Communities of wood-inhabiting fungi: Ecological requirements and responses to forest management and fragmentation

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Academic dissertation

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The woods are lovely dark and deep.

But I have promises to keep.

And miles to go before I sleep,

And miles to go before I sleep.

– Robert Frost –

CONTENTS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I	Hottola, J., Ovaskainen, O. and Hanski, I. 2009. A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. – *Journal of Ecology* 97, 1320–1328
II	Hottola, J., Penttilä, R., Siitonen, J., Tomppo, E. and Ovaskainen, O. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented forests. – *Manuscript*
III	Hottola, J. and Siitonen, J. 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. – *Biodiversity and Conservation* 17, 2559–2577
IV	Ovaskainen, O., Hottola, J. and Siitonen J. Species co-occurrence modeled by Bayesian multivariate logistic regression. – *Submitted manuscript*

CONTRIBUTIONS

The table shows the major contributions of authors to the original articles and the manuscripts. Other contributors are acknowledged in the relevant articles or manuscripts.

	I	**II**	**III**	**IV**
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ABSTRACT

Despite much research on forest biodiversity in Fennoscandia, the exact mechanisms of species declines in dead-wood dependent fungi are still poorly understood. In particular, there is only limited information on why certain forest-associated fungal species have responded negatively to habitat loss and fragmentation, while others have not. Understanding the mechanisms behind species declines would be essential for the design and development of ecologically effective and scientifically informed conservation measures, and management practices that would promote biodiversity in production forests.

In this thesis I study the ecology of polypore fungi and their responses to forest management, with a particular focus on why some species have declined more than others. The data considered in the thesis comprise altogether 98,318 dead-wood objects, with 43,085 observations of 174 fungal species. Out of these, 1,964 observations represent 58 red-listed species. The data were collected from 496 sites, including woodland key habitats (179 sites), clear-cuts with retention trees (132), mature managed forests (82), and natural or natural-like forests in southern Finland (91) and Russian Karelia (12).

I show that the most relevant way of measuring resource availability can differ to a great extent between species seemingly sharing the same resources. It is thus critical to measure the availability of resources in a way that takes into account the ecological requirements of the species. The results show that connectivity at the local, landscape and regional scales is important especially for the highly specialized species, many of which are also red-listed. It is thus likely that small habitat patches contribute only marginally to protection of red-listed species, especially if habitat quality is not substantially higher than in ordinary managed forest, as is the case with woodland key habitats. Habitat loss and fragmentation affect not only species diversity but also the relative abundances of the species and, consequently, species interactions and hence fungal successional pathways. Changes in species distributions and abundances are likely to affect the food chains in which wood-inhabiting fungi are involved, and thus the functioning of the whole forest ecosystem.

The findings of my thesis highlight the importance of protecting well-connected, large and high-quality forest areas instead of small fragments distributed across the landscape. Woodland key habitats might have the potential to contribute to maintenance of forest biodiversity as supplementing elements of the forest protection network if the key habitats were delineated larger and if harvesting of individual trees was prohibited in them. Taking the landscape perspective into account in the design and development of conservation measures is critical while striving to halt the decline of forest biodiversity in an ecologically effective manner.

SUMMARY

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1 Introduction

Habitat loss and fragmentation in boreal forests of Fennoscandia

Habitat loss and fragmentation are major threats to biodiversity worldwide, across all ecosystems (Anon. 2005). For hundreds of millions of years, since the Late Devonian, forests have been the dominant terrestrial ecosystem on Earth (Hanski 2005). The global loss of pristine forests may seem less dramatic in the boreal region than in the tropics, as pristine boreal forests have mostly been converted to production forests consisting of native tree species rather than to e.g. cultivated fields. Thus, the forest cover in the boreal region may have even increased (Kauppi et al. 2006) at the same time as forest biodiversity has descended into crisis. Boreal forests and forest landscapes have been fundamentally transformed especially in Fennoscandia (Östlund et al. 1997; Kouki et al. 2001), whereas in Siberia and Canada larger tracts of natural forests still remain.

The large-scale alteration of natural structures and processes in Fennoscandian forest landscapes has caused a severe decline of forest-associated species. Out of the 1,505 species classified as threatened in Finland, the primary cause of threat is either forest management or overgrowth of open habitats for 61% of the species (Rassi et al. 2001). These threats represent habitat loss and fragmentation from the viewpoint of the focal species. Thirty-eight percent of the threatened species in Finland live primarily in forest habitats. In Sweden, ca. 2,000 forest-associated species are considered to be threatened (Gärdenfors 2005).

Currently, only about 1.9% of the forest land in southern Finland is under protection (www.metla.fi/metinfo/tilasto/suojelu/suojelu_taulukot.html), and a large proportion of the protected forests have been previously managed (Anon. 2000). The majority of the forest land in southern Finland is privately-owned, and therefore establishing new protection areas is economically and socially difficult. Remedies have been sought during the last two decades from biodiversity-oriented forest management (e.g. woodland key habitats and retention trees) and voluntary permanent or temporary protection (Forest Biodiversity Programme for Southern Finland). The aim is to protect biodiversity as cost-effectively as possible. However, the ecological benefits of this kind of 'precision conservation' remain largely to be shown.

Attempts have been made to identify landscape-level habitat availability thresholds for species persistence to effectively direct conservation and management actions. Quantitative studies from boreal forests in Canada (Betts & Villard 2009) and Fennoscandia (Andrén 1994) suggest the landscape-level threshold in the amount of habitat ranges from 10-30%. Such thresholds are likely to vary according to species characteristics and habitat types. The spatial distribution of the habitat can be assumed to be of particular importance for sedentary species which inhabit long-lasting microhabitats (Jonsson & Ranius 2009), such as certain fungal species on large logs. It is evident that e.g. in southern Finland the amount of many habitat types is substantially below the landscape-level threshold for many forest species.

Loss of dead wood in forests

Abundant and diverse dead wood is an essential structural component in boreal forests and plays a key role in ecosystem functioning. Diverse dead wood enhances species diversity by providing a range of resources and niches suitable for a variety of species. Compared to many other microhabitats, dead wood is a relatively stable substrate and thus provides favorable conditions for growth and reproduction. Very large numbers of organisms have adapted to use dead wood as food, growing substrate or shelter, simultaneously contributing to its decomposition (Siitonen 2001; Hanski 2005; Jonsson et al. 2005; Tikkanen et al. 2006; Lonsdale et al. 2008). In Finland, it has been estimated that 20–25% (4,000–5,000 species) of all forest-inhabiting species are dependent on dead wood at least in some part of their life cycle (Siitonen 2001).

