United States
Department of
Agriculture

Forest Service

Southern
Research Station

General Technical
Report SRS–93

Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology

Brisbane, Australia
August 15–21, 2004

Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS–93. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 109 p.

In August 2004, the city of Brisbane, Australia, was host to one of the largest recent gatherings of the world's entomologists. The 22nd International Congress of Entomology featured a multitude of symposia covering a wide range of entomology-related topics. This general technical report is based on papers presented on one such symposium, "Insect Biodiversity and Dead Wood." It features contributions from around the world. Dead wood is anything but dead. It is the lifeblood of an intricate web of life in which insects feature prominently. The papers presented here consider both the basic ecology and evolutionary history of saproxylic (dead-wood dependent) insects and how such insects can be affected by management of the forests where most species live. Past management has not always been beneficial to saproxylic insects and in some parts of the world has harmed them greatly. With continued quality research, however, there is some prospect that future land management will be more accommodating to saproxylic insects.

Keywords: Arthropod diversity, coarse woody debris, fossil insects, funnel web spider, invertebrate conservation, New Forestry, saproxylic insects.

Preface

In August 2004, the city of Brisbane, Australia, was host to one of the largest recent gatherings of the world's entomologists. Several thousand delegates attended the 22nd International Congress of Entomology, which featured a multitude of symposia that together covered a wide range of entomology-related topics. This special General Technical Report is based on papers presented in a symposium entitled "Insect Biodiversity and Dead Wood." It features contributions by scientists from around the world, and these contributions clearly illustrate our growing understanding of the entomological importance of dead wood.

Dead wood is anything but dead. It is the lifeblood of an intricate web of life in which insects figure prominently. The papers presented here consider the basic ecology and evolutionary history of saproxylic (dead-wood dependent) insects, and show how these species can be affected by human management of the forests where most of them live. Past management has not always been kind to saproxylic insects, and in some parts of the world this has harmed the fauna significantly. However, there is reason to think that continued research may in the future give land managers the technical tools to accommodate saproxylic insects. Whether societies will adopt these friendlier techniques remains to be seen, but we hope the information presented in this volume will encourage them to do so.

Simon Grove, Co-convenor
Forestry Tasmania

Jim Hanula, Co-convenor
USDA Forest Service
Southern Research Station

Contents

Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology

Editors:

Simon J. Grove, Conservation Biologist
Forestry Tasmania
Southern Research Station
Hobart, Tasmania 7001, Australia

James L. Hanula, Research Entomologist
U.S. Department of Agriculture Forest Service
Southern Research Station
Athens, GA 30602-2044

EVOLUTION OF SAPROXYLIC AND MYCOPHAGOUS COLEOPTERA IN NEW ZEALAND

Richard A.B. Leschen[1]

Abstract—Beetles are an old holometabolous group dating back to the early Permian and associated with sediments containing conifers, ginkgos, and cycads. To determine the antiquity of dead wood beetles the evolution of gondwanan saproxylic and mycophagous beetles was examined in the context of available phylogenies that include New Zealand taxa. Phylogenetic position and branch lengths showed that 50 percent of the New Zealand fauna is basal and may represent old lineages dating to around 82 million years when New Zealand separated from Gondwana. Meanwhile, 60 percent of the New Zealand taxa have relatively long branches relative to overseas outgroups and this phenomenon may have resulted from the adaptation of these groups to resource shifts in changing forest communities. The resource shift hypothesis predicts that polyphagy will be widespread in mycophagous and phytophagous insects. Podocarp-broadleaf forest associations are more primitive than associations with *Nothofagus* based on species level phylogenies and forest associations of long-branched taxa.

INTRODUCTION

Though my work as a systematist is geared to develop classifications, build keys, and provide monographs that collate natural history and taxonomic data, most of the contributors and readers of this volume may be chiefly interested in the ecology of dead wood insects. I believe that the time is ripe for ecologists and systematists to build a common research program and it may be useful to introduce some of the readers to what can happen in the field of ecological phylogenetics. Moreover, it may help some ecologists to appreciate that taxonomists are not just folks who are interested in building collections, eager to obtain a few specimens in exchange for a service identification, but are scientists keen to place their knowledge about natural history in a broader scientific context.

The insect order Coleoptera is one of the most important taxa associated with dead wood (Grove 2002). It is the largest group of described organisms and beetles occupy almost every niche available in dead wood (and outside of it). Because of their immense diversity, microhabitat associations and behaviors, beetles are popular subjects for ecological studies. But what about their evolution? How did modern saproxylic communities come into existence? In this essay I report on phylogenetic work in progress and discuss the evolution of saproxylic beetles at deeper evolutionary time scales. First, I briefly review data that indicate that the earliest beetles may have been saproxylic. Then I focus on two phylogenetic questions about saproxylic beetles in New Zealand: (1) are New Zealand taxa basal with respect to other members of their clade, and (2) do they have longer branches compared to their sister taxa located in other areas? Both questions relate to the uniqueness of beetle faunas in the geologically diverse and geographically isolated archipelago of New Zealand.

ANCIENT SAPROXYLIC BEETLES

Beetles are holometabolous insects defined by a suite of adult synapomorphies that include hardened forewings or elytra that enclose the abdomen and flight wings while resting. These features are thought to be characters that form part of an adaptive complex that led to the extraordinary number of beetle species that exists today. There are four suborders, Archostemata, Adephaga, Polyphaga, and Myxophaga. The first three have many saproxylic species, and the fourth may do so (Löbl 1995). The relationships among the four suborders are controversial (see reviews in Lawrence 1999, Kukalová-Peck and Lawrence 2004, Leschen and Beutel 2004) with many studies supporting Archostemata as sister taxon to the other suborders (compare Beutel and Hass 2000 to Kukalová-Peck and Lawrence 1993, 2004). The Archostemata have a number of primitive characteristics (plesiomorphies), and the common belief that they are a primitive group in Coleoptera is matched by the fossil record. The first true beetles are Archostemata recorded from the early Permian (265 my) and placed in the family Tshekardocoleidae, a short-lived family ranging from the early Permian to early Triassic (Ponomarenko 1969, 2002). But the Archostemata, as defined by Ponomerenko (2002), may be paraphyletic (see Kukalová-Peck and Lawrence 2004) and some of its members, including Tshekardocoleidae, may be placed separately in the order Protocoleoptera.

Part of the phylogenetic debate surrounding the ordinal phylogeny of beetles is the presence of many derived characteristics in Archostemata (Lawrence 1999), a group that has undergone considerable radiation (even though it is rather depauperate at present). The suborder includes rostrate forms from the Triassic (Obrieniidae was described by Zherikhin and Gratshev (1993) as belonging among the weevils (Polyphaga), but were later transferred to Archostemata (Zherikhin 2002)), and unusual life histories, including thelytokous development with viviparous, larviform females in the family Micromalthidae (Pollock and Normark 2002).

Nevertheless, the antiquity of Archostemata is unmatched by any other beetle group, with extant genera dating back to the early Jurassic (*Omma* Newman and *Tetraphalerus* Waterhouse; Zherikhin 2002). At the Permian dawn of Coleoptera,

---

[1] Richard A.B. Leschen, New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

conifers were on the rise while the first ginkgos and cycads emerged, and so Ponomorenko (1969) and others (Crowson 1975, Kirejtshuk 2003) speculate that the early Archostemata had xylomycetophagous larvae, based on modern feeding habits. Though there are clear indications of ancient wood boring in fossil wood (Weaver and others 1997) that may have been caused by beetles, trace and fecal fossils are not affirmative (Labandeira 1998), and differentiating between species that feed on decayed or live wood (Zherikhin 2002) is problematic. Meanwhile, the most primitive groups of extant beetles have mouthparts that are associated with feeding on materials such as microfungi and algae (Crowson 1981, Lawrence 1989), and this type of microphagy (Betz and others 2003, Leschen 1993) may have been a primitive feeding mechanism. The presence of microphagous feeding mechanisms suggests that the diets of ancient beetles were not strictly wood feeding and beetles may have occurred in any decaying habitats that promote fungal growth (Personal communication. 2005. John F. Lawrence, Systematist, CSIRO Entomology, GPO Box 1700, Canberra, ACT, 2601, Australia). Because of the rise of conifers with their cork-cambium layer that is easily separated from heartwood after death, it is quite likely that the subcortical situation may have been one of the microhabitats that ancient beetles first inhabited (Crowson 1984, Ponomorenko 2002).

ANCIENT PHYLOGENETIC PATTERNS IN NEW ZEALAND

One way to gain an appreciation of the antiquity of saproxylic beetles is to study their history in New Zealand, an ancient land with an interesting mix of old endemic species and those that have colonized more recently. There are approximately 5000 described New Zealand beetle species (Klimaszewski and Watt 1997), though there may be up to 10,000 species in total, which are placed into 86 families (Leschen and others 2003): 58 of the families have species associated with dead wood. The total numbers of species rival the number for Britain (just over 4000 species), a country of similar area. But New Zealand's location and history are strikingly different from Britain's (and its fauna is too!).

New Zealand is an island archipelago in the southwestern Pacific, chiefly comprised of two main islands that are presently positioned astride the Australian and Pacific plates. Active tectonism has produced a diverse and complex landscape (Suggate and others 1978). Isolation from Gondwana began around 82 million years ago when New Zealand was separated from Australia by the development of the Tasman Basin (Cooper and Millener 1993) and the rifting of the New Zealand landmass to its present eastward location. By the Oligocene period (c. 35 my) most of New Zealand was submerged. Later, plate collision resulted in a mountain building phase which originated in the Miocene and continues to present day. The result is that the South Island is dominated by the north-south trending Southern Alps, which rise to elevations of nearly 4000 m and extend around 500 km. To the east in the rain shadow of the Southern Alps, the landscape consists of lowlands and basins. The southwest end of the South Island contains extensive fjiordlands while the northeast of the South Island terminates in sounds. The South Island is separated from the North Island by the narrow Cook Strait which was formed around 0.5 my ago (Lewis and Carter 1994) and exists only during periods of high sea-levels. During periods of glaciation and low sealevels the islands are linked. The North Island landscape, by contrast, is a result of the offshore subduction that creates north-south trending axial ranges that absorb plate compression, a volcanic arc, with lines of active volcanoes and a backarc region that is being thinned and is subsiding. The elevations of North Island ranges are lower than the Southern Alps. The north terminates in a long peninsula pointing towards New Caledonia, while the broad middle portion is dominated by East and West Capes, making the North Island appearing spindle-shaped.

The geological history of New Zealand, and its contrasting landforms, make it an ideal model system for biogeographic studies, so it is no surprise that the discipline of panbiogeography has its most fervent supporters here (Craw and others 1999, Hull 1988). New Zealand is home to a unique fauna (like the panbiogeographers). Ratite birds have undergone major extinction in New Zealand, and the once diverse group is now reduced to three species of kiwi that at are the delight of conservationists, lay people, and scientists. Because of the presence of these ratite birds, and of tuatara, tailed-frogs (Leiopelmatidae), and primitive plants like kauri (*Agathis australis* (D. Don) Lindl. (Araucariaceae)) and whisk-ferns, most biologists consider New Zealand a refuge for ancient lineages that evolved prior to the fragmentation of Gondwana. Likewise, many of the beetles may be relictual and should be of interest from an evolutionary and ecological (conservation) perspective.

So, is the dead wood beetle fauna relictual? One way to test this question is to determine the phylogenetic position of New Zealand beetles in reconstructed phylogenies (cladograms) containing taxa from other areas. Relatively basal (primitive) taxa will be located near the root of trees, while derived taxa will be located in higher branches. In figure 1 clade AB is located at the base and is considered primitive relative to, say, taxon E, which is more derived. Also, do New Zealand

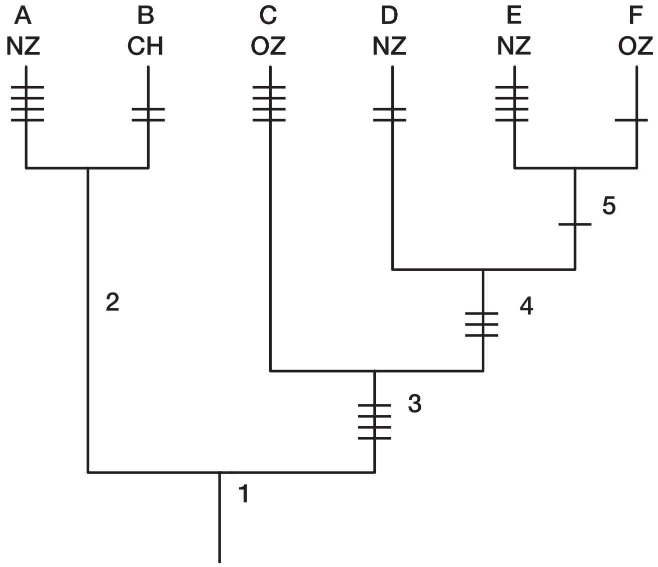


Figure 1—Five-taxon area-cladogram showing distribution of taxa A-F. The bars across each branch indicate character changes (OZ = Australia, CH = Chile, NZ = New Zealand).

taxa have longer branches than their immediate sister taxa? Between the sister pair A and B (fig. 1), A has a longer branch than B. Similarly, taxon C has a longer branch than DEF in this pairwise comparison. The power of the pairwise comparison is the assumption that the time of divergence in a common ancestor calibrates the relative rates of evolution between two sister taxa (Cracraft 1985; Eldredge and Cracraft 1980; Mitter and others 1988; Wiley 1979, 1981). A longer branch will indicate a higher rate of anagenesis compared to that present in a short-branched sister taxon.

METHODS

Addressing questions about phylogenetic location and branch length requires cladograms that include terminal taxa present in and outside of New Zealand; but there are few of these trees available. In fact, monographs and phylogenies are desperately needed to understand the ecology and systematics of all Coleoptera, an issue that limits anyone working on the New Zealand saproxylic fauna. Therefore, I include in the data set any phylogeny that includes saproxylic, leaf litter, and fungus inhabiting beetles (including sooty mould beetles in the endemic families Cyclaxyridae and Agapythidae). These other habitats may be viewed as natural extensions of dead wood since leaf litter will include coarse woody debris of small diameters and fungi of all sorts. A total of 13 phylogenies were used in this study (table 1).

Phylogenetic position in a cladogram is calculated by measuring Relative Phylogenetic Position (RPP) which is the ratio of the node number of the taxon/longest path in cladogram beginning at the root of the tree. An RPP < 0.50 is considered relatively basal, while an RPP ≥ 0.50 is relatively derived. For example, in figure 1 Taxon A is relatively basal with an RPP of 0.25 (1/4) while Taxon E is relatively derived with an RPP of 1.0 (4/4). Branch length is the number of character changes that have occurred since a taxon diverged from its nearest relative. The branch lengths for pairs of two sister taxa with one present in New Zealand and the other occurring elsewhere are compared (these are termed pairwise comparisons by Mitter and others 1988). If the branch length of the New Zealand taxon is longer than its sister taxon, then this is indicative of relatively high rate of evolution compared to its sister taxon.

Measuring these variables, though, is not straightforward. In situations when characters were not mapped onto phylogenies (Lawrence 1994), or onto terminal taxa (Ashe 1992, Hall 1999), branch length was not determined. Where multiple cladograms were published, the one selected as the preferred or reference tree in the original publication was used for this analysis. Polytomies were resolved only when they were located at the base of the tree (Lawrence 1994) or included New Zealand taxa (Pollock 1995). For cases where there is a monophyletic group of New Zealand taxa, branch length and RPP is scored at the basal node (Thayer 1985). If two or more New Zealand taxa are nearest neighbors, then RPP is taken at the basal branch (branch 4, fig. 1) while branch length is measured for the most derived taxon (branch 5, fig. 1), analogous to the situation in biogeography where a sister taxon has become extinct (Paterson and others 1999). This situation occurs in Scaphisomatini (Leschen and Löbl 2005), pilipalpine Pyrochroidae (Pollock 1995, when the trichotomy is resolved), and Cryptophagidae (Leschen 1996). In the single comparison in pilipalines and the one comparison for cryptosomatulini Cryptophagidae, there are three nearest neighbors (the two taxa used for each of the measurements are listed in table 1).

Nothofagus and podocarp-broadleaf are the two principal forest communities in New Zealand and these forest associations are listed in table 1. Association was based on information contained in original publications and specimens housed in the New Zealand Arthropod Collection, Auckland.

RESULTS

All of 13 phylogenies available for this study were morphology-based (table 1) and included 19 values for RPP and 15 pairwise comparisons for branch length. Ten of 19 (53 percent) taxa were located in basal portions of the trees, and four of these are distributed in podocarp-broadleaf forests, one in *Nothofagus*, and five in both forests. Nine of the 15 (60 percent) pairwise comparisons of branch length had longer branches compared to sister taxa, and three of these taxa are distributed in podocarp-broadleaf forests, one in *Nothofagus*, and five in both forest types. Five taxa are basal and have long branches (*Stylogymnusa*, *Notonewtonia, Agapytho*, *Cryptodacne,* and *Loberonotha*), and of these, only *Agapytho* is exclusively found in *Nothofagus.*

DISCUSSION

50 percent of the New Zealand saproxylic taxa were basal and more than half of the taxa had longer branches compared to sister taxa occurring elsewhere. The basal taxa may be relictual and I suggest that they may have had ancestors in New Zealand dating back to 82 my. Whether this pattern is present in other groups of beetles requires the analysis of cladograms for intertidal aleocharine staphylinids (Ahn 2001, Leschen and others 2002), phytophagous weevils (Kuschel and Leschen 2003), and aquatic hydraenids (Beutel and Leschen 2005; Beutel and others 2003) not included in this study.

Determining the phylogenetic position of New Zealand taxa is related to a more comprehensive biogeographic question about the relationships among Earth's biota (Pollock 1995, Sanmartín and Ronquist 2004). A more intensive study of the biogeographic affinities of New Zealand biota will be pursued in a future study that will combine phylogenetic and fossil data for widespread lineages. What is enigmatic, though, is that some old Pangaean taxa, such as Archostemata, are absent from New Zealand, which suggests that either they were absent here at the time of the fragmentation of Gondwana, or have gone extinct afterwards. One massive extinction event may have occurred in New Zealand during the Oligocene (c. 30 my) marine transgression where there is evidence of a considerable reduction in the land area. Cooper and Cooper (1995) considered this submergence a crisis that created bottle-necks in populations that led to widespread extinctions — some even believe that the entire country was completely submerged (Macphail 1997, Pole 1994). But the presence of ancient beetle lineages in New Zealand provides strong evidence against the hypothesis of total submergence.

Table 1—Taxa examined for position and branch length with their forest associations. For each study referenced, the number of terminal taxa and taxonomic level, and number of characters used are provided

Taxon	RPP	BL	Forest type	Reference
Ptiliidae				
Nellosana Johnson (3 spp.)	0.25	—	P	Hall 1999 (28 genera/48)
Leiodidae				
Catopsilius Sharp (2 spp.)	0.6	Same	P	Leschen and Newton unpubl. (Neopelatopini, 10 genera/25)
n. gen. (7+ spp.)	1.0	Lower	B	“ ”
Staphylinidae				
Metacorneolabium Steel (7 spp.)	0.1	Lower	B	Thayer 1985 (Omaliinae, 22 spp./34)
Stylogymnusa Hammond (1 sp.)	0.1	Higher	P	Ahn and Ashe 2004 (Aleocharinae, 57 spp./99)
Austrasilida Ashe (1 sp.)	0.6	—	B	Ashe 1992 (Aleocharinae, 26 spp/34)
Brachynopus Broun (2 spp.)	0.3	Lower	B	Leschen and Löbl 2005 (Scaphisomatini, 45 gen/110)
“B.” apicellum (Broun)	—	Higher	P	
“B.” rufa Broun	0.4	—	P	“ ”
Notonewtonia Leschen and Löbl (2 spp.)	0.4	Higher	B[a]	“ ”
Euderia Broun (1 spp.)	0.5	—	N	Philips (2000) (Anobiidae, 34 genera/102)
Erotylidae				
Cryptodacne Sharp (7 spp.)	0.2	Higher	B[b]	Wegrzynowicz 2002 (Erotylinae, 30 gen./85)
Loberonotha Sen Gupta and Crowson (1 sp.)	0.2	Higher	B	Leschen 2003 (Erotylidae, 57 gene/120)
Cryptophagidae				
Ostreacryptus Leschen (1 sp.)[c]	0.4	—	P	Leschen 1996 (55 genera/113)
Picrotus Sharp (2 spp.)	—	Same	B[d]	Leschen 1996 (55 genera/113)
Paratomaria Leschen (1 sp.)	0.6	—	P	Leschen 1996 (55 genera/113)
Salltius Broun (1 sp.)	—	Higher	P	Leschen 1996 (55 genera/113)
Agapythidae				
Agapytho Broun (1 sp.)	0.4	Higher	N	Leschen and others 2005 (36 genera/99)
Priasilphidae				
Priasilpha Broun (7 spp.)	0.5	Lower	B[b]	Leschen and others 2005 (36 genera/99)
Cyclaxyridae				
Cyclaxyra Broun (3 spp.)	0.9	Higher	B[d]	Leschen and others 2005 (36 genera/99)
Ulodidae				
Brouniphylax Strand + *Syrphetodes* Pascoe (15+ spp)	0.8	—	B	Lawrence 1994 (Zopheridae groups, 20 genera/31)
Pyrochroidae				
Exocalopus Broun (1 sp.)	—	Higher	B	Pollock 1995 (Pilipalpinae, 15 genera/30)
Techmessa Bates (2 spp.)	0.7	—	B	Pollock 1995 (Pilipalpinae, 15 genera/30)

RPP = Relative Phylogenetic Position; BL = branch length; B = both forest types, N = *Nothofagus*, P = podocarp-broadleaf.

[a] Most species or specimens present in podocarp-broadleaf forests.

[b] Primitive species in these groups are associated with podocarp-broadleaf forests (Skelley and Leschen, submitted in 2005; Leschen and Michaux, in press).

[c] Listed as New Zealand genus 2 and named later (Leschen 2001).

[d] Most species or specimens present in *Nothofagus* forests.

Meanwhile, the pattern in beetles is testimony to a complex geological and climatic history that influenced the biota of New Zealand since the break-up of Gondwana. Over half of the New Zealand taxa have longer branches than those of their sister taxa. Rate of anagensis, or the accumulation of character changes within a single branch, has many causes. Assuming no extinction and a constant rate of speciation with random change, I suggest that the high number of long branches present in New Zealand taxa may be indicative of lineages that persisted over time during changing vegetative landscapes, and that these groups had to adapt to periodic introductions (and losses) of new fungal and dead wood resources.

The vegetative history of New Zealand is a story of ever-changing communities associated with loss and gains of many taxa throughout the fossil record (Lee and others 2001). Losses mark each epoch, but none as great as the losses occurring during the Miocene with the extinction of 23 genera. It is also remarkable that the extinction of *Acacia*, *Eucalyptus* and other genera in New Zealand occurred as recently as the Pleistocene. Coupled with the Oligocene bottleneck, these community changes over time must have significantly influenced the evolution of saproxylic beetles. Therefore, long branches may have arisen in lineages as an adaptive response to plant community changes that facilitated resource shifts, especially in saproxylic and fungus beetles that would have had to track dramatic changes in the composition of coarse woody debris. Evidence for resource shifting is that 13 taxa listed in table 1 are associated with both *Nothofagus* and podocarp-broadleaf forests. This hypothesis predicts that saproxylic beetles may be associated with different types of coarse woody debris, and likewise, polyphagy should dominate in phytophagous and mycophagous insects as a result of resource shifting.

One line of evidence against the “resource shift hypothesis” is that beetle and plant communities may be stable in ecological time and have maintained cohesion since the last glacial maximum. Based on new data from the fossil record, communities respond to climate change and are influenced by changes in temperature (Marra 2003a, 2003b; Marra and Leschen 2004) resulting in local extinctions while species continue to survive (Marra, Maureen. [Name of manuscript unknown]. Manuscript in preparation. Author can be reached at: Landcare Research, Private Bag 3127, Hamilton, New Zealand.) (Marra, Maureen; Leschen, Richard A.B. [Manuscript in preparation]. Fossil beetles as indicators of climate change and geological history of New Zealand. Maureen Marra can be reached at: Landcare Research, Private Bag 3127, Hamilton, New Zealand). However, fossil sites are limited to a few Quaternary locations and older sites need to be examined to reconstruct older fossil communities.

The assumptions for the resource shift hypothesis may be too simplistic. For example, one cause for long-branches is the extinction of sister taxa, and this too may result in asymmetrical (unbalanced) trees (Guyer and Slowinski 1993, Heard and Mooers 2002). It would be important to examine the symmetry of phylogenetic trees of saproxylic beetles to determine if tree shape may relate to extinction events such as the Oligocene drowning rather than to resource tracking.

There is also reason to doubt that long branches and basal positions are coupled (see table 1). For example, the New Zealand kauri is the most primitive member of *Agathis,* a genus that has fossils in New Zealand dating back to the Cretaceous, and has a relatively short branch based on *rbc*L sequences (Stöckler and others 2002). The biogeographic story for plants, however, is much different from that of animals (Sanmartín and Ronquist 2004), with a greater proportion of dispersal than vicariance. It is also expected that the history of different lineages of beetles may differ, which is reflected in the asymmetry between number of basal taxa and those having higher branch lengths. Additional data from molecular clocks and fossils to determine evolutionary rates alongside natural history studies would provide tests of the resource shift hypothesis by providing divergence dates and ages for extant saproxylic taxa.

Determining ancestral community associations for New Zealand saproxylic beetles is hampered by the lack of species level phylogenies and detailed information on their geographic distributions. Thayer (1985) published the only species level phylogeny for New Zealand saproxylic beetles (*Metacorneolabium,* Staphylinidae). Otherwise, there are unpublished cladograms for species of New Zealand *Baeocera* (scaphisomatine Staphylinidae) (Leschen, Richard A.B. Unpublished, phylogeny. Leschen, author of this paper), and the endemic genera *Cryptodacne* (Erotylidae) (Skelley and Leschen 2006, submitted) and *Priasilpha* (Priasilphidae) (Leschen and Michaux 2005). When forest associations are optimized onto these cladograms, podocarp-broadleaf associations are primitive for *Baeocera*, *Cryptodacne*, and *Priasilpha*, while *Nothofagus* may be primitive for *Metacorneolabium*.

In basal and long-branched taxa that are found in both podocarp-broadleaf and *Nothofagus* forests, most of the species and/or specimens are found in association with podocarp-broadleaf forests (table 1). These data mirrors the patterns seen in the species phylogenies that podocarp-broadleaf forest associations may be more primitive than the *Nothofagus* associations. This pattern seems reasonable because of the more recent arrival of *Nothofagus* (Hill 2001, Macphail and others 1994) compared to that of podocarps in New Zealand. Even though Mill (2003) believes that the recent New Zealand podocarps represent a secondary radiation, these forests could have been continuously present since the Cretaceous. It is also possible that more derived species occur in areas dominated by *Nothofagus*, only because many of these areas were recently glaciated (Porter 1975, Trewick and Wallis 2001) and not because of a strict association with forest type.

Classifying forest types into two forest types may be problematic, particularly because the podocarp-broadleaf class includes within it the *Metrosideros* forests of Auckland Island in the New Zealand subantarctic (Campbell Plateau). Optional character state treatments could illuminate different patterns of character evolution (Leschen 1999) and when the podocarp-broadleaf class is separated into two divisions (*Metrosideros* versus podocarp-broadleaf) this creates a more complex character-state reconstruction in *Priasilpha*. The ancestral states in *Priasilpha* are made ambiguous by having a mixture of podocarp-broadleaf, *Metrosideros*, and *Nothofagus* forest associations (Leschen and Michaux 2005). One of the most primitive *Priasilpha* species occurs in the subantarctic *Metrosideros* forests, where it is sympatric with the basal species *Stylogymnusa antarctica* Hammond (table 1). In contrast to *Nothofagus*, which is recorded from New Zealand in the late Cretaceous (Lee and others 200), fossil pollen (late Paleocene; Mildenhall, 1980) and macrofossils (early Miocene, Pole 1991) of *Metrosideros* are more recent, and members of this genus tend to be climbers in New Zealand. So, it is likely that the basal position of Auckland Island taxa are related more to the age of the Campbell Plateau landmass (Michaux and Leschen 2005) than to the forest type.

The preliminary analysis here is work in progress and indeed there are several biases and problems with it. The small number of available phylogenies, all of which are morphology-based, which by their nature are composed of fewer character changes compared to molecular data, may bias the results. In fact if other groups were included in this study to broaden the questions to include all lineages of terrestrial biota, the results might well change. Also different taxonomic levels were compared across taxa (usually genus-level) and it would be valuable to use trees based on species (but this is a problem when dealing with insect diversity!). On-going work on species- and population-level phylogenies for various mycophagous beetles (e.g., Leiodidae, scaphidiine staphylinids, Nitidulidae) will help to determine ancestral forest associations. These data coupled with species level phylogenies of plant feeding taxa, such as Molytini weevils (Craw 1999), will help to reconstruct community level patterns through evolutionary and ecological time. A test that examines probability of position, character changes, and branch length in a theoretical tree space will also provide the statistical rigor needed to test the patterns illustrated here.

PROSPECTUS FOR ECOLOGICAL AND PHYLOGENETIC STUDIES ON SAPROXYLIC INSECTS

Many ecosystems in New Zealand and elsewhere are under threat, and there are species that have become extinct, or will do so very soon. In New Zealand the fauna has been reduced by human impact (Worthy and Holdaway 2002), including the accidental introductions of rodents (Holdaway 1996) and other predators that are capable of wiping out the larger species of invertebrates that are not lucky enough to have defensive secretions or find refuge on predator-free islands (e.g., Leschen and Rhode 2002). Then there is the accidental introduction of ants (Harris and Berry 2001) that will affect even the smallest arthropod taxa. So there is a need for scientists from all disciplines to combine their skills to address biological questions at all levels before species losses are further accentuated by climate change.

Much has been gained by the incorporation of phylogenetic data into ecological programs (Brooks and McLennan 1993, Gorman 1993) and there has been a recent upsurge in research on populations and species using molecules, even resulting in specialized publications such as the journal *Molecular Ecology*. While some of the papers in *Molecular Ecology* may be organismal, much of the autecological work does little for community ecology and the understanding of natural history for many groups, especially those taxa like dead wood insects that are not easily (and repeatedly) sampled for DNA studies. *Phylogenetic assembly* is a relatively new and promising field that incorporates knowledge of the community in question and the phylogenetic relationships of the co-existing organisms (see Webb and others 2002 for application and methods). Among several questions that can be addressed about communities, two questions, as covered by Webb and others (2002), are paramount: Is the distribution of species among habitats in a community nonrandom with respect to phylogeny and how are niche differences in communities arrayed on a phylogeny? Several lines of data are needed: a list of species for the local community, their geographic distributions, ecological character data, and phylogenetic data for each of the species. Obviously, a list of insects would be easier to obtain than phylogenies for each species, and in hyperdiverse areas such as tropical rainforests, even a list may be difficult without a team of collaborators. Nevertheless, the protocols of this research program to determine the origin and structure of saproxylic insect communities has the potential to elicit input from biologists of different disciplines and one can imagine the direct applications to insect conservation and management.

ACKNOWLEDGMENTS

I thank Simon Grove and Jim Hanula for the invitation to participate in this symposium, Sven Christian Lipschitz and Ragavendra Ghadakar for theoretical advice, and Thomas Buckley, Robert Hoare, Maureen Marra and John Lawrence for reviews of the manuscript. This work was supported in part by FRST (contract C09X0002).

LITERATURE CITED

Ahn, K.-J. 2001. Phylogenetic relationships of the intertidal genus *Halorhadinus* Sawada and key to the genera of the Liparocephalini (Coleoptera: Staphylinidae: Aleocharinae). Entomologica Scandinavica. 32: 123-132.

Ahn, K.-J.; Ashe, J.S. 2004. Phylogeny of the Myllaenini and related taxa (Coleoptera: Staphylinidae: Aleocharinae). Cladistics. 20: 123-138.

Ashe, J.S. 1992. Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae). University of Kansas Science Bulletin 54: 335-406.

Ashe, J.S. 2000. Mouthpart structure of *Stylogymnusa subantarctica* Hammond, 1975 (Coleoptera: Staphylinidae: Aleocharinae) with a reanalysis of the phylogenetic position of the genus. Zoological Journal of the Linnean Society. 130: 471-498.

Betz, O.; Thayer, M.K.; Newton, A.F. 2003. Comparative morphology and evolutionary pathways of the mouthparts in spore-feeding Staphylinoidea (Coleoptera). Acta Zoologica (Stockholm). 84: 179-238.

Beutel, R.G.; Anton, E.; Jäch, M.A. 2003. On the evolution of adult head structures and the phylogeny of Hydraenidae (Coleoptera, Staphyliniformia). Journal of Zoological Systematics and Evolutionary Research. 41: 256-275.

Beutel, R.G.; Haas, F. 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics. 16: 103-141.

Beutel, R.G.; Leschen, R.A.B. 2005. Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. Systematic Entomology. 30: 510-548.

Brooks, D.R.; McLennan, D.A. 1993. Historical ecology: examining phylogenetic components of community evolution. In: Ricklefs, R.E.; Schluter, D., eds. Species diversity in ecological communities: historical and geographic perspectives. Chicago, IL: University of Chicago Press: 267-280.

Cooper, A.; Cooper, R.A. 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. Proceedings of the Royal Society of London (ser. B). 261: 293-302.

Cooper, R.A.; Millener, P.R. 1993. The New Zealand biota: historical background and new research. Trends in Ecology and Evolution. 8: 429-433.

Cracraft, J. 1985. Biological diversification and its causes. Annals of the Missouri Botanical Garden. 72: 794-822.

Craw, R.C. 1999. Molytini (Insecta: Coleoptera: Curculionidae: Molytinae). Fauna of New Zealand 39. Lincoln, NZ: Manaaki Whenua Press. 68 p.

Craw, R.C.; Grehan, J.R.; Heads, M.J. 1999. Panbiogeography: tracking the history of life. New York, NY: Oxford University Press. 229 p.

Crowson, R.A. 1975. The evolutionary history of Coleoptera, as documented by fossil and comparative evidence. Atti del X Congresso Nazionale Italiano di Entomologia, Sassari 20-25 Maggio 1974, Firenze: 47-90.

Crowson, R.A. 1981. The biology of the Coleoptera. London: Academic Press. 802 p.

Eldredge, N.; Cracraft, J. 1980. Phylogenetic patterns and the evolutionary process. Method and Theory in Comparative Biology. New York, NY: Columbia University Press. 349 p.

Gorman, O.T. 1993. Evolutionary ecology and historical ecology: assembly, structure, and organization of stream fish communities. In: R.L. Mayden, ed. Systematics, historical ecology, and North American fresh water fishes. Stanford, CA: Stanford University Press: 659-688.

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

Guyer, C.; Slowinski, J.B. 1993. Adaptive radiation and the topology of large phylogenies. Evolution. 47: 253-263.

Hall, W.E. 1999. Generic revision of the tribe Nanosellini (Coleoptera: Ptiliidae: Ptiliinae). Transactions of the American Entomological Society. 125: 39-126.

Harris, R.J.; Berry, J.A. 2001. Confirmation of the establishment of three adventive ants (Hymenoptera: Formicidae) in New Zealand: *Cardiocondyla minutior* Forel, *Ponera leae* Forel, *Mayriella abstinens* Forel. New Zealand Entomologist. 24: 53-56.

Heard, S.B.; Mooers, A.Ø. 2002. Signatures of random and selective mass extinctions in phylogenetic tree balance. Systematic Biology. 6: 889-897.

Hill, R.S. 2001. Biogeography, evolution and palaeoecology of *Nothofagus* (Nothofagaceae): the contribution of the fossil record. Australian Journal of Botany. 49: 321-332.

Holdaway, R.N. 1996. Arrival of rats in New Zealand. Nature. 384: 225-226.

Hull, D. 1988. Science as a process: an evolutionary account of the social and conceptual development of science. Chicago, IL: University of Chicago Press. 586 p.

Kirejtshuk, A.G. 2003. Subcortical space as an environment for palaeoendemic and young groups of beetles, using mostly examples from sap-beetles (Nitidulidae, Coleoptera). In: Proceedings of the second pan-European conference on Saproxylic Beetles (Royal Holloway, University of London, June 2002), People's Trust for Endangered Species: 50-56.

Klimaszewski, J.; Watt, J.C. 1997. Coleoptera: family-group review and keys to identification. Fauna of New Zealand 37. Lincoln, NZ: Manaaki Whenua Press. 199 p.

Kukalová-Peck, J.; Lawrence, J.F. 1993. Evolution of the hind wings in Coleoptera. The Canadian Entomologist. 135: 181-258.

Kukalová-Peck, J.; Lawrence, J.F. 2004. Use of hind wing characters in assessing relationships among Coleopteran suborders and major Endoneopteran lineages. European Journal of Entomology. 101: 95-144.

Kuschel, G.; Leschen, R.A.B. 2003. Phylogenetic relationships of the Belinae. In: Kuschel, G. Nemonychidae, Belidae, Brentidae (Insecta: Coleoptera: Curculionoidea). Lincoln, NZ: Fauna of New Zealand 45. Lincoln, NZ: Manaaki Whenua Press: 48-55.

Labandeira, C.C. 1998. Early history of arthropod and vascular plant associations. Annual Review of Earth and Planetary Sciences. 26: 329-377.

Lawrence, J.F. 1989. Mycophagy in the Coleoptera: feeding strategies and morphological adaptations. In: Wilding, N.; Collins, M.; Hammond, P. M.; Webber, J. F., eds. Insect - Fungus Interactions. Royal Entomological Society Symposium (Series 14): 1-23.

Lawrence, J.F. 1994. The larva of *Sirrhas variegatus*, sp. nov., with notes on the Perimylopidae, Ulodidae (stat. nov.), Zopheridae and Chalcodryidae (Coleoptera: Tenebrionoidea). Invertebrate Taxonomy. 8: 329-349.

Lawrence, J.F. 1999. The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. Invertebrate Taxonomy. 13: 369-390.

Lee, D.E.; Lee, W.G.; Mortimer, N. 2001. Where have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. Australian Journal of Botany. 49: 341-356.

Leschen, R.A.B. 1993. Evolutionary patterns of feeding in selected Staphylinoidea (Coleoptera): shifts among food textures. In: Schaefer, C.W.; Leschen, R.A.B., eds. Functional Morphology of Insect Feeding. Proceedings, Thomas Say Publications: 59-104.

Leschen, R.A.B. 1996. Phylogeny and revision of the genera of Cryptophagidae (Coleoptera: Cucujoidea). Kansas Science Bulletin. 55: 549-634.

Leschen, R.A.B. 1999. Origins of symbiosis: phylogenetic patterns of social insect inquilinism in Cryptophagidae (Coleoptera: Cucujoidea). In: Byers, G. W.; Hagen, R.H.; Brooks, R. W., eds. Entomological Contributions in Memory of Byron Alexander University of Kansas Natural History Museum Special Publication 24: 85-101.

Leschen, R.A.B. 2001. A new genus of Cryptosomatulini (Coleoptera: Cryptophaginae). New Zealand Entomologist. 24: 7-9.

Leschen, R.A.B. 2003. Erotylidae (Insecta: Coleoptera: Cucujoidea): phylogeny and review. Fauna of New Zealand 47. Lincoln, NZ: Manaaki Whenua Press. 108 p.

Leschen, R.A.B.; Beutel, R.G. 2004. Ocellar atavism in Coleoptera: plesiomorphy or apomorphy? Journal of Zoological Systematics and Evolutionary Research. 42: 63-69.

Leschen, R.A.B.; Bullians, M.; Michaux, B.; Ahn, K.-J. 2002. *Baeostethus chiltoni*, a subantarctic liparocephaline (Coleoptera: Staphylinidae: Aleocharinae): a pangean relic or recent immigrant? Journal of the Royal Society of New Zealand. 32: 189-201.

Leschen, R.A.B.; Lawrence, J.F.; Kuschel, G. [and others]. 2003. Coleoptera genera of New Zealand. New Zealand Entomologist. 26: 15-28.

Leschen, R.A.B.; Lawrence, J.F.; Slipinski, A. 2005. Classification of basal Cucujoidea (Coleoptera: Polyphaga): cladistic analysis, keys, and review of new families. Invertebrate Systematics 19: 17-73.

Leschen, R.A.B.; Löbl, I. 2005. Phylogeny and classification of Scaphisomatini (Staphylinidae: Scaphidiinae) with notes on mycophagy, termitophily, and functional morphology. Coleopterists Society Monographs 3: 1-63.

Leschen, R.A.B.; Michaux, B. [In press]. Phylogeny and evolution of New Zealand Priasilphidae (Coleoptera). New Zealand Journal of Entomology.

Leschen, R.A.B.; Rhode, B.E. 2002. A new genus and species of large extinct Ulodidae (Coleoptera) from New Zealand. New Zealand Entomologist. 25: 57-64.

Lewis, K.; Carter, L. 1994. When and how did Cook Strait form? In: van der Ligen, G.J.; Swanson, K.; Muir, R., eds. Evolution of the Tasman Sea Basin. Rotterdam, Netherlands: A. A. Balkema Publishers: 119-137.

Löbl, I. 1995. New species of terrestrial *Microsporus* from the Himalaya (Coleoptera: Microsporidae). Entomolgische Blätter. 91: 129-138.

Macphail, M.K. 1997. Comment on M. Pole (1994): the New Zealand flora - entirely long-distance dispersal? Journal of Biogeography. 24: 113-117.

Macphail, M.K.; Alley, N.; Truswell, E.M.; Sluiter, I.R.K. 1994. Early Tertiary vegetation: evidence from spores and pollen. In: Hill, R.S., ed. History of the Australian Vegetation: Cretaceous to Recent. Cambridge, MA: Cambridge University Press: 189-262.

Marra, M.J. 2003a. A description and interpretation of a fossil beetles assemblage from marine isotope stage 6 from Banks Peninsula, New Zealand. New Zealand Journal of Geology and Geophysics. 46: 523-528.

Marra, M.J. 2003b. A last interglacial beetle fauna from New Zealand. Quaternary Research. 59: 122-131.

Marra, M.J.; Leschen, R.A.B. 2004. Late Quaternary paleoecology from fossil beetle communities in the Awatere Valley, South Island, New Zealand. Journal of Biogeography. 31: 571-586.

Michaux, B.; Leschen, R.A.B. 2005. East meets West: biogeology of the Campbell Plateau. Biological Journal of the Linnaean Society 86: 95-115.

Mildenhall, D.C. 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. Palaeogeography, Palaeoclimatology, Palaeoecology. 31: 197-233.

Mill, R.R. 2003. Towards a biogeogeaphy of the Podocarpaceae. Acta Horticulturae. 615: 137-147.

Mitter, C.; Farrell, B.D.; Wiegman, B. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? American Naturalist. 132: 107-128.

Paterson, A.M.; Palma, R.; Gray, R.D. 1999. How frequently do avian lice miss the boat? Systematic Biology. 48: 214-223.

Philips, T.K. 2000. A phylogenetic analysis of the New World Ptininae (Coleoptera: Bostrichoidea). Systematic Entomology. 25: 263-272.

Pole, M. 1991. The New Zealand flora - entirely long-distance dispersal? Journal of Biogeography. 21: 625-635.

Pollock, D.A. 1995. Classification, reconstructed phylogeny, and historical biogeography of Pilipalpinae (Coleoptera: Tenebrionoidea: Pyrochroidae). Invertebrate Taxonomy. 9: 563-708.

Pollock, D.A.; Normark, B.B. 2002. The life cycle of *Micromalthus debilis* (Coleoptera: Archostemata: Micromalthidae): historical review and evolutionary perspective. Journal of Zoological Systematics and Evolutionary Research. 40: 105-112.

Ponomarenko, A.G. 1969. Historical development of the Coleoptera - Archostemata. Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR. 125: 1-240.

Ponomarenko, A.G. 2002. Order Coleoptera, the beetles. In: Rasnitsyn A.P.; Quicke D.L.J., eds. History of Insects. Dordrecht, Germany: Kluwer Academic Publishers: 164-183.

Porter, S.C. 1975. Glaciation limit in New Zealand's Southern Alps: arctic and alpine research. 7: 33-37.

Sanmartín, I.; Ronquist, F. 2004. Southern Hemisphere biogeography inferred by event-based models: plant vs. animal patterns. Systematic Biology. 53: 216-243.

Skelley, P.; Leschen, R.A.B. [Submitted in 2006]. Erotylidae (Insecta: Coleoptera: Staphylinidae): Taxonomy and biogeography. Fauna of New Zealand. Lincoln, New Zealand: Maanaki Whenua Press.

Stöckler, K.; Daniel, I.L.; Lockhart, P.J. 2002. New Zealand kauri (*Agathis australis* (D.Don) Lindl., Araucariaceae) survives Oligocene drowning. Systematic Biology. 51: 827-832.

Suggate, R.P.; Stevens, G.R.; Te Punga, M.T., eds. 1978. The geology of New Zealand. Wellington, NZ: Government Printer. 2 volumes, 820 p.

Thayer, M.K. 1985. Revision, phylogeny, and biogeography of the austral genus *Metacorneolabium* Steel (Coleoptera: Staphylinidae: Omaliinae). In: Ball, G. E., ed. Taxonomy, phylogeny, and zoogeography of beetles and ants. Series Entomologica 33. Dordrecht, Germany: W. Junk: 113-179.

Trewick, S.A.; Wallis, G.P. 2001. Bridging the "beech-gap": New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. Evolution. 55: 2170-2180.

Weaver, L.; McLoughlin, S.; Drinnan, A.N. 1997. Fossil woods from the Upper Permian Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica. Australian Geological Survey Organisation Journal. 16: 655-676.

Webb, C.O.; Ackerly. D.D.; McPeek, M.A.; Donoghue, M.J. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics. 33: 475-505.

Wegrzynowicz, P. 2002. Morphology, phylogeny and classification of the family Erotylidae based on adult characters (Coleoptera Cucujoidea). Genus. 13: 435-504.

Wiley, E.O. 1979. Cladograms and phylogenetic trees. Systematic Zoology. 28: 88-92.

Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. New York, NY: Wiley-Interscience. 439 p.

Worthy, T.H.; Holdaway, R.N. 2002. The lost world of the Moa. Bloomington, IN: Indiana University Press. 592 p.

Zherikhin, V.V.; Gratshev, V.G. 1993. Obrieniidae, fam. nov., the oldest Mesozoic weevils (Coleoptera, Curculionoidea). Paleontological Journal. 27: 50-69.

Zherikhin, V.V. 2002. Ecological history of terrestrial insects. In: Rasnitsyn A.P.; Quicke D.L.J., eds. History of Insects. Dordrecht, Germany: Kluwer Academic Publishers: 331-388.

AQUATIC WOOD — AN INSECT PERSPECTIVE

Peter S. Cranston and Brendan McKie[1]

Abstract—Immersed wood provides refugia and substrate for a diverse array of macroinvertebrates, and food for a more restricted genuinely xylophagous fauna. Worldwide, xylophages are found across aquatic insect orders, including Coleoptera, Diptera, Trichoptera and Plecoptera. Xylophages often are specialised, feeding on the wood surface or mining deep within. Many feed preferentially on wood of particular species or of a particular decay class. Some of the most specialised genuine wood miners occur among the Chironomidae, and the fauna is particularly rich in Australia. Recent discoveries of unusual midges in Australia and south-east Asia allow speculation about the evolution of immersed-wood mining by Chironomidae. Subfamily Orthocladiinae contains many unrelated taxa with larval mouthpart modifications associated with gouging wood. Wood-mining chironomines, in fewer groups, mostly lack morphological differentiation. However, several early-branching clades of both subfamilies show radiation (diversity), and the condition can be inferred as ancestral, potentially associated with differential historical survival from cataclysmic extinction events.

INTRODUCTION

Coarse woody debris (CWD) in aquatic habitats fulfills many important functions, including structuring of stream channels (Bilby 1984, Gippel 1995, Gippel and others 1996), enhancement of organic matter retention (Bilby and Likens 1980) and provision of substrate for life history activities of aquatic macroinvertebrates including attachment, feeding and oviposition (Anderson and others 1984, Andrus and others 1988, Harmon and others 1986, O'Connor 1991). Wood also provides an abundant but refractory source of carbon which worldwide is fed on by an array of specialized insects, including elmid coleopterans like *Lara avara* LeConte (North America) and *Notriolus* spp. and *Simsonia* spp. (Australia), the burrowing ephemeropteran *Povilla adjusta* Navas (Polymitarcidae, Africa), the trichopterans *Lype* (Psychomyiidae, Europe) and *Triplectides* (Leptoceridae, Australia), species of the dipteran *Lipsothrix* (Tipulidae, Holarctic) and the plecopteran, *Acruroperla* (Austroperildae, Australia). However, inventories of macroinvertebrates associated with CWD tend to be dominated by species belonging to non-gouging functional groups that may use the wood substrate stochastically (e.g., McKie and Cranston 2001). Indeed, as a generalization, larval insect taxa living internally within immersed wood are underestimated. Nevertheless, a summary of the stenophagous (narrowly restricted) xylophagous mining taxa in major groupings in well-studied regions can be presented (table 1).

Few of these taxa have been studied in detail, but it is apparent that many exhibit significant ecological specialisation. Preferences for different wood species and/or decay classes can reflect both palatability and complexity of surface sculpturing of the host wood (McKie and Cranston 1998, 2001). For example, conifer woods have notably high carbon/nitrogen ratios and large quantities of secondary chemical compounds,

Table 1—Species of stenophagous xylophagous mining insects known from USA, New Zealand, and Australia

	Central Europe[a]	Oregon[b]	USA[c]	New Zealand[d]	Australia[e]
Ephemeroptera	0	3	3	0	2
Plecoptera	2	3	3	1	4
Trichoptera	4	5	5	2	3+
Col: Elmidae	1	2	2	0	> 8
Col: Ptilodactylidae	0	1	1	0	1+
Dipt: Chironominae	1	1	2	1	6+
Dipt: Orthocladiinae	3	3	5	1	7+
Dipt: Tipulidae[f]	17	Yes	Yes	Yes	Yes

Col = Coleoptera; Dipt = Diptera: Chironomidae.

[a] Hoffmann and Hering (2000) (NB. taxa listed as "probably xylophageous").

[b, c] Anderson and others 1984, Cranston and Oliver 1988.

[d] Anderson 1982.

[e] McKie and Cranston 1998, 2001.

[f] Probably multiple species in all regions, though many may be semiaquatic.

---

[1] Peter S. Cranston, Department of Entomology, University of California, Davis, CA 95616; and Brendan McKie, Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

both of which may inhibit decay and reduce suitability as a food source for macroinvertebrates (Anderson and Sedell 1979, Aumen and others 1983). More complex and/or decayed wood surfaces potentially provide more surface area for feeding and more refugia, and facilitate mining (Collier and Halliday 2000, Magoulik 1998, McKie and Cranston 1998, Spänhoff and others 2000). In subalpine Australia, dominant xylophagous taxa, (primarily Coleoptera: Elmidae), have been shown to respond to wood species, favouring native *Eucalyptus* but avoiding the alien pine, *Pinus radiata* (McKie and Cranston 1998). Similarly, the north American shredders *Lara avara* (Coleoptera: Elmidae) and *Lipsothrix* (Diptera: Tipulidae) both favour alder over coniferous wood (Anderson and others 1978, Dudley and Anderson 1987). However, while the New Zealand caddisfly *Pycnocentria funerea* (Trichoptera: Conoesucidae) varies in its feeding efficiency (assessed via faecal production) on five different wood species, it shows no aversion to introduced conifers (Collier and Halliday 2000, Collier and others 2004). Different xylophages also exploit different components of wood, some gouging at the surface (e.g., McKie and Cranston 1998) and others mining within (e.g., Cranston and Hardwick 1996), and there is evidence for differential exploitation of wood at different stages of decay (Anderson and others 1984, Collier and Halliday 2000).

In contrast to community studies, there have been few autecological studies of these obligate wood-mining insects, despite the pioneering studies by Norm Anderson's team at Oregon State University in the 1980's, including those on *Lara avara* (Steedman and Anderson 1985) and *Lipsothrix* (Dudley and Anderson 1987) are rare examples. The many chironomid miners also are poorly known and only the life history of *Xylotopus par* Coquillett has been studied in detail (Kaufmann and King 1987, Kaufmann and others 1986). Many aspects of the ecology of wood-miners remains poorly understood, not least processes of cellulose digestion.

Our studies have revealed a diverse chironomid fauna associated with immersed wood, especially in Australia (table 1). Many of these species are true wood-miners, which are difficult to sample using standard methods and consequently may be little known to most freshwater biologists. True richness of this fauna can be assessed by quantitative intercepts of their floating pupal exuviae, whose presence demonstrates completion of the life cycle in nearby wood. This contribution reviews and synthesizes research on xylophagous chironomids. We include a summary of appropriate sampling techniques, discuss what can be discerned of their phylogenetic relationships, and speculate on some less-well understood aspects of their evolutionary ecology.

METHODS USED TO STUDY AQUATIC WOOD

The most commonly employed method for studying biodiversity of macroinvertebrates, associated with immersed wood is to examine recovered sticks of various sizes and wood classes (e.g., varying in density and degree of abrasion (which depends on wood species), immersion time, water velocity, etc.). Washing sticks into a bucket with appropriate sieving allows retention of macroinvertebrates dislodged from the surface. Increasing water pressure and scrubbing with a brush removes most organisms clinging to the surfaces including those secreted in crevices. However, rigorous survey for true miners requires visual inspection of the wood while stripping off surface layers, sometimes under a dissecting microscope. Wood that shows external evidence of internal activity, such as appropriate-sized bore-holes or accumulation of frass, is worthy of such close inspection. Examination of the gut contents can confirm wood-mining habits amongst larval Chironomidae. Gut contents, visible through the body wall especially after clearance for slide preparation, consists of comminuted wood fibres and little else (Cranston 2003, Cranston and Hardwick 1996, Cranston and Oliver 1988, McKie and Cranston 2001).

Making life history associations for wood-mining taxa is difficult, because many are stenophagous and die outside their natural larval habitat. Placing immersed wood into aerated aquaria can provide some estimation of species presence (by collecting emerged adults and/or pupal exuviae at the surface), but the technique is fraught with possible mis-association and general contamination. Physical examination of large quantities of wood, though tedious and often poorly rewarded, can reveal complete life histories through fortuitous discovery of larva/pupa associations, and of pupae containing pharate adult stages.

Serendipitous, qualitative studies are important in documentation of the diversity of wood-mining species, and with experience preferred types (species and decay state) of wood for mining can be identified. Naturally this varies geographically. For example, alder (*Alnus*) is especially preferred in the northern hemisphere and other riparian soft woods elsewhere. Generally softer woods sustain higher densities and diversity of wood-miners than do harder woods, although *Eucalyptus* is favoured by surface-gougers in Australia. Wood of differing decay states may yield different densities and/or assemblages of xylophages, and this often may be more important than the taxonomic affinity of the wood in determining what species are found (Personal observation. McKie and Cranston, authors of this paper) (Spänhoff and others 2000). Although succession among aquatic xylophages according to wood decay has been little studied; some evidence exists for its occurrence (e.g., Collier and Halliday 2000). Transitions from surface feeding to deeper mining taxa are likely as the wood softens.

Quantitative and experimental studies can involve placement of wood of known history (species identity, age, size) into selected water bodies for controlled durations to study colonization dynamics (e.g., Spänhoff and others 2000). Appropriate hierarchical designs, similar to those used by Townsend and others (1997) and McKie and Cranston (2001), allow recognition of distinct preferences among locations and wood types.

DIVERSITY AND ECOLOGY OF CHIRONOMID WOOD MINERS

Only three of the 10 subfamilies of Chironomidae include larvae that are associated closely with immersed wood. These predominantly occur in the very diverse Orthocladiinae and Chironominae, with a sole example in the Diamesinae (*Pagastia*). The subfamily Tanypodinae is comprised mainly of predatory larvae that never mine but search the outer wood surfaces for prey. Amongst the other subfamilies for which larval behaviours are known, certain Australian Podonominae larvae utilize external wood surfaces, whereas Telmatogetoninae, Prodiamesinae and Buchonomyiinae show no special association with CWD.

In both Orthocladiinae and Chironominae wood mining appears to be distributed across the taxa such that there are many isolated examples, with just one or a few species often within some of the most speciose genera. For example, throughout much of the northern hemisphere, the appositely-named *Orthocladius* (*Symposiocladius*) *lignicola* Thienemann mines woods such as alder (Cranston 1982). Although *O. lignicola* may comprise several closely related entities, evidently there has been no radiation within *Orthocladius* and all potential relatives are non-mining algal grazers. Likewise, amongst the Chironominae, larvae of one or two species of *Polypedilum* in S.E. Asia and Australia mine in relatively soft immersed woods. Since close relatives in this large genus are collector-gatherers that do not mine, apparently this too is an apparent example of an evolutionarily facultative switch to living in wood, with no commensurate radiation within the substrate.

Despite the disparate occurrence of xylophagy amongst the Chironomidae, there is sporadic convergence in some morphological features associated with the mining habit. Thus menta are often either awl-like (e.g., fig. 1G), with the central tooth sagittate and protruding (e.g., several Orthocladiinae and the Chironominae *Shangomyia* Sæther and Wang) or more blade / plough-like (e.g., fig. 1F), with the distal edge flattened to recessed (the orthocladiine *Austrobrillia* Freeman and chironomine *Harrisius* Freeman), but other menta do not appear especially modified (e.g., fig. 1D). Similarly, there are some common but by no means universal modifications to the abdomen, including a flattened and/or flaccid form, reduced or no prolegs, and, in some undescribed orthocladiines, curious posterior body sclerotisation (McKie 1996).

It is presently difficult to assess the ecological significance of such morphological variation, as the ecology of xylophagous chironomids is generally poorly known, though there is certainly species-specific variation in stenophagy and patterns of resource utilisation. The evolution of wood-mining and leaf-shredding appears somewhat related among Chironomidae (thus the genera *Stenochironomus* Kieffer and *Brillia* Kieffer include both feeding modes), and there are some xylophagous species that feed on both leaves and wood (e.g., the Australian species of *Austrobrillia* and *Harrisius*). Such larvae evidently are “coarse detritus specialists” rather than obligate xylophages. Other species appear genuinely stenophagous, being found only mining within logs and failing to rear to emergence away from wood. Surveys of the wood-inhabiting fauna of south-east Australian streams revealed differential utilisation of wood by chironomid xylophages. Several taxa, including *Austrobrillia, Harrisius* and some novel orthocladiine species, were associated with the surface layers of mid-sized (diameter 2 — 5 cm) sticks (McKie 1996). In contrast, *Stenochironomus* sp. never was found associated with the wood-surface, and its presence was confirmed only after adults emerged from extremely well-decayed wood that had been kept in laboratory aquaria for several months, indicating a very deep mining habit (also see Cranston and Hardwick 1996). All such xylophages were associated most with more decayed wood from native forested streams (McKie 1996), with no species utilising fresh wood. Notably, negligible colonisation of fresh wood by xylophagous chironomids in an experimental study contrasted strongly with observations for surface gouging elmid beetles (McKie and Cranston 2001). Further details of the autecology of xylophagous chironomids generally are lacking, with only the north American lotic *Xylotopus par* Coquillett studied in detail — in Michigan, USA, it colonises wood of various decay classes, apparently has an annual life cycle, and bears a band of bacteria in its midgut that may be involved in wood digestion (Kaufmann and King 1987, Kaufmann and others 1986).

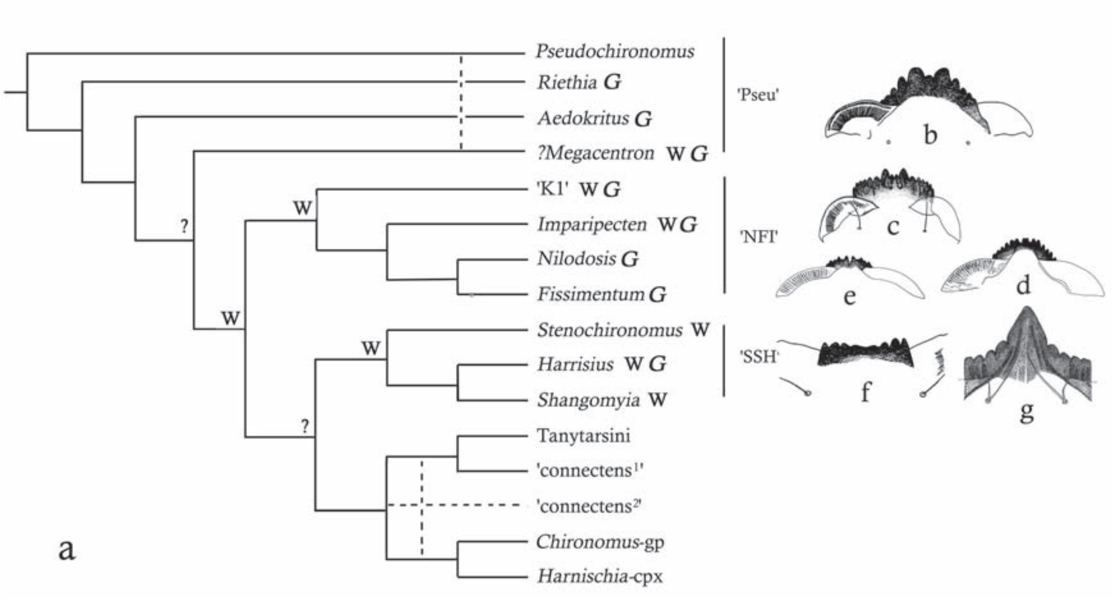


Figure 1—(A) Postulated early-nodes of subfamily Chironominae phylogeny (after Cranston 2004), broken lines represent ambiguous relationships; W = wood-mining taxa and reconstructed nodes, *G* = Gondwanan in distribution, ? — uncertain reconstruction. Menta of (B) ?*Megacentron* Freeman, (C) Australian genus ‘K1’, (D) *Imparipecten* Freeman, (E) *Nilodosis* Kieffer, (F) *Harrisius* Freeman, (G) *Shangomyia* Sæther and Wang.

