

Wood-decaying fungi in the forest: conservation needs and management options

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Abstract Wood-decaying fungi are essential for the functioning of forest ecosystems. They provide habitat for many other organisms and enable the regeneration of forests throughout the world. Since wood decomposition is a decisive process in nutrient recycling, soil formation and the carbon budget of forest ecosystems, it is receiving increasing attention from forest ecologists, pathologists and managers. Research has focussed on the factors driving the species-richness of wood-decomposing organisms and is moving on to analyse the effects of this species-richness on ecosystem functioning. Coarse woody debris (CWD) and its associated wood-decaying organisms have been drastically reduced in abundance and diversity by forestry and so these features often have potential as conservation indicators. Protective measures at a landscape level are needed for threatened wood-inhabiting fungi. These include restricting salvage operations in windthrow stands, actively encouraging the accumulation of deadwood in forests, and facilitating decay in standing trees by inoculating them with fungi. Here, we aim to collect and summarize recently produced work on deadwood ecology, pointing out research gaps and perspectives.

Keywords Biogeography · Carbon sequestration · Forest ecosystem management · Functional diversity · Landscape fragmentation · Macroecology · Morticulture · Nurse logs · Old-growth · Polypores

Introduction

Deadwoodology, the ecology of deadwood (Grove 2002), is a thriving research field, with wood-decaying fungi playing a major role in it. Wood-decaying fungi are excellent ecosystem engineers, because they directly modulate the availability of resources other than themselves for several other functional groups (Harley 1971; Jones et al. 1994; Krajick 2001; Moore et al. 2004). The fundamental ecological significance of deadwood decomposition in forests has been highlighted in several reviews and conclusions for silviculture have been drawn repeatedly (Table 1). Essentially, modern forestry needs to retain appropriate levels of deadwood in managed forests, ideally in all its forms and density levels, in order to cover the full spectrum of habitat conditions (Samuelsson et al. 1994; MacNally et al. 2001; Berg et al. 2002; Vasiliauskas et al. 2004; Christensen et al. 2005) for the sake of dependent organisms and in order to achieve sustainability of timber production.

Much information on the process of wood-decay in forest ecosystems and on the organisms associated with it is currently scattered in individual papers. Here, focusing mainly on wood-decaying fungi (rather than saproxylic arthropods, molluscs, birds and other vertebrates dependent on deadwood) and on boreal and temperate forests (where most published research on this topic has been carried out), we aim to bring together recently published knowledge and to identify gaps in research dealing with this important part of biodiversity. The review is organized as follows: in the

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Table 1 Review papers highlighting the fundamental ecological significance of deadwood decomposition in forests and/or drawing conclusions for silviculture

Main focus	Main region	References
Wood decomposition	–	Swift (1977)
Temperate ecosystems	North America	Harmon et al. (1986)
Tree death	North America	Franklin et al. (1987)
Natural forest reserves	Germany	Albrecht (1991)
Guidelines for silviculture	Germany	Ammer (1991)
Biodiversity	Scandinavia	Samuelsson et al. (1994)
Canopies	North America	Parks and Shaw (1996)
Guidelines for silviculture	Britain	Hodge and Peterken (1998)
Maintaining biodiversity	North America	McComb and Lindenmayer (1999)
Forest reserves	Germany	Meyer (1999)
Managed forests	Sweden	Fridman and Walheim (2000)
Deadwood management	North America	Harmon (2001)
Functions of CWD	China	Hou and Pan (2001)
Status and ecology of decaying wood	UK	Butler et al. (2002)
Saproxyllic insects	Australia	Grove (2002)
Decay dynamics	Scandinavia	Kruys et al. (2002)
Habitat management	Britain	Bratton (2003)
Old-growth forests	Canada	Feller (2003)
Decaying beech logs	Denmark	Heilmann-Clausen and Christensen (2003)
Forest insects	Europe	Bouget and Duelli (2004)
Retention felling	Finland	Hautala et al. (2004)
Conifer plantations	Britain	Humphrey (2005)
Deadwood management	Scandinavia	Jonsson et al. (2005)

‘For a functional ecology of decay section’, we highlight the importance of deadwood for a range of organisms, and for the regeneration of forests (Deadwood as Noah’s ark section), we discuss the issue of whether deadwood size or other related factors drive the species-richness of wood-decaying fungi (What is driving the species-richness of wood-decaying fungi? section) and point out that the question of whether the species (and functional) diversity of wood-decaying organisms affects decomposition rates has been seldom addressed, but is relevant in the context of global climate change and carbon sequestration (Species-richness of wood-decaying fungi and ecosystem functioning section). In the ‘Conservation issues in deadwoodology section’, we show that conservation biologists are increasingly focussing on wood-decaying fungi as general indicators of forest ecosystem threat (How threatened are wood-decaying fungi? section). We then draw attention to studies applying the single large or several small? (SLOSS) debate to the conservation of wood-decaying fungi (And how well are we protecting them? section), addressing the consequences of regional habitat fragmentation for the meta-population persistence of wood-decaying fungi (Landscape perspectives for wood-decaying fungi section) and studying this aspect of biodiversity in tropical forests (Biogeography of CWD and of wood-decaying fungi section). We then

attempt a comparison of the amount of deadwood in extra-tropical versus tropical forests. In the ‘Deadwood management section’, we discuss opportunities provided by various kinds of disturbance (tree pathogens, windthrow and fire) in order to increase the amount of deadwood in managed forests (Creative ideas for a permanent flow of deadwood needed section), we review studies assessing whether management guidelines aiming to improve the presence of deadwood in forests are having success (Are deadwood guidelines having any noticeable effect? section), and identify active morticulture as a new method to encourage wood-decaying organisms in forests where their presence has been unduly suppressed (Active morticulture section). The review is concluded by a recapitulation of some outstanding research questions.

For a functional ecology of decay

Deadwood as Noah’s ark

Standing and fallen decaying trees are species-rich environments, and deadwood has been recognized as providing resources for a variety of living organisms (Table 2). Wood-decay is fundamental to the formation of ecological

niches (Odling-Smee et al. 2003), the wide variety of which reflects the potential decay pathways and ecological successions, together with the variety of the starting material. This includes standing deadwood (snags), fallen logs, living trees with heartrot and dying branches. In many cases, species and (meta)populations dependent on deadwood require a particular amount of coarse woody debris (CWD) at a certain stage of decay, thus demonstrating that deadwood niches should be defined quantitatively as well as qualitatively. In Europe an example is the flagship beetle species of tree hollows *Osmoderma eremita* (Ranius 2002). Niche opportunities for wood-decaying fungi are also shaped by interspecific interactions between different species (Coates and Rayner 1985a, b, c; Boddy 2000) as well as by intraspecific interactions (including nuclear reassortment between conspecific heterokaryons, see Johanneson and Stenlid 2004). Another layer of niche-definition comes from growing evidence that fungal species are often complexes of previously undifferentiated taxonomic units

which specialize in different ecological conditions [e.g. *Armillariamellea* s.l. (e.g. Guillaumin et al. 1993), *Heterobasidionannosum* s.l. (e.g. Niemelä and Korhonen 1998), *Laetiporus* spp. (Rogers et al. 1999), *Phellinus* spp. s.l. (Fischer and Binder 2004) and *Phialocephala fortinii* s.l. (Grünig et al. 2004)].

