SILVA FENNICA
Silva Fennica 45(5) review articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Forest Naturalness in Northern Europe: Perspectives on Processes, Structures and Species Diversity

Guntis Brūmelis, Bengt Gunnar Jonsson, Jari Kouki, Timo Kuuluvainen and Ekaterina Shorohova

Brūmelis, G., Jonsson, B.G., Kouki, J., Kuuluvainen, T. & Shorohova, E. 2011. Forest naturalness in northern Europe: perspectives on processes, structures and species diversity. Silva Fennica 45(5): 807–821.

Saving the remaining natural forests in northern Europe has been one of the main goals to halt the ongoing decline of forest biodiversity. To facilitate the recognition, mapping and efficient conservation of natural forests, there is an urgent need for a general formulation, based on ecological patterns and processes, of the concept of "forest naturalness". However, complexity, structural idiosyncracy and dynamical features of unmanaged forest ecosystems at various spatio-temporal scales pose major challenges for such a formulation. The definitions hitherto used for the concept of forest naturalness can be fruitfully grouped into three dimensions: 1) structure-based concepts of natural forest, 2) species-based concepts of natural forest and 3) process-based concepts of natural forest. We propose that explicit and simultaneous consideration of all these three dimensions of naturalness can better cope with the natural variability of forest states and also aid in developing strategies for forest conservation and management in different situations. To become operational, criteria and indicators of forest naturalness need to integrate the three dimensions by combining species (e.g. red-listed-, indicator- and umbrella species) with stand and landscape level structural features that are indicative of disturbance and succession processes.

Keywords natural forest, dead wood, biological diversity, disturbances
Addresses *Brūmelis*, Faculty of Biology, University of Latvia, Kronvalda bulv. 4, Riga, LV-1586, Latvia; *Jonsson*, Department of Natural Sciences, Engineering and Mathematics, Mid Sweden University, Sundsvall, Sweden; *Kouki*, School of Forest Sciences, University of Eastern Finland, Joensuu, Joensuu; *Kuuluvainen*, Department of Forest Sciences, University of Helsinki, Finland; *Shorohova*, Saint-Petersburg State Forest Academy, Saint-Petersburg, Russia & Finnish Forest Research Institute, Vantaa Research Unit, Vantaa, Finland
E-mail guntis.brumelis@lu.lv
Received 17 November 2010 **Revised** 31 October 2011 **Accepted** 3 November 2011
Available at http://www.metla.fi/silvafennica/full/sf45/sf455807.pdf

1 Introduction

Throughout Europe, modern forest management has resulted in drastic changes in forest ecosystems (Esseen et al. 1997, Kuuluvainen 2002). The most notable changes are decline in the amount of dead wood, disappearance of very large diameter trees, and reduction of the complexity of the tree age and size structure of the stands. Together with the landscape-level fragmentation of natural forest habitats and loss of natural disturbances, these changes have caused remarkable changes to forest structure and function (Kouki et al. 2001, Auvinen et al. 2007, Kuuluvainen 2009).

Scientists, policy makers and non-governmental organizations have all recognized the importance of saving the remaining natural forests as a means to protecting forest biodiversity. In some areas this is not enough and active restoration of lost ecosystem characteristics is needed to secure biodiversity (Angelstam and Andersson 2001, Angelstam et al. 2004a). Of high priority is the protection of the remaining forests that have largely escaped the impact by man. This also includes forests that have in the past been managed non-intensively and often have regained or still retain natural structures and processes that support high biodiversity (e.g. Uotila et al. 2002, Lilja and Kuuluvainen 2005, Lommi et al. 2009, Josefsson et al. 2009).

To develop conservation and restoration programmes and to set measurable goals, it is important to define the concept of 'natural forest'. For example, if different countries aim at maintaining a specific proportion of their forests in natural stage, then some agreement and common idea of 'natural forest' are needed. However, this is often difficult, since naturalness can be defined in various ways and be regarded as a continuous and multidimensional variable (Peterken 1996). The gradient of forest naturalness is driven by a complex set of human influences of varying intensities, often difficult to quantify (Josefsson et al. 2009). Even without human influence natural forest exhibits a range of natural variability, driven by the disturbance-succession cycle (Landres et al. 1999, Keane et al. 2009). It is even more challenging to attempt to estimate the interaction between the natural range of variability and human impact.

