## Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests

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#### **Summary**

This paper reviews the biodiversity conservation issues relating to management of coarse woody debris (CWD) in the wet eucalypt production forests of Tasmania, with particular emphasis on clearfell, burn and sow (CBS) silviculture and on fuelwood harvesting. CBS is the standard silvicultural system in these forests, while fuelwood harvesting, as currently proposed, would involve the recovery of a higher proportion of felled biomass than standard CBS, as well as some pre-existing CWD.

Studies and practices from around the world are considered that have relevance to the temperate Australian forestry situation in general, and the Tasmanian situation in particular. The paper considers the ecological roles of CWD in natural forest ecosystems, emphasising its value as a key structural component and as habitat for biodiversity (especially invertebrates). Temporal continuity and spatial connectivity in supply of CWD, and presence of larger-diameter CWD, emerge as key factors determining community richness and composition. Whilst levels of CWD naturally fluctuate spatially and temporally in wet eucalypt forests, studies from northern temperate and boreal forests with similar dynamics demonstrate that, historically, management of native forests has tended to result in a gradual diminution of the CWD resource. Larger-diameter material is readily diminished through management, with potential consequences for dependent biodiversity.

Suggested mitigation measures (landscape-level and coupe-level), to accommodate biodiversity concerns and avoid a long-term conservation management problem for forest managers in Tasmania, centre on two main concerns. One is the likelihood that current standard rotation lengths used in CBS are probably too short to allow for the recruitment of sufficient CWD to replace that which is lost through harvesting, regeneration burning and natural decomposition. The other concern is that fuelwood harvesting may significantly increase the impacts of CBS on biodiversity in general and on threatened species in particular.

*Keywords:* forest management; logging; clearcutting; fuelwood; wood residues; forest fires; biodiversity; population dynamics; invertebrates; sclerophyllous forests; reviews; Tasmania

#### Introduction

In Tasmania, clearfelling, followed by regeneration burning and sowing of native eucalypt seed from local sources (called 'clearfell, burn and sow', and hereafter referred to as CBS) is the standard silvicultural system in the lowland wet eucalypt forests (Hickey et al. 2001). Whilst the extent to which clearfelling actually affects biodiversity continues to be debated, a neglected aspect of the debate is its effect on coarse woody debris (CWD). Much work remains to be done in Tasmania to determine typical natural CWD volumes in wet eucalypt forests at different stages in their development. In the present context, CWD is defined as fallen dead wood, down to a small-end diameter of 10 cm. Recentlycollected data suggest that Tasmanian wet eucalypt forests have the potential to support some of the greatest volumes of CWD in the world, rivalling or even exceeding forests in parts of the USA Pacific Northwest (Meggs 1996; Woldendorp et al. 2002a,b). Clearly, consideration of CWD and its biodiversity is an important part of assessing the ecological impact of Tasmanian forestry.

Information on CWD and its biodiversity in Tasmania is important at present because plans for introducing industrial-scale fuelwood harvesting in these forests, which may involve the recovery of some



**Figure 1.** Coarse woody debris, chiefly comprising logging waste, following clearfelling in wet *Eucalyptus obliqua* forest in southern Tasmania. Photo: Simon Grove.



**Figure 2.** Coarse woody debris, chiefly comprising logging waste, remaining in a clearfelled wet *Eucalyptus obliqua* forest in southern Tasmania following a hot regeneration burn. Photo: Simon Grove.



**Figure 3.** Coarse woody debris, chiefly comprising logging waste, from a clearfelled wet *Eucalyptus obliqua / Eucalyptus regnans* forest in southern Tasmania. The CWD has been heaped for processing into fuelwood. Note that this coupe forms part of a trial of fuelwood harvesting, and represents a 'worst case scenario' in terms of quantities and types of residue harvested. Photo: Simon Grove.

pre-existing CWD as well as a higher proportion of felled biomass than standard CBS, are well advanced. CBS generally produces large amounts of CWD as logging residue (Fig. 1). Regeneration burns reduce these amounts somewhat, but most of the larger material, including pre-existing logs, survives the burn to decay *in situ* (Slijepcevic 2001) (Fig. 2). Fuelwood harvesting could potentially recover much of this 'waste', before the coupe is burnt (Fig. 3), for electricity generation in a wood-fired power station.

The management of CWD and its ecological values has increasingly become a cornerstone of mainstream forestry in Europe and North America, following a rapid rise in awareness of its value for biodiversity (Harmon et al. 1986; Kirby and Drake 1993; Hanski and Hammond 1995; Freedman et al. 1996; Franklin 1989; Harmon 2001; Siitonen 2001). CWD management warrants greater consideration in Australian forestry too (Lindenmayer and Franklin 2002; Lindenmayer et al. 2002), but currently the literature that would assist Australian managers is sparse, since much of the international literature scarcely addresses the Australian situation. This paper arose out of an internal review for Forestry Tasmania (Grove et al. 2002) that examined issues of the management of CWD with particular reference to Tasmania's wet eucalypt forests. It is presented here to reach a broader audience, since many of the issues are common throughout the eucalypt forests of Australia. Its objectives are to review and discuss (1) the ecological functions of CWD, (2) effects of production forestry on CWD, (3) consequences of forestry-induced changes to CWD, (4) the ecological values of CWD in managed forests in Europe and North America, and (5) some recommendations for CWD management and further research in Tasmania.

#### Some of the ecological functions of CWD

CWD has many ecological functions in a natural forest, the main ones of which are reviewed here (and see also Lindenmayer *et al.* 2002). Most of the studies reported are from regions other than Australia, but many of the same ecological principles should apply to Tasmania and other parts of Australia.

#### Substrate for saproxylic and epixylic organisms

Conservation biologists increasingly recognise the value of CWD as a key substrate for a vast but often overlooked component of forest biodiversity (Speight 1989; Kirby and Drake 1993; Hallenberg et al. 1994; Hanski and Hammond 1995; Hammond 1997; Dajoz 2000). Species dependent on decaying wood microhabitats (e.g. many invertebrates and fungi) are called saproxylic (Speight 1989), while those that colonise its surface (e.g. many lichens and bryophytes) are called epixylic (e.g. Laaka 1992). Saproxylic species are a speciose functional group in native forest (Grove 2002a). In a recent Finnish study, 42% of the beetle species caught in a survey of mature boreal forest were saproxylic (Martikainen et al. 2000), while in a German study, 56% of the regional forest beetle species were considered to be saproxylic (Köhler 2000). Since beetles account for some 40% of all insect species (Grove and Stork 2000), and since Parker (1982) has estimated that the number of species of CWD-dependent beetle may outnumber all terrestrial vertebrates by at least two to one, this translates into a large number of dependent species worldwide. At the Warra Long-Term Ecological Research (LTER) site in Tasmania's southern forests, more than 350 beetle species have been collected from Eucalyptus obliqua logs (Yee et al. 2001) a large number compared to that found in many other studies (reviewed in Grove 2002a). CWD also supports many dependent species in other insect orders (especially flies, Økland 1996; Rotheray et al. 2001) and in other invertebrate taxa, such as earthworms (Hendrix 1993), mites (Johnston and Crossley 1993), velvet worms (Mesibov and Ruhberg 1991) and molluscs (Caldwell 1996). Wood-rotting fungi in CWD are also diverse (Nakasone 1993; Hoiland and Bendiksen 1996; Rydin et al. 1997; Edmonds and Lebo 1998; Lumley et al. 2000; Nordén and Paltto

2001). Many lichens (Barkman 1983; Qian *et al.* 1999) and bryophytes (Rambo and Muir 1998; Ódor and Standovár 2001) are primarily epixylic; 165 bryophyte species have recently been recorded on logs at Warra LTER site (Turner 2003). CWD in aquatic systems is relatively poor in saproxylic species but supports some specialist invertebrates whose activities enhance the value of CWD for other colonists (e.g. McKie and Cranston 1998).

#### Physical habitat structure

CWD adds greatly to the structural complexity of the forest floor. At the scale at which most forest-floor organisms operate, this structural complexity increases the range of microclimates and microhabitats available for exploitation, allowing greater numbers of individuals and species to co-exist than would otherwise be the case. For instance, a recent study on spider diversity in a Canadian forest (Buddle 2001) concluded that CWD was a habitat component favoured by many otherwise purely terrestrial species, especially web-builders. In the USA Pacific Northwest, populations of small insectivorous mammals such as shrews can be strongly correlated with the availability of CWD because of its value in augmenting feeding habitat (Lee 1995; Butts and McComb 2000). In California, Canada and Sweden, herbivorous small mammals such as voles can show similar relationships even though they do not directly depend on CWD for sustenance (Tallmon and Mills 1994; Bowman et al. 2000; Ecke et al. 2001).

CWD may serve as an equally important provider of habitat structure in aquatic systems (Bragg and Kershner 1999), though these have been little studied in the Tasmanian setting (e.g. Davies *et al.* 2001). Invertebrate communities dependent on submerged and floating dead wood can be speciose and abundant (Braccia and Batzer 2001), in turn supporting vertebrate predators, such as duck-billed platypus and (in the Northern hemisphere) salmonid fish (e.g. Flebbe 1999).

#### Nesting or denning sites

Hollow logs in Australian forests are frequently used as dens or nesting sites by a range of mammals and reptiles. In Tasmanian wet eucalypt forests, partly rotten logs can be an important nesting site for little pygmy possums (Duncan and Taylor 2001).

#### **Refuge from environmental extremes**

CWD, especially in the form of large logs, retains moisture more readily than does fine litter or the soil surface (Amaranthus *et al.* 1989). Some plants and animals that do not otherwise have any association with CWD may nevertheless depend on it for moisture in dry conditions (Clausen 1964). Salamanders in the USA are a case in point (Means *et al.* 1996). Responses to logging observed amongst some frogs in New South Wales (Margules *et al.* 1995; Lemckert 1999) can also be explained in terms of susceptibility to desiccation. Long-beaked echidnas may also resort to foraging amongst logs under dry conditions (Smith *et al.* 1989).

CWD also provides a refuge from other environmental extremes, particularly fire. For example, the persistence of litter-dwelling stag beetles in Tasmanian wet production forest (Michaels and Bornemissza 1999) was attributed to their ability to survive silvicultural burns by taking refuge beneath large logs. The preference by the endangered broad-toothed stag beetle *Lissotes latidens* of the SE Tasmanian wet forest for forest with more than 10% ground cover of CWD (Meggs and Munks 2003) may also be attributable to this effect.