In many regions of the world, a list of taxa dependent on decaying wood is equivalent to a coarse inventory of threatened species (see How threatened are wood-decaying fungi? section). The amount of evidence testifying to the ecological utility of CWD accumulated in terrestrial ecosystems is staggering, and an equally fundamental structural and functional role is played in aquatic freshwater (Gurnell et al. 1995; Krajick 2001; Gurnell et al. 2002) and saline (e.g. Robertson 1991; Gilbert and Sousa 2002; Parent et al. 2004) ecosystems. Indeed, Noah's ark was made of nothing else but floating deadwood.

Moreover, the presence of dead and decaying wood is a functional requirement not only for animal wildlife, but also

Table 2 Examples of studies recognizing deadwood as the main source of resources for living organisms (see also reviews of Table 1)

Main organism(s)	Main region	References
Mountain gorillas (<i>Gorilla beringei</i>)	Uganda	Rothman et al. (2006)
Small mammals	OR, USA	Maser et al. (1978)
Small mammals and carnivores	Switzerland	Suter and Schielly (1998)
Small mammals	NB, Canada	Bowman et al. (2000)
American martens (<i>Martes americana</i>)	BC, Canada	Porter et al. (2005)
Least shrews (<i>Cryptotis parva</i>)	SC, USA	McCay and Komoroski (2004)
Red-backed voles (<i>Clethrionomys gapperi</i>)	MT, USA	Ucitel et al. (2003)
Deermice (<i>Peromyscus maniculatus</i>)	WA, USA	Lee (2004)
Arboreal marsupials	QLD, Australia	Wormington et al. (2003)
Bats	BC, Canada	Parsons et al. (2003)
Woodpeckers	TX, USA	Conner et al. (1976)
Red-breasted nuthatch (<i>Sitta canadensis</i>)	BC, Canada	Steeger and Hitchcock (1998)
Pileated woodpecker (<i>Dryocopus pileatus</i>)	MT, USA	McClelland and McClelland (1999)
Three-toed woodpecker (<i>Picoides tridactylus</i>)	Switzerland	Butler et al. (2004)
Red-cockaded woodpecker (<i>Picoides borealis</i>)	North America	Jackson and Jackson (2004)
Forest-floor vertebrates	OR, USA	Butts and McComb (2000)
Plethodontid salamanders	OR, USA	Alkaslassy (2005)
Soil macro-arthropods	Germany	Jabin et al. (2004)
Mycetophilids (Diptera)	Norway	Økland (1996)
Insects in boreal forests	Sweden	Ehnström (2001)
Insects in polypores	Sweden	Jonsell and Nordlander (2002)
Insects in <i>Fomitopsis pinicola</i>	Finland	Komonen (2003)
Coleoptera	Germany	Kappes and Topp (2004)
Gastropods	Germany	Kappes (2005)
Molluscs in mangrove forests	Australia	Robertson (1991)
Arachnida and other litter-dwelling invertebrates	New Zealand	Evans et al. (2003)
Bryophytes	Sweden	Andersson and Hytteborn (1991)
Bryophytes	Hungary	Ódor and Van Hees (2004)
Bryophytes and lichens	Britain	Humphrey et al. (2002)

for trees. In many cases, the regeneration of a forest only happens when fallen logs decay in situ. Decaying logs create differences in substrate; in turn, different micro-sites allow species with different niche requirements to coexist, thus influencing future stand composition. There are reports of a protective effect of CWD against pathogens of seeds (in *Picea engelmannii* and *Abies lasiocarpa*, Zhong and van der Kamp 1999) and of seedlings; in *Tsuga canadensis* (O'Hanlon-Manners and Kotanen 2004), and in *Picea jezoensis* (Sakamoto and Miyamoto 2005). The enhanced survival of seedlings of at least some tree species on decaying deadwood in a forest is very widely reported (see also Harmon et al. 1986). Reports come from forests in Japan, Taiwan, Tasmania, Hawaii, Argentina, Chile, pastures in Costa Rica, rainforests in Dominica, forests across USA and Canada, in Sweden, Finland, Poland and the European Alps (Table 3). The mechanisms through which the presence of deadwood facilitates seedling survival include moisture retention, mineral recycling, provision of mycorrhizal fungi, biological control of soil-borne pathogens and, in the case of branchy fallen material, protection against browsing.

What is driving the species-richness of wood-decaying fungi?

Even though wood-inhabiting fungi are important for a whole web of other organisms, they are themselves part of the biodiversity of a forest ecosystem. Strictly speaking, measures aimed to conserve wood-decaying fungi can thus be already justified merely for the sake of these organisms. The question arises as to which factors have an influence on their species-richness.

The species-richness of wood-decaying fungi tends to increase with the amount of substrate (e.g. Sippola and Renvall 1999; Allen et al. 2000; Humphrey et al. 2000; Edman et al. 2004b; Penttilä et al. 2004; Berglund and Jonsson 2005; Heilmann-Clausen and Christensen 2005; Schmit 2005; Sippola et al. 2005; Similä et al. 2006; Ódor et al. 2006). On the basis of the species-area relationship, a 90% reduction in deadwood substrate could be followed by the extinction of 50% of wood-inhabiting species (Siitonen 2001). A positive relationship also exists between CWD size and the number of fruiting fungal species (e.g. Bader et al. 1995; Renvall 1995; Lindblad 1997; Lindhe et al. 2004). But Heilmann-Clausen and Christensen (2004) show in near-natural beech stands in Denmark that, although the number of wood-inhabiting fungal species increases with CWD size (this is expected due to the species-area curve: a sample of a larger volume is likely to contain more species), the number of species per unit of volume decreases.

The occurrence of relatively few fungal species in large CWD units can be explained by the combined effects of a number of factors. The smaller the CWD size, the larger the

surface per volume, which implies more space for fungal sporocarps. In order to sample the same CWD volume, the smaller its size, the greater the number of items, and thus the higher the individual cases of fungal infection (e.g. Takahashi and Kagaya 2005). The issue is similar to the collector curve: a sample of more individuals is likely to contain more species. Another reason is that a large item of CWD may allow more room for large fungal individuals to develop, rather than necessarily providing more space for a wider range of species. Conversely, there are some basidiomycetes that may require wood of a certain size before fruiting, although there is evidence from Bavaria that many species of the Corticiaceae and Polyporaceae produce fruit bodies even on rather thin woody substrates (Hahn and Blaschke 2005) and from Switzerland that fine and very fine woody debris, even in intensively managed forests, often provides important refuges for many wood-inhabiting fungi (Küffer and Senn-Irlet 2005a).

