Natural Variability of Forests as a Reference for Restoring and Managing Biological Diversity in Boreal Fennoscandia

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Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36(1): 97–125.

In Fennoscandia, use of the natural forest as a reference for restoration and management of forest biodiversity has been widely accepted. However, limited understanding of the structure and dynamics of the natural forest has hampered the applications of the *natural variability* approach. This is especially the case in areas, where the natural forests have almost totally vanished. This review was motivated by the idea that despite these difficulties the essential features of the natural forest can be reconstructed based on biological archives, historical documents, research done in adjacent natural areas, and modeling. First, a conceptual framework for analyzing the relationship between forest structure, dynamics and biodiversity is presented. Second, the current understanding of the structure and dynamics of natural forests at different spatiotemporal scales in boreal Fennoscandia is reviewed. Third, the implications of this knowledge, and gaps in knowledge, on research and on practical restoration and management methods aimed at forest biodiversity conservation are discussed. In conclusion, naturally dynamic forest landscapes are complex, multiscaled hierarchical systems. Current forest management methods create disturbance and successional dynamics that are strongly scale-limited when compared with the natural forest. To restore some of the essential characteristics of the natural forest's multiscale heterogeneity, diversification of silvicultural and harvesting treatments, as guided by natural disturbance dynamics, is needed to produce more variation in disturbance severity, quality, extent, and repeatability.

Keywords Biodiversity, disturbance dynamics, ecosystem management, heterogeneity, hierarchy, scaling, spatiotemporal dynamics, succession sustainable forestry
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Received 13 November 2000 **Accepted** 8 March 2002

1 Introduction

Management of natural resources is closely linked with how we view and understand ecosystem structure and function. In this respect, it is noteworthy that our perception of the functioning of forest ecosystems has changed dramatically over the past decades. Until the early 1970s, forests were thought to be systems at relative equilibrium, characterized by relative constancy in structural and compositional features, and by predictable successional development leading to a stable endpoint. This endpoint was the (climatic) climax, which was regarded as the equilibrium stage of forests (Clements 1916, Cajander 1926). This equilibrium or 'balance-of-nature' paradigm was abandoned less than 30 years ago when ecologists realized the common occurrence and important ecological role of various disturbances in all kinds of ecosystems. Multiscale heterogeneity, chance events, nonequilibrium dynamics, and 'complexity' are now seen as fundamental characteristics of forest ecosystems, where individual species are embedded in interactive communities of micro-organisms, plants, and animals (Attiwill 1994, Pickett et al. 1997, Hunter 1999). This has also been called the contemporary nonequilibrium or 'flux-of-nature' paradigm (Rogers 1997, Landres et al. 1999). This paradigm change has had a strong influence on the scientific thinking underlying the present view of ecosystem management and should also form the basis for restoration and management of forest biodiversity (Christensen et al. 1996).

Evolutionary and historical perspectives form the necessary background for all biodiversity conservation and ecosystem management (Levin 1992). The evolutionary point of view reminds us that during their evolution forest-dwelling organisms have evolved life-history strategies, i.e. ways to reproduce, disperse, survive, and grow, which utilize the spatiotemporal distribution of habitats and resources available in natural forests. Because trees are the primary producers and have a dominant influence on all forest ecosystem characteristics, understanding forest dynamics and the interaction between trees and other organisms is key to understanding forest biodiversity. To take an obvious example, hole-nesting birds are common in natural boreal forests because of the historical abundance of large, senescent trees and the evolution of woodpeckers that utilize this resource (Angelstam and Mikusinski 1994). The same is true for the wide array of organisms dependent on dead wood (Siitonen 2001). In addition to the evolutionary perspective, the human cultural history of a given landscape (e.g. the stage of naturalness) strongly influences the possibilities of carrying out restoration and management (Bradshaw et al. 1994, Fries et al. 1998).

The so-called *natural variability* approach in forest restoration and management (Attiwill 1994, Hunter 1999, Landres et al. 1999) is ultimately based on the evolutionary viewpoint, suggesting that biodiversity at different levels of ecological organization will be preserved if the natural structures and processes of forests are maintained (the 'coarse-filter' approach, Hunter et al. 1988). It is acknowledged that 'natural' is a relative concept because of the great variability in nature itself and because humans have often been an almost omnipresent component of forest ecosystems (Landres et al. 1999). In addition to the natural variability approach, at least two other conceptual approaches to restoration and management of biological diversity can be distinguished; the *species* and the *multiple aspects* approaches (Fries et al. 1998). The former is founded on island biogeography theory (MacArthur and Wilson 1967), and more recently, on metapopulation theory (Hanski and Gilpin 1997, Hanski 1999), while the latter gives more emphasis to cultural aspects, i.e. the cultural history context, related to a given landscape (Fries et al. 1998).

In Scandinavian countries, the idea of using natural forests as a model for restoration and management of biodiversity in managed forests has so far been the most influential (Haila et al. 1994, Fries et al. 1997, 1998, Angelstam 1998, Lähde et al. 1999). However, the maintenance of structural complexity has not been a goal of traditional silvicultural systems. On the contrary, during the past decades, forest management aimed at converting naturally heterogeneous forest structures to homogeneous single species even-aged stands using thinnings, clear-cutting and planting (Linder and Östlund 1998, Axelsson and Östlund 2000, Axelsson 2001). At landscape level, the management ideal was the fully regulated even-aged forest, in which each stand age class covered an equal area and the oldest age class was annually harvested providing a continuous and sustained yield of timber. It was not until the 1990s, when ecological sustainability of forest use became a significant issue in the marketing of forest products, that a major chance in forestry practices occurred. This development has been enhanced by international agreements to protect forest biodiversity.

In Sweden and Finland, management guidelines based on site-specific considerations of natural disturbance (fire) dynamics (particularly the ASIO-model; Angelstam and Rosenberg 1993, Angelstam 1998) have been influential in guiding many of the practical efforts to protect and restore forest biodiversity (Angelstam and Pettersson 1997, Fries et al. 1998, Karvonen 1999). Nevertheless, a need exists both for more detailed conceptual and theoretical models, and improved management applications based on scientific understanding of the processes maintaining biodiversity in natural boreal forests (Haila et al. 1994, Axelsson and Östlund 2000).

The purpose of this paper was 1) to present a conceptual framework for analyzing the relationship between forest structure and dynamics, and biodiversity, 2) to discuss the present understanding of the variability in structure and dynamics of natural forests at different scales in Boreal Fennoscandia, with special emphasis on Finnish conditions, 3) to analyze the main discrepancies between natural and managed forests, and 4) to discuss the implications of this knowledge, and gaps in knowledge, on research and on restoration and management methods aimed at forest biodiversity conservation.

2 Conceptual and Theoretical Considerations

2.1 The concept of Natural Forest

In theory, the concept of a natural forest is easy to define: a forest that has never been affected by human activity of any kind. However, in practice, the definition remains elusive. This is due both to the great natural variability characteristic of forest ecosystems and to the long-lasting intimate relationship and interaction between forests and humans (Landres et al. 1999). Today, the direct or indirect influence of human activity can be seen throughout Fennoscandia. Even in protected areas of southern Finland only a small share of the forest can be classified as natural or nearly natural (Working group ... 2000). In its natural state, the boreal forest is not in equilibrium but changes in structure and dynamics occur as a function of variation in climatic conditions. This means that the structure and dynamics of a natural forest cannot be simply described, rather the aim is to define the essential characteristics and their bounds of variability (Landres et al. 1999).

2.2 Heterogeneity and Biodiversity

Heterogeneity is perhaps the most important underlying concept of the contemporary paradigm in ecosystem management and conservation biology (Kolasa and Pickett 1991, Dutilleul and Legendre 1993, Mladenoff and Pastor 1994, Pickett et al. 1997, Spies and Turner 1999). In broad terms, the concept of heterogeneity can be defined as any form of environmental variation, physical or biotic, occurring in space and/or time (Ostfeld et al. 1997). Heterogeneity is inherently a multiscale phenomenon, which can be examined at different scales, both in time and space (Kolasa and Pickett 1991, Christensen 1997, Peterson and Parker 1998). Heterogeneity in forest structure can be viewed at branch, tree, tree group, stand, landscape, and geographic scales. Each of these scales interacts with the others and may have important implications to system functioning and maintenance of overall species diversity.