PHYLOGENETIC RELATIONS AMONGST WOOD-MINING CHIRONOMIDAE

In the Orthocladiinae, the wood-mining habit appears clustered within a grouping of genera with no formal name, but to which the sobriquet '*Brillia* group' sensu Sæther and Wang 1992, can be applied (Cranston 2000). It includes the genera *Austrobrillia* Freeman, *Brillia* Kieffer, *Eurycnemus* v.d. Wulp, *Euryhapsis* Oliver, *Plhudsonia* Sæther*, Neobrillia* Kawaii and *Xylotopus* Oliver and *Irisobrillia* Oliver and *Tokyobrillia* Kobayashi & Sasa probably should be included also despite their immature stages remaining unknown. Although detailed phylogenetic relationships in this most diverse subfamily remain unclear, poorly resolved or contradictory, morphological analyses are converging on the view that the '*Brillia* group' may either be sister group to the remainder of the subfamily (as 'the most basal group'; Sæther and Wang 1992, Cranston 2000) or forms a paraphyletic grade at the base of the subfamily tree.

Wood-mining also appears to be concentrated in early branching ('basal') clades of Chironominae. As with the Orthocladiinae, ideas on the phylogeny and even the monophyly of some high ranking groups of the Chironominae, remain uncertain. However, the recently elucidated life history of an unusual Oriental wood-mining taxon, *Shangomyia* Sæther and Wang, provoked a reconsideration of some of the earliest branching events, based on morphology (Cranston, 2003), as depicted in figure 1A. Thus in the likely grade (paraphyletic) 'Pseudochironomini' ('Pseu', fig. 1A) the putative larva of *Megacentron* Freeman (fig. 1B) is found in soft wood (Cranston 1996). The next postulated branch comprises an undescribed Australian genus 'K1' (fig. 1C) (Cranston 1996), *Imparipecten* Freeman (fig. 1D), *Nilodosis* Kieffer and *Fissimentum* Cranston & Nolte in the clade ('NFI' (fig. 1). Larvae of *Imparipecten* mine in immersed wood in eastern Australia (Cranston and Hardwick 1996); those of 'K1' mine wood in monsoonal tropical streams of Northern Territory. The curious cleft menta of *Nilodosis* (fig. 1E) and *Fissimentum* seems to preclude mining, but their feeding mode is poorly understood.

The next node on the tree involves a clade that clearly constitutes a radiation of mining larvae: the long-understood sister-species pair of wood- and leaf-mining genera *Stenochironomus* Kieffer and *Harrisius* Freeman (Borkent 1984) is robust. Reviewing xylophagous chironomids, Cranston and Oliver (1988) observed that mining Chironominae (such as *Stenochironomus* and *Harrisius*) (fig. 1F) lacked 'adaptive' wood-mining modifications of the mentum that appeared restricted to a convergent suite of Orthocladiinae with protruding median mental teeth. This seemed to have generality even after revelation of diverse Australian woodminers (e.g., Cranston 2000, Cranston and Hardwick 1996, McKie 1996). However, the recently-discovered wood-mining larva of the Oriental chironomine genus *Shangomyia* has the sagittate protruding median mentum (fig. 1G) of a type associated previously only with Orthocladiinae miners (Cranston 2003). Never-the-less, phylogenetic analyses place *Shangomyia* unequivocally within the *Stenochironomus* / *Harrisius* clade (Cranston 2003), although superficially they differ in many aspects of their morphology in each life history stage.

Traits such as wood-mining can be reconstructed onto nodes (branching points) from such phylogenic hypotheses Several competing optimisation schemes exist, but even with fully-sampled and robust phylogenies, quantitative ancestral node reconstructions remain controversial, perhaps little better than those derived from qualitative parsimonious reasoning. Accepting this, it is reasonable to postulate that the early radiation of the subfamily Orthocladiinae may have been associated with substantial wood mining, as argued by Cranston (2000). Similar rationale can be applied to the Chironominae with the more recently elucidated early nodes in the phylogeny (Cranston 2003). Since Orthocladiinae and Chironominae are likely sister taxa, wood-mining may be a plesiotypic behaviour prior to the diversification of the two sister subfamilies.

DATING THE EVOLUTIONARY EVENTS

Lack of a molecular phylogeny, with its ever-improving capacity to provide dates for branching events, need not exclude speculation on the timing and locations of the events postulated from the phylogenies discussed above. From the earliest days biologists accepted the notion of drifting continents (plate tectonics), and especially following the formalisations of Hennig (1960) and Brundin (1966), the modern-day distribution of organisms and postulated earth history events have been used in dating evolutionary events. The rationale, discussed for Chironomidae by Brundin (1966), Cranston (1994) and Cranston and Hare (1995) and for Diptera more widely (Cranston 2005), assumes that sister taxa that occupy separated, but once united as Gondwana, southern landmasses speciated in allopatry prior to tectonic-induced separation. This provides minimum dates for vicariance according to the geological timetable (see Sanmartín and Ronquist 2004). Several taxa in early (including postulated wood-associated) radiations include austral distributed groups, such as *Riethia* and *Megacentron,* 'K1', *Imparipecten* and *Harrisius* in Chironominae (labelled '*G'* fig. 1A), and *Austrobrillia* amongst the Orthocladiinae (Cranston 2000). The occurence of such taxa with specialised immature biology in both South America and Australia add weight to arguments that the radiation of Chironomidae at the taxonomic level of still extant monophyletic clades (genera) predates major fragmentation of Gondwana. While the early-departing African continent rarely is included, many distributions involve Australia (with its remarkably diverse xylophagous chironomid fauna — table 1) and South America, which were contiguous through Antarctica some 38 million years ago. Furthermore, the current more global distribution of the '*Brillia* group' and *Stenochironomus* and relatives suggests an even more ancient origin perhaps in Pangaea. Reconciliation of biogeographic evidence of great age with palaeodiversity demonstrated by Cretaceous (Brundin 1976, Kalugina 1980) and earlier (Evenhuis 1994) fossils suggests the evolutionary history of the Chironomidae already was well in place in the Mesozoic.

According to this scenario, wood mining may not have been a plesiotypic (ancestral) behaviour for Orthocladiinae + Chironominae as inferred above. Thus a wide spectrum of larval behaviours, from dwelling in the hygropetric zone to predatory, plus gouging of wood and shredding of leaves, was established by the dramatic end of the Cretaceous. A pre-existing wood-mining habit would have been an exaptation to a late Cretaceous / early Tertiary (K-T) world of 'greenhouse' climate — essentially allowing survival through the K-T event in an environmentally-buffered refugial habitat, namely immersed wood in streams and lakes. Furthermore, the severity of the environmental changes may have been distributed unevenly across the globe, with the southern hemisphere, and Australia in particular, serving as a refugial area, less impacted by the Chicxulub bolide collision (O'Keefe and Aherns 1989) and/or Deccan traps vulcanism (Caldeira and Ramino 1990). Such a model for such geographically-differentiated survival can be inferred from recent phylogenies of avian evolution by Cracraft (2001) and Barker and others (2004). Adding an ecological scenario of differential resistance to extinction between habitats to 'geographic resistance' provides a scenario to explain present-day patterns that appear worthy of further study.

LITERATURE CITED

Anderson, N.H. 1982. A survey of aquatic insects associated with wood debris in New Zealand streams. Mauri Ora 10: 21-33.

Anderson, N.H.; Sedell, J.R. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology. 24: 351-377.

Anderson, N.H.; Sedell, J.R.; Roberts, L.M.; Triska, F.J. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist. 100: 64-82.

Anderson, N.H.; Steedman, R.J.; Dudley, T. 1984. Patterns of exploitation by stream invertebrates of wood debris (xylophagy). Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie. 22: 1847-1852.

Andrus, C.W.; Long, B.A.; Froechlich, H.A.. 1988. Woody debris and its contribution to pool formations in a coastal stream 50 years after logging. Canadian Journal of Fisheries and Aquatic Sciences. 45: 2080-2086.

Aumen, N.G. 1990. Influence of coarse woody debris on nutrient retention in catastrophically disturbed streams. Hydrobiologia.190: 183-192.

Aumen, N.G.; Bottomley, P.H.; Ward, G.M.; Gregory, S.V. 1983. Microbial decomposition of wood in streams: distribution of microflora and factors affecting [^{14}C] lignocellulose mineralisation. Applied and Environmental Microbiology. 46: 1409-1416.

Barker, F.K.; Cibois, A.; Schikler, P. [and others]. 2004. Phylogeny and diversification of the largest avian radiation. Proceedings of the National Academy of Sciences. 101: 11040-11045.

Bilby, R.E. 1981. Role of organic debris in regulating the export of dissolved and articulate matter from a forested watershed. Ecology. 62: 1234-1243.

Bilby, R.E. 1984. Removal of woody debris may affect stream channel stability. Journal of Forestry. 82: 609-612.

Bilby, R.E.; Likens, G.E. 1980. Importance of organic debris-dams in the structure and function of stream ecosystems. Ecology. 61: 1107-1113.

Borkent, A. 1984. Systematics of the *Stenochironomus* complex. Memoirs of the Entomological Society of Canada.128: 1-269.

Bowen, K.L.; Kaushik, N.K.; Gordon, A.M. 1998. Macroinvertebrate communities and biofilm chlorophyll on woody debris in two Canadian oligotrophic lakes. Archiv für Hydrobiologie. 141: 257-281.

Brundin, L. 1976. A Neocomian chironomid and Podonominae-Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. Zoologica Scripta. 5: 139-60.

Caldeira, K.G.; Ramino, M.R. 1990. Deccan volcanism, greenhouse warming, and the Cretaceous/Tertiary boundary. Geological Society of America, Special Paper. 247: 117-123.

Collier, K.J.; Halliday, J.N. 2000. Macroinvertebrate-wood associations during decay of plantation pine in New Zealand pumice-bed streams: stable habitat or trophic subsidy? Journal of the North American Benthological Society. 19: 94-111.

Collier, K.J.; Smith, B.J.; Halliday, N.J. 2004. Colonization and use of pine wood versus native wood in New Zealand plantation forest streams: implications for riparian management Aquatic Conservation — Marine and Freshwater Ecosystems. 14: 179-199.

Cracraft, J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. Proceedings of the Royal Society of London B. 268: 459-469.

Cranston, P.S. 1982. The metamorphosis of *Symposiocladius lignicola* (Kieffer), n. gen., n. comb., a wood-mining Chironomidae (Diptera). Entomologica scandinavica. 13: 419-429.

Cranston, P.S. 1994. Biogeography. In: Chironomidae: Biology and Ecology of Non-biting Midges (ed P. Armitage, P.S. Cranston and L.C.V. Pinder), Chapman and Hall, London, Glasgow, New York, Tokyo, Melbourne, Madras., pp. 62-84. Chapter 4.

Cranston, P.S. 1996. Identification guide to the Chironomidae of New South Wales. AWT Identification Guide Number 1. Australian Water Technologies Pty Ltd, West Ryde, NSW. pp. 376.

Cranston, P.S. 2000. *Austrobrillia* Freeman: immature stages, and a new species from the neotropics. Spixiana. 23: 101-111.

Cranston, P.S. 2003. The oriental genus *Shangomyia* Sæther & Wang (Chironomidae: Diptera): immature stages, biology, putative relationships and the evolution of wood mining in chironomid larvae. Raffles Bulletin of Zoology 51: 179-186.

Cranston, P.S. 2005. Biogeographical history in the evolutionary biology of flies. (eds. D.K. Yeates and B.M Wiegmann) Columbia University Press, New York: 274-311.

Cranston, P.S.; Hardwick, R. 1996. The immature stages and phylogeny of *Imparipecten* Freeman, an Australian endemic genus of wood-mining chironomid (Diptera). Aquatic Insects. 18: 193-207.

Cranston, P.S.; Hare, L. 1995. *Conochironomus* Freeman: an Afro-Australian Chironomini genus revised (Diptera: Chironomidae). Systematic Entomology, 20: 247-64.

Cranston, P.S.; Oliver, D.R. 1988. Aquatic xylophagous Orthocladiinae — systematics and ecology (Diptera: Chironomidae). Spixiana Supplement 14: 143-154.

Dudgeon, D. 1994. The influence of riparian vegetation on macroinvertebrate community structure and functional organisation in six New (sic) Guinea streams. Hydrobiologia 294: 65-85.

Dudley, T.L.; Anderson, N.H. 1987. The biology and life cycles of *Lipsothrix* spp. (Diptera: Tipulidae) inhabiting wood in western Oregon streams. Freshwater Biology. 17: 437-451.

Evenhuis, N. 1994. Catalogue of the fossil flies of the world. Backhuys Publishers, Leiden. 600 pp.

Gippel, C.J. 1995. Environmental hydraulics of large woody debris in streams and rivers. Journal of Environmental Engineering. 121: 388-395.

Gippel, C.J.; Finlayson, B.; O'Neill, I. 1996. Distribution and hydraulic significance of large woody debris in a lowland Australian river. Hydrobiologia. 318: 179-194.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecologocal Research. 15: 133-302.

Hennig, W. 1960. Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem. Beitrage Entomologie. 10: 221-329.

Hoffmann, A.; Hering, D. 2000. Wood-associated macroinvertebrate fauna in Central European streams. International Review of Hydrobiology. 85: 25-48.

Kalugina, N.S. 1980. Cretaceous Aphroteniinae from North Siberia (Diptera: Chironomidae). *Electrotenia brundini* gen. nov., sp. nov. Acta Universitatis Carolinensis-Biologica 1978: 89-93**.**

Kaufman, M.G.; King, R.H. 1987. Colonization of wood substrates by the aquatic xylophage *Xylotopus par* (Diptera: Chironomidae) and a description of its life history. Canadian Journal of Zoology. 65: 2280-86.

Kaufman, M.G.; Pankratz, H.S.; Klug, M.J. 1986. Bacteria associated with the ectoperitrophic space in the midgut of the larva of the midge *Xylotopus par* (Diptera: Chironomidae). Applied and Environmental Microbiology. 51: 657-660.

Magoulick, D.D. 1998. Effect of wood hardness, condition, texture and substrate type on community structure of stream invertebrates. The American Midland Naturalist. 9: 187-200.

McKie, B. 1996. The community ecology of wood-associated macroinvertebrates in streams of the Brindabella Ranges, Australia. Honours Thesis, Australian National University.

McKie, B.G.L.; Cranston, P.S. 1998. Keystone coleopterans? Colonisation by wood-feeding elmids of experimentally-immersed woods in South-east Australia. Marine and Freshwater Research. 49: 79-88.

McKie, B.G.L.; Cranston, P.S. 2001. Colonisation of experimentally immersed wood in South eastern Australia: responses of feeding groups to changes in riparian vegetation. Hydrobiologia 452. 1-14.

Molles, M.C., Jr. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology. 63: 1-6.

O'Connor, N.A. 1991. The effect of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland system. Oecologia. 85: 504-512.

O'Keefe, J.D.; Aherns, T.J. 1989, Impact production of CO^2 by the bolide and the resultant heating of the Earth. Nature. 338: 247-249.

Sæther, O.A.; Wang, X. 1992. *Euryhapsis fuscipropes* sp. n. from China and *Tokyobrillia anderseni* sp. n. from Tanzania, with a review of genera near *Irisobrillia* Oliver (Diptera: Chironomidae). Annales de Limnologie. 28: 209-223.

Sanmartín, I.; Ronquist, F. 2004. Southern Hemisphere biogeography inferred by event-based models: plant vs. animal patterns. Systematic Biology. 53: 216-243.

Scheffer, T.C.; Cowling, E.B. 1966. Natural resistance of wood to microbial deterioration. Annual Review of Phytopathology. 4: 147-170.

Spanhoff, B.; Alecke, C.; Meyer, E.I. 2001. Simple method for rating the decay stages of submerged woody debris. Journal of the North American Benthological Society. 20: 385-394.

Steedman, R.J.; Anderson, N.H. 1985. Life history and ecological role of the xylophagous aquatic beetle, *Lara avara* LeConte (Dryopoidea: Elmidae). Freshwater Biology. 15: 535-546.

Tank, J.L.; Winterbourn, M.J. 1995. Biofilm development and invertebrate colonisation of wood in four New Zealand streams of contrasting pH. Freshwater Biology. 34. 303-315.

Thorp, J.H.; McEwan, E.M.; Flynn, M.F.; Hauer, F.R. 1985. Invertebrate colonization of submerged wood in a cypress-tupelo swamp and blackwater stream. American Midland Naturalist. 113: 56-68.

Townsend, C.R.; Arbuckle, C.J.; Crowl, T.A.; Scarsbrook, M.R. 1997. The relationship between land use and physiochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. Freshwater Biology. 37: 177-191.

THE USE AND APPLICATION OF PHYLOGEOGRAPHY FOR INVERTEBRATE CONSERVATION RESEARCH AND PLANNING

Ryan C. Garrick, Chester J. Sands, and Paul Sunnucks[1]

Abstract—To conserve evolutionary processes within taxa as well as local co-evolutionary associations among taxa, habitat reservation and production forestry management needs to take account of natural genetic-geographic patterns. While vertebrates tend to have at least moderate dispersal and gene flow on a landscape-scale, there are good reasons to expect many small, flightless, ecologically specialized saproxylic invertebrates to be strongly subdivided owing to low powers of dispersal, long-lived stable microhabitats and multiple generations within a single log. Phylogeographic studies have repeatedly demonstrated that, in low vagility taxa, (1) traditional morphological taxonomy underestimates genetic diversity, (2) conservation strategies focused at and above the species-level are inadequate, and (3) it is not atypical for sedentary invertebrates to exhibit high local endemism over very fine spatial scales. Phylogeography and comparative phylogeography provide an empirical framework for maximizing the conservation benefit of reserves, and directing conservation strategies and sustainable management practices outside of protected areas.

INTRODUCTION

Sustainable forestry practices are underpinned by maintaining healthy productive forests, which in turn depend on efficient cycling of nutrients throughout the system. Rotting logs on the forest floor serve as a critical arena for nutrient cycling (Grove 2002a, 2002b, 2002c), but the biology, population structure and ecology of many members of the key invertebrate groups that aid in the decomposition of coarse woody debris are poorly studied. Many log-dependent (saproxylic) invertebrates are likely to show marked population structure over very fine spatial scales owing to their ecological specialisation and inherently poor dispersal abilities (Schiegg 2000, Warren and Key 1991). Despite this, conservation planning is often based on more mobile surrogate taxa such as mammals (Stiling 1999). Thus current forest management practices probably fail to cater adequately for the economically and ecologically important and incredibly species-rich rotting log faunal assemblages. Indeed, basic questions critical in conservation management such as how often, how large, and how far apart species habitat patches should be, remain largely unanswered (Thomas and Morris 1994).

Ecological characteristics of certain fauna tend to influence their efficiency in capturing geographical patterning in biota resulting from long-acting processes such as climatic cycles (Moritz and others 2001). Because invertebrates may have considerably smaller ranges than vertebrates, they can potentially provide fine-scale information about processes that have led to current biogeographic patterns, and given that low vagility (flightless) invertebrates often show high fidelity to their preferred habitat, they are particularly likely to be efficient indicators of historical climate change in those habitats (Yeates and others 2002). For these reasons, we propose that saproxylic invertebrates may represent an exceptional community for capturing landscape history given that these animals experience their local environment at very fine spatial scales, such that even individual creek lines and gullies may represent refuges for viable populations during cool dry glacial periods (Heatwole 1987).

Phylogeography (sensu Avise 1987) is the study of geographical distributions of closely related genealogical (genetic) lineages. It makes a critical contribution to evolutionary and population biology because it concentrates on the interface of processes acting within species (population genetics) and among species (phylogenetics) (Avise 1998, 2000). Accordingly, phylogeography can identify processes that influence speciation and illuminate population history. It has become apparent that phylogeographic analysis of unrelated, co-distributed taxa (comparative phylogeography) has unique potential to address long-standing questions about the formation of organismal communities, landscape ecology, and the sources and maintenance of biodiversity. Given that we should seek to maintain evolutionary processes, it is of paramount importance to understand how historical processes have shaped contemporary genetic and species diversity in whole communities. Although the details of such processes are likely to vary from one system to another, it should nonetheless be possible to formulate conservation strategies that protect both irreplaceable (historical) genetic diversity, as well as adaptive genetic diversity (Moritz and others 2000). Furthermore, concordant phylogeographic patterns among multiple diverse taxa generate predictions about present-day patterns of genetic variation for co-distributed taxa that have yet to be sampled, thereby potentially extending the findings of such studies to regional species assemblages (Avise 1998). Consequently, phylogeographic studies are directly relevant to conservation planning, whereby management strategies can be tailored so as to maximise the benefit of nature reserves, and the great potential for production forests to compliment within-reserve conservation can be realised through sustainable low-impact management practices that take account of the evolutionary history of biota. Unfortunately, invertebrates are poorly represented in phylogeographic studies (e.g.,

---

[1] Ryan C. Garrick, Ph.D. candidate, Chester J. Sands, Ph.D. candidate, and Paul Sunnucks, Senior Lecturer, Department of Genetics, Biological Sciences Building 1, La Trobe University, Bundoora, VIC 3086, Australia, respectively.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Molecular Ecology Phylogeography Special Issue 1998, Avise 2000). Yet many invertebrates, especially sedentary terrestrial groups such as the ecologically specialised log-dependent fauna (Warren and Key 1991, Yee and others 2001), are likely to deviate from population-genetic models based on well-studied relatively large and mobile vertebrate species. For saproxylic invertebrates, management practices that maintain both spatial and temporal connectivity of dead wood are likely to be critical for retaining biodiversity (Grove 2002a, Schiegg 2000).

This review aims to inform researchers and natural resource managers of the potential benefits and applications of phylogeographic studies, with particular emphasis on invertebrates —an understudied yet exceptionally diverse group of high ecological importance (Wilson 2001). First, key considerations relating to taxon sampling are highlighted, and the array of molecular tools and analytical techniques available for answering questions about long-term population dynamics of forest invertebrate fauna and their responses to historical climate change are introduced. We then overview conservation-based applications of phylogeography, giving examples from studies of diverse invertebrate species, and illustrate the high degree of local endemism that may be typical of many saproxylic invertebrates via a case study of a log-dwelling 'giant' springtail (Collembola) from a south-east Australian temperate forest. Finally, we present some broad generalisations that can be drawn from the existing body of phylogeographic research.

TAXON SAMPLING: SPATIAL SCALE AND STRATEGY

Phylogeography usually addresses evolutionary questions at and below the level of biological species. A critical requirement is adequate sampling at an appropriate spatial scale throughout the geographic range of the populations under study (Templeton 1998, Templeton and others 1995). In the case of relatively sedentary taxa such as saproxylic invertebrates, this can be in the order of several of kilometres or less (Peterson and Denno 1998). Under a fine-scale sampling regime, precise geographic locations of contact zones among distinct genetic lineages can be identified, and the degree of population structure (i.e., genetic differentiation) can be determined with considerable accuracy. A nested sampling design (e.g., individuals within sites, sites within areas, areas within regions) allows analyses at hierarchical spatial scales, which in turn can be used to distinguish between population history and structure (Templeton and others 1995). The incorporation of independent demographic, morphological (phenotypic), and environmental data such as landscape history (e.g., geology or palaeoclimatology) and ecological information further increases the power of phylogeographic inference, and permits more sophisticated analyses that can reveal the relative influence of specific environmental and ecological components upon the present-day spatial distribution of genetic diversity (Moritz and others 2000).

MOLECULAR TOOLS IN THE 'PHYLOGEOGRAPHIC TOOLBOX'

Mitochondrial DNA

The traditional molecular marker of choice in animal phylogeographic studies has been mitochondrial DNA (mtDNA) (Avise 2000). The mitochondrial genome is usually maternally inherited (Hutchinson and others 1974), allowing interpretation of genealogical relationships that have been largely unaffected by recombination. Due to the lack of a mutation repair mechanism mtDNA sequences evolve at a much faster rate than nuclear gene sequences, making them sufficiently variable to yield information relating to evolutionary relationships at a variety of temporal scales, and across multiple taxonomic levels (Avise 2000, Harrison 1989). Further, genetic variation in mitochondrial protein-coding genes is mostly selectively neutral, such that the genetic signature of historical lineage divergence is not overwritten by natural selection (Avise 2000). Finally, the mutation rate of animal mtDNA has been widely studied, and based on calibrations using fossil and/or geological dating, coding regions in most species are believed to evolve at approximately two percent sequence divergence per million years (Brower 1994, Brown and others 1979). The application of a molecular clock permits estimates of the absolute ages of lineage splitting events, which in turn can be used to generate or test biogeographic hypotheses, and identify factors likely to have had major impacts on the evolutionary history of populations, species, and species assemblages.

However, there are several reasons why mtDNA should not be used to the exclusion of other gene regions. First, because the mitochondrial genome is inherited as a single cohesive unit, phylogeographic studies based on mtDNA alone are effectively evolutionary studies of a single molecule, not the species. Whilst mitochondrial evolution may be a good approximation of the evolutionary history of the host organism, there are well-known mechanisms by which relationships among alleles at any locus (i.e., a gene tree) will not match those of the species (Avise 2000, Ballard and Whitlock 2004). Second, some of the aforementioned beneficial characteristics of animal mtDNA do not apply in certain situations. For example, its selective neutrality has been challenged (Ballard and Whitlock 2004), and on relatively rare occasions, the presumed lack of recombination has been shown to be incorrect (Lunt and Hyman 1997). Third, in those organisms with maternally inherited mtDNA (i.e., most animal taxa), the results of any study are sex-biased: they reflect only the history of matrilines. Finally, the validity of a molecular clock is a matter of considerable debate, given that the rate of mtDNA evolution may vary among taxa, within taxa, and among the different protein-coding genes within the mitochondrial genome (Arbogast and others 2002, Ballard and Whitlock 2004). Yet despite these potential pitfalls, mtDNA makes an excellent starting point. Importantly, given the widespread use of mtDNA in phylogeographic studies, these data are connectable, and therefore permit comparisons across otherwise unrelated studies.

Nuclear DNA

The strength of phylogeographic inference is directly dependent on the number of independent lines of evidence (Templeton 2004). Accordingly, the application of multiple co-dominant nuclear DNA (nDNA) genetic markers can provide robust evidence that corroborates (or refutes) a phylogeographic hypothesis generated on the basis of mtDNA alone, thus better reflecting the history of the organism (Templeton 1998). In addition, because nDNA is bi-parentally inherited, phenomena such as hybridisation, sex-biased dispersal, and genetic introgression can potentially be identified (Sunnucks 2000). Furthermore, information on the relative frequency of nuclear genotypes (particular combinations of alleles at a locus), which potentially change over short (i.e., generation-to-generation) timescales, can uncover recent subdivision of a formerly panmictic population that would otherwise be undetectable. There are a variety of nuclear markers available for these studies (reviewed in Sunnucks 2000, Hare 2001), ranging from relatively inexpensive protein-based markers such as allozymes, to the DNA-based markers such as microsatellites (hypervariable repetitive DNA). Although more expensive, the latter class of molecular markers often provide greater resolution of population structure over very fine spatial scales.

In general, the use of nDNA sequence data in phylogeographic studies is not yet common practice owing to inherent difficulties with accounting for the distorting effects that recombination can have on genealogical relationships. However, when the signature of recombination is absent or negligible, much can be gained by the incorporation of nDNA sequence data, particularly since it allows a much deeper time frame (c.f. mtDNA) to be examined (Hare 2001). Several recent phylogeographic studies have demonstrated the benefits of obtaining nDNA frequency and sequence data from multiple regions of the genome in illuminating the evolutionary history of invertebrates (e.g., grasshoppers: Ibrahim and others 2002, crickets: Broughton and Harrison 2003, saproxylic Collembola: Garrick and others 2004).

Analyses

As is often the case with a new discipline, development of appropriate analytical techniques can represent a significant hurdle. Fortunately, phylogeography is open to well-established population-genetic analyses and phylogenetic techniques. In recent years, much progress has been made in the area of statistical phylogeography, which provides an array of procedures to explicitly test specific hypotheses (Knowles 2004, Knowles and Maddison 2002, Manel and others 2003). For example, Nested Clade Analysis (Templeton 1998, Templeton and others 1995) is a powerful technique enabling one to distinguish between alternative causes of geographical associations among genetic lineages (e.g., isolation-by-distance verses habitat fragmentation) and so separate pattern from process. Further, geographical information systems hold great potential for sophisticated genetic, geographic and environmental data analyses and model-building. The need to incorporate fine-scale abiotic and biotic ecological data into models of organismal history has been highlighted by Endler (1982) and Moritz and others (2000). While such studies are presently rare, it is already clear that they make a significant contribution to understanding processes that promote species diversification, historical biogeography of particular regions and community ecology (Moritz and others 2000). Continued integration of molecular phylogenetics and population genetics with analyses of phenotypic variation, reproductive isolation and independent evidence of landscape history and ecology will undoubtedly propel the field of phylogeography to the forefront of conservation research and planning, with direct applications in biodiversity indication, reserve design, identification of management units, and maintenance of species' evolutionary potential.

APPLICATIONS OF PHYLOGEOGRAPHY FOR INVERTEBRATE CONSERVATION

To date, there have been very few phylogeographic studies that explicitly focus on saproxylic invertebrates. Consequently, the following section primarily draws on literature dealing with relatively sedentary, ecologically specialised terrestrial invertebrates that are likely to exhibit patterns of population structure and local endemism akin to what we might expect to find in dead wood-dependent taxa.

Taxon-Specific Phylogeography: Uncovering Cryptic Biodiversity

Our perceptions of biodiversity are commonly based upon taxonomic divisions that rely on morphological features (Holland and Hadfield 2002). A repeated trend in phylogeographic studies is the uncovering of cryptic species (Arbogast and Kenagy 2001). This is of considerable relevance to conservation biology as it is becoming clear that in many invertebrates, genetic evolution out-paces morphological evolution, with the result that traditional morphological taxonomy may greatly underestimate the underlying genetic diversity present (Avise 1989, 2000).

Bond and Sierwald (2002) investigated patterns of genetic diversity in a morphologically conservative species of millipede (*Anadenobolus excisus*) endemic to Jamaica. This animal is associated with limestone formations, is presumed to have extremely limited dispersal abilities, and was believed to represent a single species on the basis of genitalic morphology—the features most commonly used to distinguish millipede taxa. Using mtDNA, these authors identified three highly divergent genetic lineages, two of which presently occur in sympatry. Based on these molecular data, it was concluded that *A. excisus* is actually a complex of three sibling species.

Similarly, Salomone and others (2002) applied phylogeography to investigate patterns of evolutionary diversification and speciation in soil-dwelling oribatid mites endemic to the Canary Islands. The three focal species in the genus *Steganacarus* have extremely limited powers of dispersal, and predominantly occur in dead organic matter in the surface layers of forest soil horizons. Owing to the paucity of unambiguous morphological characters, taxonomic relationships among the three species were uncertain. Indeed, even the morphological diagnosis of two of these species was contentious. Phylogenetic relationships inferred using molecular data were inconsistent with those based on morphology—this is perhaps unsurprising given that the usefulness of traditional taxonomic approaches to phylogeny in this genus is questionable. Interestingly, despite a lack of morphological variation among specimens of *S. carlosi* collected across three islands in the archipelago, genetic data identified three highly differentiated clades, each being restricted to a single island. Levels of divergence among these clades are comparable with those found between 'good' biological congeneric species in other terrestrial arthropod taxa, thus prompting the authors to suggest that each of the clades represent cryptic species. Comparable findings have been reported for other diverse invertebrate taxa (e.g., pseudoscorpions: Wilcox and others 1997, Onychophora: Trewick 1998, ladybird beetles: Kobayashi and others 2000).

Taxon-Specific Phylogeography: Identifying Management Units and Setting Conservation Priorities

Identifying appropriate units of conservation is a dynamic area of research and contention (Crandall and others 2000). One widely-accepted system is that of Moritz (1994)—an adaptation of Ryder's (1986) evolutionarily significant unit (ESU). Moritz (1994) defines an ESU as a collection of lineages with a shared evolutionary history. By first producing a gene tree, and then identifying lineages that are reciprocally monophyletic (i.e., share a single most recent common ancestor), ESUs can be determined relatively quickly and unambiguously. An advantage in using a phylogeographic approach is that one simultaneously identifies both the number, and the geographic range of ESUs.

Holland and Hadfield (2002) evaluated the phylogeographic structure within and among populations of three endemic Hawaiian tree snails in the critically endangered genus *Achatinella*, with a view to setting conservation priorities for *A. mustelina*. The focal species has limited dispersal abilities, occurs in fragmented populations occupying only upland montane habitats above 600m elevation, and is in a state of rapid decline owing to invasive species and human impacts. Despite the absence of clear morphological differentiation, six geographically isolated ESUs were identified from mtDNA sequence data. This information will guide a multi-faceted conservation action plan (e.g., delineation of areas for protection, identification of key sources of genetic diversity for captive propagation, and directing field translocations or reintroductions).

Similarly, Trewick (2001) used an ESU framework to make recommendations relating to the conservation of an endangered grasshopper (*Brachaspis robustus*) endemic to the South Island of New Zealand via a wider phylogeographic study that included two additional *Brachaspis* species. *B. robustus* is very rare and localised, flightless, and the species' range appears to have contracted since intensive field observations began. Although the molecular data identified three distinct *Brachaspis* lineages, these were not consistent with the three species recognised by current taxonomy. One of the lineages comprised both the endangered *B. robustus* and southern populations of the alpine-restricted *B. nivalis*, while northern *B. nivalis* populations formed a separate lineage that showed levels of genetic divergence comparable with that of among-species differences seen in other insects. Here, evidence to support the current classification of the endangered *B. robustus* as a distinct species was found to be weak inasmuch as it failed to satisfy the criteria of an ESU.

Comparative Phylogeography: Illuminating Processes Driving Evolutionary Diversification, and Testing Biogeographic Hypotheses

Population-genetic processes are numerous and complex, and they can be hard to separate in single-species studies (Bohonak 1999). Comparative phylogeography offers a means of assessing the relative role of historical (e.g., climate-induced) vicariance and dispersal ability in shaping the present-day distribution of taxa (Avise 2000).

Using a suite of flightless invertebrate taxa, Trewick and Wallis (2001) employed comparative phylogeography to test two competing biogeographic hypotheses proposed to explain the existence of areas possessing markedly lower levels of biodiversity and local endemicity in New Zealand—specifically, the "beech-gap" zone in the central South Island. Mitochondrial DNA-based genetic relationships were estimated both within and among taxa representing ten genera, which included log-dwelling velvet-worms (Onychophora), a mixture of geographically localised and widespread beetles (Coleoptera), as well as subalpine- and alpine-adapted cockroaches (Blattodea), grasshoppers and crickets (Orthoptera). Molecular data were not consistent with the 'Ancient Fault' hypothesis, given that the observed depths of divergences were relatively shallow, and should postdate contact of the Pacific and Australasian continental plates (c. 20-25 Million years before present, Mybp). In contrast, while phylogeographic patterning in nearly all taxa examined showed spatial patterns not inconsistent with the 'glacial extirpation' hypothesis (< 1.8 Mybp), this was undermined by the fact that most estimates of divergence times suggested that the differentiated forms predated the Pleistocene origin of vicariance. Thus the authors invoked a third scenario, Pliocene mountain building (c. 2-7 Mybp), as the most likely explanation for the observed patterns of endemism and inferred timing of speciation events.

Comparative Phylogeography: Revealing Common Genetic Patterns in Faunal Communities, and Identifying Surrogate Taxa for Biodiversity Indication

Through revealing the degree to which members of particular biotic assemblages have responded to climatic and geographic events in concert, comparative phylogeography can help identify biodiversity 'hotspots' and prioritize regions in need of protection (Avise 2000, Kuchta and Meyer 2001, Moritz and Faith 1998). Importantly, the greater the ecological and taxonomic diversity of the suite of species examined in comparative studies, the more widely applicable the findings will be (Zink 1996). As expected, it is clear that the level of regional and subregional endemism is much higher in low vagility (flightless) invertebrates, such as saproxylic taxa, than in vertebrates (Yeates and others 2002). While the distribution patterns of saproxylic invertebrates yield important insights into the pattern of endemism and effects of environmental change (Yeates and others 2002), comparative phylogeography has the special property of providing an empirical framework to explicitly assess the relative influence of various evolutionary processes in promoting and maintaining biodiversity. Individual species and whole communities are dynamic in space and time (Moritz and others 2000). Thus process-oriented conservation strategies are likely to be much more effective in a changing world than those that assume a static distribution of biodiversity (Bush 1996).

Moritz and others (2001) proposed that the efficiency of surrogate taxa in reflecting common biogeographic patterns that result from long-acting processes such as climate-induced vicariance is likely to depend on the spatial scale over which the species operate. To test this hypothesis, these authors examined the phylogeography of a suite of taxa with contrasting levels of local endemicity and dispersal abilities (including invertebrates, plants and vertebrates) from tropical rainforests in northeast Queensland, Australia. Results showed that, despite an overall congruence in phylogeographic patterning, the efficiency of surrogacy for biodiversity indication among taxa was highly asymmetric: the tremendously diverse and narrowly distributed invertebrates were strong predictors of conservation priorities for the less diverse and more broadly distributed vertebrates (and to a slightly lesser extent, plants), but not vice-versa. This asymmetry was attributed to the finer-scale distribution and greater species richness of the invertebrates, both of which serve to increase information content, and hence improve their ability to capture spatial patterns of biodiversity in other groups. Similar conclusions have been reached for ground-dwelling arthropods in temperate Australian forests (Ferrier and others 1999).

Hugall and others (2002) used the phylogeography of an Australian land snail (*Gnarosophia bellendenkerensis*), endemic to the tropical rainforests of northeast Queensland, to evaluate predictions based on palaeoclimatic modelling regarding the location and size of Pleistocene—Holocene refugia. This animal is a leaf litter / log generalist, and is expected to have low vagility. Findings from the snail mtDNA phylogeography were generally consistent with predictions from modelling using the BIOLCLIM procedure (Busby 1991), whereby potential former distributions for species are predicted by first deriving an environmental envelope from present-day distributions, then mapping this onto inferred palaeoclimatic surfaces. The presence of multiple refugia was corroborated by both molecular and palaeoclimatic data, and repeated temporal fluctuations in rainforest area and connectivity were cited as being the principal cause of deeply divergent geographically localised snail lineages. Interestingly, comparison with co-distributed herpetofauna (rainforest-restricted lizards and frogs) revealed that the snail phylogeography was essentially a composite of the patterns seen in each of the vertebrate species. The authors suggested that the snail captured the major population structure of other unrelated taxa owing to the finer geographic scale over which it operated.

CASE STUDY: PHYLOGEOGRAPHY OF A SAPROXYLIC ‘GIANT’ SPRINGTAIL FROM SOUTH-EAST AUSTRALIA

Using Tallaganda State Forest (SF) in south-east New South Wales, Australia, as a model system, we (together with collaborators) are employing comparative phylogeography to investigate the relative influence of habitat and species’ biology upon the present-day spatial distribution of genetic diversity in sedentary forest invertebrates. This research seeks to inform forestry management practices and guide conservation strategies by identifying areas that are home to evolutionarily distinct lineages of multiple log-dependent invertebrate taxa. In this program, phylogeographic patterns of paired representatives of a suite of co-distributed saproxylic taxa are being compared to each other, and to other very different members of the rotting-log community.

Recently, Garrick and others (2004) showed that an unusually large and extremely dorso-ventrally flattened saproxylic springtail (Collembola: Neanuridae) from Tallaganda SF exhibits very high local endemism over spatial scales of c. 10 kilometres or less (figs. 1A and 1B). Further, the spatial arrangement of genetically distinct populations was found to correspond with four ‘microbiogeographic’ regions identified a priori on the basis of topography and estimated landscape history. In particular, hydrological divisions of Tallaganda SF seem to capture the major phylogeographic structure of this taxon, to the extent that locations of abrupt genetic contact zones mirror those of major and/or minor catchment boundaries with considerable precision. Molecular data indicated that population divergences of the focal Collembolon at Tallaganda SF were likely to be of considerable antiquity, possibly originating in the late Pliocene—late Miocene (2.5 to 7 Mybp). Genetic data also detected at least two subsequent lineage-splitting events that occurred on different timescales (i.e., late Pliocene—early Pleistocene > 0.7 to 2 Mybp, and mid-late Pleistocene < 0.7 to 0.01 Mybp), all three of which correspond with major palaeoclimatological events that affected south-east Australia.

It has previously been proposed that areas of high diversity (e.g., hybrid zones, genetic clines, or historical refugia) should be targeted for conservation (Faith and others 2003, Mesibov 1994). Indeed, in this model system, the areas most likely to have repeatedly served as refugia for upland cool-loving saproxylic invertebrates during cold dry glacial periods are the commercially valuable tall moist eucalypt forests that occur in east-facing, topographically heterogeneous areas (fig. 1B). In order to conserve biodiversity, it is essential that evolutionarily important habitat types such as these be represented in the reserve system, and where they occur within production forests, the needs of saproxylic invertebrates must be afforded special consideration in management practices (Grove 2002c). Further, it is important to recognise the distinction between geographic areas that contain concentrations of ancient lineages versus those in which recently derived lineages occur. Although areas of both types are important reservoirs of biodiversity, the rationale for conserving them, and the optimal strategies for doing so, differ. In the former case, protection of irreplaceable phylogenetic diversity should focus on maintaining large continuous tracts of undisturbed native forest, while in the latter case, adaptive diversity is best protected by maintaining the ecological integrity and connectivity of habitats that contribute environmental gradients and ecotones across heterogeneous landscapes (Moritz and others 2000). In the case of saproxylic invertebrates, the loss of ecological integrity of dead wood habitats in production forests can be prevented by ensuring a spatially and temporally continuous (and adequate) supply of large-diameter commercially overmature trees, and by allowing dead wood to decompose in situ (Grove 2002a, 2002c).

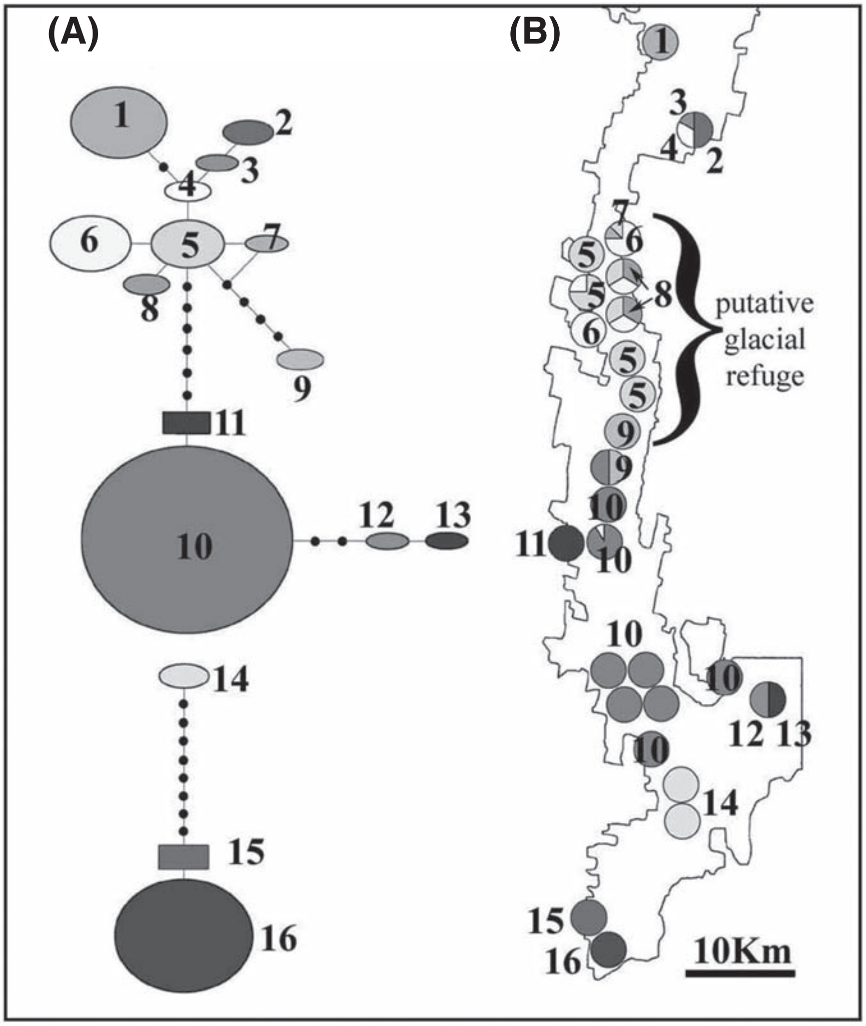


Figure 1—Phylogeography of a saproxylic springtail at Tallaganda State Forest in the Great Dividing Range of South-east Australia. (A) Statistical parsimony network depicting genealogical relationships among genetic lineages. Shaded ovals (also numbered) represent unique mtDNA sequences (where area is proportional to frequency), each single black line represents one mutational step, and solid black circles represent "missing" haplotypes, i.e., not sampled or extinct. Two disconnected networks were produced owing to the very large number of mutational steps between mtDNA lineages from the southern section of the forest (bottom network) and all other lineages (top network). (B) Map of Tallaganda State Forest showing spatial distribution of mtDNA lineages [numbered as in (A)], where each pie chart represents a single sampling site, i.e., log. This Collembolon shows very strong geographic associations among genetic lineages, and the hypothesized glacial refuge contains high evolutionary diversity.

CONCLUSIONS

Genetic diversity represents a fundamental component of biodiversity (Moritz and Faith 1998), and its conservation is critical in maintaining evolutionary processes (Frankham and others 2002). In order to achieve this, habitat reservation and forestry management needs to take account of natural genetic-geographic patterns. It is becoming clear that the predominant focus on vertebrates and vascular plants in conservation research and planning (Stiling 1999) is likely to result in management strategies that fail to cater for a large proportion of the biodiversity present in sedentary invertebrate taxa, such as the ecologically specialized saproxylic fauna. Indeed, phylogeographic studies have repeatedly demonstrated that, in these groups, (1) traditional morphological taxonomy tends to underestimate genetic diversity, (2) conservation strategies focused at and above the species-level are inadequate, and (3) it is not atypical for sedentary invertebrates to exhibit high local endemism over spatial scales in the order of several kilometers or less. Accordingly, invertebrates of low mobility have been identified as particularly effective surrogates for biodiversity indication.

Given that the proportion of total forest area that can be dedicated to the protection of biodiversity is limited, it is essential to maximize the conservation benefit of reserves and managed forest lands. There is urgent need to focus on conservation strategies and sustainable management practices outside of protected areas, as the geographic scale necessary to permit natural evolutionary and biogeographic processes to continue is often greater than can reasonably be accommodated within reserves (Moritz and others 2000). Production forestry can be tailored (if the will exists) to meet the needs of conservation. Indeed, when managed with the conservation of saproxylic fauna as a specific objective, production forests have the potential to maintain natural forest dynamics and ecological processes at the landscape-level (Grove 2002c), while still providing an economic return on timber (Grove 2002a). In contrast to organism-specific conservation strategies, the identification of areas that harbour (and more importantly, promote) the greatest proportion of biodiversity in multiple taxa offers an insight into optimal management goals that would positively impact taxonomically wide-ranging biota. Comparative phylogeography provides an empirical framework for delineating areas of congruent endemism and consequent high conservation priority, while simultaneously yielding insights into evolutionary processes driving the present-day geographic distribution of biodiversity (Avise 2000, Arbogast and Kenagy 2001, Kuchta and Meyer 2001, Moritz and Faith 1998).

ACKNOWLEDGMENTS

We thank Simon Grove and Jim Hanula for organising the Insect Biodiversity and Dead Wood symposium at the XXII International Congress of Entomology, Brisbane, 2004. The Tallaganda comparative phylogeography project is supported by the Australian Research Council (grant DP-0211156 to PS and Dave Rowell), a DEST Systemic Infrastructure Initiative Grant, and Holsworth Wildlife Research Fund grants to RCG and CJS. Noel Tait, Dave Rowell and Penny Greenslade have made critical contributions throughout the program, as have all members (past and present) of the Invertebrate Molecular Population Biology Research group at La Trobe University and the Australian National University (see http://www.latrobe.edu.au/genetics/staff/sunnucks/homepage/). This manuscript was improved by comments from Simon Grove and Jim Hanula.

LITERATURE CITED

Arbogast, B.S.; Edwards, S.V.; Wakely J. [and others]. 2002. Estimating divergence times from molecular data on phylogenetic and population genetic timescales. Annual Review of Ecology and Systematics. 33: 707-740.

Arbogast, B.S.; Kenagy, G.J. 2001. Comparative phylogeography as an integrative approach to historical biogeography. Journal of Biogeography. 28: 819-825.

Avise, J.C. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics. 18: 489-522.

Avise, J.C. 1989. A role for molecular geneticists in the recognition and conservation of endangered species. Trends in Ecology and Evolution. 4: 279-281.

Avise, J.C. 1998. The history and purview of phylogeography: a personal reflection. Molecular Ecology. 7: 371-379.

Avise, J.C. 2000. Phylogeography: the history and formation of species. Cambridge, MA: Harvard University Press.

Ballard, J.W.; Whitlock, M.C. 2004. The incomplete natural history of mitochondria. Molecular Ecology. 13: 729-744.

Bohonak, A.J. 1999. Dispersal, gene flow, and population structure. The Quarterly Review of Biology. 74: 21-45.

Bond, J.E.; Sierwald, P. 2002. Cryptic speciation in the *Anadenobolus excisus* millipede species complex on the island of Jamaica. Evolution. 56: 1123-1135.

Broughton, R.E.; Harrison, R.G. 2003. Nuclear gene genealogies reveal historical, demographic and selective factors associated with speciation in field crickets. Genetics: 163, 1389-1401.

Brower, A.V.Z. 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. Proceedings of the National Academy of Sciences of the USA. 91: 6491-6495.

Brown, W.M.; George, M., Jr.; Wilson, A.C. 1979. Rapid evolution of animal mitochondrial DNA. Proceedings of the National Academy of Sciences of the USA. 76: 1967-1971.

Busby, J. 1991. BIOCLIM—a bioclimate analysis and prediction system. In: Margules, C.R.; Austin, M.P., eds. Nature conservation: Cost effective biological surveys and data analysis Melbourne, Australia: CSIRO Publishing: 64-68.

Bush, M.B. 1996. Amazonian conservation in a changing world. Biological Conservation. 76: 219-228.

Crandall, K.A.; Bininda-Emonds, O.R.P.; Mace, G.M. Wayne, R.K. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology and Evolution. 15: 290-295.

Endler, J.A. 1982. Problems in distinguishing historical from ecological factors in biogeography. American Journal of Zoology. 22: 441-452.

Faith, D.P.; Reid, C.A.M.; Hunter, J. 2003. Integrating phylogenetic diversity, complementarity and endemism for conservation assessment. Conservation Biology. 18: 255-261.

Ferrier, S.; Gray, M.R.; Cassis, G.A.; Wilkie, L. 1999. Spatial turnover in species composition of ground-dwelling arthropods, vertebrates and vascular plants in North-east New South Wales: implications for selection of forest reserves. In: Ponder, W.; Lunney, D., eds. The other 99%. The conservation and biodiversity of invertebrates. Mosman, Australia: The Royal Zoological Society of New South Wales: 68-76.

Frankham, R.; Ballou, J.D.; Briscoe, D.A. 2002. Introduction to conservation genetics. pp. 1-20. Cambridge, England: Cambridge University Press.

Garrick, R.C.; Sands, C.J.; Rowell, D.M. [and others]. 2004. Phylogeography recapitulates topography: very fine-scale local endemism of a saproxylic 'giant' springtail at Tallaganda in the Great Dividing Range of South-east Australia. Molecular Ecology. 13: 3329-3344.

Grove, S.J. 2002a. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian tropical rainforest. Biological Conservation. 104: 149-171.

Grove, S.J. 2002b. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecological Indicators. 1: 171-188.

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

Hare, M.P. 2001. Prospects for nuclear gene phylogeography. Trends in Ecology and Evolution. 16: 700-706.

Harrison, R.G. 1989. Animal mitochondrial DNA as a genetic marker in population and evolutionary biology. Trends in Ecology and Evolution. 4: 6-11.

Heatwole, H. 1987. Major components and distributions of the terrestrial fauna. In: Dyne, G.R.; Walton, D.W., eds.,The Fauna of Australia, Vol. 1. Canberra, Australia Capital Territory: Australian Government Publishing Service: 69-100.

Holland, B.S.; Hadfield, M.G. 2002. Islands within an island: phylogeography and conservation genetics of the endangered Hawaiian tree snail *Achatinella mustelina*. Molecular Ecology. 11: 365-375.

Hugall, A.; Moritz, C.; Moussalli, A.; Stanisic, J. 2002. Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). Proceedings of the National Academy of Sciences of the USA. 99: 6112-6117.

Hutchinson, C.A., III; Newbold, J.E.; Potter, S.S.; Edgell, M.H. 1974. Maternal inheritance of mammalian mitochondrial DNA. Nature. 251: 536-538.

Ibrahim, K.M.; Cooper, J.B.; Hewitt, G.M. 2002. Testing for recombination in a short nuclear DNA sequence of the European meadow grasshopper, *Chorthippus parallelus*. Molecular Ecology. 11: 583-590.

Knowles, L.L. 2004. The burgeoning field of statistical phylogeography. Journal of Evolutionary Biology. 17: 1-10.

Knowles, L.L.; Maddison, W.P. 2002. Statistical phylogeography. Molecular Ecology. 11: 2623-2635.

Kobayashi, N.; Shirai, Y.; Tsurusaki, N. [and others]. 2000. Two cryptic species of the phytophagous ladybird beetle *Epilachna virgintioctopunctata* (Coleoptera: Coccinellidae) detected by analyses of mitochondrial DNA and karyotypes, and crossing experiments. Zoological Science. 17: 1159-1166.

Kuchta, S.R.; Meyer, D. 2001. A genealogical view of geographic variation. Molecular Ecology. 10: 2569-2576.

Lunt, D.H.; Hyman, B.C. 1997. Animal mitochondrial DNA recombination. Nature. 387: 24.

Manel, S.; Schwartz, M.K.; Luikart, G.; Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution. 18: 189-197.

Mesibov, R. 1994. Faunal breaks in Tasmania and their significance for invertebrate conservation. Memoirs of the Queensland Museum. 36:133-136.

Moritz, C. 1994. Defining 'evolutionary significant units' for conservation. Trends in Ecology and Evolution. 9: 373-375.

Moritz, C.; Faith, D.P. 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. Molecular Ecology. 7: 419-429.

Moritz, C.; Patton, J.L.; Schneider, C.J.; Smith, T.B. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics. 31: 533-563.

Moritz, C.; Richardson, K.S.; Ferrier, S. [and others]. 2001. Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. Proceedings of the Royal Society of London Series B. 268: 1875-1881.

Peterson, M.A.; Denno, R.F. 1998. The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. The American Naturalist. 152: 428-446.

Ryder, O.A. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution. 1: 9-10.

Salomone, N.; Emerson, B.C.; Hewitt, G.M.; Bernini, F. 2002. Phylogenetic relationships among the Canary Island Steganacaridae (Acari, Oribatida) inferred from mitochondrial DNA sequence data. Molecular Ecology. 11: 79-89.

Schiegg, K. 2000. Are there saproxylic beetle species characteristic of high dead wood connectivity? Ecography. 23: 579-587.

Stiling, P. 1999. Ecology: theories and applications. 3rd edition. Upper Saddle Lake, NJ: Prentice-Hall Inc.

Sunnucks, P. 2000. Efficient genetic markers for population biology. Trends in Ecology and Evolution. 15: 199-203.

Templeton, A.R. 1998. Nested clade analyses of phylogeographic data: testing hypotheses about gene flow and population history. Molecular Ecology. 7: 381-397.

Templeton, A.R. 2004. Statistical phylogeography: methods of evaluating and minimizing inference errors. Molecular Ecology. 13: 789-809.

Templeton, A.R.; Routman, E.; Phillips, C.A. 1995. Separating population structure from population history: a cladistic analysis of the geographic distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. Genetics. 140: 767-782.

Thomas, J.A.; Morris, M.G. 1994. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom. Philosophical Transactions of the Royal Society of London Series B. 344: 47-54.

Trewick, S.A. 1998. Sympatric cryptic species in New Zealand Onychophora. Biological Journal of the Linnean Society 63: 307-329.

Trewick, S.A. 2001. Identity of an endangered grasshopper (Acrididae: Brachaspis): taxonomy, molecules and conservation. Conservation Genetics. 2: 233-243.

Trewick, S.A.; Wallis, G. 2001. Bridging the "beech-gap": New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. Evolution. 55: 2170-2180.

Warren, M.S.; Key, R.S. 1991. Woodlands: past, present and potential for insects. In: Collins, N.M.; Thomas, J.A., eds. The conservation of insects and their habitats. London: Academic Press: 155-212.

Wilcox, T.P.; Hugg, L.; Zeh, J.A.; Zeh, D.W. 1997. Mitochondrial DNA sequencing reveals extreme genetic differentiation in a cryptic species complex of neotropical pseudoscorpions. Molecular Phylogenetics and Evolution. 7: 208-216.

Wilson, E.O. 2001. The diversity of life. London: Penguin Books Ltd.

Yeates, D.K.; Bouchard, P.; Monteith, G.B. 2002. Patterns and levels of endemism in the Australian Wet Tropics rainforest: evidence from flightless insects. Invertebrate Systematics. 16: 605-619.

Yee, M.; Yuan, Z.Q.; Mohammed, C. 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. Tasforests. 13: 119-128.

Zink, R.M. 1996. Comparative phylogeography in North American birds. Evolution. 50: 308-317.

PHYLOGEOGRAPHY OF TWO AUSTRALIAN SPECIES OF FUNNEL WEB SPIDER (ARANEAE: MYGALOMORPHAE: HEXATHELIDAE) IN TALLAGANDA STATE FOREST, NEW SOUTH WALES

Amber S. Beavis and David M. Rowell[1]

Abstract—Decomposing logs are habitat for invertebrate species occupying a range of ecological niches. A collaborative research project is examining patterns of genetic endemism among saproxylic (dependent on decaying wood) invertebrates across the Tallaganda region of New South Wales, Australia. An earlier study of an unnamed species of 'giant' Collembolon revealed strong population structuring suggesting that the saproxylic habitat has been a major factor influencing the evolution and speciation of some invertebrates. Two species of funnel web spiders, one in each of the genera *Hadronyche* and *Atrax,* are found throughout Tallaganda. Although ecologically similar, the *Hadronyche* species is log-dwelling whereas the *Atrax* species is ground burrowing. The niche partitioning of these species allows the separation of species and habitat as contributing factors to the patterns of local endemism found in this system. Hence, the addition of funnel web spiders to this study of log-dwelling invertebrates is central to determining whether the saproxylic habitat induces consistent and predictable outcomes in the population structuring of diverse taxa. The resolution of this issue will permit the establishment of informed conservation priorities for invertebrates in Tallaganda State Forest. The phylogeography of the *Hadronyche* and *Atrax* species was investigated using mitochondrial sequence data. We found high levels of sequence divergence (average = 0.088) in *Atrax* accompanied by spatial structuring of haplotypes, whilst *Hadronyche* displayed low sequence divergence (0.014) and an absence of any spatial structuring of haplotypes. These findings indicate differential responses of the two species to Quaternary (<0.4Mybp) glacial-interglacial cycling, namely, that *Atrax* persisted in gully refuges during glacial periods whilst *Hadronyche* became locally extinct during glacial periods and recolonised the region from outside Tallaganda during the most recent inter-glacial. The differential persistence of *Atrax* and *Hadronyche* will require the implementation of management interventions appropriate to each species.

