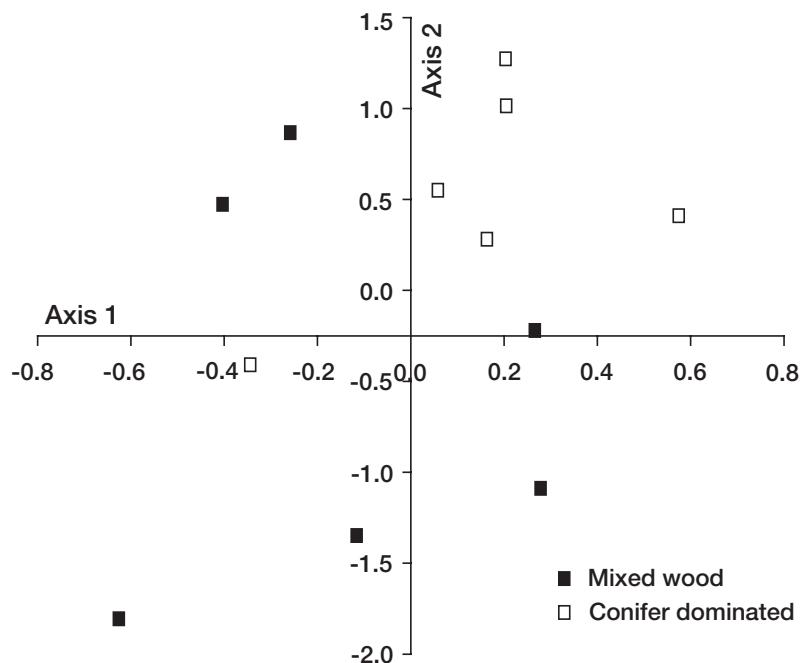

Figure 3—Nonmetric multidimensional scaling (NMS) ordination based on catch of 117 saproxylic beetle species on 12 samples of white spruce snags in coniferous dominated (CDOM) and or codominated (MX) cover types at the Ecosystem Management by Emulating Natural Disturbance experiment site, Alberta. Each point represents the sum of three traps from naturally dead trees or three traps from girdled trees from three replicates of each cover type. R^2 for axes 1 and 2 are 0.34 and 0.828, respectively; stress = 6.49 $P < 0.02$.

stands was coniferous (mainly spruce). Furthermore, in CDOM stands, the volume of coniferous CWD and the density of coniferous snags were almost three times higher than in MX stands. Thus, greater amount of spruce CWD could increase the ability of conifer specialist beetles to colonize suitable habitats in CDOM stands.

Decay—CWD is a dynamic environment characterized by often-rapid changes in chemistry, physical characteristics, to a large extent brought about by the action of fungi and other micro-organisms (Boddy 1992, Renvall 1995). The changes in CWD qualities associated with decay, and the species of fungi (and sporocarps) present at a particular time, greatly influences saproxylic beetle assemblage structure (Siitonen 2001). After the death of a tree, decomposition takes several decades, and during which there is a succession of saproxylic species (Esseen and others 1992, 1997).

Our work on saproxylic beetles of *Populus* in Alberta also shows clear faunal succession with increased decay of CWD, and that succession is most rapid during the 1-2 years immediately after tree death (Hammond and others 2001, 2004). We classified CWD as early decay (decay class 1 (DC1)), intermediate decay (DC2) or advanced (DC3) (see classification criteria in Hammond and others 2004). Although mean abundance of saproxylic beetles collected using flight-intercept traps did not differ significantly among decay classes, DC1 CWD tended to have the highest overall abundance of beetles (table 3). Species richness, estimated by rarefaction (Gotelli and Colwell 2001, Hurlbert 1971, Sanders 1968), was lowest in DC1 CWD (table 3). These patterns suggest that activity around new CWM is higher, but species diversity is lower than around more advanced decay classes. Furthermore, cluster analysis of Bray-Curtis similarity measures revealed that the assemblage of species associated with fresh CWD (DC1) was most different compared to more advanced decay classes. Early succession in CWD occurs rapidly (Hammond and others 2001, Siitonen 2001). Freshly killed wood has a lower diversity of microhabitats than more decayed material; however, it does provide large amounts of nutrient-rich resources in the form of phloem and sapwood. A distinct fauna characterized by phloeophages, xylophages and ambrosia beetles, all of which require fresh phloem or sapwood to