The available literature contains a suite of definitions and concepts of natural forests (see a review by Rouvinen and Kouki 2008). In general, virgin and primeval forests are considered as unaffected by man (Peterken 1996). However, the concept of primeval forest has little besides philosophical relevance for countries, such as Denmark and Latvia, where all forests have at some time been harvested or had previous agricultural use. Some untouched areas still exist in Sweden and Finland. For instance, along the Scandinavian mountain range in Northern Sweden high altitude natural forests still remain as a relatively unbroken chain of well-connected forests (Bryant et al. 1997). Similarly, along the Finnish-Russian border some forests have retained their natural characteristics, but are typically small and scattered (Bryant et al. 1997, Aksenov et al. 2002), and the unprotected ones are under threat of harvest (Burnett et al. 2003).

On the other hand, in Russia, which supports the greater part of undisturbed forests in Europe (MPCFE 2007), the idea of primeval forest is more relevant and pristine forest landscapes larger than 50,000 ha have been mapped in a project by Global Forest Watch (Aksenov et al. 2002). In North America, the term old-growth forest is largely used (Bergeron and Harper 2009, Wirth et al. 2009), referring to late-successional forest stands dominated by old trees and largely unaffected by recent human or natural stand-replacing disturbances. Depending on the past history of forest continuity on a particular site, the terms ancient, primary and secondary forest have been applied (Peterken 1996).

Many definitions of natural forest used in Northern Europe overlook ecologically important factors, such as the past history, natural variability and spatial scale, and thus provide inadequate interpretation of the full range of variability in forest diversity (Rouvinen and Kouki 2008, Josefsson et al. 2009). Good examples are provided by the post-disturbance phases that are an essential component of natural boreal forest landscape (e.g. Kouki et al. 2001). For example, a young forest regenerating after a stand replacing fire of an old-growth forest is still a natural forest, containing e.g. large amounts of charred dead wood. However, definitions of "natural forest" that emphasize the age of forest or trees ("old-growth”) tend to completely ignore such post-disturbance forests. A major scientific as well as applied challenge is to identify valid proxies for forest naturalness so that inherent ecosystem dynamics are also taken into account; at least these dynamics should be recognized when such proxies are suggested.

The specific aims of this paper were to 1) review the usage of the concept of forest naturalness and its multi-dimensionality in northern European conditions, 2) propose a framework for defining forest naturalness based on distinguishing different dimensions of naturalness, and 3) discuss the possibility to develop more robust and general definitions and indicators of forest naturalness.

2 Approaches to Define Forest Naturalness in Northern Europe

The hitherto taken approaches to define forest naturalness can roughly be divided into three groups: 1) structure-based concepts, 2) species-based concepts, and 3) process-based concepts of natural forest. In the following, we discuss and evaluate each of these approaches and their usage in the north European context. Finally we discuss the interdependence of these three approaches in defining forest naturalness.

2.1 Structure-Based Concepts of Natural Forest

Forest structures indicating long-term absence of human influence have commonly been used to define degree of naturalness (Lloyd 1999, Norén et al. 2002, Uotila et al. 2002, Lindholm 2003, PEFC Finland 2009). These structures include old trees, variation in tree species composition (especially occurrence of large deciduous trees), multi-layered and multi-aged tree canopies, dead wood of varying sizes and decay stages, as well as signs of natural disturbances (fire, wind, insects, and fungi). Such forest structural components may serve as good proxies for habitat suitability of many species dependent on forests minimally disturbed by human (Angelstam et al. 2004a, Smirnova 2004). Visible and measurable structural patterns can easily be translated also to quantitative targets for forest management (Bütler et al. 2004, Villard and Jonsson 2009). As such they may also be modelled allowing for prediction of future habitat suitability for target species (Ranius and Kindvall 2004, Tikkanen et al. 2007) and analysing economical trade-offs (Jonsson et al. 2006, Tikkanen et al. 2007).