Continuous production and maintenance of habitat heterogeneity at many scales is generally accepted to be important for biodiversity (Pastor et al. 1992, Pickett et al. 1997). The reasoning behind the connection between environmental heterogeneity and species diversity is straightforward: 1) heterogeneity means variation in resource/habitat availability, 2) this variation provides a range of opportunities for organisms to colonize, survive, and reproduce, and 3) the presence of multiple opportunities host a wider range of organisms characterized by different

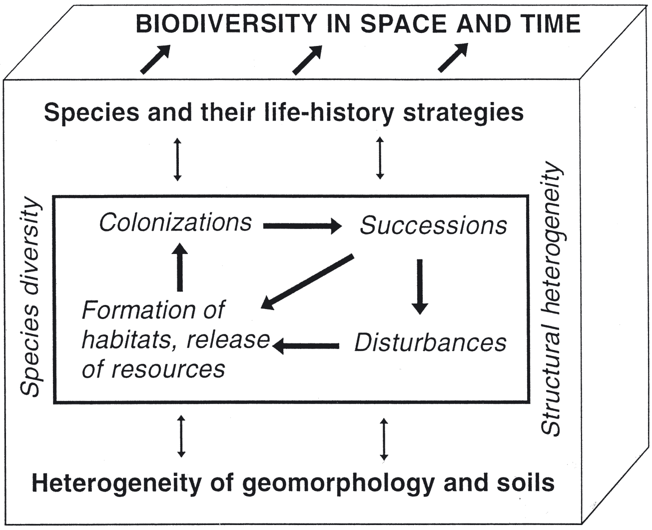

Fig. 1. The 'Sampo[1] of biodiversity' in forest ecosystems: a conceptual model of the basic processes and factors creating and maintaining heterogeneity and biodiversity within a forested area. Biodiversity is maintained by the interplay between the available range of species and their life-history characteristics, and the dynamic heterogeneity of forest structure created by disturbances and successional processes. ([1] In Finnish mythology the Sampo is a cosmological metaphor for a kind of Magic Mill capable of producing wealth.)

life-history traits, thus maintaining a higher species diversity. According to the natural variability approach, the increase in habitat heterogeneity is no goal in itself, but the goal of management must be the restoration and maintenance of such multiscale heterogeneity which will provide habitats for species populations naturally occurring in a given area, thus ensuring their viability.

Heterogeneity of forest ecosystems is often viewed as structures at a given point in time. However, it is important to realize that the observed structural heterogeneity is created and maintained by processes in time (Smith et al. 1993). These processes can broadly be grouped into two categories: 1) disturbance and 2) successional processes, both occurring over a wide range of spatial and temporal scales. Recently, the role of disturbances in maintaining forest biodiversity has been emphasized (Attiwill 1994, Pickett and White 1986). However, successional processes, e.g. the development of specific stand structures, species mixtures, and the creation of fine-scale environmental variation through biotic interactions, are equally important for habitat formation and biodiversity. In reality, disturbances and successions are closely connected since disturbance characteristics usually strongly affect successional development. The effects of both disturbance and succession on species diversity can further be divided into two broad and somewhat overlapping categories: 1) effects on availability of habitat/resource and 2) effects on the spatial pattern and quality of habitats.

In forests, disturbances and successional processes maintain species diversity but are also affected by species diversity. For example, tree species composition and structural heterogeneity of tree stands directly influence the diversity of the organisms inhabiting them. Structural heterogeneity itself affects the pattern and rate of important ecological processes such as the activity of decomposing organisms, and pathogens and pests causing finescale disturbances. These, in turn, affect the successional development of the stands, especially in the absence of severe disturbances (Holah et al. 1993, Christensen et al. 1996, Schowalter 1996). Overall, we can conclude that biodiversity is maintained by the interplay between the avail-

Fig. 2. Old deciduous trees are an important component of functional heterogeneity in the boreal forest. An old *Salix caprea* hosts a large number of epiphytic lichen species, including the foliose lichen *Lobaria pulmonaria*. Paanajärvi region, Russian Karelia, northern boreal zone (photograph by T. Kuuluvainen).

able range of species and their lifecycle characteristics, and the dynamic heterogeneity of forest structure that is the result of disturbances and successional processes. (Fig. 1).

The emphasis of ecological heterogeneity in space and time can also be seen as a link between species-oriented conservation ecology (represented by island biogeography and metapopulation theories) and the present emphasis on landscape ecology and ecosystem management. Quantification of environmental heterogeneity defines the multiscale habitat characteristics (“the theatre”) within which the organisms (“the actors”) live and (meta)population dynamics of species occur (“the play”) (see Fig. 1). The interaction between the environment and species populations is largely determined by the species’ life-history traits, which is one of the key concepts of population ecological theory. What the heterogeneity approach emphasizes is that for efficient ecosystem management and species conservation knowledge of species population dynamics must be placed in a real-world spatially explicit environmental context, where the environment cannot be simplified to “habitat” and “nonhabitat” areas (Wiens 1997).

2.3 Structural and Functional Heterogeneity

When applying the heterogeneity approach in forest ecosystem restoration and management, the concept of heterogeneity must be made operational. Therefore, it may be useful to make a distinction between structural and functional heterogeneity (Kolasa and Rollo 1991). *Structural heterogeneity* denotes any variability in system property without reference to functional effects, while *functional heterogeneity* means variability in system property affecting ecosystem processes and/or properties, such as species diversity (Fig. 2). The separation of these two types of heterogeneity is obviously only meaningful when applied to a given type of ecosystem. For example, in managed forests even relatively small input of dead wood is likely to have on effect on saproxylic species (Martikainen 2000), while in natural forests with abundant dead wood such an increase in species diversity is unlikely to occur. Defining functional heterogeneity will be a long-range task of accumulating information on the ecology of species. It is worth noting that quantifying the structural heterogeneity of natural forests forms the basis for the natural variability approach in forest landscape management, whereas functional heterogeneity can be regarded as a synthesis between the natural variability and species-oriented approaches. In the latter case the ultimate goal is to understand the response of populations to multiscale heterogeneity (Wiens 1997). This is important because imitating nature is not always possible, e.g. because of limited resources and social constraints or because areas to be restored are too small for natural-scale landscape dynamics to take place (Bunnell and Johnson 1999).

The concept of functional heterogeneity is also closely connected with the common separation between generalist and specialist species (Hansson 1997). The boreal biome is dominated by the generalists, which do well over a wide range of habitat conditions. A smaller number of species are specialists, which are strongly dependent on specific substrates or an interaction between one or several species. The main problem of ecosystem management and species conservation is how to maintain viable populations of specialist species in managed forest landscapes.

Although we have quantitative methods for measuring heterogeneity, no comprehensive theory on the heterogeneity approach exists to guide its application in ecosystem management. Instead, by analyzing existing information and learning more from individual case studies, the features of a particular system which are important for biodiversity maintenance at various scales can be defined. From the natural variability point of view to restoration and management of biodiversity, crucial questions are: What are the essential features of natural variability of forests at multiple spatiotemporal scales? How do naturally dynamic forests differ from managed forests? Are there important differences between heterogeneity created by forestry versus heterogeneity created by natural forces? To provide some answers to these questions the following section discusses the multiscale controls of heterogeneity and biodiversity in natural and managed forests.

3 Scales of Heterogeneity: Top-Down and Bottom-up Controls of Forest Structure and Biodiversity

Scale is a crucial question when considering the application of the heterogeneity concept in restoration and management of biodiversity. This means that we should be able to understand and predict how different levels of the ecological hierarchy interact to produce the habitat structures that we observe at various levels of ecological organization. For example, if we simultaneously manage for individual tree characteristics, stand structures, and landscape spatial patterns, how should these three scales be related to each other? An answer to this question may be found in studying naturally dynamic forests at different scales (Lertzman and Fall 1998). When trying to understand the dynamics of multiscale heterogeneity and habitat characteristics of a natural forest area, it is useful to distinguish between two categories of potential mechanisms, the *top-down* and the *bottom-up* controls of forest structure (Lertzman and Fall 1998; Table 1).

The *top-down view* emphasizes that the structure of any forest area is to a large extent determined by its climate, geomorphology and soils, historical factors, and the occurrence of (often large) allogenic disturbances such as like fire, storms, and insect outbreaks. This view empha-

Table 1. Factors affecting the structure and biodiversity of forest landscapes can be divided into successional and disturbance mechanisms. Controlling factors are specified to be operating at the landscape level (top-down controls) or at the stand or tree level (bottom-up controls). Allogenic disturbances are external to stand level and are often large in extent (e.g. disturbance caused by fire and storms). Autogenic disturbances are caused by biotic factors within stands (tree deaths caused by fungi, insects, and competition).

	Mechanisms	
	Succession	Disturbance
Top-down controls	Various site type controlled ecological communities Various site type controlled ecological successions	Effect of landscape structure on allogenic disturbance probability and spread
Bottom-up controls	Seed dispersal, regeneration, competition, tree and stand structures; ‘ecological engineering’ by trees	Effect of stand structure on allogenic disturbance probability and spread Small-scale autogenic (gap) disturbances

sizes the important role of the abiotic environment and allogenic disturbances. Because these factors are unique to each forest area, every landscape is a special case. The flaw in this view is that the role of deterministic succession is easily overemphasized, which leads us back to the already abandoned 'balance-of-nature' view of forest dynamics.

The *bottom-up view* emphasizes that in addition to abiotic factors, forest properties are shaped by local-scale biotic spatial interactions and processes, such as tree reproduction, dispersal, growth, competition, and death due to autogenic factors, as well as modification of environmental conditions in the trees' vicinity. The stand structures formed through local regeneration and competition processes may also affect disturbance probability of, for example, ignition and spread of fire. This view conforms to the individual-based approaches in ecology and emphasizes localscale biotic interactions as a source of multi-scale environmental heterogeneity (DeAngelis and Gross 1992, Lawton 1994).

To better understand multiscale interactions in forest ecosystems, the top-down and bottom-up interactions can be further divided into successional and disturbance mechanisms (Table 1).

