SAPROXYLIC INSECT ECOLOGY AND THE SUSTAINABLE MANAGEMENT OF FORESTS

Simon J. Grove

Division of Forest Research and Development, Forestry Tasmania, GPO Box 207, Hobart, Tasmania 7001, Australia; email: simon.grove@forestrytas.com.au

Key Words dead wood, insect conservation, logging, beetles, forestry

■ **Abstract** Saproxylic insects comprise a diverse, species-rich and dominant functional group that share a dependence on dead wood and the old trees that generate it (mature timber habitat). Recent research has highlighted their sensitivity to forest management, with managed or secondary forests generally supporting fewer individuals, fewer species, and different assemblages compared to old-growth or primary forests. This sensitivity is a product of their association with a habitat that tends to diminish in managed forests. Many species also have low powers of dispersal relative to human-induced fragmentation, making breaks in habitat continuity particularly harmful. In western Europe, many species are now regionally extinct. Information is largely lacking elsewhere, but similar ecological and management principles should apply. Measures taken to protect the habitat of hollow-dependent vertebrates may ensure the survival of some saproxylic insects, but unless their needs are expressly considered, there remains the risk that many others may be lost as forest areas shrink and management of remaining areas intensifies.

INTRODUCTION

Scope of Review

In this paper I review the literature on saproxylic insect ecology and conservation with particular reference to their relationships with forest management. I dwell particularly on the western European experience and also consider my own research findings from the tropical rainforests of northeastern Queensland, Australia. In so doing I highlight some of the common ecological traits shared by many saproxylic insects (especially the beetles, the subject of my own research) and relate these to the forest management practices that have so often led to their demise. Assuming that saproxylic insects are likely to respond similarly to these practices wherever they occur, I offer some thoughts on the extent to which they have a secure long-term future in managed forests worldwide, together with some suggestions for how their needs could better be addressed.

What are Saproxylic Insects and Why do They Have Their Own Word?

Saproxylic insects are defined as those that are "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight 1989). The saproxylic habit includes representatives from all major insect orders (especially beetles and flies), and accounts for a large proportion of the insect fauna in any natural forest (Table 1). For example, 56% of all forest beetle species in a region of Germany were considered saproxylic (Köhler 2000). Beetles alone may represent almost 40% of all arthropod species (Grove & Stork 2000), and there are at least twice as many species of saproxylic beetles as there are terrestrial vertebrates (Parker 1982)—probably many more. Saproxylic insects, then, are a species-rich and functionally important component of forest ecosystems. Other invertebrate groups, fungi, and other microorganisms could equally be described as saproxylic.

The word saproxylic was coined in France (Dajoz 1966) and has been widely adopted in Europe since the publications of Harding & Rose (1986) and Speight (1989). Publications from Canada (Hammond 1997) and Australia (Michaels & Bornemissza 1999, Grove & Stork 1999, Yee et al. 2001, Grove 2002a) have recently followed suit. Frequently used equivalent terms include deadwood (Elton 1966) and wood-living (SG Nilsson 1997). Saproxylic is a particularly useful word, because included in the definition (besides wood-feeders) are bark-feeders, feeders on wood-decomposing fungi, associated predators, parasitoids, detritivores feeding on their waste products, and other commensals. Hence, it refers to an entire functional group that has obligate associations with an array of dead-wood habitats. Mature timber habitat (Grove 2001a) is perhaps the only term in frequent use that can be used to sum up all the key habitat features on which saproxylic insects depend. Examples include standing and fallen dead wood of various diameters and in various states and stages of decay, wood-rotting and other dependent fungi (hyphae and sporocarps), fissures and crevices in bark, water- or humus-filled rot-holes and other tree cavities, sap-runs, and the tunnels and frass of wood-borers. In fire-adapted forests, charred wood is another example (Wikars 2001), as is waterlogged wood for aquatic saproxylic insects (Braccia & Batzer 2001).

"Deadwoodology": The Basics

In the context of forest management, specific concern for saproxylic insects is acute in Europe but remains at a much lower level elsewhere. Because the study of mature timber habitat and saproxylic insects may therefore be unfamiliar to many readers, I offer the following six guiding principles:

THE RICHNESS OF LIFE IN THE "ARBOREAL MEGALOPOLIS"   Larger-diameter, over-mature, senescent, moribund, decadent, or veteran trees (Read 1991) form the centerpiece of the mature timber habitat concept. They may be commercially overmature but are in their ecological prime of life and have been likened to an

TABLE 1 Examples demonstrating the richness of the saproxylic insect fauna

Country	Reference	Observations
Australia	Hammond et al. (1996)	21% of all beetle species in canopy samples from SE Queensland were xylophagous
Australia	Yee et al. (2001)	104 beetle species hand-collected from *Eucalyptus* logs in a single forest region in Tasmania
Australia	Grove (2002a)	339 saproxylic beetle species recorded from flight intercept traps in rainforest in NE Queensland
French Guyana	Tavakilian et al. (1997)	500 species of cerambycid beetle were reared from dead wood from leguminous forest trees
Indonesia	Hammond (1990)	20% of the 3488 beetle species collected in north Sulawesi were xylophagous or xylomycophagous
United Kingdom	Elton (1966)	456 species of invertebrates were recorded from dead wood habitats in a single woodland
Finland	Hanski & Hammond (1995)	287 species of saproxylic beetles were recorded in a single forest
Finland	Siitonen (2001)	20–25% of all forest-dwelling species (not just insects) were saproxylic, including about 800 beetle species
Finland	Martikainen et al. (2000)	42% of 553 beetle species sampled in old spruce forest were saproxylic
Finland	Martikainen (2001)	42% of 780 beetle species collected from dead aspen trees were saproxylic
Sweden	Palm (1959)	342 species of beetle associated with dead aspen in southern and central Sweden
Sweden	Ehnström (2001)	405 saproxylic beetle species associated with dead birch, 389 with dead Scotch pine and 354 with dead Norway spruce
Norway	Økland et al. (1996)	Nearly 700 obligate saproxylic beetle species nationally and 200 facultatively saproxylic species
Germany	Derksen (1941)	217 species of saproxylic insects in dead beech in a single forest
Germany	Köhler (2000)	56% of all forest-dwelling beetle species in north Rhineland considered saproxylic
Germany	Blab et al. (1994)	25% of German beetle species considered saproxylic
Canada	Hammond (1997)	257 species of saproxylic beetle recorded from dead aspens in one forest type
United States	Deyrup (1976)	More than 300 saproxylic insect species recorded from Douglas-fir in Washington
United States	Howden & Vogt (1951)	188 species of beetles recorded from dead pines in a single Maryland forest
United States	Savely (1939)	162 species of beetles recorded from pine and oak logs in a single North Carolina forest

arboreal megalopolis (Speight 1989) or termed megatrees (Nilsson & Baranowski 1994). They probably assume greatest relative importance in forests dominated by broadleaves, whether temperate (Speight 1989) or tropical (Grove 2002b) (Figure 1). In boreal and other coniferous or sclerophyllous forests, the standing dead trees (snags) and dead wood on the forest floor derived from megatrees may be more important (Berg et al. 1994). However, despite the importance of megatrees, we know relatively little about what lives in them, compared with what lives in snags or in dead wood on the forest floor. Some saproxylic insects are found in all three types, but many have distinct preferences (Palm 1959). In Swedish broadleaved forests megatrees support more substrate-specific species than either snags or dead wood on the forest floor and include most of the rarest and most threatened saproxylic insects (Nilsson & Baranowski 1997, Jonsell et al. 1998).