complete development, specialize on these resources and can colonize fresh CWD in large numbers. The trend of increasing species richness of fungivores, scavengers and predators with the more advanced decay classes is an expected successional response to increasing microhabitat diversity partly due to the actions of wood-decaying fungi (Siitonen 2001). Many saproxylic species are highly attracted to decayed wood because they specialize on different fungal structures such as fruiting bodies, hyphae and spores (Ehnström 2001) and on different fungal species (Lawrence 1973, Wheeler and Blackwell 1984). The predatory and scavenger species are probably mainly generalists responding to the greater diversity of food items available in later decay stages. In Europe, the majority of endangered species are found in wood of advanced decay, and such species may be most threatened by reduction of CWD in forests managed for wood production (Ehnström 2001, Siitonen 2001, Siitonen and Martikainen 1994).

Stand age and CWD diameter—Significantly higher saproxylic insect abundance and species richness are associated with old stands than with mature stands in Fennoscandia (Martikainen and others 1999, 2000), and the typical explanation is that older stands are structurally more diverse, and larger-diameter CWD provides a wider range of substrates and microhabitats, allowing colonization by a broader diversity of invertebrates (Martikainen and others 2000, Nilsson and others 2001). In Alberta, nearly twice the number of specimens and 34 percent more species were reared from CWD in old aspen stands (>105 years) compared to young stands (60-80 years), but rarefaction-standardized species richness did not differ among stands of different ages. Furthermore, abundance and species richness of beetles collected with flight-intercept traps were either similar to or had only slightly higher species richness in old stands as in mature (Hammond and others 2004). However, age affected beetle assemblage structure. Indicator species analysis (Dufrêne and Legendre 1997) showed 10 species that were indicative of old stands and classified only 3 species as indicative of mature stands (Hammond and others 2004).

Rarefaction-estimated species richness increased with CWD diameter and was highest in the ≥ 41 cm diameter class (fig. 4)

Table 3—Abundance and species richness of saproxylic beetles associated with *Populus* coarse woody debris of different decay classes in northcentral Alberta, Canada

Decay class[a]	Window-trapped beetles			Reared beetles		
	N	Mean catch[b]	Species richness[c]	N	Catch	Species richness[c]
1	95	33.6 ± 2.8	135.4 ± 3.5	8	689	55.6 ± 3.1
2	96	24.3 ± 1.6	142.4 ± 0.8	8	627	89.8 ± 3.5
3	95	24.3 ± 1.6	145.9 ± 0.3	8	426	83.9 ± 1.3

[a] Classification criteria provided by Hammond and others (2004).
[b] Means (±SE) are based on catches from individual window traps.
[c] Expected number of species ±SD in a sub-sample of 2,300 individuals and 400 individuals for window-trapped and reared beetles, respectively.
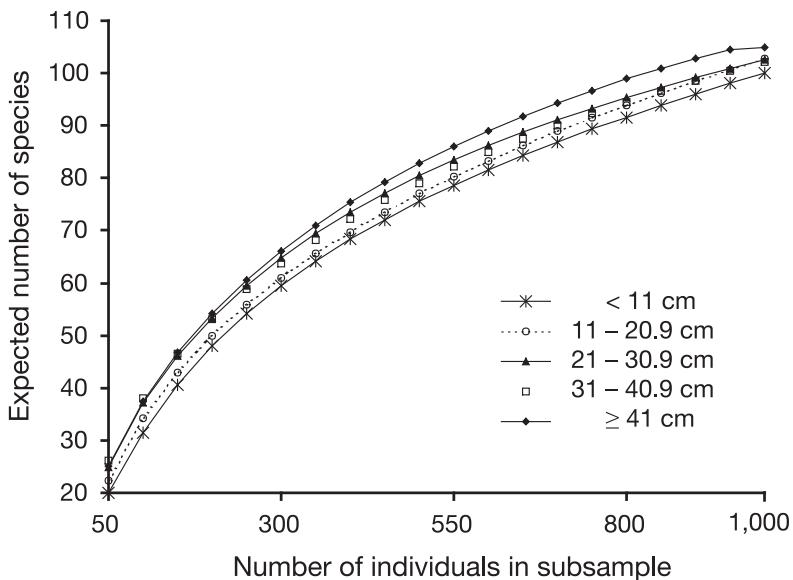
Figure 4—Rarefaction estimates of saproxylic beetle species richness collected with flight-intercept traps attached to *Populus* snags in aspen-dominated mixed wood forests in north-central Alberta. Snags are divided into 10-cm diameter at breast height classes.