In some situations, including late successional stages of eucalypt forest or rainforest in Tasmania, logs are probably the main route to successful establishment of tree seedlings (Harmon and Franklin 1989; McKenny and Kirkpatrick 1999), in part because of their moisture-retentive properties.

#### Role in carbon storage, nutrient cycling and soil conditioning

CWD acts as a long-term store of carbon (Laiho and Prescott 1999; Mackensen and Bauhus 1999), which is released gradually through decomposition (Jenisch and Harmon 2002). Decomposition is brought about by fungi and other microorganisms, often mediated by insects and other invertebrates (Swift 1977; Edmonds and Eglitis 1989; Hanula 1993; Schowalter *et al.* 1998). Decomposing CWD is the means by which many of the nutrients, carbon and energy accumulated by the living tree are returned to the soil, helping to maintain levels of organic matter and carbon therein (McFee and Stone 1966; Tate *et al.* 1993), contributing to the soil weathering process (Kayahara 1998), and making nutrients available for re-use by future trees and other organisms (Olson 1963; Laiho and Prescott 1999).

The presence of highly decayed CWD in soil also favours its colonisation by mycorrhizal fungi (Smith *et al.* 2000) which can be important for tree health.

# Heterogeneity and variation in space and time: a key ecological attribute of CWD

At the scales of space and time at which most organisms perceive it, CWD is a heterogeneous resource (Hope 1987; Sigrist and Job 1996; Pyle and Brown 1999; Allen *et al.* 2000). Different CWDdependent species have preferences for different CWD microhabitats, which is one explanation for the large number of species supported by CWD. Some of the factors contributing to this heterogeneity are discussed below.

#### The habitat value of CWD depends on how predictable its supply is in relation to population dynamics of particular species

Colonisation of CWD depends partly on its predictability of occurrence and its degree of isolation from other CWD. There are two aspects to this relationship: connectivity in space, and continuity in time (Hanski 1999a). Each exerts an influence on individual species depending on their own population dynamics. Dispersal strategies vary amongst species, with some species being extremely sedentary while others are very mobile. Whilst there is ample evidence from Europe and North America that some species associated with dead wood are relatively poor dispersers (e.g. Jonsson *et al.* 2001), the degree to which the biota is composed of sedentary or highly mobile species may vary from place to place, partly depending on the natural dynamics of CWD in the landscape (McPeek and Holt 1992). Where CWD abundance naturally fluctuates (as, for instance, in forests where CWD decays very rapidly and/or inputs are sporadic), most dependent species would be expected to be highly mobile. Where CWD abundance

tends to be more constant (as, for instance, in forests where CWD decays slowly and/or inputs are more regular), more sedentary species would be expected to predominate, and issues of habitat connectivity and continuity may become more critical (Edman and Jonsson 2001).

Exactly where Tasmania's wet eucalypt forests lie with regard to CWD dynamics at the landscape scale is unclear. Rates of decay of logs are likely to be very low, favouring sedentary species, yet inputs are naturally sporadic (influenced by wildfires with a return frequency of 20–400 y), favouring mobile species. It is likely that the forests support species assemblages with a range of dispersal abilities (as reported by Bashford 1990), with more mobile species predominating at some points in time and in some locations, while more sedentary species predominate at others.

Evidence for the importance of connectivity and continuity amongst saproxylic species is mostly derived from studies in which the availability of CWD has been artificially reduced through a long history of forest management, resulting in observable differences in habitat occupancy with isolation. In Switzerland, Schiegg (2000) found different assemblages of saproxylic beetles and flies in forests characterised by differing degrees of connectivity of CWD on the ground; plots with higher dead wood connectivity were associated with greater species richness. In a Finnish study (Siitonen 1994), specialist beetle species were more abundant in a forest containing abundant CWD than in one in which dead wood was scarce. Also in Finland, Sippola and Kallio (1995) found a positive relationship between CWD volume and beetle species richness at the stand (1 ha) scale. In Norway, Økland et al. (1996) found a positive relationship between CWD volume and beetle species richness at the broader (32 ha) but not the stand (1 ha) scale. At all scales, the diversity of dead tree parts, the number of large-diameter dead trees and the number of species of polypore fungi were all correlated with richness of beetle species and with the abundance of many species; several species were absent below a certain density of CWD. In Germany, Pfarr and Schrammel (1991) concluded that logs in areas where dead wood was scarce were still colonised by beetles as long as they occurred in a region in which most of the forest was characterised by abundant CWD. In studies in the USA (Chandler 1991) and northeastern Queensland (Grove 2002b), the greater abundance of many beetle species in old-growth compared to regrowth forest was considered to be due to the greater prevalence of suitable dead wood habitat in the old growth. In the latter study, this was borne out by the observed strong correlation between richness of saproxylic beetle species and the volume of CWD in the surrounding area (Grove 2002c).

In general, landscape-level habitat continuity is less likely to be a limiting factor for many saproxylic or epixylic species in regions which are still largely forested, such as northern Fennoscandia (Ohlson *et al.* 1997; Martikainen *et al.* 2000; Nordén 2001), and perhaps parts of Tasmania. It becomes more relevant in regions where forests are already reduced to small remnants, such as the UK (Dempster 1991; Rose 1993; Harding and Alexander 1994), and also locally in Australia's dry woodlands (Driscoll *et al.* 2000).

Whatever the dispersal ability of dependent species, many are thought to exhibit metapopulation dynamics in response to the unpredictable occurrence of their chosen habitat (Hanski 1999b). CWD is inherently a patchy resource in space and time. While a single piece of CWD (or a fungal sporocarp on CWD) may last long enough for several generations of a particular species, sooner or later it will decay away, resulting in the local extinction of that species' population, members of which will have to disperse to find another piece (Whitlock 1992; Thomas 1994). As a general principle, species able to disperse across large distances, such as many spore-dispersing fungi (Edman and Jonsson 2001; Nordén 2001) and bark-beetles (Nilssen 1984), should be able to find suitable habitat wherever it occurs in the landscape. Species with intermediate dispersal abilities, such as winged insects, some fungi (Talbot 1952; Stenlid and Gustafsson 2001) and some bryophytes (Söderström and Jonsson 1989), should be able to do so if suitable habitat patches occur within perhaps a few hundred metres of their previous patch. The most sedentary species, such as flightless or flight-reluctant saproxylic beetles (Greenslade 1972; Meggs and Taylor 1999; Jonsson et al. 2001; Ranius and Hedin 2001), velvet-worms (Barclay et al. 2000) and molluscs (Caldwell 1996; Tattersfield et al. 2001), may be dependent on finding suitable habitat patches within perhaps metres of their previous patch.

Evidence for metapopulation dynamics amongst saproxylic species is increasing (reviewed by Grove 2002a). Whitlock (1992) demonstrated the existence of a metapopulation structure in a study of the fungus-beetle *Bolitotherus cornutus* in the USA, and Ranius (2001) did so for the tree hollow-dependent scarab beetle *Osmoderma eremita* in Sweden. In Norway, Sverdrup-Thygeson and Midtgaard (1998) and Rukke and Midtgaard (1998) found that the probability of occurrence of the fungus-beetle *Bolitophagus reticulatus* decreased with distance at the scale of sporocarps on a single log, logs in a stand, and isolated forest blocks in an agricultural matrix.

## The habitat value of CWD for particular species depends on its decay stage and type

CWD exists in varying degrees of decay, from structurally intact through to an amorphous mass that merges into the soil. Many published studies have considered the succession of species occupying dead wood as it decomposes, and most report that each successional stage has its own characteristic species. Among these studies are Shigo (1967) and Kaarik (1975) for microorganisms; Dix and Webster (1995), Niemelä *et al.* (1995) and Boddy (2001) for fungi; Söderström (1988) for lichens and bryophytes; and Blackman and Stage (1924), Ingels (1933), Greenslade (1972), Stephen and Dahlsten (1976) and Marshall *et al.* (1998) for insects. A succession of insect species may occupy a single wood-rotting polypore fungal fruiting body (Jonsell *et al.* 1999).

At any particular stage of decay, different fungal and microbial communities may give rise to different types of decay (brown rots, white rots, wet or dry rots, etc.) (Meggs 1996; May and Simpson 1997). Recent work in the Warra LTER site has demonstrated clear associations between certain species or assemblages of saproxylic insect and certain types of decay (Yee *et al.* 2001). In Japan, different species of stag beetle were found to be associated with different types of decay (Araya 1993). In Finland, different beetle assemblages were associated with dead birch wood decayed by different fungi (Kaila *et al.* 1994), while in the UK and Sweden, different assemblages of insect have been found to inhabit different parts of fruiting bodies of different wood-rotting fungi (Paviour-Smith 1960; Jonsell *et al.* 2001).

# The habitat value of CWD for particular species depends on its history of exposure to fire

Many early successional species of insects, fungi, lichens and bryophytes are fire-adapted, and this extends to those dependent on CWD. Some species will colonise only charred wood or ashbeds; others compete most successfully in such situations (Evans 1971; Warcup 1990; Wikars 1995). The proportion of the forest saproxylic fauna that is fire-dependent may depend on the natural fire regime. At least in Scandinavia, tree species pre-adapted to fire disturbance support a richer and more host-specific fire-dependent biota than tree species for which fire disturbance is atypical (Wikars 2002). Some wood-rotting fungi are stimulated to produce fruiting bodies by fire (Gribb and Gribb 1971), and many apparently fire-dependent insects are associated with these fungi, especially ascomycetes (Wikars 2002). Some micropezid flies are attracted by wood smoke (Bickel 1996), presumably because it signals potential breeding sites (larvae apparently feed in fungi on dead wood). Likewise, the saproxylic buprestid beetle Melanophila acuminata has been shown to be capable of detecting infrared radiation from forest fires as a means of locating new breeding habitat (Evans 1966). Lundberg (1984), Muona and Rutanen (1994), Ehnström et al. (1995) and Wikars (1997) have all highlighted the importance of burning for the boreal forest insect faunas of Scandinavia, particularly for associates of dead wood; Danks and Foottit (1989) have also done so for Canadian boreal forest. Lundberg (1984) noted 54 Swedish beetle species for which dead burnt trees were the major habitat. Wikars (2001) and Penttilä and Kotiranta (1996) also noted the importance of fires for certain wood-rotting fungi in Scandinavia, including rare species.