Definitions required for forest inventories and assessments over large regions (national and European) and by logging companies are typically based on structural stand-level forest characteristics that can be assessed relatively quickly. These definitions stress forest characteristics such as multi-agedness and diverse size structure of forest stands, presence of several trees species and canopy layers, high amounts and continuity of dead wood and generally the lack of major human influence on structures (e.g. Norén et al. 2002, Kriteerityöryhmä 2003, Metsäntutkimuslaitos 2009, MCPFE 2007, PEFC Finland 2009, Timonen et al. 2010). For example, in the 11th Finnish national forest inventory (VMI11 2009–2013) naturalness is estimated by three independent factors: structure of tree stand, dead wood continuity, and signs of human activity. For each of these three factors, three levels are separated: (semi) natural, slightly transformed, and clearly transformed forest (Metsäntutkimuslaitos 2009).

Another example of a recent large-scale assessment is provided by the evaluation of threatened habitat types in Finland (Tonteri et al. 2008ab), where forests were classified according to site type, successional stage and dominating species. Several quality attributes related to structural (e.g. amount of dead wood and occurrence of large diameter trees) as well as functional (e.g. signs of past disturbances) properties were used in the evaluation, in addition to quantitative changes in amounts of habitat types. In this work, e.g. the amount of dead wood had clearly defined threshold values (Tonteri et al. 2008ab, Kontula and Raunio 2009).

In Denmark, where the human footprint is profound and has a very long history, and the level of naturalness of forests is at the extreme low end, some definitions do not utilize structural elements indicative of natural processes (Møller 2000). Instead, the naturalness is assessed by time period of tree-layer continuity and natural regeneration, regardless of presence of forest management. In addition, designation as a Woodland Key Habitat in Denmark is based on evidence of any habitat type, structure or species that would be difficult to maintain under conventional forestry (Kitnæs and Forfang 2001).

Although being valuable from the applied perspective, using stand structures as the only proxy for naturalness has limitations. Even if thresholds of dead wood, snags, or tree ages are reached this does not guarantee that associated species are present (for recent reviews on dead wood thresholds, see Müller and Bütler 2010, and for deadwood volume and diversity, see Lassauce et al. 2011). For example, old forest in fragmented landscape in south-western Finland hosts less red-listed polypore species compared to similar forest stands in the eastern part of the country where much more natural forest remains (Tikkanen et al. 2009, Berglund et al. 2011). Thus, the species population dynamics as well as the disturbance processes that take place at landscape scale may lead to extinction of species from individual forest fragments (e.g. Paltto et al. 2006). On the other hand, the presence of some specific structural components is not necessarily a good proxy for naturalness in every site and area (Similä et al. 2006). For example, pristine forest stands at some successional stages may have relatively low volumes of dead wood and be even-aged (Shorohova and Soloviev 2002), which does not diminish their conservation value as an integral part of the natural variability of forest structure.

Besides stand-level structures also whole landscapes may have patterns that indicate naturalness (Mladenoff et al. 1993). With the aid of modern remote sensing techniques landscape patterns and their historical development can be addressed (e.g. Löfman and Kouki 2001) and modelled (e.g. Pennanen and Kuuluvainen 2002). The naturalness of landscapes at different scales can also be estimated by thresholds that estimate the functional amount of habitat for focal species (Mikusiński et al. 2001) indicative of overall diversity (Angelstam et al. 2003, 2004b, Roberge and Angelstam 2006). The definitions of forest naturalness, however, seem not to take into account landscape-level structures explicitly.

2.2 Species-Based Concepts of Natural Forest

The structure-based definitions described above are a specific case of species-based definitions: they focus on the main tree species and their characteristics. Species-based approaches have been widely used to identify forests that are of high conservation value, which intrinsically is associated with assessment of the actual naturalness of these forest ecosystems.