3.1 Top-down Controls of Landscape Structure and Biodiversity

Landscape characteristics regulate both the range of potential ecosystem types and the behavior of disturbances, and the interaction of these two factors, which results in the potential variation of postdisturbance successional phases. The variety and spatial pattern of climatic conditions, geomorphology, hydrology, soils and water bodies, such as lakes and rivers, exert a strong influence on the potential diversity of ecological communities that can exist within a given landscape. This is also true for the potential array of successional sequences, which are related to variation in site type qualities. Landscape characteristics also affect disturbance behavior. For example, continuous upland areas are more likely to ignite and burn just because the probability of being struck by lightning is higher and fire spread is easier on continuous upland areas (Pennanen and Kuuluvainen 2002). Likewise, forests adjacent to open mires may be more susceptible to windthrow disturbances than continuous forest areas on flat terrain. Thus, landscape characteristics and the effect of these characteristics on disturbances interact to produce the existing diversity of ecosystems and their successional stages.

3.2 Bottom-up Controls of Landscape Structure and Biodiversity

The interaction among individual organisms as a source of ecological patterns has recently been emphasized in ecological literature (Huston 1992, DeAngelis and Gross 1992, Sorrensen-Cothern et al. 1993). This individual-based ecology utilizes the method of reduction, i.e. the properties of the system are derived from the relationships among the components of the system (Lomnicki 1992). The complex pattern visible in forest structure at various scales is seen as the outcome of the interference between individual trees and their environment (Pacala et al. 1993). There is indeed evidence that tree-scale spatial interactions may strongly affect forest dynamics and plant community composition (Woods 1984, Pacala and Deutschman 1995, Frelich et al. 1999, Law and Dieckmann 2000). On the other hand, many components of forest biodiversity are simply related to the amount of substrate or habitat available.

To understand these bottom-up controls of biodiversity, it is useful to examine the local-scale mechanisms through which trees often create habitats for other forest-dwelling organisms. While some organisms need habitats that emerge only after long periods of uninterrupted successional development, other organisms are adapted to utilize habitats or resources formed or released by disturbance and tree death (see Fig. 1). Tree-scale influences on functional heterogeneity can be grouped into four partly overlapping broad categories: effects of 1) tree species diversity, 2) trees as physical structures (tree architecture, forest physiognomy), 3) modification of local environment by trees, i.e. "physical ecosystem engineering" (*sensu* Jones et al. 1997), and 4) autogenic disturbances, tree death, and 5) stand structure on disturbance probability and spread.

3.2.1 Tree Species Diversity

Although the boreal biome is dominated by only a few tree species, tree species diversity is an important aspect of ecosystem functional heterogeneity. This is because the few tree species differ in their structural, ecophysiological, and life-history characteristics, thereby offering a wide variety of habitats, resources, and processes for use by other forest-dwelling organisms. The variation in tissue chemistry among tree species is one important mechanism linking species diversity to process variability since tissue chemistry controls decomposition and palatability (Pastor and Mladenof 1992). Tissue chemistry is, in turn, related to plant traits such as growth rate and size. Thus, in forest ecosystems, tree species diversity (encompassing genetic diversity) is inseparably connected with both structural and functional heterogeneity, as discussed below.

3.2.2 Trees as Physical Structures

As trees are the largest organisms in forest ecosystems, they provide a habitat and growing substrate for a wide variety of organisms, from microorganisms on leaf surfaces to large vertebrates. The combined effects of surface availability, quality, and microclimate modification may also determine species occurrence. Since tree species differ in their structure and ecophysiological characteristics (affecting e.g. leaf and bark chemistry), they also play different functional roles in supporting species diversity in the forest ecosystem (Kuusinen 1996). Structural changes occurring with tree growth and aging are also important. For instance, in *Pinus*, the branching characteristics undergo endogenous developmental changes with age (Stenberg et al. 1994). As trees mature, the loss of needles and branches strongly influence tree structure, and a decrease in leader growth leads to a more rounded crown form. These endogenous changes are superimposed on external influences, such as atmospheric forces and competition, which induce plastic changes in crown structure (Rouvinen and Kuuluvainen 1996). As a result of these internal and external processes, the crown structure of *Pinus* becomes more complex and irregular with age. Some of these structural features, such as the twisted thick branches and flat crowns of large trees, may take hundreds of years to emerge. Examples of vertebrates dependent on this structural feature are birds of prey, like the golden eagle (*Aquila chrysaetos*) and ostrich (*Pandion haliaetus*), which require large round-topped trees for nesting.

Epiphytic lichens are perhaps the single most important and species-rich group dependent on trees as physical growing surfaces. Each tree species has a characteristic species composition with at least some host-specific species (Fig. 2; Kuusinen 1996). In addition, a large number of species are dependent on specific habitats such as old deciduous trees, dead-standing trunks, and burned stumps (Esseen et al. 1997, Kuusinen 1994a, b). Some lichens have long regeneration times and need continuity in substrate availability, characteristic of old-growth forests, to be able to persist. The higher epiphyte biomass in the canopies of old-growth forest trees is essential to a diverse assemblage of invertebrates and canopy-favoring passerine birds (Pettersson 1997, Pettersson et al. 1995, Esseen et al. 1996).

3.2.3 Trees as 'Ecosystem Engineers'

In addition to providing substrate, trees largely regulate the below-canopy supply and small-scale spatial distribution of central abiotic factors including solar energy, water, carbon, and nutrients. Consequently, trees strongly influence microclimatic conditions and resource availability of other forest-dwelling organisms in their vicinity. These influences have long-term effects on ecosystem structure and functioning. For example, considering plant-plant interactions, trees usually play a dominant role in the competitive hierarchy of the forested plant community. These plant-plant interactions include competition between trees of different sizes and interactions between trees and understory vegetation (Aaltonen 1919, Woods 1984, Kuuluvainen et al. 1993, Yastrebov 1996, Økland 1999). Mature forest trees have been demonstrated to exert a strong influence on tree seedlings and understory vegetation (Aaltonen 1919, Kuuluvainen et al. 1993) as well as on soil properties (Zinke 1962, Boettcher and Kalisz 1990, Hokkanen et al. 1995, Kuuluvainen and Linkosalo 1998).

Local influences of individual trees appear to be a major source of small-scale environmental heterogeneity in forest ecosystems. The effect of trees on the observed spatial patterns of forest ecosystem properties is obviously due to multiple influences, each of which can be important for species and functional diversity. These include variation in light quantity and quality due to light interception and transmission, interception of precipitation, foliage and branch litter, root uptake of water and nutrients, root turnover, and rhizosphere effects (Kuuluvainen et al. 1993, Hokkanen et al. 1995, Kuuluvainen and Linkosalo 1998).

Local competitive interactions also create local hierarchy structures in tree populations (Kenkel et al. 1989). Asymmetry in crown structure (Rouvinen and Kuuluvainen 1996) and small-scale autocorrelation patterns of tree size and age can be observed in heterogeneous naturally evolving forests (Kuuluvainen et al. 1996, 1998, Wallenius et al. 2002). These local interactions shape the three-dimensional structure of the forest, which in turn is important as a habitat characteristic. Moreover, evidence is available that small-scale structural heterogeneity and tree-scale spatial interactions may be highly important for long-term forest regeneration and ecosystem structure (Woods 1984, Pacala and Deutschman 1995, Frelich et al. 1998, Frelich and Reich 1999).

In conclusion, our understanding of the role and ecological importance of local tree influences in creating and maintaining small-scale environmental heterogeneity by ecosystem engineering is limited. Even less is known about the importance of this heterogeneity on biodiversity at different ecological scales. It is possible that much of the effect is related to tree species in combination with tree age and size, thus emphasizing the importance of old, large trees for creating small-scale environmental heterogeneity (Kuuluvainen and Linkosalo 1998).

3.2.4 Autogenic Disturbances and Tree Death

Since trees are the primary producers of phytomass in forest ecosystems, it is not surprising that a high number of organisms use dead trees and decaying wood as a habitat and resource (Siitonen 2001). In Finland, an estimated 4000–5000 species (about 20–25%) of the 20 000 forest species are dependent on dead wood (Working group ... 2000, Siitonen 2001). Dead trees also maintain many important functions in forest ecosystems (Samuelsson et al. 1994, Siitonen 2001). Decomposing logs and woody debris store nutrients and water, affect energy and nutrient flows, and serve as seedbeds for tree regeneration. Standing dead trees (snags), stumps, and fallen logs in different stages of decay provide a variety of habitats for decomposers, plants, and animals. Conifer snags are especially important for fungi and lichens and serve as a nutrient source for invertebrates, while fallen logs seem to be important for a wide range of plants and animals (Esseen et al. 1997).

Wood-decaying fungi, in particular, are a functionally important group in boreal forest ecosystems. Due to their activity, energy and nutrients assimilated in the wood are released (Harmon et al. 1986). The best-known taxa of wood-decaying fungi are polypores and *Corticiaceae*. These are usually host-specific and adapted to use trunks of different sizes and in various stages of decay (Siitonen 1994a). Other characteristics of the host trunk, e.g. microclimate in the surrounding area and previous decay succession, can also be important for specialized species (Niemelä et al. 1995, Renvall 1995). Each polypore species causes rot of a unique chemical and physical character (Rayner and Boddy 1988). A diverse polypore flora is likely to indicate an array of dead-wood habitats and numerous fauna of other organisms living in dead trees (Økland et al. 1996).