Many Australian studies have examined the effect of forest fires on invertebrates (Bornemissza 1969; Campbell and Tanton 1981; York 1991; Neumann 1992; Friend 1995; Collett 2000; York 2001), bryophytes (Brasell and Mattay 1984) and fungi (Gribb and Gribb 1971; Warcup 1990; Taylor 1991), but these have generally not expressly considered fire dependence amongst CWD-dependent species. Packham et al. (2002) considered macrofungi in some Tasmanian southern forest sites of different ages and with different fire histories. Burnt wood and unburnt wood on the forest floor were two key environmental factors related to macrofungal community structure, the two factors having relationships with very different communities. Similarly, McMullan-Fisher et al. (2002) found that most of the macrofungi apparent in clearfelled and burnt Eucalyptus regnans forest in Victoria were growing on charred wood and burnt soil. These fungi formed a distinct community comprising species largely absent from later successional stages. Despite these last two studies, there is insufficient information to say to what extent the saproxylic and epixylic biota is fire-adapted in Tasmanian wet eucalypt forest. However, the natural fire disturbance regime is not dissimilar to that in parts of Scandinavia which support a rich fire-dependent saproxylic insect fauna (Wikars 1995).

#### The value of CWD as habitat for particular species depends on the tree taxon from which it was derived

Amongst saproxylic organisms, host-specificity is rare at the tree species level, although it is common at higher plant taxonomic levels (May and Simpson 1997; Tavakilian *et al.* 1997; Rotheray

*et al.* 2001). In German forests, Köhler (2000) found that 13% of the saproxylic beetle species were tree genus-specific. Host specificity is highest amongst organisms inhabiting freshly dead wood (Dix and Webster 1995; Hammond *et al.* 2001) which still retains chemical compounds derived from the living tree (Sigrist and Job 1996). As decomposition proceeds, host specificity declines. The situation in Tasmania is not well understood, but probably follows patterns similar to those seen elsewhere.

# The habitat value of CWD for particular species depends on its dimensions and its original position on the tree from which it was derived

CWD of different sizes, or originating from different parts of the tree (bole, branchwood) tends to support different though overlapping combinations of saproxylic species (Hoiland and Bendiksen 1996; Singh and Bhandari 1997; Schiegg 2001) and epixylic species (McAlister 1995; Rambo and Muir 1998). For saproxylic species, CWD diameter is thought to be a key characteristic determining which species make use of the resource. Some are able to use their chosen substrate whatever its dimensions (Palm 1959), but many are more particular (Elton 1966; Esaki 1996). For saproxylic insects, most studies suggest a positive relationship between the diameter of dead wood and species richness, incidence or abundance (reviewed in Grove 2002a). For instance, Kleinevoss et al. (1996) found more species of saproxylic beetle on large-diameter CWD in German forests. In the USA, Torgersen and Bull (1995) found that carpenter ants prefer large logs to smaller ones. In Finland, Siitonen and Saaristo (2000) found that the incidence of the red-listed saproxylic beetle Pytho kolwensis in spruce logs was positively correlated with log diameter.

Jonsell et al. (1998) devised models based on known habitat associations of Swedish red-listed invertebrates associated with CWD. These models predicted that most species would occur in CWD 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. Current research projects at the Warra LTER site aim to clarify the importance of log diameter in Tasmanian wet eucalypt forests (Yee et al. 2001; Grove and Bashford 2003). Various explanations exist for the apparent favourability of large-diameter CWD. First, it is a highly heterogeneous resource, allowing many specialist species to coexist (Kolström and Lumatjärvi 2000). Second, largediameter CWD takes longer to decompose, and a more stable microclimate is maintained within, favouring many species (Palm 1959). Third, large-diameter CWD supports more species of fungi, including species apparently specific to large-diameter wood (Kruys and Jonsson 1999; Nordén and Paltto 2001), on which many saproxylic insects depend. A recent study from Eucalyptus regnans forest in Victoria suggested a similar relationship with diameter for some macrofungi (McMullan-Fisher et al. 2002).

## The habitat value of CWD for particular species depends on its location and orientation

CWD in contact with the forest floor is easier to colonise for organisms that can move through or over the soil, such as collembola (Marshall *et al.* 1998) and velvet-worms (Barclay *et al.* 2000), whereas suspended CWD tends to be colonised more

by airborne organisms such as bark-beetles (Nilssen 1984), scarab beetles (Ranius and Hedin 2001) and many fungi (Nordén and Larsson 2000). Whether CWD is in sun or shade affects its moisture-retaining properties and its temperature, and therefore which species can exploit it (Buisson 1999). Species favouring cool, moist CWD will therefore predominate in shaded logs and on sites with a southerly aspect in the southern hemisphere (e.g.

on sites with a southerly aspect in the southern hemisphere (e.g. the velvet-worm *Euperipatoides rowelli* in NSW, Barclay *et al.* 2000), while those which are thermophilic or shade-intolerant will predominate in sun-exposed logs and on sites with a more northerly aspect. In Fennoscandian boreal forest, species in the latter category are in the majority, at least amongst the beetles (Økland *et al.* 1996; Martikainen 2001; Sverdrup-Thygeson and Ims 2002).

# Some potential impacts of production forestry on CWD

By managing forests so that wood can be removed before it is 'lost' to decay, CWD is often progressively depleted. However, natural CWD abundance partly depends on its rates of input and output, and whether these are in equilibrium. Logging can alter both rates, but especially the rate of input. The rate of input might temporarily increase above natural levels through the accumulation of logging residue, especially the first time a mature native forest is logged. Such a situation has been reported for Tasmanian wet eucalypt forest (Meggs 1996), and northern US beech forest (Gore and Patterson 1986). Heightened inputs to riparian areas are also likely at this stage (e.g. Campbell and Doeg 1989; Benda *et al.* 2002). Fire suppression and pest outbreaks brought on by forest management can also increase CWD levels (Edmonds and Marra 1999).

On the other hand, the rate of input of CWD will often decrease in the longer term. Reductions in dead wood may be most rapid and thorough through forest hygiene practices (Schmitt 1992), salvage logging (Maser 1996) or whole-tree, fuelwood or biomass harvesting (Tritton et al. 1987; Wall 1999). Incremental losses are also likely under almost any silvicultural system, as existing old trees die, the dead wood they produced decomposes, and the younger trees of the residual or replacement stand have a lower level of biomass and relatively small diameters. These changes may extend to adjacent aquatic systems (e.g. Liljaniemi et al. 2002). CWD may eventually be reduced from abundance to rarity. This is the long-term prognosis for managed native forests predicted by many researchers (e.g. Gore and Patterson 1986; Spies et al. 1988; Andersson and Hytteborn 1991; Bader et al. 1995; Meggs 1996; Reid et al. 1996). Goodburn and Lorimer (1999) reported that quantities of CWD on the forest floors of selectively logged hardwood forests in Wisconsin and Michigan were only about 60% those found in old-growth forests, with differences in large-diameter material being even more pronounced. In the USA Pacific Northwest, Spies and Cline (1988) predicted that log abundance would be 30% of the pre-harvest level at the end of the first 100-y rotation, and only 6% at the end of the second. 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 is none left. The situation may be similar wherever native forests are heavily

exploited for fuelwood (e.g. China: Nalepa *et al.* 2001; South Africa: DuPlessis 1995; Australia: Driscoll *et al.* 2000).

Reductions in CWD availability can be exacerbated by changes in diameter-class distributions. Managed stands tend to lack the largest-diameter trees which are often the main generators of CWD, so the proportion contributed by large-diameter material generally decreases (Grove 2001). Since small-diameter pieces would be expected to decay more rapidly than larger ones (Harmon *et al.* 1986), this can ultimately result in even less CWD in managed stands. A surge in CWD contributed by logging residue can also alter the relative proportions of CWD in different decay stages. Initially, it will elevate levels of CWD in early decay stages. As the logging residue decomposes, it contributes to pulses in successive decay stages.

Fire management is a common silvicultural tool with an effect on CWD. Often the aim is fire suppression, to avoid losses of merchantable wood to wildfire. In boreal forests, fire suppression can lead to a reduction in early successional forest and to an increase in stand density, resulting in a greater prevalence of shaded as opposed to sun-exposed CWD (Johnson et al. 2001). In other forests, such as Tasmania's wet eucalypt forests, burning following clearfelling is a standard silvicultural practice. These forests are naturally fire-prone, and wildfires of various scales and intensities, with a return interval of 20-400 y (Hickey et al. 1999; Alcorn et al. 2001), are thought to be the main source of large-scale natural disturbance. This is one reason why clearfell, burn and sow silviculture (CBS) has long been considered the most appropriate for managing these forests (Attiwill 1994). Burning is done to reduce the amount of logging residue, especially fine litter, to make sowing and/or natural regeneration easier in the resultant ash-bed (Ashton 1987).

In Tasmania's wet eucalypt forests, silvicultural alternatives that involve much lower levels of post-harvest burns than CBS are now being considered (Hickey *et al.* 2001). Because wildfire is a natural event in these forests, no-burn alternatives may signal a greater deviation from natural CWD dynamics compared to CBS. Not burning residue may initially leave more CWD, but it may be a more homogeneous resource, as it will lack charred wood and ash-beds. If a proportion of the CWD is then harvested as fuelwood, its abundance, size-class distribution and spatial arrangement will also be altered.

## Some potential ecological consequences of forestryinduced changes to CWD

Reducing the amount of CWD, and altering its distribution, composition and dynamics, can greatly affect dependent biodiversity. Writing from a UK 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 to be an underestimate (reviewed in Grove 2002a). 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'.

In Europe, a region where deforestation and forest management have been intensive and long-term, many saproxylic and epixylic species are now confined to the least intensively managed forests (Speight 1989; Hammond and Harding 1991; Stubbs 1991; Kirby and Drake 1993; McLean and Speight 1993; Fowles 1997; Key et al. 2000). European threatened species lists are often dominated by CWD-dependent species, and would probably be even more so if most such species were not so unfamiliar to the bulk of ecologists and legislators (Berg et al. 1993). Examples include lichens (Thor 1998), bryophytes (Laaka 1992), fungi (Stenlid and Gustafsson 2001) and invertebrates (Geiser 1983; Shirt 1987; Blab et al. 1994; Jonsell et al. 1998). In Sweden, logs are considered the key habitat for 28% of the 739 red-listed forest invertebrate species (Berg et al. 1995), while in the UK, the removal of dead wood is considered the main threat for 65% of the country's 150 threatened woodland insect species (Hambler and Speight 1995).