Relationships between CWD size and the number of fungal species might to some extent be dependent on the age of the part of the tree concerned, as size is partly related to age (but see Heilmann-Clausen and Christensen 2005). Age involves factors such as the presence of heartwood and the initiation of heartrot while the wood was still standing. Furthermore, the size of the units can influence moisture content as well as temperature, and these factors may affect which species are able to colonize the deadwood (Vasilaukas et al. 2005). An additional point is that larger logs take longer to decay and thus allow more time for colonization of different species of fungi (Ódor et al. 2006). Hence, from an applied point of view it is important to keep in mind that a wide range of CWD, representing differing sizes and stages of decay, is needed in order to support species of varying requirements (Niemelä et al. 1995; Høiland and Bendiksen 1996; Kruys and Jonsson 1999; Nordén et al. 2004a; Stokland and Kauserud 2004; Selonen et al. 2005; Junninen et al. 2006; Tikkanen et al. 2006). Analogously, both high and low CWD turnover regimes are needed to conserve populations with, respectively, small and large body size, given that size is inversely related to the frequency of disturbances in the ecosystem; e.g. as shown for lichens (Hestmark 1997). A problem here is that some fungal species may be present endophytically and cause decay only after tree death (Boddy 1994; Baum et al. 2003). Some of these fungi occur as mycelia in various tree species, but form fruit bodies only on particular hosts, e.g. Xylariaceae (Whalley 1996).

Species-richness of wood-decaying fungi and ecosystem functioning

Within an ecological context, the term 'functioning' has many connotations (Jax 2005) and we focus here on the

Table 3 Examples of reports of enhanced survival of seedlings of various forest tree species occurring on decaying deadwood (see also Harmon et al. 1986)

Tree species	Region	References
<i>Abies sachalinensis</i> , <i>Betula ermanii</i> , <i>Picea jezoensis</i> , <i>P. glehnii</i>	Japan	Hiura et al. (1996)
<i>Abies sachalinensis</i> , <i>Picea glehnii</i>	Japan	Takahashi (1997)
<i>Picea abies</i>	Japan	Takahashi et al. (2000)
<i>Abies mariesii</i> , <i>Tsuga diversifolia</i>	Japan	Sugita and Tani (2001)
<i>Picea jezoensis</i> , <i>Tsuga diversifolia</i>	Japan	Narukawa et al. (2003)
<i>Abies sachalinensis</i> , <i>A. mariesii</i> , <i>A. veitchii</i> , <i>Picea glehnii</i> , <i>P. jezoensis</i> , <i>Tsuga diversifolia</i>	Japan	Narukawa and Yamamoto (2003)
<i>Abies mariesii</i> , <i>A. veitchii</i> , <i>Picea jezoensis</i> , <i>Tsuga diversifolia</i>	Japan	Mori et al. (2004)
<i>Picea glehnii</i>	Japan	Noguchi and Yoshida (2004)
<i>Cryptomeria japonica</i>	Japan	Hirayama and Sakimoto (2005)
<i>Tsuga diversifolia</i>	Japan	Sugita and Nagaïke (2005)
<i>Chamaecyparis obtusa</i>	Taiwan	Liao et al. (2003)
<i>Anopterus glandulosus</i> , <i>Atherosperma moschatum</i> , <i>Eucryphia lucida</i> , <i>Nothofagus cunninghamii</i> , <i>Phyllocladus aspleniifolius</i>	Tasmania	McKenny and Kirkpatrick (1999)
<i>Cheirodendron trigynum</i> , <i>Ilex anomala</i> , <i>Melicope</i> spp., <i>Metrosideros polymorpha</i> , <i>Myrsine</i> spp.	Hawaii	Santiago (2000)
<i>Nothofagus pumilio</i>	Argentina	Heinemann et al. (2000) and Heinemann and Kitzberger (2006)
<i>Laurelia philippiana</i> , <i>Nothofagus nitida</i>	Chile	Lusk (1995)
<i>Eucryphia cordifolia</i> , <i>Laurelia philippiana</i> , <i>Nothofagus nitida</i> , <i>Tepualia stipularis</i> , <i>Weinmannia trichosperma</i>	Chile	Christie and Armesto (2003)
<i>Croton draco</i> , <i>Miconia</i> spp., <i>Verbesina tapantiensis</i>	Costa Rica	Peterson and Haines (2000)
A number of spp., including <i>Dipteryx panamensis</i> , <i>Pentaclethra macroloba</i>	Costa Rica	Slocum (2000)
<i>Cecropia schreberiana</i> , <i>Miconia mirabilis</i> , <i>M. furfuracea</i> , <i>M. tricholoma</i>	Dominica	Lack (1991)
<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i>	OR, USA	Harmon and Franklin (1989)
<i>Abies amabilis</i> , <i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	West Coast, USA	Gray and Spies (1997)
<i>Tsuga heterophylla</i>	WA, USA	Kennedy and Quinn (2001)
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	BC, Canada	Brang et al. (2003)
<i>Abies lasiocarpa</i> , <i>Picea engelmannii</i>	BC, Canada	Parish and Antos (2005)
<i>Betula papyrifera</i> , <i>Salix</i> spp., <i>Picea glauca</i>	AB, Canada	Lee and Sturgess (2001)
<i>Picea glauca</i>	AB, Canada	Stewart et al. (2001)
<i>Abies balsamea</i> , <i>Thuja occidentalis</i>	MN, USA	Cornett et al. (1997)
<i>Thuja occidentalis</i>	MN, USA	Cornett et al. (2001)
<i>Tsuga canadensis</i>	Great Lakes, USA	Rooney and Waller (1998)
<i>Pinus strobus</i>	Great Lakes, USA	Dovciak et al. (2003)
<i>Abies balsamea</i> , <i>Betula alleghaniensis</i> , <i>Tsuga canadensis</i>	NY, USA	McGee (2001)
<i>Abies balsamea</i> , <i>Picea glauca</i> , <i>Thuja occidentalis</i>	QC, Canada	Simard et al. (1998)
<i>Abies balsamea</i>	QC, Canada	Parent et al. (2003)
<i>Picea glauca</i> , <i>Thuja occidentalis</i>	QC, Canada	Simard et al. (2003)
<i>Picea abies</i>	Sweden	Hornberg et al. (1997)
<i>Pinus sylvestris</i>	Finland	Kuuluvainen and Juntunen (1998)
<i>Picea abies</i>	Finland	Kuuluvainen and Kalmari (2003)
<i>Abies alba</i> , <i>Picea abies</i>	Poland	Szewczyk and Szwagrzyk (1996)
<i>Picea abies</i>	Poland	Zielonka and Piatek (2004)
<i>Picea abies</i>	Slovenia	Diaci et al. (2005)
<i>Picea abies</i>	Italy	Motta et al. (2006)
<i>Abies alba</i> , <i>Picea abies</i>	Switzerland	Eichrodt (1970)
<i>Abies alba</i> , <i>Acer pseudoplatanus</i> , <i>Picea abies</i>	Switzerland	Stöckli (1995)
<i>Abies alba</i> , <i>Picea abies</i>	Switzerland	Hunziker and Brang (2005)