In Sweden, several groups of species have been listed as indicator species (signalarter) and used to indicate naturalness and other habitat qualities (Nitare 2000). In Finland, several polypore fungi species have been used to indicate the value and naturalness of old-growth forests (Kotiranta and Niemelä 1996). Red lists of endangered species of forest can be used to provide national guidelines for the management of biological diversity (Rassi et al. 2010), particularly when examined in connection with natural structural characteristics, such as dead wood (Hyvärinen et al. 2006, Tikkanen et al. 2006), or old age of the forests (Tikkanen et al. 2009). EU protected forest habitats (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora) include natural forests representing various stages of succession with slight or no human impact (EU 2003). The selection criteria include specialist species and typical plant communities, alongside criteria based on structures such as abundance of dead wood, variable tree size distribution and a number of generations of trees.

In Latvia, Lithuania and Estonia, for conservation purposes natural forest types (Woodland Key Habitats) are defined based on specialist species (fungi, bryophytes, lichens and invertebrates) that assumedly could not survive in stands managed for timber production, (Auzins and Ek 2001). A suite of structural characteristics such as coarse woody debris, trees with hollows and woodpecker signs are also included in the indicator-based definition. In Sweden and Finland, the woodland key habitats are sites that meet criteria based on structural characteristics, and where indicator species occur or are likely to occur (Pykälä 2007, Timonen et al. 2010).

2.3 Process-Focused Concepts of Natural Forest

In the following, disturbance and successions are referred to as key ecological processes of natural forest (Korpilahti and Kuuluvainen 2002). However, earlier definitions of natural forests were based on the Clementsian static climax community concept (Clements 1932), which ignores the prevalence of disturbances and which therefore has largely been rejected by modern ecologists. However, the traditional climax forest community concept , which is still used in scientific literature in a diluted form denoting 'old-growth' (e.g. Volkov 2003), probably formed a background for ideas of proposed higher conservation value of late-successional forests. These forests undoubtedly have priority in conservation of biological diversity, but nevertheless they only represent a subset of forests with high natural values.

The natural range of variability in forest dynamics and properties at different scales has recently been emphasized (Landres et al. 1999, Kuuluvainen 2002, Keane et al. 2009). In Northern Europe and Russia, a view of virgin forest as uneven-aged and dynamic was presented at the very beginning of development of forest science (Shorohova et al. 2009, Brūmelis et al. 2011, Hytteborn and Verwijst 2011, Jonsson and Hofgaard 2011). The studies considered age structure as indicative of successional processes within the forest community (Dyrenkov 1984).

In Russia, Bogushevsky already in 1912 argued that a primeval forest (korennoj les) state is characterized by heterogeneity of trees in age and size, implying that the dynamics of natural forest takes place at the scale of small gaps or patches. He also warned of extrapolating results acquired from one site to all sites and tree species, thus emphasizing the uniqueness of ecological context. Morozov (1912) proposed that primeval forests are in a shifting equilibrium state that is continually changing due to multiple pathways of succession. In Sweden, the storm gap theory of virgin spruce (*Picea abies* (L.) H. Karst.) forest regeneration and dynamics was presented by Sernander (1936). Thus, the basic ideas of shifting mosaic steady state dynamics (sensu Bormann and Likens 1979) and mosaic-cycle of forests (Remmert 1991) were expressed already in the early literature.

The importance of natural disturbances in affecting and maintaining the spatial pattern of forest landscape was indicated in some early studies. For example, Ivashkevich (1915) described the pattern of a virgin pine (*Pinus sibirica* Du Tour) forest in Siberia. The main features of a virgin forest (devstvennyj les) included unevenagedness, periodicity of peaks in regeneration, very slow growth of the trees during the first 100 years after a major disturbance, and patchiness in spatial distribution. Natural disturbances (wind, fire or insect induced) were assumed to lower the predominance of coniferous forests and convert them into mixed woods. Thus, the importance of natural disturbances in affecting and maintaining the spatial landscape forest pattern was obvious in these early studies.