Saproxylic beetles comprise ca. 800 species in Finland (Rutanen 1994), and 242 species have been recorded within a single stand of northern boreal old-growth forest (Siitonen 1994a). Large numbers of highly specialized species with narrow habitat requirements often act with a suitable polypore species decaying the host tree (Siitonen 1994b). Several rare epixylic bryophyte species exist which are dependent on large decaying logs, moist microclimate, and long stand continuity (Söderström 1988, 1993). The total number of bryophyte species in a typical *Picea*-dominated boreal forest can range between 80 and 150, as compared with only about 40 species of vascular plants in the understory (Söderström and Jonsson 1992). The creation of pits and mounds in tree falls is also important for the maintenance of bryophyte diversity (Jonsson and Esseen 1990), as well as for tree regeneration and maintenance of tree species mixtures in boreal forests (Hofgaard 1993, Kuuluvainen 1994, Kuuluvainen and Juntunen 1998).

3.2.5 Effect of Stand Structure on Disturbance Probability and Spread

Tree-scale interactions in disturbance events may have important consequences for the dynamics of landscape structure (Frelich et al. 1999). The key question is, what are the potential mechanisms for the propagation of disturbances across spatial scales, from a single tree up to landscape? Typically autogenic disturbances, such as death of individual trees or groups of trees due to competition or pathogens and insects attacking weakened or damaged trees, limit their influences to a very local scale. However, these local processes may increase the probability of fire ignition and spread, which may be strongly related to such factors as amount of dead wood and multilayered canopy structure. Kuuluvainen et al. (1998) detected small-scale patterns of spatial autocorrelation in tree size in a mature *Pinus sylvestris* forest and hypothesized that these local spatial hierarchies of trees may affect fire behavior by providing "stepping stones" for surface fires to become crown fires. However, at present, we have limited understanding of the effect of stand structure on the probability and spread of different disturbances in Fennoscandian boreal forests.

3.3 Importance of Multiscale Interactions and Chance Events

Although the distinction between bottom-up and top-down controls of forest structure and biodiversity is useful when analyzing potential causal factors affecting landscape dynamics, it must be kept in mind that in reality we are dealing with complex multiscale interactions. While landscape pattern and topography obviously affect the probability and spread of disturbances (e.g. fire, storm, insects), the properties of tree stands and individual trees often ultimately determine the effect of the disturbance factor. This means that landscape-level forest structure is strongly affected by the *interaction* between disturbances and stand structures and the structure and life history traits of the constituent tree populations. For example, although in *Pinus sylvestris*-dominated landscapes low- or moderate-severity fires occur frequently, large gaps seldom occur because larger *Pinus* trees with thick bark survive the fire and crown fires do not often occur (Kolström and Kellomäki 1993, Agee 1998). Thus, in natural *Pinus*-dominated forest landscapes, a considerable part of the landscape remains forest-covered, containing old trees (Axelsson and Östlund 2000), and forest dynamics are to a large extent driven by overstory tree mortality caused mainly by factors other than fire (Rouvinen and Kuuluvainen 2001, Rouvinen et al. 2002, Kuuluvainen et al. 2002b). In this case, the forest structure is determined both by allogenic disturbances (fires, top-down control) and autogenic disturbances (death of trees due to pathogens and insects, bottom-up control), and by their (possibly complex) interaction.

The simplified model scenario shown in Fig. 3 can clarify the importance of the interaction between fire disturbance and life-history characteristics of tree species. The scenario is based on a simulation model (FIN-LANDIS) developed and evaluated for simulating natural forest dynamics in boreal Fennoscandia (Pennanen and Kuuluvainen 2002). Graph A shows the age distribution of a fully regulated forest landscape (the traditional theoretical goal for sustainable yield forestry) when the rotation cycle is 100 years and each age class occupies the same area. Graphs B and C describe the age structure of two naturally dynamic forest landscapes, assuming random occurrence of fires (e.g. all successional stages are equally susceptible to fire), a 100-year fire cycle, and that individual fires are relatively small (<5%) compared with the total forest area. Graph B shows the distribution of area in terms of time since last fire. The distribution is close to the theoretical negative exponential model (Van Wagner 1978), with some deviation caused by the simulated random occurrence of fires. If we assume that all these fires are severe stand-replacing

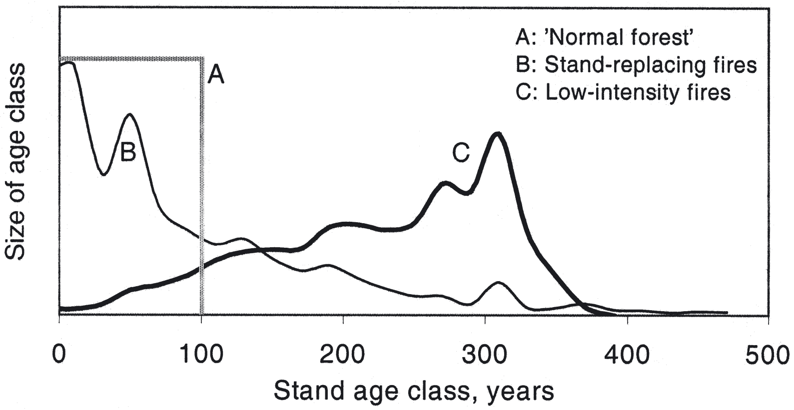

Fig. 3. A model scenario illustrating the differences in the age distribution of forests between managed and naturally fire dynamic landscapes and the effect of tree species characteristics on forest age distribution at the landscape level. Forest age is determined based on the age of the oldest surviving tree cohort. Graph A: a managed, fully regulated forest with a 100-year cutting cycle; Graph B: naturally dynamic forest with all fires stand-replacing, 100-year fire cycle, and random occurrence of fires; Graph C: same as the previous scenario, but the oldest trees survive the fires (*Pinus sylvestris* under low- or moderate-severity fire regimes). See text for additional details. The scenario is based on a simulation model (FIN-LANDIS) developed and evaluated for simulating natural forest dynamics in Fennoscandia (Pennanen and Kuuluvainen 2002). Redrawn from Working group ... (2000).

ones, this graph would also show the age distribution of the forest. However, we know that under Fennoscandian conditions, particularly in *Pinus*-dominated forests and landscapes, a considerable proportion of trees, especially large trees, survive fires. This leads to a situation where the majority of landscape area is dominated by multi-aged *Pinus* forest containing old trees (Graph C), which eventually die due to biological age limits or autogenic disturbances. This result is in accordance with some studies based on empirical materials (Östlund et al. 1997, Axelsson and Östlund 2000, Kuuluvainen et al. 2002b). If we assume that part of the fires are stand-replacing (Pitkänen 1999), the forest age structure is an intermediate between Graphs B and C.

In addition to landscape geomorphology, soil and vegetation characteristics, chance events related to allogenic disturbances, are an important factor affecting the variability of forest structures within natural forest landscapes. Fire occurrence at a given site is not only determined by flammability and location in the landscape, but also by chance events. Because of the stochastic character of fire occurrence, part of the forest, regardless of its flammability, can escape major disturbances for long periods of time.

To date, we have limited understanding of how chance events, disturbances, and successional processes interact across multiple scales to produce habitat structures in natural boreal forests. Accordingly, this topic is a major challenge for forest ecological research. The natural variability approach attempts to shed light on these important interactions operating in natural forest ecosystems and to find management applications that would ultimately lead to similar structural heterogeneity as that found in natural ecosystems. This is important because heterogeneity may be a critical aspect of long-term ecosystem dynamics and function (Landres et al. 1999).

In the following section (Section 4) an attempt is made to summarize the essential features of heterogeneity and variability of natural boreal forests in Fennoscandia. This review will provide the background to an analysis of the main differences between natural and managed forests (Section 5).

4 Defining Structural Heterogeneity of Natural Boreal Forests

Understanding the structure and dynamics of the natural forest is essential in estimating how much we have changed the managed forests from their natural state or, alternatively, how well we have succeeded in restoring a particular forest ecosystem (Landres et al. 1999, Kuuluvainen et al. 2002a). Particularly in the southern parts of boreal Fennoscandia only fragments of the natural forest are left, and it is therefore a major challenge to reconstruct the essential structural and dynamic features of the vanished natural forests. However, this can be attempted based on biological archives (Tolonen 1983, Pitkänen 1999), research carried out in adjacent boreal Scandinavia (Linder and Östlund 1992, 1998, Östlund et al.1997, Axelsson and Östlund 2000, Niklasson and Granström 2000) and in the large natural forest areas of northwestern Russia, just on the other side of the Finnish-Russian border (Volkov et al. 1997, Karjalainen and Kuuluvainen 2002, Kuuluvainen et al. 2002b, Rouvinen et al. 2002), and by using modeling to reconstruct natural forest dynamics (Pennanen 2002, Pennanen and Kuuluvainen 2002). Incorporating the landscape scale in the analyses is necessary because many essential processes of the natural boreal forest, such as forest fires and subsequent vegetation successions, occur over large areas.

In this review, the essential features of dynamic heterogeneity and variability of natural forests in boreal Fennoscandia are discussed. Due to limited knowledge, the picture often is more qualitative than quantitative. Despite this, knowledge of the main structural and dynamic features of natural forests is valuable since in an ever-changing world it is more important to know the direction of restorative actions, while the setting of specific management goals is a long process involving research, monitoring, and adaptive management (Walters and Holling 1987, Bunnell and Johnson 1999, Bergeron et al. 2002, Kuuluvainen et al. 2002a). Accordingly, even the current limited understanding of natural forests is indispensable in directing our efforts to manage and restore biodiversity in boreal forests.