INTRODUCTION

Decomposing logs on the forest floor, which constitute a part of the saproxylic environment, provide habitat for a wide array of invertebrate taxa. The saproxylic component of biodiversity, though little-studied, is diverse, containing representatives of all major insect orders (Grove and Stork 1999, Key 1993), including a disproportionately high number of threatened invertebrate species (Jonsson and Kruys 2001). In addition, many saproxylic invertebrates appear to be poor dispersers (Hammond 1984) and are ecologically specialized, occupying specific and narrow niches (Yee and others 2001). This is of conservation concern given that the saproxylic habitat is also susceptible to the impacts of current forest practices such as clearfelling, regeneration burning and intensive harvesting of coarse woody debris (Grove 2002). Consequently there is a clear need to establish conservation priorities and to implement management strategies for the saproxylic fauna. It is apt, then, that the same suite of characteristics which make saproxylic invertebrates vulnerable also cause their own population histories to be closely linked with that of their environment, thus providing a system well suited to phylogeographic analysis and subsequent establishment of informed conservation strategies.

Phylogeography is the study of the biogeographical and evolutionary processes which have determined the distributions of extant genealogical lineages (Avise 1998, 2000; Bossart and Prowell 1998; Garrick and others 2005; Moritz and others 2001). As a discipline, phylogeography has the unique power to investigate more recent evolutionary events occurring around and below the species level (Avise 1998). It has been argued that this focus upon relatively recent history has the effect that invertebrate taxa may be particularly informative study species; Moritz and others (2001) proposed that taxa that experience their environment at a fine spatial scale display the effects of long-acting environmental changes, such as glacial/ inter-glacial cycling, to a greater degree than taxa that experience their environment on a broader scale. For example, during the Quaternary, vertebrate taxa may have been driven to local extinction by climatic oscillations, and have subsequently recolonised from separate populations (Moritz and others 2001). In contrast, invertebrate taxa are often characterized by a restricted geographic range and low vagility. As such it is likely that, when exposed to climatic oscillations, many species of invertebrate survived in smaller, local, refugia, thus retaining the spatial genetic structuring which forms the basis of phylogeographic studies (Keyghobadi and others 1999, Moritz and others 2001). We propose that the restricted dispersal and habitat-specificity characteristic of many log-dwelling invertebrates provides a model system for inferring landscape history.

The Tallaganda Model

The present phylogeographic study of two unnamed species of funnel web spider is one component of a broader study encompassing a suite of saproxylic invertebrates (described in Garrick and others 2004). Focusing on the Tallaganda region (Tallaganda State Forest, Gourock National Park and

---

[1] Amber S. Beavis, PhD candidate, Division of Botany & Zoology, Australian National University, ACT, 0200; and David M. Rowell, Australia; Reader in Evolutionary Genetics.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Badja State Forest; collectively referred to as 'Tallaganda'), in south-eastern New South Wales, Australia, this study aims to investigate whether the saproxylic habitat has induced consistent and predictable outcomes in the population structuring of diverse taxa. To date, the spatial structuring of a saproxylic 'giant' springtail at Tallaganda has revealed congruence with five *a priori* microbiogeographic regions previously defined with reference to the topography and hydrology of Tallaganda in addition to an assessment of the probable palaeoclimatological history of the region (Garrick and others 2004).

Tallaganda

The Tallaganda region (35°35'S-35°44'S and 149°28'E-149°30'E) is a 100km long (north/south) by 3-20km wide (east/west) section of continuous, temperate, forest situated on the spine of the Gourock Range. The forest connects to the Great Dividing Range via Deua National Park in the south, but is otherwise ecologically and topographically isolated, being surrounded by the low-lying Southern Tablelands. The following information is taken from: CSIRO 1969, Barclay and others 2000, Bowler 1982, Frakes and others 1987, Heatwole 1987, Hope 1994, Singh 1982, State Forests of NSW 1995, White 1990, White 1994. The region is categorized into a three-tier landscape: the low-lying and geologically recent coastal plain (altitude 600m), an escarpment which has been ecologically stable over the last 20 my (altitude 1000-1500m), and the ancient (< 50-70 myo) Great Dividing Range. The forest is primarily sclerophyll forest, ranging from wet to dry types dependent upon altitude, aspect and local climate. Tallaganda is strongly affected by the orographic influence of the Great Dividing Range. The eastern, coastal, slopes are subject to high orographic rainfalls and, consequently, are typified by wet sclerophyll forest, while the western slopes are subject to a rain shadow effect and are typified by dry sclerophyll forest. The region has been subject to logging on a regular basis since the 1890's. Prior to 1949 Tallaganda State Forest was harvested using selective logging techniques, where only trees suitable for commercial use are taken. After 1949 clear-felling techniques were implemented at Tallaganda. Clearfelling is "the localized removal of most or all trees followed by burning of debris" (State of the Environment Advisory Council 1996). At Tallaganda, however, debris is left on the forest floor rather than burnt.

The Tallaganda region has been subject to a series of climate change events: the Oligocene Refrigeration (25-36 mybp), the Mid-Miocene and Terminal Miocene cooling events (7-15 mybp), a period of extended cooling and drying in the Pliocene (3-5 mybp) and, of particular relevance here, glacial/ inter-glacial cycling during the Pleistocene (over the last 2.5 my). During the Pleistocene, glacial/ inter-glacial cycling had a distinct impact on Australian flora and fauna. At glacial maxima temperatures were 9°C cooler than modern temperatures. The cooler climate resulted in altitudinal shifts in vegetation, an occurrence documented in fossil pollen data taken from Lake George (NSW) which is adjacent to Tallaganda. Forests contracted, with the upper tree line decreasing by 1200-1500m, with the result that low-lying areas such as gullies became the location of forest fragments in a matrix of treeless steppe. It is hypothesized that these isolating events affected saproxylic invertebrates, impacting on historical gene flow to the extent that the effects may be observed in the spatial structuring of modern genealogical lineages (Bowler 1982; CSIRO 1969; Frakes and others 1987; Heatwole 1987; Hope 1994; Singh 1982; State Forests of NSW 1995; White 1990, 1994).

Funnel Web Spider Species: *Hadronyche* and *Atrax*

Two undescribed species of funnel web spider (Mygalomorpae: Hexathelidae) are found in very high densities at Tallaganda: *Hadronyche* sp. 1 and *Atrax* sp. 1 (hereafter referred to as *Hadronyche* and *Atrax*) These two species are ecologically similar: both are top-level predators, feeding opportunistically on invertebrates and small vertebrates; they are of a similar size (adult females of both species having carapace widths ranging between 7-11 mm); they are long-lived, females having a maximum lifespan of approximately 20 years (Levitt 1961); both are sessile following juvenile dispersal, although males wander for a short period following maturity (Wishart 1993); they construct burrows lined with silk and with trip lines extending from their entrance (Hickman 1964, Levitt 1961). The two species exist sympatrically, however, they exhibit niche partitioning in their choice of habitat. *Hadronyche* is exclusively saproxylic, occupying burrows within decomposing logs. In contrast, *Atrax* builds ground burrows directly into the soil, the entrances to which may be found beneath logs, rocks or in open ground. Thus, *Hadronyche* appears to specialize in the saproxylic habitat, with the result that individuals are restricted to dispersing between logs, presumably resulting in a patchy distribution. In contrast, *Atrax* appears to specialize in the forest-floor habitat with the result that individuals may disperse along a gradient resulting in a continuous distribution across the forest floor. Given the ecological differences between the two funnel web spider species under study, we predicted that the population genetic structure of *Hadronyche* would reflect the species' dependence upon the log habitat and produce a phylogeny that was highly structured according to spatial parameters. In contrast, we predicted that *Atrax*, being less restricted by habitat availability, would show high gene flow and be more genetically homogeneous across its range.

The addition of funnel web spiders to this comparative phylogeographic study of saproxylic invertebrates is key to distinguishing what factors have been responsible for the patterns of genetic structuring observed in saproxylic invertebrates to date (Garrick and others 2004). *Atrax* and *Hadronyche* species show the greatest disparity of habitat type within a pair of related taxa compared to the other organisms under study (Garrick and others 2004). The inclusion of a saproxylic and a ground-dwelling mygalomorph species in this study allows us to address the question of whether the patterns of spatial structuring found in saproxylic invertebrates to date are due to the saproxylic habitat or are a factor of being a forest-floor dwelling invertebrate of low vagility.

We investigated and compared the patterns of spatial structuring for *Hadronyche* and *Atrax* using mitochondrial DNA (mtDNA) sequence from Cytochrome Oxidase subunit I (COI). MtDNA is particularly suited to intraspecific phylogeographic studies as it has a relatively high mutation rate and does not recombine (reviewed in Avise 1998). We aimed to test the prediction that the spatial distribution of genetic diversity in the log-dependent species would display distinct structure reflecting the non-continuous nature of the log habitat, while the forest-floor dwelling species would be more homogeneous across the forest, as potential burrowing sites are essentially continuous.

MATERIALS AND METHODS

Taxon Sampling

Between 2002-2004 samples were collected from throughout the Tallaganda region. *Hadronyche* individuals were extracted from their burrows in logs, and *Atrax* were collected opportunistically from around log sites. Tissue samples were stored at -20°C.

Amplification and Sequencing of Mitochondrial DNA

Sequence was collected from 51 *Hadronyche* individuals and 18 *Atrax* individuals. Genomic DNA was isolated from 1mm^3 muscle tissue using a QIAGEN DNeasy Tissue Kit. A 700 base pair (bp) region of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified using the universal primer pair Lco1490: 5'—GGTCAACAAATCATAAAGATATTGG and Hco2198: 5'—TAAACTTCAGGGTGACCAAAAAATCA (Folmer and others 1994). Using a thermal cycler, amplifications were as follows: 1 cycle of 94°C for 3 min, 65°C for 30s, 72°C for 45s; 2 cycles of 94°C for 30s, 60°C for 20s, 72°C for 45s; 2 cycles of 94°C for 45s, 55°C for 20s, 72°C for 45s; 3 cycles of 94°C for 45s, 50°C for 20s, 72°C for 45s; 94°C for 45s, 45°C for 20s, 72°C for 45s; 40 cycles of 94°C for 45s, 45°C for 20s, 72°C for 45s; 72°C for 3min. Amplification reactions consisted of 2μL of template DNA; 2U Platinum *Taq*PCRx DNA Polymerase (Invitrogen); 4μL 10X PCR Buffer, Minus Mg; 2.4μL 50mM $MgCl_2$; 1.6μL 5mM dNTps; 1μL each 10μM primer; in 40μL total volume. Polymerase chain reaction (PCR) products were purified using 3M NaAc with an ethanol precipitation. PCR products were sequenced in both directions using Big Dye Terminator (Applied Biosystems) and run on an ABI3100 Genetic Analyzer. Sequences were aligned in SEQUENCHER (version 3.0, Gene Codes Corporation, Mi). Ambiguous end regions were removed so that all individuals within each genus were analysed over the same sequence length. No stop codons were found within the reading frame. After alignment and cropping, a 500bp segment was analysed for *Hadronyche* and a 600bp segment was analysed for *Atrax*. Unique haplotypes were determined using a pairwise distance matrix.

Analysis

Sequence variation was calculated using the general time-reversible (GTR) model (Tavaré 1986) with corrected p values (using PAUP* V.4.0). The GTR model assumes that the rate of change from base *a* to *b* is the same as from base *b* to *a*. Phylogenetic relationships amongst mtDNA COI sequences were estimated for both species via a haplotype network based on statistical parsimony (Templeton and others 1992) using the program TCS V.1.13 (Clement and others 2000). Genealogical relationships were estimated for *Atrax* and *Hadronyche* separately from one another via a statistical parsimony haplotype network. This technique uses a parsimony-based algorithm to estimate the minimum number of base substitutions between haplotypes. TCS fails to connect haplotypes which differ by more than 10 substitutions. According to coalescence theory, the most common and widespread haplotype is most likely to be the ancestral haplotype (Posada and Crandall 2001). An important feature of this technique is its adherence to a 95 percent confidence limit for the acceptance of hypothetical networks.

RESULTS

Both species were abundant across Tallaganda. Comprehensive sampling was conducted for *Hadronyche*, however, *Atrax* sampling was more patchy. Fifteen haplotypes were detected for both *Hadronyche* (n = 51) and *Atrax* (n = 18). Mean corrected sequence divergence between pairs of sequences (GTR model) was 0.014 for *Hadronyche* and 0.088 for *Atrax*.

Haplotype networks for *Atrax* (see fig. 1) and *Hadronyche* (see fig. 2) were constructed using a parsimony algorithm. The haplotype 'network' showing the relationships between *Atrax* individuals was disjointed, connecting very few of the haplotypes (one group of four haplotypes; three groups of two haplotypes; five unconnected haplotypes). All connected haplotypes were found to be located at adjacent sites. The disjointed nature of the *Atrax* network may be due to two factors. First, it may be indicative of deep structure, extant haplotypes being relics from ancient population contractions or extinctions. Second, it may be due to the continued presence of extant but unsampled haplotypes.

In contrast, a haplotype network for *Hadronyche* indicated that the majority of samples represented a single haplotype. The most common haplotype formed the central hub of the network with 12 of 15 haplotypes being connected to it by a maximum of seven steps. The most common haplotype was also the most geographically widespread, occurring across the full range of the forest.

DISCUSSION

The primary aim of this preliminary study was to compare the patterns of genetic diversity over a similar spatial scale for two species of funnel web spider: *Atrax* (forest-floor dwelling) and *Hadronyche* (exclusively log-dwelling). The secondary

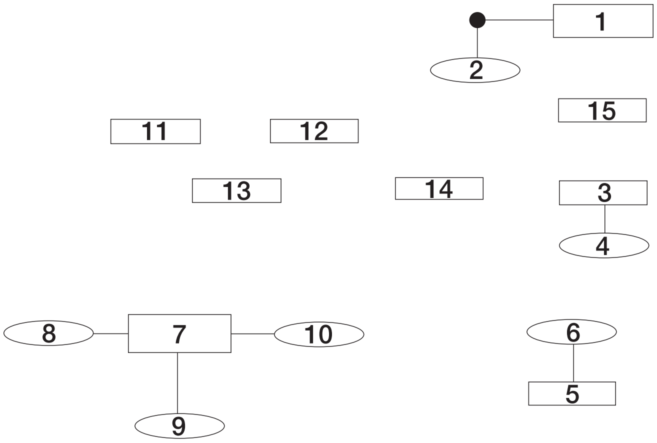


Figure 1—Haplotype network for *Atrax*. Networks were created in the program TCS version 1.13 using a maximum parsimony algorithm. Sampled haplotypes are numbered as an identifier and missing haplotypes are represented as black dots. Rectangles represent the "ancestral hub" of the network according to coalescence theory (Posada and Crandall 2001). Larger rectangles and circles represent more common haplotypes. The network for *Atrax* is disjointed with very few haplotypes being connected. Connected haplotypes were found to be located at adjacent sites.

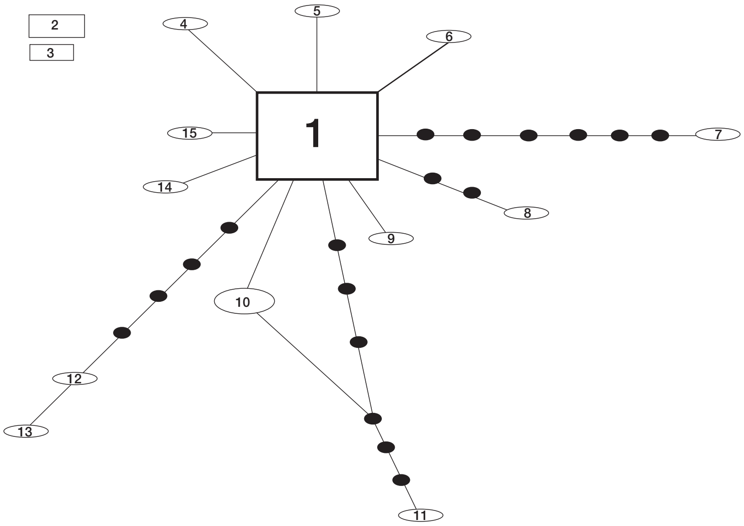


Figure 2—Haplotype network for *Hadronyche*. *Hadronyche* shows connectivity amongst haplotypes which radiate from a single common haplotype (haplotype 1). The most common haplotype was found to occur across the full range of Tallaganda.

aim of this study was to use this set of preliminary results to look for congruence between the extent of phylogeographic structuring displayed by these two species and other taxa of saproxylic organisms examined in the same model system at Tallaganda. The addition of two funnel web spider genera with different levels of log-dependence (log-dwelling versus forest floor-dwelling) allowed us to ask whether the patterns found amongst log-dwelling invertebrates are due to taxonomic factors. The data set discussed here is preliminary and, as such, is focused upon determining the parameters for the ongoing study.

All analyses indicated that we should unequivocally reject our initial hypothesis that the spatial distribution of genetic diversity in *Hadronyche* would be highly structured, while *Atrax* would be more homogeneous. Rather, the opposite was found: *Hadronyche* is surprisingly uniform across the forest whilst *Atrax* displays phylogeographic genetic structure. A key finding of this study was the order of magnitude difference between the mean sequence divergence of the two species. Typically, low sequence divergence is indicative of recent population expansion whilst high sequence divergence is congruent with an ancient origin (Hewitt 2000, Riddle 1996, Steiner and Catzeflis 2004, Zink and others 2000). Given the habitat preferences observed, this finding was unexpected and invites further investigation into the historical demographic processes responsible for the phylogeographic patterns displayed by the taxa. The patterns displayed by *Hadronyche* are characteristic of Type IV trees recognized by Avise and others (1987), namely, a shallow, unstructured, tree which is typical of a recent range expansion. The low sequence divergence (mean one percent GTR), homogeneous geographic structuring of haplotypes and the connection of 12 (of a possible 15) haplotypes to a central network hub, are consistent with recent population expansion and a lack of isolating barriers (Avise and others 1987, Zink 2002). In contrast, the deep sequence divergence (mean nine percent GTR) and the disjunct haplotype network, displayed by *Atrax* (Type I: deep haplotype trees showing geographic structuring) is congruent with a long history in the region and the presence of isolating barriers (Avise and others 1987, Zink 2002).

The repercussions of these finding within the context of conservation are twofold. First, the high sequence divergence (8.8 percent) within *Atrax*, combined with the disjointed nature of the haplotype network for this taxon, suggests that this species may be highly genetically structured over the Tallaganda region. If so, identification of evolutionarily significant units (ESUs) and management units (MUs) within *Atrax* will be necessary to ensure the conservation of genetic diversity within this species. In addition, the 8.8 percent sequence divergence within *Atrax* raises the question of whether unidentified species within this genus are present in Tallaganda. The genetic species concept has been applied to taxa displaying four percent sequence divergence (Holder and others 1999) and genetic distances of between two percent and 11 percent have been recognized as carrying a high probability of being indicative of species status (Ballard and others 2002, Bradley and Baker 2001). Given the presence of spatial structuring of *Atrax* haplotypes—which is congruent with the species being a poor disperser—and the high level of genetic variation occurring within the species, there is a clear need for an extensive study into whether current logging practices in Tallaganda have the potential to adversely impact on ground dwelling funnel web spiders both directly and via habitat fragmentation. Clearfelling, for example, where all trees in a localized area are felled in a single operation, results in extensive disturbance of soil by forestry machinery. Recorded impacts of forestry machinery include soil displacement, soil compression and a decrease in soil permeability (Horn and others 2004). Soil displacement caused by the wheel tracks of machinery may occur to depths of 56 centimetres (Horn and others 2004), which encompasses the habitat of *Atrax*. As such, the damage caused by logging practices to *Atrax* habitat may have impacts at the level of the individual and the population; however, there are currently no empirical data in this area.

Second, the unexpectedly low sequence divergence and high connectivity of the haplotype network found in *Hadronyche* raises questions about the history of this species in Tallaganda. The phylogeographic patterns are consistent with recent population expansion and a lack of isolating barriers to dispersal. Widespread dispersal can be a characteristic of organisms with highly specialized and localized habitat requirements, as individuals must disperse further to find an appropriate habitat (Jung and Croft 2001). Given that *Hadronyche* has extremely specific habitat requirements, the homogeneous spatial structuring of the species over the area of Tallaganda suggests that the species has specialized habitat requirements to the extent that widespread dispersal is required. There is observational evidence that large *Hadronyche* juveniles and adults are unable to reestablish a burrow once disturbed. A one-off dispersal event, which potentially occurs in this system, would result in the confinement of an individual to its first choice of log habitat with the result that the fate of *Hadronyche* individuals would be intrinsically linked to the fate of the log they inhabit, that is, to their local environment. Consequently, *Hadronyche* individuals may be highly sensitive to any environmental change or disturbance as is typical of habitat specialists (Bolger and others 2000, Gascon and others 1999, Lynam 1997, Vandergast and others 2004). The shallow structure of the haplotype network for *Hadronyche* supports the species' probable life history strategy, being indicative of a recent range expansion followed by a rapid radiation.

We hypothesise that the glacial—interglacial cycling affected *Hadronyche* and *Atrax* differentially according to their habitat (Hewitt 1996, Hugall and others 2002, Schoswetter and others 2002, Tribsch and others 2002). *Atrax* individuals are not dependent upon logs, however, all mygalomorph species are susceptible to desiccation due to their two pairs of book lungs which present a large surface area for water-loss (Foelix 1982, Levi 1967, Schmitz and Perry 2000) Consequently, the geographic range of *Atrax* is intrinsically linked to climate and is therefore associated with overall patterns of forestation. When, during glacial periods, conditions became drier and forests contracted to gully refuges or were locally extinguished, *Atrax* individuals would persist only in gully refuges. In contrast, because *Hadronyche* is exclusively dependent on the log habitat and individuals are confined to the one log within their lifetime, glacial events have the potential to drive *Hadronyche* to negligible population densities or to local extinction. The shallow structure of the *Hadronyche* phylogeny suggests that the taxon has recolonised Tallaganda—potentially from the adjacent areas of the Great Dividing Range—since the end of the previous glacial period.

The results of this study have two implications. First, it appears that there is some congruence between the type of phylogeographic structuring of *Atrax* and that of Collembola (Garrick and others 2004). Second, a particularly striking finding of this study is that *Hadronyche*, an exclusively log-dwelling species, exhibits different patterns of phylogeographic structuring to other saproxylic taxa, namely Collembola (Garrick and others 2004). These preliminary findings suggest that the patterns exhibited by log-dwelling taxa are not unique to the log habitat, but rather are more likely to be associated with being forest-floor invertebrates of low vagility. Whilst Collembola species and other log-dwelling taxa may be log-associated, *Hadronyche* may be the only exclusively log-dwelling species which is also unable to move between logs under unfavourable environmental conditions. Thus, it seems that being a log-associated species of low vagility results in local endemism, so the identification of appropriate conservation units should be a priority. For exclusively saproxylic species, such as *Hadronyche*, the implications of being exclusively saproxylic may be extreme and carry a very real risk for local extinction if their habitat is not adequately catered for through appropriate management.

ACKNOWLEDGMENTS

We thank Simon Grove and Jim Hanula for organising the Insect Biodiversity and Dead Wood symposium at the XXII International Congress of Entomology, Brisbane, 2004. The input provided by Paul Sunnucks is also integral to the Tallaganda project. Chester Sands and Ryan Garrick provided guidance in the phylogenetic analysis and interpretation of this data. This manuscript was improved by comments from Paul Sunnucks, Simon Grove and Jim Hanula. The Tallaganda comparative phylogeography project is supported by the Australian Research Council (grant DP-0211156 to Paul Sunnucks and Dave Rowell).

LITERATURE CITED

Avise, J.C. 1998. The history and purview of phylogeography: a personal reflection. Molecular Ecology. 7: 371-379.

Avise, J.C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Avise, J.C.; Arnold, J.; Ball, R.M. [and others]. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics. 18: 489-522.

Ballard, J.W.O.; Chernoff, B.; James, A.C. 2002. Divergence of mitochondrial DNA is not corroborated by nuclear DNA, morphology or behaviour in *Drosopha simulans*. Evolution. 56(3): 527-545.

Barclay, S.; Ash, J.E.; Rowell, D.M. 2000. Environmental factors influencing the presence and abundance of a log-dwelling invertebrate. Journal of Zoology. 250: 425-436.

Bolger, D.T.; Suarex, A.V.; Crooks, K.R. [and others]. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecological Applications. 10: 1230-1248.

Bossart, J.L.; Powell, D.P. 1998. Genetic estimates of population structure and gene flow: limitations, lessons and new directions. Trends in Ecology and Evolution. 13: 202-206.

Bowler, J.M. 1982. Aridity in the late Tertiary and Quaternary of Australia. In: Evolution of the flora and fauna of arid Australia (eds. Barker, W.R.; Greenslade, P.J.M.). pp. 35-45. Peacock Publications, Frewville.

Bradley, R.D.; Baker, R.J. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy. 82(4): 960-973.

Clement, M.; Posada, D.; Crandall, K. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology. 9(10): 1657-1660.

CSIRO (Commonwealth Scientific and Industrial Research Organisation). 1969. The lands of the Queanbeyan-Shoalhaven area, ACT and NSW. Land Research Series. Number 24. CSIRO, Melbourne.

Foelix, R.F. 1982. Biology of spiders. pp 67-68. Harvard University Press, Cambridge, Massachusetts and London, England.

Folmer, O.; Black, M.; Hoeh, W. [and others]. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit 1 from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology. 3(5): 294-299.

Frakes, L.A.; McGowran, B.; Bowler, J.M. 1987. Evolution of Australian environments. In: The Fauna of Australia, Vol. 1 (eds. Dyne, G.R.; Walton, D.W.). pp. 69-100. Australian Government Publishing Service, Canberra.

Garrick, R.C.; Sands, C.J.; Rowell, D.M. [and others]. 2004. Phylogeography recapitulates topography: very fine-scale local endemism of a saproxylic 'giant' springtail at Tallaganda in the Great Dividing Range of South-east Australia. Molecular Ecology. 13: 3315-3330.

Garrick, R.C.; Sands, C.J.; Sunnucks, P. 2006. The use and application of phylogeography for invertebrate conservation research and planning. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22^{d} International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Gascon, C.; Lovejoy, T.E.; Bierregaard, R.O., Jr. [and others]. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation. 91: 223-229.

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

Grove, S.J.; Stork, N.E. 1999. The conservation of saproxylic insects in tropical forests: a research agenda. Journal of Insect Conservation. 2: 67-74.

Hammond, P.M. 1984. Changes in the British coleopterous fauna. In: The Changing Flora and Fauna of Britain. Proceedings of a Symposium of the Systematics Association (ed. Hawksworth, D.L.). pp. 323-369. Academic Press, London.

Heatwole, H. 1987. Major components and distributions of the terrestrial fauna. In: The Fauna of Australia, Vol. 1 (eds. Dyne, G.R.; Walton, D.W.). pp. 69-100. Australian Government Publishing Service, Canberra.

Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society. 58: 247-276.

Hewitt, G.M. 2000. The genetic legacy of the Quaternary ice ages. Nature. 405(6789): 907-913.

Hickman, V.V. 1964. On *Atrax infensus* sp.n. (Araneida: Dipluridae) its habits and a method of trapping males. Papers and Proceedings of the Royal Society of Tasmania. 98: 107-112.

Holder, M.T.; Erdmann, M.V.; Wilcox, T.P. [and others]. 1999. Two living species of coelacanths. Proceedings of the National Academy of Sciences, USA. 96: 12616-12620.

Hope, G.S. 1994. Quaternary vegetation. In: History of the Australian Vegetation: Cretaceous to Recent (ed. Hill, R.S.). pp. 368-389. Cambridge University Press, Cambridge.

Horn, R.; Vossbrink, J.; Becker, S. 2004. Modern forestry vehicles and their impacts on soil physical properties. Soil and Tillage Research. 79: 207-219.

Hugall, A.; Moritz, C.; Moussalli, A.; Stanisic, J. 2002. Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis*. Proceedings of the National Academy of Sciences, USA. K99: 6112-6117.

Jonsson, B.G.; Kruys, N. 2001. Ecology of woody debris in boreal forests. Ecological Bulletins. 49: 1-218.

Jung, C.; Croft, B.A. 2001. Ambulatory and aerial dispersal among specialist and generalist predatory mites (Acari: Phytoseiidae). Environmental Entomology. 30(6): 1112-1118.

Key, R. 1993. What are saproxylic invertebrates? In: Proceedings of the Ecological Society. Dead wood matters: the ecology and conservation of saproxylic invertebrates in England. English Nature, Petersborough, UK.

Keyghobadi, N.; Roland, J.; Strobeck, C. 1999. Influence of landscape on the population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology. 8: 1481-1495.

Levi, H.W. 1967. Adaptations of respiratory systems of spiders. Evolution. 21: 571.

Levitt, V. 1961. The funnel web spider in captivity. Proceedings of the Royal Zoological Society (NSW). 1958: 80-84.

Lynam, A.J. 1997. Rapid decline of small mammal diversity in monsoon evergreen forest fragments in Thailand. In: Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities (eds. Laurance, W.F.; Bierregaard, R.O.J). pp. 222-240. University of Chicago Press, Chicago, IL.

Moritz, C.; Richardson, K.S.; Ferrier, S. [and others]. 2001. Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a triopical rainforest biota. Proceedings of the Royal Society of London—Series B: Biological Sciences. 268(1479): 1875-1881.

Posada, D.; Crandall, K.A. 2001. The effect of recombination on the accuracy of phylogeny estimation. Journal of Molecular Evolution. 54(3): 396-402.

Riddle, B.R. 1996. The molecular phylogeographic bridge between deep and shallow history in continental biotas. Trends In Ecology and Evolution. 11(5): 207-211.

Rowell, D.M. 1980. Morphology and biosystematics of the genera *Atrax* and *Hadronyche*, with notes of *Bymainiella brindabella* (Mygalomorphae: Dipluridae). Honours Thesis, Australian National University.

Schmitz, A.; Perry, S.F. 2000. Respiratory system of arachnids I: morphology of the respiratory system of *Salticus scenicus* and *Euophrys lanigera* (Arachnida, Araneae, Salticidae). Arthropod Structure and Development. 29(1): 3-12.

Schöswetter, P.; Tribsch, A.; Niklfeld, H. 2002. Several Pleistocene refugia detected in the high alpine plant *Phyteuma globulariifolium* in the European Alps. Molecular Ecology. 11: 2637-2647.

Singh, G. 1982. Environmental upheaval: vegetation of Australasia during the Quaternary. In: A History of Australasian Vegetation (ed Smith, J.M.B.). pp. 90-108. McGraw-Hill, Sydney.

State Forests of NSW. 1995. Proposed forestry operations in the Queanbeyan and Badja management area, environmental impact statement. State Forests of New South Wales, Southern region. Pennant Hills, NSW, Australia.

State of the Environment Advisory Council. 1996. Australia: state of the environment 1996. CSIRO publishing, Collingwood, VIC, Australia.

Steiner, C.; Catzeflis, F.M. 2004. Genetic variation and geographica structure of five mouse-sized opossums (Marsupialia, Didelphidae) throughout the Guinana region. Journal of Biogeography. 31: 959-973.

Tavaré, L. 1986. Some probabilistic and statistical problems on the analysis of DNA sequences. Lectures on mathematics in the life sciences. 17: 57-86.

Templeton, A.R.; Crandall, K.A.; Sing, C.A. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics. 132: 619-633.

Tribsch, A.; Schönswetter, P.; Stuessy, T. 2002. *Saponaria pumila* (Caryophyllaceae) and the Ice Ages in the European Alps. American Journal of Botany. 89: 2024-2003.

Vandergast, A.G.; Gillespie, R.G.; Roderick, G.K. 2004. Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth and the potential for accelerated evolution. Molecular Ecology. 13: 1729-1743.

White, M.E. 1990. The nature of hidden worlds. pp. 176-225. Reed Books, Balgowlah.

White, M.E. 1994. After the greening. Pp. 41-245. Kangaroo Press, Kenthurst.

Wishart, G.F.C. 1993. The biology of spiders and phenology of wandering males in a forest remnant (Araneae: Mygalomorphae). Memoirs of the Queensland Museum. 33(2): 675-680.

Yee, M.; Yuan, Z.Q.; Mohammed, C. 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus oblique* production forests: the ecology of large and small logs compared. Tasforests. 13: 119-128.

Zink, R.M. 2002. Methods in comparative phylogeography, and their application to studying evolution in the North American aridlands. Integrative and Comparative Biology. 42: 953-959.

Zink, R.M.; Blackwell-Rago, R.C.; Ronquist, F. 2000. The shifting roles of dispersal and vicariance in biogeography. Proceedings of the Royal Society of London—Series B: Biological Sciences. 267: 479-503.

WHAT CAN FOREST MANAGERS LEARN FROM RESEARCH ON FOSSIL INSECTS? LINKING FOREST ECOLOGICAL HISTORY, BIODIVERSITY AND MANAGEMENT

Nicki J. Whitehouse[1]

Abstract—This paper outlines the usefulness of using fossil insects, particularly Coleoptera (beetles), preserved in waterlogged palaeoenvironmental and archaeological deposits in understanding the changing nature of forest ecosystems and their associated insect population dynamics over the last 10,000 years. Research in Europe has highlighted the complex nature of early forest ecosystems, in particular the role of dead wood and grazing animals. This research suggests that the north European primary forest has similarities to pasture woodlands, rather than the forest manager's perception of closed canopy systems. Human activity has had a major impact on forest ecosystems, resulting in an expansion of plants and animals associated with cleared landscapes and pasture and also the local extirpation of a sizeable proportion of taxa from the forests of northern Europe. The decline in these species has been seen as resulting from habitat loss due to human impact on the forest, which intensified from about 2500 years ago onwards, coupled with subtle climate change effects. These extirpations will be discussed, with particular reference to the management of forest ecosystems for the benefit of their invertebrates (particularly those associated with dead wood), and emphasising how the record from archaeological and palaeoecological sites has significant relevance to modern woodland management and conservation. Moreover, the role of disturbances in maintaining the structure and biodiversity of the "wildwood" will be emphasied.

INTRODUCTION

Insects, recovered as fossils, potentially provide one of the most effective means of reconstructing both past environments and the details of changing climate, being very sensitive to environmental change and occupying almost every possible habitat on land and in freshwater (Elias 1994). As a group, their remains may be the most frequent identifiable fossils in terrestrial, waterlogged sediments and are similarly common in anaerobic archaeological sediments (fig. 1). Most fossil insect research has focused on Coleoptera, but increasingly, other insect groups are studied, in particular the Diptera (e.g., Brooks and Birks 2000, Panagiotakopulu 2004). Much of the following account concentrates on the former rather than the latter, as these form the basis of our understanding of the palaeoentomology of woodlands, the subject of this paper.

In particular, many investigations provide an insight into what the primeval forest may have looked like and how landscape clearance affected the insect biota, allowing the expansion of species associated with cleared landscapes. Results of these investigations highlight the enormous changes effected upon the fauna of the British Isles, particularly since the onset of agriculture, but also provide an insight into their rapid colonisation and expansion as ice sheets retreated. Inevitably, much of the following account concentrates on results from the British Isles, as this is where the majority of this work has been carried out, although reference will be made to work elsewhere where possible. Management implications are particularly concerned with the European forest habitat, whether ancient or recently planted, although where possible implications for areas elsewhere are also made. This paper includes a background section which introduces the reader to the subject of fossil beetles, an area of research which may be unfamiliar to readers of this volume.

Coleoptera nomenclature follows Lucht (1987). Information on insect biology has been obtained from the entomological database BUGS (Buckland and others 1997). Where necessary, reference is made to the current threatened status of beetles. Many species discussed in this paper are included in

Figure 1—Coleoptera fossils from palaeochannel deposits dating to the mid-Holocene from Thorne Moors, Humberhead Levels.

---

[1] Nicki J. Whitehouse, Palaeoecologist, School of Archaeology and Palaeoecology, Queens University Belfast, Belfast BT7 1NN, Northern Ireland, United Kingdom.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

the Nature Conservancy Council's *British Red Data Books: 2, Insects* (Shirt 1987). This is a comprehensive statement on the status of most threatened insects in Great Britain. The book contains three major categories based upon degrees of threat, RDB ("Red Data Book") 1, 2 and 3 (respectively endangered vulnerable and rare). A further classification of Notable species (A and B) (Hyman 1992, 1994) is also used. Notable A species are those which do not fall within RDB categories but which are none-the-less uncommon and are thought to occur in 30 or fewer 10 km squares of the National Grid, whilst Notable B taxa are those which are thought to occur in between 31 and 100 10 km squares of the National Grid. One point worth remembering is that species that are rare today may not have been so in the past, and perhaps *vice versa* (Buckland and Dinnin 1993). Dates are expressed as BC/AD for dendrochronological (= tree rings) dates (followed by the appropriate bibliographic citation) and cal BC/AD for radiocarbon dates (range calculated to 95 percent level confidence and calibrated using INTCAL 1986 calibration curve, Pearson and others 1986). Figure 2 shows the location of sites discussed in the text.

ORIGINS AND PRINCIPLES OF PALAEOENTOMOLOGY

The origins of modern palaeoentomology date back to the 1930s and 1940s when Carl Lindroth and fellow Scandinavian entomologists established the foundations of the modern discipline, but it was really when, in the mid 1950s, research activity moved to Britain and particularly to the geology department at Birmingham University (Morgan and Morgan 1987), with the work of Prof. Russell Coope, that the discipline gained wider attention. Coope began studying Quaternary insect fossils from Upon Warren, an interstadial deposit in the British Midlands dated to *c.* 40,000 radiocarbon years ago (Coope and others 1961). By making patient comparisons with modern specimens, he matched most of the material to modern species. Coope (1970, 1978, 1995, 2004) suggested that insects had remained evolutionarily stable in their morphology and their environmental requirements throughout the whole of the Quaternary period, responding to climate change by undergoing distributional shifts. The effect of such movement would keep the gene pool constantly mixed, preventing genetic isolation of populations and mutations which would result in speciation and ensuring that stasis is the norm for many Quaternary insects. Thus far, evidence for evolutionary change is extremely rare from Quaternary insect assemblages (e.g., Böcher 1986, 1997; Matthews 1970) and it seems that the overall composition of the assemblages of insect species which occur today, at least in the temperate zones, were established during late Tertiary times (Elias 1994). However, as Ashworth (2004) points out, stasis is not always corroborated by genetic evidence (e.g., Reiss and others 1999). This may possibly be true only for the northern temperate fauna, while the highly diverse tropics may be the place to look for evidence for divergence, where climatic oscillations may not have been so extreme. Moreover, this perspective may not hold true for narrow-range endemic taxa (see discussions by Ribera and Vogler 2004).

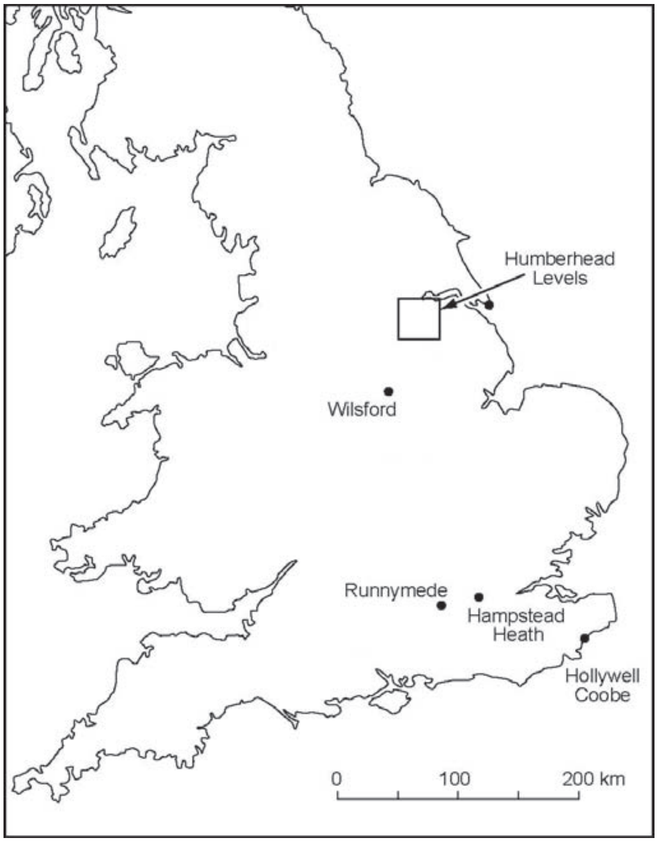


Figure 2—Location map of United Kingdom sites discussed in text.

Insect groups identified are generally the beetles (Coleoptera), because the robust exoskeleton survives well in waterlogged deposits, leaving many of their diagnostic features still evident. Identification is still very much of a specialist activity because of the range of species present in the fossil record. Other insect orders are available for analysis, such as the Chironomidae (Diptera)—this group has recently received considerable research attention (e.g., Brooks and Birks 2000; Brooks and others 1997a, 1997b; Walker and others 1991). Work on other dipterous (fly) remains is being pioneered through the work of Pete Skidmore (1995) and more recently Eva Panagiotapopolou (2004). Trichoptera (caddis) have also received some attention (e.g., Wilkinson 1984) and have recently been recognised as important environmental and climate change indicators (Greenwood and others 2003). Increasingly, there is the use of several insect groups to refine reconstruction of past environments, particularly where high quality data are required concerning periods of rapid environmental change. A good example of this approach is provided by the Kråkenes Project, which has investigated the ecosystem of this lake in western Norway during the late-glacial and early-Holocene (Birks and others 2000).

Reconstruction of past environments operates upon on the major assumption that the ecological requirements of insects have not dramatically changed. The fact that groups of species have consistently been found together suggests that the ecological requirements of most species have not altered (Kenward 1975). However, there are considerable difficulties in establishing the ecological requirements of single species and their significance in fossil faunal assemblages. Even when the biology of species is known in some detail, this may not cover all the suitable habitats, especially in situations when microhabitats may provide suitable locations while the *overall* situation may provide a rather different ecological environment (Kenward 1978). It is therefore recommended that a large number of taxa and individuals are utilised, which when examined together provide a picture of past environments and conditions, an approach known as the "mosaic" approach (Kenward 1976). The setting up of a habitat and fossil database (BUGS: http://www.umu.se/envarchlab/bugs.html) formerly at the University of Sheffield, now at the University of Bournemouth, England, has greatly facilitated the use of this approach (*cf.* Buckland and others 1997).

Sampling of material suitable for fossil beetles entails the removal of material from an exposed sediment section or bulk sampling from an archaeological or palaeoecological context (e.g., cesspit; fossil tree rot hole). Occasionally, a coring device may be used to extract material from lakes, bogs, hollows and where no section is accessible. Samples are usually removed in 5-10 cm thick contiguous "slices", usually of at least 5 litres, or entire contexts. The extraction of fossil Coleoptera follows a technique devised by Coope and Osborne (1968), using paraffin (kerosene) to concentrate remains. The identification of insect fossil material is carried out through the use of entomological keys and through direct comparison with a range of modern comparative material (Buckland and Coope 1991). Much of the sampling for fossil insects has been through the use of palaeoentomology in archaeological investigations, dating both from the prehistoric and historic periods (e.g., Buckland and others 1996; Girling 1976; Kenward and Hall 1995; Robinson 1991, 2000). There have also been studies which have examined "natural" deposits—those not directly associated with archaeological features—but which carry a record of the wider environment, as well as human impact on the landscape. Anaerobic conditions ensure excellent preservation of fossils and the often rapid built-up of deposits provides good temporal resolution. Floodplain deposits, for instance, are immensely valuable, as they provide records of fluvial histories, floodplain evolution and change, vegetation composition and structure as well as the nature and scale of human impact (e.g., Andrieu-Ponel and others 2000; Dinnin 1997; Osborne 1988, 1995; Smith and Howard 2004). Bogs and fens are also rich sources of fossil insect assemblages, although fen peats tend to be richer in insect remains than acid peats (e.g., Buckland 1979; Elias 1994; Klinger and others 1990; Ponel and others 2001; Roper 1996; Whitehouse 1997b, 2004). Wood peats are especially useful in the study of the forest faunas, as elaborated in further detail below.

Perhaps one of the greatest contributions of Quaternary entomology has been its role in helping our understanding of rapid climate change—particularly associated with the termination of the last ice age and of the nature of climate during previous interglacials. Through work on many sites, palaeoentomologists have been able to reconstruct quantified temperatures covering the last 45,000 years, showing the rate and rapidity of climate change during the late-glacial across northern Europe (*c.* 14,000 -10,000 radiocarbon years ago) (Atkinson and others 1987; Coope 1977, 1994; Coope and Brophy 1972; Coope and Lemdahl 1995; Coope and others 1998; Vandenberghe and others 1998; Walker and others 1993). Elias (1996, 1997) and Elias and others (1996) has produced similar data for the American continent, whilst Marra and others (2004) have produced promising new results for the southern hemisphere.

Despite the success in examining late glacial climatic change, Holocene climatic change (the last 10,000 years) has been less easy to infer from the Coleopteran record, although evidence from ice and ocean cores indicates that periodic changes to climatic regimes have taken place (Bond and others 1997, 2001). From the mid-Holocene onwards, palaeoecological studies highlight the increasing scale and extent of environmental change, particularly in Europe. In America, similar scales of human impact are noticeable within a few centuries of the arrival of Europeans, with concurrent dramatic environmental impacts (e.g., Baker and others 1996, Schwert 1996). Data clearly indicate that not only is human impact of considerable importance, but that it may swamp and mask low magnitude climatic events. The scale of these human impacts, particularly upon the forest, was massive, as discussed below. These studies have also provided us with valuable insights into the nature of the primeval forest ecosystem, before major human impact. Figure 2 shows the location of sites discussed in the text.

THE ANCIENT FOREST FOSSIL BEETLE RECORD

The Nature and Structure of "Wildwood"

We know from the pollen record that during the early phases of the present interglacial, rapid climatic warming enabled tree species to re-colonise areas of tundra of northern Europe, at varying rates of expansion from their respective glacial refugia (*cf.* Bennett and others 1991, Willis 1996) and according to their edaphic requirements. These "wildwoods" (also known as *Urwald*) appear to have been structurally complex and rich ecosystems, characterised by significant numbers of large, long-lived trees. Dead, dying and moribund wood appears to have been a major component of this habitat (Smith and Whitehouse 2005), often referred to as coarse woody debris (CWD) (Franklin 1988). We know this because fossil insect assemblages from this period are characterised by large numbers of species associated with this component, including primary colonisers and large numbers of secondary saproxylics (xylophages) and predators which invade wood when very rotten and feed upon the primary colonisers of rotting wood (Smith and Whitehouse 2005, Whitehouse 1997b). This wood-decomposing system has exceptional species diversity (Biström and Väisänen 1988, Harding and Rose 1986). Coarse woody debris is often thought to compose between 15-25 percent of the total wood mass in 'virgin' temperate forest habitats (Peterken 1996). This may be as high as 50 percent in undisturbed forests (Elton 1966, Warren and Key 1991), a figure which would not be inconsistent with the fossil beetle record. As a result, CWD must have been a dominant aspect of the ecology and appearance of ancient woodlands (Smith and Whitehouse 2005).

These wildwoods supported a distinctive invertebrate population of *Urwaldtiere* (*cf.* Palm 1951; undisturbed relict taxa). It is difficult to know exactly when species arrived after the retreat of the ice sheets because of the paucity of sites covering the earlier part of the Holocene, although several studies provide insights into this period (*cf.* Coope 1998; Dinnin 1997; Osborne 1972, 1974, 1980). Deposits at Holywell Coombe in

Kent, southern England, include a valuable record covering the late glacial and first millennium of the Holocene (Coope 1998). Deposits spanning the first thousand years of the Holocene indicate a community of beetles associated with open ground and light woodland. By 8630-8280 cal BC (9230 ± 75 BP, Q-2710) a suite of specialist species had already arrived, including the Notable B *Melasis buprestoides* (L.), RDB 1 *Eucnemis capucina* Ehr., RDB 3 *Dirhagus pygmaeus* (F.) and Notable B *Anaglypus mysticus* (L.) all dependant upon rotting wood and dry heart-wood of deciduous trees, whilst the non-British *Rhyncolus elongatus* (Gyll.) is normally associated with dead and rotting wood of conifers, although in this context may have been living in deciduous wood. This latter species is not on the present list of British Coleoptera, but still lives in central Europe. As tree species expanded from Europe and habitats became more diverse, their associated fauna moved northwards over the next few thousand years, including a diverse range of specialist saproxylics that no longer live in Britain and Ireland (Buckland and Dinnin 1993; Dinnin and Sadler 1999; Whitehouse 1997a, in press). By about *c.* 6000 cal BC, increased diversification of saproxylic communities seems to have occurred (Dinnin and Sadler 1999). These increases were probably caused by the availability of the full range of forest habitats at different successional stages and the arrival of the highly specialised thermophilous *Urwaldtiere* from their mainland European refugia (*cf.* Bennett and others 1991).

The fossil beetle record also provides us with valuable insights into the nature of these forests. There is strong evidence to suggest that they were subject to a range of natural disturbances including forest fires, storm damage, and floods, creating open, sun-exposed places with a considerable amount of dying and dead wood (Whitehouse 1998, 2000). Occasionally, insect attack and pathogens would also have caused defoliation and extensive tree damage *(cf.* Patterson and Backman 1988). Such small-scale disturbances are part of the natural system within forests (Kaila and others 1997) and opened up the canopy of the woodland, creating clearings, and generating a build-up of fuel upon the forest floor, thus making the forest more susceptible to fire (Danks and Foottit 1989). Early Holocene and later sediments often contain abundant charcoal indicating frequent fires (Huntley 1993, Patterson and Backman 1988, Patterson and others 1987). Local non-forest vegetation patches may have emerged quite frequently, creating semi-permanent open spaces and breaking up the canopy of the woodland.

The structure of these forest ecosystems has recently been the subject of fierce discussion, most notably by Frans Vera (2000), who has questioned many assumptions about the natural ecological state of “wildwood”. Vera’s ideas have generated intense discussion amongst conservationists, biologists and palaeoecologists (e.g., Bakker and others 2004; Blumer 2002; Bradshaw and Hannon 2004; Bradshaw and others 2003; Eriksson and others 2002; Kirby 2003, 2004; Mitchell 2005; Rackham 2003; Sutherland 2002; Svenning 2002; Whitehouse and Smith 2004). In particular, Vera suggests that the role of large herbivores in these wildwoods has been seriously underestimated and that they played an important part in maintaining substantial open areas in the forests of primeval Europe. He debunks the widespread idea that the “wildwoods” of Europe were a dense, continuous canopy (*cf.* Peterken 1996, Rackham 1986). Moreover, Vera suggests these woodlands may have been much more open, rather similar in structure to wood pasture and parkland. These concepts underpin much of our current attitude to the management of woodland and parkland and, if correct, imply that the current conservation policies of regenerating closed woodland may be flawed.

Similar arguments concerning the openness of wildwood and its comparison to pasture woodland have been made by several modern entomologists (e.g., Harding and Rose 1986) and some palaeoecologists, who have long drawn attention to the role of grazing in affecting vegetation structure (Bradshaw and Hannon 1992, Bradshaw and Mitchell 1999, Buckland and Edwards 1984, Mitchell 1990, Robinson 2000). A recent review by Whitehouse and Smith (2004) argues that whilst Vera (2000) undoubtedly challenges many traditional interpretations of vegetational history, he underestimates the complexity of the physical landscape and environmental backdrop of the wildwood, creating a model which is at times simplistic, especially when considering the diversity across Europe (*cf.* Rackham 2003). For instance, he fails to consider that forest composition, and hence structure, changes over the Holocene (*cf.* Birks 1989) or the changing climatic backdrop against which these changes were being played (e.g., Bond and others 1997, 2001). Climate variability will have impacted forests in several different ways, including making it more susceptible to disturbance and affecting the frequency and occurrence of forest fires (Bradshaw and Hannon 1992). Moreover, the assumption that animals and grazing pressure were distributed evenly across the landscape is open to question (*cf.* Bradshaw and Hannon 2004, Buckland and Edwards 1984), but more fundamentally, the role of humans in affecting animal distributions is not considered (Whitehouse and Smith 2004).

Whitehouse and Smith (2004) considered the published fossil insect data from the early Holocene to investigate whether fossil beetle data could throw any light on this debate. They concluded that, within the limits of the published record, some early-mid Holocene forest was at least partly open in character or included open areas, whilst species usually associated with the dung of grazing animals, although in small numbers, are persistent. They stress, however, that the role of grazing animals in creating these openings is far from clear on the present evidence and that new research is required to address this point. Moreover, they suggest that other disturbance agents, such as forest fires are likely to have been equally important. Similar points are made by Bradshaw and Hannon (2004), who consider the pollen, plant macrofossil and charcoal record from several Danish and Swedish sites and additionally draw attention to the role of flooding and wind-throw in the structure of “wildwood”.

Human Impacts and Loss of Biodiversity

By 8,000-4,000 cal BC there appears to be some evidence for the disturbance of primary forest indicated within the pollen and charcoal record (e.g., Edwards 1996; Smith 1970, 1981). However, there is far clearer unequivocal evidence for human disturbance during the move to agriculture in the Neolithic, *c.* 5,000 cal BC, when we know from the archaeological record that humans were starting to clear the landscape, but also managing forest areas through coppicing and pollarding (Rackham 1986, Rasmussen 1990). These changes can be observed in detail through the fossil beetle record from several archaeological sites. For instance, at West Heath, Hampstead, London, Mesolithic deposits indicate a largely undisturbed landscape, with a diverse range of undisturbed forest indicators (*Urwaldtiere*) including the lime feeder, the RDB1 *Ernoporus caucasicus* Lind. and two taxa which no longer live in Britain, *Pycnomerus tenebrans* Ol. (a species which displays a very scarce, sporadic distribution in mainland Europe, where it is considered a relict species of old forest), and *Isorhipis melasoides* (Lap.) (another ancient forest inhabitant often found in dry beech wood (Reitter 1911)). Within a relatively short period of time, perhaps 500-1,000 years, the beetles indicate a chiefly managed landscape (Girling 1989). Similarly, at Runnymede, Surrey, investigations over a decade cover a sequence of at least 6,000 years, one of the longest Holocene insect sequences studied in Britain (Robinson 2000). The Mesolithic (*c.* 7,000-5,000 cal BC) until the late Neolithic deposits (*c.* 4250-3650 cal BC, 5100 ± 100 BP, BM-3039) are characterised by an insect fauna with a strong wildwood element. By the Late Bronze Age the insect fauna reflects a largely agricultural landscape (Robinson 1991, 2000). At Wilsford, in the British Midlands, at *c.* 1880-1430 cal BC (3330 ± 90 BP, NPL-74) Osborne (1969) records a fauna that indicates grazing animals in an almost treeless landscape. These transitions from forested to cleared landscape have been observed at several other sites in Britain (e.g., Dinnin 1997), Ireland (Caseldine and others 1997) and elsewhere in Europe (e.g., Ponel and others 2001) with the result that by about 2,500 years ago mature forest beetle species, at least on the islands of Britain and Ireland, appear to represent an insignificant faunal element. Significant inroads had also been made into the forested areas almost throughout Europe. By 2,000 to 1,000 years ago it is doubtful whether anything more than patches of secondary forests remained in the lowlands, over most of the Mediterranean and parts of western Europe accessible to cultivation (Greig 1982, Speight 1989). By the onset of the scientific period when Linnaeus started to give animals and plants Latin names, Europe's forest areas had been reduced to their smallest extent since the last glaciation. Across the Atlantic, in America, massive scales of human impact are noticeable within a few centuries of the arrival of Europeans, with concurrent dramatic environmental impacts (e.g., Baker and others 1996, Schwert 1996), although populations of earlier human colonists had far greater impacts on the environment that has sometimes been commonly recognised (Cronon 1983, Russell 1997).

Associated with these enormous changes to the landscape and forest clearance, was the concurrent decline of its invertebrate inhabitants. Fossil beetle work spanning several decades of research from archaeological and palaeoecological sites suggests that Britain and Ireland have lost a large portion of their original old-growth forest Coleoptera, particularly the saproxylic species, coinciding with the loss of primeval and semi-natural forests and forests. The few studies that have examined natural successions indicate that it is still really too early to quantify the number of extirpations in Britain and Ireland. To date, 40 pre-Linnean (i.e., not including recent 18th-19th century extinctions) extirpations have been recorded amongst British Holocene Coleoptera, whilst 15 have been recorded in Irish deposits (Buckland 1979; Dinnin and Sadler 1999; Whitehouse 1997a, in press). Assessing true numbers is compounded by problems associated with the identification of species that cannot be identified on characteristics recoverable from the fossil record (i.e., based upon their head, thoraces or elytra), and some of the difficulties of identifying specialist species where modern comparative specimens are increasingly difficult to track down. These factors would suggest that these identified extirpated fossils represent a tiny proportion of the range of species which formerly lived in Ireland and Britain (Whitehouse, in press). Of the complete list, over 60 percent of species (25) are from saproxylic taxa associated with old and dead wood, with the rest coming from beetles representing a variety of threatened habitats, including those associated with wetlands and meadowland. An example of one of these species is shown in figure 3, the ostomid *Temnochila coerulea* West, with its modern distribution shown in figure 4. This species is typical of the "extirpated" taxa recovered in fossil records, being today found in central Europe, associated with ancient forest and considered an "*Urwaldrelikt*".

In addition to the "extirpations", many saproxylics which are today extremely rare or endangered are remarkably common in the fossil record. For instance, investigations of the raised mires of Thorne and Hatfield Moors, in the Humberhead Levels, for their fossil insect record include 49 rare or threatened saproxylics in addition to 18 extinct taxa (Boswijk and Whitehouse 2002; Buckland 1979; Smith and Whitehouse 2005; Whitehouse 1997a, 1997b, 2004). Here, the forest fauna is dominated by two categories of saproxylics: those that are predators of primary invaders of freshly dead trees and species that live in well-rotted, dead, fungoid wood. There is also the notable presence of species apparently associated with burnt forest, particularly pinewood (*cf.* Whitehouse 2000). The rarest species tend to be the predators, highlighting that species at the top of the food chain are often the first affected by and endangered by habitat change and manipulation.

A review of the published literature (Smith and Whitehouse 2005) for its ancient forest fauna across a series of assemblages from Britain representing different forest types suggests,

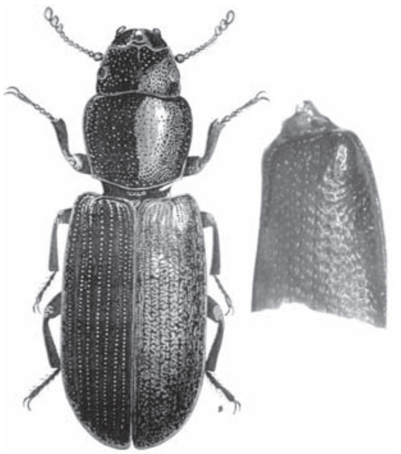


Figure 3—*Temnochila coerulea* West: on left, drawing of modern beetle by Peter Skidmore and on right fossil specimen of elytra. © Peter Skidmore (modern beetle drawing), with permission. The fossil was recovered from wood peat within the basal deposits of the bog at Thorne Moors, England (Roper 1996, Whitehouse 1997b).