Many other species dependent on dead wood are already extinct throughout most of their prehistoric range, as evidenced by their wider occurrence as subfossils in peat deposits (Buckland and Dinnin 1993) or in early entomological collections (Speight 1989; Nilsson and Baranowski 1997). Buckland and Dinnin (1993) list 17 saproxylic beetle species known in the UK only from subfossils, mostly from peat deposits dating from 4880 years BP, 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. Hammond (1974) reported the loss from the UK of a further 20 beetle species over the past two centuries, and a fifth of the remaining saproxylic cerambycid beetle fauna is now considered threatened (Twinn and Harding 1999).

Regarding effects of forestry-induced changes in CWD, one issue is how CWD distribution and dynamics in the managed forest relate to the population dynamics of dependent species. In theory, if CWD becomes so sparsely distributed that species dependent on it cannot readily cross from one piece or patch to another, then they may die out as their own patch becomes unsuitable or disappears. Likewise, if CWD vanishes temporarily from a piece of forest, then it may be recolonised only by those species for which the nearest source is sufficiently near to enable them to do so — that is, the more mobile species. Both these issues are difficult to quantify, especially when there may be several timedependent processes at work over different time-scales (e.g. decomposition of remnant logs over decades, annual or multiannual life cycles of insects, change in the mean age of stands in the landscape over several years as more and more coupes are treated). Referring to butterflies, Thomas (2000) found that the species least able to tolerate habitat fragmentation were those with medium levels of mobility. Species with higher mobility could disperse amongst widely scattered patches, while species with low mobility tended to occur at higher densities in their favoured patches and hence were less prone to extinction, at least in the short to medium term.

Studies that have examined the impacts of management-induced changes in CWD distribution and dynamics have already been mentioned above. Whilst most studies have been carried out within single blocks of forest, some have taken a landscape-scale approach. Together they suggest that effects of reduction of CWD are likely to manifest themselves at many scales; sometimes they may be evident only at the landscape scale. Fahrig (2001) found that habitat quality in the matrix was as critical as its quality in remnants. If matrix quality was high enough, species could survive in the landscape even if remnants were sparse. If it was low, however, species extinctions would be avoided only by maintaining abundant habitat remnants.

The effects of fire suppression on fire-adapted CWD-dependent biodiversity can be marked. In Fennoscandia, fire suppression threatens many fire-adapted saproxylic insects as well as thermophilic, shade-intolerant and poorly competitive species that can comprise a large proportion of the regional fauna (Wikars 1995; Økland et al. 1996; Martikainen 2001). In southern Sweden, where silvicultural burns are no longer the norm, a single wildfire site was found to support 27 endangered wood-living insect species (Ahnlund and Lindhe 1992) - many of them endangered because of fire suppression and the dominance of no-burn silviculture in the region as a whole. There is now the suggestion of similar effects in Canadian boreal forests (Pedlar et al. 2002). In a Tasmanian study, most of the fungi forming mycorrhizas with eucalypt seedlings growing on clearfelled and burnt sites were found to be fire-adapted ascomycetes belonging to 58 species (Warcup 1991). Presumably these would be much less prevalent in the absence of silvicultural burns.

## Catering for the ecological values of CWD in managed forests: North American and European experience

#### **Historical perspective**

The forestry profession's relationship with CWD continues to change to reflect the values and concerns of society. Harmon (2001) reviewed historical trends in this relationship in the USA Pacific Northwest — trends that are mirrored elsewhere. He considered that natural forest management had gone through three phases with respect to its treatment of CWD: (1) 'wasteful logging'; (2) waste reduction — salvage logging and fuelwood harvesting; and (3) CWD retention. During the first phase, primarily involving logging of old-growth forests, CWD levels either increased or declined slightly depending on intensity. In the second phase, with increasing awareness of resource limits and economic efficiency, forestry practices resulted in much lower levels of CWD. Lofroth (1998) argued that the characteristic attitude during this phase amounted to 'zero waste tolerance'. Alarm at the ecological effects of this forestry has led to the current adoption in this region of forestry standards (Harmon's third phase) that specify management practices for the retention of CWD. Harmon (2001) concluded that, for the USA Pacific Northwest, 'forest managers are moving away from a "blanket" removal of all the woody detritus possible, to leaving and even enhancing the amounts in forests'. During this period, retained CWD levels have begun to rise, though they have not generally reached natural levels.

The transition from Harmon's phase 2 to phase 3 is not proving an easy one for the forestry profession. It can lead to conflicting legislative requirements, as is the case in British Columbia (BCMoF 2000), where current standards specify the removal of CWD for forest health and hygiene reasons, while planned standards specify its retention for biodiversity. Even in Sweden, where the biodiversity value of CWD is well appreciated, there is growing pressure from industry to use 'waste' wood for fuelwood — but equally a growing resistance to doing so (Ehnström 2001). Elsewhere in Europe, industrial fuelwood is increasingly either sourced from 'traditional' plantation waste (Nuñez-Regueira *et al.* 2002) or from energy plantations (Ford-Robertson *et al.* 1993), so biodiversity concerns are fewer.

Harmon (2001) has suggested that a future phase of forest management (phase 4) in the USA Pacific Northwest might see CWD return to near-natural levels. This would require extending the current static concept of forestry standards to a more dynamic one. One shortfall of the current approach, because the main management intervention occurs at harvesting, is that the adoption of minimum standards can lead to static management of a dynamic entity. In other words, prescribing the retention of certain amounts of CWD now may not be sufficient to ensure that CWD exists in ecologically appropriate amounts through the ensuing decades and centuries. Adopting a more dynamic approach might involve landscape-scale modelling of CWD in relation to forest management and natural disturbance at all stages of the silvicultural cycle, and setting standards for each stage.

#### Legal and policy aspects

In Europe and North America, maintenance of CWD is now generally given relatively high priority in forest policy and planning. For instance, Guideline 4.2h of the Helsinki Process (developed to ensure that sustainability criteria are met at the operational level in the participating countries of Europe) states that 'standing and fallen dead wood...should be left in quantities and distribution necessary to safeguard biological diversity'. The voluntary Pan-European Forest Certification System has since adopted these criteria, and many European countries now have national or regional standards based on the Helsinki criteria and indicators (Grove 2001). In Swedish boreal forest, national Forest Stewardship Council certification criteria require not just the maintenance of CWD but its enhancement (Raivio et al. 2001). For instance, the Swedish National Board of Forestry aims to increase dead wood levels by 50% during this decade (Ehnström 2001). In Sweden and Finland, certification criteria require the re-introduction of prescribed burning following clearfelling, specifically for fire-dependent species (Raivio et al. 2001). In the USA, management standards are devised on a bioregional (or forestry regional) basis. Many such regions have standards relating to the retention of dead wood, though often referring to forests managed under selection systems and focusing on standing dead trees.

#### **Practical aspects**

Despite the legal and policy framework that exists in many parts of the world to support CWD retention and enhancement, there is little information on how this is done in practice. Most documented interventions concern techniques for maintaining or enhancing forest stand structure to cater for biota dependent on standing dead trees (Morrison and Raphael 1993; Ross and Niwa 1997; Graves *et al.* 2000; Harris 2000; Hallett *et al.* 2001). There has been comparatively little emphasis on intervention for logs on the ground. This may reflect the prevalence of selection silvicultural systems, in which catering for standing dead trees ultimately ensures that logs are catered for too. Franklin (1989) mentioned the idea of felling 'cull' trees to supplement CWD levels, but again this refers to a selection system, as do the more numerous references from the UK concerning what amounts to intensive care for dead wood (Warren and Key 1991; Kirby and Drake 1993).

### Some recommendations for CWD management and further research in Tasmania

If the conceptual model developed by Harmon (2001) of the historical development of the forestry profession's attitudes towards CWD management has any relevance in Tasmania's wet eucalypt forests, it seems that native forest management here is still in phase 1 ('wasteful logging') but considering entering phase 2 ('waste reduction'). Ecologically it would make more sense to skip phase 2 altogether, and to proceed to phase 3 or even to phase 4. In phase 3, it is envisaged that CWD levels would not drop greatly below natural levels because of the application of static forestry standards at the time of harvesting. In phase 4, it is envisaged that CWD would be maintained at near-natural levels through the prudent application of forestry standards throughout the silvicultural cycle.

Native forest management is likely to be most compatible with biodiversity conservation (including that for CWD-dependent biota) when it most closely mimics natural forest dynamics (Hansen et al. 1991). This applies the world over, even though natural forest dynamics and silvicultural systems may differ. In Tasmania's wet eucalypt forests, where wildfire is the main largescale disturbance, the use of clearfelling followed by regeneration burning may currently be allowing the survival of species that in the long-term would be disadvantaged by the 'benign neglect' approach adopted in adjacent conservation areas (Brown 1996). Thus, to some extent, the fate of many species may depend on how the production forest estate is managed. However, CBS, as currently practised, does not adequately cater for forest structural complexity (Franklin 1989) — at least at the coupe level. If it were to do so, much longer rotations might be required (Hickey 1994), coupled with strategies (such as aggregated retention) to maintain mature forest structures (e.g. commercially overmature trees, standing dead trees and large-diameter logs) within coupes throughout the silvicultural cycle.

On the basis of current understanding, the following key interim mitigation measures for reducing the potential effects of fuelwood harvesting are recommended:

- providing fuelwood primarily from coupes scheduled for conversion to plantation (since these will be managed on short rotations and will be unable to support much CWD in the long term);
- limiting the intensity and extent of fuelwood harvesting in non-conversion forest, especially for larger-diameter and longer-lived CWD;
- 3. monitoring to determine the efficacy of these interim mitigation measures.

It is also clear that ecological knowledge is currently insufficient for firm conclusions to be drawn regarding the full nature and extent of likely effects of fuelwood harvesting, or indeed of CBS. Two recent publications propose research agendas to address key gaps in knowledge: Jonsson and Kruys (2001) with respect to Scandinavian boreal forests, and Lofroth (1998) with respect to forests in British Columbia and the USA Pacific Northwest. Many of the suggestions are equally relevant in Tasmania and are incorporated here, and also appear in a recent independent review of Tasmanian fuelwood harvesting plans (Raison *et al.* 2002).