Boreal forests have experienced a large-scale reduction in the amount dead wood. Intensive forestry has reduced the mean volume of dead wood to 4-10 m^3 ha^{-1} in managed forests in most parts of Fennoscandia (Jonsson et al. 2005), whereas the typical range in Fennoscandian natural forests is 60-120 m^3 ha^{-1} (Siitonen 2001). Loss of dead wood is the primary cause of threat for 25% of threatened forest species in Finland (Rassi et al. 2001). Nilsson et al. (2001) suggest, based on general extinction models and several empirical studies, that at least 20% of original densities of large living and dead trees should be preserved in managed forests to ensure that forestry is ecologically sustainable. In southern Fennoscandia, this corresponds to 20-30 m^3 ha^{-1} of dead wood. This kind of guidelines may aid in developing biodiversity-oriented management, but it is unlikely they reflect the needs of all forest species of concern.

Dead-wood dependent fungi

There are ca. 750 species of dead-wood dependent basidiomycetes in Finland, and the corresponding number of ascomycete species is ca. 600 (Anon. 2000). Most of the wood-inhabiting basidiomycetes are aphyllophorous species, which comprise a diverse, ecologically important and taxonomically well known group of species (e.g. Eriksson et al. 1973-1988; Niemelä 2005; Kotiranta et al. 2009). Wood-inhabiting fungi are key species in forest ecosystems in the sense that they offer microhabitats and food for other organisms. Further, the saprotrophic species release the energy and nutrients stored in dead trees, and the pathogenic species kill individual trees thus contributing to the disturbance dynamics in the forest. About five percent of the poroid aphyllophorales in Finland are primarily mycorrhizal, while 25% are pathogenic and 70% are saprotrophic (Kotiranta & Niemelä 1996; Niemelä 2004). Many fungal species are, however, known to be able to switch from one nutritional strategy to another if needed (Dix & Webster 1995).

As many of the wood-inhabiting fungal species are more or less specialized in their use of resources and habitats, they are commonly used as indicators of the ecological condition of a forest in northern Europe (see Halme et al. 2009). A substantial fraction of the species have been classified as threatened or near threatened (red-listed) in Finland and Sweden (Rassi et al. 2001; Gärdenfors 2005), corresponding to one fourth of all aphyllophorous species (ca. 1,100 species, most of which are corticioids) and one third of all polypore species (poroid Aphyllophorales; ca. 260 species) in both countries. The decline of wood-inhabiting fungi is attributed mainly to intensive forest management that has reduced the availability of dead wood. Especially large logs which offer particular microclimatic conditions, physical and chemical characteristics, and long-lasting substrates for slow-growing species have been recognized as important substrates for threatened fungal species (Bader et al. 1995; Renvall 1995; Lindblad 1998; Kruys et al. 1999; Tikkanen et al. 2006). Indications of dispersal limitation have also been detected in landscapes experiencing extensive loss and fragmentation of forest habitats. In such landscapes, the abundance and viability of spores of declining fungal species are lowered (Edman et al. 2004a; Edman et al. 2004b).

All of the five aphyllophorous species that are classified as extinct in Finland are forest species, and 93% of the 115 threatened species and 97% of the 75 near-threatened species live primarily in forest habitats. Spruce is the main host-tree species for 29% of the red-listed aphyllophorous species, and the corresponding figures are 21% for pine, 6% for aspen, 8% for alders and 6% for birches. In the absence of any human influence, most red-listed boreal aphyllophorous species would occur in all of boreal Finland. Only six species are considered to be true 'taiga species' and thus restricted to northern and eastern part of boreal Finland by their natural range (Kotiranta & Niemelä 1996; Anon. 2000). Finland has a long tradition of taxonomy and surveys of polypores starting from Karsten (1859). Collections kept in botanical museums show that the distribution of many species has changed dramatically during 150 years. For instance, there are many 19th and early 20th century records from southern Finland of species (Kotiranta & Niemelä 1996, 1997) that are at present regionally extinct (e.g. *Antrodia crassa* and *Perenniporia tenuis* var. *pulchella*) or very rare (Rassi et al. 2001; Kotiranta et al. 2009). In the Finnish Red-List assessment (Rassi et al. 2001), the major threats for the red-listed aphyllophorous species include changes in the age structure of forests, decrease in the amount of dead wood, forest management actions, changes in tree species composition, construction, and small population size. The main habitats of the red-listed aphyllophorous fungi are old heathland forests and herb-rich forests (Kotiranta & Niemelä 1996; Anon. 2000; Rassi et al. 2001).

Apart from the quality of the dead-wood substrate, microclimate and characteristics of the site and landscape, the occurrence of wood-inhabiting fungi is affected by species interactions. Renvall (1995) has described various successional pathways in communities of wood-inhabiting fungi. Some of the species are specialized in very close interaction with other fungal species, thus creating predecessor-successor species pairs (Niemelä et al. 1995; Renvall 1995).

Open research questions

Despite much research on forest biodiversity in Fennoscandia (Kouki et al. 2001; Nilsson et al. 2001; Siitonen 2001; Berglund 2004; Jonsson et al. 2005), the exact mechanisms of decline of the dead-wood dependent fungi and other species groups are still poorly understood. In particular, there is only limited information on why certain forest-associated fungal, insect and bryophyte species have responded negatively to habitat loss and fragmentation, while others have not. This is in contrast with research on other taxonomical groups such as plants, birds, mammals and butterflies, where species attributes (e.g. body size and mobility) have been linked to regional and global population trends (Kattan 1992; Henle et al. 2004; Pöyry et al. 2009). Understanding the mechanisms behind species declines would be essential for developing cost-effective and scientifically informed conservation actions, but the necessary information for most forest-associated species is not available (but see Davies et al. 2004).

2 Aims of the thesis

In this thesis, I study the communities of wood-inhabiting fungi, mainly polypores, with the aim of gaining understanding of the ecological characteristics of the species and their responses to forest management. A particular focus of the research has been the question why some species have declined more than others. Knowledge on ecological requirements and responses to forestry of individual species is necessary for the design and development of ecologically effective conservation measures and management practices that would promote biodiversity in production forests.