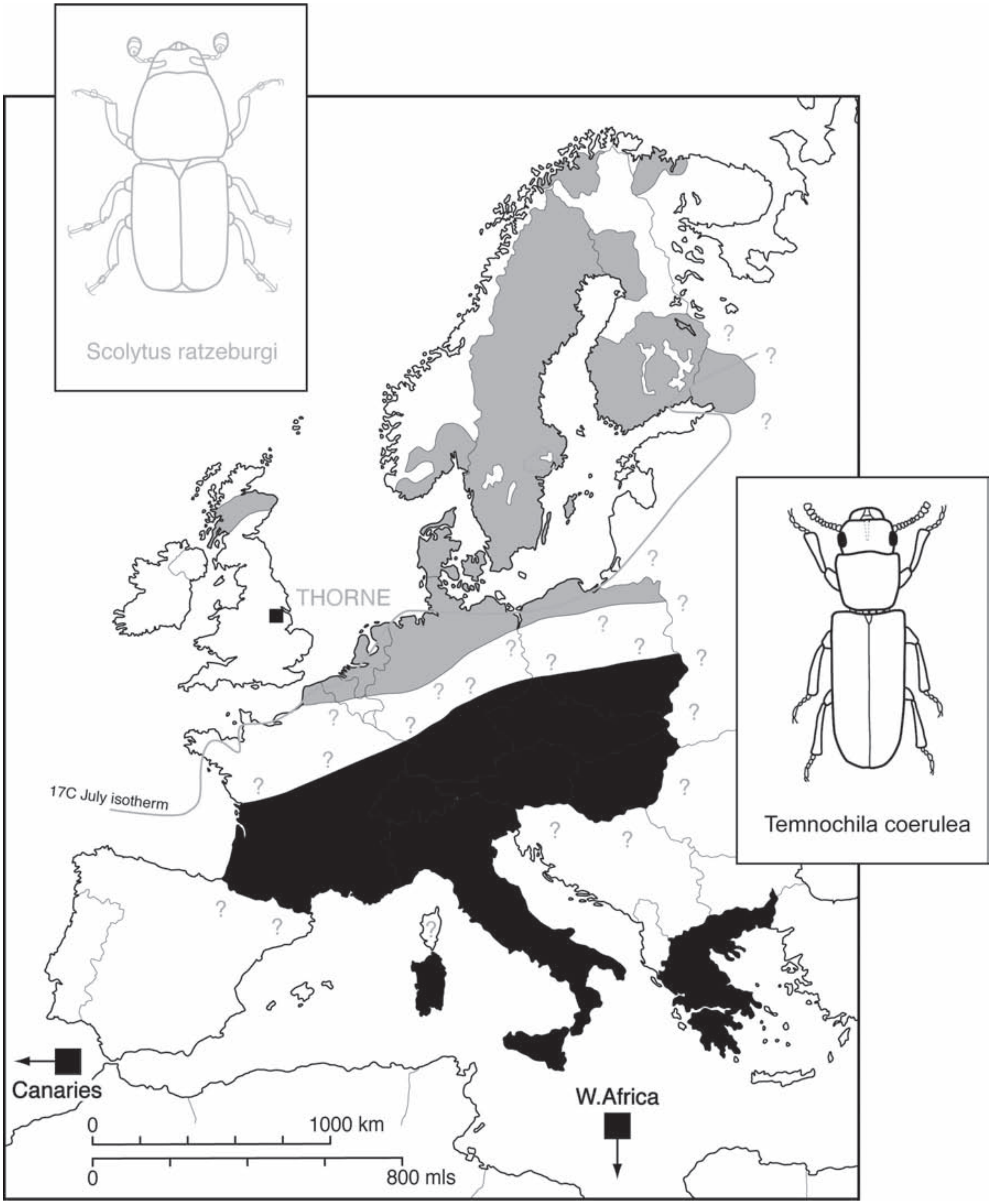


Figure 4—Modern distribution of *Temnochila coerulea* Westw (black) and *Scolytus ratzeburgi* Jans (grey), which were found together in the same deposit at Thorne Moors, Humberhead Levels, England. Arrowed boxes indicate find spots in Africa and the Canary Islands for *T. coerulea*. Redrawn with permission after an original by P.I. Buckland. © P.I. Buckland.

from the range of taxa present at many sites and the variety of niches they potentially exploited, that many of these forests were ecologically diverse and complex. For many sites, the ‘woodland’ component (this includes ‘ancient woodland’ taxa as well as other species associated with trees) accounts for *c.* 15-20 percent or higher of the terrestrial fauna present, a figure usually taken to indicate closed canopy forest (Robinson 1981). Such high levels are particularly evident at particular sites, such as woodland mires and floodplains, but this is not the case everywhere. Indeed, not all sites in the survey included large numbers of extinct, endangered or rare species, despite containing substantial forest faunas (Smith and Whitehouse 2005). Smith and Whitehouse (2005) conclude that it may sometimes be difficult to assess the extent to which individual species of beetle were rare or common in the past and therefore the extent they have declined by the present day. Nevertheless, certain groups appear to have suffered greater declines than have others—namely those associated with boreal forests (particularly pinicolous taxa, see Whitehouse 1997a, for further details) and mire forest habitats, because their habitats have declined, at least in the British Isles. More recently, large numbers of these species have declined in the boreal forests of Fennoscandia (Heliövaara and Väisänen 1984, Kaila and others 1997), following increased felling and grazing in the latter part of the 21st century (Peterken 1996). Many of the species showing contractions in populations are associated with the later stages of wood decomposition, and whilst the biology of many of these species is qualitatively well-known, quantitative information concerning the micro- and macro-habitat requirements of individual species is still scarce (Kaila and others 1997).

It is still unclear when many of these species decline or disappear from the fossil record. At least a sizeable proportion probably disappears with primary clearance during the prehistoric period, although at least some taxa survive into the medieval period (Dinnin 1997; Whitehouse, in press). There are hints that there are differences in the records between Britain and Ireland, although our knowledge of the latter's record is still very limited (Whitehouse, in press). In particular, it appears that some taxa may survive in Ireland up until the medieval period, but that high levels of post-medieval woodland clearance caused the further eradication of other less specialised taxa. The use of wood in urban areas and house structures in towns may have provided important refugia for some species during this period. In contrast, the establishment of Forests, Chases and the practises of traditional woodland management in England ensured the continued survival of some of the species which sadly have contracted in Ireland (Whitehouse, in press).

DISCUSSION: IMPLICATIONS FOR FOREST MANAGEMENT

What are the implications of this research for the management of forested areas? There are, broadly speaking, three different areas where fossil beetle research has important insights to provide the forest managers with. Firstly, the research can provide valuable insights into the structure of native forest; secondly, it provides an insight into species decline and causes of decline and therefore ways in which loss of biodiversity may be halted and even reversed; finally, it provides insights into how the forest can best be managed to ensure survival of saproxylics and encourage their return.

In terms of forest structure, forest managers need to be clear about what they are trying to achieve. The current debate concerning the level of open-ness of forests and the role of grazing animals may be particularly pertinent and it may no longer be appropriate to aim for the development of closed canopy forest. Indeed, many forest invertebrates require a mixed mosaic landscape rather than full canopy forest (Alexander 1999, Palm 1959, Ranius and Jansson 2000), whilst Similä and others (2002) have drawn attention to the high numbers of threatened insect species belonging to early successional forest. These habitats, often in glades and on forest edges, provide significant nectar sources near breeding habitat (Harding and Rose 1986). Other taxa appear to require sunny, open habitats with large amounts of dead wood, the type of habitat offered by pasture woodland suggested by Vera (2000) for past forests. As Alexander (1999, 2002) has pointed out, ancient wood pastures and parklands provide some of the most valuable habitats for many saproxylics rather than closed forest. Moreover, if the "wildwood" was uniformly dense, where did all the many light-demanding species of plants and invertebrates evolve? Eriksson and others (2002) draw attention to the fact that an explicit consideration of the original habitats of semi-natural grassland species has been overlooked in the closed forest hypothesis and highlight that many such species already existed in the landscape. The mixture of different species found in the fossil record during the early Holocene, periods when forests were largely free of human disturbance, suggests that substantial open areas did indeed exist although their extent may have varied across different forest types and areas.

From a management perspective, it is therefore crucial that forest managers are aware of the history of a forest area and its current status. They should manage the area in the most appropriate way for the species which are present, whilst being aware of opportunities for species colonisation from nearby sites and potential to create new habitats. Any management activities and their impacts on invertebrates should be monitored to ensure that biodiversity is not adversely impacted by management activities. Where it is established that the species mix is such that pasture woodland would be beneficial, managers may allow the development of open glades as well as areas with a more closed canopy. In this scenario, allowing some level of grazing by wild or domesticated animals as a management tool is likely to be beneficial, although stock levels may need to be controlled in terms of their density, by season and their effects monitored to ensure that over-grazing does not occur (Mountford and Peterken 2003). A consideration of baseline flora and fauna prior to the introduction of grazing will be essential, followed up by survey at intervals after the introduction of grazing. The use of animals as a management tool has often been perceived in negative terms by forest managers, but the development of the grazing debate and ongoing experimental work indicates the potential of this sort of approach, particularly in the management of large reserves, allowing managers to help maintain structural and species diversity within forest and encourage regeneration of light-demanding taxa (Bakker and others 2004). Current large scale ecological projects where this approach has proven beneficial include the Oostvaardersplassen reserve in the Netherlands (Kampf 2002) and the New Forest, Hampshire, UK (Kirby 2004, Mountford and Peterken 2003).

It is likely that a range of other disturbance factors, in addition to animal grazing, played equally important roles in creating open areas. Forests in the past appear to have been subject to a range of natural disturbances such as forest fires and storm damage, often creating open, sun-exposed places with considerable amounts of dying and dead wood (Kirby 2004; Whitehouse 1998, 2000). Forest fires, in particular, appear to have played an important role in maintaining an open character in at least some early Holocene forests, especially where dominated by flammable pine and birch (Bradshaw and Hannon 2004, Whitehouse 2000). Indeed, substantial numbers of the boreal insect fauna are fire-favoured (Wikars and Schimmel 2001), and this faunal element may represent the closest modern analogue for some of the early Holocene beetle assemblages which have been examined in Great Britain. As a result of such fires, local vegetation patches and islands may have emerged locally quite frequently, creating semi-permanent open spaces and opening up the canopy of the forest. Again, whilst many foresters are understandably cautious about forest fires, from an ecological perspective they can be extremely useful and add to ecosystem diversity. Moreover, ecologists are increasingly recognising that natural fires may have played a more important part than previously assumed in maintaining areas of open landscape in the past (Kirby 2004). Emulation and controlled use of these natural dynamics may be one key area in which managers may increase ecosystem structure, range and biodiversity.

Forest managers may also find it beneficial to consider the causes of saproxylic insect decline which can be seen clearly in the fossil insect record. The demise of many of the species of *Urwaldtire* has been attributed to the combined loss of undisturbed forest habitats and particularly of dead wood. Elton (1966) pointed out that if dead wood is removed from the forest ecosystem, the system is impoverished of a fifth or more of its invertebrate fauna. The apparent poor mobility of many of these saproxylic species (*cf.* Warren and Key 1991) appears to have played an important part in their decline and/or extirpation in the British Isles (Buckland and Dinnin 1993, Whitehouse 1997b), particularly with the onset of forest fragmentation and the loss of continual forest corridors. Forest history, management and temporal continuity of habitat also appear to have been significant components in the maintenance and survival of many of these saproxylic communities (Whitehouse, in press), whilst increasing geographic isolation in areas such as raised mires and other wetlands appears to have played an important role in isolating relict populations. The loss of particular types of forest, such as pinewood and its associated habitats, either through successional competition, decline in forest fires and/or the development and expansion of peatlands, seem to have all been important contributory factor for some species (Whitehouse 1997a, 2000). There is strong evidence to support the idea that climate change may also have played an important role in some local extirpation. This may have been related to changes in temperature, but also a move from a more continental climate to a wetter, more oceanic one (Buckland 1979; Dinnin and Sadler, 1999; Whitehouse and others 1997, in press). However, it is clear that extirpations are the result of a complex interplay between climate changes on the one hand and human impact on the ecosystem on the other.

From a management perspective, it is clear that managers must ensure that forests include a variety of dead, frassy wood habitats in a range of different conditions and levels of moisture, leaving wind-throws and upstanding dead wood to die in situ. Although forest managers are commonly concerned that this may encourage forest “pests” into an area which may attack healthy trees, the fossil record indicates that populations are commonly kept in check by predators of primary invaders of wood. Moreover, the availability of suitable habitats for predators is likely to ensure that any pests affecting healthy trees are more likely to be controlled because predators are provided with suitable habitats.

Continuity of habitat appears to be crucial as does ensuring that habitats are not overly isolated and fragmented; corridors of suitable habitat appear to be important. Traditional management practices including pollarding and coppicing can create the necessary diversity and range of different successional habitats for many saproxylics. This management approach may be particularly desirable where it can be established that these traditional management practises have been used in the past and therefore will be beneficial to and contributed towards the current species mix. Where there is no history of these traditional practises it may still be worthwhile considering using these approaches, depending upon the overall aims of forest management and the current species mix. Under these circumstances, managers may wish to undertake any such management under controlled conditions during initial stages and with invertebrate monitoring to establish any impacts on existing site fauna.

In some types of forests, allowing forest fires to occur on a regular basis is likely to be beneficial not only in facilitating the regeneration of some trees (e.g., *Pinus sylvestris*), but encouraging a wide range of fire-adapted and pyrophilous invertebrates (Whitehouse 2000), as well as discouraging major build-ups of forest litter layers which commonly lead to major devastating conflagrations.

CONCLUSIONS

The fossil insect record indicates that it has many useful contributions to make to any debate concerning ecosystem conservation and draws attention to the long term changes which sites have undergone. In particular, it highlights the major changes which have impacted on forest invertebrates, mostly through the activities of humans, and emphasises that we are still some way from having a good understanding of what forest ecosystems in high northern latitudes may have looked like in their ‘natural’ state.

Future research needs to take several different directions. First, many of the records discussed above come from the British Isles. We need to have a much clearer understanding of the wider context of these faunas and examine similar fossil faunas from across Europe. Is what we see in the fossil record in Britain and Ireland unique or is it just part of a wider, complex, European picture? A series of comparative sites across Europe would provide a much-needed context to these studies. Our understanding of the early “wildwood” is relatively poor, despite its potential to provide valuable answers, particularly concerning the arrival and development of the forest fauna. Our knowledge of records covering the last thousand years is surprisingly poor; this is at least partially because of a paucity of suitable peat deposits which relate to this period, but there are a variety of deposits—such as in-filled forest hollows, in-filled palaeochannels and shallow lakes—which could all be suitable for investigation and which could provide valuable insights into this period. Any such investigations would provide valuable insights into the impacts of the modern era upon many saproxylics and their implications for long term management of sites.

ACKNOWLEDGMENTS

This paper was originally presented at the XXIIth Entomology Congress, Brisbane. I would like to thank Simon Grove and Jim Hanula for inviting me to speak at the “Dead Wood” session of the Conference and for their patience in the preparation of this paper. I would like to thank the following funding bodies who provided funding to attend the meeting: the Royal Society, British Academy, and Queen's University Belfast. Aspects of the research discussed above have been funded by the Hossein Farmy Fund (University of Sheffield), as part of a PhD under the supervision of Professors Paul Buckland and Kevin Edwards and more latterly the Royal Society. It forms part of ongoing work being undertaken by the author in collaboration with other researchers. I would especially like to thank Prof. Paul Buckland for many useful discussions over the years on the advantages of a fossil insect approach. The following people are thanked for sharing their insights on the "wildwood", forest invertebrates and the fossil record: Keith Alexander; Paul Buckland; Brian Eversham; Valerie Hall; Harry Kenward; Fraser Mitchell, David Smith; Peter Skidmore, Frans Vera. Libby Mulqueeny, Queen's University Belfast, is thanked for cartographic assistance. Finally, my thanks to Simon Grove for his editorial suggestions.

LITERATURE CITED

Alexander, K. 1999. Should deadwood be left in sun or shade? British Wildlife 10: 342.

Alexander, K.N.A. 2002. The invertebrates of living and decaying timber in Britain and Ireland Peterborough. English Nature.

Andrieu-Ponel, V.; Ponel, P.; Bruneton, H. [and others]. 2000. Palaeoenvironments and cultural landscapes of the last 2000 years reconstructed from pollen and Coleopteran records in the Lower Rhône Valley, southern France. The Holocene 10: 341-355.

Ashworth, A.C. 2004. Quaternary Coleoptera of the United States and Canada. Developments in Quaternary Science 1: 505-517.

Atkinson, T.C.; Briffa, K.R.; Coope, G.R. 1989. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. Nature 325: 587-592.

Baker, R.G.; Bettis, E.A.; Schwert, D.P. [and others]. 1996. Holocene palaeoenvironments of northeast Iowa. Ecological Monographs 66(2): 203-234.

Bakker, E.S.; Olff, H.; Vandenberghe, C. [and others]. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. Journal of Applied Ecology 41, 571-582.

Bennett, K.D.; Tzedakis, P.C.; Willis, K.J. 1991. Quaternary refugia of north European trees. Journal of Biogeography 18: 103-115.

Birks, H.H.; Battarbee, R.W.; Birks, H.J.B. 2000. The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late-glacial and early-Holocene—a synthesis. Journal of Palaeolimnology 23: 91-114. [Contributions by Bradhsaw, E.G.; Brooks, S.J.; Duigan, C.A.; Jones, V.J.; Lemdahl, G.; Peglar, S.M.; Solem, J.O.; Solhøy, T. and Stalsberg, M.K.]

Birks, H.J.B. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. Journal of Biogeography 16: 503-40.

Biström, O.; Väisänen, R. 1988. Ancient forest invertebrates of the Pyhän-Häkki National Park in central Finland. Acta Zoologica Fennica 185: 1-69.

Blumer, M.A. 2002. Review of Grazing ecology and forest history. Environmental History 7: 687-9.

Böcher, J. 1986. Boreal insects in northernmost Greenland: palaeoentomological evidence from the Kap Kobemhavn Formation (Plio-Pleistocene) Peary Land. Fauna Norvegica B36: 37-43.

Böcher, J. 1997. History of the Greenland insect fauna with emphasis on living and fossil beetles. Quaternary Proceedings 5: 35-48.

Bond, G.; Kromer, B.; Beer, J. [and others]. 2001. Persistent solar influence on North Atlantic climate during the Holocene. Science 294: 2130-6.

Bond, G.; Showers, W.; Chesby, M. [and others]. 1997. A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. Science 278: 1257-1266.

Boswijk, G.; Whitehouse, N.J. 2002. *Pinus* and *Prostomis*: a dendrochronological and palaeoentomological study of a mid-Holocene woodland in eastern England. The Holocene 12: 585-96.

Bradshaw, R.; Hannon, G. 1992. Climatic change, human influence and disturbance regime in the control of vegetation dynamics within Fiby Forest, Sweden. Journal of Ecology 80: 625-32.

Bradshaw, R.; Mitchell, F.J.G. 1999. The palaeoecological approach to reconstructing former grazing-vegetation interactions. Forest Ecology and Management 120: 3-12.

Bradhsaw, R.H.W.; Hannon, G.E. 2004. The Holocene structure of north-west European temperate forest induced from palaeoecological data. In Honnay, O.; Verheyen, K.; Bossuyt, B. and Hermy, M. (eds) Forest Biodiversity: lessons from history for conservation. Wallingford, Oxfordshire: CABI Publishing, 11-26.

Bradshaw, R.H.W.; Hannon, G.E.; Lister, A. 2003. A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management 181: 267-80.

Brooks, S.J.; Birks, H.J.B. 2000. Chironomid-inferred late glacial air temperatures at Whitrig Bog, southeast Scotland. Journal of Quaternary Science 15 (8): 759-764.

Brooks, S.J.; Lowe, J.J.; Mayle, F.E. 1997a. The Late Devensian Lateglacial palaeoenvironmental record from Whiting Bog, SE Scotland. 2. Chironomidae (Insecta: Diptera). Boreas 26: 297-308.

Brooks, S.J.; Mayle, F.E.; Lowe, J.J. 1997b. Chironomid-based lateglacial climatic reconstruction for southeast Scotland. Journal of Quaternary Science 12 (2): 161-167.

Buckland, P.C. 1979. Thorne Moors: a palaeoecological study of a bronze age site; a contribution to the history of the British insect fauna. Birmingham: Dept. of Geography, University of Birmingham, Occasional Publication Number 8.

Buckland, P.C.; Amorosi, T.; Barlow, L.K. [and others]. 1996. Bioarchaeological and climatological evidence for the fate of Norse farmers in medieval Greenland. Antiquity 70: 88-96.

Buckland, P.C.; Coope, G.R. 1991 A bibliography and literature of Quaternary entomology. University of Sheffield: J.R. Collis Publications.

Buckland, P.C.; Dinnin, M.H. 1993. Holocene woodlands, the fossil insect evidence. In: Kirby, K.J. and Drake, C.M. (eds.) Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. Peterborough: English Nature, 6-20.

Buckland, P.C.; Edwards, K. 1984. The longevity of pastoral episodes of clearance activity in pollen diagrams; the role of post-occupation grazing. Journal of Biogeography 11: 243-9.

Buckland, P.I.; Yuan Zhuo, D.; Buckland, P.C. 1997. Towards an expert system in palaeoentomology. Quaternary Proceedings 5: 67-78.

Caseldine, C.; Gearey, B.; Hutton, J. [and others]. 2001. From the wet to the dry: palaeoecological studies at Derryville, Co. Tipperary, Ireland. In Raftery, B. and Hickey, J. (eds) Recent Developments in Wetland Research. Dublin: Dept. of Archaeology, University College Dublin, 99-115.

Coope, G.R. 1970. Interpretations of Quaternary insect fossils. Annual Reviews of Entomology 15: 97-120.

Coope, G.R. 1977. Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (last) cold stage. Philosophical Transactions of the Royal Society of London Series B 280: 313-340.

Coope, G.R. 1978. Constancy of insect species versus inconstancy of Quaternary environments. In L.A. Mound and N. Waldoff (eds.) Diversity of Insect Faunas (Symposia of the Royal Entomological Society of London 9). London: Blackwell, 176-187.

Coope, G.R. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. Philosophical Transactions of the Royal Society of London, Series B, 344: 19-26.

Coope, G.R. 1995. Insect faunas in ice age environments: why so little extinction? In Lawton, J.H. and May, R.M. (eds.) Extinction rates. Oxford: Oxford University Press, 55-74.

Coope, G.R. 1998. Insects. In Preece, R. C. and Bridgland, D. R. (eds.), Late Quaternary Environmental Change in North-West Europe: Excavations at Hollywell Coobe, South-East England. London: Chapman and Hall, 213-33.

Coope, G.R. 2004. Several million years of stability among insect species because of, or in spite of, ice age climatic instability? Philosophical Transactions Royal Society London B 359: 209-214.

Coope, G.R.; Brophy, J.A. 1972. Late glacial environmental changes indicated by a Coleopteran succession from North Wales. Boreas 1: 97-142.

Coope, G.R.; Lemdahl, G. 1995. Regional differences in the late-glacial climate of northern Europe based on Coleopteran analysis. Journal of Quaternary Science 10(4): 391-395.

Coope, G.R.; Lemdahl, G.; Lowe, J.J.; Walkling, A. 1998. Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9^{14}C kyr BP) interpreted from Coleopteran assemblages. Journal of Quaternary Science 13 (5): 419-433.

Coope, G.R.; Osborne, P.J. 1968. Report on the Coleopterous fauna of the Roman well at Barsley Park, Gloucestershire. Transations of the Bristol and Gloucershire Archaeological Society 86: 84-87.

Coope, G.R.; Shotton, F.W.; Strachan, I. 1961. A late Pleistocene fauna and flora from Upton Warren, Worcestershire. Philosophical Transactions of the Royal Society of London, B244: 379-421.

Cronon, W. 1983. Changes in the land; Indians, colonists and the ecology of New England. New York: Hill and Wang.

Danks, H.V.; Foottit, R.G. 1989. Insects of the boreal zone of Canada. Canadian Entomologist 121: 626-674.

Dinnin, M. 1997. Holocene beetle assemblages from the lower Trent floodplain at Bole Ings, Nottinghamshire, U.K. Quaternary Proceedings 5: 83-104.

Dinnin, M.H.; Sadler, J.P. 1999. 10,000 years of change: the Holocene entomofauna of the British Isles. Quaternary Proceedings 7: 545-62.

Edwards, K.J. 1996. A Mesolithic of the Western and Northern Isles of Scotland? Evidence from pollen and charcoal. In Pollard, T. and Morrison, A. (eds.) The early prehistory of Scotland. Edinburgh: Edinburgh University Press, 23-38.

Elias, S.; Anderson, K.H.; Andrews, J.T. 1996. Late Wisconsin climate in Northeastern USA and Southeastern Canada, reconstructed from fossil beetle assemblages. Journal of Quaternary Science 11 (5): 417-421.

Elias, S.A. 1996. Late Pleistocene and Holocene seasonal temperatures reconstructed from fossil beetle assemblages in the Rocky Mountains. Quaternary Research 46: 311-318.

Elias, S.A. 1997. The mutual climatic range method of palaeoclimate reconstruction based on insect fossils: new applications and inter-hemispheric comparisons. Quaternary Science Reviews 16: 1217-1225.

Elton, C. 1966. Dying and dead wood. In Elton, C. (Ed.), The Pattern of Animal Communities. London : Methuen, 279-305.

Elton, C.S. 1966. The pattern of animal communities. London: Methuen.

Eriksson, O.; Cousins, S.A.O.; Bruun, H.H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science 13: 743-8.

Franklin, J.F. 1988. Structural and functional diversity in temperate forests. In Wilson, E. O. (ed.) Biodiversity. Washington: National Academy Press, 166-75.

Girling, M. 1989. Mesolithic and later landscapes interpreted from the insect assemblages of West Heath Spa, Hampstead. In: Collins, D. and Lorimer, D. (eds.) Excavations at the Mesolithic site on West Heath, Hampstead 1976-1981 (British Archaeological Reports 217), York: British Archaeological Reports, 72-89.

Girling, M.A. 1976. Fossil Coleoptera from the Somerset Levels: the Abbot's Way. Somerset Levels Papers 2: 28-33.

Greenwood, M.T.; Agnew, M.D.; Wood, P.J. 2003. The use of caddisfly fauna (Insecta: Trichoptera) to characterise the late-glacial River Trent, England. Journal of Quaternary Science 18(7): 645-662.

Greig, J. 1982. Past and present lime woods in Europe. In: Bell, M. and Limbrey, S. (eds.) Archaeological Aspects of Woodland Ecology (British Archaeological Reports International Series 146), Oxford: British Archaeological Reports, 23-55.

Harding, P.T.; Rose, F. 1986. Pasture-woodlands in lowland Britain. Peterborough: Institute of Terrestrial Ecology, NERC.

Heliövaara, K.; Väisänen, R. 1984. Effects of modern forestry on north-western European forest invertebrates: a synthesis. Acta Forestalia Fennica 189: 1-32.

Kaila, L.; Martikainen, P.; Puttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation 6: 1-18.

Kampf, H. 2002. Nature conservation in pastoral landscapes: challenges, chance and constraints. In Redecker, B.; Finck, P.; Hardtle, U.; Riecken, U. and Schroder, E. (eds) Pasture landscapes and Nature Conservation. Berlin: Springer-Verlag, 15-30.

Kenward, H.K. 1975. Pitfalls in the environmental interpretation of insect death assemblages. Journal of Archaeological Science 2: 85-94.

Kenward, H.K. 1978. The analysis of archaeological insect assemblages: a new approach. York: York Archaeological Trust.

Kenward, H.K.; Hall, A.R. 1995. Biological evidence from 16-22 Coppergate, York (Archaeology of York: The Environment 14/7). York: York Archaeological Trust,

Kirby, K.J. 2003. What might a British forest-landscape driven by large herbivores look like? (Research Report 530). Peterborough: English Nature.

Kirby, K.J. 2004. A model of a natural wooded landscape in Britain as influenced by large herbivore activity. Forestry 77 (5): 405-420.

Klinger, L.F.; Elias, S.A.; Behan-Pelletier, V.M.; Williams, N.E. 1990. The bog climax hypothesis: fossil arthropod and stratigraphic evidence in peat sections from south-east Alaska, U.S.A. Holarctic Ecology 13: 72-80.

Lucht, W.H. 1987. Katalog. Die Käfer Mitteleuropas. Krefeld: Goecke and Evers.

Marra, M.J.; Smith, E.C.G.; Schulmeister, J.; Leschen, R. 2004. Late Quaternary climate change in the Awatere Valley, South Island, New Zealand using a sine model with a maximum likelihood envelope on fossil beetle data. Quaternary Science Reviews 23: 1637-1650.

Matthews, J.V., Jr. 1970. Two new species of Micropeplus from the Micropeplinae of western Alaska with remarks on the evolution of Coleoptera: Staphylinidae. Canadian Journal of Zoology 48: 779-788.

Mitchell, F.J.G. 1990. The impact of grazing and human disturbance on the dynamics of woodland in sw Ireland. Journal of Vegetation Science 1: 245-54.

Mitchell, F.J.G. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. Journal of Ecology 93: 168-177.

Morgan, A.V.; Morgan, A. 1987. Palaeoentomology—towards the next decade. Episodes 10 (1): 38-40.

Mountford, E.P.; Peterken, G.F. 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. Forestry 76 (1): 19-43.

Osborne, P.J. 1969. An insect fauna of late bronze age date from Wilsford, Wiltshire. Journal of Ecology 38: 555-566.

Osborne, P.J. 1972. Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire Philosophical Transactions of the Royal Society of London 263: 327-367.

Osborne, P.J. 1974. An insect assemblage of early Flandrian age from Lea Marston, Warwickshire, and its bearing on the contemporary climate and ecology. Quaternary Research 4: 471-486.

Osborne, P.J. 1980. The Late Devensian-Flandrian transition depicted by serial insect faunas from West Bromich, Staffordshire, England. Boreas 9: 139-147.

Osborne, P.J. 1988. A late bronze age insect fauna from the River Avon, Warwickshire, England: its implications for the terrestrial and fluvial environment and for climate. Journal of Archaeological Science, 15: 715-727.

Osborne, P.J. 1995. An insect fauna of Roman date from Stourport, Worcestershire, U.K. and its environmental implications. Circaea (The Journal of the Association for Environmental Archaeology) 12 (2): 183-189.

Palm, T. 1951. Die Holz und Rindenkäfer der nordschwedischen Laubbaume. Meddelelser Statens Skögsfors.-instituten, 40, no. 2.

Palm, T. 1959. Die Holz und Rindenkäfer der Sud- und Mittelschwedischen Laubbäume. (Opuscula Entomologica Supplementum 16) Lund: Entomologiska Sallskapet.

Panagiotakopulu, E. 2004. Dipterous remains and archaeological interpretation. Journal of Archaeological Science 31: 1675-1684.

Patterson, W.A.; Backman, A.E. 1988. Fire and disease history of forests. pp. 603-32 in Huntley B. and Webb, T. (eds.), Vegetation History. New York: Kluwer Academic.

Patterson, W.A.; Edwards, K.J.; Maguire, D.J. 1987. Macroscopic charcoal as a fossil indicator of fire. Quaternary Science Reviews 6: 3-23.

Pearson, G.W.; Pilcher, J.R.; Baillie, M.G.L. [and others]. 1986. High precision ^{14}C measurement of Irish oaks to show the natural ^{14}C variation from AD 1840-5210 BC. Radiocarbon 28(2B): 911-934.

Peterken, G.F. 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge: Cambridge University Press.

Ponel, P.; Andrieu-Ponel, A.; Parchoux, F. [and others]. 2001. Late-glacial and Holocene high-altitude environmental changes in Vallée des Merveilles (Alpes-Maritimes, France): insect evidence. Journal of Quaternary Science 16: 795-812.

Rackham, O. 1986. The history of the countryside. London: J. M. Dent and Sons Ltd.

Rackham, O. 2003. Ancient woodland. Its history, vegetation and use in England. (New Edition). Dalbeattie: Castlepoint Press.

Ranius, T.; Jansson, N. 2000. The influence on forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85-94.

Rasmussen, P. 1990. Pollarding of trees in the Neolithic: often presumed—difficult to prove. In: D. E. Robinson (ed.) Experimentation and reconstruction in environmental archaeology. (Symposia of the Association of Environmental Archaeologists 9) Oxford: Oxbow Books, 139-148.

Reiss, R.; Ashworth, A.C.; Schwert, D.P. 1999. Molecular genetic evidence for the post-Pleistocene divergence of populations of the artic-alpine ground beetle *Amara Alpina* (Paykull) (Coleoptera: Carabidae). Journal of Biogeography 26: 785-794.

Reitter, E. 1908-12. Fauna Germanica-Die Käfer des Deutchen Reiches. Stuttgart.

Ribera, I.; Vogler, A.P. 2004. Speciation of Iberian diving beetles in Pleistocene refugia (Coleoptera, Dytiscidae). Molecular Ecology 13: 179-193.

Robinson, M. 1981. Appendix I: the use of ecological groupings of Coleoptera for comparing sites. In M. Jones and G. Dimbleby (eds.) The Environment of Man: the Iron Age to the Anglo-Saxon Period. London: British Archaeological Reports, 279-281.

Robinson, M.A. 1991. The Neolithic and late bronze age insect assemblages. In Needham, S. (ed.), Excavation and Salvage at Runnymede Bridge, 1978: the Late Bronze Age Waterfront Site. London: British Museum, 277-325.

Robinson, M.A. 2000. Middle Mesolithic to late bronze age insect assemblages and an early Neolithic assemblage of waterlogged macroscopic plant remains. In Needham, S. P. (ed.), The Passage of the Thames: Holocene Environment and Settlement at Runnymede. (Runnymede Bridge Research Excavations: Volume 1). London: The British Museums Press, 146-67.

Roper, T. 1996. Fossil insect evidence for the development of raised mire at Thorne Moors, near Doncaster. Biodiversity and Conservation 5: 503-521.

Russell, E. 1997. People and land through time. Linking Ecology and History. New Haven, Connecticut: Yale University Press.

Schwert, D.P. 1996. Effect of Euro-American settlement on an insect fauna: paleontological analysis of the recent chitin record of beetles (Coleoptera) from northeastern Iowa. Ecology and Population Biology 89: 53-63.

Shirt, D.B. 1987. British red data books: 2. Insects. Peterborough: Nature Conservancy Council.

Similä, M.; Kouki, J.; Martikainen, P.; Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106: 19-27.

Skidmore, P. 1995. A dipterological perspective on the Holocene history of the North Atlantic area. Unpublished PhD thesis, University of Sheffield, England.

Smith, A.G. 1970. The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In: D. Walker and R.G. West (eds.), Studies in the Vegetation History of the British Isles. Cambridge: University Press, 81-96.

Smith, A.G. 1981. Palynology of a Mesolithic-Neolithic site in county Antrim, N. Ireland. Lucknow: Proceedings of the IVth International Palynology Conference (1976-1977), 248-257.

Smith, D.; Whitehouse, N.J. 2005. Not seeing the woods for the trees; a palaeoentomological perspective on woodland decline. in Brickley, M., Smith, W. and Smith, D.N. (eds.), 'The Fertile Ground'; Papers in Honour of Susan Limbrey. Oxford: Oxbow Books.

Smith, D.N.; Howard, A.J. 2004. Identifying changing fluvial conditions in low gradient alluvial archaeological landscapes: can Coleoptera provide insights into changing discharge rates and floodplain evolution? Journal of Archaeological Science 31: 109-120.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. (Nature and Environment Series No 42). Strasbourg: Council of Europe,

Sutherland, W.J. 2002. Conservation biology: openness in management. Nature 418: 834-5.

Svenning, J.-C. 2002. A review of natural vegetation openness in north-western Europe. Biological Conservation 104: 133-48.

Vandenberghe, J.; Coope, R.; Kasse, K. 1998. Quantitative reconstructions of palaeoclimates during the last interglacial-glacial in western and central Europe: an introduction. Journal of Quaternary Science 13 (5): 361-366.

Vera, F.W.M. 2000. Grazing ecology and forest history. Oxfordshire: CABI Publishing.

Walker, I.R.; Mott, R.J.; Smol, J.P. 1991. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. Science 253: 1010-1012.

Walker, M.J.C.; Coope, G.R.; Lowe, J.J. 1993. The Devensian (Weichselian) Lateglacial palaeoenvironmental record from Gransmoor, East Yorkshire, England. Quaternary Science Reviews 12: 659-680.

Warren, M.S.; Key, R.S. 1991. Woodlands: past, present and potential for insects. In Collins, N.M. and Thomas, J.A. (eds.) The conservation of insects and their habitats (15th Symposium of the Royal Entomological Society of London, 14-15 September 1989). London: Academic Press, 155-211.

Whitehouse, N.J. 1997a. Insect faunas associated with *Pinus sylvestris* L. from the mid-Holocene of the Humberhead Levels, Yorkshire, U.K. Quaternary Proceedings 5: 293-303.

Whitehouse, N.J. 1997b. Silent witnesses: an “Urwald” fossil insect assemblage from Thorne Moors. Thorne and Hatfield Moors Papers 4: 19-54.

Whitehouse, N.J. 1998. The evolution of the Holocene wetland landscape of the Humberhead Levels from a fossil insect perspective. Unpublished PhD thesis, University of Sheffield.

Whitehouse, N.J. 2000. Forest fires and insects: palaeoentomological research from a sub-fossil burnt forest. Palaeogeography, Palaeoclimatology, Palaeoecology 164: 231-46.

Whitehouse, N.J. [In press]. The Holocene British and Irish ancient woodland fossil beetle fauna: implications for woodland history, biodiversity and faunal colonisation. Quaternary Science Reviews.

Whitehouse, N.J.; Boswijk, G.; Buckland, P.C. 1997. Peatlands, past, present and future; some comments from the fossil record. In: Parkyn, L.; Stoneman, R. and Ingram, H.A.P. (eds.) Conserving Peatlands. Wallingford, Oxfordshire: CAB International, 54-64.

Whitehouse, N.J.; Smith, D.N. 2004. “Islands” in Holocene forests: implications for forest openness, landscape clearance and “culture-steppe” species. Environmental Archaeology 9(2): 199-208.

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

Wilkinson, B.J. 1984. Interpretation of past environments from subfossil caddis larvae. In Morse, J.C. (ed.) Proceedings of the 4th International Symposium on Trichoptera. The Hague: W. Junk, 447-452.

Willis, K.J. 1996. Where did all the flowers go? The fate of temperate European flora during glacial periods. Endeavour 20: 110-114.

BROWN ROT IN INNER HEARTWOOD: WHY LARGE LOGS SUPPORT CHARACTERISTIC SAPROXYLIC BEETLE ASSEMBLAGES OF CONSERVATION CONCERN

**Marie Yee, Simon J. Grove, Alastair MM. Richardson,
and Caroline L. Mohammed**[1]

Abstract—It is not clear why large diameter logs generally host saproxylic beetle assemblages that are different from those of small diameter logs. In a study in Tasmanian wet eucalypt forest, two size-classes of *Eucalyptus obliqua* logs (>100cm and 30-60cm diameter) were destructively sampled to assess their beetle fauna and the associations of this fauna with decomposing wood. Ninety species were collected as adults from 42 logs; at least 19 species were also collected as larvae. The two log size-classes differed in beetle assemblage composition. These differences could be explained by the observation that certain beetle species were associated with specific successional phases of decomposing wood (rotten wood types). Those that were preferentially found in brown rotted heartwood, which was common in large logs, were rare or absent in small logs. This rotten wood type seems to be a relatively stable microhabitat and accordingly, the four most strongly associated species (in the genera *Cossonus, Dryophthorus, Prostomis* and *Pycnomerus*) seem likely to have low dispersal ability. Although relatively common in this habitat, each belongs to a genus whose European counterparts have undergone drastic range reductions. Our research highlights the importance of a level of landscape planning in Tasmanian forestry, which would maintain sufficient large diameter logs in the landscape over the long term.

INTRODUCTION

Saproxylic beetle assemblages have been studied in many forest ecosystems, including the boreal forests of Scandinavia (reviewed in Siitonen 2001) and Canada (Hammond and others 2004), the temperate forests of Germany (Kleinvoss and others 1996), the Douglas Fir forests of Northwest U.S. (Edmonds and Marra 1999, Maser and Trappe 1984), and the wet eucalypt forests of Tasmania (Yee 2005). These studies demonstrate that large diameter logs host specific saproxylic beetle assemblages that are not found in smaller sized logs. The ecological processes that shape these assemblages and create the differences between large and small diameter logs are not well understood. Differences in the decomposition pathways in large and small logs, resulting in differences in rotten wood types that potentially represent different microhabitats, may influence the saproxylic beetles assemblages within those logs.

Rotten wood is defined here as wood that has undergone some degree of decomposition. Decomposition results from either one or a combination of biotic and abiotic agents (Harmon and others 1986). These include mechanical, physical-chemical processes, and the physical and metabolic actions of various organisms (Kaarik 1974, Kirk and Cowling 1984, Swift 1977). They include bacteria (Clausen 1996), xylophagous arthropods (Carpenter and others 1988, Edmonds and Eglitis 1989), basidiomycete and ascomycete fungi, and micro-arthropods (Ausmus 1977, Seastedt 1984, Sollins and others 1987, Swift 1977). Depending on the types of processes and organisms, the physical, chemical and biological wood properties change in a specific way (Rayner and Boddy 1988). This gives rise to a specific rotten wood type that can be described by its wood microstructure and chemistry, relative density, moisture content and nutrient levels (Ausmus 1977, Christensen 1984, Harmon and others 1986, Swift and Boddy 1984). To illustrate, brown rotted wood arises when 'brown-rot' fungi selectively remove cellulose and hemicellulose from the wood, leaving a residue of slightly modified lignin. By contrast, 'white-rot' fungi utilise all components of the wood cells, removing lignin, cellulose and hemicellulose and leaving the wood bleached, with a spongy, stringy or laminated structure (Kaarik 1974).

Current studies have clearly established that for the hardwood species *Eucalyptus obliqua* in Tasmanian wet eucalypt forests, large (>100 cm diameter) and small (30-60 cm diameter) logs at an intermediate decomposition stage differ in both type and spatial arrangement of rotten wood (Yee 2005). Eleven distinct rotten wood types have been classified within these logs. Although little is known of the actual decomposition processes or of the organisms involved, each type may result from a specific decomposition pathway and potentially provides a unique microhabitat for saproxylic beetles. Large diameter logs have a higher frequency of brown rotted heartwood occurring within the log centre. In small diameter logs a white rotten wood commonly occurs in the outer regions of the log. The presence of the different types of rotten wood demonstrates differing decay processes occurring in each size class of log. In large diameter logs internal decay probably established when the tree was alive, as heartrot is frequent in large old trees. Younger (smaller diameter) trees are less likely to give rise to logs with pre-existing heart rot, but such logs were more frequently rotted in their outer regions.

---

[1] Marie Yee, Conservation Planner, Division of Forest Management, Forestry Tasmania, GPO Box 207, Hobart, Tasmania 7001, Australia (formerly at Cooperative Research Centre for Sustainable Production Forestry, University of Tasmania, Private Bag 12, Hobart, Tasmania 7001, Australia); Simon J. Grove, Conservation Biologist, Division of Research and Development, Forestry Tasmania, GPO Box 207, Hobart, Tasmania 7001, Australia; Alastair MM. Richardson, Invertebrate Ecologist, School of Zoology, University of Tasmania, Private Bag 5, Hobart, Tasmania 7001, Australia; and Caroline L. Mohammed, Senior Research Scientist, CSIRO-Forestry and Forest Products and University of Tasmania, Private Bag 12, Hobart, Tasmania 7001, Australia.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Many saproxylic beetles are specially adapted to and intimately associated with the microhabitats and microclimates that occur in rotten wood (Dajoz 2000, Gilbertson 1984, Haack and Slansky 1987, Lawrence 1989, Speight 1989). For instance, in Japan the lucanids *Ceruchus lignarius* and *Aesalus asiaticus* occur more frequently in wood decomposed by brown rot fungi, whilst *Platycerus acuticollis* prefers wood decomposed by soft rot fungi (Araya 1993). Some beetle species rely on the actions of certain wood decay fungi to process and precondition the wood. Fungi can provide metabolic water and vitamins necessary for insect development, and they can produce enzymes for cellulose digestion that can be ingested by insects living within the wood. Fungi can detoxify wood that contains toxic or repellent allelochemicals, or decompose the wood to a softer and more chewable resource that can be more readily assimilated (Hanula 1996-see references within, Swift and Boddy 1984).

Saproxylic beetles may also be indirectly associated with one or more rot types through their dependence on organisms that are more intimately associated with a specific type of rot (Dajoz 2000, Speight 1989). For example, some elaterid beetles specifically prey on tipulid flies that only live in the moist wood invaded by white rot fungi (Dajoz 2000). The European *Elater ferrugineus* (Elateridae) is a predator of scarab beetles that occur in the red rotted wood of old trees (Svensson and others 2004).

In this study we investigated the saproxylic beetle assemblages found in large and small diameter logs in the wet eucalypt forest of Tasmania. Our aim was to determine whether the differences observed in the beetle assemblages between log size classes could be explained by associations between beetles and rotten wood types specific to a log size class.

METHODS

Study Location and Experimental Design

The study was conducted in wet eucalypt forest (Ashton 1982), at three localities in Tasmania's Southern Forests (fig. 1). These were in the Huon Valley, at the Warra Long Term Ecological Research (LTER) site (43º04'S, 146º41'E); in the Picton Valley, 10 km south of Warra; and in the Arve Valley, 10 km east of Warra. There were seven study sites among the three localities: four sites in single aged native forest that had regenerated from 'clearfell, burn and sow' silviculture (Hickey and others 2001) during the 1960s, and three sites in multi-aged unlogged forest that had regenerated following wildfires in the early 1900s. Within each site, three pairs of large and small *Eucalyptus obliqua* logs were sampled, and these were at an intermediate decomposition stage. In the logging regenerated forests, the studied logs were from felled trees left after the harvest. In the mature-unlogged forests, it was not possible to determine the date of tree fall but logs for the trial were selected so as to be of the same decompositional stage as those selected in the logging regenerated forests. The effect of forest type was not analysed in this study, but will be reported elsewhere (Yee 2005). Large logs were defined as those greater than 100 cm in diameter, derived from an 'old growth' tree; and small logs were 30-60 cm, derived from a 'regrowth' tree.

Sampling Method

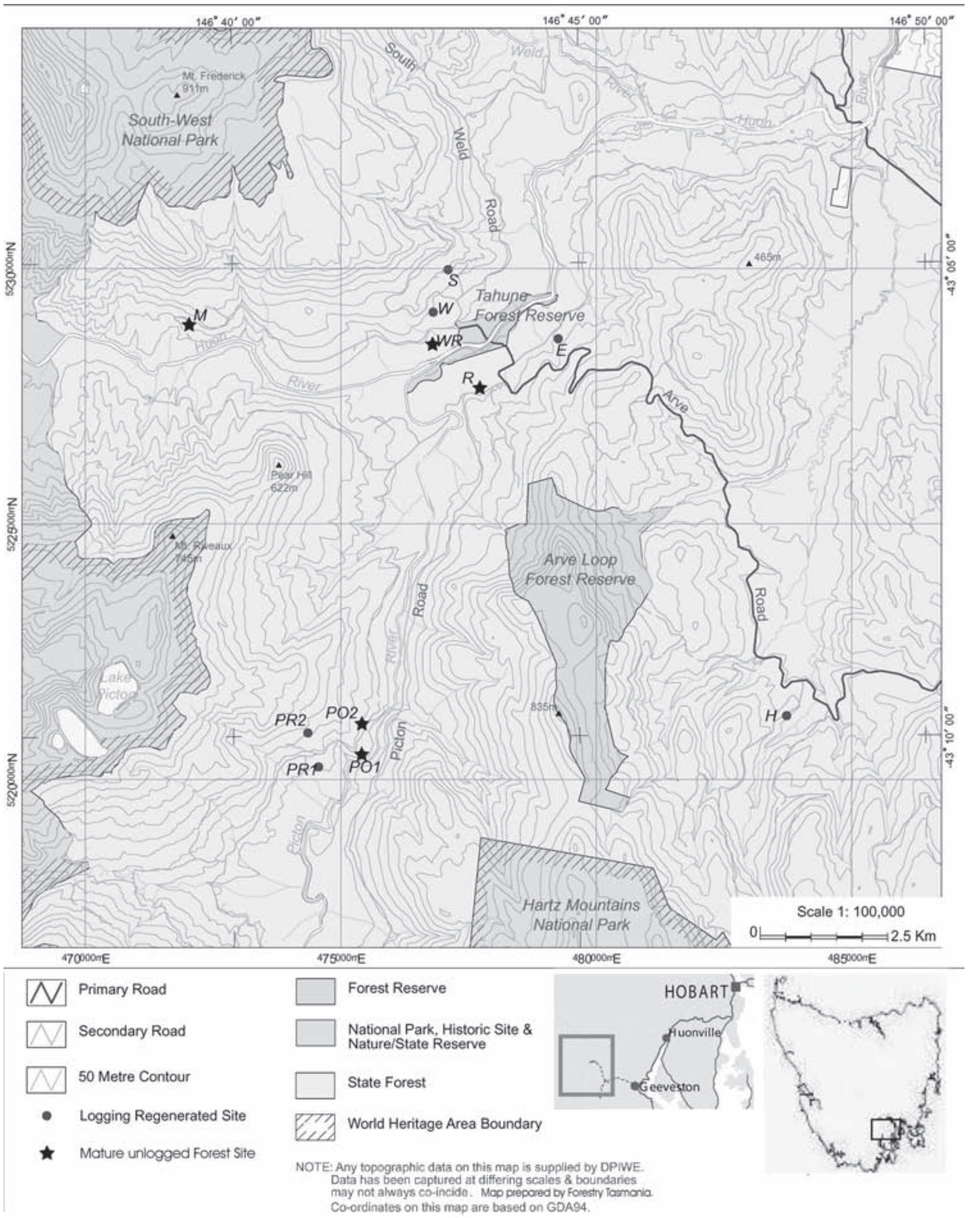
Two 1 m sections were sampled from each log, with one to two hours being spent sampling each log section. Sections were taken along the base and middle positions of the fallen tree trunk, and were at least 4 metres apart (figs. 2A and 2B). The surface of each section was examined and then the section was removed from the log using a chainsaw. The removed section was then cut into three parts to allow ease of handling. Each part was then further cut up using an axe and hammer. Because of the gross differences in volume between the log size classes, for large diameter logs only one eighth of each 1-m long section was sampled (fig. 2B). Reducing the sampled volume ensured a more comparable sampling effort between log sizes and made sampling large logs logistically feasible.

The rot types present within each section were categorised according to 11 previously characterised Rotten Wood (RW) types (see table 1). The classification system for RW types of *Eucalyptus obliqua* logs had been developed alongside this study (Yee 2005), on the basis of colour, texture, hardness and 'RW region'. RW region to some extent indicates where decomposition may have started, for example, within the log or on the log surface. This was based on the consistent spatial association of a rot type with one of five areas within the log cross-section, and the direction from which the decomposition appeared to be spreading. The five areas specified were surface (sapwood), outer heartwood, inner heartwood, localised pockets from which the decay did not appear to spread, and throughout the heartwood (fig. 3). Colour was taken as indicative of the predominant type of fungal decay in process at the time of sampling: a 'white' or a 'brown' rot.

Beetle collection was conducted with the aid of a head torch and forceps to search within the log section as it was broken up. Collected adult and larval beetles were immediately preserved in 80 percent ethanol. To minimise impacts on saproxylic beetle populations, only subsets of specimens were taken when multiple individuals of the same species were found. Additional samples of larvae with host wood were taken to the laboratory for rearing, to allow identification and to observe life history. Beetles were sorted and identified to known species using various taxonomic keys, consulting with taxonomic experts, and comparing voucher specimens with material in the Australian National Insect Collection (ANIC: CSIRO Entomology, Canberra) and Tasmanian Forest Insect Collection (TFIC: Forestry Tasmania, Hobart). Specimens have been lodged at both, but with the primary set of vouchers lodged at the TFIC.

Statistical Analyses

Data and general statistical techniques—Presence-absence data were used instead of abundance because it was considered more relevant for determining a species' association with RW type. Using such an approach also reduced the influence of factors relating to the breeding strategy and the aggregative behaviour of individual species and the confounding effects of variable sampling efforts among the different RW types. Many larvae could not be identified even to family level, were seldom encountered, and may be the larval stage of some adult beetles. Therefore, species occurring only as larvae were documented separately and excluded from statistical analyses. Larval Elateridae and Scirtidae were the



NOTE: Any topographic data on this map is supplied by DPIWE.
Data has been captured at differing scales & boundaries
may not always co-incide. Map prepared by Forestry Tasmania.
Co-ordinates on this map are based on GDA94.

Figure 1—Location of the three study areas and seven sites in southern Tasmania, showing the State forest and forest reserve boundaries.

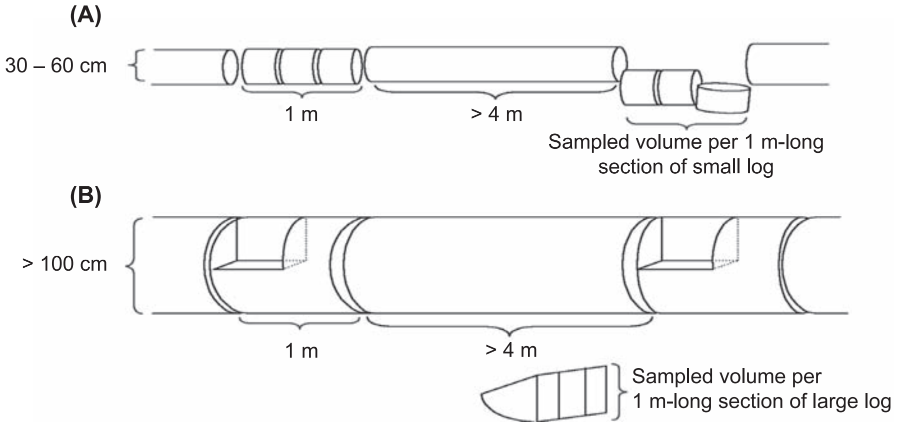


Figure 2—Schematic diagram of the destructive sampling method used for (A) small and (B) large diameter logs in wet eucalypt forests in southern Tasmania.

Table 1—Classification of 11 rotten wood types, listed in order by rotten wood origin, from Eucalyptus obliqua logs in wet eucalypt forests in southern Tasmania.

Rotten wood type	Rotten wood origin	Suspected main decomposition process	Apparent decay type
Fibrous surface rot	Surface (sapwood)	Fungal decay	Unknown
White jelly surface rot	Surface (sapwood)	Fungal decay	Unknown
Yellow dry slatey rot	Outer heartwood	Fungal decay	Unknown
White pocket rot	Outer heartwood	Fungal decay	White
White stringy rot[a]	Outer heartwood	Fungal decay	White
Brown spongy cubic rot	Outer heartwood	Fungal decay	Brown
Discolored wood	Heartwood	Unknown	NA
Wet cracks	Localised	Mechanical and other	NA
Brown blocky crumbly rot	Inner heartwood	Fungal decay	Brown
Red brown blocky fibrous rot	Inner heartwood	Fungal decay	Brown
Brown mudgut rot	Inner heartwood	Insects, fungal and other	Brown

NA = not applicable.

[a] During incipient stages of decomposition, this rotten wood type appears as dark crimson discoloured wood.

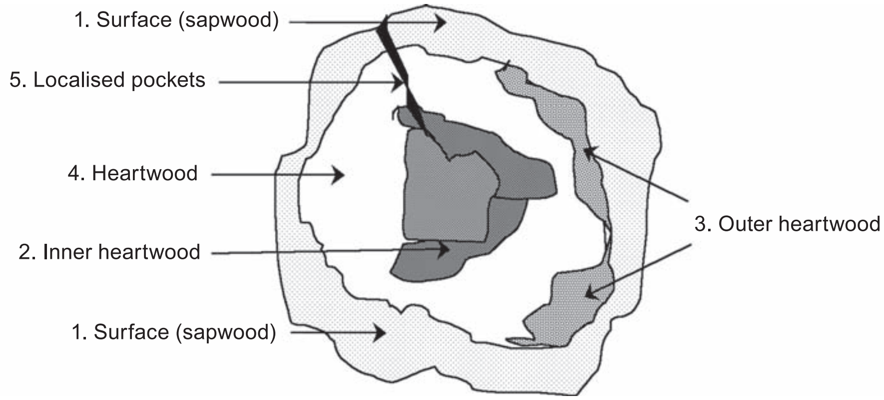


Figure 3—Stylised *Eucalyptus obliqua* log cross section showing the five main areas where rotten wood occurred, referred to as "RW region" in this paper.

exception. They were included because for these families, only larvae inhabit the log so there was no risk of double-counting. Furthermore, elaterids and scirtids are a common and important component of the saproxylic community, and are relatively easy to identify to family and morphospecies.

Two multivariate statistical methods were used, Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedures (MRPP). NMS is a non-parametric ordination technique that relates the similarity of entities (e.g., logs or rotten wood samples), based on ranked distances, in multidimensional space (McCune and Grace 2002). NMS was performed using a Sorensen (Bray-Curtis) distance measure, in *PC-ORD* (McCune and Mefford 1999), choosing the 'slow and thorough autopilot' mode. MRPP in *PC-ORD* is a non-parametric method that uses permutation procedures for testing the hypothesis of no difference between two or more *a priori* groups based on multi-species data. This method provides a test statistic, T, which describes the separation between groups: the more negative the T, the stronger the separation. It also provides a p-value, which evaluates whether the observed difference is greater than expected by chance. As recommended in the program, the method was run on an Euclidean distance measure and used the natural group weighting of n/sum (n).

Comparison of beetles between log size classes—The frequency of occurrence of individual beetle species was compared between large and small logs, using Chi-square analyses. Data comprised the presence-absence of a species within a log pooled from all RW types from both log sections. Only common species (occurring in more than 25 percent of logs) were analysed. Beetle assemblages in large and small logs were graphically compared using NMS. Beetle species occurrences and RW type vectors were overlaid onto the ordination as a joint plot. RW type data comprised the presence-absence of RW types within a log, pooled from the two 1 m-long sections. MRPP were used to test for differences in beetle assemblage composition between log size-classes.

Beetle associations with RW types/regions—Individual beetle species and assemblages were investigated for their association with RW types. Data comprised the presence-absence of species within a RW type, pooled from both log sections. Since many species were absent from over 20 percent of RW types per log, many standard statistical analyses, such as Chi-square analysis, would not have been reliable. Therefore interpretation of this aspect is limited to a discussion of observed trends on larval feeding and on species associations with rotten wood. NMS was used to determine whether RW types were characterised by similar beetle assemblages. MRPP were used to test whether the assemblages within rotten wood differed significantly among RW types. As RW region was found to be an important difference between large and small logs, species associations with RW region were also examined by overlaying RW region onto the ordination plot instead of RW type, and by testing group differences using MRPP. Beetle species vectors were also overlaid on the ordination plot as a joint plot.

RESULTS

In total, 90 species of adult beetles from 23 families were collected (appendix A). The most species-rich families were Staphylinidae (16 species), Curculionidae (12 species) and Carabidae (12 species). At least 19 of these species were also collected as larvae (appendix A), their identities being confirmed following successful larval rearing. Only 14 species occurred in over 25 percent of logs, and all of these were collected in both life stages, except *Aleocharinae* TFIC sp 34 (Staphylinidae) and *Exeiratus* TFIC sp 01 (Curculionidae), which were only collected as adults.

In total, 27 morphospecies were collected as larvae only (appendix B). Some of these may have represented the larval stages of species also collected as adults. Those larvae identified as species in the families Lycidae, Cantharidae, Cleridae and Melandryidae were not represented in the collection as adults. However, many of these larvae were only represented as singletons.

Comparison of Beetles between Log Size Classes

Sixty-three species of adult beetles were collected from large logs and 65 from small logs, with 38 species common to both. Of the 14 species that occurred in over 25 percent of logs, *Cossonus simsoni* (Curculionidae) occurred only in large logs, and *Pycnomerus* TFIC sp 02 (Zopheridae) and *Coripera deplanata* (Tenebrionidae) were significantly more frequent in large logs than in small ones ($p = 0.013$ and 0.0278 respectively) (fig. 4). Meanwhile, *Enneaphyllus aeneipennis* (Cerambycidae) only occurred in small logs.

Results from the NMS (figs. 5A and 5B) and MRPP showed that large and small logs differed significantly in their beetle assemblages (fig. 5B, separation along Axis 3; $p = 0.001$, $T = -4.5$). Ten small logs were clearly different from the cluster of large logs. Overlaying the beetle species onto the ordination plot revealed that *Enneaphyllus aeneipennis* had a strong influence on this pattern, correlating with Axis 3 ($r^2 = 0.65$). Several species correlated in the opposite direction: *Prostomis atkinsoni* (Prostomidae) ($r^2 = 0.31$), Elateridae TFIC sp 21 (Elateridae) ($r^2 = 0.24$), *Dryophthorus* TFIC sp 01 (Curculionidae) ($r^2 = 0.25$), *Pycnomerus* TFIC sp 02 (Zopheridae) ($r^2 = 0.20$) and Scirtidae YEE sp 04 (Scirtidae) ($r^2 = 0.23$). Two RW types, 'brown mudgut rot' and 'wet cracks', which are both wet RW types, also correlated with this axis ($r^2 = 0.24$ and 0.20 respectively).

