Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation[1]

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Abstract—Saproxylic insect assemblages inhabiting dead wood in Canadian forests are highly diverse and variable but quite poorly understood. Adequate assessment of these assemblages poses significant challenges with respect to sampling, taxonomy, and analysis. Their assessment is nonetheless critical to attaining the broad goals of sustainable forest management because such species are disproportionately threatened elsewhere by the reductions in dead wood generally associated with commercial exploitation of northern forests. The composition of the saproxylic fauna is influenced by many factors, including tree species, degree of decay, stand age, and cause of tree death. Wildfire and forest harvesting have differential impacts on saproxylic insect assemblages and on their recovery in postdisturbance stands. Exploration of saproxylic insect responses to variable retention harvesting and experimental burns is contributing to the development of prescriptions for conserving saproxylic insects in boreal forests. Understanding of processes that determine diversity patterns and responses of saproxylic insects would benefit from increased attention to natural history. Such work should aim to provide a habitat-classification system for dead wood to better identify habitats (and associated species) at risk as a result of forest management. This tool could also be used to improve strategies to better maintain saproxylic organisms and their central nutrient-cycling functions in managed forests.

Résumé—Les peuplements d'insectes saproxyliques qui habitent le bois mort dans les forêts canadiennes sont très diversifiés et variables, mais bien mal connus. Une évaluation adéquate de ces peuplements soulève des problèmes importants d'échantillonnage, de taxonomie et d'analyse. Leur évaluation est néanmoins essentielle pour atteindre les grands objectifs de la gestion durable des forêts, parce que ces espèces font face ailleurs à une menace démesurément élevée à cause des réductions générales du bois mort associées à l'exploitation commerciale des forêts nordiques. La composition de la faune saproxylique est influencée par plusieurs facteurs, dont l'espèce d'arbre, l'importance de la décomposition, l'âge du peuplement forestier et la cause de la mort de l'arbre. Les feux de brousse et la coupe forestière ont des impacts différents sur les peuplements d'insectes saproxyliques et sur leur récupération dans les peuplements forestiers qui se développent après la perturbation. L'examen des réactions des insectes saproxyliques aux coupes avec des taux variables de rétention et aux feux expérimentaux contribue à l'élaboration de suggestions pour la conservation des insectes saproxyliques dans les forêts boréales. Une attention plus grande portée à l'histoire naturelle des insectes saproxyiliques favoriserait une meilleure compréhension des processus déterminants de leurs patrons de diversité et de leurs réactions. Ces travaux devraient chercher à dresser un système de classification des habitats de bois mort afin de mieux identifier les habitats (et leurs espèces associées) qui sont menacés par la gestion des forêts. Un tel outil pourrait aussi servir à améliorer les stratégies pour assurer le maintien des organismes saproxyliques et de leurs fonctions centrales de recyclage des nutriments dans les forêts aménagées.

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Introduction

The abundant natural resources of Canada include approximately 10% of the world's forests spread over 417.6 million hectares of forest land (Natural Resources Canada 2003). These forests are home to about two-thirds of the nation's estimated 140 000 species, about 70% of which are arthropods (Danks 1979; Danks and Foottit 1989). Among the most diverse and characteristic assemblages of forest arthropods are "saproxylic" species: arthropods that are associated, during some part of their life cycle, with microhabitats found in or on dead and dying wood (Speight 1989). For example, in the first Canadian study of saproxylic arthropods on trembling aspen, *Populus tremuloides* Michx. (Salicaceae), Hammond (1997) collected approximately 39 000 specimens representing 5 classes, 13 orders, at least 113 families, and over 2000 species. In addition to being taxonomically diverse, saproxylic assemblages also exhibit high functional diversity, since they include 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, including the beetle (Coleoptera) families Cerambycidae, Curculionidae (Scolytinae), and Buprestidae. However, even in these groups much is unknown about insect–host relationships and species distributions. Saproxylic assemblages exhibit high spatial variability because many species have specific microhabitat associations, and such habitats are not distributed evenly within or among stands (Siitonen 2001; Hammond *et al.* 2004). There is also a temporal succession of species as the physical, chemical, and biological characteristics of wood change significantly over time, largely as the result of decay (Hammond *et al.* 2001; Jacobs *et al.* 2007*a*).

Wood, especially dead wood, provides unique structural characteristics and essential ecological elements of forests. Dead wood plays important roles in nutrient cycling and as habitat for species ranging from microorganisms to vertebrates (Franklin *et al.* 1987; Edmonds and Eglitis 1989; Cobb 2006). The large decrease in dead-wood volume, especially that classified as 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 Fennoscandian invertebrate groups (Heliövaara and Väisänen 1984; Siitonen and Martikainen 1994) and cryptogams (Anderson and Hytteborn 1991; Bader *et al.* 1995). Thus, it is increasingly accepted that dead-wood management must be incorporated into forest-ecosystem management (Franklin *et al.* 1997; Lee *et al.* 1997; Hagan and Grove 1999; Work *et al.* 2003).

Dead and dying wood occurs naturally as a consequence of low-intensity forest fires, self-thinning in immature stands, and the actions of insects and fungi (Harmon *et al.* 1986). Harvesting also produces large quantities of dead wood; however, there are many obvious physical and ecological differences between fire (and other natural disturbances) and harvesting as causes of forest disturbances and in terms of the quality and quantity of dead wood produced. Because harvesting is quickly replacing natural disturbances, especially fire, as the major stand-replacing disturbance in boreal forests in western Canada (Pratt and Urquhart 1994), widespread discussion and some experimentation are occurring to assess how harvesting practices may be adapted to better preserve the structural and habitat complexity created by natural disturbances. This work has been largely driven by the "natural-disturbance paradigm", which holds that forest management should aim to emulate the physical patterns and ecological effects of natural disturbances (especially fire) (Hunter 1993; Attiwill 1994). However, this approach to forest management requires multidisciplinary scientific input to examine a range of ecological, economic, and social-response parameters (values) if we are to be sure that such a shift in management style will make things better.

Over the last decade there has been increasing focus on saproxylic insect assemblages in Canadian forests. The purpose of this work has been to understand the natural determinants of faunal structure and succession and assess faunal responses to natural and anthropogenic disturbances. The ultimate goal of this work is to establish how operational forest practices may be adapted to minimize impacts on saproxylic assemblages. This review is a brief summary of some of the challenges to saproxylic insect research in Canada, lessons learned thus far, and a research agenda for the future. Most work to date in Canada has been carried out in the western boreal forests and provides the foundation for this review; however, excellent work is emerging in other parts of Canada and this is included where appropriate.

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Challenges

An important purpose of this review is to encourage future work on saproxylic faunas in Canada. However, those who aspire to delve into faunistics and ecological work on saproxylic arthropods need to be aware of the significant pitfalls and challenges associated with such work so that they can plan accordingly (Langor and Spence 2006). These challenges are summarized below.