The first **Chapter (I)** includes the development of a new measure for resource availability that integrates the contributions of the number, volume and diversity of resource units. We use this measure to characterize how the contrasting ecologies of common and red-listed species are reflected in their responses to habitat quality.

In **Chapter II,** our objectives are to study species' responses to connectivity at the local, landscape and regional scale, and to identify the ecological and life-history traits that are associated with vulnerability to loss of connectivity, and which may increase the risk of extinction.

Chapter III focuses on woodland key habitats, a key concept in biodiversity-oriented forest management. We compared brook-side key habitats and ordinary managed forests to find out whether they differ in their structural features and species composition, and whether the key habitats host red-listed species, as assumed.

Finally, in **Chapter IV** we attempt to disentangle the effects of resource use and interspecific biological associations in generating species co-occurrences. We model co-occurrence data on polypore communities with multivariate logistic regression, including both species-specific substrate preferences and positive or negative residual associations.

3 Material and methods

Study area and study sites

The study area extends from southwestern Finland to eastern Finland and northwestern Russia in southern and middle boreal vegetation zones (Ahti et al. 1968) in eastern Fennoscandia (Fig. 1). The history of land use in terms of duration and intensity varies between different parts of the study area (Lilja & Kuuluvainen 2005 and references therein). In the southwest-northeast direction, southwestern Finland has the longest history of intensive land use, and, consequently, the lowest proportion of natural forests remaining in the landscape. The loss of natural forests is more recent in eastern Finland and Russian Karelia, where the area of natural-like forests is larger. In the south-north direction, history of intensive land use is longer in the southern boreal vegetation zone than in the middle boreal zone. In order to study these gradients in land-use history and landscape structure, we selected three study regions, two of which extend to both southern and middle boreal vegetation zones.

I collected the material for this thesis with the help of a group of field assistants in the autumns of 2000 to 2005. The data include 179 woodland key habitats (69 brook-side key habitats, 70 key habitats on rocky outcrops and 40 herb-rich key habitats), 132 clear-cuts with retention trees, 82 mature managed forests and 54 protected natural or natural-like forests in southern Finland, and 12 natural or natural-like forests in Russian Karelia. In addition to these data, **Chapter II** includes Reijo Penttilä's data from 15 old-growth forests and 22 wind-throw sites.

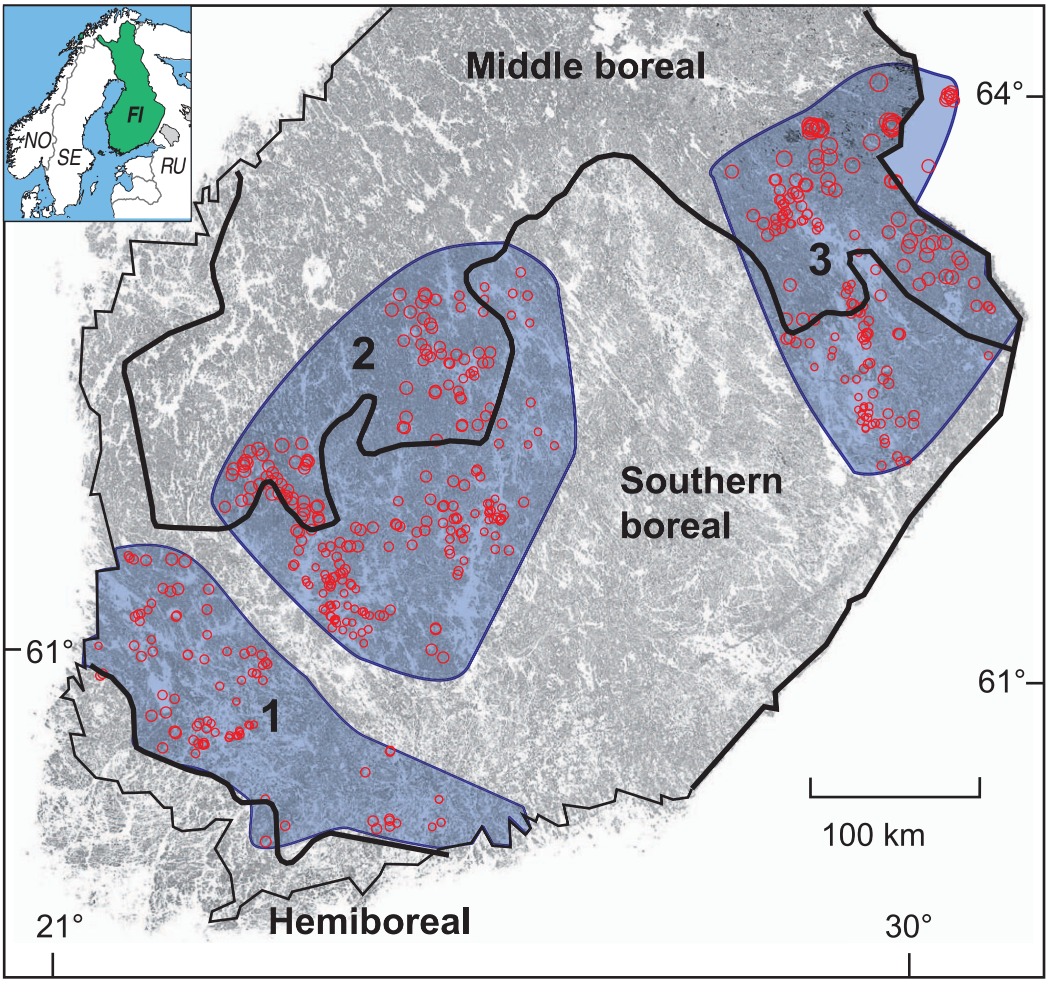

Figure 1. Locations of the study sites included in this thesis in the southern Finland and northwestern Russia. The size of each dot is proportional to the landscape-level connectivity (S2) of the focal site (see Material and Methods in **Chapter II**). Study regions: 1 = southwestern and southernmost Finland; 2 = central Finland; 3 = eastern Finland and Russian Karelia

The locations of the altogether 496 sites are shown in Figure 1. The study forests represent a range of successional stages from young to very old. Most of the forests were dominated by Norway spruce (*Picea abies* (L.) Karsten), some by Scots pine (*Pinus sylvestris* L.), and a few by deciduous tree species. The full data are described in detail in **Chapter II**.