Beetle Associations with RW Types and Origins

The relative frequencies of individual species differed among RW types. No species was restricted to a single RW type but some showed preferences for either a RW region or for an amalgamation of RW types into decay type (white or brown) (table 2). For example, the xylophagous species *Dohrnia simplex* (Oedemeridae), *Dryophthorus* TFIC sp 01, *Prostomis atkinsoni, Cossonus simsoni* and *Pycnomerus* TFIC sp 02 preferred the brown rotten heartwood (inner) types, whilst

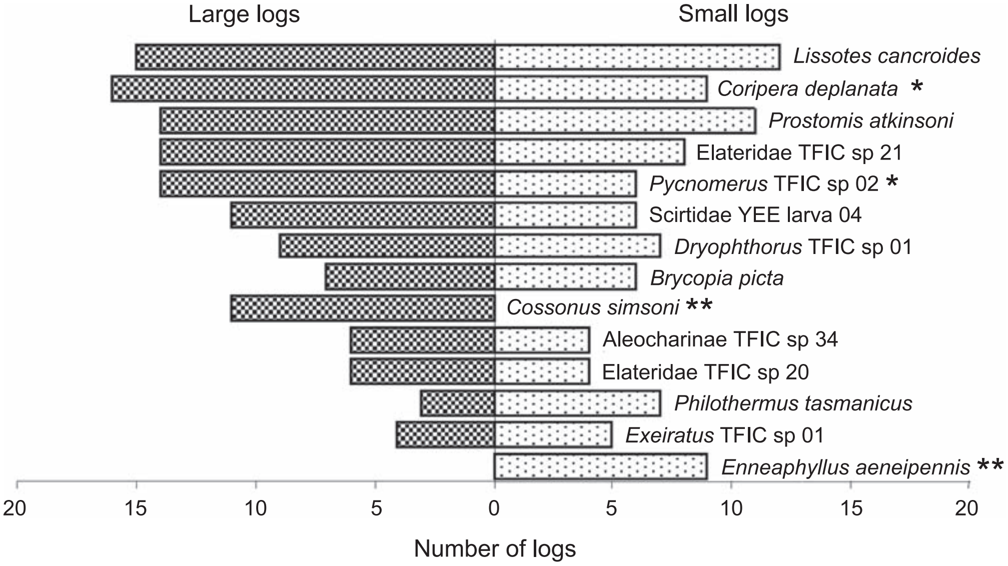


Figure 4—The frequency of common (> 25 percent of logs) saproxylic beetle species found in 21 large (left) and 21 small (right) *Eucalyptus obliqua* logs from wet eucalypt forests in southern Tasmania. Species whose occurrences differed significantly ($p < 0.05$) between the two log size classes are denoted by *, while those exclusive to a particular log size class are denoted by **.

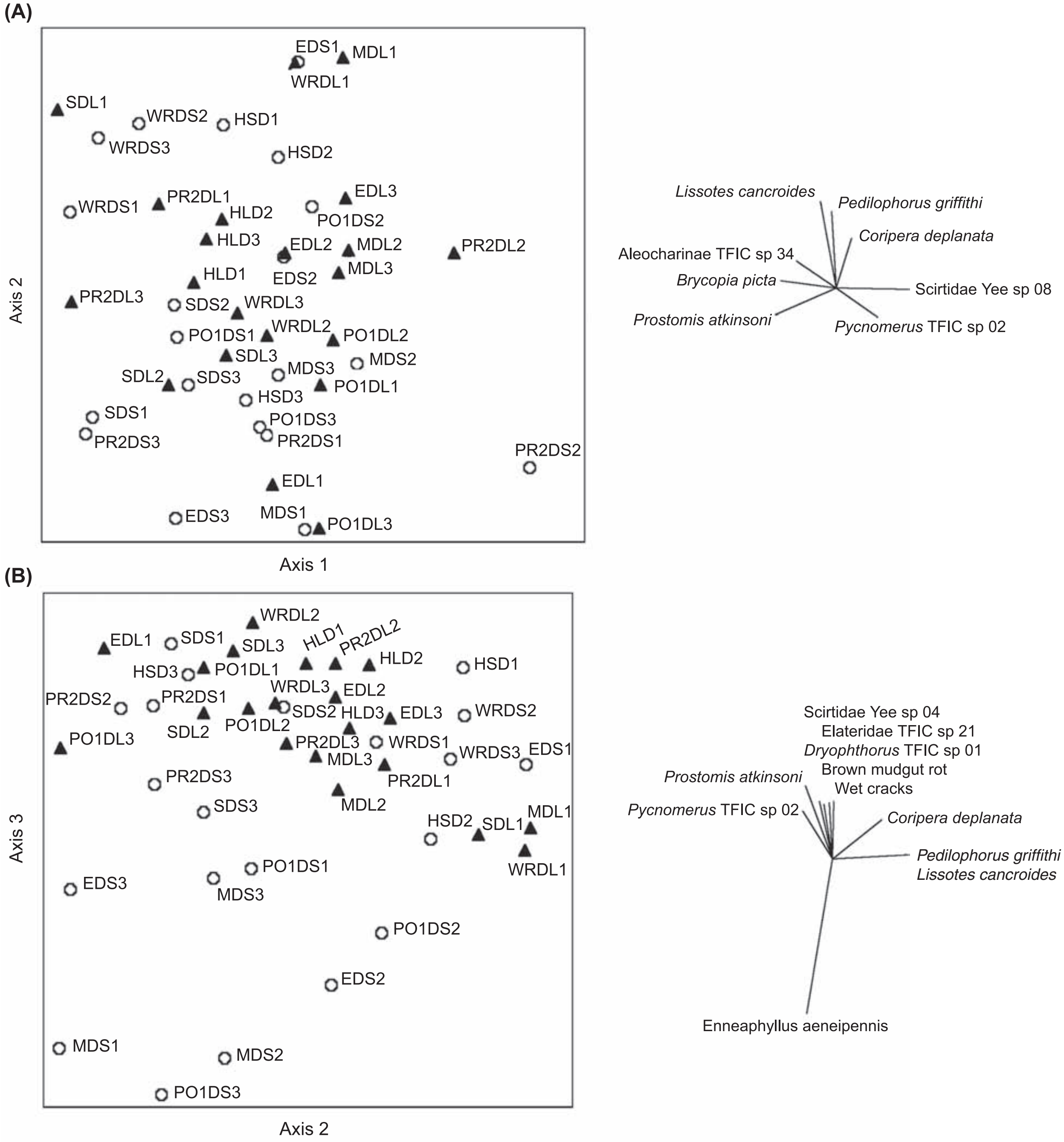


Figure 5—NMS ordination showing saproxylic beetle assemblages from 21 large (▲) and 21 small (○) *Eucalyptus obliqua* logs from wet eucalypt forests in southern Tasmania. (A) axes 1 and 2; (B) axes 2 and 3. Based on presence-absence data for saproxylic beetle species pooled from two 1-m long sections per log (single occurrences were excluded). Alphanumeric codes are log identification tags. Vectors based on beetle species occurrence and rotten wood type (refer to table 2) are overlaid as a joint plot; for greater clarity, these are displayed adjacent to the ordination. Stress = 0.18, p = 0.0196. Vector scaling 100 percent. Only vectors with $r^2 > 0.2$ are shown.

Enneaphyllus aeneipennis preferred the white rotten heartwood types. Two further xylophagous species *Coripera deplanata* and *Lissotes cancroides* (Lucanidae) were more closely associated with surface (sapwood) rotten wood than with other log areas, but their occurrence also extended into the brown rotted heartwood (inner). The saprophagous species Scirtidae YEE sp 04 (Scirtidae) was more frequent in the very wet RW types ('wet cracks' and 'brown mudgut rot'). The xylophagous *Syndesus cornutus* (Lucanidae) was restricted to brown rot, where many larvae were found feeding within brown rotted wood that was either cubic or crumbly, and occurring in either inner or outer heartwood.

Except for the distinct patterns evident for two single RW types ('brown mudgut rot' and 'fibrous surface rot'), there were no discrete clusters of the same RW type evident in ordination

Table 2—Species associated with rotten wood type, grouped by rotten wood origin and apparent decay type

RW origin[a]	SF (SP)		OH				H	IH			L	
RW type [b]	WJR	FSR	YDR	WPR	WSR	BSR	DW	RBR	BBR	BMR	WC	Total
Apparent decay type[c]	–	–	–	Wh	Wh	Br	–	Br	Br	Br	–	
Lissotes cancroides	8	14	2	1	2	1	6			3		37
Prostomis atkinsoni	1	2			2	2	5	6	5	11	2	36
Coripera deplanata	7	16		1		1	3	1		4		33
Elateridae TFIC sp 21	5	9				2	4	3	2	4		29
Dryophthorus TFIC sp 01	2	5			1		1	8	1	7		25
Pycnomerus TFIC sp 02		2				1	6	6	2	7		24
Cossonus simsoni	1	4		1		1	4	7		4		22
Scirtidae YEE sp 04		1			1		2	1	2	7	9	22
Diemenoma TFIC sp 01		3			1	1	3	4	3	2		17
Aleocharinae TFIC sp 34*aA*	3	4				1	2		1	1		12
Enneaphyllus aeneipennis		2		2	5		2			1		12
Dorhnia simplex	1						1	4	2	3		11
Exeiratus TFIC sp 01		2		1	2			3		3		11
Aleocharinae TFIC sp 13	1	2					2	1	1	3		10
Elateridae TFIC sp 20	2	7								1		10
Philothermus tasmanicus	1	1			1		2			3	2	10
Syndesus cornutus	1					3	1	3		1		9
Pedilophorus griffithi		7								1		8
Promecoderus tasmanicus	1	6					1					8
Trechimorphus diemenensis		1				1	2	2		2		8
Adelium abbreviatum	2	4					1					7
Stichonotus leai	2	4			1							7
Denticollinae TFIC sp 01	1							1		3	1	6
Elateridae TFIC sp 23	2	1					2	1				6
Dryocora cephalotes							1	1	1	2		5
Elateridae TFIC sp 19							1	2		2		5
Lissotes subcaeruleus	2						1			2		5
Macroplectus CHANDLER 'Type 1'		1					1		1	1	1	5
Scirtidae YEE sp 02										4	1	5
Scirtidae YEE sp 08							1			2	2	5
Scopodes intermedius	1	3					1					5
Sloaneana tasmaniae	1	2					1	1				5
Staphylinidae ANIC 88-0088	1	2					1	1				5
Toxeutes arcuatus						1	1	1		2		5
Curculionidae YEE sp 49							3			1		4
Dinichus terreus		3		1								4
Staphylininae TFIC sp 03	1	1					2					4

RW = rotten wood.

[a] SF (SP) = surface (sapwood); OH = outer heartwood; IH = inner heartwood; H = heartwood; L = localised.

[b] WJR = white jelly surface rot; FSR = fibrous surface rot; YDR = yellow dry slatey rot; WPR = white pocket rot; WSR = white stringy rot; BSR = brown spongy cubic rot; DW = discoloured wood; RBR = red brown soft blocky fibrous rot; BBR = brown blocky crumbly rot; BMR = brown mudgut rot; WC = wet cracks.

[c] Wh = white rot; Br = brown rot.

Number within a cell represents the number of logs in which a species occurred. Grey cells highlight more than two occurrences. Species are listed in decreasing order of most to least frequency. Species with fewer than four occurrences were excluded.

plots based on beetle assemblages (figs. 6A and 6B). That is, no single RW type had a distinct beetle assemblage. Despite this apparent lack of difference among single RW types, MRPP suggested that there were highly significant differences ($p < 0.000001$, $T = -11.4$). The ordination was re-examined by overlaying the RW region on the ordination instead of RW type, and this showed that some RW regions formed discrete clusters (figs. 7A and 7B), and this difference among RW regions was significant ($p < 0.000001$, $T = -17.6$). Species that correlated with the ordination included those that showed an association when examining individual species (table 2): *Prostomis atkinsoni* and *Pycnomerus* TFIC sp 02 were associated with the brown rotten heartwood (inner) types, *Lissotes cancroides* and *Coripera deplanata* with the surface (sapwood) RW types, and *Enneaphyllus aeneipennis* with the white rotten heartwood types.

DISCUSSION

Our results support the hypothesis that the differences in saproxylic beetle assemblages between large and small logs can be explained by the discrete decompositional processes undergone in logs of the two size classes, as reflected in the region or type of rotten wood. For example, we have shown in a concurrent study that types of brown rotten heartwood occur more frequently in large logs (Yee 2005). This study has described the clear association of two beetle species (*Cossonus simsoni* and *Pycnomerus* TFIC sp 02) with brown rotten heartwood. It is therefore reasonable to assume that one explanation for their specificity to large logs (in this study) is due to the presence of these RW types not commonly found in small logs. This argument is also supported by other related observations. Members of the family Scirtidae apparently prefer large logs (this study, Yee 2005; Grove and Bashford 2003). These beetles appear to be associated with the 'wet' RW types, such as 'wet cracks' and 'brown mudgut rot', which were more frequent in large logs (Yee 2005). Their association can be explained by their requirement for wet habitats, as larval scirtids have retained an ancestral respiratory system adapted for living in saturated environments and mouthparts designed for filtering wet detritus (Lawrence and Britton 1994). Meanwhile, the white rotten heartwood types are more frequent in small logs than in large logs (Yee 2005). In this study, one beetle species (*Enneaphyllus aeneipennis*) was restricted to this particular white rot type, and was only detected in small logs.

These log size preferences and rotten wood type associations could only be demonstrated for common species, as these occurred in sufficient numbers for statistical analysis. In theory, rarity can be positively related to habitat specificity (Rabinowitz 1981), so it seems likely that many of the less common species in this study will also have a preference for log size and/or rotten wood type preference. However, additional sampling would be needed to gain an adequate understanding of the habitat preferences of naturally rare species.

There may have been factors other than the types of rotten wood to which species may be responding. For example, the xylophagous *Coripera deplanata* was more frequent in large logs, yet showed an association for the surface (sapwood) rotten wood that is common to both log sizes. It may have preferred large logs because the sapwood layer is thicker on

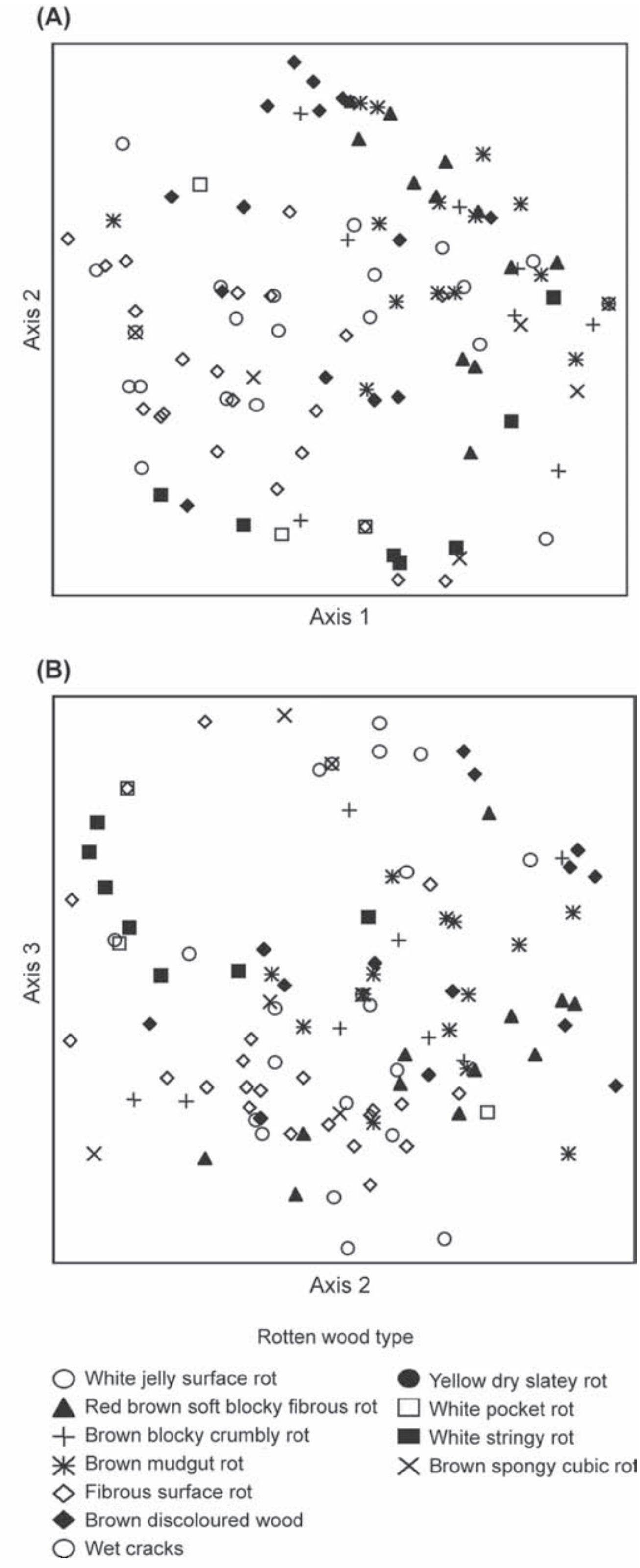


Figure 6—NMS ordination of saproxylic beetle assemblages from 119 samples of rotten wood from 42 *Eucalyptus obliqua* logs, from wet eucalypt forests in southern Tasmania, with rotten wood type (symbols) overlaid. (A) axes 1 and 2; (B) axes 2 and 3. Based on presence-absence data of 42 beetle species within a rotten wood type pooled from two 1-m long sections per log (doubletons excluded). Stress = 0.23, p = 0.0196. Samples of rotten wood with no beetles were omitted.

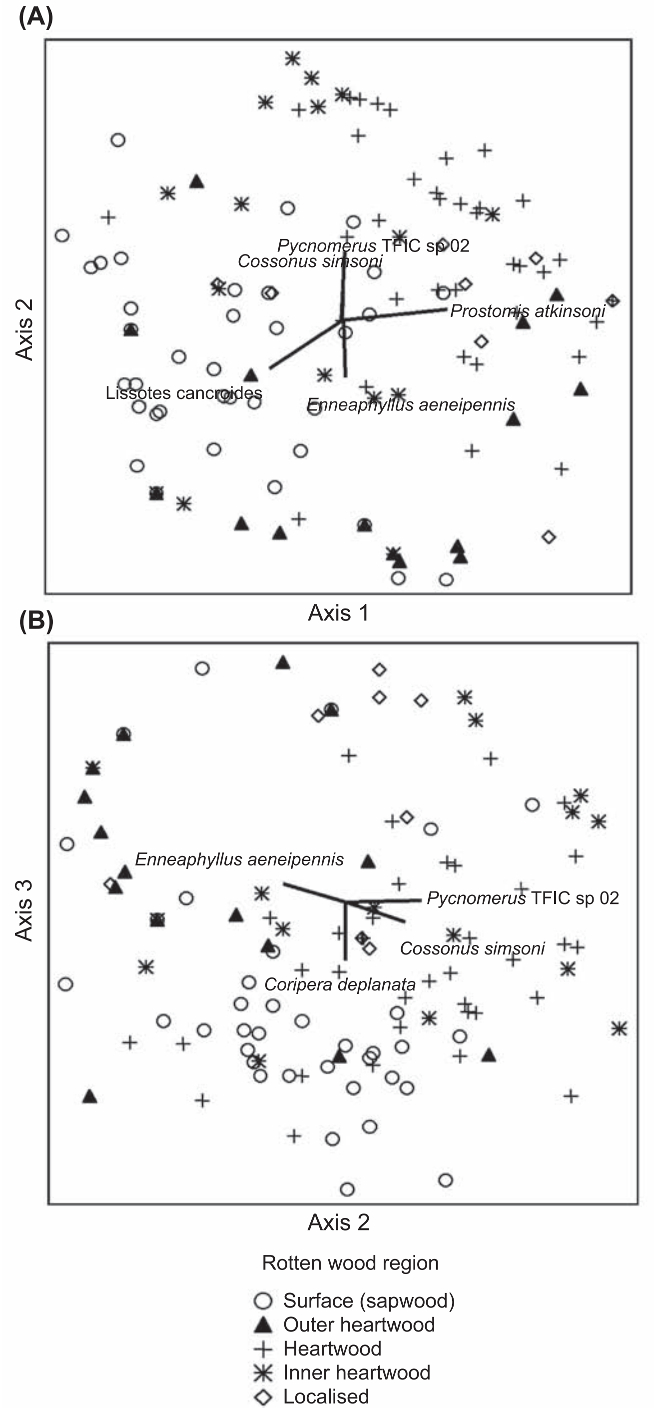


Figure 7—Same ordination as in figure 6, but with rotten wood region (symbols) overlaid. (A) axes 1 and 2; (B) axes 2 and 3. Vectors are defined by beetle species occurrence data. Vector scaling 100 percent. Only vectors with $r^2 > 0.2$ are shown.

large logs than small logs (Brack and others 1985). This is the case for the northern European sapwood feeding *Pytho kolwensis* (Pythidae) which, in a Finnish study, preferred large spruce logs over small logs for this reason (Siitonen and Saaristo 2000). Another interpretation is that *Coripera deplanata* seems to have relatively broad larval habitat associations, also occurring in the brown rotted heartwood (inner) common in large logs (Unpublished data. Dr. Simon Grove, Conservation Biologist, Forestry Tasmania, 79 Melville Street, Hobart, Tasmania, Australia). Additional sampling might reveal a better understanding of the mechanisms underlying its apparent preference for large logs.

Whatever the limitations of our study, the findings suggest that the brown rotted heartwood is an important habitat feature of large *Eucalyptus obliqua* logs. Its value may lie in its relative stability as a habitat. Habitat stability is defined as how favourable it remains for a population over a continuous period of time (Southwood 1977). In general, large logs of the size-dimensions studied here are considered to offer more stable habitats for saproxylic beetles than do smaller sized logs (Grove and Meggs 2003). This is because they tend to take longer to decompose, partly because of lower decay rates (Harmon and others 1986, Mackensen and others 2003, Stone and others 1998), and so persist longer in the landscape; they maintain more optimal moisture levels (Amaranthus and others 1989) that allow buffering against the effects of desiccation and temperature extremes; and they provide potential refuges during disturbance events, such as wildfire (Meggs and Taylor 1999, Michaels and Bornemissza 1999). In the present study, it is suspected that the brown rotted heartwood had probably originated in the living tree, entering through infection courts such as those caused by fire damage or the breakage of large branches (Greaves and others 1965, Tamblyn 1937, Wardlaw 2002). Therefore as a habitat, it might begin to sustain an assemblage of beetles from the time of tree-fall or even beforehand, thus allowing more time to sustain assemblages of species dependent on this habitat. The rotten wood in small logs, on the other hand, almost certainly owed its origin to fungal and microbial colonisation since the tree-fall event.

The apparently poor dispersal potential of species associated with the brown rotted heartwood also supports the notion that this is a relatively stable habitat for saproxylic beetles. Theoretically, species dependent on stable habitats should require lower dispersal abilities, while those in less predictable habitats would require higher ones (Southwood 1977). Species that were clearly associated with the brown rotted heartwood (*Cossonus simsoni, Prostomis atkinsoni, Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02) have characteristics that appear to fit this pattern. They are all small xylophagous species, often found living in aggregates, appeared to have sedentary behaviour and were either flightless, relatively long living or a combination of these. All except *Prostomis atkinsoni* are flightless, and flightlessness is one outcome of habitat stability (Lattin and Moldenke 1990, Stevens 1997). *Prostomis atkinsoni, Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02 seem capable of undergoing successive generations within the same log without emerging, and this interpretation is supported for *Prostomis atkinsoni* by a recent study that found genetically similar individuals at very fine spatial scales (Watson 2003). Adults and larvae of *Prostomis atkinsoni, Dryophthorus* TFIC sp 01 and *Pycnomerus* TFIC sp 02 subsisted in the original host wood material for over 25 months in the laboratory, with both adult and larval stages still alive. Furthermore, these three species were collected from partially decomposed to well-rotted inner heartwood, thus showing their capacity to feed on a broad range of decomposed wood stages; and in the laboratory they seemed to re-ingest previously consumed wood. The specificity of several of these beetle species for habitat types more common in large logs, coupled with their apparent low powers of dispersal, suggests that these species are likely to be susceptible to reductions in large logs, and the subsequent fragmentation effects that can result from intensive forestry (Nilsson and Baranowski 1997, Ranius and Nilsson 1997).

In Northern Europe, the declines in saproxylic beetles that have resulted from centuries of timber harvesting and recent intensive forest management (Grove 2002) provide examples of what may occur in Australian production forests if similar management trajectories were followed. Remarkably, each of the four species specific to the brown rotted heartwood (*Dryophthorus* TFIC sp 01*, Prostomis atkinsoni, Cossonus simsoni,* and *Pycnomerus* TFIC sp 02) belongs to a genus whose European representatives have already experienced drastic declines, with some regional extinctions. And yet, in this Australian (Tasmanian) study, they were among the most common species collected. Moreover, some of the European species appear to have similar rotten wood type preferences to those in this study. For example, *Dryophthorus corticalis*, which lives in the red heartwood rot of old standing and fallen oak (*Quercus* sp) trees, is threatened in Great Britain (Hyman 1992), Germany (Bense 2002), and the Czech Republic (Strejcek 1996). *Prostomis mandibularis,* which occurs in the red-brown muddy rot of decomposing oak logs (personal observation), is extinct in the UK (Boswijk and Whitehouse 2002) and threatened with extinction in parts of Germany (Bense 2002). A number of species from the genus *Cossonus* are threatened in several European countries: *Cossonus linearis* in central Europe (Harde 1984) and the Czech Republic (Strejcek 1996); *C. cylindricus* in Finland (Martikainen 2001); and *C. parallelepipedus* in the Czech Republic (Strejcek 1996) and Germany (Bense 2002). *Pycnomerus terebrans,* which occurs in the red rotten wood of old hardwood trees, has also become extinct in Britain (Buckland and Dinnin 1993), and is close to extinction in parts of Germany (Wenzel 2002). Considering the similarities found in this study with those of Northern European examples, it seems likely that developing an understanding of the dispersal ecology of these species will provide valuable information as to how to manage large logs over appropriate spatial and temporal scales, to ensure that such major declines and extinctions can be avoided in Tasmania and elsewhere.

In conclusion, large *Eucalyptus obliqua* logs in Tasmanian wet eucalypt forests were found to host an assemblage of beetle species that was rarely encountered in small logs, and this could be explained by the more general presence of brown rotten heartwood (inner) types within large logs. This rotten wood type had probably originated in the standing tree; however the specific decomposer organisms or processes involved in its development are unknown. Current research projects are attempting to address this issue (Harrison and others 2003a, Hopkins and others 2003) (Unpublished data. Dr. ZiQing Yuan, Plant Pathologist, Department of Primary Industries, Water and Environment, Newtown Laboratories, 13 St Johns Avenue, Newtown, Tasmania, Australia 7008). It seems that this rotten wood type is a relatively stable microhabitat, and species associated with it appear to have low dispersal potential. Considering that these species belong to genera whose European representatives have undergone serious declines, it seems they may also be susceptible to the long-term effects of intensive forest management and fragmentation. Determining how far these species disperse, whether they colonise the living tree, or at which stage they colonise the fallen log, and for how long they remain within the log, will provide valuable information as to how to manage for large logs over appropriate spatial and temporal scales. Current research projects are seeking to answer some of these questions (Harrison and others 2003b, Watson 2003). A caveat to this study is that the conclusions have mostly been drawn from the commonly collected species, and so conservation issues relating to naturally rare species still need to be addressed.

ACKNOWLEDGMENTS

Funding for this research was provided by the Australian Research Council, Forestry Tasmania, Gunns Ltd and the Cooperative Research Centre for Sustainable Production Forestry. Marie Yee was granted a University of Tasmania Strategic Scholarship and a top-up scholarship from the Cooperative Research Centre for Sustainable Production Forestry. We acknowledge and are very grateful for the field assistance of ZiQing Yuan, who single-handedly cut up the 42 logs. Study sites were located in State Forest managed by Forestry Tasmania. We are grateful to Rob Taylor of Forestry Tasmania and Sue Baker who suggested research ideas at the start of this project, and suggested possible field sites. We thank Dr Peter McQuillan, Mr Tom Weir, Dr Rolf Oberprieler, Dr John Lawrence and Dr Donald Chandler for their beetle identifications. We also thank Sarah Richards and Paul Harrington for helpful comments on earlier versions of this manuscript.

LITERATURE CITED

Amaranthus, M.P.; Parrish, D.S.; Perry, D.A. 1989. Decaying logs as moisture reservoirs after drought and wildfire. In: Alexander, E., ed. Stewardship of Soil, Air and Water Resources. Proceedings of Watershed 89. Juneau, AK: U.S. Department of Agriculture Forest Service, Region 10: 191-194.

Araya, K. 1993. Relationship between the decay types of wood and occurrence of lucanid beetles (Coleoptera: Lucanidae). Applied Entomology and Zoology. 28: 27-33.

Ashton, D.H. 1982. Tall open-forests. In: Groves, R. H., ed. Australian Vegetation. Sydney, Australia: Cambridge University Press: 121-151.

Ausmus, B.S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecological Bulletins. 25: 180-192.

Bense, U. 2002. Verzeichnis und Rote Liste der Totholzkäfer Baden-Wüttembergs. Naturschutz Landschaftspfege Baden-Wüttembergs. 74: 309-361.

Boswijk, G.; Whitehouse, N.J. 2002. *Pinus* and *Prostomis*: a dendrochronological and palaeoentomological study of a mid-Holocene woodland in eastern England. Holocene. 12: 585-596.

Brack, C.L.; Dawson, M.P.; Gill, A.M. 1985. Leaf and sapwood dimensions in eucalyptus. Australian Forest Research. 15: 1-7.

Buckland, P.C.; Dinnin, M.H. 1993. Holocene woodlands, the fossil insect evidence. In: Kirby, K.J.; Drake, C.M., ed. Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain, Vol. No. 7. Proceedings of a British Ecological Society Meeting held at Dunham Massey Park on 24 April 1992: English Nature.

Carpenter, S.E.; Harmon, M.E.; Ingham, E.R. [and others]. 1988. Early patterns of heterotroph activity in conifer logs. Proceedings of the Royal Society of Edinburgh. 94B: 33-43.

Christensen, O. 1984. The states of decay of woody litter determined by relative density. Oikos. 42: 211-219.

Clausen, C.A. 1996. Bacterial associations with decaying wood: a review. International Biodeterioration and Biodegradation. 37: 101-107.

Dajoz, R. 2000. Insects and forests: the role and diversity of insects in the forest environment. Paris: Intercept LTD, Lavoisier Publishing.

Edmonds, R.L.; Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Canadian Journal of Forest Research. 19: 853-859.

Edmonds, R.L.; Marra, J.L. 1999. Decomposition of woody material: nutrient dynamics, invertebrate/fungi relationships and management in Northwest forests. In: Meurisse, R.T.; Ypsilantis, W.G.; Seybold, C., eds. Organism functions and processes, management effects on organisms and processes, and role of soil organisms in restoration. Proceedings of the Pacific Northwest Forest and Rangeland Soil Organism Symposium, Oregon State University, USA, 17-19 March 1998. Gen. Tech. Rep. PNW-GTR-461. Corvallis, OR: U.S.Department of Agriculture Forest Service, Pacific Northwest Research Station: 68-79.

Gilbertson, R.L. 1984. Relationships between insects and wood-rotting basidiomycetes. In: Wheeler, Q.; Blackwell, M. eds. Fungus-insect relationships: perspectives in ecology and evolution. New York: Columbia University Press: 130-165.

Greaves, T.; McInnes, R.S.; Dowse, J.E. 1965. Timber losses caused by termites, decay and fires in an alpine forest in New South Wales. Australian Forestry. 29: 161-174.

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

Grove, S.J.; Bashford, R. 2003. Beetle assemblages from the Warra log decay project: insights from the first year of sampling. Tasforests. 14: 117-129.

Grove, S.J.; Meggs, J. 2003. Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. Australian Forestry. 66: 258-272.

Haack, R.A.; Slansky, F., Jr. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera. In: Slansky, F.J.; Rodriguez, J.G., eds., Nutritional ecology of insects, mites and spiders. New York: Wiley Press: 449-486.

Hammond, J.H.E.; Langor, D.W.; Spence, J.R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research. 34: 1-19.

Hanula, J.L. 1996. Relationship of wood-feeding insects and coarse woody debris. In: McMinn, J.W.; Crossley, D.A., eds. Biodiversity and coarse woody debris in southern forests. Gen. Tech. Rep. SE-94. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station: 55-81.

Harde, K.W. 1984. A field guide in colour to beetles. London: Octopus Books.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research. 15: 133-302.

Harrison, K.S.; Hopkins, A.J M.; Grove, S.J.; Mohammed, C.L. 2003b. Living trees - what lives here? Saproxylic invertebrates and wood decay fungi in living *Eucalyptus obliqua* in Tasmania's wet sclerophyll forests. In: 34th Australian Entomological Society and 6th Invertebrate Biodiversity Conference. 29 September - 3 October, Hobart, Tasmania. Orange, NSW: Australian Entomological Society.

Harrison, K.S.; Hopkins, A.J.M.; Grove, S.J.; Mohammed, C.L. 2003a. Artificial wounding of living *Eucalyptus obliqua* in Tasmania's wet sclerophyll forests. In: Ecological Society of Australia Ecology 2003 Conference. 8-10 December, Armidale, New South Wales. Canberra, ACT: Ecological Society of Australia.

Hickey, J.E.; Neyland, M.G.; Bassett, O.D. 2001. Rationale and design for the Warra silvicultural systems trial in wet *Eucalyptus obliqua* forests in Tasmania. Tasforests. 13: 155-182.

Hopkins, A.J.M.; Harrison, K.S.; Grove, S.J. [and others]. 2003. What makes a good habitat tree? Wood decay fungi and habitat formation in *Eucalyptus obliqua* in Tasmania's wet sclerophyll forests. In: Ecological Society of Australia Ecology 2003 Conference. 8-10 December, Armidale, New South Wales. Canberra, ACT: Ecological Society of Australia.

Hyman, P.S.; Parsons, M.S. 1992. A review of the scarce and threatened Coleoptera of Great Britain, Part 1. Peterborough, UK: Joint Nature Conservation Committee.

Kaarik, A. 1974. Decomposition of wood. In: Dickinson, C.H.; Pugh, G.J.F. eds., Biology of plant litter decomposition. London, UK: Academic Press: 129-174.

Kirk, T.K.; Cowling, E.B. 1984. Biological decomposition of solid wood. In: R.M. Rowell (Ed.), The chemistry of solid wood. Proceedings of a symposium at the 185th meeting of the American Chemical Society, Seattle, Washington, March 20-25, 1983. Washington, DC: American Chemical Society, Division of Paper and Textile Chemistry: 455-487.

Kleinevoss, K.; Topp, W.; Bohac, J. 1996. Buchen-Totholz im Wirtschaftswald als lebensraum für xylobionte Insekten [Dead beech wood in the commercial forest as habitat for xylobiont insects] (In German). Zeitschrift für Ökologie und Naturschutz. 5: 85-95.

Lattin, J.; Moldenke, A. 1990. Moss lacebugs in Northwest conifer forests: adaptation to long-term stability. The Northwest Environmental Journal. 6: 406-407.

Lawrence, J.F. 1989. Mycophagy in the Coleoptera: feeding strategies and morphological adaptations. In: Wilding, N.; Collins, N.M.; Hammond, P.M.; Webber, J.F., eds. Insect-fungus interactions. London, UK: Academic Press: 2-24.

Lawrence, J.F.; Britton, E.B. 1994. Australian beetles. Melbourne, Australia: Melbourne University Press.

Mackensen, J.; Bauhus, J.; Webber, E. 2003. Decomposition rates of coarse woody debris - a review with particular emphasis on Australian tree species. Australian Journal of Botany. 51: 27-37.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletins. 49: 205-218.

Maser, C.; Trappe, J.M. 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station.

McCune, B.; Grace, J.C. 2002. Analysis of ecological communities. Glenedon Beach, OR: MjM Software Design.

McCune, B.; Mefford, M.J. 1999. PC-ORD. multivariate analysis of ecological data. Version 4.17 Glenedon Beach, OR: MjM Software Design.

Meggs, J.; Taylor, R.J. 1999. Distribution and conservation status of the Mt Mangana stag beetle, *Lissotes menalcas* (Coleoptera: Lucanidae). Papers and Proceedings of the Royal Society of Tasmania. 133: 23-28.

Michaels, K.; Bornemissza, G. 1999. Effects of clearfell harvesting on lucanid beetles (Coleoptera: Lucanidae) in wet and dry sclerophyll forests in Tasmania. Journal of Insect Conservation. 3: 85-95.

Nilsson, S.G.; Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography. 20: 491-498.

Rabinowitz, D. 1981. Seven forms of rarity. In: Synge, H., ed., The biological aspects of rare plant conservation. Chichester, UK: Wiley: 205-217.

Ranius, T.; Nilsson, S.G. 1997. Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabaeidae), a beetle living in hollow trees. Journal of Insect Conservation. 1: 193-204.

Rayner, A.D.M.; Boddy, L. 1988. Fungal decomposition of wood: its biology and ecology. Chichester, UK: Wiley.

Seastedt, T.R. 1984. The role of microarthropods in decomposition and mineralisation processes. Annual Review Entomology. 29: 25-46.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecological Bulletins. 49: 11-42.

Siitonen, J.; Saaristo, L. 2000. Habitat requirements and conservation of *Pytho kolwensis,* a beetle species of old-growth boreal forest. Biological Conservation. 94: 211-220.

Sollins, P.; Cline, S.P.; Verhoeven, T. [and others]. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research. 17: 1585-1595.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology. 46: 337-365.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series. Strasbourg, France: Council of Europe.

Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in BC forests. Working Paper 30/1997. Vancouver, British Columbia: Ministry of Forests Research Branch.

Stone, J.N.; MacKinnon, A.; Parminter, J.V.; Lertzman, K.P. 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. Canadian Journal of Forest Research. 28: 788-793.

Strejcek, J. 1996. Coleoptera: Curculionoidea. In: Rozkosny, R.; Vanhara, J., eds. Terrestrial Invertebrates of the Palava Biosphere Reserve of UNESCO, III. Folia Fac. Sci.Nat. Uni. Masaryk. Bru., Biol. 94: 577-599.

Svensson, G.P.; Larsson, M.C.; Hedin, J. 2004. Attraction of the larval predator *Elater ferrugineus* to the sex pheromone of its prey, *Osmoderma eremita,* and its implication for conservation biology. Journal of Chemical Ecology. 30: 353-363.

Swift, M.J. 1977. The ecology of wood decomposition. Science Progress, Oxford.. 64: 175-199.

Swift, M.J.; Boddy, L. 1984. Animal-microbial interactions in wood decomposition. In: Anderson, J.M.; Rayner, A.D.M.; Walton, D.W.H., eds. Invertebrate-microbial interactions. Joint symposium of the British Mycological Society and the British Ecological Society, held at the University of Exeter, September 1982. British Mycological Society symposium series, Vol. 6. Cambridge, Cambridgeshire, UK: Cambridge University Press: 133-153.

Tamblyn, N. 1937. Decay in timber with special reference to Jarrah (*Eucalyptus marginata* Sm.). Australian Forestry. 2: 6-13.

Wardlaw, T.J. 2002. Studies on the extent, impact and management of stem decay in young regrowth eucalypt forests in Tasmania. Doctoral Thesis. Hobart, Australia: University of Tasmania.

Watson, S. 2003. Population genetic structure, gene flow and dispersal in the saproxylic beetle *Prostomis atkinsoni.* Honours Thesis, Melbourne, Australia: LaTrobe University.

Wenzel, E. 2002. Ammerkungen zur Koleopterenfauna des Lampertheimer Waldes in Südhessen (Ins., Col.). Vol. 2002 http://www.coleo.de/Lamperth02/LAMP-BER.html

Yee, M. 2005. The ecology and habitat requirements of saproxylic beetles native to Tasmanian wet eucalypt forests; potential impacts of commercial forestry practices. Hobart, Australia: University of Tasmania. Ph.D. dissertation.

APPENDIX A

Taxonomic list of adult saproxylic beetles hand collected from 42 *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania.

Family and subfamily	Species
Carabidae-Migadopinae	*Stichonotus leai* (Sloane 1910)
Carabidae-Trechinae	*Sloaneana tasmaniae* (Sloane 1915)
Carabidae-Trechinae	*Trechimorphus diemenensis* (Bates 1878)
Carabidae-Broscinae	[a]*Promecoderus tasmanicus* (Castelnau 1867)
Carabidae-Callistinae	*Lestignathus sp nr foveatus* (Sloane 1920)
Carabidae-Lebiinae	*Agonocheila curtula* (Erichson 1842)
Carabidae-Pentagonicinae	*Scopodes intermedius* (Blackburn 1894)?
Carabidae-Psydrinae	*Amblytelus* TFIC sp 01
Carabidae-Psydrinae	*Theprisa convexa* (Sloane 1920)
Carabidae-Pterostichinae	*Notonomus politulus* (Chaudoir 1865)
Carabidae-Pterostichinae	*Rhabdotus reflexus* (Chaudoir 1865)
Carabidae-Zolinae	*Pterocyrtus tasmanicus* (Castelnau 1867)
Ptiliidae	Ptiliidae TFIC sp 04
Leiodidae-Cholevinae	*Nargomorphus jeanneli* (Szymczakowski 1963)
Leiodidae-Cholevinae	*Nargomorphus* TFIC sp 02
Scydmaenidae	Scydmaenidae TFIC sp 04
Scydmaenidae	Scydmaenidae TFIC sp 08
Scydmaenidae	Scydmaenidae TFIC sp 10
Staphylinidae	Staphylinidae ANIC 88-0088
Staphylinidae-Pselaphinae	*Macroplectus* CHANDLER 'Type 1'
Staphylinidae-Pselaphinae	*Macroplectus tasmaniae* Raffray
Staphylinidae-Pselaphinae	*Startes CHANDLER* 'Tasmania 1'
Staphylinidae-Pselaphinae	*Tasmanityrus newtoni* (Chandler 1987)
Staphylinidae-Tachyporinae	*Sepedophilus* TFIC sp 01
Staphylinidae-Aleocharinae	Aleocharinae TFIC sp 13
Staphylinidae-Aleocharinae	Aleocharinae TFIC sp 25
Staphylinidae-Aleocharinae	Aleocharinae TFIC sp 27
Staphylinidae-Aleocharinae	Aleocharinae TFIC sp 28
Staphylinidae-Aleocharinae	Aleocharinae TFIC sp 34
Staphylinidae-Scaphidiinae	*Scaphidium* YEE sp 01
Staphylinidae-Paederinae	*Hyperomma bryophilum* (Lea 1923)
Staphylinidae-Paederinae	Paederinae TFIC sp 03
Staphylinidae-Staphylininae	*Quedius* TFIC sp 04
Staphylinidae-Staphylininae	Staphylininae TFIC sp 03
Lucanidae-Syndesinae	[a]*Syndesus cornutus* (Fabricius 1801)
Lucanidae-Lucaninae	[a]*Lissotes cancroides* (Fabricius 1787)
Lucanidae-Lucaninae	[a]*Lissotes curvicornis* (Boisduval 1835)
Lucanidae-Lucaninae	*Lissotes subcaeruleus* (Bomans 1986)
Scarabaeidae-Melolonthinae	*Heteronyx pilosellus* (Blanchard 1850)
Scarabaeidae-Melolonthinae	[a]*Phyllochlaenia* TFIC sp 01
Scarabaeidae-Melolonthinae	*Phyllochlaenia villosus* (Le Guillou 1844)
Scarabaeidae-Melolonthinae	*Telura vitticollis* (Erichson 1842)
Scirtidae	*Prionocyphon?* TFIC sp 01
Scirtidae	*Pseudomicrocara atkinsoni* (Waterhouse 1877)?
Byrrhidae-Byrrhinae	*Pedilophorus griffithi* (Lea 1907)
Byrrhidae-Byrrhinae	*Pedilophorus* nr ANIC sp 88-0313
Eucnemidae	*Neocharis tasmanicus* (Muona 1987)
Elateridae-Pityobiinae	*Tasmanelater pelionensis* (Calder 1996)
Elateridae-Agrypninae	*Agrypnus* TFIC sp 01
Elateridae-Denticollinae	Denticollinae TFIC sp 01

(continued)

APPENDIX A

Taxonomic list of adult saproxylic beetles hand collected from 42 *Eucalyptus obliqua* logs in wet eucalypt forests in southern Tasmania—continued

Family and subfamily	Species
Elateridae-Denticollinae	Denticollinae TFIC sp 16
Elateridae-Denticollinae	*Elatichrosis exarata* (Candeze 1863)
Elateridae-Denticollinae	*Enischnelater* TFIC sp 01
Elateridae-Elaterinae	*Augenotus quadriguttatus* (Erichson 1842)
Cleridae-Phyllobaeninae	*Lemidia* YEE sp 02
Nitidulidae-Cryptarchinae	*Cryptarcha laevigata*
Silvanidae-Brontinae	*Cryptamorpha* TFIC sp 01
Silvanidae-Brontinae	*Cryptamorpha victoriae* (Blackburn)?
Cryptophagidae-Cryptophaginae	*Cryptophagus tasmanicus* (Blackburn 1907)
Cryptophagidae-Cryptophaginae	*Cryptophagus* sp nr *gibbipennis* (Blackburn 1892)
Cerylonidae-Ceryloninae	[a]*Philothermus tasmanicus* (Slipinski 1988)
Corylophidae-Corylophinae	[a]*Holopsis* TFIC sp 01
Corylophidae-Sericoderinae	*Sericoderus* TFIC sp 05
Zopheridae-Zopherinae	*Docalis funerosus* (Hope 1845)
Zopheridae-Pycnomerinae	*Penthelispa fuliginosa* (Erichson 1842)
Zopheridae-Pycnomerinae	[a]*Pycnomerus* TFIC sp 02
Zopheridae-Colydiinae	*Enhypnon tuberculatus*
Tenebrionidae-Lagriinae	[a]*Adelium abbreviatum* (Boisduval 1835)
Tenebrionidae-Lagriinae	*Brycopia coelioides* (Pascoe 1870)
Tenebrionidae-Lagriinae	*Brycopia hexagona* (Carter 1920)
Tenebrionidae-Lagriinae	[a]*Brycopia picta* (Pascoe 1869)
Tenebrionidae-Lagriinae	[a]*Coripera deplanata* (Boisduval 1835)
Tenebrionidae-Zolodininae	[a]*Tanylypa morio* (Pascoe 1869)
Prostomidae	[a]*Dryocora cephalotes* (Waterhouse)
Prostomidae	[a]*Prostomis atkinsoni* (Waterhouse 1877)
Oedemeridae	[a]*Dohrnia simplex* Champion
Cerambycidae-Prioninae	[a]*Enneaphyllus aeneipennis* (Waterhouse 1877)
Cerambycidae-Prioninae	[a]*Toxeutes arcuatus* (Fabricius 1787)
Curculionidae	*Curculionidae* YEE sp 49
Curculionidae-Cryptorhynchinae	*Decilaus lateralis* (Lea 1913)
Curculionidae-Cryptorhynchinae	*Decilaus* nr *striatus/subfasciatus*
Curculionidae-Cryptorhynchinae	*Poropterus antiquus* Boheman
Curculionidae-Cryptorhynchinae	*Tyrtaeosus ustulatus* Pascoe
Curculionidae-Dryophthorinae	*Dryophthorus* ECZ sp 02
Curculionidae-Dryophthorinae	[a]*Dryophthorus* TFIC sp 01
Curculionidae-Molytinae	[a]*Dinichus terreus* (Pascoe 1887)
Curculionidae-Molytinae	*Exeiratus* TFIC sp 01
Curculionidae-Cossoninae	Cossoninae TFIC sp 06
Curculionidae-Cossoninae	[a]*Cossonus simsoni* (Lea 1910)
Curculionidae-Cossoninae	*Pentarthrum* TFIC sp 01

[a] Refers to species that were also collected in their larval form.

APPENDIX B

Taxonomic list of larval saproxylic beetles hand collected from 42 Eucalyptus obliqua logs in wet eucalypt forests in southern Tasmania.

Family	Larval morphospecies code: *Genus*
Carabidae	CARLAR15
Carabidae	CARLAR8
Staphylinidae	LAR5: *Scaphidium* sp
Scirtidae	Scirtidae YEE sp 04
Scirtidae	Scirtidae YEE sp 08
Byrrhidae	LAR29
Eucnemidae	EUCNEM2
Elateridae	Elateridae TFIC sp 23
Elateridae	Elateridae TFIC sp 19
Elateridae	Elateridae TFIC sp 20
Elateridae	Elateridae TFIC sp 21
Elateridae	Elateridae YEE sp 06
Elateridae	LAR33
Elateridae	ELAT1
Lycidae	LYCIDLAR1
Cantharidae	LAR11
Cantharidae	LAR3
Cleridae	CLER2: *Lemidia* sp
Melandryidae	LYMEX1: *Mystes* sp
Tenebrionidae	LAR10
Tenebrionidae	LAR16
Tenebrionidae	TENLAR1
Indet	LAR30
Indet	CURLAR2
Indet.	CARLAR9
Indet.	STAPHLAR1
Indet.	STAPHLAR7

THE ROLE OF DEAD WOOD IN MAINTAINING ARTHROPOD DIVERSITY ON THE FOREST FLOOR

James L. Hanula, Scott Horn, and Dale D. Wade[1]

Abstract—Dead wood is a major component of forests and contributes to overall diversity, primarily by supporting insects that feed directly on or in it. Further, a variety of organisms benefit by feeding on those insects. What is not well known is how or whether dead wood influences the composition of the arthropod community that is not solely dependent on it as a food resource, or whether woody debris influences prey available to generalist predators. One group likely to be affected by dead wood is ground-dwelling arthropods. We studied the effect of adding large dead wood to unburned and frequently burned pine stands to determine if dead wood was used more when the litter and understory plant community are removed. We also studied the effect of annual removal of dead wood from large (10-ha) plots over a 5-year period on ground-dwelling arthropods. In related studies, we examined the relationships among an endangered woodpecker that forages for prey on live trees, its prey, and dead wood in the forest. The results of these and other studies show that dead wood can influence the abundance and diversity of the ground-dwelling arthropod community and of prey available to generalist predators not foraging directly on dead trees.

INTRODUCTION

Large dead wood or coarse woody debris (CWD) with a diameter >10 cm is an important resource for many arthropods and other animals that use it for food, oviposition sites, protection from environmental extremes, and foraging habitat (Elton 1966, Grove 2002b, Harmon and others 1986). Over 400 species of insects are known to use woody debris as a food resource in the Southeastern United States (Hanula 1996), and similar or greater numbers of arthropods have been reported to use it at other locations throughout the world (Grove 2002b). In addition to their direct contribution to forest diversity, these saproxylic arthropods are an important part of the forest food web (Harmon and others 1986). However, little work has been done on the role of terrestrial CWD in the forests of the Southeastern United States (McMinn and Crossley 1996).

Most of the research involving insects and CWD has focused on obligate saproxylic species (e.g., Grove 2002a, 2002b; Jonsell and others 1998; Sippola and others 2002; Speight 1989). Elton (1966) recognized that as wood decomposes it is increasingly colonized by generalists that do not require specific tree species or even depend on woody debris as their sole habitat. Relatively little is known about later successional communities in and around woody debris, and even less is known about the overall effect of woody debris on ground-dwelling arthropod communities. Recent work has begun to focus on these relationships, though (Evans and others 2003, Jabin and others 2004, Marra and Edmonds 1998).

During the past 8 years we have studied the role of CWD in relation to ground-dwelling arthropods in pine forests of the Southeastern United States. Our research examined results of trapping near CWD in unburned and frequently burned pine stands, and the effects of annual removal of dead wood from large plots over a 5-year period on ground-dwelling arthropods. In related studies we have examined interrelationships among the endangered red-cockaded woodpecker (RCW) (*Picoides borealis*), which forages for prey on live trees, its prey, and dead wood in the forest. The results of these and other studies are summarized here and show that dead wood influences the abundance and diversity of the ground-dwelling arthropod community, and may indirectly affect the prey available to at least some generalist predators.

USE OF CWD IN FREQUENTLY BURNED HABITATS BY GROUND-DWELLING ARTHROPODS

Longleaf pine (*Pinus palustris*) and its characteristic plant communities have experienced a long-term decline for a variety of reasons. Prescribed burning is considered one of the best options for restoring and maintaining this species and the characteristic plant communities associated with it, but little was known about the effects of fire on arthropods in these ecosystems. We conducted a 5-year study on long-term (40 years) research plots on the Osceola National Forest in northern Florida to examine the effects of frequent dormant-season burning on ground-dwelling arthropods (Hanula and Wade 2003). As part of that study we wanted to determine if CWD was an important arthropod habitat in areas receiving varying dormant-season burn frequencies. We hypothesized that the presence of woody debris would be important to ground-dwelling arthropods on annually burned plots where the understory vegetation and structure are more sparse compared to unburned plots (fig. 1). In addition, we measured the amount of CWD (diameter >10 cm) to determine if 40 years of frequent burning affected its abundance.

We hypothesized that logs could increase trap captures of arthropods in two ways: (1) they could be a preferred habitat resulting in concentrations of arthropods around them, or (2) they could act as drift fences concentrating and directing arthropods that normally wander across the forest floor into nearby traps. To determine which occurred, we placed 3-m lengths of longleaf pine logs (20 to 25 cm in diameter) in the center of each plot and installed pitfall traps along them (two

---

[1] James L. Hanula, Research Entomologist, U.S. Department of Agriculture Forest Service, Southern Research Station, Athens, GA 30602–2044; Scott Horn, Entomologist, U.S. Department of Agriculture Forest Service, Southern Research Station, Athens, GA 30602–2044; and Dale D. Wade, Research Forester (now retired), U.S. Department of Agriculture Forest Service, Southern Research Station, Athens, GA 30602–2044.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Figure 1—Amount and height of vegetation on long-term burn plots on the Osceola National Forest near Olustee, FL, that received dormant season burns annually, biennially, quadrennially, or not at all over a 40-year period. The signs (arrows) in each photo are approximately the same height. Photos were taken at the end of each burn cycle so vegetation had the maximum amount of time to recover.

on each side within 0.5 m of each end) as close to the log as possible (fig. 2). A wedge-shaped piece of aluminum sheet metal was inserted in the space between the edge of each trap and the log to ground contact to prevent arthropods from bypassing the trap through the gap between the trap and the log. Four additional pitfall traps were installed along a 3-m long aluminum sheet metal drift fence located 10 m from and parallel to the center log (fig. 2). Traps were placed as the log pitfalls were except that the edge of each trap was in direct contact with the drift fence. Pitfall traps were opened for month-long periods six times per year and covered when not in use. Arthropods were identified to genus when possible.

In November 2003, we measured the volume of CWD on all plots. Down woody debris was sampled in five 10-m-wide transects equally spaced across each plot, and a 100 percent survey of standing dead wood was conducted at the same time. The midpoint diameter of standing dead trees was estimated using taper equations for Coastal Plain longleaf pine (Clark and others 1991), and CWD volume was estimated using Huber's equation (Avery 1975). Percent similarity (Southwood 1966) was used to compare arthropod communities captured in the two types of traps, and richness and the Shannon diversity index were used to measure arthropod community diversity. Calculations were based on the cumulative totals for the entire study period.

Analyses of variance were conducted to test for interactions between burn frequency and trap location, and trap location effects. Model effects were burn treatment, trap location, block, treatment x block interaction, and burn treatment x trap location interaction. We observed interactions between fire and arthropod use of logs in 30 taxa. In 11 taxa, more individuals were captured in traps near logs in some burn treatments than in other burn treatments. However, there was no consistent pattern; i.e., frequent burning was associated with greater

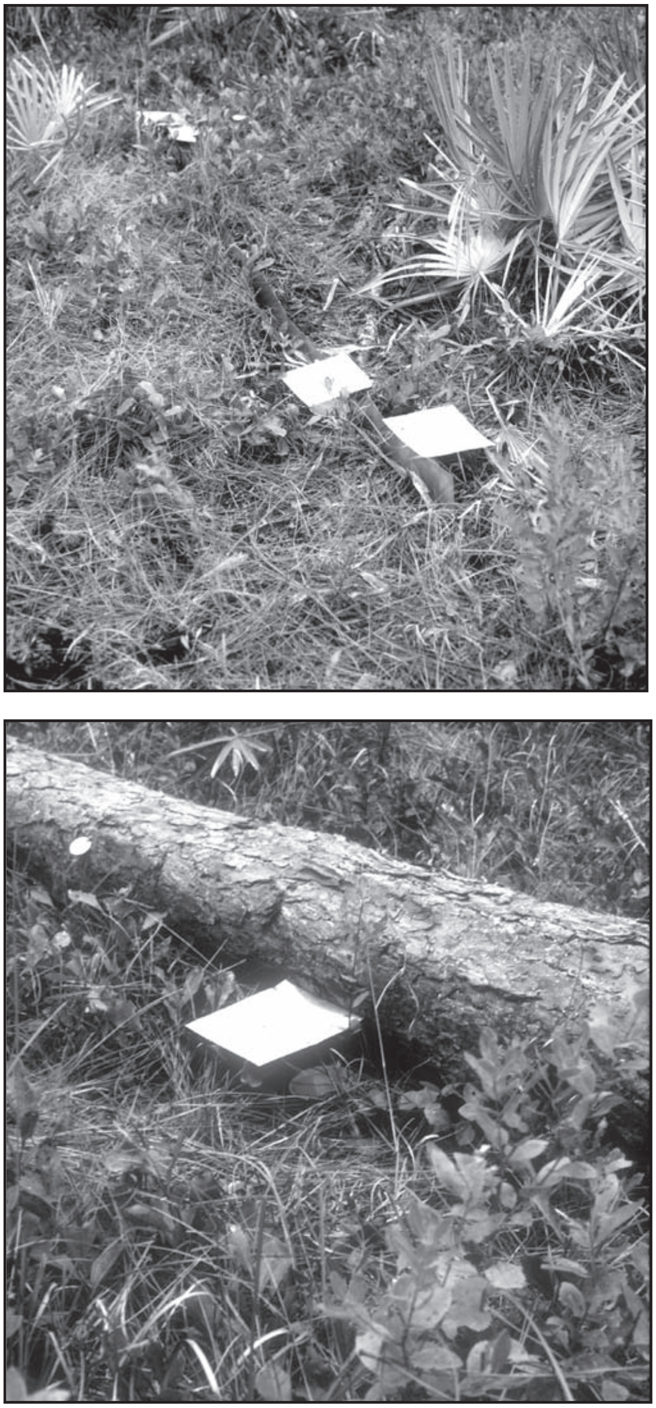


Figure 2—Pitfall traps were placed along 3-m long drift fences (top) and near 3-m sections of longleaf pine logs (bottom). Sheet metal squares were used to reduce trap flooding from rain.

numbers of some taxa near logs but infrequent or no burning was associated with greater numbers for other taxa. In only a few cases did frequent burning result in concentrations of arthropods near logs, although leaf litter, live herbaceous vegetation biomass, and structure were much lower on those plots than on unburned or quadrennially burned plots (Hanula and Wade 2003). Total volumes of CWD ranged from a mean of 8.0 m^3/ha (SE = 1.01) for unburned control plots to 9.1 m^3/ha (SE = 1.73) on annually burned plots. Volume of CWD was not significantly affected by burning, so differences in background levels of woody debris should not have affected the results.

Overall, we caught significantly more arthropods and a greater biomass of arthropods in pitfall traps near drift fences than in those near logs (fig. 3). The similarity of what was caught in the two types of traps ranged from 64.4 percent (SE = 3.6) in comparisons of annually burned plots to 69.2 percent (SE = 1.4 percent) in comparisons of similarity in the two trap locations on unburned controls. There were no significant differences in comparisons of similarity of arthropods captured in pitfall traps near logs to pitfalls near drift fences on the various burn treatments ($F_{5,3} = 1.06$, $P = 0.40$). Likewise, Shannon diversity, evenness, richness, and numbers of rare species were the same for traps near logs and drift fences regardless of burn frequency.

We captured over 932 genera in 5 years of trapping (Hanula and Wade 2003). Of those, 135 arthropod taxa were captured in higher numbers in one trap type or the other (table 1). When examining this many individual taxa one is very likely to encounter some apparently significant results simply by chance. However, the 135 taxa represent over 14 percent of the total number of arthropod taxa examined. At an alpha level of 0.05 one would only expect 5 percent to have been captured in statistically higher numbers by chance. Ninety-nine different arthropod taxa were captured in significantly ($P < 0.05$) higher numbers in pitfalls near drift fences while 36 arthropod taxa were captured in higher numbers near logs.

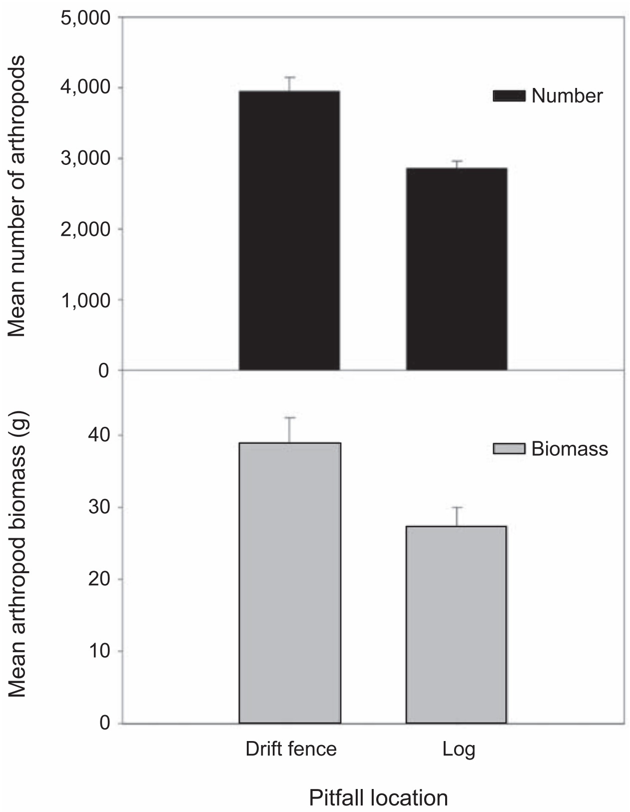


Figure 3—Pitfall traps near drift fences caught significantly higher numbers ($P < 0.0001$) and biomass ($P < 0.0001$) of arthropods than similar traps near logs.

