Ecology of Species Living on Dead Wood – Lessons for Dead Wood Management

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Dead wood has been identified as a crucial component for forest biodiversity. Recent research has improved our understanding of habitat relations for many species associated with dead wood. However, the consequences for forest management are yet to be explored. In this review we build upon the growing volume of studies on dead wood dependent species, the dynamics of dead wood and ecological theory in order to identify the challenges for forest management at the landscape level. The review has a Fennoscandian focus, but the problems and challenges are similar in many forest ecosystems. We argue that it is necessary to 1) counteract the current shortage in availability of dead wood, 2) concentrate planning at the landscape level in order to minimize isolation and reduce edge effects, 3) create a variety of dead wood types, and 4) utilise available quantitative analytical tools. This calls for new approaches to management that to a large extent includes available knowledge, and to find platforms for planning forested landscapes with diverse holdings.

Keywords landscape planning, Fennoscandian forests, woodland key habitats, saproxylic species, epixylic species, forest management, coarse woody debris

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1 Introduction

Numerous studies have shown the key importance of dead wood for biodiversity in boreal forests (see e.g. papers in Jonsson and Kruys 2001). Such studies have produced a large body of data concerning the availability of dead wood and specific species' demands. However, it remains a challenge to draw conclusions from this new knowledge for implementation in forest management. Simple statistics on the occurrence of dead wood and wood living species are valuable starting points but do not provide guidelines for management. Most studies address small-scale patterns of individual logs and specific habitat demands at the stand level, in contrast to forestry planning, which normally takes place at the landscape level (e.g. Fries et al. 1997, Raivio et al. 2001). Considering that most species are dynamic in their distribution, it is also more biologically relevant to consider the viability of forest species at the landscape level rather than within stands.

Living on dead wood requires the dependence on a dynamic and transient substrate, and often a large amount of stochasticity is involved in the dynamics. This implies that populations must be able to compensate local extinctions on individual logs and within forest stands with repeated colonisations to ensure survival at the landscape level. Understanding these colonization-extinction dynamics is essential for successful biodiversity management. However, up to now most environmental concern in forestry has focused on the individual management unit, and no reliable guidelines are available for *how* and *where* dead wood should be increased to optimise the biodiversity benefit at a landscape level. As trees are both the economically most important product extracted from the forests and the basis for species dependent on dead wood there is an obvious trade-off between the economy for individual forest owners and biodiversity conservation (Ranius et al. 2005). This implies that when a dead tree is "used" for biodiversity it is in everybody's interest that it is placed under conditions that maximise the benefit. Such conditions involve consideration of spatial, microenvironmental and stand structure factors.

In this paper we review the current knowledge, with a chosen Fennoscandian focus, of the biology of wood dependent species and the dynamics of dead wood. Our aim is to clarify the challenges to forest management regarding how and where to increase the volumes of dead wood. The answer to these questions also depends on many socio-economic factors. These factors are not reviewed, but in the discussion we point to particular issues that must be addressed in this context.

2 System Description

Here we describe the ecological context in which conservation of wood dependent species should be viewed. This includes relevant ecological theory, biology of the species and dynamics of the habitat. We do not include an extensive review of substrate demands of individual species (see Dahlberg and Stokland 2004). Rather we try to keep the landscape level in focus by addressing the major question on how and where to increase volumes of dead wood.

2.1 Theoretical Context

Dead wood is created by tree mortality, which in natural forests is caused by fire, wind, snow breakage, drought, competition, insects and pathogens (Kuuluvainen 1994, Engelmark and Hytteborn 1999). Tree mortality has a fairly large random component in space and time, and the dominant mortality factor varies strongly between different forest types (Fridman and Ståhl 2001). The decay rate varies between forest type and tree species and as a consequence of the actual decayer-community (Harmon et al. 1986, Harmon et al. 2000, Kruys et al. 2002). All this implies that species dependent on dead wood must track the availability of a fairly unpredictable habitat. Therefore, wood dependent species must compensate the extinctions with new colonisations through dispersal and establishment on new dead trees. Such a system shares many similarities with systems studied under the theory of metapopulation ecology (Hanski 1999).

A set of habitat patches may maintain viable populations even if the survival in individual patches, e.g. individual decaying tree trunks, is limited in time (Ranius 2000). At a small scale (such as individual dead wood objects or small forest stands) both the species *and* their habitat are dynamic, which is normally not considered in "classical" metapopulation ecology. However, many populations that have been described as metapopulations are associated with habitats with a limited duration of each patch, i.e. they are habitat-tracking metapopulations (Thomas 1994).

For species capable of long-distance dispersal, metapopulation models may be appropriate to use when understanding the dynamics at larger scales (larger stands and landscapes). The situation in some areas of the Fennoscandian boreal forests may correspond to a mainland-island metapopulation (sensu Harrison and Taylor 1997, Hanski 2001). Mountain forests in Sweden and the large tracts of unexploited forests in westernmost Russia may serve as dispersal sources (analogous to a mainland) for isolated forest patches (islands) in more exploited regions. However, this analogy may only hold for species capable of long-distance dispersal. For species with more limited dispersal, the survival in fragmented landscapes relies on their ability to persist without a "mainland" source. Such metapopulations rely on a positive equilibrium between colonisations and extinctions. In large parts of boreal Fennoscandia the area of interior old-growth habitat with abundant dead wood is highly fragmented and constitutes only a small fraction of the pre-forestry landscape (Bernes 1994). Here metapopulation ecology provides a framework for analysing species survival since no stable "mainland" populations serve as a continuous source of colonisers (e.g. Gu et al. 2002).

2.2 Ecological Concepts

2.2.1 Trophic Levels

Many species associated with dead wood do not live on the dead wood directly, but on other species that consume dead wood. During most decay stages, except immediately after tree death before the fungal community has developed, a large number of beetle species feeds on fungal mycelium (Esseen et al. 1997). In turn, many parasitic insects live on wood living beetles (Kenis et al. 2004). Finally, it has been shown that many fungi live associated with, likely as parasites, other fungi (Niemelä et al. 1995). There is in most of these associations a certain degree of host specificity. In a study on three species representing different trophic levels within a food chain (a bracket fungi, a moth and a specialist parasitoid), it was found that habitat loss and fragmentation truncated the food chains (Komonen et al. 2000). Thus, we should expect that parasitoids and predators strictly associated with certain wood-living species are generally more vulnerable than those species directly associated with dead wood.

2.2.2 Genetic Variation

Fragmentation of habitats may influence genetic variation and subsequently the fitness of isolated populations (e.g. references in Young and Clarke 2000), which has been discussed also for wood living species. In the fungi *Fomitopsis rosea*, Högberg and Stenlid (1999) found low heterozygosity levels for small isolated populations in southern Sweden. In a related study, Edman et al. (2004c) noted strongly decreased spore germinability in these southern populations, suggesting a link between isolation, reduced genetic variation and fitness. Similarly, for another wood living fungi, *Steccherinum robustius*, low gene flow and low genetic variation among isolated populations have been shown (Nordén 2000).

By contrast, Kauserud and Schumacher (2003) found only limited population differentiation in *F. rosea* and *Phellinus nigrolimitatus* among five studied Fennoscandian populations. Also shown is that for common species, such as *Fomitopsis pinicola*, gene flow appears to be high (Nordén 1997, Högberg et al. 1995).

Genetic studies on wood-living insects have focused on beetles in bracket fungi. Jonsson et al. (2003) compared the genetic structure of a common (*Bolitophagus reticulatus*) and a rare (*Oplocephala haemorrhoidalis*) beetle living in sporocarps of *Fomes fomentarius*. Between sites, the genetic differentiation was larger in *O. haemorrhoidalis*. It seems that gene flow between *O. haemorrhoidalis* populations has declined as an effect of recent habitat fragmentation, while *B. reticulatus* likely moves over large areas and has higher gene flow (Jonsson et al. 2003). Genetic variability was not low in either species. Knutsen et al. (2000) also studied *B. reticulatus*, however at a smaller geographic scale. They found significant genetic differentiation between trees, probably due to a founder effect (Jonsson et al. 2003). However, in accordance with Jonsson et al. (2003), they found only a very small genetic differentiation at a larger geographic scale, between their two study areas.

2.2.3 Rarity

The management of wood dependent species is complicated by the fact that the majority of the species of interest are quite rare. In a sampling study for wood-living beetles, Martikainen and Kouki (2003) showed that very large samples are required for accurate descriptions of the fauna and occurrence of red-listed species. The same conclusion can be drawn for wood fungi and bryophytes. In isolated old-growth forest patches in northern Sweden, more than 50% of the species were found in less than 5% of the studied stands (Berglund and Jonsson 2003). From these examples we can draw two conclusions: 1) to preserve the full suite of wood-associated species, large volumes of dead wood are needed and 2) inventorying and monitoring the total wood living communities is very labour intensive (e.g. Berglund et al. 2005).