Focal species

The focal species of this thesis work include all polypore species (poroid Aphyllophorales) occurring in Finland (Niemelä 2005). In addition, 16 other wood-inhabiting species that are either red-listed (Rassi et al. 2001) or indicator species (Kotiranta & Niemelä 1996), and relatively easy to identify in the field, were included in this study. Polypores are a polyphyletic form group of species that share morphological and ecological characteristics. Their taxonomy has been in turbulence in recent years, molecular systematic analyses placing previous congenerics sometimes to different phylogenetic clades.

Species and dead-wood inventories

All data used in this thesis come from systematic surveys of all downed and standing dead-wood objects in the predefined study area which in most cases was an entire forest stand. Most of the data come from sample plots with an area of 0.2. ha but ranging (depending on the data set) from 0.12 to 4.38 ha. Within the sample plots, a minimum diameter of 5 cm and a minimum length of 1.3 m were used. In addition to the sample-plot inventories, the surrounding area of the focal forest stand was inventoried for dead trees at least 15 cm in diameter. In 96 clear-cut sites, no sample plot was established but retention trees were surveyed over the whole cutting area. We recorded for each dead-wood object the tree species, diameter, type of tree, decay-stage class, and length (only for broken trees), epiphyte cover (0-100%), bark cover (0-100%) and ground contact (1 = no ground contact, 2 = less than half of the trunk in ground contact, or 3 = more than half of the trunk in ground contact). For a detailed description of the inventory method see the section Material and methods in **Chapter III**.

We recorded the presence-absence of all the focal species on each dead-wood object, counting one or several fruit bodies of a particular species on an individual dead tree as one occurrence (e.g. Bader et al. 1995; Lindblad 1998; Junninen & Kouki 2006). If only dead fruit bodies were found, the species was considered present but dead. When there was any doubt about identification in the field, a specimen was collected for later microscopical identification. Representative specimens are preserved in the Botanical Museum of the University of Helsinki, and the rest are stored at the Finnish Forest Research Institute.

In addition to dead-wood measurements and species surveys, a number of variables describing the living stand were measured. The measurement and calculation of stand characteristics is explained in detail in Siitonen et al. (2009). Some of the stand characteristics, including stand area, forest site type, development class and age of dominating trees, were acquired from habitat-mapping and forest-management plan databases.

Treatment of the data

The data considered in this thesis include altogether 98,318 dead-wood objects, with 43,085 observations of 174 fungal species, of which six are endangered (EN; 18 observations), 22 vulnerable (VU; 614 observations) and 30 near threatened (NT; 1,332 observations) according to the latest Red List of Finland (Rassi et al. 2001).

Dead perennial fruit bodies were excluded from the analyses in **Chapters I** and **III**. This was done to avoid bias in species numbers and pooled abundances; perennial fruit bodies may stay identifiable for a long time after their death. For the analyses based on the responses of individual species (**Chapters II** and **IV**), the dead perennial fruit bodies were included.

Only downed logs and species observations from downed logs were considered in the analyses in **Chapters I** and **IV**. This is because most polypore occurrences are from logs, and only a small proportion of species grow mainly or only on standing trees. In **Chapter III**, dead standing and downed trees were considered separately. In the analysis of species-specific resource use (**Chapter II**), all kinds of dead-wood objects were included.

Statistical analyses and modeling

The data were analyzed with generalized linear modeling (GLM) in **Chapters I** and **III**, and with hierarchical Bayesian logistic regression models in **Chapters I** and **IV**. Non-metric multidimensional scaling (NMDS) was used in **Chapters II** and **III**. Semi-variograms (Cressie 1993) were calculated in **Chapter I** to examine whether the residuals from GLMs were spatially correlated.

The analyses in **Chapter I** include a development of a new measure for resource availability that integrates the contributions of the number, volume and diversity of resource units.

The Bayesian approach of **Chapter II** is novel in the sense that it includes a feed-back between the log-level and site-level parameters to ask whether the occurrence probability (per log) depends on the amount of suitable resources at the site level. **Chapter IV** utilizes a multivariate version of Bayesian logistic regression, and is among the first applications of this technique in the ecological literature.

4 Results and discussion

Measuring resource availability and resource use for fungal communities

One of the key questions addressed in this thesis is how does the species composition of the fungal communities vary between different types of habitats, e.g. managed forests and woodland key habitats (**Chapter III**), or between different types of landscapes (**Chapters I** and **II**). Understanding the causes of the observed differences between communities calls for relating the structure of the communities to patterns in resource availability. It is thus critical to measure the availability of resources in a way that is relevant with respect to the ecological requirements of the species.

In **Chapter I**, we illustrate that the most relevant way of measuring resource availability can differ greatly among different species belonging to the same taxonomically coherent community and even when the species seemingly share the same resources. We show how the number, size distribution and diversity of dead-wood units are of unequal importance to common species, red-listed species, and red-listed species specialized in spruce in Fennoscandia. Species richness and pooled abundance of the common species were highest when there was a large number of logs and especially if the logs represented many tree species in both early and advanced stages of decay. The red-listed species, and especially those specialized in spruce, were most numerous and abundant when large logs were present, whereas the total number of logs (of any size) was less relevant. The number or pooled abundance of red-listed species was not affected by the diversity of tree species, which is consistent with observations concerning red-listed species requiring certain kinds of substrates instead of a diverse set of substrates. In Finland, spruce and pine host more red-listed polyporoid and corticioid species than deciduous tree species (Kotiranta & Niemelä 1996; Anon. 2000; Rassi et al. 2001). The fact that many red-listed species require large spruce or pine logs is related to the fact that such logs have also the highest commercial value and are therefore scarce in managed forests.

While in **Chapter I** we measured resource availability for entire communities, **Chapter II** addresses the same question from the perspective of individual species. Analyzing species-specific resource use in a quantitative manner requires presence-absence data from a large number of resource units of varying suitability to individual species, and thus in **Chapter II** we used the entire data set of 98,000 dead-wood objects. We quantify (for continuous variables) or classify (for categorical variables) the resource use of 119 species with respect to several dead-wood quality variables such as host-tree species, type of dead wood, decay-stage class, specificity of decay-class use and diameter. A relatively large proportion of the species were rather generalized in their resource use, 78% of them commonly using two or more tree species, and 85% using man-made as well as natural dead wood. This pattern made the grouping of the ca. twenty highly specialized species all the more distinctive, as these species were restricted to one tree species and were also specialized in many other respects, using natural rather than man-made dead wood, large dead trees, and a specific decay class. Figure 2 illustrates the differences in substrate use between a generalist species (*Asterodon ferruginosus*; Fig. 2a) and a specialist species (*Amylocystis lapponica*; Fig. 2b).