4.1 Disturbances as a Source of Heterogeneity

The structure of natural forest landscapes is mainly determined by their climate, geomorphology, soils, historical factors, and different kinds of disturbances. When considering maintenance of natural biodiversity in any given landscape matrix, disturbance becomes a central mechanism. This is because characteristics of parent soil change extremely slowly, so that within a given abiotic framework, disturbances and the resultant vegetative successions determine the characteristics and pattern of habitats for forest-dwelling organisms (Pickett and White 1985, Hansen et al. 1991, Attiwill 1994, Esseen et al. 1997).

The disturbance dynamics of natural forests are a complex phenomenon, involving such factors as fire, wind, insects, pathogens, snow, and animals, and ranging in spatial and temporal scales from large catastrophic disturbances to perturbations affecting individual trees or groups of trees. Thus, disturbances in natural forests show a wide variation in quality, size, severity, and repeatability (Engelmark 1999, Bergeron et al. 1999a, 2002; see Fig. 4 and Table 2).

Structural variability of natural forests is further increased by the co-occurrence of various disturbance factors in space and time. This is due to synergism among natural disturbance factors, i.e. the occurrence of one disturbance factor affects the probability of other disturbance factors (Fig. 5). Because of this interaction and the consequent hierarchical multiscale characteristic of natural disturbances, the often-stated conceptual dichotomy between small and large cycle (i.e. small- and large-scale disturbance and succession) can be misleading. Instead of creating a dichotomy between e.g. small- and largescale disturbances, it is more realistic to view different disturbance factors, operating and interacting at different space and time scales, as simultaneously affecting the succession in various proportions of sites in a given forest area (Figs. 5, 6). This view emphasizes site disturbance history as a prerequisite and general framework for explaining and understanding stand structures and successional changes in boreal forests (Kuuluvainen and Rouvinen 2000, Wallenius et al. 2002).

Fig. 4. The structure of natural boreal forests is shaped by a combination of autogenic and allogenic disturbances, displaying a wide range of variation in disturbance type, size, severity, and repeatability. a) The autogenic mortality of large overstory trees drives the dynamics of a natural *Pinus*-dominated landscape characterized by recurrent low-severity fires; Vienansalo wilderness, Russian Karelia, middle boreal zone (Lehtonen and Kolström 2000, Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002). b) A severely burned patch with abundant regeneration and standing dead trees within a ca. 350 ha fire area in a *Pinus* forest 31 years after fire; Vienansalo wilderness, Russian Karelia. c) A natural nonpyrogenic *Picea* forest characterized by gap-phase dynamics; Paanajärvi region, Russian Karelia, northern boreal zone. d) Large-scale wind disturbance in primeval *Picea*-dominated taiga; Komi republic, Russia, southern boreal zone (Syrjänen et al. 1994). e) A gap of complex structure caused by storm wind; Koivusuo Strict Nature Reserve, Finland, middle boreal zone. f) Beaver is a significant disturbance agent in moist forests, which are otherwise seldom affected by disturbances such as fire and windthrow; Korpiselkä, Russian Karelia, middle boreal zone. (photographs a–e by T. Kuuluvainen, f by J. Siitonen).

Table 2. A comparison of characteristics of disturbance dynamics in natural versus managed forests in Finland. The table is based on the author's personal judgement and information from various sources. See text for more details.

Characteristic	Natural forest	Managed forest
Number of disturbance factors	High	Low
Variation of disturbance quality	High	Low
Proportion of trees dying	0–100%	95–100% [1]
Remaining proportion of dead trees	100%	0–5%
Mean disturbance interval	10–500 years	80–130 years [2]
Variation in disturbance interval	High	Low
Extent of disturbances	0.001–100.000 ha	0.001–10 ha

[1] Proportion of timber harvested in clear cutting
[2] Mean interval of clear cutting

Natural disturbances also differ in their mode of temporal operation in the forest (Fig. 6). Dramatic allogenic disturbances, such as severe fires or storms, often affect large areas but are discrete events in time with possibly long return intervals. In contrast, autogenic disturbances caused by pathogenic fungi and insects operate at the scale of individual trees or groups of trees more or less continuously when viewed at the landscape level. Increasing evidence is available on the importance of insects and pathogens as determinants of boreal forest structure and composition (Kuuluvainen et al. 1998, Lewis and Lindgren 2000, Rouvinen et al. 2002). Thus, within the larger-scale disturbance matrix created by discrete allogenic disturbances, i.e. fires and occasionally by storm winds, these smaller-scale disturbances, operating in a more continuous manner, significantly affect local-scale forest structure (see Figs. 5, 6; Syrjänen et al. 1994, Rouvinen et al. 2002).

Forest fires are an important disturbance factor in most natural boreal forests (Zackrisson 1977). Before human settlement, forest fires were lit by lightning strikes (Granström 1993). Factors that may potentially affect fire ignition and spread include site type, tree species composition, forest structure, amount and decay stage of dead wood, topography, and climate. Furthermore, geographic variability likely exists in lightning density (Granström 1993). According to Johnson et al. (1998), climate is the most important factor affecting ignition probability (see also Granström et al. 1995). During dry climatic periods, fire may spread to all types of forest, perhaps excluding the moistest sites (Niklasson and Granström 2000, Pitkänen 1999). Fires ignited during periods when conditions for fire spread have been unfavorable have been small low-severity fires (Agee 1998). In Fennoscandian boreal forest landscapes, natural fire barriers, such as water bodies and peatlands, are common and have a restrictive effect on fire spread. Early human settlement has probably increased fire frequency but decreased the average size of fires (Niklasson and Granström 2000).

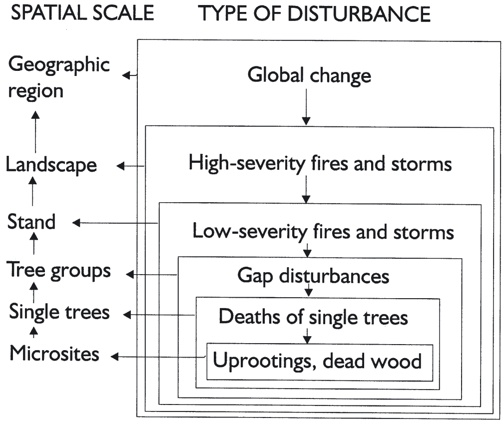

Fig. 5. An illustration of the spatial scales and the often hierarchical nested occurrence of different disturbance factors in natural forests. Structural variability of natural forests is increased by the co-occurrence of various disturbance factors in space and time (for discussion see Section 4.1).

Because the most influential fires have occurred during dry climatic periods, it is possible that no notable difference in fire frequency has

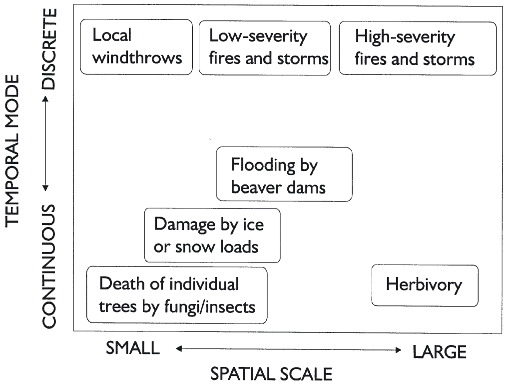

Fig. 6. Disturbances in natural boreal forests differ in their spatial extent and temporal mode of operation. Dramatic allogenic disturbances, such as severe fires or storms, often affect large areas but are discrete events in time with possibly long return intervals, whereas autogenic disturbances caused by pathogenic fungi and insects operate at the scale of individual trees or groups of trees more or less continuously when viewed at the landscape scale.

been present between mesic (*Vaccinium myrtillys* -type) and drier forest types (*V. vitis-idaea* -type) (Pitkänen 1999). However, sites moister than the *Myrtillus*-type have burned significantly less frequently, but only a few *Picea* peatlands are true fire refugia (Hörnberg et al. 1995). Moist sites occupied by deciduous trees have probably burned most seldom, because they lack the moss carpet, which burns easily, and the broad-leaved trees have prevented spread of crown fires.

Different kinds of forested wetlands are an essential component of the Fennoscandian boreal forest landscape, but their fire ecology as part of the landscape matrix is poorly understood (Sjöberg and Ericson 1997). Under normal conditions, forested peatlands burn very infrequently. However, fires have been more frequent during exceptionally dry climatic periods when the ground water table has been significantly lower than normal (Pitkänen 1999).

In addition to fire, the natural forest hosts a range of other disturbance agents that often operate at small spatial scales killing individual trees or groups of trees (Figs. 4, 5; Kuuluvainen 1994, Kuuluvainen et al. 1998). Such disturbances are caused by strong local winds, heavy ice or snow loads, floods, insects, pathogens, and some animals. The beaver, in particular, is a significant "disturber" in moist forests that seldom burn. Beavers probably played a significant role in natural swamp forest dynamics in Fennoscandia.

In general, disturbance dynamics in managed and natural forests differ substantially from each other (Attiwill 1994, Engelmark and Hytteborn 1999, Bergeron et al. 2002; see Table 2). In the managed forests of Fennoscandia, the dominant disturbance factors are wood harvesting and other silvicultural treatments, while natural disturbances are largely excluded. The structural differences between managed and natural forests can largely be attributed to differences in disturbance dynamics. In the managed forest, the disturbance (harvesting) areas and the harvest rotation are relatively constant, whereas natural forests show a wide variation in the quality, size, severity, and repeatability of disturbances (Table 2).