Taxonomy and diagnostics

A paucity of taxonomic knowledge and tools limits the scope and quality of work on saproxylic arthropod diversity in Canada (Huber and Langor 2004). Adequate keys exist for only a small fraction of the Canadian terrestrial arthropods known and described. Among saproxylic insects, Coleoptera is the best known order. Yet of the 176 identified genera of saproxylic beetles collected by Hammond (1997), at least 56 are in urgent need of revision. The situation is worse for other insect orders with large numbers of saproxylic species. For example, a recent survey of cecidomyiid flies (Diptera) in dead wood in Quebec indicated a rich fauna of 323 apparent species, of which only about half could be identified to named species (Selby 2005). The scope and quality of work on saproxylic arthropods are strongly limited by the taxonomic soundness and stability of the targeted groups and availability of diagnostic resources (*e.g.*, keys, collections, expertise) to facilitate reliable identification. Some workers advocate circumventing the taxonomic challenge by using only higher level taxa (genera, families) or morphospecies (apparent species) (Oliver and Beattie 1996; Vanderwel *et al.* 2006). However, the use of such surrogates for diversity is risky and, for many studies, quite ill-advised. 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 or family often have different habitat requirements and therefore often respond differently to ecological perturbations. Furthermore, any approach applied to biodiversity work, except that done at the species level, violates the essential scientific criterion of repeatability. Wholesale changes in local assemblages of saproxylic (and other) arthropods could easily be missed at higher taxonomic levels. However, the need for information about biodiversity presently outstrips the development of adequate taxonomic resources, and from time to time we must invoke morphospecies designations in groups that are poorly known. The quality of the result will depend greatly on the skill and experience of the designator. Ideally, to minimize the risk of poor morphospecies definition and misidentifications, the designator should be a taxonomic expert in the relevant groups. Furthermore, extensive and representative voucher collections must be retained to support reinterpretation made possible by subsequent taxonomic revisions.

Alternatives to authoritative species-level identifications are rarely acceptable in meaningful arthropod-diversity work, and research teams require access to taxonomic expertise. This expertise may be obtained through partnerships with expert taxonomists elsewhere but often the prospect of being inundated with thousands of specimens for identification generates reluctance among taxonomists to become involved. Furthermore, there is a continuing shortage of arthropod-biosystematics expertise in Canada (Huber and Langor 2004). A better solution is 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 requires a considerable investment of time before the trainee is sufficiently skilled. The usual end result of the taxonomic challenges presented by arthropods is that the selection of families for study is strongly biased toward those that are taxonomically well known and for which identification skills and tools are readily available or fairly easily learned. Because groups vary significantly in their responses to disturbance (Buddle *et al.* 2006), we achieve little protection against unwanted faunal change by monitoring only taxa that are relatively easily dealt with taxonomically. In fact, a history of such a bias in choice of taxa monitored is doubtless linked to the recent discovery that in Fennoscandia, many once-common saproxylic species have been reduced to rare or locally extirpated (Siitonen and Martikainen 1994).

Sampling

Effective sampling is necessary for faunistic work on saproxylic assemblages and for experimental designs focusing on impacts and mitigation. Saproxylic insects have been sampled in two

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basic ways, either through use of activity-based traps or by directed search. Use of activity-based traps yields large numbers of specimens, but species proportions depend on species-specific activity and propensity to be trapped. Directed-search methods yield fewer specimens per unit effort but, with sufficient effort, provide better information about habitat associations and relative abundance. Each approach has advantages and biases (Hammond 1997; Langor *et al.* 2006), as summarized below.

In much of the work on saproxylic beetles carried out in western Canada and northern Europe, flight-intercept traps attached to the boles of snags, logs, and stumps have been employed (Hammond 1997; Kaila 1993; Cobb 2006; Jacobs *et al.* 2007*a*). These inexpensive traps can be deployed quickly in large numbers, are easily checked, and are nondestructive to CWD. However, it cannot be assumed that all species collected in a trap utilize the CWD to which the trap is attached, nor that all saproxylic species using a particular substrate will be collected (Ranius and Jansson 2002; Jacobs 2004; Wikars *et al.* 2005; Saint-Germain *et al.* 2006). Also, baited and unbaited flight-intercept traps unattached to dead wood have been used to sample stand-level saproxylic assemblages (Chénier and Philogène 1989; Bishop 1998) but such traps often do not collect as high a diversity of saproxylic species (especially rare species) as do intercept traps attached directly to dead wood (D.W. Langor, unpublished data). 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, this approach is not effective for collecting species deeper in the wood or on snags.

Rearing of insects from CWD is a good way of associating saproxylic species with specific pieces of CWD. One disadvantage of rearing is that the collection of CWD from the field and transportation to rearing cages is disruptive and may result in escape of highly vagile species or alteration of the properties of the CWD (*e.g.*, moisture, fungal growth, physical damage) in ways that cause high mortality of some taxa (Hammond 1997). Also, rearings are labour-intensive and the cost of infrastructure (*e.g.*, cages, rearing space) limits sampling. Furthermore, recovery of arthropods by rearing depends on when CWD is collected relative to the habits of the species using the dead wood. Species with stages that live strictly in dead wood for extended periods will be well represented, but those that depend, for example, on dead wood as critical foraging habitats may be largely missing from such samples. Emergence traps attached to CWD in the field will sample only species emerging from CWD. Although larger "sleeve-style" traps may sample large areas of CWD, they can be expensive to construct and deploy. Emergence traps will generally sample only insects within CWD at the time the trap is placed. As a result, in Canada, emergence traps have generally not been used broadly for sampling saproxylic fauna except for some groups of bark- and wood-boring insects (*e.g.*, Langor and Raske 1987). However, a study commenced in 2007 is exploring the utility of emergence traps to sample arthropods associated with logs and snags (D.W. Langor, unpublished data).

Hand-collecting by destructively dismantling CWD has been increasingly used in European studies of saproxylic faunas (Siitonen 2004; Martikainen and Kouki 2003; Ranius and Jansson 2002; Martikainen and Kaila 2004; Wikars *et al.* 2005; Hyvärinen *et al.* 2006). This method not only allows sampling of the contents of CWD, but also allows the collector to make natural-history observations regarding specific microhabitats, food, *etc.* (*e.g.,* Palm 1951, 1959). Such value-added observations are greatly needed for most of Canada's saproxylic fauna and will support much-improved interpretation of faunal activity and responses to disturbance. Hand-collecting and cage-rearing may be done in the winter months if appropriate facilities are available. However, hand-collecting is extremely time-consuming, requires excellent natural-history skills, and is destructive. Although collecting under the bark is relatively easy and yields good numbers of subcorticulous insects, it is much more work to exhaustively sample habitats deeper in the wood, work that will yield a quite different assemblage of species (Siitonen 2004). Many specimens collected by hand are larvae and are difficult or impossible to identify to species using available resources because the taxonomy of saproxylic arthropod larvae in North America is still in its infancy. Most importantly, because hand-collection protocols are difficult to standardize and replicate, this method does not lend itself easily to statistical modeling for ecological inference. Modern "science" tends to spurn and belittle natural history in competition for funding and limited journal space, even though the lack

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of such basic information severely constrains our ability to achieve modern scientific analyses of groups like saproxylic arthropods.

In practice, 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 various collecting methods 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. Furthermore, stratification of sampling may be required to ensure adequate representation when there is subtle variation in habitats (*e.g.*, Vance *et al.* 2003). If resources permit, it is generally desirable to utilize more than one collecting method within a study, especially for faunistic inventories (Hammond 1997).

Range of natural variation.

Baseline information about distribution and abundance of species and assemblage composition under conditions deemed to be "normal" provides a model against which assemblage responses to anthropogenic disturbances may be compared. As well, understanding the range of natural variation and its determinants may permit improved prestratified sampling and replication within experimental designs. Effective biodiversity monitoring requires understanding how abundance and diversity are affected by environmental conditions (Spence 2006). Compared with our European counterparts, we remain at the early stages of such work in Canada, in part because our fauna has been insufficiently studied. Although the importance of faunistic work is frequently underestimated, it results in a treasury of information about the composition of assemblages and species distributions 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 seasonality. Thus, reliance on range of natural variation to establish response thresholds for arthropod ecological indicators offers little promise without understanding how abundance and diversity are normally affected by environmental conditions. Fortunately, in Canada most types and successional stages of forests remain in their natural stage, providing an opportunity to gather the baseline data required to assess future trends.