Based on extensive literature reviews, three main types of disturbance regimes have been distinguished for boreal forests (Angelstam 1998, Angelstam and Kuuluvainen 2004, Kuuluvainen 2009, Shorohova et al. 2009): 1) stand replacing disturbances followed by even-aged stand development (with proposed sub-types of monodominant and compositional change dynamics (Shorohova et al. 2009), 2) partial disturbances creating cohort stand dynamics and 3) fine-scale gap dynamics. Each of these stand dynamics types create specific stand structures, characterized by directional successional change and successional stages (type 1), more or less fluctuating dynamics (type 2), or a shifting steady state dynamics (type 3). Incorporating the dynamic features created by disturbance and successional processes means that deductions of naturalness from structure have to be carried out in context of the disturbance-successional cycle of the forest in concern. This also poses requirements to observational scale, as the full range of forest dynamics usually only take place at landscape or even regional scales.

2.4 Interdependence of the Components of Natural Forests

It becomes evident from the discussion above that forest naturalness has been and can be defined at different levels and using variable criteria, depending on the actor and the needs (see also Rouvinen and Kouki 2008). However, it appears that usually the definitions are clearly interdependent and many examples of interrelationships between forest structures, processes and species can be provided. To take an example, a natural dry Scots pine (*Pinus sylvestris* L.) forest, with a long history of cohort dynamics driven by recurrent surface fires, is identified by a multi-aged structure of separate cohorts (e.g. Kuuluvainen et al. 2002), i.e., the presence of the process can be deduced from the structure. This represents the well-known relationship between structure and process in forest ecosystems (Bormann and Likens 1979). The coarse woody debris profile (Stokland 2001) reflects disturbance history and represents another structure-process interrelationship, which can serve as a 'dynamic target' for conservation and restoration of coarse woody debris (Harmon 2001).

The importance of coarse wood debris for many threatened species is well known (Siitonen 2001, Jonsson et al. 2005, Tikkanen et al. 2006). The quantity of structures needed to support biodiversity can be estimated (Müller and Bütler 2010, Lassauce et al. 2011). For example, it is estimated that 18 m^3 ha^{-1} snag volume is needed in an area of 100 ha for presence of three-toed woodpecker, *Picoides tridactylus* (L.) (Bütler et al. 2004). It has been suggested at least 20 m^3 ha^{-1} is required for threatened polypore fungi to occur, but the threshold will differ depending on forest type and availability of dead wood in the surrounding landscape (Penttilä et al. 2004, Junninen and Komonen 2011).

Also the presence of species can indicate a past history of natural processes. On fire scarred and charred pine stumps lichens of the genus *Hypocenomyce* may be present for centuries after the fire. Yet their presence indicates a certain level of continuity in forest fires. However, the presence of structural indicators of natural processes does not always mean that biodiversity will be high. For example, a large forest stand with abundant dead wood in intensively managed Southern Swedish landscape does not host as high biological diversity as present in intact forest landscapes of Russia, since few forests in Fennoscandia have escaped management (e.g. Kouki et al. 2001, Löfman and Kouki 2001). In fragmented landscapes where stands with sufficient quality are in short supply, demographic and environmental stochasticity can lead to local species extinctions (Lande et al. 2003) and immigration/emigration and regional stochasticity can lead to extinction of metapopulations at a landscape scale (Hanski 1991). Thus, the landscape scale is important in inventory of natural forests, if used to assess biological diversity (Angelstam et al. 2004b, Penttilä et al. 2004, Rouvinen and Kouki 2008).

Estimates can be made of expected species richness in a landscape based on species-area relationships (MacArthur and Wilson 1967, Tikkanen et al. 2009, Wallenius et al. 2010). Thus, on a landscape scale, the relationships between species diversity and extent of remaining natural forest can be tested. Population sizes of target species can also be estimated for landscapes by building habitat suitability models (Tikkanen et al. 2007). Forest habitat demands have been, for example, determined for capercaillie, *Tetrao urogallus* L. (Suchant and Braunisch 2004); black grouse, *Tetrao tetrix* L. (Angelstam 2004); hazel grouse, *Bonasa bonasia* (L.) (Jansson et al. 2004); Siberian jay, *Perisoreus infaustus* (L.) (Edenius et al. 2004) and Siberian flying squirrel, *Pteromys volans* (L.) (Reunanen et al. 2004) and these have been used to define management targets (Tikkanen et al. 2007, Villard and Jonsson 2009). It then seems reasonable to expect that national forest inventory data collected on proportion of area of natural forests and structures known to enhance biological diversity would be related to the existing population sizes of specialist species (cf. Hottola et al., in prep.).