2.3 Species Dynamics

2.3.1 Dispersal

Theoretical models have suggested that a high frequency of local extinctions imply a high selection pressure for dispersal ability, as the possible benefit of dispersal increases when there are many empty but suitable habitat patches (for a review see Johnson and Gaines 1990). Comparisons between insects living in different habitats support this prediction: insects associated with an ephemeral habitat that dooms them to extinction within a few generations have a high dispersal propensity, while the dispersal of insects in habitats with a longer persistence is more limited (Southwood 1962, Den Boer et al. 1980, Roff 1994, Denno et al. 1996). Different types of dead wood have different longevity, and it has been suggested that this would generate differences in the dispersal biology of the inhabiting insects (Nilsson and Baranowski, 1997). Empirical studies support this view: a beetle, *Osmoderma eremita*, which lives in decaying trunks that may persist over many decades or even centuries, has a very low dispersal propensity (Ranius and Hedin 2001) compared to species occurring only one or a few years during the early stage of decay (e.g. bark beetles as *Ips typographus*; Forsse and Solbreck 1985).

Regarding dispersal, much attention has been given to a tenebrionid beetle, *Bolitophagus reticulatus*, living on sporocarps of *Fomes fomentarius*. It is an abundant and widespread species, present also in forests with low amounts of dead wood (Jonsell and Nordlander 2002, Jonsell et al. 2003). Within stands, the species has a frequency of occurrence per tree that increases with habitat size (number of fruitbodies per tree) and decrease with the degree of isolation (Rukke and Midtgaard 1998, Sverdrup-Thygeson and Midtgaard 1998). However, when different sites are compared, there is no correlation between habitat density per forest stand and the frequency of occurrence per tree of the beetle (Rukke and Midtgaard 1998, Jonsell et al. 2003). In a flight-mill experiment, Jonsson (2003) showed that the species is able to fly for extended periods, corresponding to a distance of several kilometres. This suggests that *B. reticulatus* has the capacity to colonise suitable habitat patches far away. Jonsell et al. (2003) observed that almost all long distance dispersals occurred during a single week in the summer, which may explain the previous difficulties in observing flying beetles. Moreover, during a later stage of its adult life the beetle resorbes its flight muscles and can then move only by walking (Jonsson 2003). Perhaps suitable trees standing close to each other typically are inhabited by the same population of *B. reticulatus*, with extensive dispersal between trees by walking on the ground. This may explain why the species often is most abundant where the local density of trees with fruitbodies is high (Jonsson 2003). Thus, based on the occupancy pattern within stands, it had been suggested that *B. reticulatus* had limited dispersal, while further studies showed this not to be the case. This example highlights the need for additional in-depth studies to understand dispersal patterns of individual species.

Bolitophagus reticulatus is a common species, and its dispersal may not be representative of threatened beetles. That is, *B. reticulatus* might be common simply because of its ability for long-distance dispersal. To test this hypothesis, Jonsson (2003) compared the dispersal biology of *B. reticulatus* with a red-listed beetle, *Oplocephala haemorrhoidalis*, that also lives in fruiting bodies of *Fomes fomentarius*. A similar proportion of individuals of the two species were able to fly several kilometres, but *B. reticulatus* more often had functional flight muscles and was more inclined to take off than *O. haemorrhoidalis*. In addition, *O. haemorrhoidalis* females had fewer but larger eggs than *B. reticulatus*. Jonsson (2003) therefore suggested that *O. haemorrhoidalis* is a weaker colonizer than *B. reticulatus*, due to a lower dispersal rate and a lower probability of establishing a population, even though the dispersal range of the two species is similar.

Fungi and bryophytes disperse mainly by small sized spores that are produced in vast numbers. It is thus tempting to assume that most are good dispersers. In relation to other species groups, this is generally true; however, this does not imply that dispersal is not a limiting factor. By using monocaryotic mycelia as bait on species-specific spore traps, Edman and co-workers studied the dispersal ability of a range of wood living fungi. Results showed that spores of species normally only reproducing in old-growth forests did occur in landscapes with very few or no old-growth patches (Josefsson 2002, Edman et al. 2004a). However, there is still a strong correlation between spore deposition and the amount of old-growth forest in the surrounding landscape, indicating that the amount of spores deposited locally is strongly influenced by the occurrence of the species in the surrounding landscape (Nordén and Larsson 2000, Edman et al. 2004a). Further, on experimental logs, the colonisation was much more rapid on sites with high spore production (i.e. semi-natural forests) than in managed stands with low volumes of dead wood (Fig. 1; Edman et al. 2004b). As an example, *Fomitopsis rosea* (a red-listed fungus) successfully colonised only on sites where it was already present, despite the occurrence of spores on sites where it was absent (Edman et al. 2004b). This suggests that the mere occurrence of spores is not in itself sufficient for colonisation. Most likely, colonisation probability is extremely low for individual spores, and a high deposition is necessary for success.

Bryophyte spores are usually somewhat larger than fungal spores, and in addition many wood dependent bryophytes produce large sized asexual propagules (gemmae). This suggests that wood living bryophytes have more restricted dispersal abilities than wood-fungi. The only published spore dispersal study for wood living bryophytes is on the liverwort *Ptilidium pulcherrimum* (with a spore diameter of about 20 µm; Söderström and Jonsson 1989) which showed strongly decreasing spore deposition within the first 10 m from the dispersal source. However, at the stand level, it was estimated that more than 300 spores were deposited per square meter of logs per year. Most other studies on wood living bryophytes have focused on the relation between sexual and asexual reproduction, pointing to the importance of asexual reproduction in maintaining the local population, even though asexual propagules are large and with more limited dispersal than spores (Kimmerer 1994, Laaka-Lindberg et al. 2003, Pohjamo and Laaka-Lindberg 2004)

To date, no landscape-level study on the dispersal ability of wood living bryophytes has been reported. However, an analysis of British mosses and hepatics (including wood living species; Longton 1992, Laaka-Lindberg et al. 2000) showed that species not producing sporophytes

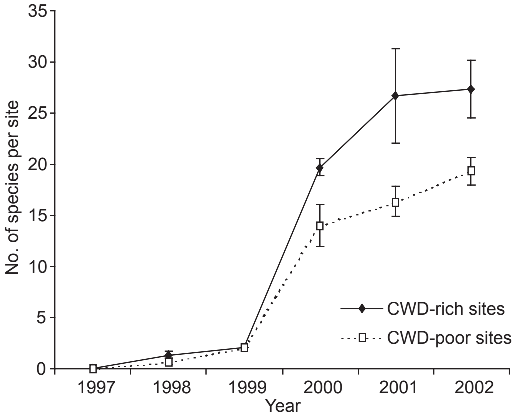

Fig. 1. (From Edman et al. 2004b) Number of wood fungi species (±SE; N = 3) on 30 transplanted fresh Norway spruce logs during the first six years after transplantation. The number of colonised species was higher on sites with abundant natural dead wood (dead wood-rich sites; mean 43 m^3 ha^{-1}) compared to sites with low abundance of natural dead wood (dead wood-poor sites; mean $3m^3$ ha^{-1}).

are strongly over-represented among rare species in Britain, suggesting that dispersal may significantly reduce overall distribution.

2.3.2 Population Establishment

Colonization is the joint result of successful dispersal and successful establishment. Establishment conditions for wood living species have rarely been studied, but include biotic interactions, abiotic conditions, wood quality, as well as chance and timing.

The fungal spore contains very little nutrient supplies, so establishment relies on encountering favourable local conditions. Also, the wood is usually already colonised by other species and thus represents a hostile environment to the coloniser (Boddy 2001). For some species, insect vectors may facilitate the establishment. One example is *Amylostereum areolatum*, which has a mutualistic relationship with wood wasps (*Sirex* species; Vasiliauskas et al. 1998). Another example is blue stain fungi, which is transported into the sapwood by bark beetles (Dowding 1984).

Little is known about bryophyte and lichen establishment on dead wood in boreal forests. The only work that has addressed this topic seems to be the studies of *Tetraphis pellucida* and *Dicranum flagellare* (Kimmerer 1993, 1994, Kimmerer and Young 1996). In this system, small-scale disturbance on individual logs was extremely important in the dynamics of the species, suggesting that the availability of space is a crucial factor, and that establishment in closed communities is difficult. For boreal epiphytic lichens Hillmo and Ott (2002) showed that the establishment from asexual propagules was slow and required more than two years before visible thalli occurred. However, the establishment rates of vegetative diaspores sown on experimental twigs were as high in young stands as in old-growth stands (Hillmo and Såstad 2001). If this pattern were also relevant for lichens on dead wood, it would indicate that establishment is more a function of dispersal ability and substrate availability than microclimate differences between managed and old-growth stands.