even though there was only a third of the number of snags in that class compared with other diameter classes (fig. 5). The number of rare species seemed to increase linearly with increasing snag diameter, peaking in the 21-30.9-cm class; however, there was almost one unique species for every snag sampled in the largest diameter class (fig. 5). Indicator species analysis identified 15 species that were significant indicators of large (≥41-cm) diameter snags, and many of these are the same as those indicative of old stands, whereas only 4 species were indicative of smaller diameter classes. Ordination of

saproxylic beetles captured by flight-intercept traps resulted in better separation on the basis of snag diameter class than on the basis of stand age, and the separation of assemblages increased as the weight of rare species was increased. As large snags are recruited in old stands, this appears to increase structural and microhabitat diversity. It may be that increased sampling effort is required in old stands and for large diameter CWD to adequately sample the wider variety of microhabitats present. An improved understanding of CWD microhabitats and development of a biologically meaningful
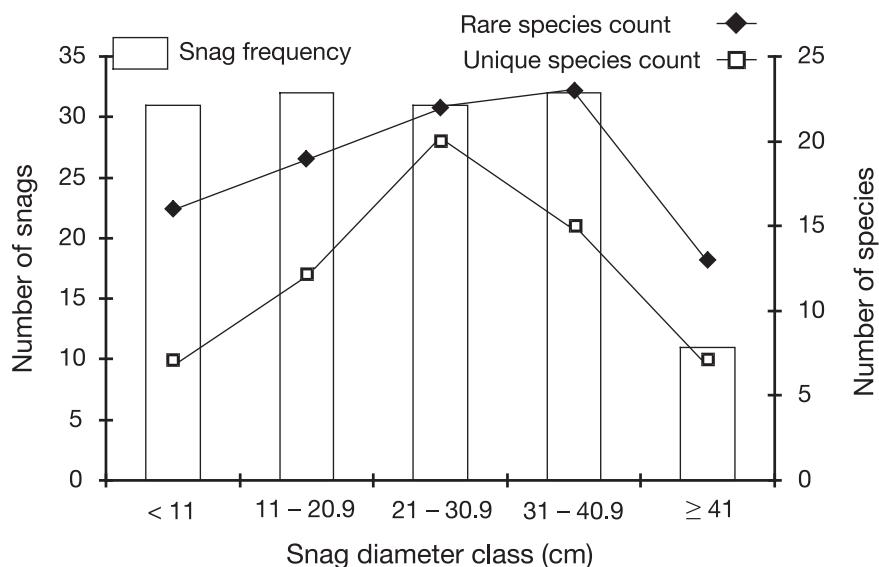

Figure 5—Number of *Populus* snags of each of five diameter classes sampled by flight-intercept traps, and the number of rare (singletons + doubletons) and unique saproxylic beetle species collected in each diameter class.

CWD classification system would help in stratification of sampling to achieve a better understanding of saproxylic fauna.