- 1. Refine local models of the dynamics of CWD and incorporate sensitivity analyses, and develop them as tools for risk management.
- 2. Review the degree to which alternative silvicultural systems currently being trialled in wet eucalypt forest at Warra may address some of the concerns regarding management of dead wood raised in this review.
- 3. Investigate the feasibility of extending the length of CBS rotations.
- 4. Investigate the extent, composition and ecology (especially dispersal ability) of local biota dependent on dead wood (in CWD, standing dead trees and living trees), and the effects of different silvicultural systems on these (including no-burn and low-burn options).
- 5. Develop robust landscape-level planning tools that address concerns for biodiversity at all appropriate scales.
- 6. Assess the extent to which mitigation measures used elsewhere in the world can be applied in Tasmania.

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#### References

- Ahnlund, H. and Lindhe, A. (1992) Endangered wood-living insects in coniferous forests some thoughts from studies of forest-fire sites, outcrops and clearcuttings in the province of Sormland, Sweden. *Entomologisk Tidskrift* **113**, 13–23.
- Alcorn, P.J., Dingle, J.K. and Hickey, J.E. (2001) Age and stand structure in a multi-aged wet eucalypt forest at the Warra silvicultural systems trial. *Tasforests* 13, 245–260.
- Allen, R.B., Buchanan, P.K., Clinton, P.W. and Cone, A.J. (2000) Composition and diversity of fungi on decaying logs in a New Zealand temperate beech (*Nothofagus*) forest. *Canadian Journal* of Forest Research **30**, 1025–1033.
- Amaranthus, M.P., Parrish, D.S. and 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. Forest Service Region 10, Juneau, AK, USA, pp. 191–194.
- Andersson, L.I. and Hytteborn, H. (1991) Bryophytes and decaying wood
  a comparison between managed and natural forest. *Holarctic Ecology* 14, 121–130.
- Araya, T.E. (1993) Relationship between decay types of dead wood and occurrence of Lucanid beetles (Coleoptera: Lucanidae). *Applied Entomology and Zoology* 28, 27–33.
- Ashton, D.H. (1987) Tall eucalypt forests. In: Brown, M.J., Jarman, S.J. and Williams, K.J. (eds) *The Tall Eucalypt Workshop*. Forestry Commission, Hobart, pp. 5–20.

- Attiwill, P.M. (1994) Ecological disturbance and the conservative management of eucalypt forests in Australia. *Forest Ecology and Management* 63, 301–346.
- Bader, P., Jansson, S. and Jonsson, B.G. (1995) Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biological Conservation* 72, 355–362.
- Barclay, S., Ash, J.E. and Rowell, D.M. (2000) Environmental factors influencing the presence and abundance of a log-dwelling invertebrate, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). *Journal of Zoology* 250, 425–436.
- Barkman, J.J. (1983) De betekenis van dood hout voor mossen en korstmossen [Dead wood as a substrate for moss and lichen communities]. (In Dutch with English summary.) Nederlands Bosbouwtijdschrift 55, 65–70.
- Bashford, D. (1990) The dispersal of ground beetles into different aged eucalypt plantations in north eastern Tasmania. *Tasforests* 2, 43–51.
- BCMoF (2000) A Short-term Strategy for Coarse Woody Debris Management in British Columbia's Forests. British Columbia Ministry of Forests.
- Benda, L.E., Bigelow, P. and Worsley, T.M. (2002) Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, USA. *Canadian Journal of Forest Research* 32, 1460–1477.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J. (1993) Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8, 718–731.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J. (1995) Threat levels and threats to red-listed species in Swedish forests. *Conservation Biology* 9, 1629–1633.
- Bickel, D.J. (1996) Smoke flies (Diptera: Platypezidae) and the Sydney bushfires. *Australian Entomological Magazine* **23**, 77–78.
- Blab, J., Nowak, E., Trautmann, W. and Sukopp, H. (1994) Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland. Kilda-Verlag, Greven.
- Blackman, M.W. and Stage, H.H. (1924) On the succession of insects living in the bark and wood of dying, dead and decaying hickory. *Technical Bulletin, New York State College of Forestry* 17, 3–268.
- 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.
- Bornemissza, G. (1969) The re-invasion of burnt woodland areas by insects and mites. *Proceedings of the Ecological Society of Australia* **4**, 138.
- Bowman, J., Sleep, D., Forbes, G. and Edwards, M. (2000) The association of small mammals with coarse woody debris at log and stand scales. *Forest Ecology and Management* **129**, 119–124.
- Braccia, A. and Batzer, D.P. (2001) Invertebrates associated with woody debris in a southeastern US forested floodplain wetland. *Wetlands* 21, 18–31.
- Bragg, D. and Kershner, J. (1999) Coarse woody debris in riparian zones. Journal of Forestry **97**, 30–35.
- Brasell, H.M. and Mattay, J.P. (1984) Colonisation by bryophytes of burned *Eucalyptus* forest in Tasmania, Australia: changes in biomass and element content. *The Bryologist* 87, 302–307.
- Brown, M.J. (1996) Benign neglect and active management in Tasmania's forests: a dynamic balance or ecological collapse? *Forest Ecology and Management* **85**, 279–289.
- Buckland, P.C. and 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*. English Nature, Peterborough, pp. 6–20.

- 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.
- Buisson, R. (1999) Should deadwood be left in sun or shade? *British Wildlife* **10**, 342.
- Butts, S.R. and McComb, W.C. (2000) Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. *Journal of Wildlife Management* **64**, 95–104.
- Caldwell, R.S. (1996) Macroinvertebrates and their relationship to coarse woody debris with special reference to land snails. In: McMinn, J.W. and Crossley, D.A.J. (eds) *Biodiversity and Coarse Woody Debris in Southern Forests*. USDA Forest Service, Washington, DC, pp. 49–54.
- Campbell, A.J. and Tanton, M.T. (1981) Effects of fire on the invertebrate fauna and litter of a eucalypt forest. In: Gill, A.M., Groves, R.H. and Noble, I.R. (eds) *Fire and the Australian Biota*. Australian Academy of Science, Canberra, ACT.
- Campbell, I.C. and Doeg, T.J. (1989) Impacts of timber harvesting and production on streams: a review. *Australian Journal of Marine and Freshwater Research* **40**, 519–539.
- Chandler, D.S. (1991) Comparison of some slime-mold and fungus feeding beetles (Coleoptera) in an old-growth and 40-year-old forest in New Hampshire. *Coleopterists' Bulletin* **45**, 239–256.
- Clausen, E. (1964) The tolerance of hepatics to desiccation and temperature. *The Bryologist* **67**, 411–417.
- Collett, N.G. (2000) Catastrophic wildfire and its short-term effects on families of Order Coleoptera (beetles) in *Eucalyptus regnans* forest in the Central Highlands of Victoria. *Australian Forestry* **63**, 7–21.
- Dajoz, R. (2000) Insects and Forests. Intercept, Andover.
- Danks, H.V. and Foottit, R.G. (1989) Insects of the boreal zone of Canada. *Canadian Entomologist* **121**, 625–690.
- Davies, P., Cook, L., Risdon, M. and Walker, R. (2001) Stream biological research at Warra. *Tasforests* **13**, 101–108.
- Dempster, J.P. (1991) Fragmentation, isolation and mobility of insect populations. In: Collins, N.M. and Thomas, J.A. (eds) *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 143–154.
- Dix, N. and Webster, J. (1995) Colonization and decay of wood. In: Dix, N.J. and Webster, J. (eds) *Fungal Ecology*. Chapman and Hall, New York, pp. 145–169.
- Driscoll, D., Mikovits, G. and Freudenberger, D. (2000) *Impact and Use of Firewood in Australia*. CSIRO Sustainable Ecosystems, Canberra, ACT.
- Duncan, A.M.R. and Taylor, R.J. (2001) Occurrence of pygmy possums, *Cercartetus lepidus* and *C. nanus*, and their nest sites in logged and unlogged dry and wet eucalypt forest in Tasmania. *Australian Forestry* 64, 159–164.
- DuPlessis, M.A. (1995) The effects of fuelwood removal on the diversity of some cavity-using birds and mammals in South Africa. *Biological Conservation* **74**, 77–82.
- Ecke, F., Lofgren, O., Hornfeldt, B., Eklund, U., Ericsson, P. and Sorlin, D. (2001) Abundance and diversity of small mammals in relation to structural habitat factors. *Ecological Bulletins* **49**, 165–171.
- Edman, M. and Jonsson, B.G. (2001) Spatial pattern of downed logs and wood-decaying fungi in an old-growth *Picea abies* forest. *Journal of Vegetation Science* **12**, 609–620.
- Edmonds, R.L. and 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. and Lebo, D.S. (1998) Diversity, production, and nutrient dynamics of fungal sporocarps on logs in an old-growth temperate rain forest, Olympic National Park, Washington. *Canadian Journal* of Forest Research **28**, 665–673.
- Edmonds, R.L. and 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. and Seybold, C. (eds) Proceedings of the Pacific Northwest Forest and Rangeland Soil Organism Symposium, Corvallis, OR, 1998, USDAFS Pacific Northwest research Station, Portland, OR, pp. 68–79.
- Ehnström, B. (2001) Leaving dead wood for insects in boreal forests suggestions for the future. *Scandinavian Journal of Forest Research* Supplement **3**, 92–98.
- Ehnström, B., Langström, B. and Hellqvist, C. (1995) Insects in burned forests — forest protection and faunal conservation (preliminary results). *Entomologica Fennica* 6, 109–117.
- Elton, C. (1966) Dying and dead wood. In: Elton, C. (ed.) *The Pattern* of Animal Communities. Methuen, London, pp. 279–305.
- Esaki, K. (1996) Emergence patterns and host wood diameter preference of seven cerambycid beetle species emerging from *Pinus parviflora* dead branches. *Elytra* **24**, 383–387.
- Evans, W.G. (1966) Perception of infrared radiation from forest fires by Melanophila acuminata DeGeer (Buprestidae, Coleoptera). Ecology 47, 1061–1065.
- Evans, W.G. (1971) The attraction of insects to forest fires. In: Tall Timbers Conference on Ecological Animal Control by Habitat Management. Tall Timbers Research Station, Tallahassee, Florida, pp. 115–127.
- Fahrig, L. (2001) How much habitat is enough? *Biological Conservation* **100**, 65–74.
- Flebbe, P.A. (1999) Trout use of woody debris and habitat in Wine Spring Creek, North Carolina. Forest Ecology and Management 114, 367–376.
- Ford-Robertson, J.B., Mitchell, C.P. and Watters, M.P. (1993) Short rotation coppice energy plantations: technology and economics. *Journal of Sustainable Forestry* **1**, 23–40.
- Fowles, A.P. (1997) The Saproxylic Quality Index: an evaluation of dead wood habitats based on rarity scores, with examples from Wales. *The Coleopterist* **6**, 61–66.
- Franklin, J. (1989) Toward a new forestry. American Forests 95, 37-44.
- Freedman, B., Zelanzny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G. and Woodley, S. (1996) Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental Reviews* 4, 238–265.
- Friend, G.R. (1995) Fire and invertebrates a review of research methodology and the predictability of post-fire response patterns. In: McCaw, W.L., Burrows, N.D., Friend, G.R. and Gill, A.M. (eds) Landscape Fires '93: Proceedings of an Australian Bushfire Conference. Perth, 1993. CALMscience Supplement 4, 165–174.
- 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: Gepp, J. (ed.) *Rote Listen gefährdeter Tiere* [*Red Lists of Threatened Species*]. Österreichs Bundesministerium für Gesundheit und Umweltschutz, Vienna, pp. 131–137.
- Goodburn, J.M. and Lorimer, C.G. (1999) Population structure in oldgrowth and managed northern hardwoods; an examination of the balanced diameter distribution concept. *Forest Ecology and Management* **118**, 11–29.