The main difference between the establishment of insects in comparison to cryptogams is the involvement of active behaviour, especially emission of and attraction to chemical compounds. For instance, it has been found that insects associated with fruiting bodies of bracket fungi are attracted by the odour emitted by specific fungi species (Jonsell and Nordlander 1995). When the first wood insects have arrived to a suitable habitat, they may attract other individuals by emitting aggregation and sex pheromones (e.g. Jonsson et al. 1997, Larsson et al. 2003). It has been found that such pheromones emitted by a wood-living beetle are used by a predator to locate its prey (Svensson et al. 2004). Our knowledge on these odours is only based on a few experimental studies, and therefore we do not know at which spatial scales they are effective and how much they actually mean for the probability of successful colonisation in different situations.

Presence of a particular species is obviously a first necessary step for population establishment. However, from a management and conservation perspective it is more important that the species actually reproduce. For wood dependent cryptogams this may be conferred from the occurrence of sporocarps (fungi), apothecia (lichens), capsules (bryophytes), or asexual means of reproduction. Usually these structures are evident during inventories and may be fairly easily noted.

The insect fauna on dead wood is often surveyed by window traps (for methods see Kaila 1993, Økland 1996, Ranius and Jansson 2002, Martikainen and Kouki 2003), which may be problematic, as it cannot be ascertained if the collected insects actually use the dead wood substrate. Typically, a relatively large proportion of the collected insects are “tourists”, in that they are caught coincidentally or are attracted by dead wood but not using it as a larvae substrate. Bark peeling (e.g. used by Siitonen and Saaristo 2000) and emergence traps (e.g. used by Lindhe and Lindelöw 2004) are in many cases more useful survey methods, as the obtained sample contains species found in, and presumably using, the substrate.

2.3.3 Habitat Requirements and Population Development

Once established, the subsequent population development depends on how well the species is able to use available resources. Dahlberg and Stokland (2004) provide a review of the types of dead wood utilised by different species in Sweden. This review is likely to be highly relevant also for all other parts of the western Taiga.

Many species show some degree of specificity to dead wood of particular tree species (Boddy 2001, Jonsell et al. 1998, 2004). However, strict host specific species seems to be rather few, and taken Sweden as an example, only around 130 species out of almost 7000 wood living species, have been identified as only occurring on one host tree species (Dahlberg and Stokland 2004). Regarding invertebrates, species in early successional stages of dead wood are more confined to particular tree species (Jonsell et al. 1998), while in later successional stages other factors, especially the presence of different decaying fungi (Kaila et al. 1994), are more important (Jonsell et al. 1998). The majority of the wood-living species in Sweden are associated with deciduous trees, however the individually most species rich tree is Norway spruce with at least 1200 associated species. Of the deciduous trees, birch, oak and aspen are the most species rich (Dahlberg and Stokland 2004). For red-listed species, oak is the most important host tree followed by Norway spruce. Given the overall importance of deciduous trees for wood dependent species, it is notable that the standing volumes of conifers in Finland, Sweden and Norway are 3 to 5 times higher than that of deciduous trees (Stokland et al. 2003).

Most invertebrate species either prefer sun exposure or are indifferent, while only a few prefer shaded dead wood (Jonsell et al. 1998). Shade-intolerant tree species appear to harbour more sun-preferring invertebrate species when compared to more shade-tolerant tree species. Norway spruce is more shade-tolerant than, for instance, aspen and birch. When dead wood of aspen (Martikainen 2001, Sverdrup-Thygeson and Ims 2001) and birch (Kaila et al. 1997) has been studied, more beetle species have been found in sun-exposed than shaded situations, while in Norway spruce, there is no difference in species richness between sun-exposed and shaded logs (Wikars, Sahlin and Ranius unpublished). When Lindhe et al. (in press) studied high stumps on clear-cuts, they also found a higher proportion of species favoured by sun-exposed conditions in aspen and a lower proportion in spruce, but surprisingly, they also found a relative low proportion of such species in birch. In contrast to the invertebrates, there is evidence that most wood-fungi and bryophytes are confined to more shaded environments as occurring in forest interiors (Söderström 1981, Snäll and Jonsson 2001, Moen and Jonsson 2003). For wood living bryophytes in isolated old-growth forest patches in northern Sweden, negative effects of edges extended about 50 m into forest stands (Moen and Jonsson 2003). Also for red-listed wood fungi, reduced occurrence was noted at the edges of woodland key habitats (Snäll and Jonsson 2001). Thus, the preference for sun-exposed *vs*. shaded conditions varies among species groups, implying that no general pattern exists.

Species composition of deadwood-dependent organisms varies markedly through the process of wood decay. In general, the majority of species dependent on dead wood seems to prefer dead wood at intermediate stages of decay (Dahlberg and Stokland 2004). This general patterns contrasts to red-listed invertebrates, where most species occur during the earlier stages of decay (Jonsell et al. 1998), and to fungi and bryophytes where many species also occur on later stages (Dahlberg and Stokland 2004). The preference for later decay stages is most apparent for red-listed wood-living fungi and bryophytes (Bader et al. 1995, Kruys et al. 1999).

In addition to decay stage, size of the dead wood piece is often positively correlated with species occurrences, as many wood living species prefer dead wood of large dimensions (e.g. Kruys et al. 1999, Siitonen and Saaristo 2000, Ranius and Jansson 2000, Jonsell et al. 2001, Dahlberg and Stokland 2004; see however Lindhe et al. in press). More than 50% of the wood dependent species in Sweden primarily occur on logs larger than 20 cm diameter and about 15% of the species are confined to dead wood with a diameter of more than 40 cm (Dahlberg and Stokland 2004). However, care should be taken not to interpret this to mean that small-sized logs are unimportant. The reason for the observed preference (as analysed) is two-fold: a true dependence on the conditions offered by the large-diameter dead wood and, in some studies, a sampling artefact from large dead wood representing a larger area or volume of habitat. Two studies indicate that, based on volume, small-diameter logs may indeed be an important substrate for wood living fungi and bryophytes (Kruys and Jonsson 1999, Nordén et al. 2004).

Although tree species, decay stage and dead wood diameter are the most well studied factors, also other aspects of dead wood are important. Such factors include the occurrence of hollows in trees, wood from slow growing trees, burnt wood and wood in streams which all host a number of specific species. For instance, a total of 405 species, including 175 red-listed species, have been found on burned wood in Sweden (Dahlberg and Stokland 2004).

2.3.4 Extinctions

Extinction of deadwood dependent organisms at the level of a single log is deterministic, as sooner or later the log will decay beyond its suitability as substrate. For many beetles only the first stages of decay are important, thus their occurrence on individual logs is restricted to a few years (Esseen et al. 1997, Jonsell et al. 1998). This differs from species (mainly wood fungi and bryophytes) that utilize advanced stages of decay, which may survive for decades on a single log. For example, inventories of the old-growth polypore *Phellinus nigrolimitatus* and the corticoid fungus *Columnocystis abietina* showed that 73% and 75%, respectively, of the logs inhabited by these species in the first inventory were still occupied eight years later (Berglund et al. 2005).

Extinctions at the stand level, however, are more stochastic, and the risk is a function of the balance between log-level extinctions and colonizations. Local extinctions are more likely among species with small populations, which seems to be common for many wood living species (e.g Berglund and Jonsson 2003, Martikainen and Kouki 2003). To date, only a limited number of studies have addressed extinctions at the stand level. Gustafsson et al. (2002) has constructed a stochastic model on the dynamics of wood fungi at stand level. Their results highlight the need for further studies on the population demography, e.g. what factors control time from germination to fruit body development and spore production. These basic factors are so far known for only a few species.

Decreased amount of dead wood may cause extinctions, especially for species with limited dispersal or narrow habitat demands. However, populations of such species may persist at the individual log or stand for extended periods even if the low habitat density in the landscape makes it impossible to balance extinctions with colonisations in the longer run. This is in short is the *extinction debt* (Tilman et al. 1994, Hanski 2000), which is currently much discussed. Given the relative slow dynamics of forest succession and the rapid decrease in the area of interior old-growth habitat, it is unlikely that all species have tracked the changes in the Fennoscandian forest landscape, meaning that current species distribution patterns are a consequence of much greater habitat availability in the previous forest landscape (Gu et al. 2002). Therefore many species are currently changing their distribution pattern. This has been analysed theoretically by Hanski (2000) and studied empirically by Berglund and Jonsson (2005), Penttilä (2004) and Gu et al. (2002).