Impacts of Forest Management

Assessment of the impacts of forest harvesting practices on arthropod biodiversity have increased rapidly over the last 12 years and is a favorite topic for first forays into the field of forest biodiversity. In Canada, a great amount and variety of work has focused on epigaeic assemblages, especially carabid and staphylinid beetles and spiders (Biological Survey of Canada 2004), and a little work has assessed the impacts of forestry practices on saproxylic beetles (Hammond 1996, Hindmarch and Reid 2001, Kehler and Bondrup-Nielsen 1999, Spence and others 1997). In all cases, arthropods responded to human-caused disturbances in terms of abundance, species richness or species composition. Consequently, it is now mundane to solely ask whether arthropods respond to forestry practices. A much more meaningful point of enquiry concerns how biotic responses to anthropogenic disturbances compare to natural disturbances of equivalent scale. Such work can be anticipated to lead to practical results by focusing on the question of how forest management may be adapted to better approximate the results of natural disturbances.

Fire and harvesting as disturbances—Natural disturbances such as fire, insect outbreaks, fungi and windfall have long shaped the boreal forest landscape, creating a shifting habitat mosaic including patches of different sizes, shapes, composition, age and juxtaposition. Wildfire is usually the most important disturbance in Canadian boreal forests. The use of natural disturbance as a forest management paradigm by which to achieve sustainable management of the boreal forest has been widely advocated (e.g., Hunter 1993, Angelstam 1997, Haila and others 1994). This approach flows from the observation that the flora and fauna of boreal forests are pre-adapted to conditions associated with large-scale natural disturbances,

especially wildfire. Thus, forestry practices that emulate some obvious macro-characteristics of these natural disturbances (e.g., variable retention, shape and design of cutting, rotation schedule, maintenance of dead wood on land-base) might be a useful approach to large-scale forest harvesting, *sensu* the Natural Disturbance Hypothesis (Hunter 1993). However, the Natural Disturbance Hypothesis remains largely untested with respect to the main emulations being presently employed by the forest industry throughout the boreal region (Spence and others 1999, Work and others 2003). It is important that we understand the impact of forest practices on biodiversity, since mounting evidence indicates that the number and identity of species occurring in an ecosystem relates in a meaningful way to ecosystem stability (Naeem 2002, Tilman and others 2001).

We examined how saproxylic beetle assemblages of *Populus* occurring in boreal-mixedwood stands of north-central Alberta differ following forest harvesting and natural wildfire, and assessed the successional trajectories of assemblages over time to explore the relative impacts of fire and harvesting on arthropod biodiversity. We used a natural chronosequence design in which the fauna was compared among 1-2, 14-15, and 28-29 year old stands (two replicates of each) originating from either wildfire or clear-cutting. Clear-cuts older than 30 years were not available for study since harvesting *Populus* in Alberta is a relatively recent practice. Saproxylic beetles were captured using one flight-intercept trap (Hammond 1997) attached to each of six snags in each stand.

Beetle catch was similar across most treatments with the exception of the 1-2-year-old harvested stands that yielded 3-4 times more beetles than other stands (fig. 6), largely due to greatly increased numbers of the bark beetle *Trypodendron retusum* (LeConte), two species of bark beetle predators in the genus *Rhizophagus*, and a staphylinid beetle, *Carphacis nepigonensis* (Bernhauer), a scavenger often associated with
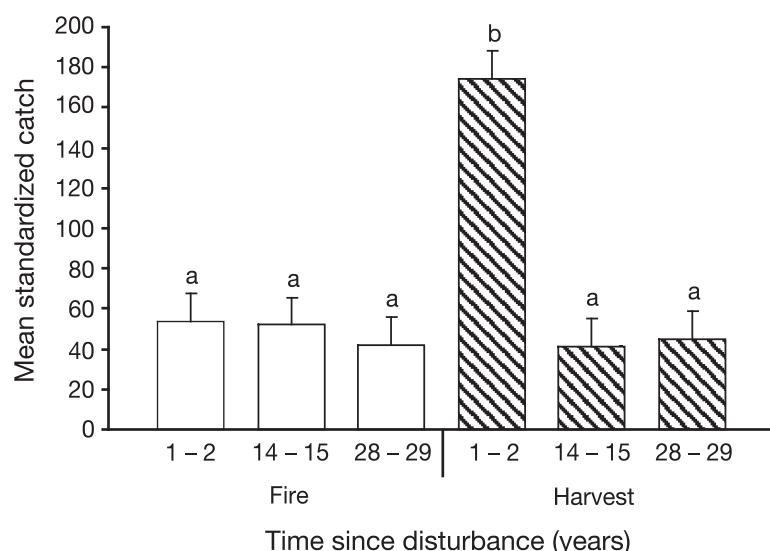