functional relationships between wood decomposition and species-richness of wood-inhabiting fungi only. It is mainly through fungal activity that organic matter is mineralized in forest ecosystems (Rayner and Boddy 1988). The particular fungal species which colonize functional and dysfunctional wood of veteran trees are also a frequent determinant of the age attained by these trees (Lonsdale 2004). Deadwoodologists have thus investigated the species-richness of wood-decaying fungi at different stages of decomposition (e.g. Lumley et al. 2001; papers reviewed in Heilmann-Clausen and Christensen 2003), but the effect of species-richness on decomposition rates has seldom been addressed (Boddy et al. 1989; Boddy 2000; Heilmann-Clausen and Boddy 2005; DeLong et al. 2005). An exception is a 13-year study of the decomposition of logs of *Cyrilla racemiflora* in forests of Puerto Rico, which provides evidence that high rates of wood decay are correlated with a high diversity of species and of functional groups of wood-inhabiting organisms (Torres and González 2005). Any influences of a more complex wood-colonizing community on decomposition rates are likely to be concurrent with the effect of seasonal variations in temperature and moisture availability (Progar et al. 2000; see also Toljander et al. 2006).

Moving from species-richness to functional diversity of the decaying community (Heilmann-Clausen 2001; Marcot 2002; Urcelay and Robledo 2004), the question arises of whether this diversity is a factor in determining the different rates of decomposition of CWD of different decay classes and tree species (Mackensen et al. 2003; Yatskov et al. 2003). Answering this question is important because the action of deadwood decomposers and consequent durability of CWD are a source of uncertainty in the role of terrestrial ecosystems as global carbon sinks (Krankina and Harmon 1995; Yin 1999; Chambers et al. 2000; Liski et al. 2003; Mackensen et al. 2003; Yatskov et al. 2003; Hood et al. 2004; Laiho and Prescott 2004; Edman et al. 2006; Liu et al. 2006). On the associated and equally relevant function of wood-decaying fungi as recyclers of nutrients, we refer to the review of Laiho and Prescott (2004) for northern coniferous forests. Similar syntheses are needed for other biomes.

Conservation issues in deadwoodology

How threatened are wood-decaying fungi?

In view of the several ecological functions of wood-decaying fungi, conservation biologists are increasingly focusing on these organisms and on the degree of threat to them (e.g. Molina et al. 2001; Parmasto 2001; Buchanan and May 2003). Thus, for instance, the proportion of fungal species dependent on deadwood is estimated to be 20–25%

in Finland (Siitonen 2001). Likewise, 40% of the threatened species in Finland are assumed to be dependent on old-growth forest (Penttilä et al. 2004). In Sweden, 25% of all threatened species are thought to occur mostly in old living trees and fallen logs (Berg et al. 1994), 20% of the 670 native Aphyllophorales are endangered (Edman and Jonsson 2001) and nearly 40% of the 2120 red-listed organisms related to forest and woodland habitats are saproxylic (one fourth of which are fungi; Lindhe et al. 2004). In Bavaria, 25% of wood-decaying fungi species are assessed as threatened (Albrecht 1992). These proportions mean every time something slightly different, but remain invariably substantial.

One thing is clear: both deadwood (e.g. Angelstam et al. 2003; Sippola et al. 2004) and wood-decaying fungi (e.g. Bader et al. 1995; Norstedt et al. 2001) are first-rate indicators for conservation value of forest patches. The question of whether the former or the latter is a better indicator should not lead to a dead-end. We need to preserve both decaying wood and wood-decaying organisms and happily the presence of the two is often positively correlated. Nonetheless, there are hints from boreal Fennoscandia that the use as indicators of corticoids and polypores can provide different management guidelines at different scales (Berglund et al. 2005). This is not surprising, given their different preferences for woody substrate. Moreover, there are differences between rare and common wood-decaying species in their value as indicator species for key woodland habitats in Finland (Sippola et al. 2005). Wood-disk traps colonized by homokaryotic mycelia provide here the way to detect low rates of spore deposition, both in the study of rare species and of long-distance dispersal (Edman and Gustafsson 2003; see also Landscape perspectives for wood-decaying fungi section).

Unfortunately, one problem is also that nature reserve selection exercises based on the presence of different kinds of wood-decaying organisms can give different results (e.g. Virolainen et al. 2000; Nordén and Appelqvist 2001; Saetersdal et al. 2005; Juutinen et al. 2006). The way out is again a choice of indicator species from several taxonomic groups, whenever possible not merely involving a single functional group, but reflecting the requirements of different organisms (Jonsson and Jonsell 1999; Berglund and Jonsson 2001; Roberge and Angelstam 2004; Similä et al. 2006). This use of the precautionary principle makes sense also in the light of the still rarely scrutinized relationship between the number of wood-decaying species and tree species-richness in different forest types (but see Hattori 2005; Kulhánková et al. 2006). No significant correlation is found in Finland, probably because of the low number of tree species in boreal forests (Sippola et al. 2004). However, a positive correlation is reported from a nemoral forest in Denmark (Heilmann-Clausen et al. 2005). Moreover,

a meta-analysis at a global scale shows a positive relationship between the overall species-richness of macrofungi and that of trees (Schmit et al. 2005; see also Biogeography of CWD and of wood-decaying fungi section). This implies that the protection of the latter can often help to safeguard the former (e.g. Andersson and Östlund 2004). But more research is needed to address whether this is true more specifically for wood-decaying fungi and other ecological groups (e.g. mycorrhizal fungi, litter-decaying organisms and successors to saproxylic organisms or fungi associated with charred deadwood). This is currently unclear because analyses of the community structure or rate of decomposition by fungi in CWD have been predominantly based on single tree species.

And how well are we protecting them?

For a given amount of money invested in conservation, the effectiveness of protective measures can be very different depending on the number, size and location of protected areas. Hence, the SLOSS debate is being kindled in the conservation of wood-decaying fungi. Götmark and Thorell (2003) find a negative density-area relationship between the number of large trees, snags and logs per unit area and the reserve size in southern Sweden. This result would imply that smaller protection areas could be more efficient, since they seem to contain a higher density of deadwood. Similarly, Berglund and Jonsson (2003) find that rare species are disproportionately well-represented in small patches of high habitat quality in Sweden, but on the other hand they also find, from species-accumulation curves, that large old-growth forest patches are more species-rich in polypore species than combinations of small patches of an equal area. The importance of small habitat patches is confirmed by Rolstad et al. (2004), who find in southeastern Norway that Norway spruce (*Picea abies*) CWD in concentrated patches of <1 ha supports wood-decaying fungi just as well as CWD spread out on a larger area. This is not confirmed by Gjerde et al. (2004), who show that in the 5% most species-rich 1-ha woodland patches across Norway, only 20–25% of red-listed species (not only including polypores, but also macrolichens, bryophytes and vascular plants) are represented. In order to protect the other 75–80% of endangered species, mature forests need thus to be preserved in more extensive patches. Also the findings by Penttilä et al. (2004) in Finland suggest that the conservation of threatened polypore species may be better served by enlarging the size of patches of suitable habitat (old-growth forests) than by attempting to increase the overall quality of managed forests.