3 Problems in Definitions and Data Compatibility

At the European level quantitative and qualitative information of the state and management of forests is collected nationally using Ministerial Conference on the Protection of Forests in Europe MCPFE (UNECE/FAO) criteria and indicators (MCPFE 2007). The MCPFE Criterion 4 on maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems includes the indicators tree species composition, regeneration, *naturalness*, introduced tree species, deadwood, genetic resources, landscape pattern, threatened forest species and protected forests.

In the MCPFE (2007) inventory, forests undisturbed by man are defined as showing natural forest features, such as natural tree composition, occurrence of dead wood, natural age structure and natural regeneration processes, the area of which is large enough to maintain its natural characteristics, and no known human intervention or long enough ago to have allowed the natural species composition and processes to have become re-established. At the other end of the scale, plantations are stands of introduced species or intensively managed stands of indigenous species, with one or two species, even age and regular spacing. Semi-natural forests are considered as those that are not natural, nor plantations. Modified natural forests are a subclass of semi-natural forests that are near natural. They show characteristics of forests undisturbed by man, such as natural forest dynamics, but which have clear indication of human activities.

As the definition of naturalness lack thresholds, interpretation of the definition varies between countries. For example, using the MCPFE definitions, Latvia has reported that the proportion of natural forest area is 0.5% of total forest area, while 7.4% was reported by its neighbour Estonia (MCPFE 2007). Similar differences between neighbours also are apparent for Finland (3.8%) and Sweden (17.6%). It seems unlikely that such large differences in estimated area of natural forests undisturbed by man would exist if assessed by standard methods using the same definitions. Given that Estonia, Latvia and Lithuania reported high coverage of modified natural forest (63%, 79% and 74%, respectively), it seems odd that Fennoscandian countries appear to lack this subclass of semi-natural forests. Thus, standardization of the definition of natural forest with threshold values for structures is clearly needed.

The MCPFE inventory indicator list includes number of threatened forest species. Such lists are aimed on a national level to direct forest management towards conservation of biological diversity. However, the lists of threatened species differ between countries due to biogeographical differences, past legacy of industrial forestry, and level of research conducted. Thus, it remains unclear how numbers of threatened species could be related to forest naturalness. We suggest that the assessment of naturalness of forests could include indicator lists of forest specialist species. The EC forest specialist bird indicator list (EEA 2004) is a step in this direction, but the species included in this list are mostly widespread species that can successfully utilize urban and recreation forest, such as blackbird (*Turdus merula* L.), Great Tit (*Parus major* L.) and Wren (*Troglodytes troglodytes* (L.)). The EC specialist forest bird list does not include Capercaillie, Three-toed woodpecker and Black woodpecker (*Drycopus martius* (L.)), which have more specific habitat demands for old coniferous forest (Virkkala and Rajasärkkä 2007). Woodpecker species, many of which have become extinct or form relict populations in some northern Europe countries, have in Poland been shown to be good/sensitive indicators of overall bird diversity (Mikusiński et al. 2001). The woodpecker species also differ in preferred habitat, eg. coniferous versus deciduous forest. Thus, separate lists for biogeographical regions are needed, and also for different forest types (eg. coniferous, deciduous and mixed), as habitat preference differs largely between species. In this respect differentiation of mean dead wood volumes by forest type (coniferous, mixed, deciduous) is also needed to establish relationships with population sizes of specialist species using different habitats.