Table 1—A list of arthropod taxonomic groups (order, family, or genus) captured in significantly ($P < 0.05$) higher numbers either in pitfall traps near drift fences or in pitfall traps near logs (within each row the lowest taxonomic level is significant)

Order	Family	Genus or subfamily
Scorpiones	Buthidae	*Centruroides*
Araneae	Ctenizidae	*Ummidia*
	Zoridae	*Zora*[a]
	Gnaphosidae	*Callilepis*
		Drassyllus
		Herpyllus[a, b]
		Sergiolus
	Theridiidae	*Dipoena*
	Linyphiidae	*Ceratinops*[a]
		Erigone[a]
		Meioneta
	Tetragnathidae	*Pachygnatha*[a]
	Thomisidae	*Ozyptila*[a]
	Corrinnidae	*Scotinella*[a]
	Agelenidae	*Cicurina*[a]
	Hahnidae	*Hahnia*
		Neoantistea[a]
	Lycosidae	*Allocosa*[a]
		Hogna
		Immatures[a]
		Pardosa
		Pirata[b]
		Schizocosa
		Sosippus
		Varacosa
	Salticidae	*Corythalia*[b]
		Habronattus
		Phlegra
		Sitticus[a]
Opiliones	Gagrellidae	*Leiobunum*
	Phalangidae[a]	
Isopoda[a]		
Spirobolida	Spirobolidae	*Narceus*
Lithobiomorpha	Lithobiidae	
Orthoptera	Tettigoniidae	*Atlanticus*
	Acrididae	Conocephalinae
	Gryllacrididae	*Ceuthophilus*
	Gryllidae	*Anaxipha*[a]
		Cycloptilum
		Gryllinae[a, b]
		Gryllus
		Miogryllus[a]
		Mogoplistinae[a, b]
		Orocharis
		Pictonemobius
Blattaria	Blattellidae	*Cariblatta*
Isoptera	Rhinotermitidae	*Reticulitermes*
Hemiptera	Reduviidae	*Repipta*[b]
		Stenopoda
Homoptera[b]	Cicadellidae	
	Delphacidae[a, b]	
	Cixiidae[b]	*Oliarus*[a, b]
	Achilidae[b]	*Catonia*[a, b]
	Aphididae	
Coleoptera	Carabidae	Larvae[a]
		Anisodactylus
Coleoptera (continued)		*Cyclotrachelus*
		Megacephala[a, b]
		Pasimachus
		Piemus[b]
		Pterostichini[b]
		Pterostichus
		Scaritini
	Dytiscidae	*Hydaticus*
	Scydmaenidae	
	Staphylinidae	Larvae[a]
		Aleochariinae[b]
		Osoriinae[b]
		Oxyteninae
		Steninae[b]
	Scarabaeidae	*Aphodius*[b]
		Bolbocerus
		Canthon
		Onthophagus
		Trox
	Elateridae	Larvae[b]
	Lycidae	*Plateros*[b]
	Cantharidae	*Larvae*[a]
	Endomychidae[b]	*Epipocus*[a, b]
	Melandryidae[b]	*Eustrophinus*[b]
	Tenebrionidae[b]	*Helops*
		Platydema[b]
	Cerambycidae[a, b]	*Prionus*[b]
	Chrysomelidae	*Metachroma*
		Myochrous
	Curculionidae	*Hylobius*
		Ips[b]
		Sphenophorus
Mecoptera	Panorpidae	*Panorpa*
Diptera	Tipulidae[b]	
	Mycetophilidae	Unidentified[a, b]
		Orfelia[a]
	Sciaridae	*Bradysia*[b]
		Corynoptera[a]
		Epidapus
		Pseudosciara[b]
		Sciara[a, b]
	Culicidae	*Culex*
	Chironomidae[b]	
	Empididae	*Drapetis*[b]
	Dolichopodidae[b]	*Medetera*[b]
	Phoridae	*Megaselia*
	Sphaeroceridae	*Leptocera*
Lepidoptera	Arctiidae	Larvae
	Noctuidae	Larvae
Hymenoptera	Diapriidae	
	Scelionidae	
	Mutillidae	*Dasymutilla*
		Timulla
	Pompilidae	*Priocnemella*
	Formicidae	*Formica*
		Leptothorax
		Monomorium
		Odontomachus
		Pheidole

[a] Denotes significant interaction between fire frequency and trap location.

[b] Groups that were captured in higher numbers near logs.

Without species-level identifications and studies it is difficult to know if these organisms are dependent on CWD or occasional users that can survive in its absence. However, the results of this study show that a variety of arthropods were captured in higher numbers near CWD. Some of these were clearly saproxylic and fed on dead wood, e.g., some Curculionidae, while others such as spiders and planthoppers were not. The fact that traps along drift fences were more efficient in capturing arthropods, as demonstrated by the much higher numbers of arthropods captured in those traps, suggests that the taxa that were caught in greater abundance in pitfalls near logs spent more time in that habitat and that logs were not just acting as drift fences for these organisms. Clearly, logs provide a resource that benefits these arthropods, but more detailed studies are needed to determine what role logs play in their biology and population dynamics.

DOES ANNUAL REMOVAL OF CWD AFFECT FOREST FLOOR ARTHROPODS?

This question is being addressed as part of a larger interdisciplinary effort to investigate how CWD affects the diversity and abundance of animal populations in mature, managed loblolly pine (*P. taeda*) forests (McCay and others 2002). The evidence is clear that CWD is important to animals in upland forests and that many organisms would disappear without it. A number of arthropod species that are not dependent on woody debris use it as a resource, but their association with it is not clear. However, few studies have been conducted under conditions that remove confounding factors to insure that CWD is the likely reason for observed differences in species abundance (Harmon and others 1986, McCay and others 2002). Loblolly pine was chosen for this study because it is the most common and commercially important species of tree in the Southern United States, where it makes up over one-half of the standing pine volume and occupies about 11.7 million ha (Baker and Langdon 1990). Loblolly pine management is often more intensive than management of other species in this region or similar species in other regions of North America. The large area covered by loblolly pine forests makes them important to regional biodiversity, and intensive management has the potential to reduce CWD in these forests. If CWD is important not only to species that depend on it for food but also to other species, then this impact will be even greater. Thus, the question addressed in this study was whether maintaining low levels of CWD by regularly removing it would affect the diversity and abundance of the general forest floor arthropod community.

The study was initiated in the summer of 1996 at the Savannah River Site, an 80 270-ha U.S. Department of Energy nuclear production facility and a National Environmental Research Park located in the upper Atlantic Coastal Plain Physiographic Province near Aiken, SC. Both longleaf and loblolly pine forests are prevalent on the site, covering approximately 14 924 ha and 25 677 ha, respectively (Knox and Sharitz 1990). Historically, longleaf pine dominated the dry, sandhill habitats, while loblolly pine was found mostly in riparian areas. The site now contains artificially regenerated, even-aged stands of loblolly, longleaf, and slash pines (*P. elliottii*).

The study was a randomized complete block design consisting of four blocks of four treatments. Blocks consisted of even-aged stands of 45-year-old loblolly pine large enough to accommodate four treatment plots. The stands selected for the study had received periodic thinning and prescribed burns. Treatment plots were 9.3-ha squares. Each plot consisted of a 6-ha core area and a 3.3-ha buffer zone to reduce edge effects. The entire 9.3-ha plot was treated, but CWD measurements and arthropod sampling were conducted only in the central 6-ha area. Treatments included a control in which all woody debris was left in place and woody debris removal in which both standing (snags) and fallen (logs) CWD was removed annually.

CWD was removed from the plots during January to February 1997, February to March 1998, March 1999, January 2000, and April to May 2001. At each annual removal all CWD was removed. Wood was removed by crews who used chainsaws to fell standing dead trees and to cut logs into sections that could be lifted by hand onto a trailer pulled by a small tractor or all-terrain vehicle. The initial removal treatment was more invasive than later ones, but removal of CWD caused little noticeable damage to the understory plants, litter, or soil.

All dead wood >10cm in diameter was measured annually in a 4-ha area in the center of each treatment plot. Volumes for logs and portions of standing dead trees < 2 m long were estimated using Huber's formula (Avery 1975), and regional volume equations (Clark and others 1991) were used to calculate volumes of larger snags.

Arthropods were sampled in each plot with 15 pitfall traps identical to those used in a previous study (Hanula and others 2002). Pitfalls were evenly spaced in three lines of five traps with approximately 50 m between traps within lines and 80 m between lines. Traps were opened for 1 week every 2 months and covered when not in use. Arthropod sampling began in November 1997 so only one sample was collected that year. Four were collected in 1998, six in 1999, five in 2000, and two in 2001. Macroarthropods from the 15 traps per plot were pooled into a single sample, preserved in 70 percent alcohol, sorted to morphologically similar groups, and identified to morphospecies by trained entomologists using a reference collection. If possible, following identification, 30 or more specimens were oven-dried at 40 °C for 48 hours and weighed to estimate biomass. In many cases biomass estimates were available from previous studies conducted in similar habitats (e.g., Hanula and Franzreb 1998), so those estimates were used to calculate biomass for this study. All immature insects and spiders were ovendried and weighed because of variation in their sizes.

Arthropod community characteristics were compared using Shannon's diversity index, evenness, morphospecies richness, and Horn's (1966) simplification of Morista's index (1959) for measuring community overlap. Differences in biomass and abundance were compared using a two-way analysis of variance (SAS 1982). Data were transformed using a $\log_{10}(x+1)$ or $\sqrt{x + 0.5}$ transformation to stabilize the variance.

In the year 2000, the volume of CWD averaged 0.5 m^3/ha (SE = 0.20) on removal plots and 10.8 m^3/ha (SE = 2.4) on control plots. About 40 percent of the dead wood on the plots was in the form of standing dead trees, and CWD volume was relatively consistent throughout the treatment blocks.

An average of 8,581 arthropods (SE = 1,013.5) were captured in pitfall traps per control stand, and an average of 9,981 (SE = 598.9) were captured per CWD removal stand. CWD removal had no significant effect on the average number of arthropods caught per plot or the average biomass ($\bar{x} = 108.9$ g per control plot, SE = 6.51; $\bar{x} = 148.5$ g per removal plot, SE = 28.1).

Although removal of CWD did not result in a reduction in total number of forest floor arthropods, it did result in a significant overall reduction in morphospecies diversity ($P < 0.06$; $H' = 4.27$ on control plots, SE = 0.16; $H' = 3.61$ on CWD removal plots, SE = 0.18) and evenness ($P < 0.07$; J = 0.70 on control plots, SE = 0.03; J = 0.59 on CWD removal plots, SE = 0.03) for the 5 years combined. When morphospecies diversity in each year of the study is examined (table 2) it is found that CWD removal resulted in significant reductions in diversity and evenness in 1998 and 1999 but that both diversity and evenness were similar for the two treatments by 2000 and into 2001. Although overall diversity of ground-dwelling arthropods was reduced by CWD removal, morphospecies richness (control = 444.3 ± 5.6 species; removal = 434.3 ± 6.2 species) and the numbers of rare (< 5 captured) morphospecies (control = 304.8 ± 11.1 species; removal = 305.3 ± 13.3 species) were unaffected.

Community similarity was 58.5 percent (SE = 4.60) for comparison of control stands to stands with CWD removed. To provide a standard, we compared faunal similarity in half of the control stands with faunal similarity in the other half. Faunal similarity among similar untreated stands was 72.8 percent, considerably higher than in the comparison of control to treated stands.

Thirteen families of arthropods were significantly affected by removal of CWD (table 3). Of those, 3 families benefited from removal and the remaining 10 were reduced. The latter included three families of spiders, three families of beetles including the Carabidae, two families of Hemiptera, one family of Diptera, and Xystodesmidae millipedes.

These data show that 5 years of removal of CWD lowered overall diversity and community similarity of arthropods in mature loblolly pine stands. Total number and biomass of ground-dwelling arthropods captured in pitfalls were unaffected by annual removal of dead wood, although the removal clearly affected many organisms that lived in the logs but were not sampled using pitfall traps. Likewise, organisms that stay close to logs and do not move readily would not be sampled adequately. However, removal of wood had an impact on a number of groups whose association with woody debris is not clearly understood, and it is important to understand how these organisms interact with dead wood. Five years is not a long time in the life of a forest, so it is difficult to know if the trends we observed will continue. However, our results show that the relatively low levels of CWD found in our study areas play a role in the biology of a diverse array of arthropods.

INTERRELATIONSHIP OF AN ENDANGERED WOODPECKER, ITS PREY, AND CWD

The RCW constructs nest cavities in live pine trees and spends approximately 95 percent of its time foraging on the boles and branches of mature live pines. For this reason its relationship to CWD, unlike many other woodpeckers, is not readily apparent.

As a high-profile endangered species, RCW has received a lot of attention and research. Much of that effort has focused on its foraging behavior and territories, but prior to 1990 only two studies examined the diet of RCW and neither of these studies was definitive (Beal 1911, Harlow and Lennartz 1977). In 1985 the RCW recovery plan (U.S. Fish and Wildlife Service 1985) focused attention on foraging habitat and the lack of understanding about the arthropod prey in it, and how forest management affects prey abundance and availability. Therefore, we studied the diet of RCW and how those arthropods are associated with live and dead trees.

One of the first goals was to develop a detailed understanding of the diet. To do this we monitored 31 groups of RCW over 5 years at 4 sites in the Southeastern United States using automatic cameras to record nest visits with prey (Hanula and Engstrom 2000, Hanula and Franzreb 1995, Hanula and others 2000). Collectively, RCW used 41 different arthropods to feed nestlings, but 9 of these arthropods made up over 90 percent of the diet. Wood cockroaches (*Parcoblatta* spp.) (Blattaria: Blattellidae), were recorded in over 6,500 nest visits and represented 54.7 percent of the diet of all 31 RCW groups combined. RCW consistently used the same types of

Table 2—Shannon diversity (H′), evenness (J), and morphospecies richness for arthropods captured in pitfall traps in 9.3-ha plots receiving annual removal of all coarse woody debris ≥ 10 cm in diameter from 1996 to 2001 at the Savannah River Site, Barnwell County, SC

	H′ (mean ± SE)		J (mean ± SE)		Richness (mean ± SE)	
Year	Control	Removal	Control	Removal	Control	Removal
1997	2.7 ± 0.26	1.8 ± 0.42	0.6 ± 0.06	0.4 ± 0.08	101 ± 6.9	75 ± 14.3
1998	4.1 ± 0.09[a]	3.4 ± 0.21	0.8 ± 0.02[a]	0.6 ± 0.04	207 ± 7.6	197 ± 8.2
1999	4.1 ± 0.08[a]	3.6 ± 0.11	0.8 ± 0.01[a]	0.7 ± 0.01	216 ± 4.0	222 ± 13.1
2000	3.4 ± 0.32	3.1 ± 0.21	0.7 ± 0.06	0.6 ± 0.04	155 ± 2.3	158 ± 4.1
2001	2.8 ± 0.30	2.7 ± 0.19	0.6 ± 0.06	0.6 ± 0.03	98 ± 8.4	92 ± 8.0

SE = standard error.

[a] Controls were significantly different ($P < 0.05$) from removals within a given year.

Table 3—Mean (SE) number of arthropods captured in pitfall traps in 9.3-ha plots receiving annual removal of all coarse woody debris with diameters ≥ 10 cm from 1996 to 2001 at the Savannah River Site, Barnwell County, SC

Family	Control	CWD removal	P > F
Araneae			
Clubionidae	20.8 (2.14)	12.8 (2.95)	0.007
Hahniidae	384.3 (131.2)	173.5 (80.3)	0.05
Lycosidae	370.3 (41.6)	291.5 (34.9)	0.01
Coleoptera			
Carabidae	330.0 (45.8)	258.8 (34.2)	0.04
Meloidae	1.25 (0.63)	0.25 (0.25)	0.06
Diptera			
Phoridae	259.8 (58.3)	115.5 (27.6)	0.04
Homoptera			
Cicadellidae[a]	1 (0.4)	4.5 (0.96)	0.02
Hemiptera			
Largidae	15.0 (6.26)	3.75 (1.75)	0.06
Lygaeidae	10.5 (1.66)	5.5 (1.32)	0.03
Reduviidae[a]	4.5 (0.96)	7.3 (1.49)	0.01
Hymenoptera			
Mutillidae[a]	22.3 (4.15)	35.0 (8.12)	0.04
Polydesmida			
Xystodesmidae	80.3 (37.3)	42.3 (27.3)	0.03

SE = standard error; CWD = coarse woody debris.

[a] Denotes more captured in CWD removal plots. The remaining families were captured in significantly higher numbers in control plots.

prey despite differences in location, forest type, physiography, or year of observation (table 4) (Hanula and Horn 2004). In every case wood cockroaches were the most frequently used prey making up about half of the diet at three of the four sample locations and about a quarter of it at the fourth.

Most arthropods found on tree boles do not live there exclusively (Hanula and Franzreb 1998) so we were interested in finding other habitats that might be important to them. We found that prey of RCW were primarily detritivores and predators based on published records of their behavior and feeding habits (table 4). In addition to prey able to move freely between

Table 4—Proportions of the most common prey groups fed to red-cockaded woodpecker nestlings at four locations in the Southeastern United States sampled during 1993 to 1997 (from Hanula and Horn 2004)

	Nest visits (percent)			
Prey item	Upper Atlantic Coastal Plain[a b c]	Lower Atlantic Coastal Plain[b]	Piedmont[b]	Gulf Coastal Plain[c]
Wood cockroach	59.6	26.0	49.9	46.8
Woodborer larva	7.3	1.2	0.5	2.9
Caterpillar	7.7	9.1	9.3	8.9
Spider	6.4	7.2	5.2	8.3
Ants	2.5	7.2	0	1.1
Centipede	5.6	4.9	3.2	6.7
Insect larva	2.4	1.3	4.1	7.4
Insect larvae	1.9	6.0	1.0	2.5
Year studied	1993–1997	1994	1995	1995–1997

[a] Data from Hanula and Franzreb 1998.
[b] Data from Hanula and others 2000.
[c] Data from Hanula and Engstrom 2000.

habitats, the RCW also fed on woodborer larvae taken from dead pine trees or dead limbs in live trees. Therefore, only a small proportion of the diet is composed of herbivores dependent on live vegetation and, in most cases, those prey feed on pine cones (Hanula and Horn 2004).

Dead Wood as Prey Habitat

Since the RCW feed primarily on detritivores and predators, what habitats are important to these arthropods? We believe that detritus, particularly standing and fallen dead trees, provides important habitat for arthropods that spend time on tree boles where they are preyed upon by RCW and other bark-foraging birds.

Support for this comes from a number of studies. First, diet studies show that RCW feed on wood cockroaches, centipedes, spiders, and ants (Beal 1911, Hanula and Engstrom 2000, Hanula and Franzreb 1995, Hanula and others 2000, Hess and James 1998); i.e., detritivores, predators, and omnivores. All of these major prey items are commonly found in or on dead wood. Second, dead branches of live trees contain as much or more arthropod biomass as any other part of the tree (Hanula and Franzreb 1998, Hooper 1996). Hooper (1996) found more arthropod biomass in dead branches than in bark at other positions on the tree bole. Likewise, Hanula and Franzreb (1998) found dead branches contained as much arthropod biomass as bark at the base of the tree, and both of these locations contained more biomass than any other position on tree boles. Third, wood cockroaches are abundant in standing dead trees (snags) and downed dead wood (logs). Snags contained almost three times as many as logs on the ground (fig. 4), but snags and logs on the ground contained approximately equal numbers of wood cockroaches because log volumes were nearly three times as great as volumes of standing dead trees (Horn and Hanula 2002a).

Horn and Hanula (2002b) estimated that in their study area a hectare of mature loblolly pine forest contained approximately 725 wood cockroaches in logs and snags. However, an average of 10.8 wood cockroaches per live tree were collected when entire tree boles were sprayed with insecticide (Horn and Hanula 2002a). The study area contained an average of 156 trees per ha, so if each tree contained ca. 11 cockroaches, there were approximately 1,716 wood cockroaches per ha on live trees—more than twice as many as found in logs and snags (fig. 5). However, the stands contained an average volume of 8.6 m^3/ha of dead wood over 10 cm in diameter compared to 188 m^3/ha of live trees. Therefore, dead trees contained almost 10 times more wood cockroaches per unit volume than live trees (fig. 5). The fact that wood cockroaches are more concentrated in dead wood suggests that it is important to their biology.

Larvae of wood-boring beetles (Coleoptera: Cerambycidae or Buprestidae), which are found in dead trees or dead branches of live trees, are also common and important prey of RCW. Likewise, the two common ant prey, carpenter ants (*Camponotus* spp.) and *Crematogaster* spp. ants, are found nesting in dead branches of live trees (Hanula and Franzreb 1998) and in dead trees. In fact, carpenter ants were six times more abundant in dead branches than at any other sample position on live trees. *Crematogaster* spp. ants were equally abundant in dead branches and in the bark 1.5 m above the ground. Both sample positions contained five times the numbers of ants found at the midbole or crown sample locations.

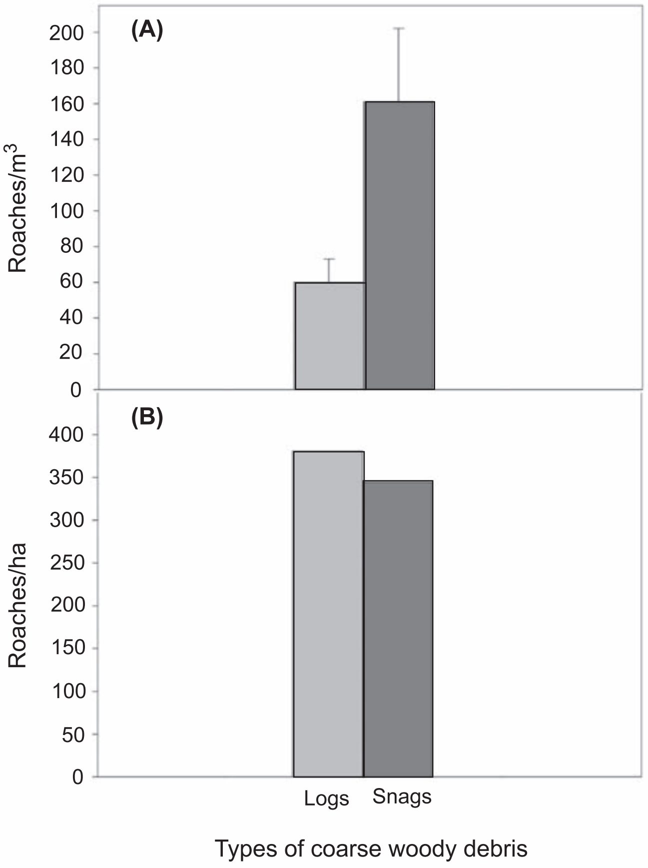


Figure 4—Densities (A) of wood cockroaches were significantly higher ($P = 0.0003$) in standing dead trees (snags) than in logs in loblolly pine stands on the Savannah River Site, SC. Estimated numbers (B) of wood cockroaches per hectare at the same location (from Horn and Hanula 2002b).

If logs and snags are important habitat for arthropods that serve as prey for RCW, what happens when they are removed from the system? We are currently investigating that question on the large-scale, long-term research plots on the Savannah River Site mentioned above. In addition to installing pitfall traps, we attached crawl traps (Hanula and New 1996) to 15 trees widely distributed throughout the plots and monitored them monthly from October 1997 to September 1999. Burlap bands also were placed on 30 trees per plot and monitored monthly from July 1998 to September 1999 (Horn 2000).

Arthropod abundance on tree boles as measured under the burlap bands was significantly ($P < 0.04$) reduced by removal of CWD but arthropod abundance in crawl traps was not (Horn 2000). No one group, e.g., ants or wood cockroaches, was significantly affected by the removal, but all groups in general were reduced slightly, resulting in the overall significant reduction in arthropod abundance beneath burlap bands. Although interesting, these preliminary results are not clear evidence of an essential role of CWD in the food web supporting RCW. Burlap bands are an efficient, nonlethal sampling method for assessing arthropods available for foraging by

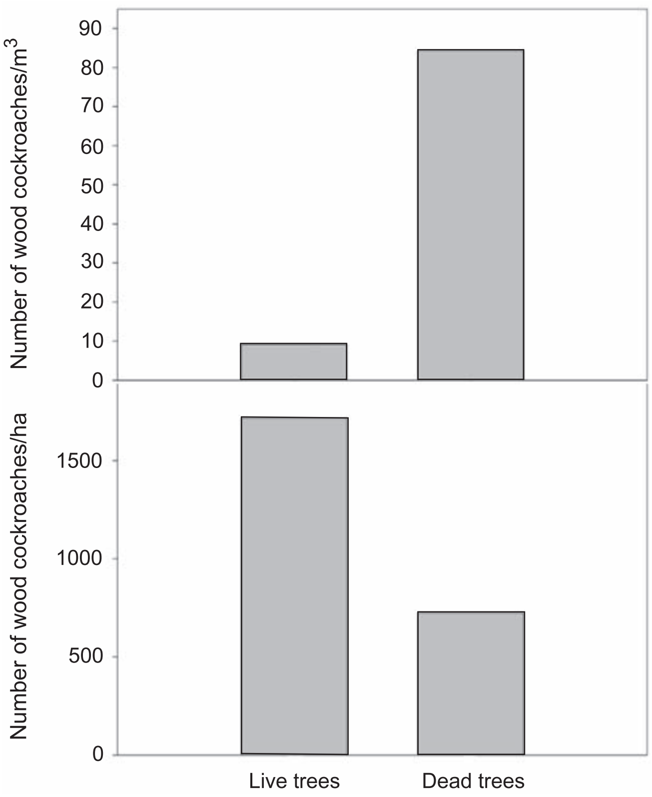


Figure 5—The number of Parcoblatta spp. wood cockroaches per unit volume (top) found in live and dead pine trees, and estimated number per unit area (bottom) in the same habitats. Wood cockroaches are concentrated in dead trees but the volume of live trees is much greater so approximately equal numbers occur in both habitats on a given hectare of pine forest (from Hanula and Horn 2004).

woodpeckers and they sample them in proportions similar to the proportions the woodpeckers actually use (Hanula and Horn 2004). They were particularly effective in sampling wood cockroaches, but abundance of these insects beneath burlap bands and in crawl traps were not affected by removal of woody debris. Thus, one of the main prey of RCW, wood cockroaches, were not reduced by the removals even though so many can be found in dead trees. The results show that the initial 2 to 3 years of CWD removal had some effect. Whether long-term absence of woody debris will affect the community of arthropods that RCW depend on is unclear, but it is a question that we are currently investigating. Likewise, it is not known whether absence of dead wood in a forest would affect population viability of RCW. Few studies have looked at such linkages. However, MacNally and others (2002) demonstrated that the brown treecreeper (*Climacteris picumnus*) in an Australian floodplain forest responded rapidly to the addition of woody debris, and Lohr and others (2002) found that removing dead wood from an upland pine forest in South Carolina reduced overall breeding bird abundance and richness as well as the abundance of several species. These studies from very different habitats are indicative of the importance of dead wood in forests and the subtle relationships between woody debris and other organisms. Clearly, more work is needed on how CWD is affecting these species.

SUMMARY

The role of CWD in the ecology of forest floor arthropods in the Southeastern United States is not clear. Logs did not increase the total abundance or biomass of arthropods captured near them and annual removal of woody debris did not result in a general decrease in arthropod abundance. However, a number of arthropods from a wide variety of taxonomic groups were captured in higher numbers near logs, and removal of CWD resulted in lower overall diversity and evenness of ground-dwelling arthropods on large scale plots. In addition, CWD removal negatively affected the abundance of a number of arthropod families. What is not clear is whether these groups were affected by the physical removal, i.e., they were removed with the wood, or whether the removal affects their ability to maintain populations within a forest. Studies are underway to determine if removal over extended periods results in further declines in their populations, and if addition of large amounts of standing or down woody debris results in population increases. Other studies are underway on the biology of specific groups, particularly wood cockroaches because of their importance as prey for the RCW, to determine their specific habitat needs and relationship to woody debris. Clearly, wood cockroaches were abundant in dead wood and are important as prey of the RCW, but whether a certain level of dead wood input is necessary to sustain populations of either the wood cockroaches or the woodpeckers is not yet clear. Dead wood in forests does influence populations of a variety of generalist, ground-dwelling arthropods, but determining to what degree and how critical it is to sustaining their populations will require further study.

ACKNOWLEDGMENTS

Funding for this work was provided in part by the U.S. Department of Energy, Savannah River Operations Office through the U.S. Department of Agriculture Forest Service, Savannah River, under Interagency Agreement DE–AI09–00SR22188 and by The Nature Conservancy's A.W. Mellon Foundation Ecosystem Research Program. We also thank the numerous colleagues, cooperators, graduate students, and technicians who worked with us on these projects. Finally, we thank Simon Grove and Staffan Lindgren for helpful comments on earlier drafts of this paper.

LITERATURE CITED

Avery, T.E. 1975. Natural resources measurements. New York: McGraw-Hill Book Co. 339 p.

Baker, J.B.; Langdon, O.G. 1990. *Pinus taeda* L. Loblolly pine. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture Forest Service: 497-512. Vol. 1,

Bartlett, M.S. 1947. The use of transformations. Biometrics. 3: 39-52.

Beal, F.E.L. 1911. Food of the woodpeckers of the United States. Biological Survey Bulletin. 37: 22-23.

Clark, I.A.; Souter, R.A.; Schlaegel, B.E. 1991. Stem profile equations for southern tree species. Res. Pap. SE–282. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station. 113 p.

Elton, C.S. 1966. Dying and dead wood. In: The pattern of animal communities. New York: John Wiley and Sons: 279-305.

Evans, A.M.; Clinton, P.W.; Allen, R.B.; Frampton, C.M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management. 184: 251-262.

Grove, S.J. 2002a. The influence of forest management history on the integrity of saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation. 104: 149-171.

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

Hanula, J.L. 1996. Relationship of wood-feeding insects and coarse woody debris. In: McMinn, J.W.; Crossley, D.A., Jr., eds. Biodiversity and coarse woody debris in southern forests: Proceedings of a workshop on coarse woody debris in southern forests: effects on biodiversity. Gen. Tech. Rep. SE–94, Asheville, N.C: U.S. Department of Agriculture Forest Service, Southern Research Station: 55-81.

Hanula, J.L.; Engstrom, R.T. 2000. Comparison of red-cockaded woodpecker (*Picoides borealis*) nestling diet in old-growth and old-field longleaf pine (*Pinus palustris*) habitats. American Midland Naturalist. 144: 370-376.

Hanula, J.L.; Franzreb, K.E. 1995. Arthropod prey of nestling red-cockaded woodpeckers in the upper Coastal Plain of South Carolina. Wilson Bulletin. 107: 485-495.

Hanula, J.L.; Franzreb, K.E. 1998. Source, distribution, and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. Forest Ecology and Management. 102: 89-102.

Hanula, J.L.; Horn, S. 2004. Availability and abundance of prey for the red-cockaded woodpecker. In: Costa, R.; Daniels, S.J., eds. Red-cockaded woodpecker: road to recovery. Blaine, WA: Hancock House Publishers: 633-645.

Hanula, J.L.; Lipscomb, D.; Franzreb, K.E.; Loeb, S.C. 2000. Diet of nestling red-cockaded woodpeckers at three locations. Journal of Field Ornithology. 71: 126-134.

Hanula, J.L.; Meeker, J.R.; Miller, D.R.; Barnard, E.L. 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. Forest Ecology and Management. 170: 233-247.

Hanula, J.L.; New, K.C.P. 1996. A trap for capturing arthropods crawling up tree boles. Res. Note SRS–3. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 8 p.

Hanula, J.L.; Wade, D.D. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. Forest Ecology and Management. 175: 163-184.

Harlow, R.F.; Lennartz, M.R. 1977. Foods of nestling red-cockaded woodpeckers in coastal South Carolina. Auk. 94: 376-377.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research. 15: 133-302.

Hess, C.A.; James, F.C. 1998. Diet of the red-cockaded woodpecker in the Apalachicola National Forest. Journal Wildlife Management. 62: 509-517.

Hooper, R.G. 1996. Arthropod biomass in winter and the age of longleaf pines. Forest Ecology and Management. 82: 115-131.

Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist. 100: 419-424.

Horn, S. 2000. Relationship of coarse woody debris to red-cockaded woodpecker prey diversity and abundance. Athens, GA: University of Georgia. 141 p. M.S. thesis.

Horn, S.; Hanula, J.L. 2002a. Comparison of arthropod prey of red-cockaded woodpeckers on the boles of longleaf and loblolly pines. Wildlife Society Bulletin. 30: 131-138.

Horn, S.; Hanula, J.L. 2002b. Life history and habitat associations of the broad wood cockroach, *Parcoblatta lata* (Blattaria: Blatellidae) and other native cockroaches in the Coastal Plain of South Carolina. Annals of the Entomological Society of America. 95: 665-671.

Jabin, M.; Mohr, D.; Kappes, H.; Topp, W. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak-beech forest. Forest Ecology and Management. 194: 61-69.

Jonsell, M.; Weslien, J.; Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity Conservation. 7: 749-764.

Knox, J.N.; Sharitz, R.R. 1990. Endangered, threatened and rare vascular flora of the Savannah River Site. Aiken, SC: Savannah River Site National Environmental Research Park Program, Savannah River Ecology Laboratory.

Lohr, S. 2002. Importance of coarse woody debris to avian communities in loblolly pine forests. Conservation Biology. 16: 767-777.

MacNally, R.; Horrocks, G.; Pettifer, L. 2002. Experimental evidence for potential beneficial effects of fallen timber in forests. Ecological Applications. 12: 1588-1594.

Marra, J.L.; Edmonds, R.L. 1998. Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates on clear-cut and forested sites on the Olympic Penninsula, Washington. Environmental Entomology. 27: 1111-1124.

McCay, T.S.; Hanula, J.L.; Loeb, S.C. [and others]. 2002. The role of coarse woody debris in southeastern pine forests: preliminary results from a large-scale experiment. In: Laudenslayer, W.F., Jr.; Shea, P.J.; Valentine, B.E. [and others], eds. Proceedings of the symposium on the ecology and management of dead wood in western forests. Gen. Tech. Rep. PSW–GTR–181. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Experiment Station: 135-144.

McMinn, J.W.; Crossley, D.A., Jr. 1996. Biodiversity and coarse woody debris in southern forests. Gen. Tech. Rep. SE–94. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 146 p.

Morista, M. 1959. Measuring of interspecific association and similarity between communities. Ser. E (Biol.). Mem. Fac. Sci. Kyushu Univ. 3: 65-80.

SAS. 1982. SAS user's guide: statistics. Cary, NC: SAS Institute. 584 p.

Sippola, A.-L.; Siitonen, J.; Punttila, P. 2002. Beetle diversity in timberline forests. A comparison between old-growth and regeneration areas in Finnish Lapland. Annales Zoologici Fennici. 39: 69-86.

Southwood, T.R.E. 1966. Ecological methods, with particular reference to the study of insect populations. London: Butler and Tanner. 391 p.

Speight, M.C.D. 1989. Life in dead trees – a neglected part of European wildlife heritage. Environmental Conservation. 16: 354-356.

U.S. Fish and Wildlife Service. 1985. Red-cockaded woodpecker recovery plan. Atlanta. 88 p.

THE FINE SCALE PHYSICAL ATTRIBUTES OF COARSE WOODY DEBRIS AND EFFECTS OF SURROUNDING STAND STRUCTURE ON ITS UTILIZATION BY ANTS (HYMENOPTERA: FORMICIDAE) IN BRITISH COLUMBIA, CANADA

Robert J. Higgins and B. Staffan Lindgren[1]

Abstract—Coarse woody debris (CWD) is increasingly recognized in Canada for its contribution toward biodiversity. It is a particularly vital resource in subboreal forests as nesting habitat for ants (Formicidae). Wood, which has low specific heat, provides a thermally favorable environment in this cool climate. Ants contribute to the physical breakdown of wood, and colonies are a significant food source for many vertebrates. However, this resource differs significantly between harvested and non-harvested stands. This study examined the physical attributes of CWD in 8-10 year old harvested and non-harvested stands while also examining the associated ant fauna. We found no significant difference in volume or total surface area between stand types. However, in harvested stands CWD is smaller in diameter, shorter, has less bark and has less evenly distributed decay classes as compared to non-harvested stands. In addition, the lack of earliest decay class and the physical damage evident on the majority of CWD pieces in harvested stands creates concern regarding the long term availability of CWD in harvested stands. Ants exploit available CWD in harvested stands but the community structure of this fauna appears to be young in these 8-10 year post-harvest stands. Larger ant species such as *Camponotus herculeanus* and *Formica aserva* were present but not common in these stands. They seem to require larger pieces of CWD and stumps for nesting habitat than is the average for CWD in harvested stands. The desirability of these ants as prey for bears and birds makes management of their nesting habitat of interest for conservation biology. Ants were largely excluded from non-harvested stands, probably because of cool and humid conditions. Historically, the ant fauna of this landscape was probably restricted to natural gaps and disturbed areas.

INTRODUCTION

In recent years there has been a move away from considering coarse woody debris (CWD) as unsalvaged waste (Maser and others 1979) and toward an appreciation of this resource as a significant contributor toward both forest ecological processes (Lofroth 1998, Maser and others 1994, Stevens 1997) and as habitat for many species (Keisker 2000). This change in attitude has been reflected by review publications in North America (Laudenslayer and others 2002), England (Hodge and Peterken 1998), Australia (Grove 2002, Waldendorp and others 2002), and Fennoscandia (Jonsson and Kruys 2001). In Canada, recognition of the role of CWD within forest ecosystems has grown, and it has now been included by some forestry companies as a critical filter habitat and biodiversity indicator within their Canadian Standards Association sustainable forest management certificate (Todd 2002).

Ants (Hymenoptera: Formicidae) constitute one of the most abundant and ubiquitous animal taxa in the world. In one of the few studies on comparative biomass in ecosystems, Fittkau and Klinge (1973) reported that the biomass of ants in the Amazon constituted over 25 percent of total animal biomass, and was more than twice that of all vertebrates combined. Ants are also one of the most widely distributed taxa, ranging from the tropics (Fittkau and Klinge 1973) to the northern treeline, with sporadic colonies found some distances beyond this (Francoeur 1983). Further, they are known to contribute significantly to ecosystem processes that include but are not limited to: pest management (Carlson and others 1984, Torgersen and Mason 1987, Way and Khoo 1992), soil nutrient turnover (Wagner and others 1997), seed dispersal (Gorn and others 2000, Heithaus 1981), grain consumption (Brown and others 1979), predation (McNeil and others 1978), and decomposition of organic material (Haines 1978). In addition, and of particular relevance to the forests of British Columbia, ants serve as a significant food source for birds (Bull and others 1995, Knowlton and others 1946, Torgersen and Bull 1995) and bears (Noyce and others 1997, Raine and Kansas 1990, Swenson and others 1999) thus playing an important role in the forest food web.

Ants (Hymenoptera: Formicidae) are a thermophilic taxon that in cooler climates must select nesting habitats which maximize daily heat gain (Hölldobler and Wilson 1990). In boreal and subboreal forests three common strategies are employed: (1) nesting under rocks; (2) the construction of thatched nests from forest litter, and; (3) nesting in dead wood (Hölldobler and Wilson 1990). Ideal nesting substrate should gain heat quickly, be of sufficient mass to hold that heat as ambient temperature declines, and be elevated above the soil to maximize insolation. Of these cooler climate nesting strategies, CWD best meets these criteria throughout the colony lifecycle.

North American literature directed at surveying the ant fauna of specific geographical regions illustrate the increasing

---

[1] Robert J. Higgins, PhD candidate, University of Northern British Columbia, Natural Resources and Environmental Studies, 3333 University Way, Prince George, B.C., V2N 4Z9; and B. Staffan Lindgren, Professor, University of Northern British Columbia, Ecosystem Science and Management, 3333 University Way, Prince George, B.C., V2N 4Z9.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

dependence of ants upon CWD with increasing latitude. While just less than 10 percent of species use dead wood as nesting habitat in Nevada, which has an average latitude of 38° N (Wheeler and Wheeler 1986), just over 35 percent used dead wood in North Dakota (average latitude 48° N) (Wheeler and Wheeler 1963), and just under 60 percent of species collected near Prince George British Columbia were dead wood associated (latitude 53° N) (Lindgren and MacIsaac 2002). Further, the latitude effect is mirrored by cooling climate. Colorado, at the same approximate latitude as Nevada, has a much greater percentage of dead wood dependent ants than Nevada. That is, 33 percent of the ant fauna is dead wood dependent in Colorado (Gregg 1963), compared to just less than 10 percent in Nevada (Wheeler and Wheeler 1986).

Currently, forest managers have few criteria upon which to base decisions regarding CWD management. Attention has been given to easily measured parameters such as volume and total surface area, the latter often expressed as percentage ground cover. It is then assumed that maintaining volume or total surface area of CWD in harvested plots, as compared to non-harvested plots will maintain the ecological functionality of CWD. However, as will be discussed, there are significant differences in the physical attributes of CWD between harvested and non-harvested sites.

The objective of our study is to examine variations in the physical attributes of CWD between harvested and non-harvested sites in the subboreal spruce biogeoclimatic zone of British Columbia. Attributes associated with utilization by ants are highlighted along with the effect of surrounding stand structure.

PROCEDURES

Coarse Woody Debris in Harvested and Non-Harvested Stands

Using records obtained from Houston Forest Products (Weldwood Canada), non-harvested and 8-10 year old harvested sites were identified in pine (*Pinus contorta* var. *latifolia*) leading stands within the subboreal spruce (SBS) biogeoclimatic zone and moist cold (SBSmc) subzone (Meidinger and Pojar 1991). Pine leading stands were chosen given the commercial significance of this species in the area. Stands were identified within a 100-km radius of Houston, British Columbia (54° 23' 59" N - 126° 40' 0" W). Four non-harvested sites and four 8-10 year old post-harvest sites were identified. Within each, a 1-ha sampling plot was randomly positioned at least 50 m away from an edge (i.e., road, stream, significant elevation change, forest or cutblock edge).

Coarse woody debris was sampled within two sets of 4X100 m strip plots randomly placed within the 1-ha sampling plot. Coarse woody debris was defined as any piece of dead wood within the strip plot with a maximum diameter of 10 cm or greater, including stumps. Each piece within the plot was measured for large and small diameter at strip edge, large end diameter, length in plot, and total length. The percentage bark retained was estimated visually and it was noted if the piece was in contact with the ground or elevated (i.e., greater than half of its total length off the ground). The decay class was determined for the sapwood and heartwood following Maser and others (1979). Woody debris of decay class 2, the most common solid wood decay class found in recently harvested stands, often exhibited signs of mechanical damage and was recorded as either 2A (no damage) or 2B (damaged) following Lloyd (2002). Stumps within the harvested plots were included in the assessment and analyzed separately from the downed woody debris. Both stumps and CWD were identified to species where possible.

The physical attributes of the CWD were recorded within 12.5-m segments within the 4X100 m transect, thus creating 50-m^2 sub-samples. The surface area of CWD pieces was derived by taking the average of the large and small end diameters at the plot boundaries and multiplying by the length. Volume was calculated as a frustrum using the large and small end diameters at the plot boundary and length in the plot. Total area and volume within the 50-m^2 sub-sample was then used as the basis of the estimate of CWD volume per hectare.

Environmental Attributes of Study Sites

Direct insolation in the harvested and non-harvested sites was approximated by determination of canopy cover. Canopy cover was assessed photographically using a Nikon Coolpix 990 digital camera fitted with a 0.63X wide angle lens. Within each plot, 5 randomly chosen points were used to photograph the canopy from a height of 1m. A 12X9 dot grid was then used to assess canopy cover on each photograph.

Temperature in the forest duff was monitored for approximately a one month period from July 7 to August 11, 2003 using iButton (Dallas Technologies) temperature dataloggers placed approximately 1 cm below the surface of the forest litter at two random points within each plot. The dataloggers recorded temperature every 30 minutes.

Ant Utilization of Coarse Woody Debris

Ant utilization of CWD was assessed within the 4X100 m strip plots indicated above. After measuring the physical attributes of CWD, each piece of wood was opened by hatchet and assessed for ant fauna. Ants were collected for species identification in the lab and the position of the ant or colony within the CWD was recorded.

To assess the ant fauna of the site that was not directly nesting within CWD, Nordlander style pitfall traps (Nordlander 1987) were set in place along four randomly placed 80-m long transects. These traps were placed at 20-m intervals along each 80-m transect (5 traps per transect, for a total of 20). Pitfall traps were left in place for one month and samples were collected at the end each second week.

Statistical Analysis

All data were assessed for normality using the Anderson-Darling test. Sample data failing to meet normality were then analyzed non-parametrically using the Mann-Whitney test.

RESULTS AND DISCUSSION

Coarse Woody Debris in Harvested and Non-Harvested Stands

The mean volume of CWD reported here (table 1) for non-harvested stands is lower than the 159 m^3/ha previously reported for this biogeoclimatic zone and subzone in a review by Lofroth (1998). This is not surprising given the great variability noted for this resource. However, the volume reported here is similar to volumes reported in a review of boreal forest CWD in Fennoscandia (Siitonen 2001).

Siittonen (2001) notes an order of magnitude reduction in CWD volumes following harvesting. Such a reduction has not been seen in this study where in fact, post-harvest volumes are higher than those found in non-harvested stands (table 1). This is likely due to the values placed upon woody material in Fennoscandia for fuel and chip production (Ehnström 2001). The reduction in volume in Fennoscandia has been associated with placing many CWD dependent invertebrate species at risk (Ehnström 2001). In response to this Ehnström (2001) recommends that CWD retention following harvesting be increased by approximately 50 percent. Following this recommendation, Ehnström (2001) discusses the need to manage the quality of the CWD as well as the total volume. As will be seen, observations from our study support that recommendation.

While we found no reductions in CWD volume and the related parameter, total surface area, variations in the physical attributes of the CWD between harvested and non-harvested sites are evident (table 2). Stumps differ fundamentally from downed woody debris with respect to physical attributes such as length (i.e., height in the case of stumps), and are not present within the non-harvested stands. Thus, they have been removed from the dataset presented in table 2. Coarse woody debris in which stumps have been excluded is referred to here as downed woody debris (DWD). DWD pieces in harvested plots are smaller in diameter, shorter, have lower bark retention, and differ in the distribution of decay classes when compared to non-harvested stands.

Table 1—Average total surface area and total volume of coarse woody debris in four harvested and four non-harvested stands within the subboreal spruce moist cold biogeoclimatic zone and subzone of British Columbia (each estimate is derived from a 50-m^2 subplot)

	Average total surface area covered by CWD	Average total volume of CWD
	m^2/ha ± SD	*m^3/ha ± SD*
Non-harvested stands	656 ± 622 n = 57	83.8 ± 87 n = 57
Harvested stands (8-10 years post-harvest)	684 ± 904 n = 61	119.9 ± 184 n = 61
Mann-Whitney two sample test	p = .9499	p = .1082

CWD = coarse woody debris.

Table 2—Physical attributes of downed woody debris in four harvested and four non-harvested stands within the subboreal spruce moist cold (SBSmc) biogeoclimatic zone and subzone of British Columbia

	Mean large end diameter	Mean total length	Mean percentage bark	Mean sapwood decay class	Mean heartwood decay class
	cm ± SD	*m ± SD*	- - - - - - - -	*± SD*	- - - - - - - -
Non-harvested stands	18.9 ± 6.8 n = 321	12.9 ± 7.5 n = 324	29 ± 39 n = 322	2.5 ± 0.8 n = 323	2.4 ± 1 n = 323
Harvested stands (8-10 years post-harvest, DWD)	16.5 ± 6.8 n = 439	3.7 ± 3.7 n = 439	8.6 ± 18.8 n = 439	2.4 ± 0.6 n = 432	2.4 ± 0.7 n = 418
Mann-Whitney Test	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.0001$	$p = 0.2776$

DWD = downed woody debris.

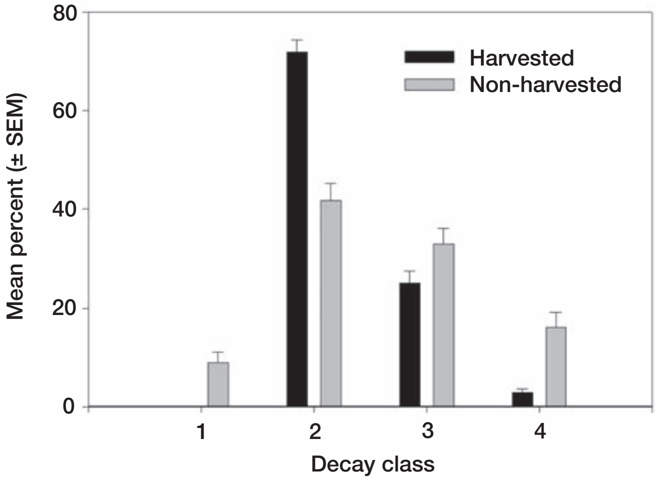


Figure 1—Percentage distribution of sapwood decay classes for coarse woody debris sampled in four non-harvested and four 8 to 10 years postharvest stands (non-harvested: n = 323; harvested: n = 701). Decay classifications follow Maser and others (1979).

It might seem surprising that a significant difference was seen in sapwood decay class between harvested and non-harvested stands given the similar average decay class (table 2). However, an examination of the distribution of decay classes between stand types (fig. 1), shows a strongly leptokurtic distribution in harvested stands, with just over 70 percent of all pieces in decay class 2, as compared to just over 40 percent in non-harvested stands. Decay class 1 was virtually absent in harvested stands, with only a single piece recorded. As a consequence this cohort will not be available for contributing toward later decay classes as stand succession progresses.

Also evident was the high degree of physical damage (i.e., crushed wood and splintering) to decay class 2 wood in harvested stands, presumably as a result of the activity of heavy machinery. In harvested plots, 63 percent of decay class 2 stumps (n=177) and 59 percent of DWD (n=301) displayed evidence of such mechanical damage. While this characteristic was almost certainly exploited by pioneering ant species (e.g., *Leptothorax canadensis* and *Myrmica alaskensis)* for access to nesting sites it could also allow more water penetration that may increase the rate of decay and, thus, the rate of removal of this resource from the stand. Exacerbating this potential increase in the rate of decay is the observation that 85 percent of pieces of CWD in the 8-10 year old post-harvest stand were in full contact with the ground, as compared to 53 percent of pieces in non-harvested stands.

Environmental Attributes of Study Sites

Harvested stands differed from 8-10 year old non-harvested stands in attributes such as canopy cover and soil litter temperature. Mean canopy cover in non-harvested stands was 78 percent ±9.24 (SD) as compared to 3.0 percent ±8.0 (SD) in harvested stands. As expected, the mean overall temperature of soil litter in the harvested stands was significantly higher than in non-harvested stands (table 3). In addition, the temperature range in harvested stands exceeded that of non-harvested stands in both daily high and low temperatures. However, this was most pronounced for daily highs (table 3).

Naturally, the higher canopy cover of non-harvested stands moderates the daily temperature fluctuations on the ground (table 3). Ants are thermophilic and are averse to cool moist conditions (Hölldobler and Wilson 1990) prevalent in forests of the subboreal spruce (SBS) moist cold (mc) biogeoclimatic zone and subzone. Thus, the low temperatures and high humidity explain the almost complete absence of ants in mature forests in this area (see below). If we assume that the canopy cover seen today in non-harvested stands is typical of that found historically on this landscape, then the ant fauna was likely restricted to naturally created gaps and disturbances arising from factors such as windthrow, insect disturbance and fire. In harvested stands, the fauna and flora must be capable of tolerating large fluctuations in daily temperature either physiologically or behaviorally. Nesting in CWD offers one mechanism of behaviorally controlling temperature.

Coarse woody debris has a low specific heat capacity (1.23kJ/kg/C at 25 °C (Wenzl 1970) compared to water (4.2 kJ/kg/C at 25 °C) (Lide 1991)). Thus, the temperature of woody debris should rise quickly from the absorption of energy as long as the wood is not excessively wet. As a consequence coarse woody debris offers a nesting substrate that can gain heat quickly when exposed to direct sunlight (e.g., in the low canopy cover of a harvested stand) and through its bulk hold some of that heat through the night. It also provides a physical matrix that allows an ant colony to reposition itself to optimize temperature and humidity or at least avoid deleterious conditions. Finally, the CWD is elevated above early successional ground flora allowing for direct exposure to sunlight.

Table 3—Temperature variations over a 1-month period (July 11, 2003 to August 11, 2003) in four harvested (8 to 10 years postharvest) and four non-harvested stands (all differences are statistically significant at $\alpha = 0.05$ as determined by the Mann-Whitney two-sample test)

Stand type	Mean temperature	Mean daily low temperature	Mean daily high temperature
		(°C ± SD)	
Harvested	14.2 ± 7.3	6.1 ± 2.1	26.5 ± 5.5
Non-harvested	10.6 ± 2.7	7.6 ± 1.5	15.1 ± 2.2

Ant Utilization of Coarse Woody Debris

A profound difference is evident in ant utilization of CWD between harvested and non-harvested stands. While 49 percent of CWD pieces (including stumps) (n=739) in harvested stands hosted ant colonies, only 3 percent of pieces (n=333) in non-harvested sites hosted ants. Further, within harvested stands ant utilization was higher for stumps than downed woody debris. On average 61 percent of stumps hosted ant colonies as compared to 41 percent of downed woody debris.

In total, 9 species of ants were collected from coarse woody debris in both harvested and non-harvested plots (appendix). However, of these, only 4 were collected within non-harvested stands whereas all 9 were present in the harvested stands. Of a total of 398 colonies of ants sampled from 1,072 pieces of CWD in this study only 11 separate colonies were located in non-harvested stands. Foraging activity was essentially absent in non-harvested stands. In total only 16 individual ants were collected in all pitfall traps set in non-harvested stands compared to 566 in harvested stands. However, even this larger number represents only 0.2 ants/trap/day. This low rate of ant capture in 8-10 year old post-harvested stands suggests that the community structure of the ant fauna is fairly young. Preliminary data (unpublished) from post-harvest stands just 5 years older has yielded 1.1 ants/trap/day, almost an order of magnitude increase.

The majority of species of ants were CWD dependent. Of the 11 species collected through all techniques, 9 were found nesting within CWD. Given that ant colonies were common in post-harvest CWD but little activity was occurring in the general stand, it is reasonable to suggest that CWD is acting as an important initiation point for ant colonization in harvested stands. However, it appears that many colonies had yet to mature and begin to fill available foraging space. In addition, of the two species not directly recorded in CWD in this study (*Polyergus breviceps* and *Myrmica fracticornis*), *P. breviceps* is known to use both CWD and soil for nesting (Wheeler and Wheeler 1963). In preliminary data from unpublished 15 year old post-harvest stands we have found evidence to suggest that soil nesting species do begin to establish. Mature colonies of a few soil nesting species of the *Formica fusca* group have been found in these older stands. However, it is possible that some of these nests may have originally established in CWD because pieces of rotten wood are often found in the center of such nests (Lindgren and MacIsaac 2002).

Given the low number of ants in non-harvested sites, the examination of the physical attributes of CWD associated with ant colonies has been limited to harvested plots. For each species present more than 10 times within the CWD survey, the physical attributes of the DWD and stumps hosting that species was compared to the overall physical attributes of all of the DWD and stumps in these stands (table 4).

Ant preferences for specific attributes of CWD however were not often clear. The most abundant species of ant colonizing CWD was *Leptothorax canadensis*. Given the average size of this ant (2.5-3.5 mm) and small colony sizes (few dozen) it is likely that it can use any CWD piece as nesting habitat. Lindgren and MacIsaac (2002) report finding this species in fragments of woody debris only 10 X 15 cm in size.

Although physically larger ant species (6-10 mm) such as *Camponotus herculeanus* and *Formica aserva* were not well established in 8-10 year old post-harvest plots some insight can be gleaned from our data about their nesting preferences. *C. herculeanus* did show a significant preference for larger pieces of CWD and *Formica aserva* was usually found in stumps rather than pieces of downed woody debris which generally had lower end diameters (table 3). These larger ants, and in particular their associated larvae, pupae, and female alates (queens) are a preferred food source for both black and grizzly bears (Noyce and others 1997, Swenson and others 1999) as well as birds (Torgersen and Bull 1995). We saw no evidence of bear foraging for ants in stumps or DWD in the 8-10 year old post-harvest sites but preliminary evidence from 15 year old stands shows signs of bear foraging on 20 percent (n=156) of stumps and 8 percent of DWD (n=185). The lack of bear foraging in 8-10 year old post-harvest stands further supports the suggestion that the ant community of these stands is immature.

We are currently expanding the range of stand types studied to further follow the relationship between CWD and ants. In particular we are beginning to examine later seral stages in harvested and naturally disturbed (burned) stands.

ACKNOWLEDGMENTS

This project would not have been possible without funding from Houston Forest Products (Weldwood Canada) and the National Science and Engineering Research Council of Canada. In addition, we have benefited greatly from the tireless field assistance of Duncan McColl, Laurel MacDonald, Lisa Zukewich, Anne Macleod, and David DeWitt.

Table 4—A comparison of the physical attributes of all downed woody debris and stumps in 8- to 10-year-old harvested plots with the same attributes associated with utilization by six species of ants, using the Mann-Whitney two-sample test

	Type of CWD	Average end diameter	Average length	Percentage bark	Sapwood decay class	Heartwood decay class
		cm ± SD	*m ± SD*	- - - - - - - - - - - - - - - - *± SD* - - - - - - - - - - - - - - -		
Overall CWD in harvested stands	DWD (n = 439)	16.5 ± 6.8	3.7 ± 3.7	8.6 ± 18.8	2.4 ± 0.6	2.4 ± 0.7
	Stumps (n = 333)	29.8 ± 13.7	0.33 ± 0.2	37.2 ± 32	2.3 ± 0.5	2.3 ± 0.6
CWD occupied by ant species						
Camponotus herculeanus	DWD (n = 7)	26.2[a] ± 4.8 p = 0.002	3.0 ± 2.4 p = 0.57	5.0 ± 3.0 p = 0.67	2.4 ± 0.5 p = 0.74	2.7 ± 0.8 p = 0.35
	Stumps (n = 5)	36.1 ± 8.2 p = 0.2	0.4 ± 0.1 p = 0.22	37.5 ± 37.4 p = 0.8	2.2 ± 0.4 p = 0.69	2 ± 0
Formica accreta	DWD (n=5)	12.5 ± 1.4 p = 0.12	6.5 ± 3.6 p = 0.1	0 ± 0	2.5 ± 0.6 p = 0.63	2.7 ± 0.5 p = 0.28
	Stumps (n = 6)	27.5 ± 9.8 p = 0.53	0.33 ± 0.0 p = 0.52	43 ± 31.4 p = 0.66	2.1 ± 0.4 p = 0.57	2.3 ± 0.5 p = 0.91
Formica aserva	DWD (n = 9)	18.1 ± 8.0 p = 0.57	4.6 ± 3.2 p = 0.32	16.0 ± 24.6 p = 0.15	2.6 ± 0.7 p = 0.38	2.6 ± 0.7 p = 0.5
	Stumps (n = 17)	35.8 ± 11.0 p = 0.09	0.31 ± 0.1 p = 0.76	36 ± 31.2 p = 0.96	2.4 ± 0.5 p = 0.65	2.5 ± 0.5 p = 0.22
Formica neorufibarbis	DWD (n = 19)	22.9[a] ± 13.5 p = 0.04	4.9 ± 5.2 p = 0.33	6.4 ± 10.3 p = 0.47	2.7 ± 0.8 p = 0.11	2.9[a] ± 0.8 p = 0.02
	Stumps (n = 28)	40.3[a] ± 13.6 p = 0.001	0.37 ± 0.2 p = 0.42	35 ± 34.1 p = 0.72	2.3 ± 0.5 p = 0.66	2.3 ± 0.5 p = 0.89
Leptothorax canadensis	DWD (n = 150)	16.3 ± 6.4 p = 0.99	4.2 ± 3.7 p = 0.16	7.7 ± 16.7 p = 0.45	2.3 ± 0.5 p = 0.67	2.4 ± 0.6 p = 0.27
	Stumps (n = 79)	30.7 ± 13.4 p = 0.51	0.33 ± 0.1 p = 0.51	38.1 ± 32.8 p = 0.89	2.1[a] ± 0.4 p = 0.04	2.2 ± 0.9 p = 0.23
Myrmica alaskensis	DWD (n = 24)	14.5[a] ± 5.3 p = 0.048	6.2[a] ± 5.2 p = 0.04	2.1 ± 3.8 p = 0.22	2.6 ± 0.8 p = 0.48	2.8 ± 0.9 p = 0.12
	Stumps (n = 36)	30.3 ± 10.8 p = 0.84	0.35 ± 0.3 p = 0.11	50.5[a] ± 28.8 p = 0.01	2.4 ± 0.5 p = 0.23	2.5 ± 0.8 p = 0.52

DWD = downed woody debris; CWD = coarse woody debris.