Figure 6—Mean (±SE) standardized catch (number of specimens per 150 trap days) of saproxylic beetles in boreal *Populus* stands of three ages and originating from fire or clearcut harvesting, Alberta.

bark beetle galleries. Interestingly, the youngest harvested stands also had the lowest species richness, as estimated by rarefaction (fig. 7). The highest species richness occurred in 14-15 year old burned stands, but there were no clear patterns in species richness associated with age of stand or disturbance type. Ordination showed that a 3-dimensional solution was optimal for the data (fig. 8). The arthropod faunas of harvest-origin and pyrogenic stands were most dissimilar in the 1-2 years following disturbance, and most similar at 28-29 years, indicating some convergence of faunal succession trajectories over time. Although it is still not possible to clearly project forward another 40-50 years to when the oldest stands will reach maturity, these initial results give some confidence that saproxylic assemblages may achieve a reasonable degree of recovery following harvesting. Data on epigaeic beetles (Carabidae, Staphylinidae) and spiders indicate a similar convergence of faunal composition by 28-29 years post-disturbance; however, there was still a very large difference from fauna of >70-year-old stands (Buddle and others 2000, 2005).
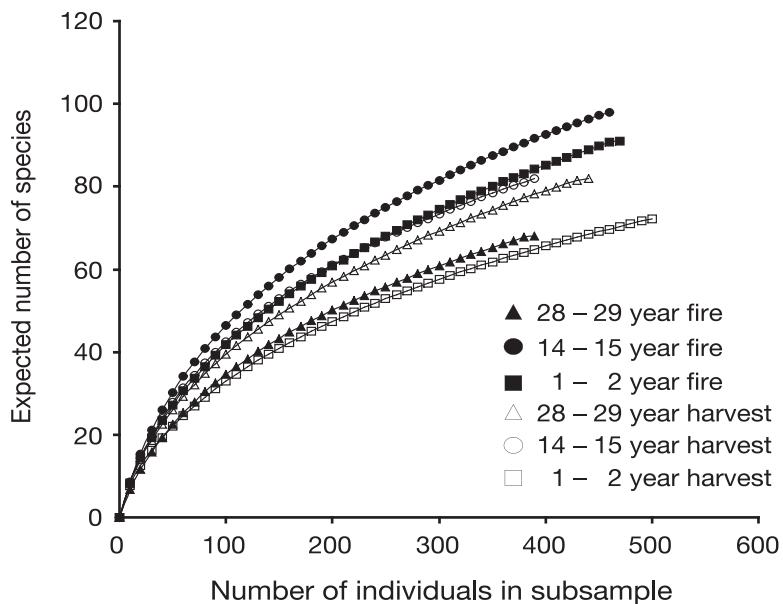