THERE'S DIVERSITY IN DECAY   A key source of saproxylic insect diversity is the range of decay stages and types that occur within dead wood, each providing habitats for different assemblages. As wood decomposes it is colonized by a succession of saproxylic insect species (Blackman & Stage 1924, Kletecka 1996, Hammond et al. 2001), as are the fruiting-bodies of wood-rotting ascomycetes and basidiomycetes (Jonsell et al. 1999). Insects that colonize living or freshly dead wood often show narrow host specificity (Hamilton 1978); the same applies for species on wood-decaying fungi (Kaila et al. 1994). Host specificity is rare at the tree species level but common at higher plant taxonomic levels (e.g., Tavakilian et al. 1997). In German forests Köhler (2000) found that 13% of the saproxylic beetle species were tree genus specific. As decomposition proceeds host specificity drops off, though there remains a big difference between the fauna of hardwoods and that of softwoods (Savely 1939, Ås 1993). Within either, decay type is important (Harmon et al. 1986, Jonsell et al. 1998). For instance, there is a big difference in the fauna depending on whether the wood was decayed by white-rot or brown-rot fungi (Araya 1993, Wood et al. 1996, Yee et al. 2001). Further differences are attributable to wood moisture content and exposure to sun (Martikainen 2001).

ALL DEAD WOOD IS GOOD, BUT BIGGER IS BETTER   Size is important for saproxylic insects. Some are able to make use of their chosen substrate whatever its dimensions (Palm 1959), but most are more particular (Elton 1966), which results in different assemblages in substrates of different sizes. Most studies suggest a positive relationship between tree or dead-wood diameter and species richness, incidence, or abundance (Table 2), with larger-diameter material being especially important for rare and threatened species (e.g., Warren & Key 1991). Various explanations exist for this phenomenon. First, larger-diameter trees and dead wood are highly heterogeneous habitats, allowing many specialist species to occupy them at the same time (Kolström & Lumatjärvi 2000). Second, larger-diameter
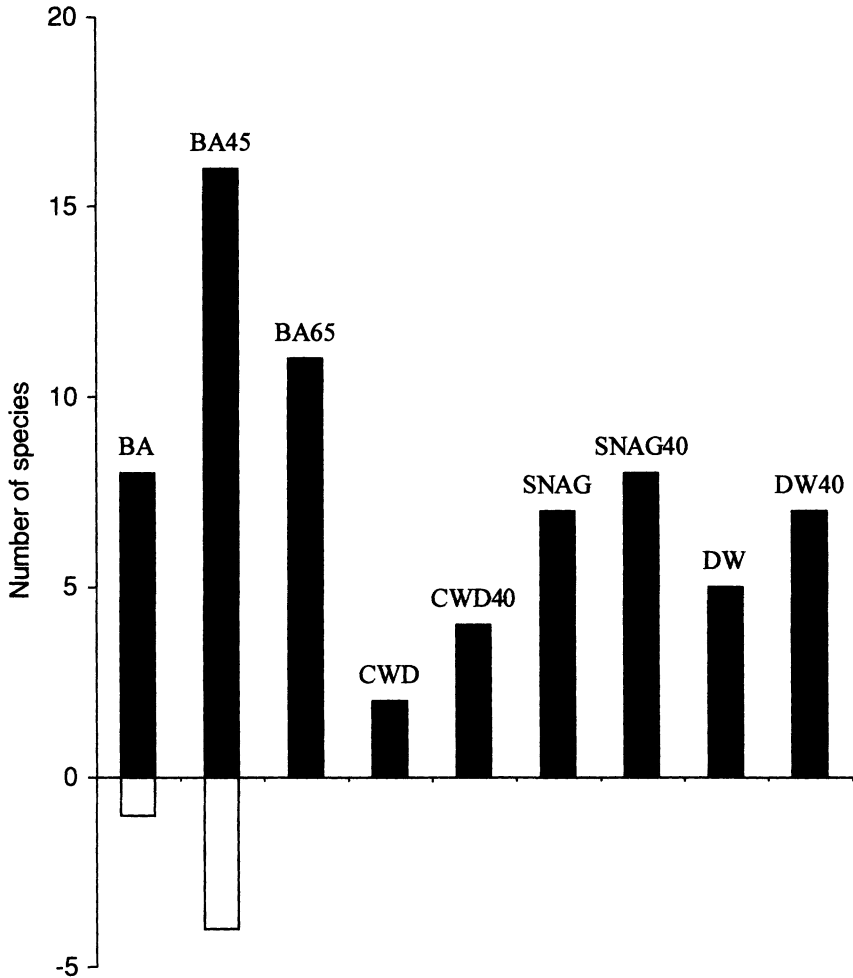
Figure 1 Numbers of saproxylic beetle species showing significant correlations (p < 0.05; Pearson two-tailed) in abundance with mature timber habitat attributes across the author's 81 study plots in the Daintree lowlands of northeastern Queensland, Australia. Based on all species represented by five or more individuals (n = 118). Correlations above the horizontal axis (*black bars*) are positive; correlations below the horizontal axis (*white bars*) are negative. Note that some species may contribute to more than one column. BA, basal area; BA45, basal area of trees >45 cm dbh (diameter at 1.5 m); BA65, basal area of trees >65 cm dbh; CWD, volume of coarse woody debris on the forest floor; CWD40, volume of CWD >40 cm dia (mid-point diameter); SNAG, volume of snags; SNAG40, volume of snags >40 cm dia; DW, total volume of dead wood; DW40, total volume of dead wood >40 cm dia.

TABLE 2 Examples demonstrating relationships between saproxylic insects and mature timber habitat diameter

Country	Reference	Relationship[a]	Observation
Australia	Grove (2002b)	+	Larger-diameter living trees a better predictor of saproxylic beetle species richness and assemblage composition than total basal area in lowland tropical rainforest
Australia	Yee et al. (2001)	+	Saproxylic beetle fauna of rotting logs varied by rot type, with some types primarily found in larger-diameter logs
Finland	Kolström & Lumatjärvi (2000)	+	Model of forest-stand structure linked to database of saproxylic beetle habitat requirements Predicted that retaining aspen trees in managed conifer stands would result in a progressive increase in saproxylic species as tree diameter increased. Thinning aspen along with conifers would not allow this increase
Finland	Väisänen et al. (1993)	+	Number of species of subcortical beetles in trees in a managed forest positively correlated with diameter
Finland	Siitonen & Saaristo (2000)	+	Incidence of threatened saproxylic beetle *Pytho kolwensis* in spruce logs positively correlated with diameter
Finland	Martikainen et al. (2000)	+	Number of saproxylic beetle species per plot positively correlated with abundance of larger-diameter living and dead trees
Sweden	Jonsell et al. (1998)	+	Models based on known habitat associations of threatened saproxylic invertebrates predicted that most would occur in dead wood in the largest diameter class, including 178 not found in smaller-diameter classes. Only 94 species would occur in the smallest, with only 13 of these not found in larger classes
Sweden	Ranius & Jansson (2000)	+	Species richness of saproxylic beetles in hollow oaks positively related to tree diameter, especially amongst threatened species and those associated with sporocarps of wood-rotting fungi
Sweden	T Nilsson (1997)	+	Probability of occurrence of saproxylic beetle *Bolitophagus reticulatus* increased with tree diameter
Norway	Thunes et al. (2000)	+	Sporocarps of wood-rotting fungus *Fomitopsis pinicola* harbored more saproxylic beetle species on larger trees

(Continued)

TABLE 2   *(Continued)*

Country	Reference	Relationship[a]	Observation
Germany	Kleinevoss et al. (1996)	+	Higher saproxylic beetle species richness on larger-diameter dead wood
United Kingdom	Elton (1966)	−/+	Assemblage composition of smaller-diameter dead wood intermediate between that of larger-diameter dead wood and leaf litter
United States	Edmonds & Eglitis (1989)	+	Higher incidence of the cerambycid beetle *Monochamus scutellatus* on larger-diameter Douglas-fir logs
United States	Torgersen & Bull (1995)	+	*Camponotus* (carpenter) ants prefer larger logs to smaller ones
United States	Hespenheide (1976)	−/+	Some species of buprestid beetle have particular branch-diameter preferences, whereas others make use of a wide range of diameters
Japan	Araya (1993)	−	The lucanid beetle *Prismognathus acuticollis* occurred more predictably in smaller-diameter logs

[a]+, positive relationship; −, negative relationship

pieces take longer to decompose, and a more stable microclimate is maintained within, favoring many species (Palm 1959). Third, larger-diameter pieces support more species of fungi, including species specific to larger-diameter wood (Kruys & Jonsson 1999, Nordén & Paltto 2001), on which many saproxylic insects depend.