Paucity of research

Despite the increasing focus on saproxylic arthropods in Canada, the huge physical size of Canada and the large number of native tree species (approximately 180) and variety of forest ecotypes demand a much greater research effort even to understand the basic distribution and habitat requirements of common saproxylic species. Most work to date has been focused on Coleoptera, and largely limited to three groups of bark- and wood-boring beetles (Scolytinae, Buprestidae, Cerambycidae) that contain many native and exotic pest species, and are taxonomically relatively well studied (Bousquet 1991; Biological Survey of Canada 2006). Comprehensive studies that include the full order of Coleoptera are largely focused on two tree species at a few locations in Alberta and Quebec. Furthermore, it is interesting that there is little serious focus on saproxylic groups other than Coleoptera, perhaps 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). The seemingly low interest of the Canadian research community in pursuing work on saproxylic faunas is puzzling, as 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 presented by this assemblage, except for some of the bark- and wood-boring groups that have been well studied because of their direct economic importance.

Faunistic inventories and assemblage composition

Discovery of new provincial or national records and undescribed species of saproxylic insects in Canada seems to be common to most biodiversity studies (*e.g.*, Hammond 1997; Bishop 1998; Dollin 2004; Selby 2005; Majka and Pollock 2006) and underscores our poor understanding of the Canadian fauna. Recent species-level work has greatly added to our knowledge of the composition of saproxylic insect assemblages. However, few such benefits are derived from work where taxa are identified only to family or higher taxon levels. Coleoptera has been the focus of nearly all studies, so

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knowledge of this order has increased substantially. Also, most of the detailed work completed to date has focused on fauna of species of *Populus* L. (Salicaceae) in north-central Alberta. This cumulative faunistics work provides a good baseline inventory, albeit for one order of insects 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 3 years (Hammond 1997). Of these, 46 species were new provincial records and 6–10 species were undescribed (taxonomic resolution is still pending). Of two subsequent studies of saproxylic beetles associated with *Populus* in other locations in north-central Alberta, one has yielded an additional 12 species, 10 of which are new provincial records (Jacobs 2004), and the other an additional 47 species, 13 of which are new provincial records (H.E.J. Hammond and D.W. Langor, unpublished data). As each new study (locality) has added new species to the provincial inventory, it is anticipated that further work will continue to turn up additional species, even in Alberta. Of the 59 new records of saproxylic species on *Populus* found since Hammond (1997), most were of fungivores (21 species), predators (17 species), and bark- and wood-borers (12 species). Hammond *et al.* (2004) found that only 142 of 257 species collected were shared between the two localities studied. With such high beta diversity, 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 much less complete, although work on spruces, *Picea* A. Dietr. (Pinaceae), in boreal Canada is now in progress (Jacobs *et al.* 2007*b*).

In terms of trophic roles, fungivores usually dominate abundance and species richness in saproxylic assemblages (Table 1; Hammond *et al.* 2004; Jacobs *et al.* 2007*a*). Although predators have been reported to be equal in species richness to fungivores (Hammond *et al.* 2004), it is likely that many of the predators captured from dead wood, especially the diverse families Carabidae and Staphylinidae, may not be truly saproxylic and do not have any affinity for dead wood. Although fungivores usually dominate saproxylic assemblages, the earliest colonization phase tends to be dominated by bark- and wood-borers, especially bark beetles (Scolytinae) and their associated predators (Hammond *et al.* 2001). However, as the phloem and sapwood are deteriorated by microorganisms 1–2 years following intial colonization, bark- and wood-borers decrease rapidly in abundance and species richness, giving way to fungivores and scavengers.

Many families of saproxylic beetles can be readily identified because of the availability of recent keys, good reference collections, and expertise in North America and Europe. However, a few major families and subfamilies remain difficult to identify accurately. The most notable group is the Aleocharinae (Staphylinidae), which is hyperdiverse and relatively poorly studied in Canada compared with many other staphylinid subfamilies (Klimaszewski 2000). It is estimated that one-third of the species of Staphylinidae in Canadian forests are aleocharine (Klimaszewski *et al.* 2007). Thus, extrapolation from the 78 species of non-aleocharine staphylinids collected by Hammond (1997) yields an estimate of about 39 species of Aleocharinae that were not identified. Interestingly, this estimate is similar to the 49 aleocharine species Palm (1959) collected from the European aspen, *Populus tremula* L. (Salicaceae), in southern Sweden (out of a total fauna of 342 beetle species). Rapid advances in the taxonomy of this subfamily now allow the possibility of species-level determinations for many genera. However, as approximately 30% of specimens require dissections of the genitalia to permit identification, and taxonomic skills reside among only a few experts, this subfamily remains relatively inaccessible, given limited budgets and time for most studies. Other families in dire need of revision are Latridiidae, Cryptophagidae, and 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 for each study are preserved, the advent of new taxonomic knowledge and tools will allow old data sets to be revisited and updated.

The family-level composition of saproxylic beetle assemblages varies from study to study in Canada (Table 1), and variability is influenced by geographic region, forest type, sampling method, and sampling intensity.

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Table 1. Numbers of saproxylic beetle species, by family, collected from coarse woody debris in five forest types in Canada.

	Alberta		Quebec	Nova Scotia	
Family and trophic role[a]	*Populus* forest (Hammond 1996)	*Populus*–conifer forest (Jacobs 2004)	Black spruce forest (Saint Germain *et al.* 2004)	Red spruce forest (Bishop 1998)	Mixed conifer forest (Dollin 2004)
Aderidae; ?	1	0	0	1	1
Anobiidae; WB	10	8	0	8	4
Anthribidae; F	3	0	0	0	0
Bostrichidae; WB	1	0	0	0	0
Buprestidae; WB	6	0	3	1	2
Byrrhidae; ?	0	0	1	0	1
Cantharidae; P	2	1	?	0	13
Carabidae; P, S	18	9	1	7	17
Cephaloidae; WB	0	1	0	2	1
Cerambycidae; WB	7	8	13	24	21
Cerylonidae; F	0	1	0	1	2
Ciidae; F	10	6	1	5	6
Clambidae; F	0	1	0	1	1
Cleridae; P	1	1	2	2	4
Coccinellidae; P, F	4	0	0	0	3
Colydiidae; P	0	1	0	0	1
Corylophidae; F	3	1	?	0	1
Cryptophagidae; F	14	8	2	7	3
Cucujidae (including Laemophloeidae, Silvanidae); P	5	3	2	3	4
Curculionidae (including Scolytidae, Nemonychidae); WB	8	24	17	24	39
Dermestidae; S	4	1	0	0	0
Elateridae; S, P	11	4	18	44	31
Endomychidae; F	3	0	0	3	1
Erotylidae; F	3	3	0	3	1
Eucinetidae; F	0	1	0	1	0
Eucnemidae; ?	4	1	0	4	2
Histeridae; P	4	2	0	2	7
Lampyridae; P	0	1	1	2	2
Latridiidae; F	18	9	4	8	8
Leiodidae; F, S	14	3	0	9	4
Lucanidae; S	1	0	0	1	1
Lycidae; P	1	1	1	5	4
Lymexylidae; WB	1	1	0	0	0
Melandryidae (including Tetratomidae); S, F	9	8	1	16	15
Mycetophagidae; F	2	2	0	1	3
Nitidulidae; F	10	5	5	3	9
Oedemeridae; WB	0	0	0	1	0
Ptiliidae; F	3	1	?	0	1
Pyrochroidae; F	2	2	0	3	1
Pythidae; WB	0	1	0	1	3
Rhipiphoridae; ?	1	0	0	0	0

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Table 1 (*concluded*).