[a] Denotes significance at $\alpha = 0.05$.

LITERATURE CITED

Bolton, B. 1995. A new general catalogue of the ants of the world. Cambridge: Harvard University Press.

Brown, J.H.; Reichman, O.J.; Davidson, D.W. 1979. Granivory in desert ecosystems. Annual Review Ecology and Systematics. 10: 201-227.

Bull, E.L.; Torgersen, T.R.; Blumton, A.K. [and others]. 1995. Treatment of an old-growth stand and its effects on birds, ants, and large woody debris: a case study. Gen. Tech. Rep. PNW-GTR-353. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station. 12 p.

Carlson, C.E.; Campbell, R.W.; Theroux, L.J.; Egan, T.H. 1984. Ants and birds reduce western spruce budworm feeding injury to small Douglas-fir and western larch in Montana. Forest Ecology and Management. 9: 185-192.

Ehnström, B. 2001. Leaving dead wood for insects in boreal forests—suggestions for the future. Scandinavian Journal of Forest Research. Suppl. 3: 91-98.

Fittkau, E.J.; Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica. 5(1): 2-14.

Francoeur, A. 1983. The ant fauna near the tree-line in northern Quebec (Formicidae, Hymneoptera). Nordicana. 47: 177-180.

Gorn, S.N.; Gorb, E.V.; Punttila, P. 2000. Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: a case study. Acta Oecologica. 21: 293-301.

Gregg, R.E. 1963. The ants of Colorado. Boulder: University of Colorado Press.

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

Haines, B.L. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica,* in Panama. Biotropica. 10(4): 270-277.

Heithaus, E.R. 1981. Seed predation by rodents on three ant-dispersed plants. Ecology. 62: 136-145.

Hodge, S.J.; Peterken, G.F. 1998. Deadwood in British forests: priorities and a strategy. Forestry 71: 99-112.

Hölldobler, B.; Wilson, E.O. 1990. The ants. Cambridge, MA: Harvard University Press.

Jonsson, B.G.; Kruys, N., eds. 2001. Ecological bulletins: ecology of woody debris in boreal forests. 49. 283 p.

Keisker, D.G. 2000. Types of wildlife trees and coarse woody debris required by wildlife of north central British Columbia. Working Paper 50: Victoria, BC: Ministry of Forests Research Program. p 92.

Knowlton, G.F.; Roberts, R.S.; Wood, S.L. 1946. Birds feeding on ants in Utah. Journal of Economic Entomology. 39(4): 547-548.

Laudenslayer, W.F., Jr.; Shea, P.J.; Valentine, B.E. [and others], tech. eds. 2002. Proceedings of the symposium on the ecology and management of dead wood in Western forests. Nov 2-4 1999; Reno, NV. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station. 949 p.

Lide, D.R., ed. 1991. Handbook of chemistry and physics. 72nd ed. Boston, MA: CRC Press.

Lindgren, B.S.; MacIsaac, A.M. 2002. A preliminary study of ant diversity and of ant dependence on dead wood in central interior British Columbia. In: Laudenslayer, W.F.Jr.; Shea, P.J.; Valentine, B.E.; Weatherspoon, C.P.; Lisle, T.E., tech. eds. Proceedings of the symposium on the ecology and management of dead wood in western forests; Nov 2-4 1999; Reno, NV. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station: 111-119.

Lloyd, R. 2002. A comparison of coarse woody debris in harvested and unharvested sites: second year report. Report for the Morice and Lakes Innovative Forest Practices Agreement: IFPA No. 442.01. 33 p.

Lofroth, E. 1998. The dead wood cycle. In: Voller J, Harrison S, eds. Conservation biology principles for forested landscapes. Vancouver BC: University of British Columbia Press. p. 185-214.

Maser, C.; Anderson, R.G.; Cromack, K., Jr. [and others]. 1979. Dead and down woody material. In: Thomas, J., ed. Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. Washington DC: Agric. Handbook 553. U.S. Department of Agriculture Forest Service.

Maser, C.; Cline, S.P.; Cromack, K., Jr. [and others]. 1994. What we know about large trees that fall to the forest floor. Gen. Tech. Rep. PNW-229. Portland Oregon: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station: 25-46.

McNeil, J.N.; Delisle, J.; Finnegan, R.J. 1978. Seasonal predatory activity of the introduced red wood ant, *Formica lugubris* (Hymenoptera: Formicidae) at Valcartier, Quebec, in 1976. Canadian Entomologist 110: 85-90.

Meidinger, D.; Pojar, J., comp. and eds. 1991. Ecosystems of British Columbia. Special Report Series No. 6. Victoria: BC: British Columbia Ministry of Forestry. 330 p.

Nordlander, G. 1987. A method for trapping *Hylobius abietis* (L.) with a standardized bait and its potential for forecasting seedling damage. Scandinavian Journal Forest Research 2: 199-213.

Noyce, K.V.; Kannowski, P.B.; Riggs, M.R. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal Zoology 75: 1671-1686.

Raine, R.M.; Kansas, J.L. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. In: Darling, L.M.; Archibald, W.R., eds. Proceeding of the Eighth International Conference of Bear Research and Management. Victoria, BC: International Association for Bear Research and Management: 297-304.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins: Ecology of woody debris in boreal forests. 49: 11-41.

Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in BC forests. Working Paper 30. Victoria, BC: Research Branch, B.C. Ministry of Forests. 26 p.

Swenson, J.E.; Jansson, A.; Riig, R.; Sandegren, F. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology. 77: 551-561.

Todd, M. 2002. Sustainable forest management indicator annual report (2002), indicator #05: coarse woody debris. Houston, BC: Houston Forest Products.

Torgersen, T.R.; Bull, E.V. 1995. Down logs as habitat for forest dwelling ants-the primary prey of pileated woodpeckers in northeastern Oregon. Northwest Science. 69: 294-303.

Torgersen, T.R.; Mason, R.R. 1987. Predation on egg masses of the Douglas-fir tussock moth (Lepidoptera: Lymnatriidae). Environmental Entomology. 16: 90-93.

Wagner, D.; Brown, M.J.F.; Gordon, D.M. 1997. Harvester ant nests, soil biota and soil chemistry. Oecologia. 112: 232-236.

Waldendorp, G.; Keenan, R.J.; Ryan, M.F. 2002. Coarse woody debris in Australian forest ecosystems. A Report for the National Greenhouse Strategy, Module 6.6 (Criteria and Indicators of Sustainable Forest Management): Canberra, Australia Capital Territory: Department of Agriculture, Fisheries and Forestry, Bureau of Rural Sciences. 75 p.

Way, M.J.; Khoo, K.C. 1992. Role of ants in pest management. Annual Review of Entomology. 37: 479-503.

Wenzl, H.F.J. 1970. The chemical technology of wood. New York: Academic Press. 692 p.

Wheeler, G.C.; Wheeler, J. 1986. The ants of Nevada. Los Angeles, CA: Natural History Museum of Los Angeles.

Wheeler, G.C.; Wheeler, J. 1963. The ants of North Dakota. Grand Forks: University of North Dakota Press.

APPENDIX

Ant species collected in the subboreal spruce, moist cold (SBSmc) biogeoclimatic zone and subzone in British Columbia, Canada. Taxonomy follows Bolton (1995).

FAMILY FORMICIDAE

Subfamily Myrmicinae
Leptothorax canadensis Provancher
Myrmica alaskensis Wheeler
Myrmica incompleta Provancher
Myrmica fracticornis Forel

Subfamily Formicinae
Camponotus herculeanus (Linnaeus)
Camponotus noveboracensis (Fitch)
Formica fusca group
  Formica accreta Francoeur
  Formica neorufibarbis Emery
Formica rufa group
  Formica obscuriventris Mayr
Formica sanguinea group
  Formica aserva Forel
Polyergus breviceps Emery

SAPROXYLIC BEETLES IN A SWEDISH BOREAL FOREST LANDSCAPE MANAGED ACCORDING TO 'NEW FORESTRY'

Stig Larsson, Barbara Ekbom,
L. Martin Schroeder, and Melodie A. McGeoch[1]

Abstract—A major threat to biodiversity in Swedish forests is the decline of Coarse Woody Debris (CWD), which is an essential resource for many organisms and plays an essential role for the structure and function of boreal forests. Removal of CWD in commercial forestry has depleted important resources for many rare wood-living (saproxylic) beetles. Replenishment of CWD has been a prominent goal of revised forest management practices (new forestry), through practices such as retention of living trees on clear-cuts, creation of standing dead wood such as snags, and abstinence from removal of wind-felled trees. In an ongoing project in central Sweden the dynamics of CWD as well as beetle species richness and composition are being studied in a landscape where the new forestry has been applied. Our data show that the new management practices have contributed a substantial amount of CWD; new-forestry final cuttings, for example, contained 18 percent of spruce CWD in the landscape. We found a total of 184 saproxylic beetle species in the study landscape. Of these, 16 species are currently included in the Swedish Red List. The highest number (11) of these rare species were found in unmanaged stands, but there were also many (9) species found on new-forestry clear-cuts. We tentatively conclude that the new management practices have improved living conditions for some species of saproxylic beetles, manifested as recruitment of rare species from CWD retained under the new-forestry silviculture.

BIODIVERSITY IN BOREAL FORESTS

The boreal region extends over vast areas and is the second largest forest biome, after the tropical rainforests, comprising 16.6 million km^2. Although the boreal forest is structurally much less diverse than forests at lower latitudes, boreal diversity is still impressive. For example, at least 4,000 species of saproxylic (wood-living) species alone have been recorded from boreal Finland (Siitonen 2001).

The history of management differs radically between boreal Fennoscandia and Russia/Canada, and thus the proportion of pristine habitat that remains is also very different in the two areas. Commercial logging has been practiced in most parts of Fennoscandia for at least one tree generation (>100 years) and for two or three generations in the southern part. The degree to which biological communities have been influenced by this long history of forestry is largely unknown, although an estimated 2,000 species of invertebrates and lower plants are threatened (red-listed) in Swedish boreal habitats (Gärdenfors 2000). Boreal Russia/Canada has a much shorter logging history over most of the area so, conceivably, fewer species have achieved threatened status in these areas.

Because of the very dissimilar logging histories within the boreal region conservation efforts need to be designed and carried out depending on the amount of pristine habitat remaining. In Fennoscandia, with its long history of intensive forestry, considerable focus has been on developing methods to maintain and restore biodiversity in the managed landscape.

Management for biodiversity in Fennoscandia has been in operation since the mid 1990s and was rapidly implemented by integrating conservation measures into silvicultural practices. The basic idea is that commercial forestry can be maintained as long as enough care is taken to preserve and restore features in the managed forest that are of importance for a sustainable diversity of flora and fauna ('New Forestry'; cf. Larsson and Danell 2002). Protected areas (national parks, nature reserves, 'key habitats') do play an important role in Fennoscandian conservation planning. But recently the main focus of conservation efforts has been the management of the matrix, the area interspersed between pieces of protected land (Ehnström 2001, Vanha-Majamaa and Jalonen 2001). Key physical structures that contribute to biodiversity have been identified and management practices designed to enhance them have been developed. Landscape and stand structures considered important include old-growth stands, coarse woody debris, large patches of deciduous trees, burnt forest, and buffer zones along streams. The certification criteria presently in use require actions to be taken in order to preserve and actively restore these elements in the landscape (Anon. 2000).

Although it seems obvious that there is a limit to how much habitat that can be removed before biological diversity starts to decline, it is not at all clear how much habitat is required for the ecosystem to be sustainable and populations to remain viable. The practices introduced in Fennoscandia for matrix management were largely based on informed guesses from biologists with long experience in the natural history of forest organisms. The urgent need to preserve species judged to be threatened by modern forestry justified recommendations that were considered the best available, although recommendations were supported only by meagre scientific data (Larsson and Danell 2001). This approach has increasingly been questioned

---

[1] Stig Larsson, Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden; Barbara Ekbom, Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden; L. Martin Schroeder, Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, SE-750 07 Uppsala, Sweden; and Melodie A. McGeoch, Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

because managing the matrix for preserving biodiversity is not without costs (Raivio and others 2001). Ideally, the methods used should result in as much conservation benefit as possible.

CWD—A RESOURCE IN SHORT SUPPLY

Coarse woody debris (CWD) is commonly considered to be a resource in short supply in commercially managed forests (Siitonen 2001). Many organisms depend on CWD and, because of the shortage of it in today's managed forests, many wood-dependent species have become rare. The Swedish red list, for example, has 501 species of beetles, 33 species of lichens, 55 species of mosses, and 382 species of fungi considered to be dependent on CWD (Dahlberg and Stokland 2004).

The amount of CWD in the undisturbed landscape is one to two orders of magnitude higher than in managed Fennoscandian boreal forest (Siitonen 2001). In the natural landscape CWD is created by natural disturbances such as fires, insect and disease outbreaks, and windstorms (Angelstam 1997, Kuuluvainen 2002). In the commercial forest landscape clear-cuts have sometimes been considered comparable to natural disturbances. At harvest, however, CWD is commonly destroyed (Hautala and others 2004). Biodiversity-oriented forestry aims to minimize destruction of existing CWD and to produce new CWD.

The degree to which CWD-dependent organisms respond to the increase in CWD following biodiversity-friendly harvesting is essentially unknown. It is also largely unknown how the spatial distribution of CWD in the landscape influences putative positive effects of the new management practices. Because CWD in Fennoscandian boreal landscapes is likely to be very aggregated, we expect organisms with dissimilar dispersal capacities to respond differently to retention of CWD at clear-cutting.

It is clearly a challenge to design research programs that can assess the benefit of the new forestry in terms of long-term maintenance of biodiversity. Most likely, organisms with different life histories (reproduction, dispersal capacity, territoriality) will show different temporal and spatial responses to management practices, and thus, the scale of study will be important. Further, the suite of forestry practices in use are likely to be of variable importance for different types of organisms, e.g., CWD for organisms dependent on dead wood and burnt habitats for fire-dependent organisms. Thus, in order for research to be operational, efforts will need to focus on a subset of organisms, a subset of forestry practices, and ideally, for the majority of organisms, be executed at the landscape level.

Currently a number of research projects are underway in Sweden and Finland aiming to elucidate how certified forest management contributes to preservation of biodiversity. The present paper focuses on results from an on-going landscape-wide project in the south boreal region of Sweden, aimed at quantifying the efforts to manage CWD. Assemblages of saproxylic beetles, a species-rich group of organisms of great concern in Swedish nature conservation (Ehnström 2001), are studied. The aim of this project is to estimate, at the landscape level, the amount of CWD that results from the new forestry, and to determine the degree to which saproxylic beetles are affected by this relative increase in CWD.

Study Site

The study landscape, a management unit of Holmen Skog AB (www.holmenskog.com), is located close to Delsbo in central Sweden (62°N, 16°E) and consists of stands that typically have been managed for at least one rotation period. The size of the landscape is 24549 ha of which 20294 ha is productive forest land; small lakes, low productive forest land, and bogs make up the remaining 4155 ha. The landscape is typical for the middle-boreal region (Sjörs 1999) with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) the dominate tree species. Birch (*Betula pendula, B. pubescens*) and aspen (*Populus tremula*) are the most common deciduous tree species, but they rarely constitute more than a small proportion of the managed forest.

The landscape consists of 2,173 management blocks (stands), and in addition, three legally protected nature reserves (table 1). Of the company-managed area, 375 stands (1920 ha) have been designated 'set-asides', i.e., they will not be commercially managed but do not have legal protection (see below). The 17723 ha forest that is commercially managed is dominated by stands harvested in the 1960s and the 1970s; more than half of the area (9459 ha) is in the age class 15-59 years. This age class holds a significant number of stands planted with the exotic lodgepole pine (*Pinus contorta*); stands with >50 percent lodgepole pine cover an area of 5787 ha. There are 853 mature stands (>60 yrs) covering an area of 5511 ha, corresponding to 31 percent of the commercially managed area, or 22 percent of the entire landscape. Most of the mature stands are dominated by Scots pine, or a mix of Scots pine and Norway spruce. Spruce-dominated mature stands (>40 percent spruce) cover an area of 1841 ha (33 percent). Only a small fraction of the area of mature stands (2 percent) has a substantial (>40 percent) amount of deciduous trees.

NEW FORESTRY

Because Holmen Skog AB is certified according to FSC (Forest Stewardship Council, see www.fsc-sweden.org) their land has been managed for almost ten years using silvicultural methods developed for preservation and restoration of biodiversity. At present, there are a number of silvicultural practices performed at final harvest stipulated by FSC standards. It is required that a certain number of living trees be retained on clear-cuts, at present ten trees (DBH>15 cm) per ha must be left. These retained patches, small in size (<<1 ha), most likely contribute future CWD because there is a high probability that trees in these wind-exposed habitat islands will be blown down during heavy storms (Esseen 1994). It is further stipulated by current certification that naturally fallen trees, frequently from stands along clear-cut edges, should be left unless the volume exceeds 3 m^3/ha, in which case there might be an increased risk for bark beetle infestation. According to FSC it is recommended that a few artificial snags should be created per ha at final harvest. These snags are usually cut at a height of 3-5 meters and should be representative of the harvested stand with respect to tree species and diameter. In the study landscape artificial snags were systematically introduced around 1995 and are presently supposed to be created at a density of three per ha. According to the FSC

Table 1—Composition of the study landscape at Delsbo, central Sweden, and sampling efforts in the different stand categories

Stand category	Stands	Area	No. of sampled stands: CWD	No. of sampled stands: Beetles	No. of sampled objects: Beetles
	number	*ha*			
Managed forest					
0 – 2 years	20	343	0	0	0
3 – 7 years	47	666	20	19	115
8 – 14 years	82	1,744	10	0	2
15 – 59 years	796	9,459	11	2	0
≥ 60 years spruce	331	1,841	14	13	103
≥ 60 years pine	493	3,447	9	5	35
≥ 60 years deciduous	29	123	5	5	9
Unmanaged forest					
Set-asides	375	1,920	11	9	74
Reserves	3 (6 + 6 + 2)[a]	751	14	14	139
Sum forest	2,176	20,294	94	67	477
Nonforest		4,155			
Entire landscape		24,449			

CWD = coarse woody debris.

[a] The reserves were larger than the managed stands. Therefore, the reserves were divided into subareas, six for the larger ones (427 and 242 ha) and two subareas for the small one (82 ha).

protocol prescribed burning, aimed at creating suitable resources for fire-dependent organisms, is required on dry mesic sites on an area corresponding to 5 percent of the final harvest area. In addition to creating habitats for fire-specialists, burns also result in the creation of CWD, the amount being dependent on substrate availability and fire intensity. Of course, if burning is carried out on a clear-cut, with substrate mainly consisting of slash, only small amounts of CWD will be created. Prescribed fires for conservation purposes in the study landscape occurred in 1997 (40 ha), 1999 (32 ha), and in 2002 (15 ha). In addition, a wildfire occurred in 2002 on about 10 ha.

The 375 areas classified as set-asides constitute about 9 percent of the forest area in the landscape. The small areas retained at clear-cut could, in principle, be regarded as set-asides, but they are not formally included in this category. A more substantial contribution to set-asides comes from so-called ‘key objects’. These are generally small stands (in the study landscape: mean area 5.1 ha, range 0.3-94 ha) of unusually high conservation value that have been identified using the same criteria as for ‘key-habitats’ (Hansson 2001). A second category of set-asides includes habitats that do not meet the criteria for key habitats but for other reasons are considered valuable for biodiversity. For example, deciduous tree species are considered to be present in much lower proportions (often <5 percent) in the managed boreal landscape compared to the unmanaged landscape (Angelstam and Andersson 2001). For this reason it has been stipulated that the proportion of deciduous trees should increase to 5-20 percent.

Silvicultural methods motivated by concerns about biodiversity, as described above, were gradually introduced into forest management from around 1995 and eventually formalized in the FSC regulation beginning in 2000. From a CWD point of view management practices in connection with final harvest can be assumed to be of particular interest. In the study landscape, 67 stands have been harvested during the period 1995-2002, totalling an area of 1009 ha (5 percent of the forested area). The majority of these stands should have been exposed to the new-forestry principles. Older clear-cuts, 8 years and older and harvested before the new forestry was introduced, are expected to have much less, if any, intentionally preserved or created CWD.

Sampling Program

In order to investigate the effect of new-forestry practices on availability of CWD and associated saproxylic beetle assemblages, we stratified the forest landscape into nine categories based on stand age and type of management using information from the Holmen Skog AB database and additional information about the forest reserves (see table 1). The first two categories, 0-2 years and 3-7 years, represent clear-cuts on which creation of high stumps and green tree retention have been practiced at final cutting. However, CWD occurring on the youngest clear-cuts was not included in the study because this quality of wood is not suitable for the subset of saproxylic beetles that is the focus of this study. Thus, no sampling was performed in this type of stand.

In each stand category, except reserves, a random sample of stands located throughout the landscape was selected (table

1). All three nature reserves within the landscape were sampled. Because reserves were larger than managed stands the two largest were divided into six sub-areas (denoted stands) of approximately equal size and the smallest was divided into two sub-areas. In each chosen stand, amounts of CWD and beetle abundance were estimated. Sampling of logs (downed woody debris) was carried out using a Line Intersect Sampling method (Marshall and others 2000). Four transects of 100 m were sampled in each stand. The same transects were used to delimit sampling plots for snags (standing dead wood). The plot extended 10 m on each side of the transect forming a 20 x 100 m rectangle. The following data were for each piece of CWD: classification as snag or log, intact or broken/cut snag, diameter (at transect line for logs and at DBH for snags), height of snags, tree species, percentage of surface area covered by bark, and decay class. The classification into decay classes (1-6) was based on the hardness of the wood (Siitonen and Saaristo 2000). The volume of snags was estimated using tree-specific functions with diameter at 1.3 m and height as input variables. Bark area on single snags was calculated by using the formula for the surface area of a cone as an approximation. Volume of logs per ha was calculated for each transect using formulae from Marshall and others (2000). Surface area was estimated by modifying the formula for "total projected area" by replacing diameter with circumference. Surface area for each object was multiplied by the proportion of remaining bark. For each stand, an average for each variable was calculated based on the four intersect lines. Further details concerning sampling can be found in Ekbom and others (2006).

Snags and logs in decay classes 2-3 from spruce, pine, and birch were sampled for beetles. Bark was peeled off and broken into small pieces that were sifted through a course net. The resulting fine fraction was placed in Tullgren funnels, where beetles were extracted under a lamp. This method was chosen because we wanted to only sample beetles actually using CWD in different stand categories. Ten objects of CWD were sampled in each stand. In stands where ten suitable objects were not available all appropriate objects were sampled. In some stands no suitable objects were found, and hence the number of stands sampled for beetles is lower than the number of stands sampled for CWD (table 1). Each sample consisted of 0.5-1.0 m^2 bark. All beetle adults were identified to species or genus level.

CWD in the Landscape

The total volume (m^3/ha) of CWD found in nature reserves and set-asides was about twice that of managed stands (Ekbom and others 2006). Bark area (m^2/ha) on CWD in nature reserves and set-asides was not significantly different from that found in managed spruce-dominated stands older than 60 years. The amount of bark found on clear-cuts and other old-managed stands was about half as much as that found in nature reserves, set-asides, and old-managed spruce stands. In young forest stands (8-59 years), bark was a sparse resource; these stands contained 10-20 times less CWD bark area than other stands. Most of the volume of CWD was pine, but the greater portion of bark area was on deciduous and spruce CWD.

The area of new-forestry final cuttings made up 4.9 percent of the landscape but they contained 8.7 percent of total CWD bark and 18.4 percent of spruce CWD bark available in the landscape. If new forestry is practised then the volume of CWD would increase by 4.5 percent at the landscape level when compared to the possibility that no CWD at all is left at final cutting (table 2). All CWD was obviously not removed under the previous management regime because the old clear-cuts (7-14 years) we inventoried were not devoid of CWD. Results from the CWD inventories are in broad agreement with simulations performed to compare past management with management according to new-forestry practices (Ranius and Kindvall 2004). In simulations, the volume of CWD roughly doubled in young stands after only 20 years. Although there is room for improvement, new management practices have increased the availability of resources for saproxylic beetles associated with bark.

Table 2—Estimates of available substrate (the volume and bark area of CWD of different tree species) in the landscape at Delsbo, central Sweden. The percentage increase in substrate attributable to "new forestry" is calculated by assuming that under earlier management regimes no CWD at all would be left on clear-cuts

		All tree species		Spruce		Pine		Deciduous	
Stand type	Area	Volume	Bark area	Volume	Bark area	Volume	Bark area	Volume	Bark area
	ha	m^3	m^2	m^3	m^2	m^3	m^2	m^3	m^2
Clear-cut	1,009	13,281	125,974	3,513	47,729	7,015	19,426	2,753	58,819
Managed, excluding clear-cut	16,714	223,007	921,843	16,133	155,146	160,411	284,801	46,463	481,896
Unmanaged	2,753	73,505	525,571	7,878	103,947	54,159	135,317	11,468	286,307
Total area in clear-cut (percent)	4.9								
Increase in CWD in managed forest attributed to "new forestry" (percent)		4.5	8.7	14.6	18.4	3.3	4.6	4.8	7.7

CWD = coarse woody debris.

Beetle Species Richness and Assemblages

A total of 184 species and 10,804 individuals of saproxylic beetle adults were recorded from a total of 67 sampled stands (table 3). Beetle species richness was positively correlated with available bark area on a stand by stand basis (r = 0.47, $p<0.0001$, n = 51; McGeoch, M.A. and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa). For all stand categories increased CWD bark generally resulted in enhanced species richness. Unsurprisingly, the highest number of species (126) was found in reserves, followed by old-managed stands (combined spruce-, pine-, and birch-dominated; 105 species). Clear-cuts were found to have almost as many species (97) as the old-managed stands. The young-managed stands had very little CWD (Ekbom and others 2006), and consequently, had very few saproxylic beetle species. The rather low number of species (81) found in set-asides is difficult to explain; approximately the same number of individuals were collected (table 3). Fewer set-aside stands were sampled, but there were as many beetle individuals sampled in set-asides as in the reserves, and thus rarefaction estimates for the two habitats have roughly the same precision (McGeoch and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa).

As expected, beetle assemblage structure, i.e., the combined consideration of species richness, relative abundance, and species composition, varied among stand types. Canonical correspondence analysis (CCA) showed that beetle assemblage on clear-cuts was very different from that in old-managed stands, set-asides and nature reserves (McGeoch and others. Contribution of managed boreal forest stands to the conservation of saproxylic beetle diversity. Manuscript submitted. Author can be reached at Department of Conservation Ecology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa). It is interesting that the assemblages found in old-managed stands differed from set-asides and reserves. Likewise, Similä and others (2002) found the beetle assemblage of early succession pine forest in Finland to differ from that in mature pine forest stands, and Kaila and others (1997) found distinct birch beetle assemblages associated with clear-cuts and mature forests.

Occurrence of Rare Saproxylic Beetles

For the purpose of this paper we define rare species as those that are currently included on the Swedish Red List (Gärdenfors 2000), although we recognize that rare organisms need not be red-listed, or vice versa. A total of 16 species of rare saproxylic beetles were found in the 67 stands (table 4). The highest number (11) was found in the reserves. But there were also many species (9) found on the clear-cuts. Old-managed stands and set-asides were intermediate with six rare species each.

Data in this study are based on the method of sieving insects from bark samples. Thus, we know that the specimens that were collected have indeed been living under the bark (no 'tourists' included). Determining beetle assemblages from sieving underestimates the true number of saproxylic beetles because the method does not usually extract insects living inside the wood or in fungal fruiting bodies. For example, Wikars and others (2005) concluded that 18 percent of spruce-living saproxylic species collected by emergence traps, an efficient but arduous method, mainly live inside wood; most of these species would not be sampled by sieving.

A great advantage of sieving bark from a particular decay class is that the quality of CWD can be reasonably well defined. Because samples were taken from logs and snags in decay stages 2-3 few beetle species feeding on fresh cambium, e.g., bark beetles, were found. The fraction of CWD that we have studied is characterized by a high density of fungal mycelium in the space between bark and wood. Interactions between fungi and insects are likely to be important in the dynamics of CWD, and of utmost importance in the preservation of the organisms (Jonsell and Weslien 2003, Jonsell and others 2001). The biology of the rare species found in this microhabitat in our study is not known in detail, but it can safely be assumed that the majority of them are associated with fungi (Personal communication. 2004. Lars-Ove Wikars, Scientist, Department of Entomology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden). The click beetle *Harminius undulatus* and the staphylinids are considered mainly to be predators, but even these species may occasionally consume fungal tissue.

Table 3—Total number of saproxylic beetle species and individuals recorded as adults from the different stand categories at the study landscape at Delsbo, central Sweden

Stand type	Stands	Total species	Total individuals
	- - - - - - - -	*number*	- - - - - - - -
Reserve	14	126	2,366
Set-aside	9	81	2,502
Old managed (total)	23	105	4,233
Old managed (spruce)	13	89	3,327
Old managed (pine)	5	57	679
Old managed (deciduous)	5	30	227
Young managed	2	18	158
Clear-cut	19	97	1,545
Total	67	184	10,804

Table 4—Red-listed saproxylic beetle species recorded as adults in the 482 sieved CWD objects from the study landscape at Delsbo, central Sweden

		Individuals				
Family and species	Red-list category[a]	Clearcut	Old managed	Set-aside	Reserve	Total
		number				
Scydmaenidae						
Eutheia linearis Mulsant	NT	1	0	0	0	1
Staphylinidae						
Olisthaerus megacephalus (Zetterstedt)	NT	0	1	0	0	1
Olisthaerus substriatus (Paykull)	NT	0	0	1	14	15
Euryusa castanoptera Kraatz	NT	0	0	0	1	1
Elateridae						
Harminius undulatus (De Geer)	NT	0 (21)	0 (51)	0 (13)	1 (6)	1(91)
Silvanidae						
Dendrophagus crenatus (Paykull)	NT	3 (5)	3 (16)	5 (4)	5 (3)	16 (28)
Endomychidae						
Leiestes seminigra (Gyllenhal)	NT	0	0	0	1	1
Corticariidae						
Enicmus planipennis Strand	NT	2	0	2	4	8
Corticaria lapponica (Zetterstedt)	NT	1	5	0	2	8
Corticaria fennica Johnson	VU	0	1	0	0	1
Cisidae						
Ennearthron laricinum (Mellie)	NT	4	4	1	13	22
Mycetophagidae						
Mycetophagus fulvicollis Fabricius	VU	1	0	0	0	1
Tenebrionidae						
Bius thoracicus (Fabricius)	VU	0	0	0	1	1
Upis ceramboides (Linnaeus)	VU	2 (6)	0	0	0	2 (6)
Melandryidae						
Orchesia fasciata (Illiger)	VU	1	0	0	1	2
Zilora ferruginea (Paykull)	NT	0	0	7	7	14
Total		15 (32)	14 (67)	16 (17)	50 (9)	96 (125)

CWD = coarse woody debris; VU = vulnerable; NT = near threatened.
Numbers in parentheses are larvae.
[a] Red-list categories are according to Gärdenfors (2000).

Rare species made up 5-10 percent of the total number of species, with no appreciable differences among stand types. Many species were represented by only one individual (singletons) (table 4), which is so often the case when studying rare organisms. Differences among stand types with regard to proportion of singletons (range 0.33-0.44) were negligible.

As mentioned earlier, many of the new-forestry initiatives aim at increasing the amount of CWD in connection with final harvest. Of the nine rare species on clear-cuts three were exclusively found there (*Upis ceramboides*, *Eutheia linearis*, and *Mycetophagus fulvicollis*). Of these, *E. linearis* and *M. fulvicollis* were found as singletons. Thus, it is difficult to know whether they commonly occur on clear-cuts, although Jonsell and Weslien (2003) reported another *E. linearis* singleton from a clear-cut. *Upis ceramboides* was collected from three clear-cuts. This species is known to colonize early succession habitats, and thus can be presumed to be favoured by increased CWD on clear-cuts.

It is interesting that six rare species were found both in reserves and on clear-cuts. These two stand types represent end points in the forest succession, and clearly provide very different environments for beetles. Nevertheless, these stand types shared a considerable number of species. It will be difficult to adequately interpret this observation until the habitat requirements of the species are better known. It is possible that this subset of saproxylic beetles accepts a wide range of stand types, as long as there is CWD of suitable quality. If so, then the new-forestry initiative of creating CWD at final harvest may reduce the risk of local extinction for some species. But it is also possible that the observed rare species on clear-cuts are simply remnants from the harvested stands. Future studies will have to specifically address this question.

CONCLUDING REMARKS

The managed boreal forest landscape contains a small fraction of CWD, compared with the pristine forest (Siitonen 2001). Under natural conditions significant amounts of CWD are produced in maturing stands through ageing and self-thinning, and in the early succession phase following disturbances such as fire, insect and disease outbreaks, and wind storms (Ranius and others 2004). The Fennoscandian attempts to increase CWD in the managed forest landscape have, to a large extent, been linked to operations at final harvests, i.e., mimicking CWD production in early succession habitats. This means that, at the landscape level, most of the additional CWD resulting from the new forestry is to be found on, or in close proximity to, clear-cuts. Less has been achieved with respect to increasing the amount of CWD in mature stands.

The amount of CWD that is retained and produced at final harvest, about 14 m^3/ha at the study landscape, is an improvement compared to the situation in Sweden in the 1960s and 1970s when virtually nothing was left. However, one must bear in mind that the amount of CWD present on today's clear-cuts is only a small fraction of what was produced after natural disturbances in the pristine boreal landscape (cf. Siitonen 2001). The question, then, arises as to whether or not present management of CWD significantly decreases the risk of local extinction for CWD-dependent organisms.

Data collected in this study support the notion that saproxylic beetles benefit from the new silvicultural methods. A considerable number of saproxylic beetle species was found to utilize CWD retained and created on clear-cuts, including species that are considered threatened (red-listed) (also cf. Jonsell and Weslien 2003). Not surprisingly, the beetle assemblage on clear-cuts differed from those in the intact stands. However, it is probably premature to conclude that restoring CWD at final harvest will only benefit saproxylic beetles that are exposed-habitat specialists. Clear-cuts and reserves shared a number of species (e.g., six red-listed). Perhaps such species accept a broad range of habitats, given that the appropriate resource is available (cf. Martikainen 2001).

Coarse woody debris with intact bark is a resource that is crucial for many beetle species, including many red-listed, that are associated with saproxylic fungi. In the present study we restricted sampling to this resource, and thus, any conclusions are limited to this subset of CWD-associated beetles. This is a problem when communicating with forest managers and scientists studying other CWD organisms, because silvicultural practices were developed in order to preserve and restore a multitude of organisms, not only saproxylic beetles living under bark. On the other hand, in order for the scientific method to be successful it is essential that the study object be clearly defined. With respect to CWD, it is obviously of little relevance to consider decay categories not used at all by the study organism. Estimates of total volumes of CWD, including the full range of decay classes, are difficult to relate to specific organisms because few, if any, grow and reproduce in all categories of CWD.

The fact that saproxylic beetles can be found in CWD on clear-cuts is intriguing, but not conclusive evidence that the management practices included in the new forestry have reduced the risk of species disappearance from the boreal landscape. We found some support for the conjecture that saproxylic beetles are limited by the availability of their resource, i.e., beetle species richness correlated positively, on a stand by stand basis, with available bark area. Thus, it is conceivable that an increase in bark area in the landscape could enhance species richness. However, precise predictions are not possible at this stage. One major uncertainty is the form of the relationship between bark area and species richness (or any other response variable, e.g., population density of rare species). There are good theoretical reasons to assume that thresholds are important (Fahrig 2002), and that threshold values differ depending on the species considered. The existence of thresholds calls for more intensive studies of the spatial distribution of CWD in the landscape, in particular the distribution of CWD in relation to the dispersal capacity of the beetles.

Finally, there is an important spatio-temporal aspect as to the value of new-forestry CWD. The category of CWD that we have studied has a turnover of about 10-20 years, depending on tree species and habitat (Kruys and others 2002, Ranius and others 2004). Assuming that, at the landscape level, harvesting occurs with the same intensity over time the input of CWD will roughly equal the disappearance of this category of CWD through decomposition. Each 'cohort' of CWD will then last 10-20 years. The arrangement of this cohort of CWD in the landscape should be designed to facilitate colonization and successful reproduction by target organisms.

ACKNOWLEDGMENTS

We thank Ola Kårén and Thomas Ranius for valuable comments on the manuscript. Support for this project came from the project "Conservation of Biodiversity in Managed Forest" financed by the Faculty of Forestry at the Swedish University of Agricultural Sciences. Holmen Skog AB generously hosted our field study, assisted in many ways with practical arrangements, and shared their stand database.

LITERATURE CITED

Anon. 2000. Svensk FSC-standard för certifiering av skogsbruk. Svenska FSC-rådet. 37 pp. (In Swedish.)

Angelstam, P. 1977. Landscape analysis as a tool for the scientific management of biodiversity. Ecological Bulletin. 46: 140-170.

Angelstam, P.; Andersson, L. 2001. Estimates of the needs for forest reserves. Scandinavian Journal of Forest Research Supplement. 3: 38-51.

Dahlberg, A.; Stokland, J.N. 2004. Vedlevande arters krav på substrat —sammanställning och analys av 3600 arter. Skogsstyrelsen, Rapport 7-2004. (In Swedish with English summary).

Ehnström, B. 2001. Leaving dead wood for insects in boreal forests —suggestions for the future. Scandinavian Journal of Forest Research Supplement. 3: 91-98.

Ekbom, B.; Schroeder, L.M.; Larsson, S. 2006. Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. Forest Ecology and Management. 221: 2-12.

Esseen, P.A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth forest. Biological Conservation. 68: 19-28.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications. 12: 346-353.

Gärdenfors, U. 2000. The 2000 red list of Swedish species. Uppsala; ArtDatabanken, SLU. 397 pp.

Hansson, L. 2001. Key habitats in Swedish managed forests. Scandinavian Journal of Forest Research Supplement. 3: 52-61.

Hautala, H; Jalonen, J; Laaka-Lindberg, S; Vanha-Majamaa, I. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation. 13: 1541-1554.

Jonsell, M.; Nordlander, G.; Ehnström, B. 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. Ecological Bulletins. 49: 173-194.

Jonsell, M.; Weslien, J. 2003. Felled or standing retained wood—it makes a difference for saproxylic beetles. Forest Ecology and Management. 175: 425-435.

Kaila, L.; Martikainen, P.; Punttila, P. 1997. Dead trees left in clearcuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation. 6: 1-18.

Kruys, N.; Jonsson, B.G.; Ståhl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications. 12: 773-781.

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

Larsson, S.; Danell, K. 2001. Science and the management of boreal forest diversity. Scandinavian Journal of Forest Research Supplement. 3: 5-9.

Marshall, P.L.; Davis, G.; LeMay, V.M. 2000. Using line intersect sampling for coarse woody debris. Forest Research Technical Report. TR-003, Ecology. Vancouver, BC: Vancouver Forest Region, Canada. 19 p.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletins. 49: 205-218.

Raivio, S.; Normark, E.; Pettersson, B.; Salpakivi-Salomaa, P. 2001. Science and the management of boreal forest biodiversity—a forest industries' view. Scandinavian Journal of Forest Research Supplement. 3: 99-104.

Ranius, T.; Jonsson, B.G.; Kruys, N. 2004. Modeling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. *Canadian Journal Forest Research*. 34: 1025-1034.

Ranius, T.; Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation. 119: 51-59.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forest as an example. Ecological Bulletins. 49: 11-41.

Siitonen, J.; Saaristo, L. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation. 94: 211-220.

Similä, M.; Kouki, J.; Martikainen, P.; Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation. 106: 19-27.

Sjörs, H. 1999. The background: geology, climate and zonation. Acta Phytogeographica Suecica. 84: 5-14.

Vanha-Majamaa, I.; Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research Supplement. 3: 79-90.

Wikars, L-O.; Sahlin, E.; Ranius, T. 2005. A comparison of three methods to estimate species richness of saproxylic beetles in logs and high stumps of Norway spruce. Canadian Entomologist. 137: 304-324.

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

David W. Langor, John R. Spence, H.E. James Hammond, Joshua Jacobs, and Tyler P. Cobb[1]

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

---

[1] David W. Langor, Research Scientist, Natural Resources Canada, Canadian Forest Service, 5320-122 Street, Edmonton, Alberta, Canada, T6H 3S5; John R. Spence, Professor and Chair, Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada, T6G 2H1; H.E. James Hammond, Technician, Canadian Forest Service; 5320-122 Street, Edmonton, Alberta, Canada, T6H 3S5; Joshua Jacobs, M.Sc. Student, Department of Renewable Resources, University of Alberta; Edmonton, Alberta, Canada, T6G 2H1; and Tyler P. Cobb, Ph.D. Student, Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada, T6G 2H1.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

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 northcentral Alberta, and from 16 sites in central and southern Sweden (Palm 1959)

	Species	
Family[a]	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)

	Species	
Trophic role	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

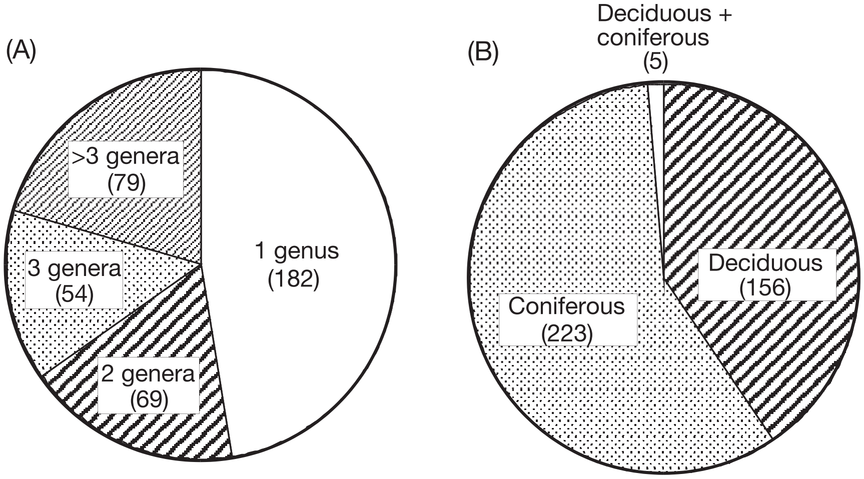


Figure 1—Host specificity of species of Scolytidae and Buprestidae in trees in Canada. (A) Proportion of beetle species utilizing 1, 2, 3, or > 3 host genera. (B) Proportion of beetle species utilizing deciduous hosts, coniferous hosts, or both. Numbers in parentheses indicate the number of species of each category.

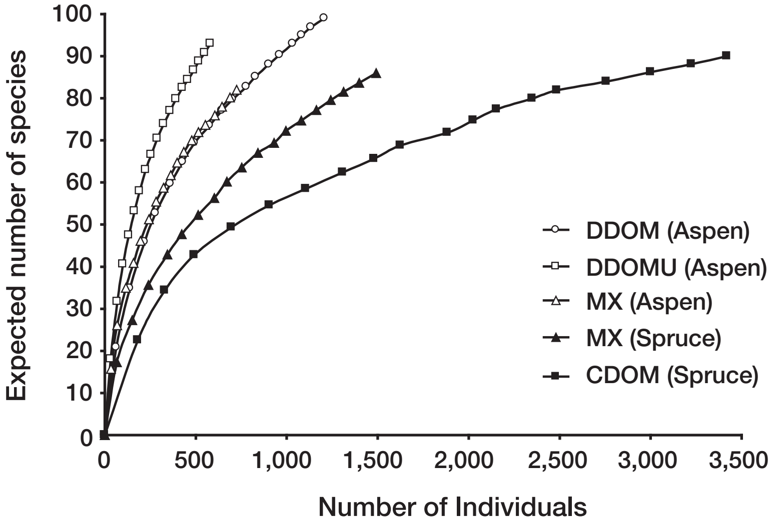


Figure 2—Rarefaction estimates of saproxylic beetle species collected using flight-intercept traps on white spruce and trembling aspen snags in each stand cover type at the Ecosystem Management by Emulating Natural Disturbance experimental site, Alberta.

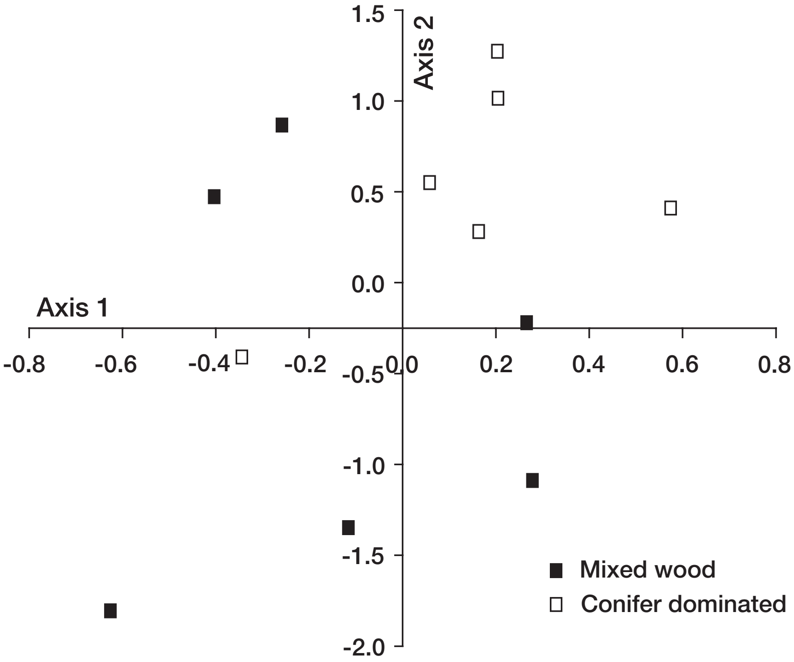


Figure 3—Nonmetric multidimensional scaling (NMS) ordination based on catch of 117 saproxylic beetle species on 12 samples of white spruce snags in coniferous dominated (CDOM) and or codominated (MX) cover types at the Ecosystem Management by Emulating Natural Disturbance experiment site, Alberta. Each 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

	Window-trapped beetles			Reared beetles		
Decay class[a]	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.

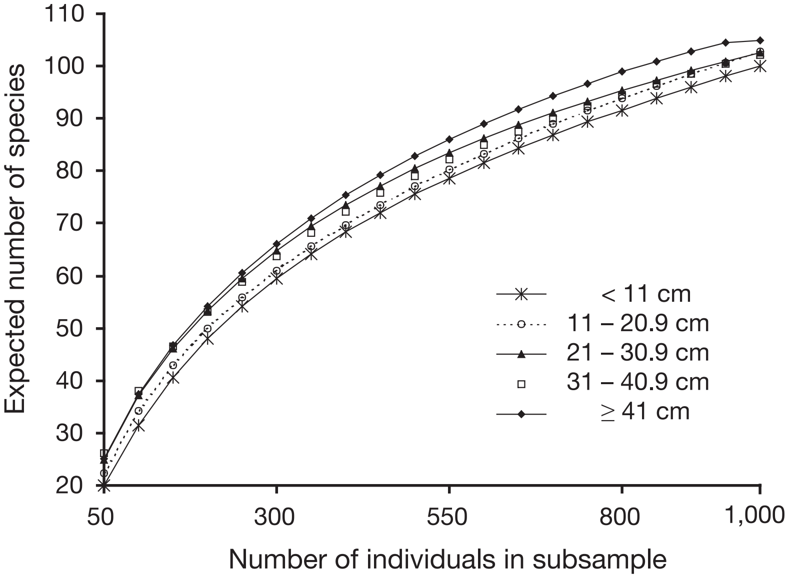


Figure 4—Rarefaction estimates of saproxylic beetle species richness collected with flight-intercept traps attached to *Populus* snags in aspen-dominated mixed wood forests in north-central Alberta. Snags are divided into 10-cm diameter at breast height classes.

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

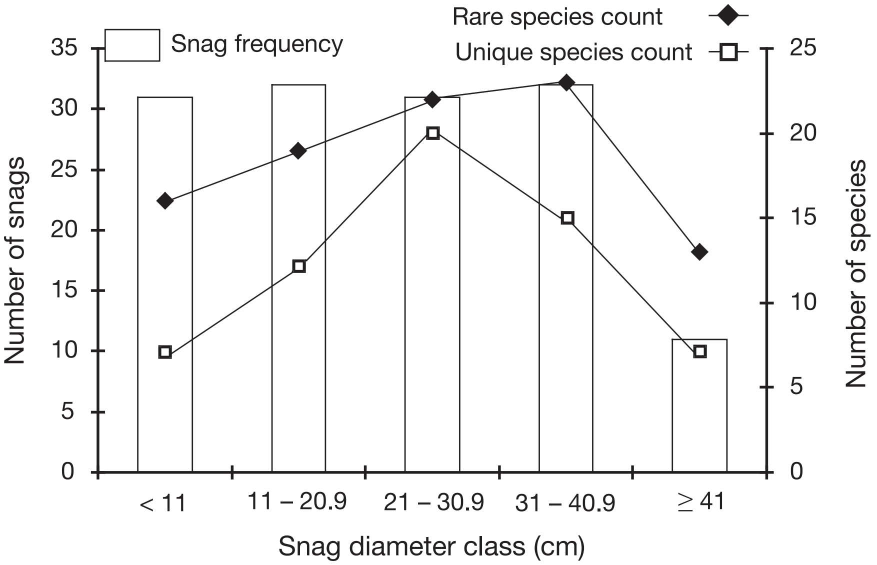


Figure 5—Number of *Populus* snags of each of five diameter classes sampled by flight-intercept traps, and the number of rare (singletons + doubletons) and unique saproxylic beetle species collected in each diameter class.

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

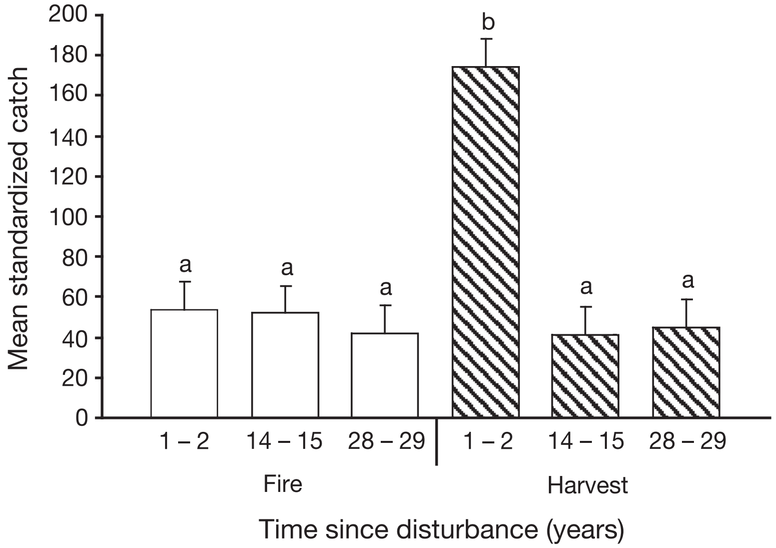


Figure 6—Mean (±SE) standardized catch (number of specimens per 150 trap days) of saproxylic beetles in boreal *Populus* stands of three ages and originating from fire or clearcut harvesting, Alberta.

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).

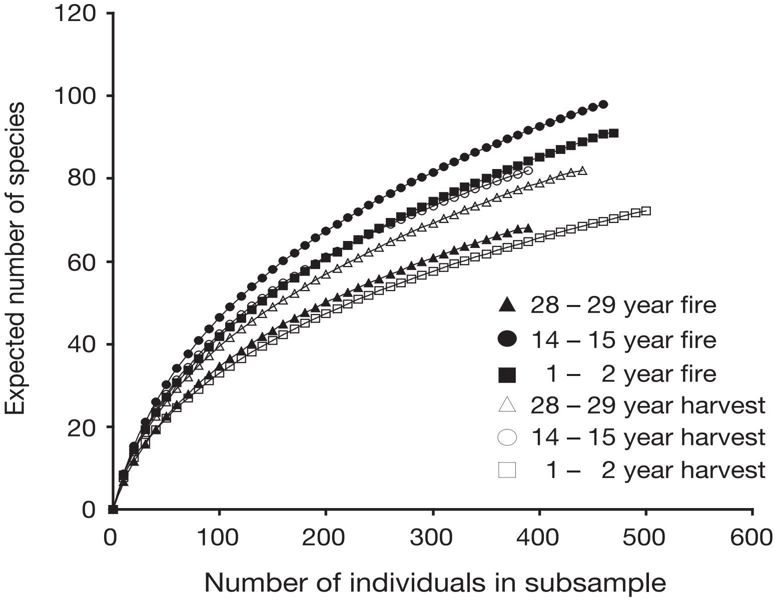


Figure 7—Rarefaction-estimated species richness of saproxylic beetles in boreal *Populus* stands of three ages and originating from fire or clearcut harvesting, Alberta.

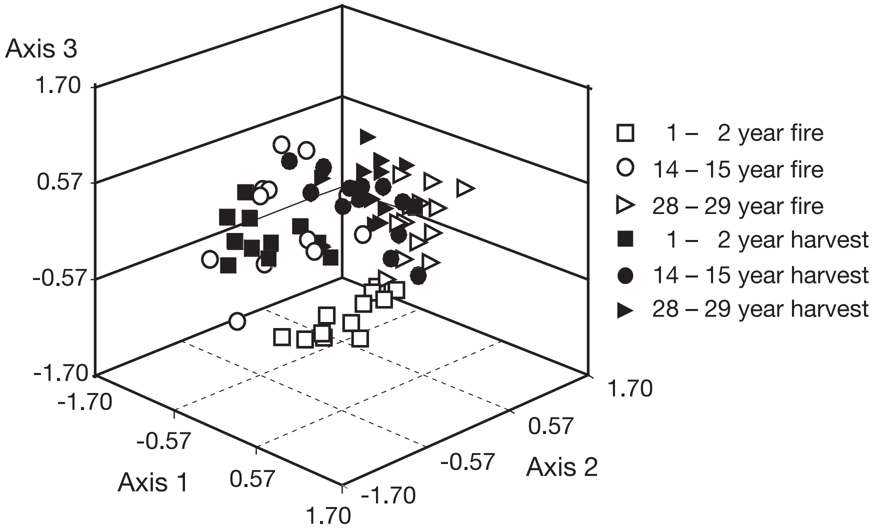


Figure 8—Nonmetric multidimensional scaling (NMS) ordination of 211 species of saproxylic beetles collected using flight-intercept traps in Alberta boreal *Populus* stands of three ages and originating from fire or clearcut harvesting. Each point represents the fauna associated with a snag (12 snags 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

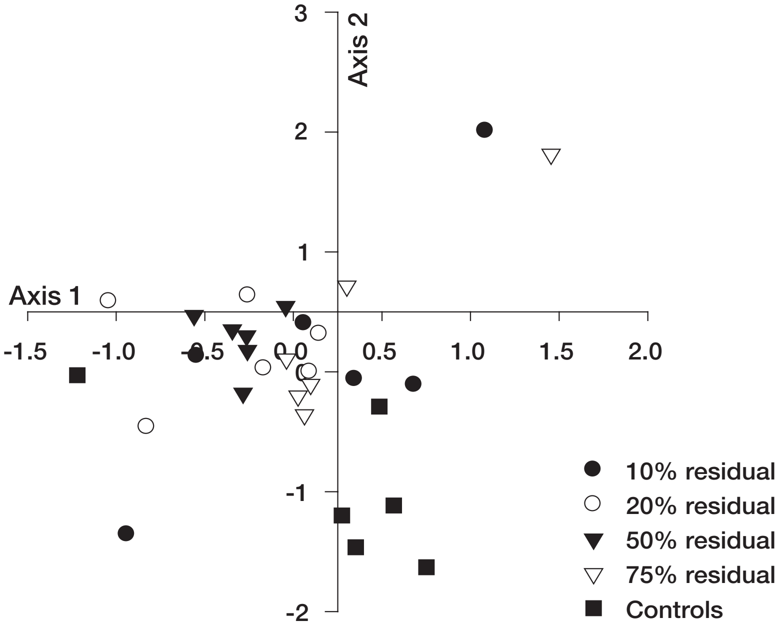


Figure 9—Nonmetric multidimensional scaling (NMS) ordination based on catch of 47 species of bark- and wood-boring beetles in controls and 4 variable retention harvesting treatments in coniferous dominated (CDOM) stands at the Ecosystem Management by Emulating Natural Disturbance experiment site, Alberta. 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 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 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.

LITERATURE CITED

Anderson, L.I.; Hytteborn, H. 1991. Bryophytes and decaying wood—a comparison between managed and natural forest. Holarctic Ecology 14: 121-130.

Angelstam, P. 1997. Landscape analysis as a tool for the scientific management of biodiversity. Ecological Bulletins 46: 140-170.

Bader, P.; Jansson, S.; Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355-362.

Biological Survey of Canada. 2004. Forest arthropod biodiversity projects in Canada. http://www.biology.ualberta.ca/bsc/english/forestprojectssummary.htm [Date accessed: September 23, 2004].

Boddy, L. 1992. Development and function of fungal communities in decomposing wood. In: In Carroll, G.C.; Wicklow, D.T., eds. The fungal community: its organization and role in the ecosystem. New York: Marcel Dekker, Inc.: 749-782.

Bousquet, Y., ed. 1991.Checklist of beetles of Canada and Alaska. Publication 1861/E. Ottawa, Ontario: Agriculture Canada. 430 p.

Bright, D.E., Jr. 1976. The insects and arachnids of Canada: the bark beetles of Canada and Alaska (Coleoptera: Scolytidae). Publication 1576. Ottawa, Ontario: Canadian Department of Agriculture (pt. 2). 241 p.

Bright, D.E., Jr. 1987. The insects and arachnids of Canada: the metallic wood-boring beetles of Canada and Alaska. Publication 1810. Ottawa, Ontario: Agriculture Canada (pt. 15). 335 p.

Buddle, C.M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. Agricultural and Forest Entomology 3: 241-251.

Buddle, C.M.; Langor, D.W.; Pohl, G.R.; Spence, J.R. [In press]. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biological Conservation. 128: 346-357.

Buddle, C.M.; Spence, J.R.; Langor, D.W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-36.

Danks, H.V. 1979. Canada and its insect fauna. Memoirs of the Entomological Society of Canada, Ottawa. 573 p.

Danks, H.V.; Foottit, R.G. 1989. Insects of the boreal zone of Canada. Canadian Entomologist 121: 625-690.

Dufrêne, M.; Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible assymetrical approach. Ecological Monographs 67: 345-366.

Ehnström, B. 2001. Leaving deadwood for insects in boreal forests—suggestions for the future. Scandinavian Journal of Forest Research Supplement 3: 91-98.

Ehnström, B.; Axelsson, R. 2002. Insekts gnag I bark och ved. ArtDatabanken SLU. 512 p.

Esseen, P.A.; Ehnström, B.; Ericson, L.; Sjöberg, K. 1992. Boreal forests—the focal habitats of Fennoscandia. In: Hansson, L., ed. Ecological principles of nature conservation. Elsevier: 252-325.

Esseen, P.A.; Ehnström, B.; Ericson, L.; Sjöberg, K. 1997. Boreal forests. Ecological Bulletin 46: 16-47.

Franklin, J.F.; Berg, D.A.; Thornburgh, D.A.; Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Washington, DC: Island Press.

Franklin, J.F.; Shugart, H.H.; Harmon, M.E. 1987. Tree death as an ecological process. Bioscience 37: 550-556.

Gandhi, K.J.K.; Spence, J.R.; Langor, D.W.; Morgantini, L.E. 2004. Harvest residuals as stand analogues of fire residuals. Canadian Journal of Forest Research 34: 1319-1331.

Gotelli, N.J.; Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Granström, A. 2001. Fire management for biodiversity in the European boreal forest. Scandinavian Journal of Forest Research Supplement 3:62-69.

Hagan, J.M.; Grove, S.L. 1999. Coarse woody debris. Journal of Forestry 97: 6-11.

Haila, Y.; Hanski, I.K.; Niemelä, J. [and others]. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Annales Zoologici Fennici 31: 187-202.