DEAD WOOD IS DYNAMIC AND SO ARE ITS INHABITANTS   Dead-wood abundance partly depends on its rates of input and output (wood growth and decay) and whether these are in equilibrium. Equilibrium is most likely in those old-growth forests in which the normal disturbance regime is one of small-scale gap replacement. If disturbance dynamics are more sporadic (e.g., occasional wildfires, windstorms, or earthquakes), then dead wood abundance may vary greatly depending on the time since the last disturbance event (Siitonen 2001, Spies et al. 1988).

A region's saproxylic insect fauna will presumably be pre-adapted to its normal disturbance regime (McPeek & Holt 1992). Species whose habitat is naturally long-lived and/or abundant are usually poor dispersers (e.g., many specialists of tree hollows) (Nilsson & Baranowski 1997; Ranius & Hedin 2001) compared with those whose habitat is scarce and/or ephemeral (e.g., many scolytine beetles on wind- or fire-damaged trees) (Nilssen 1984). Alteration of disturbance dynamics of a forest through management may have knock-on effects on saproxylic insects

(Schiegg 2000). The most likely alteration is a reduction in mature forest stands, potentially threatening many species (Ranius 2002) while turning a few others into pests (Heliövaara & Väisänen 1984, Safranyik & Linton 1999). Alternatively, fire suppression can lead to a reduction in early successional stages and an increase in stand density (Johnson et al. 2001), threatening many fire-adapted, thermophilic or shade-intolerant saproxylic insect species, which can comprise a large proportion of the regional fauna (Økland et al. 1996, Martikainen 2001).

Ecologists are familiar with metapopulation dynamics operating over the scale of kilometers among habitat patches measured in hectares (Hanski 1999, Thomas 2000), but for some saproxylic insect species, metapopulation dynamics may operate among habitat patches measured in cubic meters (Table 3). Individual trees, logs, snags, or fungal sporocarps can host several generations of a particular species, but eventually the entire population will become extinct once the resource decomposes, while new substrate patches appear for colonization elsewhere. If forest management alters patch abundance and distribution, then the population dynamics of species dependent on them may break down, leading to landscape-level extinction. For example, a common harvesting practice in forests pre-adapted to wildfires is clearfelling. Although often justified on the grounds of mimicking natural disturbance (Attiwill 1994), the resulting dead wood dynamics may be very different (Harmon et al. 1986, Price et al. 1998, Grove et al. 2002). Not only has much of the wood been harvested, but the remainder is fragmented and positioned entirely on the ground, where it may decay so rapidly that little remains within a few decades. Saproxylic insects may then face a critical habitat continuity gap, during which metapopulation dynamics might well break down, even though dead wood levels might subsequently increase later in the silvicultural cycle.

CONNECTIONS IN SPACE AND TIME: CONTINUITY IS THE KEY   One of the key management issues for saproxylic insects is the maintenance of ecological continuity in space (connectivity) and in time. In much of western Europe ecological continuity (or lack of it) is thought to be a major limiting factor for many of the less vagile saproxylic insect species (Speight 1989). Following millennia of intensive use (Thirgood 1989), there are probably few remaining patches of forest that have experienced sufficient ecological continuity to support anything close to the natural complement of saproxylic insect species (see "Saproxylic Insects and the Unsustainable Management of Forests," below). This has led to European conservationists paying particular attention to old-forest species, which are confined to primary forest, despite there being many mature secondary forests in the region (Speight 1989, Martikainen et al. 1999, Siitonen & Saaristo 2000). In the United Kingdom a suite of such species can be used to discriminate between mature woodland dating from the eighteenth century or earlier and the other 78% of the forest estate, which consists of more recently established plantations or regrowth (Fowles 1997). However, where forests are less fragmented and/or

TABLE 3 Examples demonstrating relationships between saproxylic insects and availability of mature timber habitat

Country	Reference	Observation
Australia	Grove (2002b)	Basal area of larger-diameter trees the best predictor of saproxylic beetle abundance and assemblage composition; coarse woody debris volume a better predictor of species richness in lowland tropical rainforest
Finland	Martikainen et al. (2000)	Total volume of dead wood provided the best predictor of beetle species richness
Finland	Siitonen (1994a)	Specialist beetle species were more abundant in a forest containing abundant dead wood than in one in which dead wood was scarce
Finland	Sippola & Kallio (1995)	Positive relationship between dead-wood volume and beetle species richness at the stand (1 ha) scale
Finland	Komonen et al. (2000)	Number of saproxylic trophic levels based on the bracket fungus *Fomitopsis rosea* decreased from three in intact old-growth forest to one in fragmented old-growth forest
Finland/ Russia	Siitonen (1994b)	On the Russian side of the border dead aspen trees were common, but on the Finnish side they were rare. On the Russian side they supported a much richer beetle fauna than on the Finnish side, including 2 species extinct in Finland and 18 species regarded as nationally rare in Finland, compared with 5 rare species on the Finnish side
Sweden	Jonsell et al. (1999)	Fungus beetles showed differing abilities to colonize sporocarps, dependent on distance and the nature of the intervening land. Most of the species studied could persist in the managed forest landscape if suitable breeding substrate were created or maintained at the landscape (1 km^2) scale. To some extent larger habitat patches compensated for isolation
Sweden	Nilsson & Baranowski (1997)	Beetle species specializing on tree-hollows in living trees (a rare but long-lived resource) less vagile than species living in dead wood on the forest floor (a commoner but less persistent resource). Logged forest supported all species living in dead wood on the forest floor but not several tree-hollow species, even though the trees there were now large enough to support suitable hollows
Norway	Thunes et al. (2000)	The major factor influencing the number of species of beetles and the number of threatened species on dead sporocarps of the bracket fungus *Fomitopsis pinicola* was the amount of dead wood in and around the sampling site. Some of the species colonizing dead sporocarps were also able to live in dead wood and only occurred on sporocarps when dead wood was abundant

(Continued)

TABLE 3 (*Continued*)

Country	Reference	Observation
Norway	Rukke (2000)	Incidence of beetle species associated with the bracket fungus *Fomes fomentarius* related to degree of isolation of habitat trees, as well as to habitat size at tree and landscape scale
Norway	Sverdrup-Thygeson & Midtgaard (1998)	Probability of occurrence of the tenebrionid fungus-beetle *Bolitophagus reticulatus* increased with tree diameter and with the number of dead sporocarps on the tree and decreased as the distance to surrounding inhabited trees increased
Norway	Økland et al. (1996)	Positive relationship between dead-wood volume and beetle species richness at the landscape (32 ha) but not the stand (1 ha) scale. At all scales diversity of dead tree parts, number of large-diameter dead trees and number of polypore fungi species all correlated with beetle species richness and with abundance of many species; several species absent below a certain density of dead wood
Switzerland	Schiegg (2000)	Different species of beetle and fly found in forests with differing degrees of connectivity of dead wood; plots with higher dead-wood connectivity associated with higher species richness
Canada	Kehler & Bondrup-Nielsen (1999)	Probability of occurrence of the tenebrionid fungus-beetle *Bolitotherus cornutus* decreased with distance at the scale of sporocarps, logs, and forest blocks in an agricultural matrix. At any scale, distance proved the most consistent indicator of isolation
USA	Chandler (1991)	Greater abundance of many beetle species in old-growth compared with regrowth forest attributed to the greater prevalence of suitable dead-wood habitat in old growth

where occasional catastrophic disturbance is the norm, the present availability of the right dead-wood habitat may have greater significance for saproxylic species than does its continuity over time. This is held to be the case in the boreal forests of Fennoscandia (Kouki et al. 2001) and might also be true elsewhere.