Family and trophic role[a]	Alberta		Quebec	Nova Scotia	
	Populus forest (Hammond 1996)	*Populus*–conifer forest (Jacobs 2004)	Black spruce forest (Saint Germain *et al.* 2004)	Red spruce forest (Bishop 1998)	Mixed conifer forest (Dollin 2004)
Rhizophagidae; P	4	3	0	1	1
Salpingidae; P	2	0	1	1	0
Scaphidiidae; F	2	0	0	4	0
Scraptiidae; ?	2	0	0	4	5
Scydmaenidae; P	1	1	0	2	2
Sphindidae; F	2	1	0	3	2
Staphylinidae (excluding Aleocharinae; including Pselaphidae); P, S, F	104	32	?	42	39
Tenebrionidae (including Zopheridae, Lagriidae); F	5	0	0	7	15
Throscidae; F	0	0	0	2	2
Trogossitidae; P	4	2	0	0	1
Total	310	158	>74	259	286

Note: Designation of families is according to Bousquet (1991).
[a]WB, bark- and wood-borers; P, predators; F, fungivores; S, scavengers; ?, unknown.

Langor *et al.* (2006) made a comparison of species richness and faunal composition of the saproxylic fauna associated with *Populus* in Canada (using data from Hammond 1997 and unpublished work) and southern Sweden (Palm 1959). The two 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*. Of these, 12 were restricted to *P. tremula* and 17 overwintered only in the CWD. Although Staphylinidae, Latridiidae, and Leiodidae were among the most species-rich families in both Alberta and Sweden, the distribution of species among families differed significantly, as did trophic structure. Predators and fungivores dominated the faunas in Alberta and Sweden, but predators were most dominant in Alberta and fungivores 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 particular affinity for dead wood. When carabids and staphylinids were eliminated from analyses, the distribution of species among families and trophic groups did not differ significantly between Sweden and Alberta (Langor *et al.* 2006). 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 of Sweden, where the inventory is fairly complete. This raises the question of whether the longer history of forestry practices in Sweden may have caused a reduction in faunal diversity.

Determinants of assemblage structure

CWD is immensely variable in terms of easily observed qualities (*e.g.*, species, degree of decay, size, orientation), as well as more subtle differences in such qualities as species of fungi present, moisture content, *etc.*, all of which influence saproxylic insect composition and abundance (Siitonen 2001). Furthermore, the range of natural variation in saproxylic assemblage composition and abundance is enormous. For example, Hammond *et al.* (2004) placed two flight-intercept traps separated by 1.5 m in vertical height on the bole of each *Populus* snag. Percent similarity among fauna captured in the two traps on each snag averaged only 38% (range 0%–68%). Such high variability

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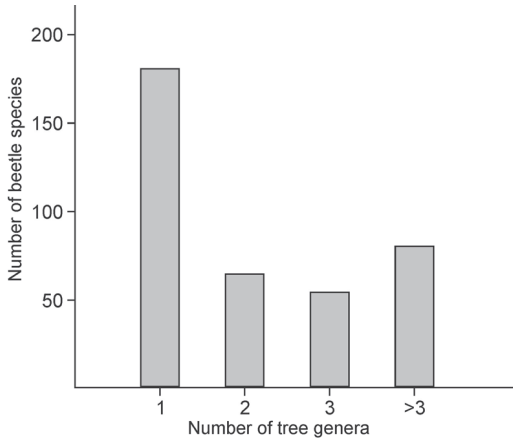
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among samples, also evident at other spatial scales, greatly increases the challenge of designing good experiments to ensure that sampling of saproxylic faunas is adequate for making meaningful comparisons and, ultimately, improving management for biodiversity on landscapes subject to industrial forestry. However, despite the high natural variability, progress has been made in understanding the major determinants of saproxylic assemblage structure in Canada.

Regional variation

Regional variation in faunal composition is evident. Hammond *et al.* (2001, 2004) sampled saproxylic beetle assemblages in boreal *Populus* at two locations in northern Alberta. Only 55% of the 257 species collected were shared between localities and percent similarity between regions was only 56% for reared beetles and 64% for window-trapped beetles. The two localities, separated by 500 km and 1.5° latitude, belong to the Boreal Plains Ecozone but were in two different ecoregions (Ecological Stratification Working Group 1995). The faunal differences between these two sites were interpreted as a function of differences in biophysical characteristics tempered by dispersal. Differences 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 *et al.* 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 (*Populus balsamifera* L. (Salicaceae)) are distributed from coast to coast and from the far south to treeline in the north, and both species occur in almost all of Canada's ecozones and ecoregions. The large geographic variation in the saproxylic beetle assemblage associated with just these two 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 choice of indicators, and embraced in monitoring programs.

Fig. 1. Host specificity of species of Scolytinae and Buprestidae in trees in Canada.



Host species

Information about host tree species as a determinant of saproxylic assemblage structure is most complete for the bark- and wood-boring Curculionidae (Scolytinae), Buprestidae, and Cerambycidae. These groups have been well collected and studied because many species are of economic importance. Of the 213 species of Scolytinae and 171 species of Buprestidae known to occur on trees in Canada (Bright 1976, 1987), almost half (182 species) are known from only one tree genus (Fig. 1), 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 five species are known to breed in both coniferous and deciduous hosts.

Variation of the total saproxylic beetle fauna (all trophic groups) among white spruce (*Picea glauca* (Moench) Voss (Pinaceae)) and aspen snags was assessed at the Ecosystem Management by Emulating Natural Disturbance Project (EMEND) research site 90 km northwest of Peace River, Alberta (Jacobs *et al.* 2007*a*). Three mixedwood stands were sampled with flight-intercept traps placed on white spruce and aspen snags that had been dead for 1–7 years. In total, 114 species were collected, 56 from both hosts, 22 only from aspen, and 36 only from spruce. Indicator analysis (Dufrêne and Legendre 1997) designated 12 species as indicative of spruce or aspen trees; 5 species were indicative of aspen, including 1 ambrosia beetle (Scolytinae), the beetle's specialist predator, and 3 fungivores; and 7 species were indicative of spruce, all of which were bark beetles

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Table 2. Abundance and species richness of saproxylic beetles associated with *Populus* coarse woody debris of different decay classes in north-central Alberta, Canada (summarized from Hammond *et al.* 2004).

	Window-trapped beetles			Reared beetles		
Decay class[a]	*n*	Catch[b]	Species richness[c]	*n*	Catch[d]	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 *et al.* (2004).
[b]Number of beetles (mean ± SE), based on catches from individual window traps deployed from April to early September and standardized to 155 trap-days.
[c]Expected number of species (mean ± SD) in a subsample of 2300 and 400 window-trapped and reared beetles, respectively.
[d]Mean number of beetles standardized to the volume of the largest wood sample: 535 020 cm^3.

and their specialist predators. This work suggests that fungivores, scavengers, and generalist predators may be less host-specific than species requiring fresh phloem or sapwood and their specialist predators. However, one must use caution in interpreting the results from flight-intercept traps, as the trap catch may not adequately represent the species resident in the snag to which the trap is attached. Nonetheless, it is widely recognized that host tree species exerts a strong influence on the composition of saproxylic insect assemblages (*e.g.*, Palm 1951, 1959; Siitonen 2001; Lindhe and Lindelöw 2004; Selby 2005).