More generally, how are we to assess the effectiveness of protected areas for the conservation of fungal wood-decaying species? Kruys et al. (1999) state that, given that <1%

of the forest land in the non-mountainous regions of Sweden is protected, in view of inevitable local extinctions over time, protected areas can at best function as temporary refuges and sources of dispersal for threatened wood-inhabiting species. They thus argue that the whole landscape should be managed taking into account deadwood retention objectives (see also Ranius and Kindvall 2004). Currently, however, where sanitation measures are the rule, the average deadwood volumes in managed forests are so low that many species dependent on deadwood are confined to protected areas (Rouvinen and Kouki 2002, see also Ranius and Fahrig 2006). Complementarity analyses (e.g. Virolainen et al. 2000; Juutinen and Mönkkönen 2004; Mayer et al. 2006) are needed so as to select a network of protected forests containing enough naturally occurring deadwood that would be needed to meet conservation targets within a given country or supranational region. If such an approach is ignored by politicians and foresters, the science will become meaningless. Even in Europe, the last temperate forest which is believed to retain some primeval areas, Białowieża, Poland, is rapidly vanishing (Wesolowski 2005).

Landscape perspectives for wood-decaying fungi

There is an increasing recognition that the conservation biology of saproxylic organisms has to be addressed from the perspective of the landscape and not only of the forest stand (e.g. Gu et al. 2002; Berglund et al. 2005; Jonsson et al. 2005; Vanderpoorten et al. 2005; Ekbom et al. 2006; Junninen et al. 2006). This approach can benefit from regional gap analyses, such as Angelstam et al. (2003) present for a suite of birds, a beetle and for lichens dependent on a humid micro-climate. They show that patches of a certain size and connectivity are needed for the persistence of the target species; the inference is that the same is needed for wood-decaying fungi. Additionally, the quality of the landscape matrix should be taken into account, so as to improve the chances of success when implementing conservation measures for fungi dependent on decaying wood. In Scotland, Humphrey et al. (2000) show that the number of macrofungal species of conservation importance (including mainly mycorrhizal species and only a few wood-decaying species) in conifer plantations is higher if plantations are close to patches of natural forest. However, they add that the dispersal ecology of these species is poorly understood and that in many cases propagules may have been transported in association with the root system of planting stock. Along with Sverdrup-Thygeson and Lindemayer (2003), these authors argue that the matrix in which suitable habitat patches are embedded has to be understood not only spatially but also chronologically; i.e. in terms of the continuity of the presence of deadwood. In Sweden, where spatial

and temporal patterns of human activity can be related to the present-day local and regional presence distribution of old-growth forest, this activity has evidently influenced the abundance of viable spores of two endangered wood-decaying organisms, *Fomitopsis rosea* and *Phlebia centrifuga* (Edman et al. 2004a, b). Similarly, the importance of chronological continuity for the survival of species of saproxylic invertebrates has been demonstrated in the UK (Alexander 1998).

The above data suggest that the negative effects of lack of deadwood are operating not only through loss of habitat but also through fragmentation (Kouki et al. 2001; Berglund and Jonsson 2003, 2005; Pharo et al. 2004). This is confirmed by modelling, experimental and empirical work. Strange et al. (2004) apply a variety of site-selection strategies to a Danish database of occurrences of wood-decaying species, subject to a budget constraint. They show that the inclusion of spatial connectivity in models would markedly affect the selection of reserves in an intended network. Edman et al. (2004c) experimentally placed freshly cut logs in Swedish plots containing varying amounts of CWD and thus differing in their pool of wood-decaying species. Despite the potentially confounding transmission of species from stands where logs were cut, colonization by fungal species is found to be higher in sites rich in deadwood. Siitonen et al. (2005) find less old-growth indicator fungi at the edge of forests in comparison with interiors within a fragmented landscape in eastern Finland, but this edge effect is not simple, since it varies with the age of the forest because of interacting factors.

All these studies imply that, although fungal species can maintain viable populations by dispersing within old-growth stands (e.g. Komonen 2005; see also Kauserud et al. 2005), their dispersal can be disrupted by forest fragmentation. Therefore, conservation measures are inadequate if they aim merely to increase the amount of CWD in managed forests without connecting forest patches (see also Penttilä et al. 2006). Although the relationships between forest history, habitat fragmentation and dispersal of wood-decay fungi are still rather poorly understood, especially for some species (e.g. *F. rosea*, Högberg and Stenlid 1999; Kauserud and Schumacher 2003a), it is becoming increasingly clear that fragmentation can be a problem, particularly for wood-decaying species which show limited gene flow between regions (e.g. *Datronia caperata*, Parrent et al. 2004). On the contrary, the detrimental effects of fragmentation may be more easily overcome by species of wood-inhabiting basidiomycetes whose spores remain viable during long-distance dispersal (e.g. *Trichaptum abietinum*, Kauserud and Schumacher 2003b; or *Fomitopsis pinicola*, Högberg et al. 1999), although their spore load at long distances is inevitably much smaller than that of locally established species (Rishbeth 1959; de Jong et al. 1990;

Nordén 1997; Nordén and Larsson 2000; Hallenberg and Küffer 2001).

Biogeography of CWD and of wood-decaying fungi

Traditionally, research on wood-decaying fungi has concentrated mainly on temperate and boreal ecosystems in developed countries (Harmon et al. 1986). Yet, the same questions of conservation and functional ecology are being increasingly investigated in temperate and boreal regions of developing countries (e.g. Mukhin and Kotiranta 2001; Greslebin and Rajchenberg 2003; Dai et al. 2004; Afyon et al. 2005) and in warm mixed and tropical forests (e.g. Lodge and Cantrell 1995; Rodriguez et al. 1995; Ryvardeen 1998; Goes-Neto et al. 2000; Lindblad 2001; Ortega and Navarro 2004; Groposo and Loguercio-Leite 2005; Torres and González 2005). Is the level of threat of wood-decaying fungi in the tropics similar to that in boreal regions? The answer might be determined by the greater rarity of fungal tropical species (Gilbert et al. 2002) and their lower host specialization (Lindblad 2000; Gilbert and Sousa 2002), both possibly influenced by higher tree species diversity (Ferrer and Gilbert 2003). However, the assessment of rarity of wood-decaying tropical species may be biased by a relative lack of studies.