DEAD WOOD IS NOT WASTE WOOD   For classically trained foresters and for many members of the public, wood allowed to rot or burn is wood that has gone to waste ("zero waste tolerance") (Lofroth 1998). Yet in nature waste recycling is a critical ecological process. Decomposing dead wood is the means by which a large proportion of the nutrients and energy accumulated by the living tree is returned to the soil (Laiho & Prescott 1999). Dead wood also acts as a medium-term store

of carbon (Mackensen & Bauhus 1999). As decomposition progresses dead wood becomes incorporated into soil, helping to maintain levels of organic matter and carbon (Tate et al. 1993). Decomposition is brought about primarily by the activity of fungi and other microorganisms but is often mediated by saproxylic invertebrates (Swift 1977, Edmonds & Eglitis 1989, Schowalter et al. 1992, Hanula 1996). Quite apart from their own rights to existence, saproxylic insects are a principal source of food for other forest-dwelling organisms such as woodpeckers (Hanula & Franzreb 1998, Torgersen & Bull 1995).

CONSERVATION AND MANAGEMENT ISSUES

Death by a Thousand Cuts: How Humans and Saproxylic Insects Compete for Trees

Over the past few thousand years humans have increasingly ended up competing with saproxylic insects for timber (Hagan & Grove 1999). A small minority of saproxylic species such as some bark beetles (Peltonen 1999, Weslien & Schroeder 1999) can compete successfully with humans and are therefore termed pests. The vast majority are more likely to end up on the losing side, resulting in managed forests supporting altered saproxylic insect species assemblages, often coupled with lower numbers and fewer species overall (Table 4). By managing forests so that we can remove wood before it is lost to decay, we progressively eliminate mature timber habitat.

Elimination of mature timber habitat may be most rapid and thorough through excessive forest hygiene (Schmitt 1992), salvage logging (Maser 1996), or fuelwood or biomass harvesting (Tritton et al. 1987, Wall 1999, Grove et al. 2002). In other situations its loss may be more insidious and may start with a temporary increase in visible dead wood through wasteful logging practices (Harmon 2001) or fire suppression and pest outbreaks brought on by management (Edmonds & Marra 1999). However, with successive silvicultural cycles an incremental loss is likely: As existing old trees die, the dead wood they produce decomposes, and the younger, more healthy trees of the managed forest do not live long enough to generate sufficient replacement habitat. Mature timber habitat may thus be reduced from abundance to rarity. Goodburn & Lorimer (1998) reported that levels of dead wood on the forest floor of selectively managed hardwood forests in Wisconsin and Michigan were only about 60% those of old-growth forests, with differences in larger-diameter material being even more pronounced. Fennoscandian production forests provide a more extreme example, with coarse woody debris levels falling by 90–98% over the past century (Siitonen 2001). In other parts of Europe it is not even possible to say how much dead wood an old-growth forest would have had, because there are none left. Writing from a British perspective, Elton (1966) stated that "if fallen timber and slightly decayed trees are removed [from a natural forest] the whole system is gravely impoverished of perhaps more than a fifth of its fauna." If anything, this is likely an underestimate, as the studies in Table 1 suggest.

TABLE 4 Examples of relationships between saproxylic insects and forest management[a]

Country	Reference	N[b]	S[c]	C[d]	Observations
Australia	Grove 2002a	+	+	+	Analyses of data concerning 339 saproxylic beetle species in old-growth, selectively logged and regrowth tropical rainforest. Differences subtle but consistent
Australia	Michaels & Bornemissza 1999	+	+	NR	Lucanid beetle species richness and abundance lower in regrowth forest than in recent clear-fells owing to continued presence of old-growth logs in clear-felled areas
Finland	Martikainen et al. 2000	+	+	+	78% of 232 saproxylic beetle species more abundant in old-growth than in managed mature forest; almost no overlap in assemblage composition
Finland	Martikainen et al. 1999	+	+	NR	Scolytine beetles in old-growth, overmature, and managed mature forest
Finland	Väisänen et al. 1993	NR	NR	+	Among saproxylic beetles living subcortically in dead trees, proportion of scolytines much higher in managed forest; proportion of rare species higher in old growth
Poland	Gutowski 1986	+	0	+	Cerambycid beetles in old-growth versus managed forest. More species present only in old-growth than only in managed forest
Germany	Schmitt 1992	NR	+	+	Recorded more species of saproxylic beetle in logs and more threatened species in unmanaged than in adjacent managed forest. Managed forest assemblages more dominated by scolytines
Canada	Spence et al. 1996	+	+	+	Several saproxylic beetle species found in old-growth that were rare or absent in mature managed forest
United States	Chandler & Peck 1992	+	+	NR	More species and individuals of leiodid beetles in old-growth versus "regrowth" (former clear-cut) forest
United States	Chandler 1991	+	NR	NR	More individuals of saproxylic beetles in old-growth versus regrowth forest

[a] Relationships are expressed with respect to "old-growthness"; +, positive relationship; 0, no relationship; NR, not reported
[b] N, abundance of individuals
[c] S, species richness
[d] C, assemblage composition

Referring to North American forests, Huston (1996) stated, "No other manageable property of the forest environment has a greater impact on biodiversity than coarse woody debris. Even [timber] harvesting... probably has a greater effect on total forest biodiversity through the alteration and removal of coarse woody debris than through its effect as a disturbance that 'resets' forest succession."

The situation may be equally critical wherever native forests are heavily exploited for fuelwood [e.g., China (Nalepa et al. 2001), South Africa (DuPlessis 1995), Australia (Driscoll et al. 2000)]. It may also be comparable to parts of the eastern United States, where the extensive mature forests are the result of "old-field" succession and are less than 200 years old. Within my study area in northeastern Queensland, the volume of dead wood on the forest floor in selectively logged tropical rainforest averaged about 80% that of nearby old growth, with much greater deficiencies among larger-diameter material (Grove 2001b). Differences were more marked among living trees, and in these forests it appeared to be the loss of larger-diameter trees from logged forest that was the main cause of the differences in the saproxylic beetle fauna (Grove 2002b) (Figure 2). This is likely also the case in forests managed by selection silviculture elsewhere.

Saproxylic Insects and the Unsustainable Management of Forests: A 5000-Year European Experiment

The history of forest use and abuse in western Europe is not unique but is well documented. Forests had scarcely reached their maximum post-glacial extent when farmers started clearing them. Over the following millennia forest cover was drastically reduced, and the structure and composition of remaining fragments greatly altered (Thirgood 1989). By 1000 A.D., there was probably no truly natural forest left in Europe outside Fennoscandia (Greig 1982).