Decay

CWD is a dynamic environment characterized by often-rapid changes in chemistry and physical characteristics, brought about to a large extent by the action of fungi and other microorganisms (Boddy 1992; Renvall 1995). The changes in CWD quality associated with decay, and the species of fungi (especially sporocarps) present at a particular time, influence the structure of saproxylic beetle assemblages (Siitonen 2001). After the death of a tree, decomposition takes several decades, during which time there is a succession of saproxylic species (Esseen *et al.* 1992, 1997).

Work on saproxylic beetles in Canada also shows clear faunal changes with increased decay of CWD; these changes are most rapid during the 1–2 years immediately after tree death (Hammond *et al.* 2001, 2004; Vanderwel et al. 2006; Jacobs *et al.* 2007*a*). The most detailed work has been done on *Populus* CWD in boreal Alberta. CWD decay was assessed according to the following decay classes (DC): early (DC1), intermediate (DC2), and advanced (DC3) (see classification criteria in Hammond *et al.* 2004). Although mean abundance of saproxylic beetles collected using flight-intercept traps did not vary significantly among decay classes, DC1 CWD tended to have the highest overall abundance of beetles (Table 2), a pattern also reported in eastern Canada for Coleoptera in pine (*Pinus* L. (Pinaceae)) logs (Vanderwel *et al.* 2006) and for *Picea*-associated assemblages in boreal Alberta (Jacobs *et al.* 2007*a*). However, species richness in *Populus*, estimated by rarefaction (Sanders 1968; Hurlbert 1971; Gotelli and Colwell 2001), was lowest in DC1 CWD (Table 2). Therefore, although saproxylic beetle activity is higher around new CWD, species diversity is lower than around more advanced decay classes. About 3 times as many species are uniquely associated with older decay classes as with new CWD (Hammond 1996). Furthermore, cluster analysis based on Bray–Curtis similarity measures revealed that the assemblage of species associated with fresh CWD (DC1) was most dissimilar to those of the two more advanced decay classes.

Early succession in CWD occurs rapidly (Hammond *et al.* 2001; Siitonen 2001; Jacobs *et al.* 2007*a*). 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, specializes on these resources and can colonize fresh CWD in large numbers. The trend of species richness of fungivores, scavengers, and predators to increase with the more advanced decay classes (Hammond *et al.* 2004; Vanderwel *et al.* 2006) is an expected successional response to increasing microhabitat diversity that is partly due to the

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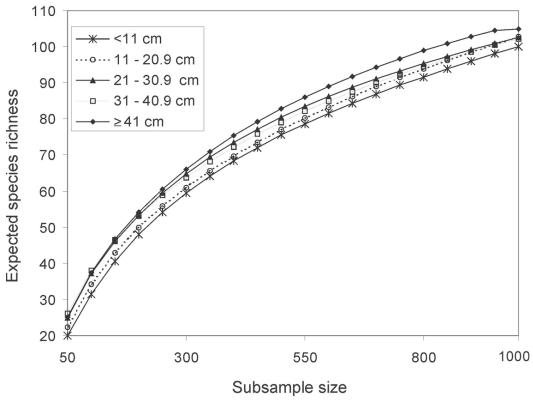
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actions of wood-decaying fungi (Siitonen 2001). Many saproxylic species are highly attracted to decayed wood because they specialize on different fungal structures such as fruiting bodies, hyphae, and spores (Ehnström 2001) and on different fungal species (Lawrence 1973; Wheeler and Blackwell 1984). The predatory and scavenger species are 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

In Fennoscandia, significantly higher abundance and species richness of saproxylic insects are associated with old stands rather than with mature stands (Martikainen *et al.* 1999, 2000); 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 *et al.* 2000; Nilsson *et al.* 2001). In Alberta, in a relatively unharvested landscape consisting of a mixture of stands ranging from 40 to >105 years since disturbance, nearly twice the number of specimens and 34% more species were reared from CWD in old aspen stands (>105 years of age) than in young stands (60–80 years of age); however, rarefaction-standardized species richness did not vary among stands of different ages. Furthermore, in old stands, abundance and species richness of beetles collected with flight-intercept traps were similar to, or species richness was only slightly higher than, in mature stands (Hammond *et al.* 2004). However, age clearly affected beetle assemblage structure. Indicator-species analysis showed 10 species that were indicative of old stands and classified only 3 species as indicative of mature stands (Hammond *et al.* 2004). In Nova Scotia, saproxylic and fungivorous beetles in the family Nitidulidae were most abundant in managed hemlock (*Tsuga* Carrière (Pinaceae)) – hardwood stands but most diverse in old-growth stands, and species composition differed between the two ages of stands (Zeran *et al.* 2006). Stand age also significantly affected species richness of saproxylic beetles in mixed spruce–hemlock–pine stands in Nova Scotia: stands >80 years of age had much higher species richness (Dollin 2004).

Fig. 2. Rarefaction estimates of expected species richness by subsample size (number of individuals) for saproxylic beetles collected with flight-intercept traps attached to *Populus* snags in aspen-dominated mixedwood forests in north-central Alberta. Snags are divided into 10 cm diameter-at-breast-height classes.

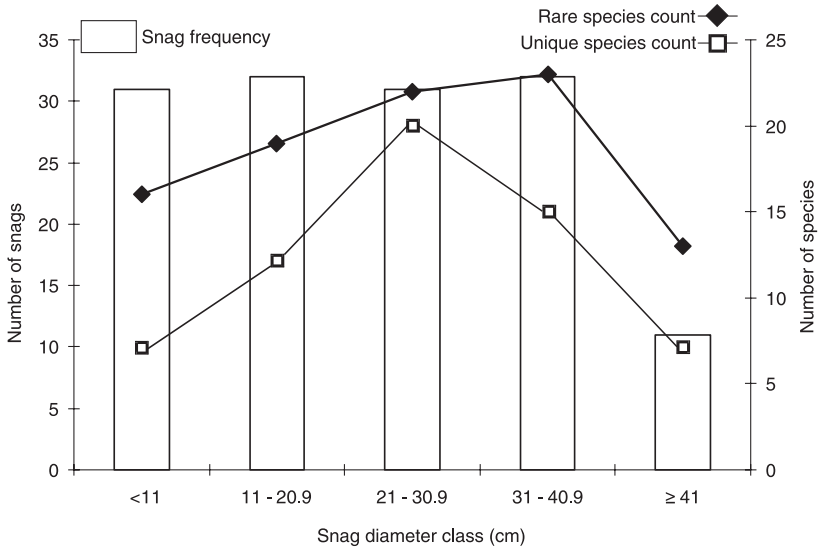


Rarefaction-estimated species richness increased with *Populus* CWD diameter and was highest in the ≥41 cm diameter at breast height (DBH) class (Fig. 2), even though that size class included only one-third the number of snags as other diameter classes (Fig. 3). Number of rare species seemed to increase linearly with snag diameter, peaking in the 21–30.9 cm DBH class; however, there was almost one unique species for every snag sampled in the largest diameter class (Fig. 3). Indicator-species analysis identified 15 species that were significant indicators of large (≥41 cm DBH) snags, and many of these are the same as those that are 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, structural and microhabitat diversity appears to increase. 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. Collectively these results suggest that an improved understanding of CWD microhabitats and development of a biologically meaningful CWD-classification system would help in stratification of sampling to achieve a better understanding of the saproxylic fauna.