In apparent contradiction to the results of **Chapter I**, diversity of logs did explain significantly the occurrence of red-listed species in the study of **Chapter III**. However, unlike in **Chapter I**, in this case our diversity measure included also the size (diameter class) of logs. Deciduous dead wood is obviously crucial for red-listed species specialized to use it, but deciduous-specialists contribute less to the total number of red-listed species than species decaying spruce and pine. The number of red-listed species increases more rapidly with the increment of conifer wood than deciduous wood since deciduous-dwellers have declined less than conifer-dwellers in boreal Fennoscandia. The importance of large logs for red-listed species has been demonstrated in several studies (e.g. Bader et al. 1995; Lindblad 1998; Tikkanen et al. 2006), but our finding that the common species are actually proportionately less abundant on large logs than on small logs raises interesting questions about the role of species interactions (**Chapter IV**) in community dynamics of wood-inhabiting fungi.

Specialist species require connectivity at three spatial scales

Species traits have been linked vulnerability to loss of connectivity in plants and animals. Habitat fragmentation harms especially such species that have specialized habitat requirements, low natural abundance, high population fluctuations, low ability to persist over unfavorable environmental conditions, intermediate or low dispersal power, and low reproductive potential. Good dispersal ability is essential for tolerating loss of connectivity if the risk of local extinction is high but to a lesser extent if the species have sufficiently stable local dynamics (Henle et al. 2004). Regarding fungi, studies linking species traits and fragmentation sensitivity are few.

In the study presented in **Chapter I** we show that the occurrence of red-listed species is affected by the area of the focal forest stand and its connectivity to the surrounding larger expanses of old-growth forest, whereas the species richness and pooled abundance of the common species were explained mainly by the local availability of resources. Given that the fungi have the ability to disperse (at least theoretically) for long distances, even hundreds of kilometers, it was intriguing to see that the spatial context mattered greatly within a region that has been fragmented relatively recently and where the area and connectivity of natural-like forests is still