It was not just wolves, bears, and lynx that retreated. As forests were cleared and the remaining fragments were managed for firewood, poles, and timber, mature timber habitat and saproxylic insects also began to vanish (Speight 1989). Their prehistoric extinction in the United Kingdom is well documented. Buckland & Dinnin (1993) list 17 saproxylic beetle species known in the United Kingdom only from subfossils, mostly from peat deposits dating from about 2900 B.C., and speculate that the list will grow with further excavations. None of these species is yet globally extinct, but most now survive only in tiny refugia elsewhere in Europe. Many belong to genera containing species that are currently common in other parts of the world (e.g., *Rhysodes, Prostomis, Pycnomerus, Dromaeolus, Platycerus, Cerambyx,* and *Eremotes*) and provide a clear reminder of what any region stands to lose if the processes that operated in western Europe are repeated elsewhere.

The 5000-year-long trend in forest loss in western Europe has now largely been reversed, with the expansion of secondary woodlands and plantations. However, the extinction of saproxylic insects continues apace. For instance, Hammond (1974) reported the loss from the United Kingdom of a further 20 beetle species over
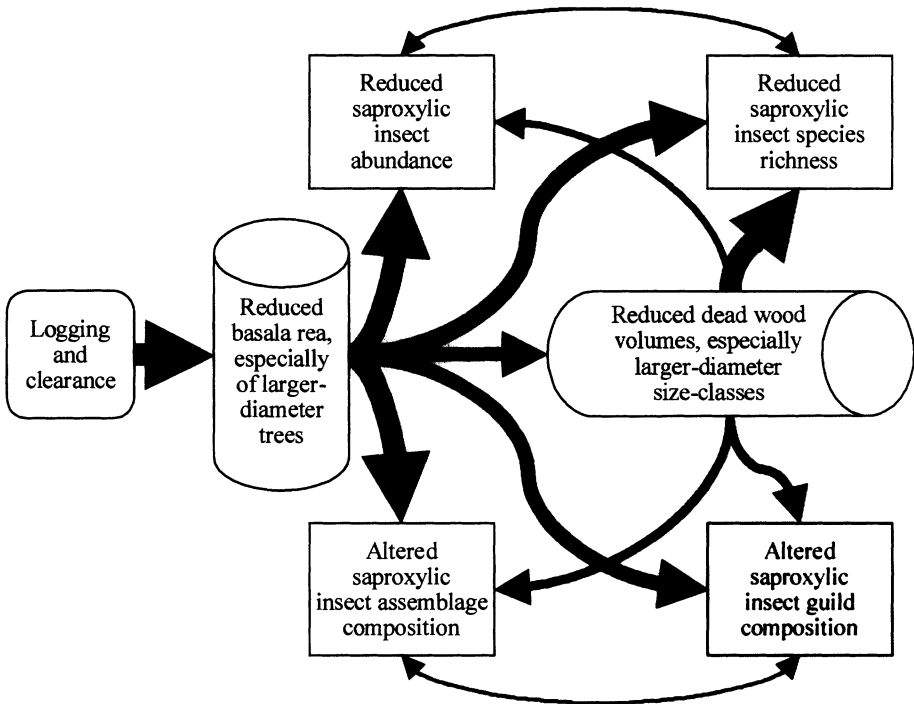
Figure 2   Likely impacts of logging and forest clearance on mature timber habitat, and consequences for the saproxylic insect fauna. Based on the main findings of the author's research on saproxylic beetles in northeastern Queensland. The thickness of each arrow is approximately proportional to the strength of the relationship as gauged by correlations, analyses of variance, or multivariate analyses as discussed in Grove (2002b). Relationships concerning guild composition are derived from the author's unpublished data.

the previous two centuries, and a fifth of the remaining UK cerambycid beetle fauna is now considered threatened (Twinn & Harding 1999). Today extinction is mostly driven by increasingly intensive forest management (Hanski & Hammond 1995, Siitonen 2001) coupled with the delayed effects of past fragmentation. In Fennoscandia, fire suppression and no-burn silviculture is one of the main threats to saproxylic species (Martikainen 2001, Johnson et al. 2001). Saproxylic insects now comprise a disproportionately large percentage of nationally rare and threatened species in Europe (Geiser 1983, Shirt 1987). For instance, in Sweden, of the 739 threatened forest invertebrate species, old living trees are considered a key habitat for 33%, logs 28%, and snags 35% (Berg et al. 1994). The removal of mature timber habitat is considered the main threat for 65% of the United Kingdom's 150 threatened woodland insect species (Hambler & Speight 1995).

Many saproxylic species now survive in Europe only as relictual populations, "hanging on by the tips of their tarsi" (Buckland & Dinnin 1993) in small patches

of forest or pasture woodland—or even single trees—which for historical reasons did not experience the same loss of mature timber habitat. In the absence of positive management, the ultimate extinction of some such species (truly the "living dead") is almost inevitable through stochastic events (Thomas 2000).

Silviculture, Morticulture, and the Living Dead: Catering for Saproxylic Insects in Managed Forests

The forestry profession is increasingly aware of its responsibilities towards dead wood management ["morticulture" (Harmon 2001)], especially in North America (Franklin 1989) and northern Europe (Siitonen 2001). Done well, morticulture should cater for saproxylic insects. Whereas it is unrealistic to expect even sustainably managed commercial forests to retain a full complement of saproxylic insect species at the stand level, they ought to be able to at the landscape level. Some brief suggestions for how to do so follow.

At the landscape level the bottom line is that management should retain sufficient elements of natural forest dynamics to maintain the ecological processes in which mature timber habitat is involved—especially the chance for trees to live to ecological maturity and decay without intervention. Sufficient trees or patches should be retained to allow for some landscape-level temporal and spatial habitat continuity (Martikainen 2001, Grove et al. 2002). Management should also allow for the occasional occurrence of pest and disease outbreaks, windthrow, and fire if these are normal disturbance events. At the stand level there are many measures that can be taken (e.g., Grove 2001a, Ehnström 2001). For all forest types these should include using reduced-impact logging techniques, avoiding incidental damage to logs and snags, and avoiding harvesting of woody debris. Additional measures for selectively logged forests should include retaining habitat trees and legacy trees and avoiding silvicultural refinement. Additional measures for forests subjected to clearfelling should include extending rotations long enough for mature timber habitat to accumulate between felling cycles (at least over part of the production forest estate), a preference for small logging coupes and/or aggregated retention, and separating consecutive logging coupes to ensure that there is always some mature forest in the production forest matrix.

In regions where species are regionally extinct through a history of forest fragmentation and intensive use (as in western Europe), reintroductions are the only option. If they still survive as "living dead" in refugia, then morticultural management of refugia and the surrounding matrix may yet save them from extinction. Managing refugia is perhaps best developed in the United Kingdom, where most of the remaining key sites are cultural landscapes (such as royal hunting parks), now owned by nature conservation organizations (Alexander 1995), allowing a level of intensive care that would be uneconomical for commercial forestry. An example is the reinstatement of pollarding (Read 1991). Originally carried out to provide a supply of pole-wood above the reach of browsing animals, it incidentally helps prolong tree life, providing the necessary mature timber habitat and habitat

continuity for a wide range of saproxylic insects and other organisms. In North America other suggestions for enhancing mature timber habitat in production forests have included the use of explosives (Bull & Partridge 1986) to produce snags from living trees, attracting bark beetles to living trees with pheromones to produce snags for "wildlife" (Ross & Niwa 1997), and the felling of "cull" trees to supplement coarse woody debris (Franklin 1989). Killing trees with herbicides has also been promoted, but the resultant snags provide much poorer conditions for saproxylic insects than do those resulting from natural tree death (Aulen 1991).

Management Indicators: The Way Forward for Sustaining Saproxylic Insects?

In Europe enough is now known about saproxylic insects for their potential use in identifying key sites for nature conservation or for monitoring the sustainability of forest management. Many taxonomic groups have been promoted for this purpose, especially beetles (Harding & Rose 1986, Harding & Alexander 1994, Nilsson et al. 1995). However, their use still remains the domain of entomologists and academics, rather than forestry practitioners. No such level of knowledge—or indeed interest—appears to exist in any other part of the world, so their chances of being widely adopted as indicators are slim.