Not only the status of wood-decaying fungi but also that of deadwood has gone largely unreported from tropical regions (Delaney et al. 1998; Grove 2001). But studies are beginning to fill this gap. Are levels of standing and fallen CWD lower in temperate and boreal old-growth forests than in tropical rainforests? This would be expected on the basis of high productivity in the tropics, given that there is a positive relationship between productivity and deadwood volumes within temperate and boreal forests (Harris 1999; Spetich et al. 1999; Feller 2003). On the other hand, the rate of decomposition is also higher at the higher mean temperatures of tropical forests and is often accelerated by the activities of termites. From a study of available data, we have not been able to find evidence that CWD is more abundant in the tropics. The volume of CWD (average $118 \text{ m}^3 \text{ ha}^{-1}$, SD $40 \text{ m}^3 \text{ ha}^{-1}$) reported from nine recent rainforest surveys we were able to find [multiple plots in Borneo and plots in Ecuador (Gale 2000), tropical Australia (Grove 2001), Costa Rica (Clark et al. 2002) and Brazil (Keller et al. 2004; Rice et al. 2004)] does not differ significantly (ANOVA: $F_{1,17} = 1.4$; $P = 0.25$), from that of nine selected old-growth or mature forests at higher latitudes [average $94 \text{ m}^3 \text{ ha}^{-1}$, SD $43 \text{ m}^3 \text{ ha}^{-1}$; plots in Canada, Alberta (Lee et al. 1997) and Newfoundland (Sturtevant et al. 1997), USA, New York (McGee et al. 1999), Sweden (Jonsson 2000), multiple plots in Canada, Ontario (Pedlar et al. 2002) and in Finland (Rouvinen et al. 2002)]. Similarly high values are reported also from temperate

rainforests of Chile (Carmona et al. 2002), from unmanaged forests of southern New South Wales (MacNally et al. 2002b) and from *Fagus* forests in different temperate countries (Piovesan et al. 2005).

A higher species-richness of wood-decaying organisms at tropical latitudes might be extrapolated from the findings (1) of positive site productivity–diversity relationships for polypores in six forests over a latitudinal extent of 1,350 km in Norway (Gjerde et al. 2005), (2) of a higher species-richness of wood-inhabiting aphylloroid basidiomycetes in fallen woody material at lower altitudes in Swiss forests (Küffer and Senn-Irlet 2005b) and (3) of a positive species–energy availability (expressed in terms both of log volume and density) relationship for macrofungal wood-inhabiting species in Puerto Rico (Schmit 2005). Assuming such a pattern, a mechanism enabling more fungal species to coexist in tropical deadwood could be a finer partitioning of resources. This would also assume a comparable level of CWD volumes in tropical forests and extra-tropical ones, which may be expected given that not only deadwood production but also decay rates increase with increasing forest productivity (Stephenson and van Mantgem 2005; Storaunet et al. 2005). This is also confirmed by analyses of Pregitzer and Euskirchen (2004), and of Woldendorp and Keenan (2005). However, any lack of statistical significance in the differences in deadwood volumes between biogeographical regions may be the consequence of confounding factors (e.g. survey methodology, plot area, topography and recent disturbance).

Deadwood management

Creative ideas for a permanent flow of deadwood needed

At the risk of circularity, one argument for the importance of gap perturbations and stand-replacing events due to supposed forest ‘pests’ and tree pathogens is that their by-product is a continuous supply of deadwood in forests (Harmon et al. 1986; McGee 2000; Rouvinen et al. 2002; Müller-Using and Bartsch 2003; Storaunet and Rolstad 2004; McPherson et al. 2005). This unrelenting deadwood flow is part of the ecological memory of forests (Peterson 2002) and should be emulated by forest managers. The next step for applied ecosystem management is indeed to allow an acceptable amount of disease in a particular forested landscape, gauging it on the baseline provided by an understanding of the conditions that predated modern forestry (e.g. Edmonds et al. 2000; Manion 2003; Crow and Perera 2004). The view that tree decay and diseases are necessarily deleterious is rather anthropocentric (Cooke and Rayner 1984). The incidence of damage has, however, sometimes been increased by human activity, which has been a factor

in the chronological changes in the incidence and severity of forest disease. For instance, in many managed forests, the occurrence of *H. annosum* s.l. has long been exacerbated by an unnatural abundance of cut stumps, which act as a selective substrate for this and similar root rot fungi (Redfern and Stenlid 1998). Stumps probably also favour *Armillaria* spp. (Prospero et al. 2003). The potential use of non-pathogenic saprotrophic wood-decaying fungi as antagonistic factors against *H. annosum* s.l. is reviewed by Holdenrieder and Greig (1998) and Korhonen and Holdenrieder (2005).

Windthrow gaps, if left to their natural development, are nowadays potential deadwood islands in a CWD-deprived matrix (Bouget and Duelli 2004). They provide a great opportunity to increase deadwood abundance in managed forests faster than can be achieved applying biodiversity-oriented silvicultural practices (Ranius and Kindvall 2004). In central European forests, this opportunity was arguably missed with the overzealous clearing of stands overthrown by Hurricane Lothar at the end of 1999. In Switzerland, as of November 2004, 80% of the ca. 14 million m³ of wood-windthrow had been cleared (BUWAL 2004). It has been shown that for Hurricane Hugo in the United States the economic surplus generated by salvage averaged \$6.25 million for each additional percentage in the volume of salvaged timber up to the observed salvage rate (16%) (Prestemon and Holmes 2004). But when salvage rates are much higher, it may be not only ecologically but also economically sensible to retain windthrow trees in the forests (Baur et al. 2003).

Are deadwood guidelines having any noticeable effect?

With the possible exception of tropical forests (Keller et al. 2004), managed forests generally show CWD levels significantly lower than those of unmanaged forests (e.g. Guby and Dobbertin 1996; Green and Peterken 1997; Fridman and Walheim 2000; Jenkins et al. 2004; Gibb et al. 2005; Köster et al. 2005; Marage and Lemperiere 2005; Storaunet et al. 2005; Ekbom et al. 2006), except that the differences may be statistically non-significant when logging is selective (Rouvinen et al. 2002). This implies that, in many cases, the naturalness of a forest can be assessed from the amount of deadwood present (Rouvinen et al. 2005). Issues surrounding deadwood are therefore becoming relevant also for forest certification, with best practice guidelines often encouraging the retention of a higher volume of deadwood in managed forests.