- Gore, J.A. and Patterson, W.A.I. (1986) Mass of downed wood in northern hardwood forests in New Hampshire: potential effects of forest management. *Canadian Journal of Forest Research* 16, 335–339.
- Graves, A.T., Fajvan, M.A. and Miller, G.W. (2000) The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. *Canadian Journal of Forest Research* 30, 1214–1220.
- Greenslade, P.J.M. (1972) Distribution patterns of *Priochirus* species (Coleoptera: Staphylinidae) in the Solomon Islands. *Evolution* **26**, 130–142.
- Gribb, A.B. and Gribb, J.W. (1971) Polyporus fruiting following a bush fire. *Queensland Nature* **20**, 59.
- Grove, S.J. (2001) Extent and composition of dead wood in Australian lowland tropical rainforest with different management histories. *Forest Ecology and Management* **154**, 35–53.
- Grove, S.J. (2002a) Saproxylic insects and the sustainable management of forests. *Annual Review of Ecology and Systematics* **33**, 1–23.
- Grove, S.J. (2002b) 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. (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. and 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. and Stork, N.E. (2000) An inordinate fondness for beetles. *Invertebrate Taxonomy* **14**, 733–739.
- Grove, S.J., Meggs, J. and Goodwin, A. (2002) A Review of Biodiversity Conservation Issues relating to Coarse Woody Debris Management in the Wet Eucalypt Production Forests of Tasmania. Forestry Tasmania, Hobart, 72 pp.
- Hallenberg, N., Söderström, L. and Appelqvist, T. (1994) Wood decomposing and epixylic organisms. In: Angelstam, P., Bondrup-Nielsen, S., Stenseth, N.C. and Stokland, J.N. (eds) *Biodiversity* and Management of Boreal Forests. Oxford University Press, Oxford.
- Hallett, J.G., Lopez, T., O'Connell, M.A. and Borysewicz, M.A. (2001) Decay dynamics and avian use of artificially created snags. *Northwest Science* 75, 378–386.
- Hambler, C. and Speight, M.R. (1995) Biodiversity conservation in Britain science replacing tradition. *British Wildlife* **6**, 137–147.
- 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. and Spence, J.R.S. (2001) Early colonization of *Populus* wood by saproxylic beetles. *Canadian Journal of Forest Research* 31, 1175–1183.
- Hammond, P.M. (1974) Changes in the British coleopterous fauna. In: Hawksworth, D.L. (ed.) *The Changing Flora and Fauna of Britain*. Academic Press, London, pp. 323–369.
- Hammond, P.M. and Harding, P.T. (1991) Saproxylic invertebrate assemblages in British woodlands: their conservation significance and its evaluation. In: Read, H.J. (ed.) *Pollard and Veteran Tree Management*. Corporation of London, London, pp. 30–37.
- Hansen, A.J., Spies, T.A., Swanson, F.K. and Ohmann, J.L. (1991) Conserving biodiversity in managed forests: lessons from natural forests. *BioScience* 41, 382–392.
- Hanski, I. (1999a) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87, 209–219.
- Hanski, I. (1999b) *Metapopulation Ecology*. Oxford University Press, Oxford.

- Hanski, I. and Hammond, P.M. (1995) Biodiversity in boreal forests. *Trends in Ecology and Evolution* 10, 5–6.
- Hanula, J.L. (1993) Relationship of wood-feeding insects and coarse woody debris. In: McMinn, J.W. and Crossley, D.A. (eds) Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service, Athens, GA, pp. 55–81.
- Harding, P.T. and Alexander, K.N.A. (1994) The use of saproxylic invertebrates in the selection and conservation of relic forest in pasture-woodland. *British Journal of Entomology and Natural History* 7, 21–26.
- Harmon, M.E. (2001) Moving towards a new paradigm for woody detritus management. *Ecological Bulletins* 49, 269–278.
- Harmon, M.E. and Franklin, J.F. (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70, 48–59.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Lienkaemper, G.W., Cromack, K.J. and Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**, 133–302.
- Harris, R.B. (2000) Estimating large snag recruitment needs in regeneration timber harvests. Western Journal of Applied Forestry 15, 140–146.
- Hendrix, P.F. (1993) Earthworms, biodiversity, and coarse woody debris in forest ecosystems of the southeastern USA. In: McMinn, J.W. and Crossley, D.A. (eds) Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service, Athens, GA, pp. 43–48.
- Hickey, J.E. (1994) A floristic comparison of vascular species in Tasmanian oldgrowth mixed forest with regeneration resulting from logging and wildfire. *Australian Journal of Botany* 42, 383–404.
- Hickey, J.E., Su, W., Rowe, P., Brown, M.J. and Edwards, L. (1999) Fire history of the tall eucalypt forests of the Warra ecological research site, Tasmania. *Australian Forestry* 62, 66–71.
- Hickey, J.E., Neyland, M.G. and Bassett, O.D. (2001) Rationale and design for the Warra silvicultural systems trial in wet *Eucalyptus obliqua* forests in Tasmania. *Tasforests* 13, 155–182.
- Hoiland, K. and Bendiksen, E. (1996) Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sor-Trondelag County, Central Norway. *Nordic Journal of Botany* 16, 643–659.
- Hope, S.M. (1987) Classification of decayed *Abies amabilis* logs. *Canadian Journal of Forest Research* **17**, 559–564.
- Huston, M.A. (1996) Models and management implications of coarse woody debris impacts on biodiversity. In: McMinn, J.W. and Crossley, D.A. (eds) Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service, Athens, GA, pp. 139–143.
- Ingels, L.G. (1933) The succession of insects in tree trunks as shown by the collection from various stages of decay. *Journal of Entomology* and Zoology 25, 57–59.
- Jenisch, J.E. and Harmon, M.E. (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiology* 22, 77–89.
- Johnson, E.A., Miyanishi, K. and Bridge, S.R.J. (2001) Wildfire regime in the boreal forest and the idea of suppression and fuel buildup. *Conservation Biology* 15, 1554–1557.
- Johnston, J.M. and Crossley, D.A. (1993) The significance of coarse woody debris for the diversity of soil mites. In: McMinn, J.W. and Crossley, D.A. (eds) Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service, Athens, GA, pp. 82–87.
- Jonsell, M., Weslien, J. and Ehnström, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7, 749–764.

- Jonsell, M., Nordlander, G. and Jonsson, M. (1999) Colonization patterns of insects breeding in wood-decaying fungi. *Journal of Insect Conservation* 3, 145–161.
- Jonsell, M., Nordlander, G. and Ehnström, B. (2001) Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. *Ecological Bulletins* 49, 173–194.
- Jonsson, B.G. and Kruys, N. (2001) Ecology of coarse woody debris in boreal forests: future research directions. *Ecological Bulletins* 49, 279–281.
- Jonsson, M., Jonsell, M. and Nordlander, G. (2001) Priorities in conservation biology: a comparison between two polyporeinhabiting beetles. *Ecological Bulletins* **49**, 195–204.
- Kaarik, A. (1975) Succession of microorganisms during wood decay. In: Liese, W. (ed.) *Biological Transformation of Wood by Microorganisms*. Springer, Berlin, pp. 39–51.
- Kaila, L., Martikainen, P., Punttila, P. and Yakovlev, E. (1994) Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. *Annales Zoologici Fennici* **31**, 97–107.
- Kayahara, G. (1998) Effects of decaying wood on the weathering of soils in coastal British Columbia, Canada. *Northwest Science* 72, 74–76.
- Key, R.S., Drake, C.M. and Sheppard, D.A. (2000) Conservation of invertebrates in England: a review and framework. *English Nature Science* 35, 1–68.
- Kirby, K.J. and Drake, C.M. (1993) Dead Wood Matters: The Ecology and Conservation of Saproxylic Invertebrates in Britain. English Nature, Peterborough.
- Kleinevoss, K., Topp, W. and 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.
- 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]. (In German.) Landesamt für Agrarordnung NRW, Löbf.
- Kolström, M. and Lumatjärvi, J. (2000) Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. *Forest Ecology and Management* **126**, 113–120.
- Kruys, N. and Jonsson, B.G. (1999) Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research* 29, 1295–1299.
- Laaka, S. (1992) The threatened epixylic bryophytes in old primeval forests in Finland. *Biological Conservation* **59**, 151–154.
- Laiho, R. and Prescott, C.E. (1999) The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research* 29, 1592–1603.
- Lee, S.D. (1995) Comparison of population characteristics of three species of shrews and the shrew-mole in habitats with different amounts of coarse woody debris. *Acta Theriologica* **40**, 1–415.
- Lemckert, F. (1999) Impacts of selective logging on frogs in a forested area of northern New South Wales. *Biological Conservation* **89**, 321–328.
- Liljaniemi, P., Vuori, K.M., Ilyashuk, B., and Luotonen, H. (2002) Habitat characteristics and macroinvertebrate assemblages in boreal forest streams: relations to catchment silvicultural activities. *Hydrobiologia* **474**, 239–251.