As an alternative, mature timber habitat could well provide useful structural surrogates for saproxylic insects (e.g., Thunes et al. 2000), and incorporating such surrogates into guidelines, criteria, and indicators is perhaps our best chance of addressing the needs of saproxylic insects worldwide. One advantage is that habitat is more readily measurable than are the saproxylic insects themselves (Hodge & Peterken 1998). Measuring the basal area or standing volume of larger-diameter living trees is a simple procedure and merely an extension of a standard forestry activity. Snags and dead wood are slightly more difficult to measure accurately owing to their natural patchiness (Siitonen 1994a, Sippola et al. 1998, Grove 2001b). Currently, most initiatives assume that snags and dead wood on the forest floor are the key features. This may be so in forests where occasional large-scale disturbances are the norm, but as this review has demonstrated, it is not the whole picture, especially in forests where smaller-scale disturbances operate.

European guidelines for certification and sustainable management increasingly promote the retention and maintenance of dead wood and old trees (UKFC 1998, PEFC 1999). The level of management concern for coarse woody debris, snags, and dependent vertebrates in North America (Fenger 1996, Hagan & Grove 1999, Harmon 2001) and Australia (Gibbons & Lindenmayer 2001, Woldendorp et al. 2001) provides some hope that the needs of some saproxylic insects will be addressed by default. In the tropics nearly all available sustainable forest management guidelines are too general to refer specifically to the mature timber habitat, with one main exception (CIFOR 1999). Much work remains to be done worldwide to develop more appropriate guidelines and to get them implemented (Grove 2001a).

CONCLUSION

From European studies it is clear that saproxylic insects are peculiarly susceptible to forest management, in no small part owing to their dependence on a suite of habitats that is naturally abundant in unmanaged forest but often rare in long-managed forests. Many species may have low powers of dispersal, with populations governed by metapopulation dynamics. These characteristics make evolutionary sense, but do not favor survival in managed and fragmented forest settings, where spatial and temporal breaks in habitat continuity can lead to population declines and extinctions.

I hope this review has demonstrated that saproxylic insects deserve much greater consideration amongst forest managers and their ecologist advisers. Sustaining saproxylic insects may not be any more challenging than sustaining other forest biota, but unless their needs are specifically addressed there remains a serious risk that we will lose a large proportion of the forest fauna from our managed forests before we even know it. One only has to look at western Europe to see what might happen if we fail to act.

The *Annual Review of Ecology and Systematics* is online at
http://ecolsys.annualreviews.org

LITERATURE CITED

Alexander KNA. 1995. Historic parks and pasture-woodlands: the National Trust resource and its conservation. *Biol. J. Linn. Soc. London* 56 (Suppl.):155–75

Araya TE. 1993. Relationship between decay types of dead wood and occurrence of lucanid beetles (Coleoptera: Lucanidae). *Appl. Entomol. Zool.* 28:27–33

Ås S. 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in decidu-ous forest fragments in boreal forest. *Ecography* 16:219–28

Attiwill PM. 1994. Ecological disturbance and the conservation management of eucalypt forests in Australia. *For. Ecol. Manage.* 63:301–46

Aulen G. 1991. Increasing insect abundance by killing deciduous trees—a method of improving the food situation for endangered woodpeckers. *Holarct. Ecol.* 14:68–80

Berg A, Ehnström B, Gustafsson L, Hallingbäck T, Jonsell M, Weslien J. 1993. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* 8:718–31

Blab J, Nowak E, Trautmann W, Sukopp H. 1994. *Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland.* Greven, Ger: Kilda

Blackman MW, Stage HH. 1924. On the succession of insects living in the bark and wood of dying, dead and decaying hickory. *Tech. Bull. NY State Coll. For.* 17:3–268

Braccia A, Batzer DP. 2001. Invertebrates associated with woody debris in a southeastern US forested floodplain wetland. *Wetlands* 21:18–31

Buckland PC, Dinnin MH. 1993. Holocene woodlands, the fossil insect evidence. In *Dead Wood Matters: The Ecology and Conservation of Saproxylic Invertebrates in Britain,* ed. KJ Kirby, CM Drake, pp. 6–20. Peterborough, UK: English Nat.

Bull EL, Partridge AD. 1986. Methods of killing trees for use by cavity nesters. *Wildl. Soc. Bull.* 14:142–46

Chandler DS. 1991. Comparison of some slime-mold and fungus feeding beetles (Coleoptera) in an old-growth and 40-year-old forest in New Hampshire. *Coleopt. Bull.* 45:239–56

Chandler DS, Peck SB. 1992. Diversity and seasonality of leiodid beetles (Coleoptera: Leiodidae) in an old-growth and a 40-year-old forest in New Hampshire. *Environ. Entomol.* 21:1283–91

CIFOR. 1999. *C&I Toolbox Series No. 2: The CIFOR Criteria and Indicators Generic Template.* Bogor, Indonesia: Cent. Int. For. Res. 53 pp.

Dajoz R. 1966. Ecologie et biologie des coléoptères xylophages de la hêtraie. [Ecology and biology of xylophagous beetles of the beechwood] *Vie Milieu* 17:525–636 In French with English summ.

Derksen W. 1941. Die Succession der pterygoten Insekten im abgestorben Buchenholz [The succession of pterygote insects in fallen beech wood]. *Z. Morphol. Ökol. Tier.* 37:683–734. In German

Deyrup MA. 1976. *The insect community of dead and dying Douglas-fir: Diptera, Coleoptera, and Neuroptera.* PhD thesis. Univ. Seattle

Driscoll D, Mikovits G, Freudenberger D. 2000. *Impact and Use of Firewood in Australia.* Canberra, ACT: CSIRO Sustainable Ecosystems

DuPlessis MA. 1995. The effects of fuelwood removal on the diversity of some cavity-using birds and mammals in South Africa. *Biol. Conserv.* 74:77–82

Edmonds RL, Eglitis A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Can. J. For. Res.* 19:853–59

Edmonds RL, Marra JL. 1999. Decomposition of woody material: nutrient dynamics, invertebrate/fungi relationships and management in Northwest forests. In *Proc. Pac. Northwest For. Rangeland Soil Organism Symp.,* ed. RT Meurisse, WG Ypsilantis, C Seybold, pp. 68–79. Corvallis, OR: USDA For. Ser. Gen. Tech. Rep. PNW-GTR-461

Ehnström B. 2001. Leaving dead wood for insects in boreal forests—suggestions for the future. *Scand. J. For. Res. Suppl.* 3:91–98

Elton C. 1966. Dying and dead wood. In *The Pattern of Animal Communities,* ed. C Elton, pp. 279–305. London: Methuen

Fenger M. 1996. Implementing biodiversity conservation through the British Columbia Forest Practices Code. *For. Ecol. Manage.* 85:67–77

Fowles AP. 1997. The Saproxylic Quality Index: an evaluation of dead wood habitats based on rarity scores, with examples from Wales. *Coleopterist* 6:61–66

Franklin J. 1989. Toward a new forestry. *Am. For.* 95:37–44

Geiser R. 1983. Rote Liste ausgewählter Familien xylobionter Käfer (Coleoptera) in Österreich [Red list of threatened xylobiont beetle families (Coleoptera) in Austria] (In German). In *Rote Listen Gefährdeter Tiere*

[*Red Lists of Threatened Species*], ed. J Gepp, pp. 131–37. Wien, Austria: Österr. Bundesminist. Gesundh. Umweltschutz

Gibbons P, Lindenmayer D. 2001. *Tree Hollows and Wildlife Conservation in Australia*. Canberra: CSIRO. 240 pp.