2.3.5 Continuity

It has been hypothesized that wood dependent species with restricted colonization ability should be confined to sites with a continuous occurrence of suitable habitat over time (Nilsson and Baranowski 1997). The habitat continuity over recent times may be assessed by analysing the occurrence of certain structures, e.g. logs in different decay and size classes (Stokland 2001). Given that such an approach has a limited temporal extent, and that much larger time scales might be relevant for the fauna and flora, it has been suggested that certain indicator species should be surveyed (Nilsson et al. 1995). However, this approach also has been criticized, mainly because of the lack of reliable data correlating potential indicator species with forest continuity (Rolstad et al. 2002) and because the general importance of continuity has been questioned (Nordén and Appelqvist 2001).

Nevertheless, several studies on wood dependent species suggest that the occupancy of individual species (Siitonen and Saaristo 2000, Sverdrup-Thygeson and Lindenmayer 2003) or species richness of some certain groups (Nilsson and Baranowski 1997, Alexander 1998, Jonsell and Nordlander 2002) is positively correlated with historical continuity. However, to be able to draw firm conclusions, it is important that current habitat quality is controlled for and that historical data are used. Among these studies, only one – Siitonen and Saaristo (2000) – have tried to both control for current habitat amount and quality and use historical data, while other – Alexander (1998), Sverdrup-Thygeson and Lindenmayer (2003) – used historical data. Therefore it is in most of the studies impossible to draw conclusions about the casual relationship between species richness and historical factors *per se*. Additional studies have shown no relationship between species richness and historical continuity. A study of cryptogams in swamp forests found no relationship between species considered to indicate natural forest and the known long-term continuity of the forest (Ohlson et al. 1997). Rolstad et al. (2004) studied wood living fungi, and found no evidence for dispersal limitation, concluding that the spatiotemporal distribution of dead wood was of minor importance, at least on scales of hectares and 100 years.

Although a number of studies have addressed the importance of continuity, there is for the vast majority of species no information on their dependence on habitat continuity. Anyway, it is obviously a better starting point to include sites where the focal species occur in suitable sites than relying on the species dispersal ability for colonization of new suitable habitats (Fig. 1., See Edman et 2004b for an empirical example and Huxel and Hastings 1999 for a relevant theoretical analysis). Also, given the current extent of fragmentation of the landscape, the importance of local continuity may be increasing since the potential for re-colonization is decreasing.

2.4 Dead Tree Dynamics

2.4.1 Tree Mortality

The rate of tree death is related to, for instance, tree species composition, stand age, and forest management. Stokland et al. (2003) analysed and summarized the National Forest Inventory data from Norway, Sweden and Finland. For trees larger than 5 cm diameter at breast height (dbh), the total natural mortality ranged between 0.11 and 0.31 m^3 ha^{-1} $year^{-1}$ with the lowest value in Finland and the highest in Norway. However, the data also clearly show that the mortality rate is much higher in small diameter trees. In conifers the mortality was 2 to 3 times higher in trees <10 cm dbh than in larger trees.

Ranius et al. (2004) analysed data from the Swedish National Forest Inventory (NFI) specifically for spruce dominated old forests that have not been managed, at least during the last 25 years. The estimated average annual mortality of Norway spruce with a diameter exceeding 10 cm was 0.36%, while the corresponding figure for managed forests younger than normal cutting age was 0.09–0.21% (Ranius et al. 2003). Because the standing volume is, on average, lower in a managed forest in comparison to an old unmanaged, the amount of dead wood generated annually is several times higher in the unmanaged forest.

Very little data is available concerning between-year variation in mortality rates in boreal forests, but some variation is present and influences the predictability of habitat availability, especially for species dependent on freshly dead trees. For Norway spruce in an old-growth landscape, the mortality rate between different 5-year periods varied almost an order of magnitude, but also during periods of low mortality fresh logs tended to be relatively abundant (Jonsson 2000). In forests dominated by large-scale disturbances as forest fires, an average mortality rate is basically irrelevant. Here the actual fire characteristics will determine a large part of the tree mortality for extended periods of time (Siitonen 2001).

2.4.2 Decay Rates

In an unmanaged forests, decay of dead wood may balance the input through tree mortality. The decay is performed by a vast number of species, where insects and fungi particularly play an important role. Therefore, a reduction of biodiversity may also affect decomposition rates of a given area.

Decay has been measured in at least three ways: time to "disappearance" of the dead wood unit (usually equalling about 80–90% mass loss), mass loss functions and decay stage transitions. Estimates of the time to disappearance have mostly been conducted at areas where old plots have been revisited (Hytteborn and Packham 1987, Liu and Hytteborn 1991, Hofgaard 1993). These studies suggest that downed Norway spruce logs on average disappear from the forest floor within 50 to 120 years given a gradient from southern to northern Sweden (Ranius et al, 2004). However, the data are too scarce to allow for any broader generalisations regarding the relationship between latitude and decomposition rate (see however Jonsson 2000, Kruys et al. 2002, Storaunet and Rolstad 2002 for examples from particular regions).

Mass loss functions are usually modelled by a negative exponential model:

$$Y_t = Y_0 e^{-kt} \qquad (1)$$

where Y_t is the mass at time t, Y_0 the initial mass and k the decay rate constant. A few studies (Naesset 1999, Krankina and Harmon 1995, Tarasov and Birdsey 2001) have reported decay rate constants for boreal Europe, giving ranges from 0.03 to 0.05 corresponding to a 90% mass loss over 45 to 75 years. Somewhat surprising, only minor differences were observed between Norway spruce and Scots pine, while birch had significantly faster decay (Krankina and Harmon 1995).

In an attempt to model decay stage dynamics, Kruys et al. (2002) developed a stage transition approach and parameterised this for Norway spruce logs in boreal Sweden. Their approach is based on the probability of a particular log to move from one decay stage to the next during a certain time period. Their data have also been used in a similar model of decay stage dynamics that required a mean and standard deviation for the time a dead wood unit remains in a certain decay stage (Ranius et al. 2003). With these approaches the fate of individual logs may be followed and future decay stage distributions in a forest stand predicted (Fig. 2).

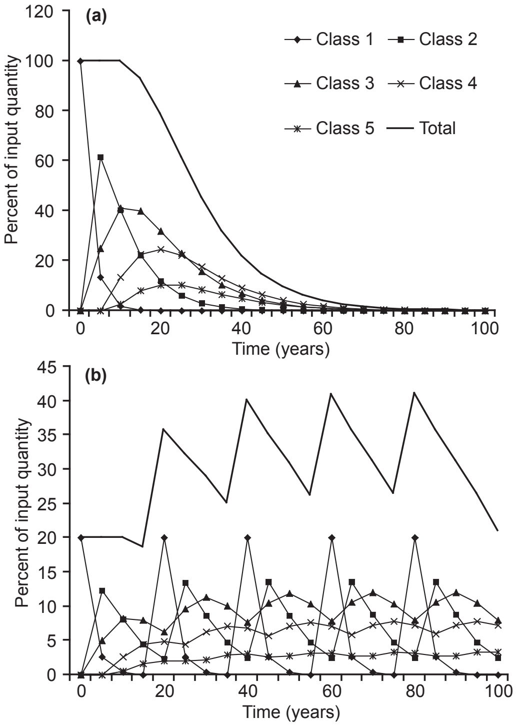

Fig. 2. (From Kruys et al. 2002) Two scenarios are presented where a certain quantity of dead wood (Σ = 100%) is entered into each system and allowed to pass through the decay model. In (a) all the quantity is entered at year 0, whereas (b) shows a situation where 20% is entered at each of years 0, 20, 40, 60 and 80. The decay classes range from undecayed (class 1) to medium decayed (class 5).

2.4.3 Stand Models

By combining mortality data and decay rates, the temporal pattern of dead wood-availability can be modelled. In the simplest case a constant input and decay is assumed. If forest management is considered, knowledge about how dead wood is destroyed or removed is also necessary (Ranius et al. 2003). However, since stand development models for managed forests are present and becoming increasingly sophisticated, more realistic models can be created. This has been done in two studies of Norway spruce forests conducted by Ranius et al. (2003, 2004). In the first, dead wood availability in managed forests

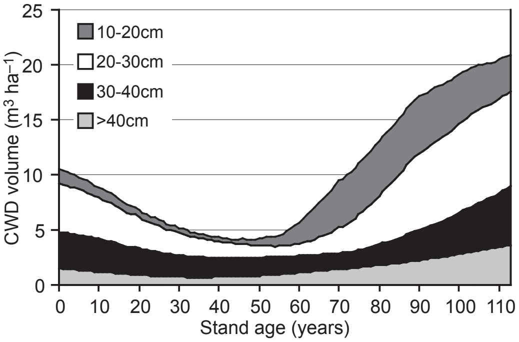

Fig. 3. (From Ranius et al. 2003) Result from a simulation model predicting dead wood-volumes in managed forests. Figure shows average (1000 replicates) amount of coarse woody debris (m^3 ha^{-1} of stems with a diameter larger than 10 cm), divided into different diameter classes. Parameter values are typical for biodiversity-oriented forestry.