- Lindenmayer, D.B. and Franklin, J.F. (2002) *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*. Island Press, Washington, DC.
- Lindenmayer, D.B., Claridge, A.W., Gilmore, A.M. and Michael, P. (2002) The ecological role of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota. *Pacific Conservation Biology* 8, 121–140.
- Lofroth, E. (1998) The dead wood cycle. In: Voller, J. and Harrison, S. (eds) Conservation Biology Principles for Forested Landscapes. UBC Press, Vancouver, BC, pp. 185–214.
- Lumley, T.C., Abbott, S.P. and Currah, R.S. (2000) Microscopic ascomycetes isolated from rotting wood in the boreal forest. *Mycotaxon* **74**, 395–414.
- Lundberg, S. (1984) Den brända skogens skalbaggsfauna i Sverige [The beetle fauna of burnt forest in Sweden]. (In Swedish with English summary.) *Entomologisk Tidskrift* **105**, 129–141.
- Mackensen, J. and Bauhus, J. (1999) *The Decay of Coarse Woody Debris*. Australian Greenhouse Office, Canberra, ACT.
- Margules, C.R., Davies, K.F., Meyers, J.A. and Milkovits, G.A. (1995) The responses of some selected arthropods and the frog *Crinia signifera* to habitat fragmentation. In: Bradstock, R.A., Auld, T.D., Keith, D.A., Kingsford, R.T., Lunney, D. and Sivertsen, D.P. (eds) *Conserving Biodiversity: Threats and Solutions*. Surrey Beatty and Sons Pty Ltd, Chipping Norton, NSW, pp. 94–103.
- Marshall, V.G., Setala, H. and Trofymow, J.A. (1998) Collembolan succession and stump decomposition in Douglas-fir. *Northwest Science* **72**, 84–85.
- Martikainen, P. (2001) Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletins* **49**, 205–218.
- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. and Rauh, J. (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation* 94, 199–209.
- Maser, C. (1996) Salvage logging the loss of ecological reason and moral restraint. *International Journal of Ecoforestry* 12, 176–178.
- May, T.W. and Simpson, J.A. (1997) Fungal diversity and ecology in eucalypt ecosystems. In: Williams, J. and Woinarski, J. (eds) *Eucalypt Ecology: Individuals to Ecosystems*. Cambridge University Press, Cambridge, pp. 246–277.
- McAlister, S. (1995) Species interactions and substrate specificity among log-inhabiting bryophyte species. *Ecology* **76**, 2184–2195.
- McFee, W.W. and Stone, E.L. (1966) The persistence of decaying wood in humus layers of northern forests. *Soil Science Society of America, Proceedings* **30**, 513–516.
- McKenny, H.J.A. and Kirkpatrick, J.B. (1999) The role of fallen logs in the regeneration of tree species in Tasmanian mixed forest. *Australian Journal of Botany* **47**, 745–753.
- McKie, B.G.L. and Cranston, P.S. (1998) Keystone coleopterans? Colonization by wood-feeding elmids of experimentally immersed woods in south-eastern Australia. *Marine and Freshwater Research* 49, 79–88.
- McLean, I.F.G. and Speight, M.C.D. (1993) Saproxylic invertebrates — the European context. In: Kirby, K.J. and Drake, C.M. (eds) *Dead Wood Matters: The Ecology and Conservation of Saproxylic Invertebrates in Britain*. English Nature, Peterborough, pp. 21–32.
- McMullan-Fisher, S.J.M., May, T.W. and Keane, P.J. (2002) The macrofungal community and fire in a mountain ash forest in southern Australia. *Fungal Diversity* **10**, 57–76.

- McPeek, M.A. and Holt, R.D. (1992) The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140, 1010–1027.
- Means, D.B., Palis, J.G. and Baggett, M. (1996) Effects of slash pine silviculture on a Florida population of flatwoods salamander. *Conservation Biology* **10**, 426–437.
- Meggs, J.M. (1996) Pilot Study of the Effects of Modern Logging Practices on the Decaying-log Habitat in Wet Eucalypt Forest in South-east Tasmania: Report to the Tasmanian RFA Environment and Heritage Technical Committee. Forestry Tasmania, Hobart, Tasmania. 74 pp.
- Meggs, J.M. and Munk, S.A. (2003) Distribution, habitat characteristics and conservation requirements of a forest-dependent threatened invertebrate *Lissotes latidens* (Coleoptera: Lucanidae). *Journal of Insect Conservation* 7, 137–152.
- Meggs, J.M. and 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.
- Mesibov, R. and Ruhberg, H. (1991) Ecology and conservation of *Tasmanipatus barretti* and *T. anophthalmus*, parapatric onychophorans (Onychophora: Peripatopsidae) from northeastern Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 125, 441–447.
- Michaels, K. and 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.
- Morrison, M.L. and Raphael, M.G. (1993) Modeling the dynamics of snags. *Ecological Applications* **3**, 322–330.
- Muona, J. and Rutanen, I. (1994) The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zoologici Fennici* **31**, 109–121.
- Nakasone, K.K. (1993) Diversity of lignicolous basidiomycetes in coarse woody debris. In: McMinn, J.W. and Crossley, D.A. (eds) Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service, Athens, GA, pp. 35–42.
- Nalepa, C.A., Li, L.I., Wen-Hua, L.U. and Lazell, J. (2001) Rediscovery of the wood-eating cockroach *Cryptocercus primarius* (Dictyoptera: Cryptocercidae) in China, with notes on ecology and distribution. *Acta Zootaxonomica Sinica* 26, 184–190.
- Neumann, F.G. (1992) Responses of foraging ant populations to high intensity wildfire, salvage logging and natural regeneration processes in *Eucalyptus regnans* regrowth forest of the Victorian central highlands. *Australian Forestry* **55**, 29–38.
- Niemelä, J., Renvall, P. and Penttilä, R. (1995) Interactions of fungi at late stages of wood decomposition. *Annales Botanici Fennici* **32**, 141–152.
- Nilssen, A.C. (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. *Annales Entomologici Fennici* 50, 37–42.
- Nilsson, S.G. and Baranowski, R. (1997) Changes in the distribution of southern click beetles dependent on dead trees (Coleoptera: Elateridae and Lissomidae) in Sweden. (In Swedish with English summary.) *Entomologisk Tidskrift* **118**, 73–98.
- Nordén, B. (2001) Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation* **10**, 779–791.
- Nordén, B. and Larsson, K-H. (2000) Basidiospore dispersal in the oldgrowth forest fungus *Phlebia centrifuga* (Basidiomycetes). *Nordic Journal of Botany* 20, 215–219.
- Nordén, B. and Paltto, H. (2001) Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. *Biological Conservation* **101**, 1–8.

- Nuñez-Regueira, L., Proupin-Castiñeiras, J. and Rodriguez-Anon, J.A. (2002) Energy evaluation of forest residues originated from *Eucalyptus globulus* Labill. in Galicia. *Bioresource Technology* 82, 5–13.
- Ódor, P. and Standovár, T. (2001) Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of managementinduced differences in dead wood. *Ecological Bulletins* **49**, 219–230.
- Ohlson, M., Söderström, L., Hornberg, G., Zackrisson, O. and Hermansson, J-O. (1997) Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation* **81**, 221–231.
- Økland, B. (1996) Unlogged forests: important sites for preserving the biodiversity of mycetophilids (Diptera: Sciaroidea). *Biological Conservation* **76**, 297–310.
- Økland, B., Bakke, A., Hågvar, S. and Kvamme, T. (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation* 5, 75–100.
- Olson, J.S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **44**, 322–331.
- Packham, J.M., May, R.M., Brown, M.J., Wardlaw, T.J. and Mills, A.K. (2002) Macrofungal diversity and community ecology in mature and regrowth wet eucalypt forest in Tasmania: a multivariate study. *Austral Ecology* 27, 149–161.
- Palm, T. (1959) Die Holz- und Rinden-Käfer der süd- und mittelschwedischen Laubbäume [The wood- and bark-beetles of south and mid-Swedish broadleaves]. (In German.) *Opuscula Entomologica* 16 (Suppl.), 1–374.
- Parker, S.P. (1982) Synopsis and Classification of Living Organisms. McGraw-Hill, New York.
- Paviour-Smith, K. (1960) The fruiting-bodies of macrofungi as habitats for beetles of the family Ciidae (Coleoptera). *Oikos* 11, 43–71.
- Pedlar, J.H., Pearce, J.L., Venier, L.A. and McKenney, D.W. (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. *Forest Ecology and Management* 158, 189–194.
- Penttilä, R. and Kotiranta, H. (1996) Short-term effects of prescribed burning on wood-rotting fungi. *Silva Fennica* **30**, 399–419.
- Pfarr, U. and Schrammel, J. (1991) Fichten-Totholz im Spannungsfeld zwischen Naturschutz und Forstschutz [Dead woody material of Norway spruce cause for strained relations between nature conservation and forestry]. (In German with English summary.) *Forstwissenschaftliches Centralblatt* **110**, 128–134.
- Pyle, C. and Brown, M.M. (1999) Heterogeneity of wood decay classes within hardwood logs. *Forest Ecology and Management* 114, 253–259.
- Qian, H., Linka, K. and Song, X. (1999) Cryptogams on decaying wood in old-growth forests of southern coastal British Columbia. *Journal* of Vegetation Science 10, 883–894.
- Raison, R.J., Kirschbaum, M.U.F., McCormack, R.J., Attiwill, P.M. and Richardson, A.M.M. (2002) *Review of the Science Relevant to the Sustainable Use of Native and Plantation Forest-harvesting Residues for Energy Production in Tasmania*. A report to Forestry Tasmania. CSIRO Forestry and Forest Products, Canberra. http:// www.aph.gov.au/senate/committee/ecita\_ctte/renewable\_energy/ submissions/sub36a.doc
- Raivio, S., Normark, E., Pettersson, B. and Salpakivi-Salomaa, P. (2001) Science and the management of boreal forest biodiversity — forest industries' views. *Scandinavian Journal of Forest Research* Suppl. 3, 99–104.
- Rambo, T.R. and Muir, P.S. (1998) Bryophyte species associations with coarse woody debris and stand ages in Oregon. *The Bryologist* 101, 266–276.