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Fig. 3. Number of *Populus* snags of each of five diameter classes sampled using flight-intercept traps, and the number of rare (singletons + doubletons) and unique saproxylic beetle species collected in each diameter class.



Forest management and biodiversity

Harvesting now rivals natural agents (*e.g.*, wildfire, windthrow, insects, and diseases) as the major disturbance and stand initiator in Canadian forests (Pratt and Urquhart 1994). Science aimed at understanding and mitigating ecological consequences of industrial forest management has generally not kept pace with the rapidly increasing rate and extent of harvesting. Consequently, the forest-science community is challenged to assess ecological effects and to find ways to maintain ecological processes in managed forests as a requirement of sustainable forest management. As many ecological processes are poorly understood and difficult to monitor, one approach to assessing ecological functions 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 (Spence *et al.* 1999*a*; Langor and Spence 2006). Although this approach has been hotly debated (*e.g.*, McCann 2000) and remains largely untested, there is a growing consensus that ecosystem processes are maintained, at least in part, by ensuring the continuity of the plant, animal, and microbial species living within a community (Naeem *et al.* 1999; Naeem 2002; Hooper *et al.* 2005).

In Canada and the northern United States of America, assessment of the impacts of forest-harvesting practices on arthropod biodiversity has increased rapidly over the last 15 years, with epigaeic assemblages (carabid and staphylinid beetles and spiders (Araneae)) receiving most of the attention (Biological Survey of Canada 2006). However, the impacts of forestry practices on saproxylic beetles have received only recent attention and have been more cursorily assessed (Hammond 1996; Spence *et al.* 1997; Bishop 1998; Kehler and Bondrup-Nielsen 1999; Hindmarch and Reid 2001; Dollin 2004; Safranyik *et al.* 2004; Zeran *et al.* 2006, 2007; Jacobs *et al.* 2007*b*). In all cases to date, saproxylic arthropods have responded to human-caused disturbances in terms of abundance, species richness, and species composition. Comparing biodiversity response patterns following anthropogenic disturbances with those following natural disturbances of equivalent scale can lead to practical solutions by focusing on how forest management may be adapted to better approximate the results of natural disturbances.

Comparison of forestry and natural disturbances

Natural disturbances such as fire, insect outbreaks, fungi, and windfall help shape the boreal-forest landscape by creating a shifting habitat mosaic. This mosaic includes patches that vary in size, shape, composition, age, and

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juxtaposition. Wildfire is usually the most important disturbance in Canadian boreal forests. The natural-disturbance paradigm for forest management has been widely advocated as the best way to achieve sustainable management of the boreal forest (*e.g.*, Hunter 1993; Haila *et al.* 1994; Angelstam 1997). This approach is grounded in the assumption that the biota of boreal-forest ecosystems is preadapted to conditions associated with large-scale natural disturbances, especially wildfire. Thus, emulation of some obvious macrocharacteristics of these natural disturbances (*e.g.*, variable retention, shape and design of cutting, rotation schedule, maintenance of dead wood on the land base) should be a useful approach to large-scale forest harvesting *sensu* the natural-disturbance hypothesis (Hunter 1993). However, there has been little empirical testing of the natural-disturbance hypothesis with respect to the main emulations currently employed by the forest industry in boreal Canada (Spence *et al.* 1999*b*; Work *et al.* 2003). It is important that we understand the relative impact of forest practices on biodiversity, compared with effects of natural disturbances, since mounting evidence indicates that the number and identity of species occurring in an ecosystem relate in a meaningful way to ecosystem stability (Tilman *et al.* 2001; Naeem 2002).

The ecological conditions in burned forests obviously differ from those in harvested forests and from those that characterize trees killed by other agents in unburned forests. Among other things, burned stands include large amounts of dead-wood substrate (Pedlar *et al.* 2002) and open stand conditions characterized by higher temperatures (Wikars 1992). Many saproxylic insects are strongly associated with burned trees and forests (Jacobs 2004; Saint-Germain *et al.* 2004*a*, 2004*b*). Saint-Germain *et al.* (2004*a*, 2004*b*), for example, reported over 40 species of saproxylic Coleoptera captured in burned black spruce, *Picea mariana* (Mill.) B.S.P. (Pinaceae), forests in Quebec but not found in unburned forests. Similarly, in Alberta, Jacobs (2004) reported 32% and 38% more saproxylic beetle species in severely burned portions of a spruce-dominated stand than in lightly burned and unburned portions, and 53 of 124 species were found only in burned stands. Although these two studies show the ecological importance of wildfire in terms of creating unique niches for saproxylic assemblages, they do not directly compare harvesting and wildfire as ecological disturbances.

The structure of the saproxylic beetle assemblage in burned stands was directly compared with that in harvested stands in *Populus*-dominated boreal–mixedwood stands in north-central Alberta (D.W. Langor, unpublished data). The chronosequence study compared the successional trajectories of assemblages over time to explore the relative impacts of fire and harvesting on arthropod biodiversity. Faunas were compared among stands aged 1–2, 14–15, and 28–29 years originating from either wildfire or clear-cutting. Beetle catches in window traps attached to snags were similar across most treatments with the exception of the 1- to 2-year-old harvested stands, which yielded 3–4 times more beetles than other stands (Fig. 4), largely because of greatly increased numbers of the bark beetle *Trypodendron retusum* (LeConte) (Scolytinae), two other species of bark beetle, and a scavenger often associated with bark beetle galleries. However, despite the much higher abundance of beetles, the youngest harvested stands had the lowest species richness, as estimated by rarefaction (Fig. 5). The highest species richness occurred in 14- to 15-year-old burned stands, but there were no clear patterns in species richness associated with stand age or disturbance type. Ordination (Fig. 6) showed that 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 significant convergence of the faunas 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 suggest that saproxylic assemblages will 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, the assemblages in each disturbance type still differed significantly from those of >70-year-old stands (Buddle *et al.* 2000, 2006).

Bishop (1998) directly compared saproxylic beetle assemblages among mainly red spruce, *Picea rubens* Sarg. (Pinaceae), stands in Nova Scotia disturbed by fire, wind, thinning, and clear-cutting. There were no significant differences among stand disturbance types in terms of mean beetle abundance, mean species richness, and mean species diversity (alpha diversity).

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Fig. 4. Standardized catch (number of specimens per 150 trap-days; mean ± SE) of saproxylic beetles in Alberta boreal *Populus* stands of three ages originating from fire or clear-cut harvesting.