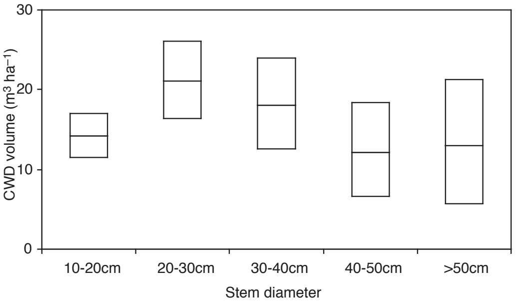

Fig. 4. (From Ranius et al. 2004) Amount of dead wood in an old-growth forest with Norway spruce, divided into size classes predicted by a computer simulation model. Mean values and 95% confidence limits from a replicate consisting of 250 subsequent years (average from 1000 replicates).

was modelled by stochastic equations giving both average values and variation in dead wood amount over the management cycle (Fig. 3). A related model was developed for old-growth forests where equilibrium between growth and mortality was assumed (Fig. 4). Both studies demonstrate that dead wood dynamics can be incorporated into forest management strategies and used as tools for "morticulture" (sensu Harmon 2001).

3 Current Status

Several authors have previously provided reviews or reports of dead wood on regional or national level in Fennoscandia (for instance Kruys et al. 1999, Fridman and Walheim 2000, Siitonen 2001, Stokland et al. 2003). The specific aim of this section is to summarise the situation and place it in relation to the previous sections on species demands.

The boreal forests of Fennoscandia can be viewed as a patchwork of predominantly managed stands with different compositional characteristics, such as tree species, age classes and productivity. Taking northern Sweden as an example, about 42% of the forested land is younger than 40 years old, and about 22% is between 40 and 80 years (Forestry statistics 2003). Mature forests (81–120 years) constitute 20%, while old forests (>121 years) only cover about 16% of the forested land (Forestry statistics 2003). Still this is one of the richest regions in Fennoscandia in terms of fraction of older forests. Only the low-productivity portions of northeasternmost Finland have significantly higher fraction of old forests, with landscapes composed of more than 40% of stands older than 120 years. In the middle-, south- and hemiboreal parts of Fennoscandia, only 4–6% of the forest is over-mature (Stokland et al. 2003).

Volumes of dead wood in managed forests range from 4–10 m^3 ha^{-1} within most parts of Fennoscandia. Only the north-boreal zone of Finland has higher values (25 m^3 ha^{-1}; Stokland et al. 2003). In general, the volume of dead wood increases with increasing stand age in Sweden, from an average of 2.1 m^3 ha^{-1} in stands up to 40 years to 19.7 m^3 ha^{-1} in stands older than 140 years (Fridman and Walheim 2000). However, it is only forests more than 60 years of age where volumes start to increase strongly (Ranius et al. 2003). These amounts of dead wood are considerably lower than the levels observed in old-growth natural forests where volumes typically reach levels of 70–100 m^3 ha^{-1} (e.g. Siitonen 2001).

Regarding dead wood quality, individual tree size and the stage of decay are two primary concerns. The diameter distribution of dead wood in the managed landscapes is strongly biased towards small diameter classes (Kruys et al. 1999, Fridman and Walheim 2000), with large dead wood being highly infrequent. Only 10–20% of available logs are larger then 30 cm in managed Swedish forests (Fridman and Walheim 2000). Similarly, the distribution of decay classes is skewed, with late decay stages being under-represented in relation to the situation in unmanaged forests. Dead wood in later decay stages disappears from the managed forests due to normal decay as well as destruction from forestry operations, especially at final cutting (Hautala et al. 2004). Large dead wood is rare in managed forests simply because trees are cut before they succumb to senescence or natural disturbance.

At present, approximately 1% of the productive forestland in Sweden has been assigned a 'semi-protected' status as a woodland key habitat (WKH). These habitats have components of natural forests and are presumed to host or potentially host threatened species. WKH's generally have larger volumes of dead wood (national mean of about 20 m^3 ha^{-1}) than the surrounding landscape, although on average significantly less than old-growth forests (Jönsson and Jonsson, unpublished). Most WKH's are small (median size: 1.4 ha), and occur as isolated stands in the otherwise managed landscape. Aune et al. (2005) studied edge effects and isolation patterns of WKH's in northernmost Sweden (Norrbotten County). Five thousand WKH stands were included in the analysis. A calculation of core area (compensating for a 50 m edge effect) showed that less than 30% of the total WKH area is core area. Of this, most is concentrated in the largest 10% WKH's. Aune et al. (2005) also concluded that, although isolation is a species-dependent effect, only species with very high dispersal ability may efficiently move within the studied network of WKH's and nature reserves.

In addition to the fact that old forests constitute only a small proportion of the landscape, the size of forest patches has also decreased. In a study of forest history in a 170 km^2 area in northern Sweden, Axelsson and Östlund (2001) showed that the percentage of multi-aged forests had decreased from 95% in 1891 to 3% in 1997. They also compared patch sizes of mature and old forests between 1914 and 1997. Constituting 71% and 20% of the landscape in 1914 and 1997 respectively, the mean patch size decreased from 241 to 24 ha. Similarly, the range in patch sizes decreased during the same time period, and the largest patch decreased from constituting 67% of the landscape to only 2%.

New forestry methods, including green-tree retention and setting aside forest stands, have the potential to increase the proportion of dead wood in larger diameter classes (Ranius et al. 2003). New forestry methods mainly concern activities during thinning and at final cutting, making the increases at the landscape level quite slow (Ranius and Kindvall 2004). For species demanding, for instance, large dead trees in closed forest stands or dead wood from slow-growing trees, these methods may prove to be insufficient. Also of major concern is the fact that stands coming into semi-mature and mature stages in the future have likely regenerated after clear-cutting and have been well managed from a forest production perspective. Such stands would have low volumes of dead wood to start with (Fridman and Walheim 2000), and commercial thinning would have lowered their natural mortality (Mäkinen and Isomäki 2004a, 2004b).

4 Discussion

In this discussion we build upon the review above to emphasize the consequences faced by dead wood dependent species. We focus on the situation in Fennoscandian boreal forests, however, the problems are general to many forest ecosystems (Harmon 2001, Grove 2002). During the last decade forest practises have changed (e.g. Raivio et al. 2001) such that various environmental concerns are now routinely taken into account. For example, small stands are set aside at harvesting, dead wood and tree groups are left, and edge zones are created along watercourses. These practises will improve the situation for those wood dependent species that can utilize dead trees in open exposed habitats and that have the potential to disperse among scattered habitats (e.g. Martikainen 2001). However, we believe that the real challenge lies in creating habitats for species that are naturally rare, demand interior forest conditions and have limited dispersal ability. Given the overall low abundance of dead wood and the lack of extensive areas of old-growth forests, these species will continue to face severe problems in the future.

4.1 Temporal Considerations

This review shows that the temporal aspects must be considered in any planning process that aims to increase the survival potential for wood dependent species. Particularly in managed forests, many wood dependent species will be confined to the mature stages where some dead wood has accumulated (cf Siitonen 2001, Ranius et al. 2003) and forest interior conditions prevail. Presently, the situation in Fennoscandian boreal forests is unfavourable for these species since stands currently entering the mature stage are usually strongly influenced by intense management and therefore contain very low volumes of dead wood (Fridman and Walheim 2000, Jönsson and Jonsson, unpublished). Dead wood volumes will likely increase once the current practises (cf Raivio et al. 2001) lead to stands with a larger component of dead wood; however, this may take several decades (Ranius and Kindvall 2004). Many species may thus be facing a prolonged period with a low abundance of dead wood. To counteract this deficit, at least two actions are necessary: increase the protection of remaining dead wood-rich forests with high biological values, and create dead wood during thinning operations. Other alternatives include artificially increasing the amount of dead wood in recently set aside forest reserves (done in southern Finland: Ympäristöministeriö 2003) and prolonging rotation times in mature stands rich in dead wood.