- Ranius, T. (2001) Constancy and asynchrony of Osmoderma eremita populations in tree hollows. Oecologia 126, 208–215.
- Ranius, T. and Hedin, J. (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* **126**, 363–370.
- Reid, C.M., Foggo, A. and Speight, M. (1996) Dead wood in the Caledonian pine forest. *Forestry* **69**, 275–279.
- Rose, F. (1993) Ancient British woodlands and their epiphytes. *British Wildlife* **5**, 83–93.
- Ross, D.W. and Niwa, C.G. (1997) Using aggregation and antiaggregation pheromones of the Douglas-fir beetle to produce snags for wildlife habitat. Western Journal of Applied Forestry 12, 52–54.
- Rotheray, G.E., Hancock, G., Hewitt, S., Horsfield, D., MacGowan, I., Robertson, D. and Watt, K. (2001) The biodiversity and conservation of saproxylic diptera in Scotland. *Journal of Insect Conservation* 5, 77–85.
- Rukke, B.A. and Midtgaard, F. (1998) The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented landscape. *Ecography* 21, 561–572.
- Rydin, K., Diekmann, M. and Hallingbäck, T. (1997) Biological characteristics, habitat associations, and distribution of macrofungi in Sweden. *Conservation Biology* **11**, 628–640.
- Schiegg, K. (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* **7**, 290–298.
- Schiegg, K. (2001) Saproxylic insect diversity of beech: limbs are richer than trunks. *Forest Ecology and Management* 149, 295–304.
- Schmitt, M. (1992) Buchen-Totholz als Lebensraum für xylobionte Käfer [Dead beech wood as habitat for xylobiont beetles]. (In German.) *Waldhygiene* **19**, 97–191.
- Schowalter, T.D., Zhang, Y.L. and Sabin, T.E. (1998) Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. *Ecography* 21, 3–10.
- Shigo, A.L. (1967) Succession of organisms in discoloration and decay of wood. In: Romberger, J.A. and Mikola, P. (eds) *International Review of Forestry Research II*, New York, pp. 237–299.
- Shirt, D.B. (1987) British Red Data Books: 2. Insects. Nature Conservancy Council, Peterborough.
- Sigrist, M-H.P. and Job, D. (1996) Mycological, entomological and physical-chemical study of decaying *Betula pendula* trunks: I. Spatial distribution of the physical-chemical state and mycoflora of trunks. (In French with English summary.) *Canadian Journal* of *Botany* 74, 1657–1664.
- Siitonen, J. (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. (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* **49**, 11–42.
- Siitonen, J. and Saaristo, L. (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation* **94**, 211–220.
- Singh, A.P. and Bhandari, R.S. (1997) Colonization, succession and preference for tree portion by insects on felled West Himalayan spruce, *Picea smithiana*. *Indian Forester* **123**, 656–663.
- Sippola, A. and Kallio, R. (1995) Species composition of beetles (Coleoptera) in different habitats within old-growth and managed forests in Finnish Lapland. In: Sippola, A., Alaraudanjoki, P., Forbes, B. and Hallikainen, V. (eds) Northern Wilderness Areas: Ecology, Sustainability, Management. Arctic Centre, Rovaniemi, pp. 59–77.

- Slijepcevic, A. (2001) Loss of carbon during controlled regeneration burns in *Eucalyptus obliqua* forest. *Tasforests* **13**, 281–290.
- Smith, A.P., Wellham, G.S. and Green, S.W. (1989) Seasonal foraging activity and micro-habitat selection by echidnas (*Tachyglossus aculeatus*) on the New England Tablelands. *Australian Journal of Ecology* 14, 457–466.
- Smith, J.E., Molina, R., Huso, M.M.P. and Larsen, M.J. (2000) Occurrence of *Piloderma fallax* in young, rotation age, and oldgrowth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, USA. *Canadian Journal of Botany* 78, 995–1001.
- Söderström, L. (1988) Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nordic Journal of Botany* **8**, 89–97.
- Söderström, L. and Jonsson, B.G. (1989) Spatial pattern and dispersal in the leafy hepatic *Ptilidium pulcherrimum*. *Journal of Bryology* **15**, 793–802.
- Speight, M.C.D. (1989) *Saproxylic Invertebrates and their Conservation*. Council of Europe, Strasbourg.
- Spies, T.A. and Cline, S.P. (1988) Coarse woody debris in forests and plantations of coastal Oregon. In: Maser, C., Tarrant, R.F., Trappe, J.M. and Franklin, J.F. (eds) *From the Forest to the Sea: A Story of Fallen Trees*. USDA Forest Service PNW-GTR, Portland, Oregon, pp. 5–23.
- Spies, T.A., Franklin, J.F. and Thomas, T.B. (1988) Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69, 1689–1702.
- Stenlid, J. and Gustafsson, M. (2001) Are rare wood decay fungi threatened by inability to spread? *Ecological Bulletins* 49, 85–92.
- Stephen, F.M. and Dahlsten, D.L. (1976) The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. *Canadian Entomologist* **108**, 283–304.
- Stubbs, A.E. (1991) Insects in dead wood in standing and fallen trees. In: Fry, R. and Lonsdale, D. (eds) *Habitat Conservation for Insects* — A Neglected Green Issue. Amateur Entomologists' Society, Middlesex, pp. 58–67.
- Sverdrup-Thygeson, A. and Ims, R.A. (2002) The effect of forest clearcutting on the community of saproxylic beetles on aspen. *Biological Conservation* **108**, 347–357.
- Sverdrup-Thygeson, A. and Midtgaard, F. (1998) Fungus-infected trees as islands in boreal forest: spatial distribution of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae). *Ecoscience* **5**, 486–493.
- Swift, M.J. (1977) The ecology of wood decomposition. Science Progress, Oxford 64, 175–199.
- Talbot, P.B.H. (1952) Dispersal of fungus spores by small animals inhabiting wood and bark. *Transactions of the British Mycological Society* **35**, 123–128.
- Tallmon, D. and Mills, L.S. (1994) Use of logs within home ranges of California red-backed voles on a remnant of forest. *Journal of Mammalogy* 75, 97–101.
- Tate, K.R., Ross, D.J., O'Brien, B.J. and Kelliher, F.M. (1993) Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. *Soil Biology and Biochemistry* **25**, 1601–1612.
- Tattersfield, P., Seddon, M.B. and Lange, C.N. (2001) Land-snail faunas in indigenous rainforest and commercial forestry plantations in Kakamega Forest, western Kenya. *Biodiversity and Conservation* 10, 1809–1829.

- Tavakilian, G., Berkov, A., Meurer-Grimes, B. and Mori, S. (1997) Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guyana. *Botanical Review* 63, 303–355.
- Taylor, R.J. (1991) Plants, fungi and bettongs: a fire-dependent coevolutionary relationship. Australian Journal of Ecology 16, 409–412.
- Thomas, C.D. (1994) Extinction, colonisation, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8, 373–378.
- Thomas, C.D. (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 267, 139–145.
- Thor, G. (1998) Red-listed lichens in Sweden: habitats, threats, protection and indicator value in boreal coniferous forests. *Biodiversity and Conservation* **7**, 59–72.
- Torgersen, T.R. and Bull, E.L. (1995) Down logs as habitat for forestdwelling ants — the primary prey of pileated woodpeckers in northeastern Oregon. *Northwest Science* **69**, 294–303.
- Tritton, L.M., Martin, C.W., Hornbeck, J.W. and Pierce, R.S. (1987) Biomass and nutrient removals from commercial thinning and whole-tree clear-cutting of central hardwoods. *Environmental Management* 11, 659–666.
- Turner, P.A.M. (2003) The ecology and conservation of bryophytes in Tasmanian wet eucalypt forest. PhD thesis. School of Geography and Environmental Studies, University of Tasmania.
- Twinn, P.F.G. and Harding, P.T. (1999) Provisional Atlas of the Longhorn Beetles (Coleoptera, Cerambycidae) of Britain. Natural Environment Research Council, Abbots Ripton.
- Wall, J. (1999) Fuelwood in Australia: impacts and opportunities. In: Hobbs, R.J. and Yates, C.J. (eds) *Temperate Eucalypt Woodlands in Australia: Biology, Conservation, Management and Restoration.* Surrey Beatty and Sons, Chipping Norton, NSW, pp. 372–381.
- Warcup, J.H. (1990) Occurrence of ectomycorrhizal and saprophytic discomycetes after fire in a eucalypt forest. *Mycological Research* 94, 1065–1069.
- Warcup, J.H. (1991) The fungi forming mycorrhizas on eucalypt seedlings in regeneration coupes in Tasmania. *Mycological Research* 95, 329–332.

- Warren, M.S. and 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*. Academic Press, London, pp. 155–203.
- Whitlock, M.C. (1992) Nonequilibrium population structure in forked fungus beetles: extinction, colonization, and genetic variation among populations. *American Naturalist* 139, 952–970.
- Wikars, L-O. (1995) Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Annales Zoologici Fennici* **32**, 375–384.
- Wikars, L-O. (1997) Brandinsekter i Orsa Finnmark: biologi, utbredning och artbevarande [Pyrophilous insects in Orsa Finnmark, Central Sweden: biology, distribution, and conservation]. (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, 1–2.
- Woldendorp, G., Keenan, R.J., and Ryan, M.F. (2002a) Coarse Woody Debris in Australian Forest Ecosystems: A Report for the National Greenhouse Strategy, Module 6.6. Bureau of Rural Sciences, Canberra, 75 pp.
- Woldendorp, G., Spencer, R.D., Keenan, R.J. and Barry, S. (2002b) An Analysis of Sampling Methods for Coarse Woody Debris in Australian Forest Ecosystems: A Report for the National Greenhouse Strategy, Module 6.6. Bureau of Rural Sciences, Canberra, 84 pp.
- Yee, M., Yuan, Z-Q. and 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.
- York, A. (1991) The response of ant communities to fire-induced habitat disturbance. *Australian Journal of Ecology* **16**, 261.
- York, A. (2001) Pyrophilic or pyrophobic? The response of forest beetle communities to an altered fire regime. In: *Proceedings of the Australasian Bushfire Conference*, 3–6 July 2001, Christchurch, NZ. Forest Research Institute, Rotorua, pp. 267–272.