Figure 7—Rarefaction-estimated species richness of saproxylic beetles in boreal *Populus* stands of three ages and originating from fire or clearcut harvesting, Alberta.
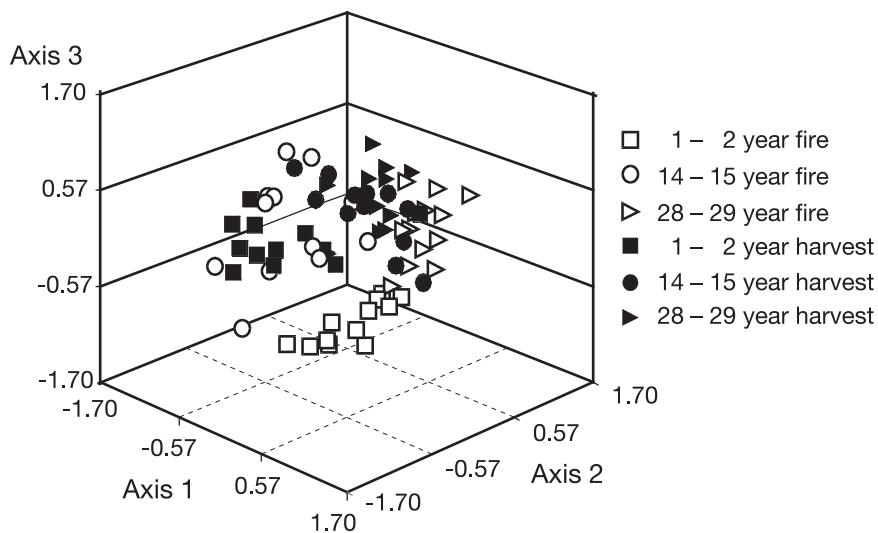

Figure 8—Nonmetric multidimensional scaling (NMS) ordination of 211 species of saproxylic beetles collected using flight-intercept traps in Alberta boreal *Populus* stands of three ages and originating from fire or clearcut harvesting. Each point represents the fauna associated with a snag (12 snags of each treatment combination). R^2 for axes 1, 2, and 3 are 0.256, 0.286, and 0.224, respectively; stress = 16.7, P = 0.002

Adaptive Forest Management

Variable retention harvesting (VRH) is starting to be employed at various locations in Canada in an attempt to leave more structural complexity on the landscape for the benefit of biodiversity conservation. VRH also affects CWD succession by increasing the input of CWD into these systems. At the EMEND study site, we assessed the short-term effects of different levels of dispersed residual structure on saproxylic beetles in white spruce dominated stands (Jacobs 2004). Although CWD volume was relatively unaffected by harvesting treatments (Langor, unpublished), it is expected that altered microclimate and physical structure affecting dispersal will promote change in the saproxylic beetle increasingly as the amount of residual structure in treatments decreases.

The 15 compartments studied were ca. 10 ha in size and dominated at canopy level by white spruce. In the winter of 1998/1999, three replicates of four VRH treatments (75 percent, 50 percent, 20 percent and 10 percent residual) were applied to the compartments using a uniform shelterwood system. The experiment also contained non-harvested controls (100 percent residual). Three 'natural' white spruce snags (dead 5-8 years and still retaining most of their bark and small branches) and three trees killed by girdling just after harvesting were sampled with flight-intercept traps in each compartment in 2000-2001. The goal of using girdled trees and natural snags was to increase the diversity of beetles sampled and to compare fauna among snags at different stages of decay. In general, NMS ordinations indicated no clear influence of harvesting, and saproxylic assemblage structure was much more strongly influenced by the type of snag (girdled versus naturally dead, which represent different decay classes). The one exception is the bark- and wood-boring beetles (fig. 9). Assemblages from controls were quite different from those of other treatments and control samples clustered mainly in the lower right portion of the plot. Also, samples from 50 and 75 percent residuals formed fairly tight clusters in close proximity to each other, but 75 percent residual was slightly more similar to controls than 50 percent. Samples from the other two treatments were highly variable and formed no distinct clusters. Thus, preliminary data indicate that even minimal harvesting (25 percent) can have an impact on saproxylic beetles, and that this impact generally increases as more wood is removed from the stands. Interestingly, one bark beetle species, *Xylechinus montanus* Blackman, that is a significant indicator of control stands, is a congener of *X. pilosus* (Ratzeburg), a forest interior specialist in northern Europe (Peltonen and Heliövaara 1998). If there are major benefits of VRH for saproxylic assemblages, they should logically become more evident over the long term when the residual structure begins to influence CWD dynamics.