But are these guidelines having real consequences; i.e. have levels of CWD been increasing over the last years in managed forests, as is reported in protected forests: e.g. an old-growth oak forest in IN, USA (Spetich and Parker 1998), and sub-alpine pine forests in the European Alps

(Risch et al. 2003)? In selected Appalachian water catchments, CWD is more abundant in areas harvested 18 years earlier but managed under best practice (including retention of 15 m unharvested zones along streams) than in unharvested control plots. Also, the various decay classes of CWD are more evenly represented in plots harvested by best management practices than in conventionally harvested plots, in which CWD consists mostly of slash left behind after harvest (McClure et al. 2004). Similarly, the application of best management practices is reported to have led to an increase in snag density in northern Arizona mixed-conifer forests between 1997 and 2002 (Ganey and Vojta 2005). The latter study does not, however, show the same effect in ponderosa forests and there have even been suggestions that intensive forest management can unintentionally produce more snags thanks to an increased live tree density following clear felling (Ferguson and Archibald 2002). Due to a relative lack of empirical data on the subject, simulations have been used to predict the amount of CWD produced from long-term application of deadwood-friendly management practices (Ranius et al. 2003). Modelling work in Sweden suggests that adopting certification requirements will double the amount of CWD in forests, but that this will take more than one century (Ranius and Kindvall 2004).

Sweden is one of the countries at the forefront in this field. In that country, the Forest Stewardship Council requires that in certified forests representative fresh windfalls are retained (FSC 2005). The unconditional ban on cutting in the few remaining European old-growth stands (advocated by Bobiec et al. 2000) could thus be extended to a large-scale case-by-case presumption against clearing deadwood from stands following windthrow (see Creative ideas for a permanent flow of deadwood needed section). But such a ban may be superfluous in marginal regions, since extreme weather may act on the supply side not only positively (with increased output due to salvage operations) but also negatively (with decreased output due to more difficult access to forests, and also with lower quality of timber) (DeWalle et al. 2003). What is clear is that we need CWD management practices that achieve a sustainable protection of deadwood biodiversity, while minimizing economic drawbacks to the forestry sector (Schiegg 1998; Heilmann-Clausen and Christensen 2004; Ranius et al. 2005; Jonsson et al. 2006). In the long-term, CWD reduction in managed forests may end up in reducing site productivity and tree height (Debeljak 2006).

Because of conflicting interests, this is indeed a politically difficult topic. For instance, in fire-prone forest ecosystems there is the potential for a conflict between biodiversity enhancement as well as forest regeneration facilitation through deadwood retention and fire risk reduction through fuel management (e.g. Ucitel et al. 2003; Bury

2004; Sanchez-Flores and Yool 2004; Donato et al. 2006; Passovoy and Fulé 2006). In regions afflicted by storms, the numerous damaged trees in a windthrow area, although desirable for all the reasons discussed in this review, can become a source of infestation by bark beetles (Wichmann and Ravn 2001; Eriksson et al. 2005), with perceived risk rates of further infestation often significantly higher than actual ones (e.g. Eriksson et al. 2006; Flint 2006). The presence or absence of particular bark beetles can have major implications for a policy of retaining deadwood. For example, *Ips typographus* is not native to the UK, where there is thus much less obsession with sanitation than in many continental countries. This could change, however, if *I. typographus* were to become established in the UK (Evans 1997).

On the particular issue of bark beetles, the need is greater than ever, not only for further research, but also for more public relations work by forest managers informing people that moderate populations of bark beetle can in certain cases contribute to overall ecosystem functioning (see Bouget and Duelli 2004; Fayt et al. 2005). For instance, they can help to diversify forests which have become spruce monocultures. This can be considered desirable where these are outside their natural range and do not have a slope protection value (Wermelinger 2004). In the latter context, broken trees, snags and logs are beneficial inasmuch as they confer protection against avalanches and rock fall (e.g. Frey and Thee 2002; Kupferschmid et al. 2003; Schönenberger et al. 2005; Ammann 2006). The problem is that on steep slopes avalanches and gravity itself tend to make deadwood rarer than elsewhere. Hence, here rapid decay is not welcome, and models estimating time from tree death to the present time (Storaunet 2004) need to incorporate decay and mortality factors (e.g. Janisch and Harmon 2002; Rademacher and Winter 2003; Garber et al. 2005; Mäkinen et al. 2006) so as to build tools predicting how long a perceptible protective effect will last (e.g. Kupferschmid and Bugmann 2005; Ammann 2006; see also Russell et al. 2006).

Active morticulture

Steep protection forests aside, the creative catabolic transformation of CWD into biodiversity, energy, CO₂ and nutrients (Swift 1977) should be facilitated by forest management in equally creative ways. Of course, the provision of CWD at an adequate spatiotemporal scale needs to be balanced against timber production (and fire risk in dry climate; Are deadwood guidelines having any noticeable effect? section). However, given that clean forestry has been a long-standing operating paradigm, there is scope for some exaggeration on the other side now. If morticulture as a new paradigm means connecting dead and live

trees (Harmon 2001), then, along with the traditional planting of a tree for every new-born child, a dead tree per hectare of logged forest should be retained as well (Harris 2001). Similarly, salvage logging in burnt forests should retain large-diameter snags in clumps so as to preserve habitat for cavity-excavating species (Chambers and Mast 2005).

Understanding the interconnections between saproxylic organisms (e.g. Torgersen and Bull 1995; Bull and Wales 2001), even though praiseworthy, is not enough and needs to be complemented with the active creation of dead trees by cutting tops and girdling (e.g. Aulen 1991; Hallett et al. 2001; Cavalli and Mason 2003; Penttilä et al. 2004; Lilja et al. 2005; Ranius et al. 2005) or by inoculating standing living trees with wood-decaying fungi, where this has been shown usefully to hasten the development of decay-based habitat (e.g. Baker et al. 1996; Lewis 1998; Carey et al. 1999; Jack et al. 2003). There is also evidence that mechanical harvesters can effectively spread fungal inoculum across logs (Uzunović et al. 2004). It may, however, require time to obtain results and to convince people that these actions are not vandalism. In the Coast Range of Oregon, Filip et al. (2004) show that inoculation of Douglas-fir trees with *Phellinus pini* and *Fomitopsis cajanderi* creates internal decay within 5 years, but that a longer time is needed for the decay column to grow large enough to be used by cavity-nesting birds. In the Gila National forest, New Mexico, Parks et al. (1999) find that 20% of 102 ponderosa pines killed so as to reduce the spread of dwarf mistletoe (*Arceuthobium* spp.) contained woodpecker cavities 7–9 years after the treatment, which consisted either of basal burning or girdling.

Spreading wood-decaying fungi from tree to tree may be nothing unnatural, since woodpeckers themselves appear to contribute to the process (Farris et al. 2004). However, this kind of commendable hands-on research is hampered by the need to obtain results in a short period. In the dry

sclerophyll forests of southeast Queensland, the average tree age for cavities to begin to appear is estimated at 186–230 years in five of six tree species [the sixth species needs longer; Wormington et al. (2003)]. It should thus be mandatory for long-term grants to be allocated in order to allow researchers to monitor the development of snags created with different methods and of decay in trees inoculated with different fungi until significant differences become evident (Brandeis et al. 2002).