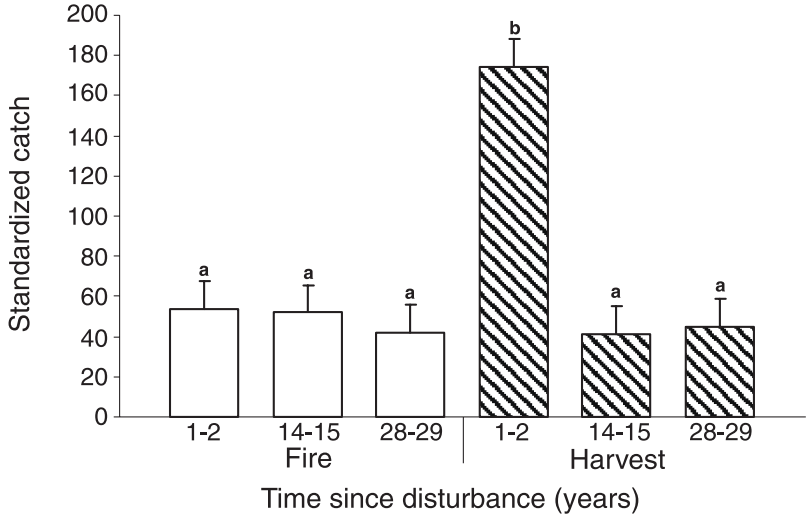
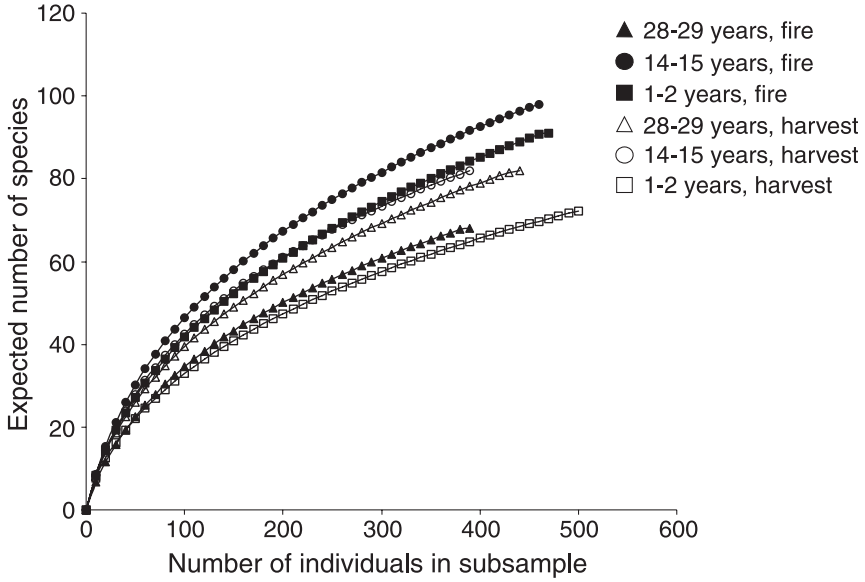


Fig. 5. Rarefaction-estimated species richness of saproxylic beetles in Alberta boreal *Populus* stands of three ages originating from fire or clear-cut harvesting.



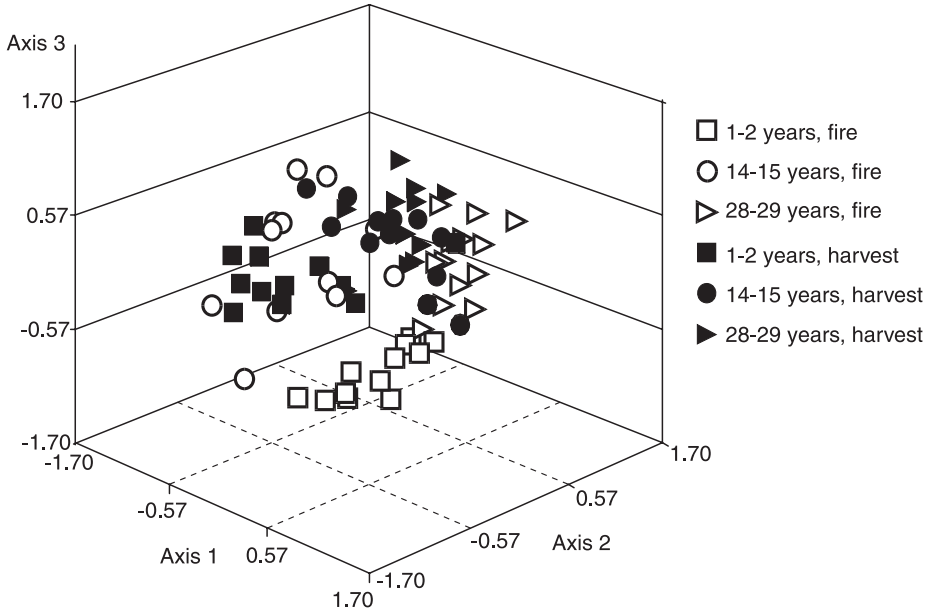
However, beta diversity (heterogeneity) varied greatly among stands: windthrown >burned >thinned >clear-cut. Therefore, clear-cut harvesting tends to ecologically homogenize stands compared with thinning. The saproxylic assemblages associated with each disturbance type were somewhat distinctive; burned stands were most distinct (14 indicator species), followed by thinned (6 species), clear-cut (4 species), and windthrown (3 species).

Comparison of the effects of fire and harvesting on biodiversity clearly indicates that clear-cutting does not strongly emulate wildfire with respect to faunal response. There may be some options for harvesting that create ecological conditions and habitats that better approximate those created following fire, including variable-retention harvesting (VRH) and residual burning following harvesting. These options are receiving attention through several ongoing studies in the

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Fig. 6. Nonmetric multidimensional scaling ordination of 211 species of saproxylic beetles collected using flight-intercept traps in Alberta boreal *Populus* stands of three ages originating from fire or clear-cut harvesting. Each point represents the fauna associated with a snag (12 snags for each treatment combination). R^2 values for axes 1, 2, and 3 are 0.256, 0.286 and 0.224, respectively; stress = 16.7, P = 0.002.



Canadian boreal forest and elsewhere in the boreal zone.

Adaptive forest management

VRH has recently been employed at various locations in Canada in an attempt to leave more structural complexity on the landscape to benefit biodiversity conservation (Work *et al.* 2003). VRH also affects CWD succession by increasing the input of CWD into these systems. The short-term effects of different levels of dispersed residual structure on saproxylic beetles were assessed in white spruce dominated stands at the EMEND site in Alberta (Jacobs 2004; Jacobs *et al.* 2007*b*). Four VRH treatments (75%, 50%, 20%, and 10% residual structure) were applied to the compartments using a uniform shelterwood system. The experiment also includes nonharvested controls (100% residual structure). Although overall CWD volume was relatively unaffected by harvesting treatments (D.W. Langor, unpublished data), snag density was highest in controls and decreased with residual volume (Jacobs et al. 2007*b*). In general, harvesting significantly affected saproxylic beetle assemblages the second summer following harvest. The effects were most evident in comparisons between control stands and harvested stands, regardless of harvest intensity. The following summer only fungivores were still showing significant effects of harvesting in comparison with the control treatments. The data from EMEND suggest that even minimal harvesting can have an impact on saproxylic beetles. Interestingly, one bark beetle species, *Xylechinus montanus* Blackman (Scolytinae), 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.

Although the influence of quantity of residual structure in harvested stands on saproxylic faunas has received some attention, the spatial patterns and quality of living and dead wood residual structure has not yet been examined in detail in Canada. In Europe, saproxylic beetles have been shown to be vulnerable to habitat fragmentation manifested as large distances between (*i.e.*, decreased connectivity of) dead-wood habitats: areas with more dead-wood connectivity had higher species diversity than those with clumped habitat distribution (Schiegg 2000*a*, 2000*b*). This work indicates that dead-wood distribution is critical for survival

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of some species and should be considered in forest-management plans.