4.2 Succession as a Source of Heterogeneity

4.2.1 Tree Successions

In natural forests, the variability of disturbance dynamics is reflected in high variation in initial and later stages of vegetation successions. In addition to disturbance type and severity, tree successions are influenced by factors such as the presence and location of seed trees, variability of seed years in relation to occurrence of disturbance events, and species composition of the predisturbance forest (e.g. surviving trees and sprouting species). Moreover, even from similar initial states, succession can evidently lead to several pathways and structural/compositional endpoints (McCune and Allen 1984, Abrams et al. 1985). These all increase the variability and heterogeneity of stand structures in natural forests.

Forest succession on a given site never reaches a stable structural and compositional endpoint, as suggested by the traditional climax concept (Clements 1916). For example, even without a fire, natural *Picea* forests maintain, as a consequence of gap-phase dynamics, a significant component of deciduous trees (Kuuluvainen et al. 1998). Because forests are characterized by continuous and sometimes unpredictable change, the traditional stand-level climax-concept has largely been abandoned in forest ecology literature (Glenn-Lewin and van der Maarel 1992).

At local scale, disturbance severity can vary from stand-replacing disturbances, killing all trees, to ones killing only individual trees, sometimes small understory trees (light surface fires) (Sarvas 1938, Engelmark 1999, Engelmark and Hytteborn 1999, Rouvinen et al. 2002). When discussing forest regeneration and stand development, it is important to make a distinction between these two extremes. Only a severe (crown) fire is capable of killing all trees, while even severe storms leave some of the understory trees alive. Thus, different disturbance agents, although being comparable in severity, create different starting points for successions.

An even-aged stand structure may develop if the succession starts after a stand-replacing fire disturbance and if regeneration occurs fairly rapidly. However, even under favorable conditions, the regeneration cohort takes several years to form after the disturbance (Sarvas 1938, Vanha-Majamaa et al. 1996). Single-cohort stand would probably not be common in the natural forest but could occur after severe crown fire events in young dense stands and in multilayered *Picea*-dominated forests (Axelsson and Östlund 2000). It is noteworthy that only in these single-cohort stands is the distinction of separate successional phases, such as establishment, thinning, maturation, transition, and shifting gap phase, truly meaningful (Spies 1996).

In most disturbance events, only a portion of the trees die, with the surviving trees remaining as part of the living structure of the forest (Agee 1998). This leads to the development of a multilayered, unevenly aged forest (Östlund et al. 1997, Axelsson and Östlund 2000, Kuuluvainen et al. 2002b, Rouvinen et al. 2002). Disturbance type has a strong effect on age structure of the developing forest: fire kills smaller and younger trees, while larger trees often survive; storms, by contrast, kill bigger, older trees and leave the smaller, younger trees of the dominant tree layer alive. The disturbance type also affects tree species diversity of the remaining forest, as the understory layer usually hosts more tree species than the dominant layer (Kuuluvainen et al. 1998).

In natural conditions in Fennoscandia, forest successions composed mainly of mixtures of *Picea*, *Pinus*, and *Betula* were predominant, with scattered occurrence of *Populus tremula* and *Salix caprea*; the mixture of species varied mainly according to site type, disturbance history, and successional stage (Pitkänen 1999, Axelsson and Östlund 2000).

4.2.2 Tree Decay Successions

When a disturbance event kills trees and facilitates forest regeneration, it also starts another successional sequence, the decay succession of dead trees. Thus, disturbance dynamics regulate the dead wood dynamics of the forest. After a severe disturbance event, dead trees can comprise up to several hundred cubic meters (Siitonen 2001). In this case, the amount of dead wood first decreases during succession, as deaths of larger trees take a long time. This decline slows down when trees of the regeneration cohort start to die due to self-thinning. This is also the phase when the early successional deciduous trees, such as *Populus* and *Betula*, contribute most to the dead wood volume, especially on fertile sites. In late successional phases, the total amount of dead wood will increase as large trees start to die and fall down (Siitonen 2001).

However, the described pattern of dead wood succession may not be common in naturally dynamic landscapes. It may occur in *Picea*-dominated forests after severe allogenic disturbances (fire, storms) but appears to be less common in *Pinus*-dominated forests characterized by low- or moderate-severity fire regimes (Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002) and in nonpyrogenic forests dominated by autogenic disturbances (Zackrisson et al. 1995, Kuuluvainen et al. 1998). In *Pinus*-dominated forests, fire usually kills smaller trees, and dead wood dynamics are regulated by other causes of overstory mortality (Axelsson and Östlund 2000, Rouvinen and Kuuluvainen 2001, Rouvinen et al. 2002). Because the death of overstory trees is partly a stochastic process both in space and time (Rouvinen et al. 2002), the input of large dead wood can vary greatly at local scale over short periods but remain relatively constant when viewed over

Fig. 7. Old *Pinus sylvestris* trees covered with a thick heat-insulating bark, although damaged by fire (fire scars), may survive several fire episodes. Because of this feature *Pinus*-dominated forests typically consist of different age cohorts, which form a patchy and multilayered canopy structure. Vienansalo wilderness, Russian Karelia, middle boreal zone. (photograph by T. Kuuluvainen).

larger areas and longer periods of time (Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002). This kind of dead wood dynamics is also typical of nonpyrogenic *Picea* forests characterized by gap-phase dynamics (Jonsson 2000, Kuuluvainen et al. 2001).

The amount of dead wood in natural forests in Fennoscandia is estimated to vary from 20 to120 m^3ha^{-1}, depending on site fertility, successional stage, disturbance history, and climatic conditions (Siitonen 2001). Amounts of dead wood are highest in fertile *Picea*-dominated forests in southern Fennoscandia and lowest in dry *Pinus*-dominated forests in northern Fennoscandia.

4.3 Characteristics of Forest Dynamic Heterogeneity at Stand Scale

4.3.1 Pinus-dominated Forests

In Fennoscandia, fire is an essential characteristic of the ecology of *Pinus sylvestris* -dominated forests (Zackrisson 1977, Esseen et al. 1997, Lehtonen 1997, Lehtonen and Kolström 2000, Engelmark and Hytteborn 1999). Because stems of older *Pinus* trees are covered with a thick heat-insulating bark, larger trees may survive even several fire episodes, and therefore, the forest remains to some extent canopy-covered (Fig. 7; Agee 1998, Östlund et al. 1997, Kuuluvainen et al. 2002b). Stand-replacing fires may, however, occur (Pitkänen 1999) in young and dense stands or in forests with a dense multilayered *Picea* understory (see Fig 4b).

Pinus-dominated forests typically consist of different age cohorts which form a patchy and multilayered canopy structure (Lähde et al. 1994, Volkov et al. 1997, Axelsson and Östlund 2000); the older cohorts have survived the fires and the younger ones have emerged within some years after surface fires (Aaltonen 1919, Sarvas 1938, Kuuluvainen et al. 1998, Kuuluvainen and Rouvinen 2000). In *Pinus*-dominated forests on medium fertile sites, a similar fire-induced age structure can be observed, but the age structure may be affected in early succession by a more abundant deciduous tree component and in later successional stages by a more abundant ingrowth of *Picea*. If severe fires do not occur this type of *Pinus* forest may perpetuate itself through the death of single or multiple dominant trees, due to old age, fungi, and bark beetles (Rouvinen et al. 2002), and subsequent regeneration in the formed gaps. The formed gaps may provide a competitive advantage to deciduous and *Picea* trees that are abundant in the understory of old *Pinus* forests (Fig. 4a; Kuuluvainen and Juntunen 1998, Kuuluvainen et al. 1998, 2002b). However, even a light surface fire shifts the tree species composition in favor of *Pinus* by killing deciduous and *Picea* trees in the understory and enhancing conditions for *Pinus* regeneration (Sarvas 1938, Kuuluvainen and Rouvinen 2000).

To summarize, the structure and composition of *Pinus*-dominated forests are typically determined by the spatial and temporal interplay between low-severity fires, affecting death and regeneration of understory trees (allogenic disturbance), and the gap formation and consequent release of understory trees due to deaths of single or multiple dominant trees caused by old age, pathogens, and insects (autogenic disturbance; Volkov et al. 1997, Rouvinen et al. 2002).

4.3.2 Picea-dominated Forests

Natural nonpyrogenic *Picea*-dominated forests are characterized by gap-phase dynamics, where the deaths of dominant trees and consequent regeneration occur continuously at local spatial scales (Sernander 1936, Dyrenkov et al. 1991, Hofgaard 1993, Kuuluvainen et al. 1998). The gap structures formed by living and dead trees can be complex (Fig. 4e). Trees of all ages and sizes occur throughout the forest and separate regeneration cohorts may not exist. The dynamics of this type of forest are driven by small-scale autogenic disturbance agents, such as pathogenic fungi and bark beetles, which kill single or groups of weakened or damaged trees (Kuuluvainen et al. 1998). Dead trees eventually fall and form uprooting spots (pits and mounds) and decayed logs, which are favorable regeneration microsites for trees (Fig. 8, Hofgaard 1993, Kuuluvainen 1994). Despite the lack of fire, deciduous trees like *Betula* spp. and *Salix caprea* are able to maintain themselves as a significant component of the forest by utilization of gaps through efficient seed dispersal, sprouting, and rapid growth (Kuuluvainen 1994, Kuuluvainen et al. 1998).