Goodburn JM, Lorimer CG. 1998. Cavity trees and coarse woody debris in old growth and managed northern hardwood forests in Wisconsin and Michigan. *Can. J. For. Res.* 28:427–38

Greig J. 1982. Past and present limewoods in Europe. In *Archaeological Aspects of Woodland Ecology*, ed. M Bell, S Limbrey, pp. 89–99. Oxford: Br. Archaeol. Rep.

Grove SJ. 2001a. Developing appropriate mechanisms for sustaining mature timber habitat in managed natural forest stands. *Int. For. Rev.* 3:272–84

Grove SJ. 2001b. Extent and composition of dead wood in Australian lowland tropical rainforest with different management histories. *For. Ecol. Manage.* 154:35–53

Grove SJ. 2002a. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biol. Conserv.* 104:149–71

Grove SJ. 2002b. Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. *Ecol. Indicators* 1:171–88

Grove SJ, 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, Aust.: For. Tasmania Tech. Rep. 22:1–72

Grove SJ, Stork NE. 1999. The conservation of saproxylic insects in tropical forests: a research agenda. *J. Insect Conserv.* 3:67–74

Grove SJ, Stork NE. 2000. An inordinate fondness for beetles. *Invertebr. Taxon.* 14:733–39

Gutowski JM. 1986. Species composition and structure of the communities of longhorn beetles (Col., Cerambycidae) in virgin and managed stands of Tilio-Carpinetum sta-chetosum association in Bialowieza Forest (NE Poland). *J. Appl. Entomol.* 102:380–91

Hagan JM, Grove SL. 1999. Coarse woody debris: humans and nature competing for trees. *J. For.* 97:6–11

Hambler C, Speight MR. 1995. Biodiversity conservation in Britain—science replacing tradition. *Br. Wildl.* 6:137–47

Hamilton WD. 1978. Evolution and diversity under bark. In *Diversity of Insect Faunas*, ed. LA Mound, N Waloff, pp. 154–75. London: R. Entomol. Soc. London

Hammond HEJ. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta—a review of taxa and collection methods. *Can. Entomol.* 129:1009–33

Hammond HEJ, Langor DW, Spence JRS. 2001. Early colonization of *Populus* wood by saproxylic beetles. *Can. J. For. Res.* 31:1175–83

Hammond PM. 1974. Changes in the British coleopterous fauna. In *The Changing Flora and Fauna of Britain*, ed. DL Hawksworth, pp. 323–69. London: Academic

Hammond PM. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rainforest in the Toraut region. In *Insects and the Rain Forests of South East Asia (Wallacea)*, ed. WJ Knight, JD Holloway, pp. 197–254. London: R. Entomol. Soc. London

Hammond PM, Kitching RL, Stork NE. 1996. The composition and richness of the tree-crown Coleoptera assemblage in an Australian subtropical forest. *Ecotropica* 2:99–108

Hanski I. 1999. *Metapopulation Ecology*. Oxford: Oxford Univ. Press. 313 pp.

Hanski I, Hammond PM. 1995. Biodiversity in boreal forests. *Trends Ecol. Evol.* 10:5–6

Hanula JL. 1996. *Relationship of wood-feeding insects and coarse woody debris*. See McMinn & Crossley 1996, pp. 55–81

Hanula JL, Franzreb K. 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the

red-cockaded woodpecker. *For. Ecol. Manage.* 102:89–102

Harding PT, Alexander KNA. 1994. The use of saproxylic invertebrates in the selection and conservation of relic forest in pasture-woodland. *Br. J. Entomol. Nat. Hist.* 7:21–26

Harding PT, Rose F. 1986. *Pasture-Woodlands in Lowland Britain.* Huntingdon, UK: Inst. Terr. Ecol. 89 pp.

Harmon ME. 2001. Moving towards a new paradigm for woody detritus management. *Ecol. Bull.* 49:269–78

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133–302

Heliövaara K, Väisänen R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta For. Fenn.* 189:5–30

Hespenheide HA. 1976. Patterns in the use of single plant hosts by wood-boring beetles. *Oikos* 27:61–64

Hodge SJ, Peterken GF. 1998. Deadwood in British forests: priorities and a strategy. *Forestry* 71:99–112

Howden HF, Vogt GB. 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill.). *Ann. Entomol. Soc. Am.* 44:581–95

Huston MA. 1996. *Modeling and management implications of coarse woody debris impacts on biodiversity.* See McMinn & Crossley, 1996, pp. 55–81

Johnson EA, Miyanishi K, Bridge SRJ. 2001. Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. *Conserv. Biol.* 15:1554–57

Jonsell M, Nordlander G, Jonsson M. 1999. Colonization patterns of insects breeding in wood-decaying fungi. *J. Insect Conserv.* 3:145–61

Jonsell M, Weslien J, Ehnström B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers. Conserv.* 7:749–64

Kaila L, Martikainen P, Punttila P, Yakovlev E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. *Ann. Zool. Fenn.* 31:97–107

Kehler D, Bondrup-Nielsen S. 1999. 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

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]. *Z. Ökol. Nat.schutz* 5:85–95. In German

Kletecka Z. 1996. The xylophagous beetles (Insecta, Coleoptera) community and its succession on Scotch elm (*Ulmus glabra*) branches. *Biologia (Bratislava)* 51:143–52

Köhler F. 2000. *Totholzkäfer in Naturwaldzellen des nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung* [*Saproxylic Beetles in Nature Forests of the Northern Rhineland. Comparative Studies on the Saproxylic Beetles of Germany and Contributions to German Nature Forest Research*]. Recklinghausen: Landesamt Agrarordnung NRW. 351 pp. In German

Kolström M, Lumatjärvi J. 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. *For. Ecol. Manage.* 126:113–20

Komonen A, Penttilä R, Lindgren M, Hanski I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90:119–26

Kouki J, Lofman S, Martikainen P, Rouvinen S, Uotila A. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scand. J. For. Res. Suppl.* 3:27–37

Kruys N, Jonsson BG. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Can. J. For. Res.* 29:1295–99

Laiho R, Prescott CE. 1999. The contribution of coarse woody debris to carbon, nitrogen, and

phosphorus cycles in three Rocky Mountain coniferous forests. *Can. J. For. Res.* 29:1592–1603

Lofroth E. 1998. The dead wood cycle. In *Conservation Biology Principles for Forested Landscapes*, ed. J Voller, S Harrison, pp. 185–214. Vancouver, Can.: UBC Press

Mackensen J, Bauhus J. 1999. *The Decay of Coarse Woody Debris*. Canberra, Aust.: Aust. Greenhouse Off. 41 pp.

Martikainen P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecol. Bull.* 49:205–18

Martikainen P, Siitonen J, Kaila L, Punttila P, Rauh J. 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *For. Ecol. Manage.* 116:233–45

Martikainen P, Siitonen J, Punttila P, Kaila L, Rauh J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* 94:199–209

Maser C. 1996. Salvage logging—the loss of ecological reason and moral restraint. *Int. J. Ecofor.* 12:176–78

McMinn J, Crossley DA, eds. 1996. *Biodiversity and Coarse Woody Debris in Southern Forests*. Athens GA: USDA For. Ser. Gen. Tech. Rep. SE-94

McPeek MA, Holt RD. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* 140:1010–27

Michaels K, Bornemissza G. 1999. Impact of clearfell harvesting on lucanid beetles (Coleoptera: Lucanidae) in wet and dry sclerophyll forests in Tasmania. *J. Insect Conserv.* 3:85–95

Nalepa CA, Li LI, Wen-Hua LU, Lazell J. 2001. Rediscovery of the wood-eating cockroach *Cryptocercus primarius* (Dictyoptera: Cryptocercidae) in China, with notes on ecology and distribution. *Acta Zootaxon. Sin.* 26:184–90

Nilssen AC. 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. *Ann. Ent. Fenn.* 50:37–42

Nilsson SG. 1997. *Grynocharis oblonga* L. (Coleoptera: Trogossitidae): a specialized wood beetle with a relict distribution. *Entomol. Tidskr.* 118:1–9. In Swedish with English summ.