PRIORITY FUTURE DIRECTIONS

Our experiences of working with saproxylic beetles over the last 10 years have provided much practical experience with this fauna, baseline data on assemblage structure and variation in boreal mixedwood forests of north-central Alberta, some understanding of the determinants of faunal structure and long-term, legacy experiments that will help identify optimal forest management prescriptions to better incorporate biodiversity objectives into resource planning. It seems
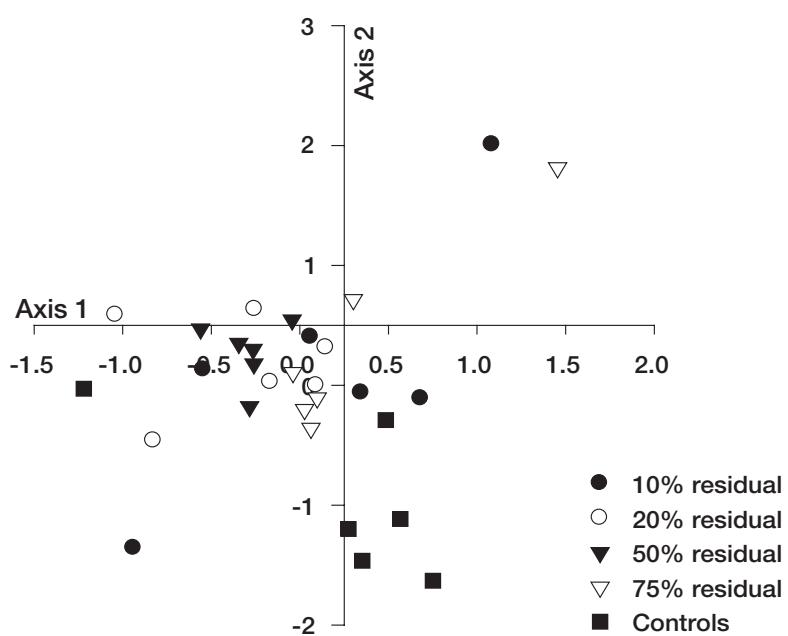

Figure 9—Nonmetric multidimensional scaling (NMS) ordination based on catch of 47 species of bark- and wood-boring beetles in controls and 4 variable retention harvesting treatments in coniferous dominated (CDOM) stands at the Ecosystem Management by Emulating Natural Disturbance experiment site, Alberta. Each point represents the sum of three traps from naturally dead trees or three traps from girdled trees from each of three replicates. R^2 for axes 1 and 2 are 0.424 and 0.400, respectively; stress = 15.8 *P* < 0.02.

unlikely that work done without long-term context will have much management significance given the range of natural variation that we observed. In particular, a race to declare taxa as indicators so that expensive monitoring programs can begin will have results more dependent on luck than science (Langor and Spence 2004). The insights gained and lessons learned over the last decade also provide some direction for future research endeavors.

Taxonomy

Although the importance of taxonomy to biodiversity science (and many other fields of biological science) is well advocated, those in positions to aid the cause of taxonomy in Canada usually pay only 'lip-service' to this relationship. Even when, on those rare occasions, new resources for taxonomy become available, they tend to be largely focused on economically-important groups, especially in agriculture, or on advanced investigations with molecular biology aimed at resolving finer points of phylogeny that are urgently required to support work with useful management implications. Saproxylic faunas include many families and genera poorly known taxonomically. Consequently, a large proportion of sampled species cannot be practically or accurately dealt with, even though some groups such as mycetophilid flies can be highly useful indicator groups (Økland 1996). Thus, we require continued investment in taxonomy and systematic infrastructure, including focus on some diverse and potentially useful saproxylic families. This certainly requires training of young taxonomists to continue describing and cataloging the North American fauna.