Although moist *Picea*-dominated forests are usually characterized by small-scale autogenic disturbances, they may periodically be susceptible to large-scale devastating disturbances, especially if this type of *Picea*-dominated forest covers large continuous areas (Fig. 4d). Under these conditions, forest fires ignited during prolonged drought periods can be severe and stand-replacing (Sirén 1955, Volkov et al. 1997, Axelsson and Östlund 2000, Gromtsev 2002). Deciduous trees, especially *Betula* and sometimes *Populus*, may dominate the following successions (Sirén 1955).

Fig. 8. *Picea*-dominated forests on moist fertile sites are typically driven by gap-phase dynamics, where the deaths of individual trees or groups of trees occur at local spatial scales. Gaps are characterized by a heterogeneous structure with pits and mounds, and decayed logs, which form favorable regeneration microsites for trees. Komi republic, Russia, southern boreal zone. In southern Scandinavia these sites have largely been converted to agricultural lands. (Photograph by T. Kuuluvainen,).

4.4 Characteristics of Forest Dynamic Heterogeneity at Landscape Scale

Quality, severity, extent, and repeatability of disturbances largely regulate the forest structural mosaic within a given landscape (Spies and Turner 1999). In natural forests, disturbance dynamics are a complex hierarchical phenomenon where different kinds of autogenic and allogenic disturbance agents affect forest structure at a given site (Fig. 5). At present, we do not know the relative importance of different disturbance agents in naturally dynamic forest landscapes in Fennoscandia. However, evidence exists that the role of fire, as an abrupt violent disturbance, may have been overemphasized in relation to other disturbance agents, usually operating continuously at small spatial scales (Kuuluvainen 1994, Axelsson and Östlund 2000, Lewis and Lindgren 2000, Rouvinen et al. 2002).

In natural conditions, forest fires would have in most cases been an important landscape-level disturbance factor. When examining the effect of forest fires on landscape structure, the area must be sufficiently large for forest fires to occur regularly and the fires should not cover a large part of the area. Because in natural forests fires can be substantial (up to 50 000–100 000 ha, Niklasson and Granström 2000), large areas are needed to examine natural fire-induced landscape mosaics. In natural conditions, forest fires may cause both equilibrium and nonequilibrium landscape structures, depending on landscape matrix characteristics. Such characteristics include tree species composition, climatic conditions, and the overall landscape mosaic of forests, wetlands, and different kinds of water bodies (Agee 1999).

In landscapes characterized by dry or dryish *Pinus* forests, often located in watershed areas, the occurrence of recurrent low-severity fires is likely to have a stabilizing effect on landscape structure (Agee 1999, Axelsson and Östlund 2000). Repeated light surface fires leave larger *Pinus* trees alive and enhance its regeneration, while killing other tree species, and thus, prevent their invasion. Gaps created due to death of single and multiple dominant trees facilitate the spotty recruitment of understory *Pinus* to the dominant canopy layer (Aaltonen 1919, Sarvas 1938, Rouvinen et al. 2002). Recurrent surface fires also lower the probability of crown fire occurrence by preventing the formation of dense understories and keeping the main canopy partly open (Östlund et al. 1997, Agee 1998).

Larger areas of fertile *Picea*-dominated forest, which in southern boreal Fennoscandia would occur on present agricultural lands, are most likely to be characterized by alternating periods of equilibrium and nonequilibrium, which are related to fluctuations in climatic conditions. In this type of moister forest, fires are relatively rare (fire-return interval could be up to several hundreds years, Hyvärinen and Sepponen 1988, Wallenius 2002), but during prolonged drought periods fires can potentially be devastating and widespread (Sirén 1955, Volkov et al. 1997, Axelsson and Östlund 2000). Severe storms could also occasionally create large-scale destruction in this type of forest (Syrjänen et al. 1994). These large-scale disturbances can periodically result in drastic fluctuations in landscape structure when viewed over long periods of time. However, between severe allogenic disturbance events, these *Picea*-dominated landscapes are characterized by near-equilibrium dynamics driven by small-scale gap formation due to autogenic disturbances (Kuuluvainen et al. 1988, Hofgaard 1993, Engelmark 1999, Engelmark and Hytteborn 1999).

In most cases, natural forest landscapes in boreal Fennoscandia are composed of mixtures of *Pinus*- and *Picea*-dominated forests, with variable proportions of deciduous trees (Pitkänen 1999). As a consequence, the dynamics of natural forest landscapes are typically an intermediate form of the two modes described above, in which equilibrium and nonequilibrium phases alternate. Different forest types and the abundance of peatlands and water bodies often restrict the extent of fires. On the other hand, most influential fires occur during dry climatic periods, when fires may ignite and spread in all types of forests (even in peatlands) irrespective of site type, successional state, and stand structure (Johnson et al. 1998). Thus, large fires would affect landscape structure most, although small fires are more numerous (Niklasson and Granström 2000). Pitkänen (1999) estimated that in central eastern Finland before human settlement about half of the fires have been stand-replacing. These results do not mean, however, that the resulting landscape structures would have been homogeneous. Because of the physical heterogeneity of landscape mosaic, even a large fire inevitably includes unburned areas and the severity of fire varies substantially within the landscape (Sarvas 1938). All this contributes to high diversity of post-fire structures and successional pathways typical of naturally dynamic forest landscapes.

It is practically impossible to determine one natural fire-return interval or fire cycle for any given forest landscape because fire regimes are known to vary through time according to climatic fluctuations (Johnson et al. 1998). As a consequence, a natural forest landscape mosaic can be interpreted as the result of a dynamically fluctuating historical fire regime. Keeping these restrictions in mind, it may be useful to estimate mean characteristics of the fire cycle for a specific period of time (Landres et al. 1999). For example, Pitkänen (1999) estimated, using palaeoecological methods, that before human settlement in northern Karelia the mean fire-return interval in both *Picea*- and *Pinus*-dominated forests has been up to 180 years (Pitkänen, pers. comm.). Wallenius (2002) estimated that the fire rotation of a natural *Picea*-dominated landscape was at least 300 years but possibly much longer. In northern Sweden before human settlement, fire occurred once every ten years per 10 000 ha (Niklasson and Granström 2000). In many dendroecological studies, higher fire frequencies have been documented (e.g. Lehtonen 1997), but these studies usually cover time periods when human activity has strongly affected fire regime (Niklasson and Granström 2000).

Generalizations of fire cycles are easily misleading because considerable variation usually exists in the fire regime within a landscape. This is partly due to the stochastic nature of fire ignition. As a result, purely by chance, some sites may remain unburned for long periods of time irrespective of their flammability (Pennanen and Kuuluvainen 2002). In addition, landscape configuration affects fire regime such that continuous upland areas have burned more often than fragmented areas of the same site type. This is because the probability of ignition and spread is higher on larger continuous elevated areas compared with small forest patches surrounded by e.g. peatlands. Topographic features also have an effect; drier south-facing slopes have burned more often than moister north-facing slopes.

In many cases, fires are the most important allogenic disturbance factor in natural boreal forests. Fire intensity varies considerably, usually being low or moderate in severity, leaving a considerable number of trees alive at landscape scale. In such cases, autogenic disturbance factors, such as pathogens and insects, play a significant role in forest dynamics. As a result, the dominant canopy cover is open and patchy at a smaller scale but relatively continuous at larger scales (Axelsson and Östlund 2000). Multi-aged mixed *Pinus-Picea-Betula* forests predominate in natural forests, but the relative proportions of tree species vary considerably in space and time (Östlund et al. 1997, Pitkänen 1999, Axelsson and Östlund 2000). While stand-replacing disturbances are relatively rare in time, fire events during prolonged drought periods can lead to stand replacement and establishment of single-cohort stands dominated by deciduous species over large areas (Sirén 1955, Volkov et al. 1997, Axelsson and Östlund 2000).

In conclusion, in natural forests, landscape-level disturbance dynamics are driven by a combination of allogenic and autogenic disturbance agents, both being affected by a multitude of factors including climate, geomorphology, soils, tree species composition, and the amount and spatial pattern of peatlands and water bodies. Moreover, it must be kept in mind that because landscape characteristics vary from one area to the next, and because a stochastic component is involved in disturbance occurrence, each landscape and time period is likely to be a special case (Landres et al. 1999). Because of these reasons generalizations of disturbance (fire) cycles as mean values and using them as a basis of determining cutting rotations at stand level (Angelstam 1998) can lead to landscape structures that are far removed from any natural ones (see Fig. 3).

5 Main Discrepancies between Natural and Managed Forest

A necessary step in using the natural forest as a reference in restoring and managing natural habitat structure and forest biodiversity is to analyze the main differences between current (habitat) structure and dynamics and those of potential natural vegetation (Axelsson and Östlund 2000, Palik et al. 2000, Kuuluvainen et al. 2002a). In the following section, the main structural differences between naturally dynamic and managed forest are discussed separately in two broad forest groups, in *Pinus*- and in *Picea*-dominated forests.

In Fennoscandia, the currently dominant harvesting method both in *Pinus*- and *Picea*-dominated forests is clear-cutting. In Finland, for instance, about 2/3 of harvested area is clearcut, with retention trees left in groups of 10–20 trees (Working group... 2000). In addition, in *Pinus*-dominated forests, seed tree and shelter-wood cuttings are practiced (1/3 of harvested area); the seed trees are removed some years after harvesting. All these harvesting methods result in forest patches of size 0.5–10 ha, incorporating small groups of older trees (retention trees).