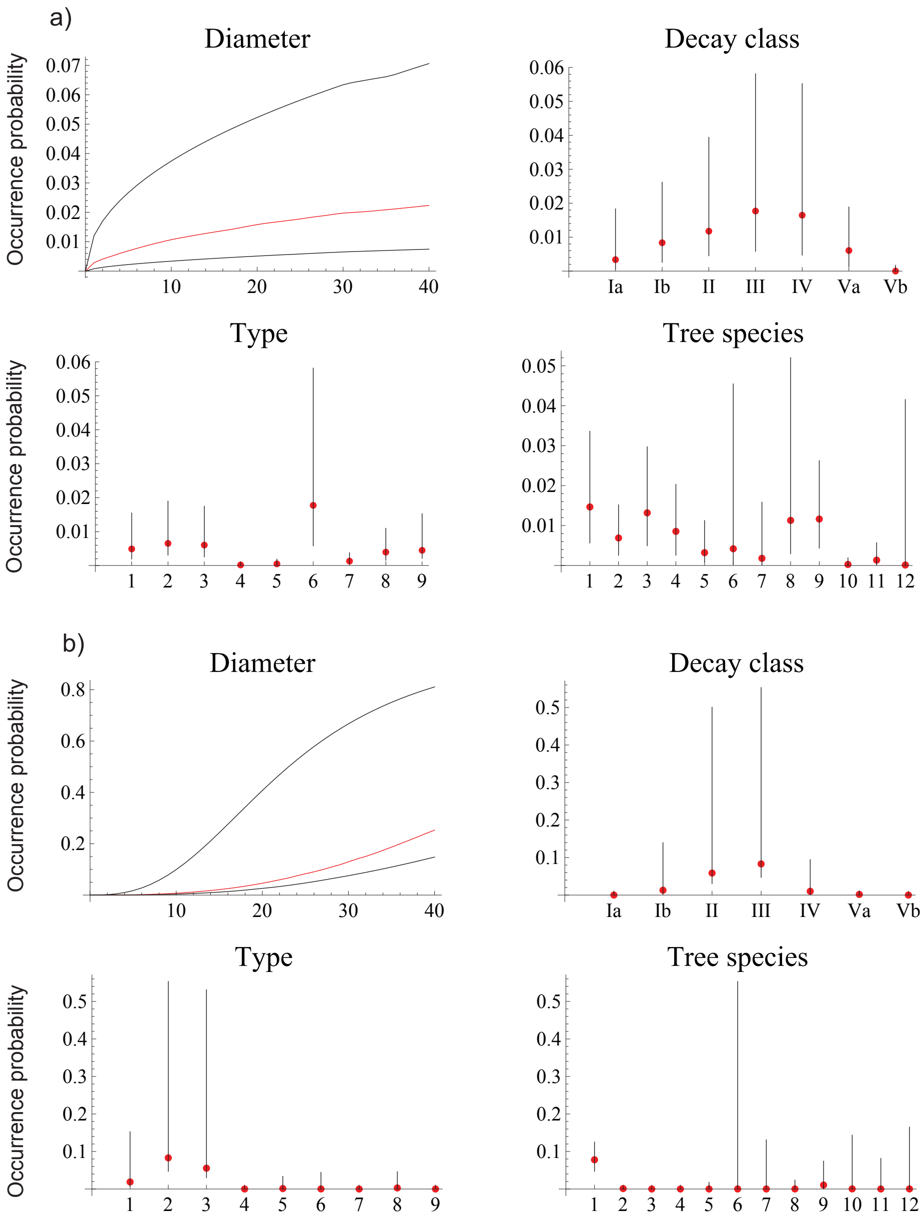

Figure 2. Resource use of a generalist and a specialist species. The panels show the dependence of occurrence probabilities of a) a generalist species, *Asterodon ferruginosus* (n = 661), and b) a specialist species, *Amylocystis lapponica* (n = 188) on tree diameter (cm), decay-stage class, dead-wood type and host-tree species. The median values (red) and the 95% confidence limits (black) for the predicted occurrence probabilities are based on the posterior density of the substrate-level regression coefficients (see **Chapter II**). In each case, we assumed that the resource unit has diameter 25 cm and consists of the most suitable resource type except for the focal variable, and that the resource unit is located on a site that is favorable (at the 90% quantile of sites ordered according to their suitability, based on variables such as naturalness, closedness, and connectivity to neighboring forests, see **Chapter II**) for the focal species. For an explanation of the decay-stage classification, see Hottola and Siitonen (2008). Dead-wood types: 1 = uprooted log, 2 = broken log or branch, 3= broken or uprooted log, 4 = entire dead standing tree, 5 = broken snag, 6 = natural stump, 7 = cut stump, 8 = cut bolt, 9 = logging-residue top or entire cut tree. Tree species: 1 = spruce, 2 = pine, 3 = juniper, 4 = unidentified coniferous tree species (spruce or pine), 5 = birch, 6 = aspen, 7 = alder, 8 = rowan, 9 = goat willow, 10 = other deciduous tree species, 11 = unidentified deciduous tree species, and 12 = unidentified tree species.

relatively high as compared to the rest of the southern Finland. The results from **Chapter I** contributed to our hypothesis that the most important traits making it difficult for red-listed species to occur in isolated fragments of natural forest are dispersal limitation and ecological specialization, the latter leading to low overall prevalence, which amplifies the effects of environmental and demographic stochasticities. In Chapter **II** we test these hypotheses in more detail with species-specific data including the entire community of wood-inhabiting polypores. These analyses are based on the presence or absence of each species on a large number of substrate units with variation in characteristics that are relevant for wood-inhabiting fungi. The data include variation in the connectivity of the sites to the old forest in the surrounding landscape, making it possible to analyze how site-level and landscape-level variables affect the distribution and abundance of the species.

It is evident that dead-wood dependent fungi suffer from a large-scale reduction in the area of natural-like forests and the amount of dead wood in forests (Siitonen et al. 2001; Edman et al. 2004c; Heilmann-Clausen & Christensen 2005; Odor et al. 2006; Penttilä et al. 2006), but it has not been known whether loss of connectivity as opposed to the general loss of habitats and resources affects a large fraction of wood-inhabiting fungi. In **Chapter II**, we analyze the resource use and site-level preferences of a large number of fungal species, and examine species' responses to connectivity at three spatial scales. The local scale is the stand-level, in which we use the local density of resources as a site-level variable. At the landscape scale, we measured the amount of old forest within a radius of five km from the focal forest stand, and at the regional scale we considered the location of the study site along the gradient in land-use history across southern Finland.

We related species' responses to connectivity to their resource-use patterns, life-history traits and red-list status. A group of species that are highly specialized in their substrate preferences stood out in these analyses: the very same species that were specialized in resource use also showed a clear preference for natural forests and a closed canopy. Further, they proved to be dependent on connectivity at local, landscape and regional scales. In contrast, the more generalized species in terms of resource use were either indifferent or showed a preference for open canopies or managed forest, possibly reflecting the role of species interactions in shaping community composition (**Chapter IV**). The generalist species may benefit from reduced competition in habitats where specialists are decreasing.

We considered a number of life-history traits to study which species attributes are associated with connectivity dependence. Out of these, spore size and the ability to form asexual chlamydospores were significantly negatively correlated with vulnerability to fragmentation. Thick-walled, durable and desiccation-tolerant chlamydospores may enable species to tolerate harsh conditions such as periods of drought. A possible causal explanation for the small spore size of the specialists is that as the resources for the highly specialized species are scarce in space and time, it is especially important for these species to be in the right place at the right time. From this follows that it is beneficial to maximize the number rather than the size of spores produced. As the resources for generalists are abundant and predictable in the landscape, the optimal strategy is to produce few but high-quality offspring (Krebs & Davies 1984). Large spores may provide an advantage in the establishment phase, but the role of spore size in dispersal is equivocal (Kauserud et al. 2008) and remains to be tested in further studies. It is possible that specialists are specialists to some extent because of the small size of their spores. Small spores carry low nutrient supply, which makes the spatial and temporal window for establishment narrower than for generalist species that tend to have larger spores.

To summarize, our results (**Chapters I** and **II**) show that highly specialized species suffer from loss of connectivity at all spatial scales, while generalist species may even benefit of isolation. The causal reason for the latter is likely to be the disappearance of specialized and often more competitive species (**Chapter IV**). We conclude that the threshold condition for the persistence (Hanski & Ovaskainen 2000) of many specialized species is apparently not met regionally in forest landscapes with little natural forests remaining, hence these species are likely to be absent from small fragments of favorable habitat. Our findings highlight the importance of concentrating the conservation efforts to protecting large and high-quality areas instead of small fragments distributed across the landscape. This is the only way to minimize the detrimental effects of fragmentation on threatened species and to prevent other ecologically specialized species of becoming threatened.

Woodland key habitats provide little value for conservation of red-listed polypores

Recognizing that the vast majority of forest land (98.1% in southern Finland; www.metla.fi/metinfo/tilasto/suojelu/suojelu_taulukot.html) is managed and that establishing large protected areas on other than state-owned land (8.5% in southern Finland) is economically and socially difficult, it becomes clear that actions to promote biodiversity within managed forests are of importance. Forest management practices have been modified in most European countries through governmental and administrative policies to better sustain biodiversity starting from the early 1990s. In Finland, the current recommendations for forest management practices came into force in the beginning of the 1990s, and the new forest legislation came into operation in 1997.

The most substantial measures that take forest biodiversity into account in forest management are preservation of valuable habitats and retention of living and dead trees on cutting areas. The new Forest Act includes the concept of woodland key habitats. They are small habitat patches with presumed high value for the preservation or future development of biodiversity. By definition they are small in area (mean 0.62 ha), easily distinguished from their surroundings, and in natural or natural-like state. Their total area covers 60,000 ha, which corresponds to 0.5% of forestry land in private forests (Yrjönen 2004). The Forest Act does not provide exact area criteria, but in practice it is interpreted so that habitats larger than one ha are seldom assigned as Forest Act habitats (Kotiaho & Selonen 2006), thus only the smallest patches of these habitat types get a legal status. Woodland key habitats fall into the concept of so-called 'precision conservation' in managed forests with the idea that preserving small but species-rich habitat patches is a cost-effective means of protecting threatened forest species. On the grounds of the results from **Chapter II**, this concept has indisputable weak points that make the potential of woodland key habitats in promoting forest biodiversity very limited. Minimizing the total area needed for conservation can actually maximize the extinction debt (Hanski 2000; Ovaskainen 2002). In **Chapter III**, we study in greater detail the value of key habitats for the protection of red-listed fungi.