Current harvesting practices may also be better adapted to emulate wildfire disturbance by leaving some residual structure in harvested blocks combined with burning of live and dead wood in the blocks following harvesting to create conditions and structure more akin to those following wildfire (*e.g.*, scorched CWD and charcoal). This treatment has recently been implemented at the EMEND site and work is underway to assess the responses of saproxylic and epigaeic arthropods.

Multiple disturbances and ecosystem function

It may be reasoned that pyrophilous species are not likely to become endangered under scenarios of increased fire activity associated with climate change (Stocks *et al.* 1998). However, the increasing application of salvage logging in burned stands (Lindenmayer and Noss 2006; Cobb 2006; Schmiegelow *et al.* 2006) calls this reasoning into question, as evidence is mounting that salvage logging has adverse ecological consequences for postfire plant regeneration (Donato *et al.* 2006; Greene *et al.* 2006), birds (Morissette *et al.* 2002; Nappi *et al.* 2004), and epigaeic beetles (Koivula *et al.* 2006; Phillips *et al.* 2006). Because postfire salvage logging involves the combination of two different disturbances on the same sites, the ecological consequences of this practice for biodiversity may be cumulative (Lindenmayer and Noss 2006). Recent work on ground beetles (Carabidae) in Alberta supports this notion, as combinations of wildfire and forest harvesting on the same sites simplified assemblages to a greater extent than either disturbance alone (Cobb 2006). For pyrophilous saproxylic species, removal of burned, dead wood may be particularly damaging and may upset ecological links between these species and nutrient cycling in forests recovering from fire (Cobb 2006). However, until the functional roles of most species, in addition to their response to disturbance combinations, have been sufficiently studied, the ecological consequences of such practices as postfire salvage logging will undoubtedly be complicated and difficult to predict.

Future directions

An increasing emphasis on the simultaneous goals of biodiversity conservation and sustainable forest management in North America and elsewhere has led to a growing interest in the study of saproxylic insects and the ecology of dead wood. In Canada, work on saproxylic insects over the last 15 years has provided much practical experience with this fauna, baseline data on assemblage structure and its variation, some understanding of the determinants of faunal structure, and several long-term, legacy experiments that will help identify forest-management prescriptions that better incorporate biodiversity objectives into resource planning. It seems 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 designate taxa as indicators so that expensive monitoring programs can begin will produce results that are more dependent on luck than on science (Langor and Spence 2006). The insights gained and lessons learned also provide some direction for future research endeavours. This assessment of the current state of knowledge about saproxylic arthropod assemblages also provides insight into areas of future work that is necessary to ensure that saproxylic assemblages remain viable in the extensively managed forest land base of Canada.

Taxonomy

Although the importance of taxonomy to biodiversity science (and many other fields of biological science) is well advocated, words and good intentions have generally not been supported with decisive action to ensure the long-term viability of this area of science. Even when, on 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 using molecular biology aimed at resolving phylogenetic issues, rather than on support for urgently required work with useful management implications, including taxonomic monographs and keys to facilitate identification of difficult groups. Saproxylic faunas include many families and genera that are 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 indicators (Økland 1996). Thus, we require continued investment in taxonomy and systematic infrastructure, including a focus on some diverse and potentially useful saproxylic families. This

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certainly requires training of young taxonomists to continue describing and cataloging the North American fauna and renewed support for museums and collections that ensure an adequate national biological inventory.

Natural history

Even for those saproxylic beetle species that can be readily identified, there is a dearth of information about biology and microhabitat requirements. Without such information, descriptions of population trends, which are necessary for the development of conservation priorities or "red lists", are preliminary at best. Therefore, the value of basic biological and ecological information, generated through detailed natural-history observations, should not be underestimated or trivialized. Such information will add greatly to the growing wealth of data about species' responses to disturbances and, when synthesized for a large number of species, will likely help identify sensitive microhabitats at risk as a result of 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 information is unlikely to emerge spontaneously from a haphazard set of tight, focused experiments designed to test particular aspects of the day's fashionable ecological theory.

Our biological knowledge of the Canadian saproxylic fauna arises from relatively few studies in a limited number of forest types (*e.g.*, aspen-dominated, midsuccessional forests) and is largely focused on beetle assemblages. Clearly, more work is needed in a wider range of forest types and on non-beetle species. With basic survey data on hand, we may begin to focus productively on more detailed work on saproxylic insect ecology. For example, saproxylic insects are generally considered to be important contributors to the process of wood decomposition either through direct feeding activity or by vectoring cellulolytic fungi. However, aside from a few studies on ambrosia beetles, there has been little effort to assess this functional role directly (*e.g.*, Cobb 2006). Moreover, there is also a paucity of detailed work on interactions between saproxylic insects and their predators (invertebrate and vertebrate) as well as species-specific fungal associations. Such data are urgently required to support and inspire scientific studies of ecosystem function.

Classification of dead wood

Our current classification systems for CWD are relatively crude and have little basis in sound biological criteria. Most systems order CWD in classes (up to 7) that are largely focused on degree of decay. Even CWD diameter, which is known to affect saproxylic assemblage structure (Grove 2002), is not included in most classification systems. Also, such systems are difficult to apply to tree species other than the one for which the system was developed. An improved dead-wood classification, especially for CWD, should be based on such criteria as species, size, decay, orientation (standing or fallen), presence of cavities and fungal fruiting bodies (and species), degree of sun exposure, nutrients, *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 coupled with improved knowledge of the natural history of saproxylic species will support identification of habitat surrogates for saproxylic arthropods that are easy to measure and readily incorporated into biodiversity-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 comprehensive studies are few and this complicates extrapolation of results across large landscapes, even of the same forest type. Thus, we must also learn to use preplanned and retrospective studies that connect to key points emerging from large experiments to help us understand what features generalize well. When possible solutions to problems are suggested, we must build them into ongoing forest-management activities and evaluate their impact. 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 *et al.* 2003).

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If conservation of saproxylic insects is to be a high priority in the development of guidelines for sustainable forest management, species-specific responses to various disturbances and mitigation procedures require further study. Management of dead wood may prove to be a particularly useful mitigation tool, but in the case of the Canadian fauna, detailed associations of saproxylic assemblages with dead-wood quality and quantity are poorly understood. Similarly, our understanding of community- and species-level responses to combinations of natural and forestry-related disturbances (*e.g.*, postfire salvage logging), as well as interactions with other disturbances such as road building, oil and gas exploration, or exotic species invasions, is rudimentary in most cases. Although the last decade of research on saproxylic insects in North America has advanced our knowledge of this group, many aspects still require attention before we can be confident about conservation of these assemblages in the context of sustainable forest management.

In summary, saproxylic organisms are perhaps the best equivalent to "a canary in the coal mine" that we have as an early-warning system 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.*, Siitonen 2001), 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 dead wood" represent a large fraction of the biological diversity in forest environments and the arthropod–fungus 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. Thus, these arthropods are closer to the fundamental level of 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 nonmigratory lifestyles 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, provides cold comfort about the fate of such creatures (and those that depend on them) as they become concentrated in small pockets of disconnected residual structure and are possibly doomed to become extinct (*e.g.*, Siitonen and Saaristo 2000). Nonetheless, our present understanding of the range of natural variation of diversity and abundance of saproxylic organisms in North America suggests that we need to better classify our knowledge by contingency (see Siitonen 2001) to effectively conserve this fauna through improved forest management. Clearly, the best present approach involves 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 *et al.* 2004), but we have much to learn before we can be confident about conserving these interesting creatures and the full range of ecological function that depends on their existence and activities.

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