Natural History

Even for those species that we can comfortably identify, there is a dearth of information about biology and microhabitat affiliations. The value of such information, generated through detailed natural history observations, should not be underestimated nor trivialized. Such information will add great value to the growing wealth of data about species responses to disturbances and, when synthesized for a large number of species, will likely point towards sensitive microhabitats at risk due to forest management. Likewise, detailed observations can provide some useful insights into ecological roles of species and ultimately lead to a better understanding of ecosystem processes. This bank of information is unlikely to emerge spontaneously from a hap-hazard set of tight, focused experiments designed to test particular aspects of the day's fashionable ecological theory.

Dead Wood Classification

Our current classification systems for coarse woody debris are relatively crude and are not based on sound biological criteria. Most systems, ranging in classes from 1-7, are largely focused on degree of decay. Even CWD diameter, which is known to affect saproxylic assemblage structure, is not included in most classification systems. An improved dead wood classification, especially for CWD, should be based on criteria such as species, size, decay, orientation (standing or fallen), presence of cavities and fungal fruiting bodies (and species), degree of sun-exposure, etc. Such a classification system can only be developed with substantial investment in natural history and a systematic examination of the full range of CWD variation in forests. A better CWD classification system and sufficient natural history knowledge will enable

identification of habitat surrogates for saproxylic arthropods that are easy to measure and readily incorporated into bio-diversity monitoring programs.

Adaptive Management

Finally, we are just beginning to invest in highly integrated, multidisciplinary, long-term experiments to identify optimal forest management practices (e.g., amount, quality and dispersion of residual structure) that balance ecological (including biodiversity), economic and social values. The benefits of these legacy experiments will magnify with time, if we are wise enough to support them in the long term. However, such experiments are very few, which makes it difficult to extrapolate results across large landscapes, even of the same forest type. Thus, we must also learn to use pre-planned and retrospective studies that connect to key points emerging from large experiments to help us understand what features generalize well. When possible solutions present themselves, we must build them into ongoing forest management activities so that they can be quickly evaluated. This demands that both industries and governments become better prepared to invest in the process of improving our efforts to conserve biological diversity and other forest values, as opposed to wanting rigid legalistic descriptions of the perfected scientific approach (Work and others 2003).

In summary, saproxylic organisms are perhaps the best equivalent to 'a canary in the coal mine' we have for evaluating forest management. They are one of the few groups of organisms for which the actual effects of boreal forestry practices have been convincingly documented (Siitonen and Martikainen 1994). Despite the present existence of a taxonomic impediment in North America, European work, particularly that in Fennoscandia (e.g., Ehnström and Axelsson 2002), provides a full measure of confidence that the fauna can be mastered given resources, time and attention. Saproxylic organisms that 'feed, need or breed in deadwood' represent a large fraction of biological diversity in forest environments and the arthropod-fungal connection is of great ecological importance to the nutrient cycling and soil processes that underpin forest production (McGill and Spence 1985). Saproxylic species specialize in various fine-scale aspects of forest environments that most vertebrates perceive as coarse-grained and are thus closer to the level of the fundamental ecosystem chemistry that ultimately controls the growth and development of forest constituents. And, lastly, unlike vertebrates, a subset of saproxylic species has low powers of dispersal restricting them to non-migratory life-styles and dependence on local conditions. The modern landscape focus, thought by some to be the magic bullet for conserving biodiversity on landscapes subjected to industrial forestry, will likely be cold comfort for such creatures (and those that depend on or value them) they become concentrated in small pockets of disconnected residual and are possibly doomed for extinction (e.g., Siitonen and Saaristo 2000). Nonetheless, our present understanding of the RNV for diversity and abundance of saproxylic organisms in North America, suggests that we need knowledge better classified by contingency (see Sittonen 2001) in order to effectively conserve this fauna through improved forest management. Clearly, the final approach will require leaving more structure on harvested landscapes than has been common in the past. Our earliest experiments suggest that location and composition of residual patches will also be

important management elements (Gandhi and others 2004), but we have much to learn before we can be confident about conserving these interesting creatures and the full range of their ecological significance.

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