Nilsson SG, Arup U, Baranowski R, Ekman S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conserv. Biol.* 9:1208–15

Nilsson SG, Baranowski R. 1994. Indikatorer på jätteträdskontinuitet—svenska förekomster av knäppare som är beroende av grova, levande träd [Indicators of megatree continuity—Swedish distribution of click beetles (Coleoptera, Elateridae) dependent on hollow trees]. *Entomol. Tidskr.* 115:81–97. In Swedish with English summ.

Nilsson SG, Baranowski R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography* 20:491–98

Nilsson T. 1997. *Spatial population dynamics of the black tinder fungus beetle*, Bolitophagus reticulatus (*Coleoptera: Tenebrionidae*). PhD thesis. Univ. Uppsala, Sweden. 44 pp.

Nordén B, Paltto H. 2001. Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. *Biol. Conserv.* 101:1–8

Økland B, Bakke A, Hågvar S, Kvamme T. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers. Conserv.* 5:75–100

Palm T. 1959. Die Holz- und Rindenkäfer der süd- und mittelschwedischen Laubbäume [The wood- and bark-beetles of south and mid-Swedish broadleaves]. *Opusc. Entomol.* 16 (Suppl.):1–374. In German

Parker SP. 1982. *Synopsis and Classification of Living Organisms*. New York: McGraw-Hill. 1232 pp.

PEFC. 1999. Pan Eur. For. Certif. Website: http://www.pefc.org/

Peltonen M. 1999. Windthrows and dead-standing trees as bark-beetle breeding

material at forest-clearcut edge. *Scand. J. For. Res.* 14:505–11

Price K, Pojar J, Roburn A, Brewer L, Poirier N. 1998. Windthrown or clearcut—what's the difference? *Northwest Sci.* 72:30–32

Ranius T. 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biol. Conserv.* 103:85–91

Ranius T, Hedin J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* 126:363–70

Ranius T, Jansson N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95:85–94

Read HJ. 1991. *Pollard and Veteran Tree Management.* London: Corp. London. 60 pp.

Ross DW, Niwa CG. 1997. Using aggregation and antiaggregation pheromones of the Douglas-fir beetle to produce snags for wildlife habitat. *West. J. Appl. For.* 12:52–54

Rukke BA. 2000. Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. *Ecography* 23:492–502

Safranyik L, Linton DA. 1999. Spruce beetle (Coleoptera: Scolytidae) survival in stumps and windfall. *Can. Entomol.* 131:107–13

Savely HE. 1939. Ecological relations of certain animals in dead pine and oak logs. *Ecol. Monogr.* 9:321–85

Schiegg K. 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* 7:290–98

Schmitt M. 1992. Buchen-Totholz als Lebensraum für xylobionte Käfer [Dead beech wood as habitat for xylobiont beetles]. *Waldhygiene* 19:97–191. In German

Schowalter TD, Caldwell BA, Carpenter SE, Griffiths RP, Harmon ME, et al. 1992. Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. In *Tropical Ecosystems: Ecology and Management*, ed. KP Singh, JS Singh, pp. 373–83. New Delhi, India: Wiley Eastern

Shirt DB. 1987. *British Red Data Books: 2. Insects.* Peterborough, UK: Nat. Conserv. Counc.

Siitonen J. 1994a. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Ann. Zool. Fenn.* 31:89–95

Siitonen J. 1994b. Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scand. J. For. Res.* 9: 185–91

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49:11–42

Siitonen J, Saaristo L. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol. Conserv.* 94:211–20

Sippola A, Kallio R. 1995. Species composition of beetles (Coleoptera) in different habitats within old-growth and managed forests in Finnish Lapland. In *Northern Wilderness Areas: Ecology, Sustainability, Management*, ed. A Sippola, P Alaraudanjoki, B Forbes, V Hallikainen, pp. 59–77. Rovaniemi, Finland: Arctic Cent.

Sippola A, Siitonen J, Kallio R. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scand. J. For. Res.* 13:204–14

Speight MCD. 1989. *Saproxylic Invertebrates and their Conservation.* Strasbourg, Fr: Counc. Eur. 79 pp.

Spence JR, Langor DW, Niemelä J, Carcamo H, Currie CR. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33:173–84

Spies TA, Franklin JF, Thomas TB. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689–702

Sverdrup-Thygeson A, Midtgaard F. 1998. Fungus-infected trees as islands in boreal forest: spatial distribution of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae). *Ecoscience* 5:486–93

Swift MJ. 1977. The ecology of wood decomposition. *Sci. Prog.* 64:175–99

Tate KR, Ross DJ, O'Brien BJ, Kelliher FM. 1993. Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. *Soil Biol. Biochem.* 25:1601–12

Tavakilian G, Berkov A, Meurer-Grimes B, Mori S. 1997. Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guyana. *Bot. Rev.* 63:303–55

Thirgood JV. 1989. Man's impact on the forests of Europe. *J. World For. Resour. Manage.* 4:127–67

Thomas CD. 2000. Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. London Ser. B* 267:139–45

Thunes KH, Midtgaard F, Gjerde I. 2000. Diversity of Coleoptera of the bracket fungus *Fomitopsis pinicola* in a Norwegian spruce forest. *Biodivers. Conserv.* 9:833–52

Torgersen TR, Bull EL. 1995. Down logs as habitat for forest-dwelling ants—the primary prey of pileated woodpeckers in northeastern Oregon. *Northwest Sci.* 69:294–303

Tritton LM, Martin CW, Hornbeck JW, Pierce RS. 1987. Biomass and nutrient removals from commercial thinning and whole-tree clear-cutting of central hardwoods. *Environ. Manage.* 11:659–66

Twinn PFG, Harding PT. 1999. *Provisional Atlas of the Longhorn Beetles (Coleoptera, Cerambycidae) of Britain*. Abbots Ripton, UK: Nat. Environ. Res. Counc. 96 pp.

UK For. Comm. 1998. *The UK Forestry Standard: The UK Government's Approach to Sustainable Forestry*. Edinburgh: For. Comm.

Väisänen R, Biström O, Heliövaara K. 1993. Sub-cortical Coleoptera in dead pines and spruces: Is primeval species composition maintained in managed forests? *Biodivers. Conserv.* 2:95–113

Wall J. 1999. Fuelwood in Australia: impacts and opportunities. In *Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration*, ed. RJ Hobbs, CJ Yates, pp. 372–81. Chipping Norton, Aust.: Surrey Beatty & Sons

Warren MS, Key RS. 1991. Woodlands: past, present and potential for insects. In *The Conservation of Insects and their Habitats*, ed. NM Collins, JA Thomas, pp. 155–203. London: Academic

Weslien J, Schroeder LM. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *For. Ecol. Manage.* 115:267–75

Wikars L-O. 2001. The wood-decaying fungus *Daldinia loculata* (Xylariaceae) as an indicator of fire-dependent insects. *Ecol. Bull.* 49:263–68

Woldendorp G, Keenan RJ, Ryan MF. 2001. *Coarse Woody Debris in Australian Forest Ecosystems*. Canberra, Aust.: AFFA Bur. Rural Sci.

Wood GA, Hasenpusch J, Storey RI. 1996. The life history of *Phalacrognathus muelleri* (Macleay) (Coleoptera, Lucanidae). *Aust. Entomol. Mag.* 23:37–48

Yee M, Yuan Z, 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.* 13:119–28