In *Pinus*-dominated forests, the structure and dynamics created by current management are in general different from the potential forest structure of these sites, which would in many cases be characterized by multi-aged and multisized stands and the more or less continuous presence of old *Pinus* trees (Östlund et al. 1997, Axelsson and Östlund 2000, Kuuluvainen et al. 2002b, Rouvinen et al. 2002, Wallenius et al. 2002). This kind of landscape structure would also most likely be fairly stable in time. Some evidence exists that stand-replacing fires may have been more common in forests before human influence. For example, Pitkänen (1999) estimated, using palaeoecological methods, that before human settlement in northern Karelia approximately half of the fires could have been severe stand-replacing disturbances, thus potentially corresponding to clear-cuts in terms of degree of tree mortality. Even taking this into account, the landscape structures and dynamics created by current management practices are drastically different from natural forests both at local and landscape scales (Fig. 3).

In natural *Picea*-dominated forests, which typically occur on medium-fertile to fertile sites, severe stand-replacing disturbances (fires) can occasionally occur, sometimes covering large areas (Sirén 1955, Volkov et al. 1997), thus resembling the effect of clear-cuts in terms of degree of tree mortality. Deciduous trees, especially *Betula* and sometimes *Populus*, would often dominate the post-fire succession. However, in natural forests, such severe disturbances are rare in time (Gromtsev 2002, Wallenius 2002). In the absence of or during hundreds of years between severe disturbances, *Picea* forests are dominated by small-scale disturbances, creating multi-aged and multisized stand structures (Dyrenkov et al. 1991, Kuuluvainen et al. 1998). Thus, on *Picea* sites, both even-aged deciduous forests and multi-aged *Picea* forests, and the successional stages between these two phases, could occur. In conclusion, in *Picea*-dominated forests, current clear-cut harvesting can create stand structures that at local scale are occasionally similar to those found in natural forests. However, at landscape scale, the situation is different because the natural forest is characterized by a wide range of variation in disturbance type, size, severity, and repeatability (see Fig. 3, Table 2).

6 Implications for Forest Management and Research

A naturally dynamic forest landscape is a complex multiscaled hierarchical system. In management aimed at restoration and biodiversity conservation, it is necessary to be aware of this complexity and try to understand it but not to be paralyzed by it (Bunnell 1999). Even limited and more qualitative information can be used in directing restoration efforts and in improving management practices for biodiversity conservation. Nevertheless, because of the complexity of the system to be managed, research and monitoring must be included as integral components of long-term restoration projects (adaptive management, Walters 1986, Walters and Holling 1990, Kuuluvainen et al. 2002a).

When using natural forests as a reference for restoring and managing biodiversity, it is important to focus on broad goals not details. Goals often cannot be defined as static entities but rather as envelopes of natural variability. In most cases, we already know how we should change current practices of forest management to better imitate the structural complexity and dynamics of natural forests. However, to do this, we must make full use of the existing information.

In managed forests, mimicking of the natural forest in all of its aspects is often not a realistic goal, because of economic and perhaps social constraints (Armstrong et al. 1999, Bunnell and Johnson 1999), as well as logical constraints. For example, mimicking natural fire dynamics may not be possible in many cases because management areas are too small for incorporating larger fire effects (Table 2). A feasible goal of planning and management could be to imitate the occurrence and effects of natural disturbance agents operating at realistic spatio-temporal scales in a given planning area. In this context, the management problem is to how to allocate the available resources most efficiently in terms of biodiversity conservation.

Some authors have suggested that the landscape scale is the most relevant scale of biodiversity restoration and management (Franklin 1993, Urban 1993). However, although it is evident that incorporating the landscape scale in management is necessary, no single scale can be selected as a basis of biodiversity management in boreal forests (Bunnell 1999). If, for instance, the management only focuses on landscape-level characteristics, the importance of structural features at a lower level of ecological organization may be overlooked (Axelsson and Östlund 2000). Thus, for managing forest dynamic heterogeneity, what is needed is a *hierarchical multiscale* approach.

One potential solution to the problem of how to apply hierarchical multiscale management could be to manage for disturbances and structures at three nested operational scales, i.e. at landscape, stand, and patch/microhabitat. Managing at the landscape scale would aim at a similar mosaic of stand structures and successional stages as found in natural landscapes. This would require defining the targets both for the share of different structural stages on different site types and for the connectivity properties of the landscape matrix. Stand-scale management would aim at maintaining those general structural features and their variability, which are known to be important for biodiversity. The third, patch/microhabitat scale management would aim at ensuring the formation and variability of specific fine-scale habitats important for biodiversity, such as soil disturbances (pit/mound complexes), large living trees, and standing and fallen dead trees. This management procedure would aim at creating habitat characteristics created by the nested hierarchical disturbance dynamics operating in natural forests (see Fig. 5).

It is evident that forest management interferes with ecosystem interactions operating across multiple scales, which creates dynamic heterogeneity typical of natural boreal forests. A major challenge in research is to achieve a better understanding of cross-scale dynamics of heterogeneity and biodiversity in the natural boreal forest. To accomplish this, research must apply a combination of different methods at different scales. For example, experimental research is feasible at microsite/patch and stand scales but very difficult and expensive at landscape scale. At larger spatial and temporal scales, retrospective analyses, using biological archives or historical stand surveys, are useful (Niklasson and Granström 2000, Pitkänen 1999, Axelsson and Östlund 2000). Also useful is research based on ground surveys and/or remote-sensing analyses of existing natural forest ecosystems (Syrjänen et al. 1994, Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002, Wallenius 2002). One reason for this is that structure can often be used to make inferences about dynamics (Kuuluvainen et al. 1998). Finally, realistic landscape models are necessary because empirical studies are seldom possible at landscape or larger scales (Pennanen 2002). However, the parameterization and evaluation of landscape simulation models can only be based on empirical material and experiments (Pennanen and Kuuluvainen 2002). In this respect, landscape-level simulation models can be viewed as a way to integrate and operationalize the existing empirical knowledge, as well as to reveal gaps in the current knowledge bases. In general, a better coordination between empirical studies of various kinds and modeling is needed (Mladenoff and Baker 1999). More attention is also needed on scaling the results of studies from one hierarchical level to the next. An important topic of research is the interaction between human-caused disturbances and the occurrence of natural disturbances (Radeloff et al. 2000, Sinton et al. 2000). Because human interventions always interfere with natural processes, restorative actions may have unexpected consequences on natural disturbances.

7 Conclusions

Compared with the natural forest, current forest management creates disturbances and successional dynamics that are strongly scale-limited. Although recent management guidelines aim at increasing structural components important for biodiversity (e.g. by protection of key biotopes and leaving dead and retention trees) and at promoting landscape connectivity (e.g. by using ecological corridors), it is obvious that the current silviculture is too monotonous and is applied too narrowly at space and time scales to restore some of the essential characteristics of multiscale heterogeneity found in natural forests. Thus, to restore structures and dynamics similar to those found in natural forests, current methods of forest management and silviculture need to be revised.

If forest management aims at restoring the characteristics of multiscale heterogeneity of the natural boreal forest, diversification of cutting treatments is necessary to produce more variation in disturbance severity, quality, extent, and repeatability. This means that forests at similar sites should be treated differently and the share of harvested trees should vary considerably within the landscape. A first important step in this direction is to avoid carrying out the same procedures everywhere (Bunnell and Johnson 1999). The set of cutting regimes applied should be based on landscape-specific analysis of potential ecosystem diversity and natural disturbance regime (Angelstam 1998, Bergeron et al. 1999b, Palik et al. 2000, Pennanen and Kuuluvainen 2002, Rouvinen et al. 2002). Here, the landscape-specific variability in natural disturbance dynamics is more important than mean values. In particular, generalizations of disturbance (fire) cycles as mean values and using them as a basis of determining cutting rotations can lead to landscape structures that are far outside the natural bounds of landscape variability. Retrospective gap analyses can be used for setting goals for landscape-level restoration (Bradshaw et al. 1994, Axelsson and Östlund 2000). Moreover, properly evaluated spatially explicit models of natural disturbance dynamics could be used as tactical-level planning tools for long-term management aimed at landscape restoration (Baker 1993, Mladenoff and Baker 1999, Pennanen and Kuuluvainen 2002).

A feasible way of practicing forestry while simultaneously restoring and maintaining some of the essential features of natural forest structures and dynamics at multiple scales is to move from clear-cutting dominated harvesting to management where a range of partial harvesting methods, inspired by tree mortality patterns found in natural forests, are applied (Bergeron et al. 2002, Pennanen and Kuuluvainen 2002, Rouvinen et al. 2002). Clear-cutting could be applied but on a limited portion of the land area. This type of forest management, based on the hierarchical multiscale variability approach and aimed at maintaining structural complexity, would also conform to the precautionary or 'coarse-filter' principle in biodiversity conservation (Hunter et al. 1988). Management aimed at restoring and maintaining some of the basic features of the natural forest would be an attractive choice in areas where recreation and ecotourism are important sources of income in addition to forestry. Overall, an urgent need exists to develop new forest management practices, based on the natural variability approach, which would be acceptable from ecological, economic and sociocultural points of view.

Acknowledgements

I am indepted to the members of our research group for ideas, discussions and inspiring collaboration. I thank Lars Östlund and one anonymous reviewer for constructive comments and Carol Pelli for linguistic corrections. This work was financed by the Academy of Finland and is part of the Finnish Biodiversity Research Programme FIBRE (1997–2002).

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Total of 155 references