Hammond, H.E.J. 1996. Arthropod biodiversity of *Populus* spp. coarse woody material in north-central Alberta. M.Sc thesis. Edmonton, Alberta: Department of Entomology, University of Alberta. 212 p.

Hammond, H.E.J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. Canadian Entomologist 129: 1009-1033.

Hammond, H.E.J.; Langor, D.W.; Spence, J.R. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31: 1175-1183.

Hammond, H.E.J.; Langor, D.W.; Spence, J.R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34: 1-19.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody depris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Heliövaara, K.; Väisänen, R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. Acta Forestalia Fennica 189: 1-32.

Hindmarch, T.D.; Reid, M.L. 2001. Thinning of mature lodgepole pine stands increases scolytids bark beetle abundance and diversity. Canadian Journal of Forest Research 31: 1502-1512.

Huber, J.T.; Langor, D.W. 2004. Systematics: it's role in supporting sustainable forest management. Forestry Chronicle 80: 451-457.

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

Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

Jacobs, J.M. 2004. Saproxylic beetle assemblages in the boreal mixedwood of Alberta: succession, wildfire and variable retention forestry. M.Sc thesis. Edmonton, Alberta: Department of Biological Science, University of Alberta. 124 p.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 29: 21-23.

Kehler, D.; Bondrup-Nielsen, S. 1998. Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus,* at different spatial scales in fragmented and continuous forests. Oikos 84: 35-43.

Langor, D.W.; Raske, A.G. 1987. Emergence, host attack and overwintering of the eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Scolytidae), in Newfoundland. Canadian Entomologist 119: 975-983.

Langor, D.W.; Spence, J.R. 2004. Arthropods as ecological indicators of disturbance in forest ecosystems. Unasylva 54(3-4): 15.

Lawrence, J.F. 1973. Host preferences in ciid beetles (Coleoptera: Ciidae) inhabiting fruiting bodies of basidiomycetes in North America. Bulletin of the Museum of Comparative Zoology 145: 163-212.

Lee, P.C.; Crites, C.; Nietfeld, M. [and others]. 1997. Characteristics and origins of deadwood material in aspen dominated boreal forests. Ecological Applications 7: 691-701.

Martikainen, P.; Siitonen, J.; Kaila, L. [and others]. 1999. Bark beetles (Coleoptera: Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. Forest Ecology and Management 116: 233-245.

Martikainen, P.; Siitonen, J.; Punttila, P. [and others]. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94: 199-209.

McCann, K.S. 2000. The diversity-stability debate. Nature 405: 228-233.

McGill, W.B.; Spence, J.R. 1985. Soil fauna and soil structure: feedback between size and architecture. In: Ball, G.E.; Spence, J.R. eds. Faunal Influences on Soil Structure. Quaestiones Entomologicae 21: 645-654.

Naeem, S. 2002. Ecosystem consequences of biodiversity loss: the evolution of a paradigm. Ecology 83: 1537-1552.

Naeem, S.; Chapin, F.S.; Costanza, R. [and others]. 1999. Biodiversity and ecosystem functioning: maintaining natural life support processes. Issues in Ecology 4: 1-12.

Natural Resources Canada, 2003. The state of Canada's forests 2002-2003. Ottawa, Ontario: Natural Resources Canada, Canadian Forest Service. 95 p.

Nilsson, S.G.; Hedlin, T.; Niklasson, M. 2001. Biodiversity and its assessment in boreal and nemoral forests. Scandinavian Journal of Forest Research Supplement 3: 10-26.

Økland, B. 1996. Unlogged forest: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation 76: 297-310.

Oliver, I.; Beattie, A.J. 1996. Designing a cost-effective invertebrate survey. Ecological Applications 6: 594-607.

Palm, T. 1951. Die Holz- und Rinden-Käfer der nordscwedischen Laubbäume. Meddelanden från Statens Skogsforskningsinstitut 40(2): 1-242.

Palm, T. 1959. Die Holz- und Rinden-Käfer der süd- und mittelscwedischen Laubbäume. Opuscula Entomologica Supplemt 16: 1-375.

Peltonen, M.; Heliövaara, K. 1998. Incidence of *Xylechinus pilosus* and *Cryphalus saltuarius* (Scolytidae) in forest-clearcut edges. Forest Ecology and Management 103: 141-147.

Pratt, L.; Urquhart, I. 1994. The last great forest. Edmonton, Alberta: NeWest Press. 222 p.

Renvall, P. 1995. Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1-51.

Saint-Germain, M.; Drapeau, P.; Hébert, C. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of Northeastern North America. Biological Conservation 118: 583-592.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. American Naturalist 102: 243-282.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11-41.

Siitonen, J.; Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9: 185-191.

Siitonen, J.; Saaristo, L. 2000. Habitat requirements of a threatened boreal old-growth species, *Pytho kolwensis* Sahlberg (Coleoptera, Pythidae), in Finland. Biological Conservation 94: 211-220.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series 42. Strasbourg: Council of Europe. 79 p.

Spence, J.R.; Langor, D.W.; Hammond, H.E.J.; Pohl, G. 1997. Beetle abundance and diversity in a boreal mixedwood forest. In: Watt, A.D.; Stork, N.E., eds. Forests and Insects, Proceedings of the 18th Royal Entomological Society Symposium. London, U.K.: Chapman and Hall, 285-299.

Spence, J.R.; Volney, W.J.A.; Lieffers, V.J. [and others]. 1999. The Alberta EMEND project: recipe and cooks' argument. In: Veeman, T.S.; Smith, D.W.; Purdy, B.G.; Salkie, F.J.; Larkin, G.A., eds. Science and practice: sustaining the boreal forest. Edmonton, Alberta: Sustainable Forest Management Network, 583-590.

Tilman, D.; Reich, P.B.; Knops, J. [and others]. 2001. Diversity and productivity in a long-term grassland experiment. Science 294: 843-845.

Wheeler, Q.D.; Blackwell, M. 1984. Fungus-insect relationships: perspectives in ecology and evolution. New York: Columbia University Press.

Wikars, L.O. 1992. Forest fires and insects. Entomologisk Tidskrift 113: 1-11.

Work, T.T.; Spence, J.R.; Volney, W.J.A.; Burton, P.J. 2003. Sustainable forest management as license to think and to try something different. In: Burton, P.J.; Messier, C.; Smith, D.W.; Adamowicz, W.L., eds. Towards sustainable management of the boreal forest. Ottawa, Ontario: NRC Research Press: 953-970.

A RESEARCH AGENDA FOR INSECTS AND DEAD WOOD

Simon J. Grove[1]

Abstract—In recent years, great advances have been made in our knowledge of the ecology, evolutionary biology, biogeography and management of saproxylic insects and their dead wood habitat. There is now a greater level of awareness of the need to cater to their requirements in today's managed forest landscapes. However, having raised the profile of saproxylic insects, researchers are now being called upon to translate knowledge gains into management principles. This throws up new research challenges, many of which can only be addressed through adaptive management. This paper outlines and prioritises some of those challenges.

INTRODUCTION

This paper is unabashedly focused on a research agenda that may aid the conservation of saproxylic insects and their habitat. Whilst the focus is on terrestrial systems, it is recognised that aquatic systems deserve a similar level of attention; this paper makes occasional specific reference to aquatic systems but many of the broader principles will apply equally to terrestrial and aquatic systems. Research on 'pest' aspects of saproxylic insects is beyond the scope of this paper.

THE RESEARCH CONTEXT

No single research agenda would be appropriate for every single region because, around the world, there are great differences in the ecology and management of forests. These differences in turn influence the ecologies and the functional integrity of saproxylic insects (Grove 2002a). Two prominent influences act more or less orthogonally: (a) the natural disturbance regime to which the forests are historically adapted; and (b) the relative dominance of natural versus human-induced ecological processes. Further aspects for consideration are the historical and present level of ecological understanding of these forests and their saproxylic insect biodiversity; and the extent to which there is, or would be, opportunity to use this understanding to influence management.

In deciding priorities for a particular region, the following issues require consideration:

- Natural disturbance dynamics—What are the forest's natural disturbance dynamics? Have they evolved to cope with occasional wildfires, cyclones or pest outbreaks that can re-set the successional clock for entire forest stands? Or are they in a more or less steady state, where normal disturbance constitutes individual trees falling (e.g., as a result of windthrow, lightning, disease or old age) followed by successional infilling of the gaps created? More likely, are they somewhere in between these two extremes, e.g., occasional rare major disturbances, interspersed with more frequent smaller disturbances, resulting in a mosaic of age-classes? To what extent are current patterns of dead wood distribution and abundance in equilibrium with the current stand structure?
- Biogeography—To what extent can the forest be considered a single biogeographical unit? Is it naturally fragmented, or are there (or have there been) other internal obstacles to continuous occupation by some species, such as faunal breaks (Mesibov 1994), resulting in substantial natural turnover of species from one part of the forest to another? Is the origin of the entire forest so recent that one area would naturally support much the same set of species as any other?
- Management history—To what extent has human management altered the forest's ecological integrity, in terms of its ability to continue to respond to natural processes at ecologically relevant spatial and temporal scales? Ecologically, how far removed is the current forest from its natural predecessor? Is it fragmented, to the extent that its natural functioning is hindered? Is it in a state of transition from a 'natural' to an 'anthropogenic' forest? Has human intervention been so consistent, and/or been going on for so long, that the forest's ecology has been remoulded, with surviving biodiversity now dependent on human management? Or is it no longer possible to say what a pre-human forest would have looked like? To what extent has management affected the dead wood resource and its saproxylic fauna?
- Level of ecological understanding of forests and their saproxylic insects—How well can we already answer the above questions? How important is it, for management purposes, to know what species live in the forest and what they do? Is it more important to have the tools to be able to 'scale up', i.e., to address 'whole-of-landscape' management issues? In which case, do we understand enough about the natural and historical processes shaping our forests and their biodiversity to be able to make management recommendations? How desirable or realistic is it to seek to maintain—or recreate—conditions necessary for the survival of a saproxylic insect fauna typical of a truly natural (pre-human?) forest, versus one that is robust in response to further natural or human-induced change?
- The opportunity for scientific input into land management—If we don't know the answers to the above questions, how much difference would it make to our management if we were to do the research to find out? Is further research just an excuse for delaying management? Will anybody take

---

[1] Simon J. Grove, Conservation Biologist, Forestry Tasmania, GPO Box 207, Hobart, Tasmania 7001, Australia.

Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

notice of our findings? Is the purpose of continued research more to maintain or raise awareness of the issue so saproxylic insect conservation creeps higher up the political agenda? Do our institutions have the capacity to do the research, and do our management agencies have the capacity to heed its findings, given the economic constraints operating to greater or lesser degrees worldwide? Do these constraints suggest that we need to prioritise our research on the basis of maximising social or political impact rather than scientific merit?

SOME GUIDING PRINCIPLES FOR DEVELOPING A RESEARCH PROGRAMME

- Get the management agencies and public on board—The public generally views nature as the more visible components of biodiversity, such as trees, birds and mammals. However, conserving these species does not necessarily ensure the conservation of saproxylic insects. Dead wood may well support a fifth of all forest-dependent animals (Elton 1966, Grove 2002a), so its management is not a trivial conservation issue. Peer-reviewed science may not be enough to engage either the public or the agencies who manage land on the public's behalf. More populist articles, posters, leaflets, web sites, public presentations, field days for adults and children, and media appearances are likely to have greater impact, as long as the delivered message reflects our understandings as researchers so that scientific integrity is maintained. Social research may need to be considered as part of the overall research agenda alongside ecological research (Bartuska 2002).
- Use an adaptive management research framework where feasible—Much good ecological science is never implemented because it doesn't clearly suit the potential user, or is sidelined by politics and economics. Even conservation managers may prefer traditional methods over new scientific evidence (Pullin and others 2004). One of the most productive ways of progressing our understanding of saproxylic insects, while at the same time improving our chances of conserving them, is by encouraging incremental change through adaptive management (Jonsson and Kruys 2001). Using this process, one can begin to answer key management questions such as: (1) what should our goals be and how do we measure progress in reaching them?; (2) how can we most effectively take action to achieve conservation?; and (3) how can we learn to do conservation better? (Salafsky and others 2002). Active adaptive management has been defined as the systematic acquisition and application of reliable information to improve natural resource management over time (Wilhere 2002). Effectively, forestry or conservation management can be treated as a giant long-term ecological experiment. This means working with management agencies, to ensure that their management practices are documented along with the impacts they have on saproxylic insects or their habitat. Larsson and others (2005) present a case study of one such experiment. If the agencies can be persuaded to try a range of alternative management scenarios, their effectiveness can also be tested. One can also be opportunistic about the form studies take, by riding on the back of existing management plans or activities. One example would be to take advantage of tree-felling to learn about the habitat associations of saproxylic insects by sampling them directly from their habitat (Tavakilian and others 1997). By feeding back research findings to management agencies, management practices can evolve through a process akin to natural selection: the less desirable practices may be dropped while the better are propagated, because they are perceived as being both superior and more readily applicable to managers and policy makers (Grove and Stork 1999).
- Promote long-term monitoring—If management agencies are uncomfortable with researchers 'taking over' the forest, then establishment of dedicated research areas could be explored. The international network of Long Term Ecological Research (LTER) sites provides a useful model for targeting research to fill gaps in our ecological understanding (Grove 2004). Long-term monitoring is especially relevant to studies in forests because of the long time-frames in which ecological and management processes operate. Promoting long-term monitoring requires: (1) identifying innovative ways to secure long-term funding that can be guaranteed beyond typical political and institutional time-frames; and (2) education of funding bodies to ensure they recognise that useful results may take a prolonged period to obtain and that monitoring is not a second-rate science (Lindenmayer 1999).
- Promote interdisciplinary research—Saproxylic insects interact with other ecosystem components (especially fungi and dead wood), all of which are influenced by management. As Speight (1989) noted, "the relationships existing between saproxylic fungi and saproxylic invertebrates are clearly so intimate that the survival of members of one group is frequently dependent on the presence of members of the other…[however]…few accounts deal with fungi and invertebrates". Untangling these and other relationships requires researching more than just the insects, and may require researchers from a range of disciplines and with a range of skills. A cohesive package of research stands a greater chance of influencing management than does a disparate set of individual studies. This is the basis for Forestry Tasmania's coarse woody debris research package.
- Promote natural history and autecological studies—Many researchers shy away from natural history studies, yet an understanding of insect natural history is fundamental to understanding the many relationships between insects and their environment (Miller 1993), and hence the implications of our management of that environment. Autecological research has the potential to throw light on numerous aspects of a species' life relevant to conservation (Cheesman 2000). Where saproxylic insects are already scarce, it may be unethical or simply unfeasible to carry out statistically rigorous, fully replicated experiments, and strict codes of conduct may have to be applied to ensure that the species are not unduly threatened (Kirby and Drake 1993). Natural history studies can also help elucidate relationships between saproxylic insects and fungi. Even being able to define a species as saproxylic often requires knowledge of its natural history—and a lack of this knowledge can limit the analytical power of scientific studies (Grove 2002a, Yee and others 2005). Stable isotopes are increasingly being employed to ascertain the trophic level at which an organism feeds (Blüthgen and others 2003), and this is a field that could usefully be applied to putative saproxylic species.

- Promote advances in insect taxonomy—The 'taxonomic impediment' remains a constraint to our understanding of species and their ecological relationships (New 1996). There continues to be a lively debate about whether we really need to know the scientific names of all the insects that we work with, or whether parataxonomic units will suffice (Derraik and others 2002). Much depends on the use to which the resultant data are put (Krell 2004). For purely local studies (e.g., Basset and others 2004), a full scientific name may be superfluous, but for comparisons across studies or regions, they become more and more important. This presupposes that the species in question have been formally described—which in many parts of the world they have not. There is a global need for a sufficiently large pool of dedicated taxonomists to describe these species (Valdecasas and Camacho 2003). Identifying many saproxylic insect species currently requires great skill, plus access to comparative material which is not always readily available. Making taxonomic information more widely available through images and/or keys on the World Wide Web is a rapidly developing field. I have not referred to any particular web sites (because they change so frequently) but many of the relevant national and international research agencies are going down this route.
- Consider recent advances in insect surveillance—Methods for marking insects were reviewed recently (Hagler and Jackson 2001), and highlighted a number of advances that may be of interest to those studying saproxylic insects (see that paper for details). Additional techniques that deserve scrutiny include lasers to mark individual beetles (Griffiths and others 2001), and pheromone detectors to monitor otherwise inaccessible populations of rare insects (Svensson and others 2003). The time may fast be approaching when rapid chemical or genetic screening of samples for species-level information may come to our aid. With regard to these technologies, Gaston and O'Neill (2004) posit that "vision and enterprise are perhaps more limiting at present than practical constraints on what might possibly be achieved". For tracing individual insects, DNA-surveillance is also a possibility for the future, as now applied to whales (Baker and others 2003). The use of genetic markers is now an important tool in assessing insect dispersal ability (Sunnucks 2000, Watson 2003).
- Consider recent advances in software and hardware—Most present-day ecological studies are designed to be analysed with classical statistics. Yet advances in computing power increasingly allow the use of alternative approaches. These may appeal to those studying saproxylic insects, bearing in mind the frequent difficulties of fulfilling the requirements for classical analyses when studying species-rich assemblages or those where the most important species are rare or cryptic. Sometimes these new approaches are extensions to existing ones, enabling, for instance, the development of non-parametric probability estimates through randomisation procedures (e.g., Colwell and Coddington 1996, Manly 1997). Anderson (2001) and Anderson and Willis (2003) have extended their use by developing non-parametric multivariate equivalents of standard parametric univariate tests. But increasingly, techniques are available that make use of Bayesian statistics (Swinburne 2002, ter Braak and Etienne 2003), or use other non-classical statistics to explore, for example, effects of large-scale or unreplicated disturbances (Parr and Chown 2003). Another example is the development of software for determining the spatial scale of species' response to habitat fragmentation, again relying on randomisation procedures (Holland and others 2004). Modelling software is becoming more sophisticated, increasing its ease of use by mainstream ecologists (e.g., Muetzelfeldt and Massheder 2003) and/or increasing its power for complex analyses such as population viability analysis (Garrick and others 2004, Grimm and others 2004, Schtickzelle and Baguette 2004) and landscape-level prediction of habitat formation contingent on wildfire return intervals (Mackey and others 2002).

  Miniaturised electronics are finding increasing uses in field studies, too. For instance, probes attached to dataloggers could be used to record temperature or humidity at different depths within a log or tree hollow over extended periods. Self-contained 'iButtons' (Maxim/Dallas Semiconductor Corporation) can perform a similar function, and because they contain a transceiver the information can be uploaded to a computer or reader remotely. Cameras tripped by infrared light beams could be used for photographing insects visiting hollows or flowers, rather than for the mammals which are the normal subject (e.g., Silveira and others 2003). Radio transmitters can now be made small enough to attach to individual beetles (Hedin and Ranius 2002), and GPS transmitters are also being manufactured smaller.

THE RESEARCH AGENDA

If, having considered the above, it is decided that further research on saproxylic insects, or the forests they inhabit, is warranted, then some suggestions follow. I have divided the ideas into 'ecological' and 'management' categories, depending on their focus, and have then grouped these ideas into three spatial scales at which the research is perhaps most appropriately conducted.

Ecologically Oriented Research: Small Scale

1. Developing standard techniques for sampling saproxylic insects—What are the relative merits of destructive versus passive sampling? What techniques are best for each of these types of sampling? Many papers have compared or promoted different techniques (e.g., Glen 1976, Grove 2000, Grove and Bashford 2003, Hanula and New 1996, Morewood and others 2002, Økland 1996, Owen 1992, Yee and others 2001). Factors to consider include the risks associated with disturbing or oversampling scarce species or their habitat; speed; selectivity; maintenance and sorting effort required; and the range of 'extra' ecological information obtained (Cheesman 2000). Different principles may operate in different regions, but the development of some standardised protocols would aid comparability among studies.
2. Autecological research on key saproxylic species—We will never understand the ecologies of every single saproxylic insect species, but in most regions it would be useful to know more about key species. 'Key' species might be defined as those with highest conservation needs, or those with a clearly important ecological role (e.g., ecosystem engineers, Jones and others 1996). Recent Fennoscandian examples where an understanding of

autecology has provided management insights include Jonsson (2003), Midtgaard and others (1998) and Ranius (2002). See the sections on insect surveillance and natural history above for further ideas.

3. Understanding relationships between saproxylic insects and fungi—These relationships are complex (Wilding and others 1989) and poorly understood in most regions, though Fennoscandia is relatively well served by recent studies (e.g., Jonsell and others 2001). How species-specific are fungus-insect relationships? Do saproxylic fungi depend on saproxylic insects any more or less than the insects depend on the fungi, or on the specific rotting wood types that they help to create (Yee and others 2005)? To what extent can we generalise about insect-fungus relationships from one species to the next, on the basis of taxonomic relatedness?

4. Understanding relationships between saproxylic insects and decomposition—Do ecosystems really need all these saproxylic insects? How much redundancy is there in the system (Srivastava 2002), and how would the forest function without them? Would fungi and other organisms be as efficient at breaking down decaying wood (and hence nutrient cycling) in the absence of saproxylic insects? Exclusion nets were used in a recent Finnish study (Müller and others 2002), and would seem to offer great potential for further studies.

5. Investigating the value of nectar sources for saproxylic insects—Many saproxylic insects emerge as adults and can be found at nearby flowers (Kirby 1992). To what extent are these nectar sources vital for their breeding success; are some plant species more important than others; and how near do they need to be to the larval habitat? This is more than a trivial issue in some heavily managed European forests, where nectar sources can be artificially low or where the survival of every individual member of a rare saproxylic insect species matters.

6. Investigating the value of burnt wood for saproxylic insects—Burnt wood is a natural component of many forest ecosystems, and an unnatural one in others. To what extent does it have unique values for saproxylic insects? And to what extent does burning intensity affect the ability of a log or standing dead tree to support saproxylic insects? These questions, and related ones on fungi, are the subject of recent studies in Fennoscandia (Penttilä and Kotiranta 1996; Wikars 2001, 2002) but other regions have apparently received less attention (though see Saint-Germain and others 2004 for a Canadian example). They would certainly be pertinent in Australia.

7. Investigating the value of dead wood for non-saproxylic insects—Dead wood is known to be important as a structural element for many terrestrial and aquatic plants and animals, but in terms of species numbers, is dead wood more or less important for non-saproxylic insects than for saproxylic insects? There have been some recent studies on the value of logs on the forest floor for non-saproxylic invertebrates (e.g., Andrew and others 2000, Evans and others 2003, Hanula and others 2005) but comparative studies are warranted.

Ecologically Oriented Research: Medium Scale

8. Investigating the extent of overlap in saproxylic insect faunas of logs, trees and litter—Which elements of a forest ecosystem deserve greatest conservation or management attention for saproxylic insects: logs on the ground, or the living or dead trees that generate the logs? There is some suggestion that this may vary by forest type (Grove 2002b). In many situations, we do not know the extent to which logs, old living trees and standing dead trees support different saproxylic insect assemblages, nor the extent to which apparently saproxylic species can utilise fine woody debris and litter (though see Nordén and others 2004 for fungi). In most parts of the world, we know little about the saproxylic insect fauna of tree hollows (though see Ranius 2002), compared to what we know about their use (probably at different spatial scales) by birds and mammals (Gibbons and Lindenmayer 2001). Schulz and Ammer (1996) have reported on the importance of upturned root plates for insect biodiversity, while Schiegg (2001) has compared the importance for saproxylic insects of logs derived from tree limbs and tree trunks. The fauna utilising subterranean dead wood (dead roots) is generally poorly known.

9. Investigating the role of fire in shaping saproxylic insect faunas—Fire can be a positive or a negative force for saproxylic insects (Enfrestøl 2003, Hanula and Wade 2003, Madoffe and others 2000, Moretti and Barbalat 2004, Wikars 1997), depending on the natural disturbance dynamics of the forest. In most regions we do not know what would be the implications for saproxylic insects of changing those dynamics. We often do not even know which species are fire-dependent rather than simply disturbance-dependent, but experiments such as those of Wikars (2002) can help us to find out.

Ecologically Oriented Research: Large Scale

10. Investigating the extent to which ecological traits among related saproxylic insect species are conserved across the globe—Given that we will never be able to investigate the autecology or natural history of more than a tiny proportion of the world's saproxylic species, to what extent can we deduce a species' ecology from that of related species studied elsewhere? There is some evidence for conservation of ecological traits among beetles (Leschen 2005), but a few studies across regions, for a range of saproxylic taxa, might further elucidate this.

Management Oriented Research: Small Scale

11. Investigating the value of artificially killed dead wood for saproxylic insects—Do artificially killed trees, branches or stumps offer the same opportunities for saproxylic insects as naturally killed ones? In some situations they probably do, because natural tree death can be as sudden as artificial tree death, for instance following a severe windstorm (Alexander 1994, Bouget and Duelli 2004) or hurricane (Whigham and others 1991). Likewise, in forests where wildfires are a major influence, silvicultural regeneration burns might be expected to offer some of the same opportunities to saproxylic insects as wildfires—though this requires investigation. But in other situations, trees only naturally fall over once major decay has set in, and the resultant dead wood is

likely to have different properties (structural, chemical and biological) from dead wood originating from felling a healthy tree (Boddy 2001). In these cases and some others, the result may be differences in saproxylic fauna (Shea and others 2002, Yee and others 2005). In other situations, trees may be deliberately wounded to provide habitat for saproxylic insects and other wildlife (Bull and others 1981, Green 1995), or stumps may be cut artificially high to leave additional habitat (Jonsell and others 2004). Are artificial stumps and wounds functional analogues for the real things? To what extent should we expect an intact saproxylic insect fauna to survive in a forest where artificial tree falls are the norm?

12. Investigating the value of relocating relocating saproxylic insects or the dead wood on which they depend. Should we seek to help endangered saproxylic insects recolonise lost ground, as those interested in lichens may do for their organisms (Lidén and others 2004)? More realistically, managers may need to relocate dead wood, either for conservation reasons (Grove and Tucker 2000) or for safety or aesthetic reasons. What factors determine its value for saproxylic insects in its new environment? For instance, to what extent does its positioning in a sunny or shady location affect its suitability for different species (Buisson 1999, Økland 2002), or for its rate of decay (Yin 1999)? Thermophilic organisms such as ants could clearly be affected by this (Higgins and Lindgren 2005). A range of similar questions applies to dead wood introduced into aquatic systems (Lester 2003, Lisle 2002, Wallace and Benke 1984), and to the choice of location for leaving standing dead trees in clearcuts (Sverdrup-Thygeson and Ims 2002).

Management Oriented Research: Medium Scale

13. Investigating dispersal and colonisation abilities of saproxylic insects—How readily can saproxylic insects colonise new habitat, and how is their ability to colonise influenced by factors such as flightedness, wing musculature, behaviour, physical distance, fragmentation and matrix quality (Bunnell and others 2002, Paradise 1998)? Are poor dispersers at more risk from human-induced fragmentation than good dispersers, or should those with intermediate powers of dispersal be of greatest concern? Is fragmentation leading to genetic losses or changes in surviving populations (Thomas and others 1998)? We can partially answer some of these questions for a few species (e.g., Ranius and Hedin 2001, Starzomski and Bondrup-Nielsen 2002, Watson 2003), but studies in other regions would also be beneficial so that we can better target the scale at which we manage for dead wood. Genetic markers (Garrick and others 2005, Sunnucks 2000) probably offer the best hope except for a few large (and perhaps rare) species, where direct surveillance of individuals is feasible (Ranius and Hedin 2001). New software may also prove valuable in inferring dispersal abilities by reinterpreting existing spatially explicit datasets for suites of saproxylic species (Holland and others 2004).

14. Developing appropriate criteria for the identification of important sites for saproxylic insects—In regions where the saproxylic insect fauna is well known, and where its conservation management is a major priority (e.g., the UK, Fennoscandia), there is a clearly defined need to prioritise sites for conservation. This requires collation of existing baseline information, and carrying out inventories for each key site (Cheesman 2000). The question then arises as to what to do with the information, which has limited value in its raw form. Alexander (2004) recommended the adoption of an index of ecological continuity, in which different saproxylic beetle species contribute different scores to the overall site index. The index correlates well with what have long been considered the ‘best’ (and usually the best protected) sites in England. Sverdrup-Thygeson (2001) found that the use of a similar index, based on fungi, to demarcate woodland key habitats in Norway did not fully capture the best sites for saproxylic beetles, suggesting that indices may need to be based on more than one taxonomic group. Despite this, the approach deserves greater consideration in other regions as knowledge of saproxylic insects (and fungi) increases.

15. Investigating the feasibility of using structural surrogates for saproxylic insect faunas—To what extent is it fair to use the occurrence of logs or old trees to gauge the suitability of a forest for saproxylic insects, or to monitor the effects of management (Stokland 2001)? It would generally be easier to monitor structural surrogates than to monitor the insects themselves (York 1999). In relatively intact forests, this may be appropriate (Grove 2002c) but does the relationship still hold in heavily modified ones?

16. Assessing the impact of fuelwood and firewood harvesting on saproxylic insects—The long-term collection of firewood can have major impacts on habitat availability for saproxylic insects (Hall and Farrell 2001), but there have been few scientific studies of its effects (Meggs 2002). The same presumably applies to industrial fuelwood, especially where it is harvested from native forests (Grove and Meggs 2003). It is sometimes difficult to persuade the public, or foresters, that such ‘waste’ wood deserves to be left in situ rather than harvested (Trockenbrodt and others 2002, Yee and others 2001). Further studies could only help.

17. Assessing the impact of feral saproxylic insects and other non-native species on native saproxylic insects—Other than pest species, feral saproxylic insects receive little attention, despite their widespread occurrence. Non-native bark beetles and longhorned beetles affect many parts of the world and are often the subject of control programmes, but what effect do they or other feral saproxylic species have on native species? Are they ‘ecosystem engineers’ (Crooks 2002)? For example, the feral weevil *Sipalus gigas* is one of the larger xylophagous insects in the rainforests of NE Queensland. Are there ‘sleeper’ feral saproxylic species that have yet to spread far, but which could potentially do so if steps are not taken to prevent them? A related issue concerns the effects of feral vertebrates on the dead wood resources that saproxylic insects require. In the UK, feral grey squirrels kill or wound many trees; is this harming or helping saproxylic species? In Australia, feral pigs root around amongst rotting logs, fragmenting them and consuming saproxylic insects directly. Feral lyrebirds in Tasmania similarly fragment rotting logs and redistribute fine woody debris on the forest floor in their search for invertebrates (Tanner 2000).

Management Oriented Research: Large Scale

18. Developing suitable landscape-scale predictive models—Forest managers traditionally model tree growth and yield, but tend not to consider tree death (other than by felling) and decay (Peng 2000). Ecologists are increasingly developing models for standing dead trees (Wilhere 2003) and coarse woody debris (Grove and others 2002, Mellen and Ager 2002, Rademacher and Winter 2003, Ranius and Kindvall 2004, Ranius and others 2003). Bringing the two model types closer together would increase the visibility of dead wood as a legitimate component of forest management (Mellen and others, 2002), and would increase model power. We could then begin to ask 'what if?' type questions with a direct relevance for saproxylic insects. For instance, what if climate change were to cause increases in log decay rates or tree growth rates or storm frequency (Opdam and Wascher 2004)? What if a pest outbreak were to cause mass tree mortality? What if forest policy were changed so that clearfell coupe size were reduced but coupe dispersion increased? What if fuelwood harvesting claimed an additional proportion of coarse woody debris that would otherwise be left after harvest?

    Another kind of modelling, population viability analysis, also promises to be a useful approach for saproxylic insects, as outlined above, especially if it can be linked to these other landscape-level modelling processes. Current software was mostly developed with vertebrates or plants in mind. It appears ill suited to modelling saproxylic insects (Jonsson and Kruys 2001) because if each log is treated as a patch, this creates too many patches for the analysis unless the spatial extent of the analysis is limited. Fox and others (2004) circumvented this problem in their study of a Tasmanian velvet-worm by treating each forestry coupe as a patch. Further research is needed to find ways around such limitations.

19. Developing techniques for maintaining or recreating forest landscapes suitable for saproxylic insects—The concept of 'new forestry', with its philosophy of maintaining complex ecosystems rather than simply the regeneration of trees (Franklin 1989), is increasingly being applied in many parts of the world (Armstrong and others 2003, Heitzman 2003, Larsson and others 2005, Lindenmayer and Franklin 2002). To what extent is it being successful in maintaining suitable conditions for saproxylic insects? In regions where habitat restoration is being pursued, what can be done to aid the restoration of suitable habitat for saproxylic insects across the forest landscape, beyond killing or wounding trees or relocating logs (see above)? Should the focus be on expanding existing sites of conservation importance? Should we consider translocation of saproxylic species to new sites beyond their dispersal range? Can we use studies of saproxylic insects of past forest landscapes as a guide to the future (Clark 2003; Whitehouse 2004, 2005)?

A CASE STUDY: FORESTRY TASMANIA'S COARSE WOODY DEBRIS RESEARCH PACKAGE

In Australia generally, managing production forests with the maintenance of CWD in mind requires a level of understanding of CWD that in most cases does not exist. In recognition of this, Forestry Tasmania (FT), as manager of Tasmania's state forests, has developed a research package comprising a number of related projects. These are aimed at (a) improving our understanding of the CWD resource and its dynamics; and (b) improving our understanding of the successional processes and habitat needs of CWD-dependent biodiversity. From these, the aim is (c) to develop management prescriptions at a range of scales, alongside suitable indicators to monitor their effectiveness. While some of the projects are being pursued in-house, most are collaborative or are being conducted by other agencies, with FT support. Details of the research package will be presented elsewhere, but the individual components are listed below:

A. Understanding the dead wood resource and its dynamics
    1. Harmonise methodologies for recording CWD in operational inventories
    2. Refine CWD model
    3. Improve model parameter estimates (decay rate, stag fall, fire-loss, CWD volume)
    4. Evaluate model robustness through sensitivity analysis and field validation

B. Understanding successional processes and habitat needs of dead wood dependent biodiversity
    1. Adopt curation standards for Tasmanian Forest Insect Collection
    2. Investigate role of fungal communities in CWD production in ageing trees
    3. Investigate effects of tree ageing on the development of structural complexity
    4. Determine the contribution of living trees of different ages as habitat for CWD-dependent invertebrates
    5. Evaluate relationship between log diameter and CWD-dependent biodiversity
    6. Determine overlap in CWD-dependent biodiversity between logs and trees of differing ages
    7. Investigate dispersal ability in a range of CWD-dependent species using genetic markers
    8. Investigate autecology of a range of CWD-dependent species of differing dispersal abilities
    9. Compare elements of CWD biodiversity in silvicultural and wildfire regrowth
    10. Evaluate the extent of fire dependence amongst CWD-dependent biodiversity

C. Developing prescriptions and suitable indicators to monitor their effectiveness
    1. Develop interim prescriptions and mitigation measures
    2. Develop a range of feasible landscape-level management scenarios
    3. Conduct population viability analyses for key CWD-dependent species
    4. Establish benchmark plots within the Warra LTER site to monitor CWD-dynamics over time

5. Develop a set of structural and biodiversity indicators (from outputs of A and B)
6. Simulate CWD dynamics and populations of key CWD-dependent species at the landscape level under different management scenarios to find optimal solutions
7. Refine interim prescriptions and mitigation measures based on landscape models
8. Validate indicators through field studies, refine and incorporate into FT management and planning systems

There is an infinite number of possible research questions that we could have sought to address in this package. We cannot afford to research something just because it is interesting, although having an interest in the research clearly helps levels of motivation. Our rationale has been to prioritise on the basis of (a) feasibility and (b) likely cumulative impact. For this reason, we have restricted our studies to one tree species, *Eucalyptus obliqua*, since this is ecologically and commercially the dominant species in the lowland wet eucalypt forests where forestry activities are particularly controversial. We have focused our research, where possible, at the Warra LTER site in southern Tasmania, because this enables individual projects to feed off one another and secures a level of funding that would not have been forthcoming had the projects been scattered around the State. *E.obliqua* forests are subject to periodic wildfires, and the main silvicultural intervention is clearfelling, followed by a hot burn and aerial reseeding with locally native eucalypt seed. They naturally have some of the highest volumes of CWD in the world, and levels can exceed 1000 m^3/ha after clearfelling, so CWD management is already a reality. We are bringing a different perspective to its management, from one that views CWD (or 'slash') as something to be reduced to acceptable levels through burning, or profitably harvested for fuelwood, to one that promotes CWD as habitat in need of sustaining across the forest landscape. Many members of the public see the current model of slash management as a sign of wasteful harvesting, but our stance is that it is ecologically more wasteful to remove it than is to leave it in the forest. But we are not out to shut forestry down. We are looking for solutions for the industry, rather than creating problems. We aim to 'have our cake and eat it'—to continue to manage these forests for timber and other products while sustaining adequate levels of CWD alongside other natural values

The reality is that research has different values for different sectors of society. For some senior agency officials and for government, we emphasise that the cost of this research is a small part of the price we pay for the social licence to continue doing business. Our research helps us to demonstrate that we manage the public forests sustainably and adaptively, through continuous improvement. Research projects are titled with this in mind. Many people are sceptical about forestry's intentions and integrity in Tasmania and would not normally credit Forestry Tasmania with this level of innovation. So we continue to promote our research widely, using language that can be understood by non-scientists. Accordingly we have presented the research package at public meetings and in the media, as well as through more academic channels such as our web site and university seminars.

There is also a sense that, when it comes to dead wood, simply doing the science is as important as finding new things out. By researching, and doing so openly, we are saying to the world, 'this stuff's important; we're prepared to spend our time, taxpayers' money and intellectual effort on it. We're lucky to have it. Value it!'

SUMMARY

No one research agenda will suit every region. Much depends on how the local forests work; how spatially diverse and expansive they are; what form human management of the forests has taken and for how long; how much is already know about the forests and their saproxylic insects; and what opportunities exist for research to inform management.

There is so much that we could research that I offered in this paper some guiding principles for selecting suitable projects. Getting the public, or at least the management agencies, on board is almost a prerequisite. Adaptive management is seen as a promising way forward for conducting research in 'real-life' situations. Research is likely to yield greater impact if it is interdisciplinary. Long-term monitoring is valuable because of the time-frames over which forests and forestry work. Insect taxonomy and natural history studies are often undervalued but provide a strong foundation for other research. Technological advances, for example in insect surveillance, computer software and electronic hardware, continue to extend the boundaries of what research is feasible.

Research can be broadly divided between 'ecologically' and 'management' oriented research, and considered at three spatial scales. Ecologically-oriented research may include: developing standard techniques for sampling saproxylic insects; autecological research on key saproxylic species; investigating relationships between saproxylic insects and fungi and between saproxylic insects and decomposition; elucidating the value of nectar sources and burnt wood for saproxylic insects; elucidating the value of dead wood for non-saproxylic insects; investigating the extent of overlap in saproxylic insect faunas of logs, trees and litter; investigating the role of fire in shaping saproxylic insect faunas; and investigating the extent to which ecological traits among related saproxylic insect species are conserved across the globe. More management-oriented research may include: investigating the value of artificially killed dead wood for saproxylic insects; investigating the value of relocating dead wood for saproxylic insects; investigating dispersal and colonisation abilities of saproxylic insects; developing appropriate criteria for the identification of important sites for saproxylic insects; investigating the feasibility of using structural surrogates for saproxylic insect faunas; assessing the impact of fuelwood and firewood harvesting on saproxylic insects; assessing the impact of feral saproxylic insects and other non-native species on native saproxylic insects; developing suitable landscape-scale predictive models; and developing techniques for maintaining or recreating forest landscapes suitable for saproxylic insects.

ACKNOWLEDGMENTS

The ideas presented here are based on numerous discussions with colleagues besides the published sources listed below.

Particular thanks are extended to Roger Key, Jeff Stone, Rob Higgins, Bill Laudenslayer, Marie Yee, Wendy Wright, Rebecca Lester, Staffan Lindgren and Jim Hanula for their constructive and timely inputs. The paper also incorporates some of the ideas presented in the reviews of Bartuska (2002), Cheesman (2000), Grove and Stork (1999), Jonsson and Kruys (2001), Lindenmayer (1999), and Wu and Hobbs (2002), and the conference proceedings compiled by Laudenslayer and others (2002).

LITERATURE CITED

Alexander, K.N.A. 1994. The use of freshly downed timber by insects following the 1987 storm. In: Kirby, K.J. and Buckley, G.P. (Ed.), Ecological responses to the 1987 great storm in the woods of South-East England. Peterborough, UK: English Nature, Science Report 23: 134-150.

Alexander, K.N.A. 2004. Revision of the index of ecological continuity as used for saproxylic beetles, Peterborough, UK: English Nature. Report 574.

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

Anderson, M.J.; Willis, T.J. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology. 84: 511-525.

Andrew, N.; Rodgerson, L.; York, A. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf litter in the conservation of ant biodiversity. Austral Ecology. 25: 99-107.

Armstrong, G.W.; Adamowicz, W.L.; Beck, J.A., Jr. [and others]. 2003. Coarse filter ecosystem management in a nonequilibrating forest. Forest Science. 49: 209-223.

Baker, C.S.; Dalebout, M.L.; Lavery, S.; Ross, H.A. 2003. WWW. DNA-surveillance: applied molecular taxonomy for species conservation and discovery. Trends in Ecology and Evolution. 18: 271-272.

Bartuska, A.M. 2002. Dead wood management issues and opportunities: future directions. In: Laudenslayer, W.F.Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 947-949.

Basset, Y.; Novotný, V.; Miller, S.E. [and others]. 2004. Conservation and biological monitoring of tropical forests: the role of parataxonomists. Journal of Applied Ecology. 41: 163-174.

Blüthgen, N.; Gebauer, G.; Fiedler, K. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia. 137: 426-435.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins. 49: 43-56.

Bouget, C.; Duelli, P. 2004. The effects of windthrow on forest insect communities: a literature review. Biological Conservation. 118: 281-299.

Buisson, R. 1999. Should deadwood be left in sun or shade? British Wildlife. 10: 342.

Bull, E.L.; Partridge, A.D.; Williams, W.G. 1981. Creating snags with explosives. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station.

Bunnell, F.L.; Wind, E.; Boyland, M. 2002. How should we spatially distribute dying and dead wood? In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 739-752.

Cheesman, O.D. 2000. Conservation of saproxylic invertebrates in the UK: a coordinated approach to BAP activities, and the wider research agenda. Wallingford, UK: CABI Bioscience.

Clark, S.H.E. 2003. Insect faunas associated with the fossil remains of *Pinus sylvestris* L. in blanket peat from northeast Scotland. Scottish Geographical Journal. 119: 39-52.

Colwell, R.K.; Coddington, J.A. 1996. Estimating terrestrial biodiversity through extrapolation. In: Hawksworth, D.L. (Ed.), Biodiversity: Measurement and Evaluation. London, UK: Chapman and Hall: 101-118.

Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos. 97: 153-166.

Derraik, J.G.B.; Closs, G.P.; Dickinson, K.J.M. [and others]. 2002. Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. Conservation Biology. 16: 1015-1023.

Elton, C. 1966. Dying and dead wood. In: Elton, C. (Ed.), The pattern of animal communities. London, UK: Methuen: 279-305.

Enfrestøl , A. 2003. Distribution of woody debris and saproxylic insects in burnt and unburnt lowland dipterocarp rainforest, East Kalimantan. Masters thesis, Oslo, Norway: Agricultural University of Norway.

Evans, A.M.; Clinton, P.W.; Allen, R.B.; Frampton, C.M. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. Forest Ecology and Management. 184: 251-262.

Fox, J.C.; Mesibov, R.; McCarthy, M.A.; Burgman, M.A. 2004. Giant velvet worm (*Tasmanipatus barretti*) in Tasmania, Australia: effects of planned conversion of native forests to plantations. In: Akcakaya, H.R.; Burgman, M.A.; Kindvall, O.; Wood, C.C.; Sjogren-Gulve, P.; Hatfield, J.S.; McCarthy, M.A., eds. Species conservation and management: case studies. New York: Oxford University Press: 150-161.

Franklin, J. 1989. Toward a new forestry. American Forests. 95: 37-44.

Garrick, R.; Sands, C.; Blacket, M. [and others]. 2006. Comparative phylogeography of saproxylic invertebrates. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22^{d} International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Garrick, R.C.; Sands, C.J.; Rowell, D.M. [and others]. 2004. Phylogeography recapitulates topography: very fine-scale local endemism of a saproxylic ‘giant’ springtail at Tallaganda in the Great Dividing Range of south-east Australia. Molecular Ecology 13: 3315-3330.

Gaston, K.J.; O’Neill, M.A. 2004. Automated species identification: why not? Philosophical Transactions of the Royal Society of London, Series B. 359: 655-667.

Gibbons, P.; Lindenmayer, D. 2001. Tree hollows and wildlife conservation in Australia. Canberra, Australia: CSIRO Publishing.

Glen, D.M. 1976. An emergence trap for bark-dwelling insects, its efficiency and effects on temperature. Ecological Entomology. 1: 91-94.

Green, E.E. 1995. Creating decaying trees. British Wildlife. 6: 310-311.

Griffiths, G.; Winder, L.; Bean, D. [and others]. 2001. Laser marking the carabid *Pterostichus melanarius* for mark-release-recapture. Ecological Entomology. 26: 662-663.

Grimm, V.; Lorek, H.; Finke, J. [and others]. 2004. META-X: generic software for metapopulation viability analysis. Biodiversity and Conservation. 13: 165-188.

Grove, S.J. 2000. Trunk window trapping: an effective technique for sampling tropical saproxylic insects. Memoirs of the Queensland Museum. 46: 149-160.

Grove, S.J. 2002a. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation. 104: 149-171.

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

Grove, S.J. 2002c. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecological Indicators. 1: 171-188.

Grove, S.J. 2004. Ecological research coverage at the Warra LTER site, Tasmania: a gap analysis based on a conceptual ecological model. Tasforests. 15: 43-54.

Grove, S.J.; Bashford, R. 2003. Beetle assemblages from the Warra log decay project: insights from the first year of sampling. Tasforests. 14: 117-129.

Grove, S.J.; Meggs, J. 2003. Coarse woody debris biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. Australian Forestry. 66: 258-272.

Grove, S.J.; Meggs, J.; Goodwin, A. 2002. A review of biodiversity conservation issues relating to coarse woody debris management in the wet eucalypt production forests of Tasmania. Hobart, Australia: Forestry Tasmania.

Grove, S.J.; Stork, N.E. 1999. The conservation of saproxylic insects in tropical forests: a research agenda. Journal of Insect Conservation. 3: 67-74.

Grove, S.J.; Tucker, N. 2000. The importance of mature timber habitat in forest management and restoration: what can insects tell us? Ecological Management and Restoration. 1: 68-69.

Hagler, J.R.; Jackson, C.G. 2001. Methods for marking insects: current techniques and future prospects. Annual Review of Entomology. 46: 511-543.

Hall, T.E.; Farrell, T.A. 2001. Fuelwood depletion at wilderness campsites: extent and potential ecological significance. Environmental Conservation. 28: 241-247.

Hanula, J.L.; Horn, S.; Wade, D.D. 2006. The role of dead wood in maintaining arthropod diversity on the forest floor. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22[d] International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Hanula, J.L.; New, K.C.P. 1996. A trap for capturing arthropods crawling up tree boles, Research Note SRS-3. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station.

Hanula, J.L.; Wade, D.D. 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. Forest Ecology and Management. 175: 163-184.

Hedin, J.; Ranius, T. 2002. Using radio telemetry to study dispersal of the beetle *Osmoderma eremita*, an inhabitant of tree hollows. Computers and Electronics in Agriculture. 35: 171-180.

Heitzman, E. 2003. “New forestry” in Scotland. Journal of Forestry. 101: 36-39.

Higgins, R.J.; Lindgren, B.S. 2006. The fine-scale attributes of coarse woody debris associated with utilization by ants. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22[d] International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Holland, J.D.; Bert, D.G.; Fahrig, L. 2004. Determining the spatial scale of species’ response to habitat. Bioscience 54: 227-233.

Jones, C.G.; Lawton, J.H.; Shachak, M. 1996. Organisms as ecosystem engineers. pp.130-147 *In*: Samson, F. B.; Knopf, F. L., eds. *Readings in Ecosystem Management.* Springer-Verlag, New York. (Reprinted from Jones, C. G.; Lawton, J. H.; Shachak, M. 1994. Organisms as Ecosystem Engineers. Oikos 69: 373-386).

Jonsell, M.; Nitterus, K.; Stighall, K. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation. 118: 163-173.

Jonsell, M.; Nordlander, G.; Ehnström, B. 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. Ecological Bulletins. 49: 173-194.

Jonsson, B.G.; Kruys, N. 2001. Ecology of coarse woody debris in boreal forests: future research directions. Ecological Bulletins. 49: 279-281.

Jonsson, M. 2003. Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. Ecological Entomology. 28: 159-167.

Kirby, K.J.; Drake, C.M. 1993. Annex 1 in dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. Peterborough, UK: English Nature.

Kirby, P. 1992. Habitat management for invertebrates: a practical handbook. Sandy, UK: Royal Society for the Protection of Birds.

Krell, F.-T. 2004. Parataxonomy vs. taxonomy in biodiversity studies—pitfalls and applicability of ‘morphospecies’ sorting. Biodiversity and Conservation. 13: 795-812.

Larsson, S.; Ekbom, B.; Schroeder, L.M.; McGeoch, M.A. 2006. Saproxylic beetles in a boreal forest landscape managed for coarse woody debris. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22[d] International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Laudenslayer, W.F., Jr.; Shea, P.J.; Valentine, B. [and others], eds. 2002. The ecology and management of dead wood in western forests. Proceedings of a Symposium, Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station.

Leschen, R. 2006. Wood, elytra, and antiquity: geologic and phylogenetic history of dead wood coleoptera. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22[d] International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Lester, R. 2003. Wood to water: the effectiveness of re-introduction of woody debris as a biodiversity enhancement tool in streams in agricultural environments. Monash, Australia: Monash University.

Lidén, M.; Pettersson, M.; Bergsten, U.; Lundmark, T. 2004. Artificial dispersal of endangered epiphytic lichens: a tool for conservation in boreal forest landscapes. Biological Conservation. 118: 431-442.

Lindenmayer, D.B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. Forest Ecology and Management. 115: 277-287.

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

Lisle, T.E. 2002. How much dead wood in stream channels is enough? In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E. eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 85-94.

Mackey, B.; Lindenmayer, D.; Gill, M. [and others]. 2002. Wildlife, fire and future climate: a forest ecosystem analysis. Collingwood, Australia: CSIRO Publishing.

Madoffe, S.S.; Bakke, A.; Tarimo, J.A. 2000. The effect of fire on the diversity and abundance of wood-living beetles in a miombo woodland, Tanzania. Southern African Forestry Journal. 187: 51-57.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte-Carlo methods in biology, 2nd Edition. London, UK: Chapman and Hall.

Meggs, J.M. 2002. Potential impacts of firewood harvesting on invertebrate biodiversity. In: Miller, J. (Ed.), Firewood Conferences 2000-2002. Hobart, Australia: Tasmanian Conservation Trust: 178-181.

Mellen, K.; Ager, A. 2002. A coarse woody debris dynamics model for the western Cascades. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds. Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 503-516.

Mellen, K.; Marcot, B.G.; Ohmann, J.L. [and others]. 2002. DecAID: a decaying wood advisory model for Oregon. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E. [eds.], Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 527-534.

Mesibov, R. 1994. Faunal breaks in Tasmania and their significance for invertebrate conservation. Memoirs of the Queensland Museum. 36: 133-136.

Midtgaard, F.; Rukke, B.A.; Sverdrup-Thygeson, A. 1998. Habitat use of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae): effect of basidiocarp size, humidity and competitors. European Journal of Entomology. 95: 559-570.

Miller, J.C. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. Biodiversity and Conservation. 2: 233-241.

Moretti, M.; Barbalat, S. 2004. The effects of wildfires on wood-eating beetles in deciduous forests on the southern slope of the Swiss Alps. Forest Ecology and Management. 187: 85-103.

Morewood, W.D.; Hein, K.E.; Katinic, P.J.; Borden, J.H. 2002. An improved trap for large wood-boring insects, with special reference to *Monochamus scutellatus* (Coleoptera: Cerambycidae). Canadian Journal of Forest Research. 32: 519-525.

Muetzelfeldt, R.; Massheder, J. 2003. The Simile visual modelling environment. European Journal of Agronomy. 18: 345-358.

Müller, M.M.; Varama, M.; Heinonen, J.; Hallaksela, A.-M. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. Forest Ecology and Management. 166: 165-181.

New, T.R. 1996. Taxonomic focus and quality control in insect surveys for biodiversity conservation. Australian Journal of Entomology. 35: 97-106.

Nordén, B.; Ryberg, M.; Gotmark, F.; Olausson, B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation. 117: 1-10.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology. 93: 195-209.

Økland, B. 2002. Canopy cover favours sporocarp-visiting beetles in spruce forests. Norwegian Journal of Entomology. 49: 29-39.

Opdam, P.; Wascher, D. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation. 117: 285-297.

Owen, J.A. 1992. Experience with an emergence trap for insects breeding in dead wood. British Journal of Entomology and Natural History. 5: 17-20.

Paradise, C.J. 1998. Colonization and development of insects in simulated treehole habitats with distinct resource and pH regimes. Ecoscience. 5: 39-45.

Parr, C.L.; Chown, S.L. 2003. Burning issues for conservation: a critique of faunal fire research in southern Africa. Austral Ecology. 28: 384-395.

Peng, C. 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management. 132: 259-.

Penttilä, R.; Kotiranta, H. 1996. Short-term effects of prescribed burning on wood-rotting fungi. Silva Fennica. 30: 399-419.

Pullin, A.S.; Knight, T.M.; Stone, D.A; Charman, K. 2004. Do conservation managers use scientific evidence to support their decision-making? Biological Conservation. 119: 245-252.

Rademacher, C.; Winter, S. 2003. Coarse woody debris in natural beech forests: generic predictions of the simulation model BEFORE-CWD of quantity, spatial distribution and availability. Forstwissenschaftliches Centralblatt. 122: 337-357.

Ranius, T. 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodiversity and Conservation. 11: 931-941.

Ranius, T.; Hedin, J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia. 126: 363-370.

Ranius, T.; Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation. 119: 51-59.

Ranius, T.; Kindvall, O.; Kruys, N.; Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. Forest Ecology and Management. 182: 13-29.

Saint-Germain, M.; Drapeau, P. Hebert, C. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of Northeastern North America. Biological Conservation. 118: 583-592.

Salafsky, N.; Margoluis, R.; Redford, K.H.; Robinson, J.G. 2002. Improving the practice of conservation: a conceptual framework and research agenda for conservation science. Conservation Biology. 16: 1469-1479.

Schiegg, K. 2001. Saproxylic insect diversity of beech: limbs are richer than trunks. Forest Ecology and Management. 149: 295-304.

Schtickzelle, N.; Baguette, M. 2004. Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. Oikos. 104: 277-290.

Schulz, U.; Ammer, U. 1996. Opened root plates and their contribution to the insect biodiversity of forests. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie. 11: 677-681.

Shea, P.J.; Laudenslayer, W.F., Jr.; Ferrell, G.; Borys, R. 2002. Girdled versus bark beetle-created ponderosa pine snags: utilization by cavity-dependent species and differences in decay rate and insect diversity. In: Laudenslayer, W.F. Jr.; Shea, P.J.; Valentine, B.; Weatherspoon, C.P.; Lisle, T.E., eds., Ecology and management of dead wood in western forests: proceedings of a symposium. Reno, Nevada, November 1999. Gen. Tech. Rep. PSW-181, Albany, CA: U.S. Department of Agriculture Forest Service, Pacific NW Research Station: 145-154.

Silveira, L.; Jacomoa, A.T.A.; Diniz-Filho, J.A.F. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biological Conservation. 114: 351-355.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Strasbourg, France: Council of Europe.

Srivastava, D.S. 2002. The role of conservation in expanding biodiversity research. Oikos. 98: 351-360.

Starzomski, B.M.; Bondrup-Nielsen, S. 2002. Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae). Ecoscience. 9: 20-27.

Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins. 49: 71-84.

Sunnucks, P. 2000. Efficient genetic markers for population biology. Trends in Ecology and Evolution. 15: 199-203.

Svensson, G.P.; Larsson, M.C.; Hedin, J. 2003. Air sampling of its pheromone to monitor the occurrence of *Osmoderma eremita*, a threatened beetle inhabiting hollow trees. Journal of Insect Conservation. 7: 189-198.

Sverdrup-Thygeson, A. 2001. Can 'continuity indicator species' predict species richness or red-listed species of saproxylic beetles? Biodiversity and Conservation. 10: 815-832.

Sverdrup-Thygeson, A.; Ims, R.A. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation. 108: 347-357.

Swinburne, R. 2002. Bayes's theorem. Oxford, UK: Oxford University Press.

Tanner, Z. 2000. Ecological impacts of the superb lyrebird in Tasmania. Honours thesis. Hobart, Australia: University of Tasmania.

Tavakilian, G.; Berkov, A.; Meurer-Grimes, B.; Mori, S. 1997. Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guyana. The Botanical Review. 63: 303-355.

ter Braak, C.J.F.; Etienne, R.S. 2003. Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. Ecology. 84: 231-241.

Thomas, C.; Hill, J.; Lewis, O. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology. 67: 485-497.

Trockenbrodt, M.; Imiyabir, Z.; Josue, J. 2002. Hollow logs and logging residues from Deramakot Forest Reserve, Sabah, Malaysia. Forest Ecology and Management. 165: 141-150.

Valdecasas, A.G.; Camacho, A.I. 2003. Conservation to the rescue of taxonomy. Biodiversity and Conservation. 12: 1113-1117.

Wallace, J.; Benke, A. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. Canadian Journal of Fisheries and Aquatic Sciences. 41: 1643-1652.

Watson, S. 2003. Dispersal and gene flow in *Prostomis atkinsoni* (Coleoptera). Honours thesis. Melbourne, Australia: LaTrobe University.

Whigham, D.F.; Olmsted, I.; Cabera Cano, E.; Harmon, M.E. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatán Peninsula. Biotropica. 23: 434-441.

Whitehouse, N.J. 2004. Mire ontogeny, environmental and climatic change inferred from fossil beetle successions from Hatfield Moors, eastern England. Holocene. 14: 79-93.

Whitehouse, N.J. 2006. What can forest managers learn from research on subfossil insects? In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the 22^{d} International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Wikars, L.-O. 1997. Pyrophilous insects in Orsa Finnmark, Central Sweden: biology, distribution, and conservation (Brandinsekter i Orsa Finnmark: biologi, utbredning och artbevarande). [In Swedish, with English summary]. Entomologisk Tidskrift. 118: 155-169.

Wikars, L.-O. 2001. The wood-decaying fungus *Daldinia loculata* (Xylariaceae) as an indicator of fire-dependent insects. Ecological Bulletins. 49: 263-268.

Wikars, L.-O. 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation. 6: 1-12.

Wilding, N.; Collins, N.M.; Hammond, P.M.; Webber, J.F. 1989. Insect-fungus interactions. London, UK: Academic Press.

Wilhere, G.F. 2002. Adaptive management in habitat conservation plans. Conservation Biology. 16: 20-29.

Wilhere, G.F. 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. Forest Ecology and Management. 174: 521-539.

Wu, J.G.; Hobbs, R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecology. 17: 355-365.

Yee, M.; Grove, S.J.; Richardson, A.; Mohammed, C. 2006. Brown rot in inner heartwood: why large logs support characteristic saproxylic beetle assemblages of conservation concern. In: Grove, S.J.; Hanula, J.L., eds. Insect biodiversity and dead wood: proceedings of a symposium for the International Congress of Entomology. Gen. Tech. Report SRS-XX. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 15-22.

Yee, M.; Yuan, Z.-Q.; Mohammed, C. 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. Tasforests. 13: 119-128.

Yin, X.W. 1999. The decay of forest woody debris: numerical modeling and implications based on some 300 data cases from North America. Oecologia. 121: 81-98.

York, A. 1999. Ecologically sustainable management: the utility of habitat surrogates for assessing terrestrial invertebrate diversity in temperate forests. In: Ponder, W.; Lunney, D., eds. The other 99%: the conservation and biodiversity of invertebrates. Mossman, Australia: Royal Zoological Society of New South Wales: 34-39.

Index of Authors

Cover photo: Staphylinids in Tasmanian Forest Insect Collection

DISCLAIMER

PESTICIDE PRECAUTIONARY STATEMENT

Papers published in these proceedings were submitted by authors in electronic media. Some editing was done to ensure a consistent format. Authors are responsible for content and accuracy of their individual papers and the quality of illustrative materials.

August 2006

Southern Research Station
P.O. Box 2680
Asheville, NC 28802

The Forest Service, United States Department of Agriculture (USDA), is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives—as directed by Congress—to provide increasingly greater service to a growing Nation.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD).

To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.