4.2 Spatial Considerations

From both management and conservation perspectives, the decision on where to increase volumes of dead wood should take place on the landscape level (cf Raivio et al. 2001, Kuuluvainen et al. 2002). By landscape we refer to the planning scale applied by most forest companies in Fennoscandia, i.e. in the range of 5000–30 000 ha. However, from a biological point of view, the "landscape" means different things for different organisms depending on their dispersal ability. This should be kept in mind when performing forest management for a multitude of species and forest products – scale is species dependent.

A starting point to answer *where* is by mapping the occurrence of valuable semi-natural forest stands. In model attempts by Hanski (2000) and Huxel and Hastings (1999) it was shown that the scenario with "blind" management generated the worst outcome in terms of survival possibilities. Thus, a prime objective is to identify localities with high habitat quality and with the largest populations of the species in concern (threatened species, keystone species, or other focal species). These sites should form the core of a successful management plan. Otherwise colonisation in other protected or restored sites within the particular landscape will depend on the species' long-distance dispersal ability – an ability that is largely unknown for most species and also questioned for many (Ranius and Hedin 2001, Edman et al. in 2004a, Edman et al. in 2004b). As many dead wood dependent species are rare, the populations will be large enough to ensure local survival for longer time periods only in sites with large volumes of dead wood. Thus, even if a fair number of suitable logs occur scattered among small stands in the landscape, many species may be dependent on abundant dispersal from a few large source populations.

The reliance on woodland key habitats as survival points and dispersal sources in the managed landscape is currently strong in Fennoscandia (Nitare and Norén 1992, SUS 2001). However, the overall low volumes of dead wood in these stands is problematic: in Sweden they contain only about 20% of natural volumes of dead wood (Jönsson and Jonsson unpublished). In addition, they are strongly influenced by edge effects and may be isolated, given the assumed dispersal ability of most wood dependent species (Aune et al. 2005). The risk is thus obvious that woodland key habitats will not be able to maintain their original dead wood dependent species over a longer time perspective – i.e. they may hold an extinction debt to be paid for in the future (e.g. Hanski 2000, Berglund and Jonsson 2005). Nevertheless, areas like the Fennoscandian woodland key habitats are in many forest regions the best starting point for a successful management of forest biodiversity.

4.3 Landscape Planning

Successful landscape planning requires spatial data on both stand structure and the distributions of species that should be preserved. Although efforts have been made to provide this basis, our knowledge is limited, and the need for additional forest inventories is evident. Based on relevant data, deficiencies of certain forest types and hotspots for particular species can be identified. The next step is to maximise the benefit from stands set aside from intensive harvesting, either as fully preserved or with low-intensity harvesting. Here isolation and edge effects are especially important considerations (Aune et al. 2005). When the most valuable habitats are very small and isolated, focus must be on creating buffer zones and increasing habitat connectivity. Given economical constraints, this might imply that some stands, which today have high biological values may have to be "sacrificed", if they are too small and isolated to maintain viable populations of the species in the long run. This should not be taken as an excuse to harvest small semi-natural forests, as these may indeed be important for more easily dispersed species. The point is that when specific target species and species groups are set, not all sites may be of equal importance. Thus we argue to focus on sites where investment gives the best return in the form of increased population viability. This of course calls for a more analytic approach to landscape planning. In such analyses, levels of isolation related to the species in concern together with long-term predictions on the change in availability of dead wood in space and time must be included (cf Ranius and Kindvall 2004). This strongly suggests that the metapopulation tool box (Hanski 1999, Morris and Doak 2002) should be applied in order to conduct population viability analysis. Preferably this analysis should include a set of species with varying demands that covers a larger set of dead wood dependent species (e.g. Angelstam 1998).

4.4 Challenges for the Future

As the number of species directly or indirectly dependent on dead wood is very large (for instance, in Fennoscandia probably in the range between 5000–7000 species; Siitonen 2001, Dahlberg and Stokland 2004), it will not be possible to give quantitative estimates on habitat demands and general guidelines for forest management that are appropriate for all species. For instance, estimates on required volumes of dead wood have been suggested from correlations between species occurrence and current dead wood volumes (e.g. Penttilä et al. 2004, de Jong et al. 2004). However, as the goal should be to preserve overall biodiversity, relationships between dead wood volumes and individual species are insufficient. Of more use would be the relationship between dead wood volumes (and quality) and the total number of dead wood dependent species that occur in viable populations. Because habitat requirements vary widely between wood living organisms, it is unreasonable that there is one target dead wood volume that would meet the needs of all species (Ranius 2005). For these reasons, we refrain from making such a recommendation, and instead conclude with four attainable management goals: 1) counteract the current shortage in dead wood availability; 2) concentrate planning at landscape level in order to minimize isolation and reduce edge effects; 3) create a variety of dead wood; and 4) utilise available quantitative analytical tools. Each of these is addressed in the following paragraphs.

Current changes in forest management in Fennoscandia provide some assurance that forests of the future will provide better habitats for wood living species. However, the current shortage requires attention and at least three actions seems necessary: to increase the protection of remaining semi-natural forests with abundant dead wood, to create dead wood during thinning operations, and possibly also to prolong rotation times in mature stands rich in dead wood.

Although species dispersal abilities differ, we should expect that some species could benefit from increased connectivity among suitable habitats. Such an increase would not pose problems to species with high dispersal ability. A focus on landscapes and landscape segments with viable populations of threatened wood dependent species and concentration of older stands with higher volumes of dead wood (high internal ecological memory sensu Bengtsson et al. 2003) increases the potential success of management efforts. To create landowner platforms for landscape planning can be difficult. For large forest companies this may be done at the corporate level where landscape plans can be compared and adjusted. For example, this is currently practiced in Sweden on land owned by the Swedish-Finnish forest company Stora Enso. How to do this for small forest owners is more difficult to envisage (see however Kurttila et al. 2002). Nevertheless, as the maintenance of forest biodiversity continues to be a pressing societal concern, such planning dialogues needs to be established.

There is no particular type of dead tree, standing or fallen, small or large, shaded or sun-exposed, in early or late decay, or belonging to a particular tree species that is suitable to all wood dependent species. Due to the large number of species associated with dead trees, it is reasonable to assume that all types of dead wood have particular associated species. Advocating for the creation of a variety of dead wood calls for increased knowledge among practitioners so that they actually "see" the types of dead wood that should be created or retained. A focus only on numbers and volumes is not sufficient. In this context, it is quite fortunate that recent research has provided abundant information on the habitat associations for many wood dependent species (Dahlberg and Stokland 2004). The successful transfer of this knowledge from science to practise would no doubt increase the variety of dead wood types in Fennoscandian forests.

The theoretical foundation for landscape-level population viability analysis has been laid. The lack of data on the species to parameterise population viability models is currently a limitation, but ongoing research will give these models more credibility and provide input from a wider range of organisms. The inclusion of quantitative analytical tools in forest biodiversity management may seem easy in theory but requires new approaches to planning and management. Applying quantitative landscape analysis and performing population viability analyses, as a part of forest management, requires a significant increase in resources both economically and regarding analytic capacity. However, for what use do scientists develop tools if they do not intend to see them put into practise? Further, to what purpose do forestry authorities and forest owners allocate resources on various conservation practises if they are not fine-tuned to meet the conservation goals? National, corporate and private economy, as well as the credibility of the forest certification systems, calls for an efficient use of the hectares and volumes that are set aside to protect biodiversity. There is thus a strong incentive to apply the best available knowledge and techniques in this context. It is also by such quantitative analyses that the answers to the urgent questions on how much and where are given. There is no reason to believe that any particular combination of quality and quantity of dead wood at any certain spatial scale is sufficient for survival of all species, as requirements are species specific (cf Angelstam et al. 2003). Thus, there is a need to define specific conservation goals (in terms of focal species or species groups that should be maintained at certain spatial scales) before critical quantitative thresholds can be given. General rules of thumb may have large impact on management, but are potentially counterproductive since they risk allocating either too little (increased extinction risks) or too much (increased costs).

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References

Alexander, K.N.A. 1998. The links between forest history and biodiversity: the invertebrate fauna of ancient pasture-woodland in Britain and its conservation. In: Kirby, K.J. & Watkins C. (eds.). The ecological history of European forests. CAB International, Oxon. p. 73–80.

Angelstam, P. 1998. Towards a logic for assessing biodiversity in boreal forest. In: Bachmann, P., Köhl, M. & Päivinen, R. (eds.). Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Dordrecht. p. 301–313.

Angelstam, P.K., Bütler, R., Lazdinis, M., Mikusinski, G. & Roberge, J.-M. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation — dead wood as an example. Annales Zoologici Fennici 40: 473–482.

Aune, K., Jonsson, B.G. & Moen, J. 2005. Isolation and edge effects among woodland key habitats in Sweden: making fragmentation into forest policy? Biological Conservation, in press.