Brook-side key habitats constitute the most important key habitat type in terms of area and timber volume. Their area is one third of the total area of all key habitats in private forests, and half of the total area in state-owned forests (Yrjönen 2004). In **Chapter III** we show that brook-side key habitats host as few red-listed species (0.28 species per 0.2 ha sample plot) as similar-sized control plots in production forests (0.24 species). This result is consistent with the results of Junninen and Kouki (2006), who studied different types of woodland key habitats and ordinary managed forests in eastern Finland. Key habitats are more species-rich than ordinary managed forests because they have more dead wood, and in the case of brook-side key habitats, more deciduous dead wood and thus a higher proportion of deciduous-associated species. Hence, woodland key habitats do not measure up to the expectations in preserving red-listed species, but by providing types of resources lacking in the

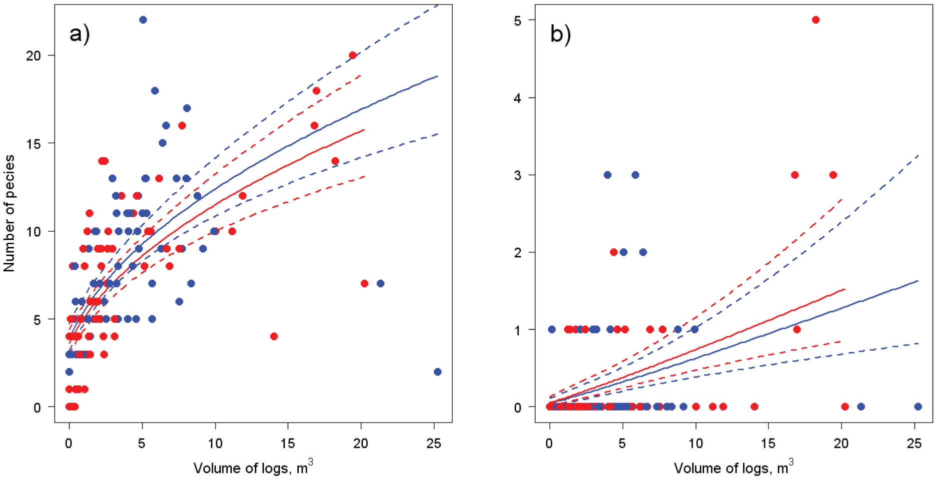

Figure 3. Volume of logs and the number of a) all species and b) red-listed species in brook-side key habitats (blue) and ordinary managed forests (red) within the whole stand. Lines indicate predictions with estimated standard errors from fitted GLM objects. The two types of forests do not differ in the average number of all species ($F_{1,136} = 0.921$, $p = 0.339$) or red-listed species ($F_{1,136} = 0.281$, $p = 0.596$) per unit volume of logs.

rest of the forest landscape they may support the common species that are not sensitive to forest fragmentation.

Figure 3 shows the number of all species and red-listed species against the total volume of logs in key habitats and production forests within the entire stand. The average area of a stand is larger in production forests (1.7 ha) than in key habitats (0.7 ha). The two types of forests do not differ in the average number of all species or red-listed species per unit volume of logs. This suggests that the number of species present does not depend on the spatial distribution of dead wood at the scale of a forest stand, as earlier suggested by Edman & Jonsson (2001) and Rolstad et al. (2004). Unlike in **Chapter II**, we did not see a threshold effect in the amount of resources for red-listed species in key habitats (**Chapter III**). This is probably because the amount of resources in key habitats was not quantified in a species-specific manner, and because key habitats were poor in red-listed species due to relatively low amount of dead wood and possibly also because of effects of isolation.

Our results give support to the view that key habitats host somewhat higher species diversity than similarly-sized managed forests mainly because of their larger amount of dead wood. However, the difference in species richness is small, and red-listed species are few both in brook-side and herb-rich key habitats (mean number 0.38 per 0.2 ha sample plot). Key habitats on rocky outcrops deviate from this pattern, as they have less dead wood and lower species diversity than ordinary managed forests, but more red-listed species (0.47) relative to their low dead-wood volume. The results concerning key habitats are consistent with the results from **Chapter I**, i.e. the common species occur also in isolated forests as long as resource units are numerous, while the red-listed species are dependent on connectivity and certain kinds of resource units (large logs).

None of the key habitats in our study was completely unmanaged, as evidenced by abundant cut stumps in most key habitats (up to 1,385 cut stumps per ha). Provided that the key habitats would be left unmanaged, they will develop towards a more natural-like state in the course of time. However, in Finland selective logging is allowed in key habitats, making it possible to cut the only host tree for red-listed species, as demonstrated for epiphytic lichens by Pykälä (2007).

Unlike in **Chapter II**, we did not find logs in eastern Finland to host more red-listed species per unit volume than logs in southwestern Finland. There were more occurrences of red-listed species in eastern Finland, but not more than the larger dead-wood volumes would allow us to anticipate. The volume and diversity of dead wood in key habitats increased along the gradient in land-use history from southwest to northeast. The lack of response of red-listed species in key habitats to the gradient may be merely due to too few occurrences of red-listed species to detect a response.

In the light of the results in **Chapter II**, it is not surprising to see that red-listed wood-inhabiting fungi do not occur in woodland key habitats. Their small area and often consequent low amount of dead wood, combined with isolation within the matrix of managed forests, do not fulfill the prerequisites for the occurrence of red-listed species. It is noteworthy that Finnish woodland key habitats are by definition small in area and clearly smaller than key habitats in e.g. Sweden (average area 3.1 ha; Anon. 2007). However, protection of key habitats does not burden the governmental conservation budget, and it is clearly a more appropriate option from the biodiversity point of view than cutting them down. Delineating larger woodland key habitats and prohibiting even light harvesting would be obvious improvements and might aid in getting woodland key habitats to contribute to maintenance of forest biodiversity. However, taking into account the results of **Chapters I**, **II** and **III** shows that creating large forest reserves has the highest priority.