Research gaps

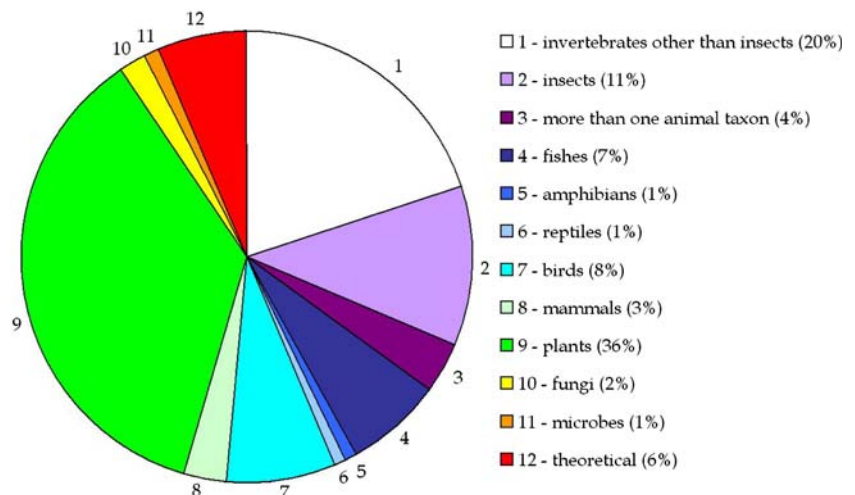
The main conclusions of this review are the following:

- (1). Research on deadwood-dependent fungi shows that these organisms are a vital link in the functioning of forest ecosystems.
- (2). Forest management practices which threaten these fungi need to be modified in order to achieve sustainability of forest ecosystems.
- (3). A whole series of management options is available to increase the presence of deadwood and its dependent organisms in forests, balancing this requirement with the risk of fires and upsurges in bark beetle populations.

Notwithstanding the studies discussed in this and in other reviews (Table 1), wood-decaying fungi are still a neglected part of biodiversity relative to other taxa. Figure 1 shows that the proportion of studies of species-richness dealing with fungi in general (studies of wood-rotting fungi are in turn only a fraction of this proportion) is only a tiny slice of the whole cake currently analyzing biodiversity.

Given their functional importance in ecosystems (Schwarze et al. 2000; For a functional ecology of decay section), lignicolous fungi have been the object of many empirical studies. In general, however, much of the research on organisms dependent on decaying wood (Deadwood as

Fig. 1 Proportion of papers dealing with species-richness of different taxa in a random sample of 100 papers per year retrieved with the keyword ‘species-richness’ in the UK version of Web of Science® (1991–2004; n = 1,400). Note: microbes do not include micro-fungi, and invertebrates other than insects do not include Protozoa (which were grouped together with microbes)



Noah's ark section), although substantial, has been descriptive and could have been more compelling if experimentally proving that (1) augmenting levels of deadwood is followed by an increased species abundance (MacNally et al. 2002a; Pretty and Dobson 2004; Patrick et al. 2006) or (2) that a depletion of CWD is followed by a reduction in abundance, as considered by McCay and Komoroski (2004). The latter authors point out that weak treatment effects may be due to CWD levels already being lower than normal in control plots. Research is needed to unravel the influence of various factors (deadwood size, diversity, age and decay class) not only on the species-richness of wood-decaying fungi (What is driving the species-richness of wood-decaying fungi? section), but also on their species-composition (e.g. Rubino and McCarthy 2003; Nordén et al. 2004b; Heilmann-Clausen and Christensen 2005; Küffer and Senn-Irlet 2005a, b). It would be interesting to establish (1) whether pioneer tree species tend, possibly for reasons of wood chemistry, to be colonized by a different functional group of wood-decaying species and (2) whether CWD from such trees is an exception to positive relationship between unit size and fungal species-richness (Küffer and Senn-Irlet 2000; Nordén and Paltto 2001; see also Hibbett and Donoghue 2001). As for ecosystem functioning (Species-richness of wood-decaying fungi and ecosystem functioning section), there is scope for addressing the interspecific interactions between the vast diversity of saprotrophs and the very few fungal pathogens inhabiting wood (which are potentially controlled by other saprotrophic organisms) and the therefore low risk of diseases posed by CWD accumulation (Hamdan et al. 2005; Woods et al. 2006). Similarly, we need data on potential influences on tree health by the presence of CWD in forests. What about deadwood dearth as a limiting factor for tree establishment at the treeline in different regions of the world? We would like to see more investigations of the role of the functional diversity of lignicolous fungi in the context of climate change and carbon sequestration (Treseder and Allen 2000), and there is much potential for forest canopy cranes to be used also for deadwood and mycological studies (Ishii and Kadotani 2006; Unterseher and Tal 2006).

As for outstanding conservation issues in deadwoodology (Conservation issues in deadwoodology section), in order to make a proper measurement of global trends in the status of biodiversity threat (How threatened are wood-decaying fungi? section), wood-decaying organisms should be included in red list indices. It would be interesting to know whether the level of threat to wood-decaying organisms in different countries is significantly affected by some other factor (e.g. forest cover or deadwood removal by humans). Are the statistics for deadwood availability and for the status of threatened species, as established in some countries, similar in different biogeographical regions? Is

the conservation budget of countries a significant factor here? Similarly, we need to know more about the importance of edge effects in the SLOSS debate (And how well are we protecting them? section). For example, is the value of small remnants of old-growth habitats diminished by fragmentation (Aune et al. 2005)? There are contradicting results from studies evaluating the effect of habitat fragmentation on spore dispersal and viability of metapopulations of wood-decaying fungi. The issue would thus benefit from further investigation.

At the landscape level (Landscape perspectives for wood-decaying fungi section), there is the need for further integration of human impacts on wood-decaying fungi: e.g. environmental pollution (Stavishenko et al. 2002) or genetic impacts on the resident mycobiota by large-scale application of single genotypes (Vainio et al. 2001). Another neglected area of research is the availability of CWD in urban areas. At the biogeographical level (Biogeography of CWD and of wood-decaying fungi section), there is a whole series of outstanding research questions involving, e.g. latitudinal gradients in the species-richness of wood-decaying fungi, the influence of energy availability on large-scale patterns in mycodiversity and mainland versus island comparisons in the diversity and abundance of wood-decaying organisms (Huhndorf et al. 2004).

Regarding deadwood management (Deadwood management section), there is not only the necessity of a permanent flow of deadwood in forests (Creative ideas for a permanent flow of deadwood needed section), but of a constant monitoring of this process (Are deadwood guidelines having any noticeable effect? section). Hurricanes, 'pest' outbreaks, and forest fires can provide an increase of deadwood as well as many research opportunities to follow in situ the succession of wood-decaying organisms on freshly colonized substrates. We need more comparative research on how different cultures perceive the presence and abundance of deadwood in managed and natural forests (e.g. Kohsaka and Handoh 2006), as well as public relations work in relation to the ecological role of bark beetles as deadwood providers. Active morticulture is just one of the many fascinating research and management avenues in current deadwoodology.

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