Axelsson, A.-L. & Östlund, L. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management 147: 109–122.

Bader, P., Jansson, S. & Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72: 355–362.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. 2003. Reserves, resilience and dynamic landscapes. Ambio 32: 389–396.

Berglund, H. & Jonsson, B.G. 2003. Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. Biological Conservation 112: 319–328.

— & Jonsson, B.G. 2005. Verifying an extinction debt in north Swedish boreal forests. Conservation Biology, in press.

— , Edman, M. & Ericson, L. 2005. Temporal variation of wood-fungi diversity at different spatial scales in boreal old-growth Picea abies forests – Implications for monitoring. Ecological Applications, in press.

Bernes, C. 1994. Biological diversity in Sweden. Monitor 14, Swedish Environmental Protection Agency.

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.

Dahlberg, A. & Stokland, J. 2004. Vedlevande arters krav på substrat – en sammanställning och analys av 3600 arter. Skogsstyrelsen, Jönköping. [in Swedish].

de Jong, J. Dahlberg, A., Almstedt, M., Jonsson, B.G., Hysing, E. & Silfverling, G. 2004. Mer död ved i skogen – en förutsättning för tusentals arters överlevnad. Fauna och Flora 99(2): 36–41. [in Swedish].

Den Boer, P.J., Van Huizen, T.H.P., Den Boer-Daanje, W. & Aukema, B. 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). Entomologia Generalis 6: 107–134.

Denno, R.E., Roderick, G.K., Peterson, M.A., Huberty, A.F., Dobel, H.G., Eubanks, M.D., Losey, J.E. & Langellotto, G.A. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. Ecological Monographs 66: 389–408.

Dowding, P. 1984. The evolution of insect – fungus relationships in the primary invasion of forest timber. In: Anderson, J.M. (ed.). Invertebrate – Microbial interactions. Cambridge University Press, Cambridge. p. 133–155.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B.G. & Ericson, L. 2004a. Spore composition of wood-decaying fungi: importance of landscape composition. Ecography 27: 103–111.

— , Kruys, N. & Jonsson, B.G. 2004b. Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on experimental logs. Ecological Applications 14: 893–901.

— , Gustafsson, M., Stenlid, J. & Ericson, L. 2004c. Abundance and viability of fungal spores along a forestry gradient – responses to habitat loss and isolation? Oikos 104: 35–42.

Engelmark, O. & Hytteborn, H. 1999. Coniferous forests. Acta Phytogeographica Suecica 84: 55–74.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16–47.

Forsse, E. & Solbreck, C. 1985. Migration in bark beetle Ips tyopgrahus L.: duration timing and height of flight. Zeitschrift für angewandte Entomologie 44: 1787–1795.

Forestry statistics 2003. Official statistics of Sweden. Swedish University of Agricultural Sciences. Umeå, Sweden.

Fries, C., Johansson, O., Pettersson, B. & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89–103.

Fridman, J. & Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management 131: 23–36.

— & Ståhl, G. 2001. A three-step approach for modelling tree mortality in Swedish forests. Scandinavian Journal of Forest Research 16: 455–466.

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

Gu, W., Heikkilä, R. & Hanski, I. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17: 699–710.

Gustafsson, M., Allmér, J. & Stenlid, J. 2002. A demographic model approach to study the ecology of Fomitopsis rosea. In: Gustafsson, M.H. Distribution and dispersal of wood-decaying fungi occurring on Norway spruce logs. PhD-thesis Swedish University of Agricultural Sciences, Uppsala, Sweden.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press. 313 p.

— 2000. Extinction debt and species credit in boreal forests: modeling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37: 271–280.

— 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88: 372–381.

Harmon, M.E. 2001. Moving towards a new paradigm for woody detritus management. Ecological Bulletins 49: 269–278.

— et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

— , Krankina, O.N. & Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus dynamics. Canadian Journal of Forest Research 30: 74–84.

Harrison, S. & Taylor, A.D. 1997. Empirical evidence for metapopulation dynamics. In: Hanski, I. & Gilpin, M.E. (eds.). Metapopulation biology. Ecology, genetics and evolution. Academic Press, San Diego. p. 27–42.

Hautala, H., Jalonen J., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity and Conservation 13: 1541–1554.

Hillmo, O. & Såstad, S. 2001. Colonization of old-forest lichens in a young and an old boreal Picea abies forest: an experimental approach. Biological Conservation 102: 251–259.

— & Ott, S. 2002. Juvenile development of the cyanolichen Lobaria scrobiculata and the green algal lichens Platismatia glauca and Platismatia norvegica in a boreal Picea abies forest. Plant Biology 4: 273–280.

Hofgaard, A. 1993. 50 years of change in a Swedish boreal old-growth Picea abies forest. Journal of Vegetation Science 4: 773–782.

Högberg, N. & Stenlid. J. 1999. Population genetics of Fomitopsis rosea – A wood-decay fungus of the old-growth European taiga. Molecular Ecology 8: 703–710.

— , Stenlid, J. & Karlsson, J.O. 1995. Genetic differentiation in Fomitopsis pinicola (Schwarts: Fr) Karst studied by means of arbitrary primed-PCR. Molecular Ecology 4: 675–680.

Huxel, G.R. & Hastings A. 1999. Habitat loss, fragmentation and restoration. Restoration Ecology 7: 309–315.

Hytteborn, H. & Packham, J.R. 1987. Decay rate of Picea abies logs and the storm tap theory: a re-examination of Sernander plot III, Fiby urskog, central Sweden. Arboricultural Journal 11: 299–311.

Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal – theoretical models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics 21: 449–480.

Jonsell, M. & Nordlander, G. 1995. Field attraction of Coleoptera to odours of the wood-decaying polypores Fomitopsis pinicola and Fomes fomentarius. Annales Zoologici Fennici 31: 97–107.

— & Nordlander, G. 2002. Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. Forest Ecology and Management 157: 101–118.

— , Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749–764.

— , Nordlander, G. & Ehnström, B. 2001. Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. Ecological Bulletins 49: 173–194.

— , Schroeder, M. & Larsson, T. 2003. The saproxylic beetle Bolitophagus reticulatus: its frequency in managed forests, attraction to volatiles and flight period. Ecography 26: 421–428.

— , Nittérus, K. & Stighäll, K. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation 118: 163–173.

Jonsson, B.G. 2000. Availability of coarse woody debris in an old-growth boreal spruce forest landscape. Journal of Vegetation Science 11: 51–56.

— & Kruys, N. (eds.) 2001. Ecology of woody debris in boreal forests. Ecological Bulletins 49.

Jonsson, M. 2002. Dispersal ecology of insects inhabiting wood-decaying fungi. PhD-thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

— 2003. Colonisation ability of the threatened tenebrionid beetle Oplocephala haemorrhoidalis and its common relative Bolitophagus reticulatus. Ecological Entomology 28: 159–167.

— , Nordlander, G. & Jonsell, M. 1997. Pheromones affecting flying beetles colonizing the polypores Fomes fomentarius and Fomitopsis pinicola. Entomologica Fennica 8: 161–165.

— , Johannesen, J. & Seitz, A. 2003. Comparative genetic structure of the threatened tenebrionid beetle Oplocephala haemorrhoidalis and its common relative Bolitophagus reticulatus. Journal of Insect Conservation 7: 111–124.

Josefsson, H. 2002. Long-distance dispersal in wood-decaying basidiomycetes. MSc-thesis Dept of Ecology and Environmental Sciences, Umeå University.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 4: 21–23.

— , Martikainen, P., Punttila, P. & Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoologici Fennici 31: 97–107.

— , Martikainen, P. & Punttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation 6: 1–18.

Kauserud, H. & Schumacher, T. 2003. Genetic structure of Fennoscandian populations of the threatened wood-decay fungus Fomitopsis rosea (Basidiomycota). Mycological Research 107: 155–163.

Kenis, M., Wermelinger, B. & Grégoire, J.-C. 2004. Research on parasitoids and predators of Scolytidae – a review. In: Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C. & Evans, H.F. (eds.). Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer Academic Publishers, Dordrecht. p. 237–290.

Kimmerer, R.W. 1993. Disturbance and dominance in Tetraphis pellucida: A model of disturbance frequency and reproductive mode. The Bryologist 96: 73–79.

— 1994. Ecological consequences of sexual versus asexual reproduction in Dicranum flagellare and Tetraphis pellucida. The Bryologist 97: 20–25.

— & Young, C.C. 1996. Effect of gap size and regeneration niche on species coexistence in bryophyte communities. Bulletin of the Torrey Botanical Club 123: 16–24.