Species interactions

A single downed log may contain many fungal species, which may take part in numerous and diverse interactions. Up to tens of species may be visible as fruit bodies and many more are likely to be present as vegetative mycelia (Allmér et al. 2006; Ovaskainen et al. 2009) at any given time. Considering the high diversity, and the fact that the resources are not renewed within a single log, one may expect severe competition for resources between individuals, both conspecific and of different species. Facilitation is another common type of interaction, and even mutualistic relationships between wood-inhabiting fungi may occur (Hendry et al. 1998). Competition is most intense on large logs of the intermediate decay stages (Boddy 2000; Woodward & Boddy 2008).

Direct interactions take place at the mycelial level inside the log, hence they are difficult to study in the field (see however Woods et al. 2006). In laboratory conditions the outcomes of interactions are affected by the chosen abiotic environment. Inferences concerning species interactions can also be drawn from occurrence data on fruit bodies collected in the field. A complication however is that positive and negative correlations in the occurrence of two species can result from similar or dissimilar habitat requirements as well as from interspecific interactions.

In **Chapter IV** we focus on 22 species of polypores that are abundant in the present data, and ask if some of these species occur together (as fruit bodies) more or less often than expected by chance. We address the question with the help of a multivariate logistic regression model, which accounts for species-specific resource use and residual correlations between each species pair. When analyzing occurrence patterns without taking the quality of logs (e.g. diameter and decay class) into account, the majority of the species pairs showed a positive correlation in their occurrences. This was however largely due to species often preferring similar kinds of logs. When taking into account the resource use of each species, many of the positive correlations vanished, or even turned out to be negative, i.e. species were occurring together less often than what would be predicted based on their resource-use patterns only.

We extracted signals of both positive and negative associations between fungal species, most of which do not have an apparent explanation, hence calling for controlled experiments to reveal the mechanisms behind the observed patterns. Many of the significant positive and negative correlations were between an early-successional decayer and a mid- or late-successional decayer, in support of the view that the succession of the species community is to a substantial extent driven by the primary decayers (Niemelä et al. 1995; Renvall 1995; Heilmann-Clausen & Boddy 2005).

The loss and fragmentation of natural-like forests and the reduction in the amount of suitable substrates result not only in the overall decline in species diversity but also in changes in the relative abundances of the species (Debinski & Holt 2000; **Chapters I** and **II**). This process leads to changes in species interactions, which in turn feed back to the demographic dynamics by suppressing some species and favoring others. We hypothesize that interspecific competition is the likely reason for some common species being less numerous in species-rich natural forests than in species-poor managed forests. Inferior competitive ability of the generalist and often more common species may be a general pattern, possibly reflected also in how the common species benefit from a large number of individual resource units whereas the specialized and often rare species are superior competitors only on the type of logs which are especially suitable for them (**Chapter I**).

5 Synthesis and perspectives

This thesis shows that the most relevant way of measuring resource availability can differ to a great extent between species seemingly sharing the same resources. It is thus critical to measure the availability of resources in a way that is relevant in relation to the ecological requirements of the species. Connectivity at the local, landscape and regional scales is important especially for the highly specialized species, many of which are also red-listed. Small habitat patches with quality that is not substantially higher than the quality of ordinary managed forests, such as woodland key habitats, do not sustain red-listed species. Habitat loss and fragmentation affect not only species diversity but also the relative abundances of species, species interactions and fungal successional pathways. These changes are likely to affect the food chains in which wood-inhabiting fungi are involved, and thus the functioning of the whole forest ecosystem.

The results of my thesis can be applied in the evaluation of the adequacy of the current conservation practices, such as leaving retention trees and protecting key habitats. Leaving living and dead retention trees on clear-cut areas has become an integral component of good silvicultural practice in Fennoscandia and North America and an element in forest certification schemes. Little research has however been done on the ecological benefits of this investment (see however Lindhe et al. 2004; Junninen et al. 2007). According to the forest statistics, typical retention levels are 6 m^3 ha^{-1} on state-owned land and 4 m^3 ha^{-1} on private land (Siitonen & Ollikainen 2006). Roughly one third of the volume is downed and standing dead wood. More than 95% of commercial forest land (21 million ha) in Finland is certified according to the PEFC (Programme for the Endorsement of Forest Certification schemes) system, which requires that 5-10 retention trees are retained per hectare of clear-cut forest. According to our results, the minimum certification requirement, e.g. five spruce trees with a diameter of 10 cm (totaling ca. 0.2 m^3; Laasasenaho 1982) is likely to benefit red-listed polypore species extremely little, and even less so if the retention trees are birches. Our results strongly suggest that more and larger logs should be retained to substantially promote biodiversity (Chapters I and II).

Our results (Chapter III) showed that woodland key habitats contain only marginally more red-listed wood-decaying fungi than ordinary managed forests. A further point of uncertainty concerning woodland key habitats is whether the species that exist there now will disappear through time as all the surrounding managed forest is eventually cut down. Wood-inhabiting fungi have been shown to respond slowly to changes in landscape structure (Paltto et al. 2006). Berglund and Jonsson (2008) showed that recently (10-20 years ago) isolated key habitats hosted more fungal species, both red-listed and widespread species, than key habitats that had been isolated much longer and hence had had time to gradually lose their species.

A key result of the thesis is that a given log is much more likely to host a red-listed species if it is located in eastern Finland (rather than in southwestern Finland), if it is well connected to the surrounding forests, and if it is located in a forest patch that has a high abundance of dead wood. Thus, in developing cost-effective conservation measures, the landscape perspective needs to be taken into account, well-connected and large enough protected areas being critical while attempting to halt the decline of forest biodiversity. This observation also indicates a need for future research, as systematic large-scale conservation would require systematic information about relevant habitat quality variables, especially the amount of dead wood. The Finnish multi-source national forest inventory (Tomppo et al. 2008) combines field inventories, satellite imagery and digital map data to provide detailed information about the living stand for the whole of Finland with a spatial resolution of 25x25 m. Along with the development of airborne laser scanning methodology (Maltamo et al. 2009a; Maltamo et al. 2009b) and increased emphasis on dead wood in the field inventories, I hope that reliable and systematic high-resolution data on the amount and quality of dead wood will be available in the future.

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