Knutsen, H., Rukke, B.A., Jorde, P.-E. & Ims, R.A. 2000. Genetic differentiation among populations of the beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape. Heredity 84: 667–676.

Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90: 119–126.

Krankina, O.N. & Harmon. M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air and Soil Pollution 82: 227–238.

Kruys, N. & 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.

— , Fries, C., Jonsson, B.G., Lämås, T. & Ståhl, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Canadian Journal of Forest Research 29: 178–186.

— , Jonsson, B.G. & Ståhl, G. 2002. A stage-based matrix model for decomposition dynamics of woody debris. Ecological Applications 12: 773–781.

Kurttila, M., Uuttera, J., Mykrä, S., Kurki, S. & Pukkala, T. 2002. Decreasing the fragmentation of old forests in landscapes involving multiple ownership in Finland: economic, social and ecological consequences. Forest Ecology and Management 166: 69–84.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annales Zoologici Fennici 31: 35–51.

— , Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J. & Tukia, H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fennica 36(1): 409–422.

Laaka-Lindberg, S., Hedderson, T.A. & Longton, R.E. 2000. Rarity and reproductive characters in the British hepatic flora. Lindbergia 25: 78–84.

— , Korpelainen, H. & Pohjamo, M. 2003. Dispersal of asexual propagules in bryophytes. Journal of the Hattori Botanical Laboratory 93: 319–330.

Larsson, M.C., Hedin, J., Svensson, G.P., Tolasch, T. & Francke, W. 2003. Characteristic odor of Osmoderma eremita identified as a male-released pheromone. Journal of Chemical Ecology 29: 575–587.

Lindhe, A. & Lindelöw, Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203: 1–20.

— , Lindelöw, Å. & Åsenblad, N. (in press). Saproxylic beetles in standing dead wood – density in relation to substrate sun-exposure and diameter. Biodiversity and Conservation (in press).

Liu, Q. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval Picea abies forest. Journal of Vegetation Science 2: 391–402.

Longton, R.E. 1992. Reproduction and rarity in British mosses. Biological Conservation 59: 89–98.

Mäkinen, H. & Isomäki, A. 2004a. Thinning intensity and growth of Scots pine stands in Finland. Forest Ecology and Management 201: 311–325.

— & Isomäki, A. 2004b. Thinning intensity and growth of Norway spruce stands in Finland. Forestry 77: 349–364.

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

— & Kouki, J. 2003. Sampling the rarest: threatened beetles in boreal forest inventories. Biodiversity and Conservation 12: 1815–1831.

Moen, J. & Jonsson, B.G. 2003. Edge effects on liverworts and lichens in forest patches in a mosaic boreal forest and wetland. Conservation Biology 17: 380–388.

Morris, W.F. & Doak, D.F. 2002. Quantitative conservation biology. Theory and practice of population viability analysis. Sinauer Press. 480 p.

Naesset, E. 1999. Decomposition rate constants of Picea abies logs in southeastern Norway. Canadian Journal of Forest Research 29: 372–381.

Niemelä, T, Renvall, P. & Penttilä, R. 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici 32: 141–152.

Nilsson, S.G. , Arup, U., Baranowski, R. & Ekman, S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. Conservation Biology 9: 1208–1215.

— & Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20: 491–498.

Nitare, J. & Norén, M. 1992. Nyckebiotoper kartläggs i nytt projekt vid Skogsstyrelsen. Svensk Botanisk Tidskrift 86: 219–226. [in Swedish].

Nordén, B. 1997. Genetic variation within and among populations of Fomitopsis pinicola. Nordic Journal of Botany 17: 319–329.

— 2000. Dispersal ecology and conservation of wood-decay fungi. PhD-thesis, Göteborg University, Sweden.

— & Larsson, K.-H. 2000. Basidiospore dispersal in the old-growth forest fungus Phlebia centrifuga (Basidiomycetes). Nordic Journal of Botany 20: 215–219.

— & Appelqvist, T. 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity and Conservation 10: 779–791.

— , Ryberg, M., Götmark, F. & Olausson, B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117: 1–10.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 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. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology 93: 195–209.

Penttilä, R., Siitonen, J. & Kuusinen, M. 2004. Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. Biological Conservation 117: 271–283.

Pohjamo, M. & Laaka-Lindberg, S. 2004. Reproductive modes in the epixylic hepatic Anastrophyllum hellerianum. Perspectives in Plant Ecology, Evolution and Systematics 6: 159–168.

Raivio, S., Normark, E., Pettersson, B. & Salpakivi-Salomaa, P. 2001. Science and the management of boreal forest biodiversity – Forest industries' views. Scandinavian Journal of Forest Research, Suppl.: 99–104.

Ranius, T. 2000. Minimum viable metapopulation size of a beetle, Osmoderma eremita, living in tree hollows. Animal Conservation 3: 37–43.

— 2005. Hur mycket död ved behövs i skogen. Svensk Botanisk Tidskrift, 99: 60–61. [in Swedish].

— & Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95: 85–94.

— & Hedin, J. 2001. The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows. Oecologia 126: 363–370.

— & Jansson, N. 2002. A comparison of three methods to survey saproxylic beetles associated with old oaks. Biodiversity and Conservation 11: 1759–1771.

— & Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation 119: 51–59.

— , Kindvall. O., Kruys, N. & Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. Forest Ecology and Management 182: 13–29.

— , Kruys, N. & Jonsson, B.G. 2004. Modelling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Canadian Journal of Forest Research 34: 1025–1034.

— , Ekvall, H., Jonsson, M. & Bostedt, G. 2005. Cost-efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. Forest Ecology and Management 206: 119–133.

Roff, D.A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. American Naturalist 144: 772–798.

Rolstad, J., Gjerde, I., Gundersen, V.S. & Sætersdal, M. 2002. Use of indicator species to assess forest continuity: a critique. Conservation Biology 16: 253–257.

— , Saetersdal, M., Gjerde, I. & Storaunet, K.O. 2004. Wood-decaying fungi in boreal forests: are species richness and abundances influenced by small-scale spatiotemporal distributions of dead wood? Biological Conservation 117: 539–555.

Rukke, B.A. & Midtgaard, F. 1998. The importance of scale and spatial variables for the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented forest landscape. Ecography 21: 561–572.

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

— & Saaristo, L. 2000. Habitat requirements and conservation of Phyto kolwensis, a beetle species of old-growth boreal forest. Biological Conservation 94: 211–220.

Snäll, T. & Jonsson, B.G. 2001. Edge effects on wood-inhabiting fungi used as indicator species. Ecological Bulletins 49: 255–262.

Söderström, L. 1981. Distribution of bryophytes in spruce forests on hill slopes in central Sweden. Wahlenbergia 7: 141–153.

— & Jonsson, B.G. 1989. Spatial pattern and dispersal in the leafy hepatic Ptilidium pulcherrimum. Journal of Bryology 15: 793–802.

Southwood, T.R.E. 1962. Migration of terrestrial arthropods in relation to habitat. Biological Review of the Cambridge Philosophical Society 37: 171–214.

Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins 49: 71–84.

— , Eriksen, R., Tomter, S.M., Korhonen, K., Tomppo, E., Rajaniemi, S., Söderberg, U., Toet, H. & Riis-Nielsen, T. 2003. Forest biodiversity indicators in the Nordic countries. TemaNord 2003:514. Nordic Council of Ministers, Copenhagen, Denmark.

Storaunet, K. & Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Canadian Journal of Forest research 32: 1801–1812.

SUS 2001. Skogsvårdsorganisationens utvärdering av skogspolitikens effekter – SUS 2001. Skogstyrelsen, Jönköping. [in Swedish].

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

Sverdrup-Thygeson, A. & Midtgaard, F. 1998. Fungus infected trees as islands in boreal forests: Spatial distribution on the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae). Écoscience 5: 486–493.

— & Ims, R.A. 2001. The effect of forest clear-cutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation 106: 347–357.

— & Lindenmayer, D.B. 2003. Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. Forest Ecology and Management 174: 353–363.

Tarasov, M.E. & Birdsey, R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecological Bulletins 49: 137–148.

Thomas, C.D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conservation Biology 8: 373–378.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Vasiliauskas, R., Stenlid, J. & Thomsen, L.M. 1998. Clonality and genetic variation in Amylostereum areolatum and A. chailletii from northern Europe. New Phytologist 139: 751–858.

Ympäristöministeriö 2003. Ennallistaminen suojelualueilla. Ennallistamistyöryhmän mietintö. Suomen ympäristö 618. Ympäristöministeriö, Helsinki. [in Finnish].

Young, A.G. & Clarke, G.M. 2000. Genetics, demography and viability of fragmented populations. Cambridge University Press. 438 p.

Total of 137 references