4 An Approach Based on Three Dimensions of Forest Naturalness

As becomes evident from the previous discussion, forest naturalness is a dynamic entity encompassing different dimensions at any given point of time. Thus, there is a quest for approaches that are able to integrate different dimensions of forest naturalness. Ideally, a definition of natural forests should incorporate the idea of natural and human-induced variability of ecosystems while addressing the main dimensions of naturalness. These dimensions include, as discussed above, forest structure, processes and species composition (Angelstam 1998, Kuuluvainen 2002, Rouvinen and Kouki 2008). Although ecologically linked, their combinations can vary somewhat independently within wide limits due to the variability of human impact, and natural disturbance and successional dynamics (Fig. 1).

Criteria covering forest structure, processes and species composition can be derived to quantitatively rank naturalness of woodlands within this framework (Trass et al. 1999). Table 1 attempts to provide qualitative thresholds for the different dimensions of naturalness in European forests. Primeval forests undisturbed by man show clear signs of natural disturbance, such as fire and windthrow, which are reflected by forest structures (eg. dead wood and large diameter trees), as well as support the natural species in viable populations (Table 1, see forest 1 in Fig. 1 and Fig. 2a). A small coniferous forest stand in a fragmented landscape might still contain abundant natural structures, but the full ranges of succession processes would be limited by fragment size, and the species pool would be affected by reduced connectivity (see forest 2 in Fig. 1 and Fig. 2b), leading to risk of local and eventually regional extinction (Hanski 1991, Lande 2003).

A secondary forest stand that developed on an alluvial floodplain previously used for hay cutting in the mid 1900's in eastern Europe might support high biological diversity of woodpeckers, due to an abundance of structural elements, such as large diameter aspen (*Populus tremula* L.) with age close to its maximum, and CWD. Thus, a stand of pioneer species such as aspen can develop natural structural features over a relatively short period of time (Bergeron and Harper 2009), but it may not rank high in naturalness on the dimension of processes. Natural processes can be reintroduced in a landscape, for example by fire. However, if there are no large diameter dead trees that typically provide large amounts of dead wood for several specialist post-disturbance species, the initial post-fire succession may fail to attract several early-successional species (Muona and Rutanen 1994, Hyvärinen et al. 2005, 2006). Nevertheless, such a forest would rank high on the process scale (see forest 3 in Fig. 1 and Fig 2c). As an extreme case, a planted and thinned pine (see forest 4 in Fig. 1 and Fig. 2d) or spruce stand would be lacking in structures, processes and species.

We argue that information on the dimensions of naturalness of stands at variable scales can aid in developing strategies for forest management. For example, in the boreo-nemoral region (Sjörs 1963), which has undergone a long legacy of industrial forestry and land-use conversion to agriculture, it might be expected that the forests with highest value for conservation of biological diversity are mesic woodland with an abundance of deciduous species (Lõhmus et al. 2005). Woodland key habitats, which are forests that rank the highest in naturalness within the region, generally lack the pre-industrial structure of the past primeval forest (Ericsson et al. 2005, Jönsson et al. 2009). Thus, in the south boreal region, the appropriate strategies for management might be aimed to ensure temporal and spatial continuity of old deciduous trees, particularly aspen (Kouki et al. 2004). It would be equally important to retain a larger component of coniferous

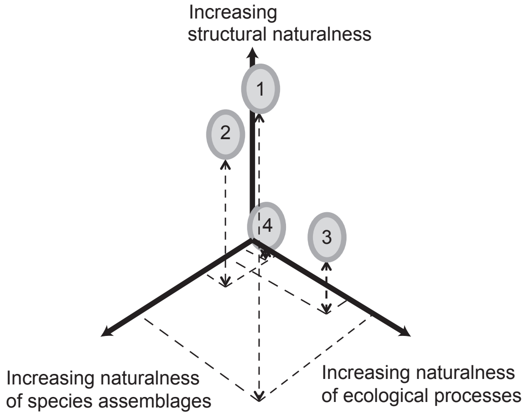

Fig. 1. An illustration of four potential states and combinations of forest naturalness in the structure-species-processes space (naturalness increases with the axes). Forest 1 represents a natural forest landscape with all natural species and processes fully incorporated (see Fig. 2a). Forest 2 represents an isolated small forest fragment with still rather natural structures but too small to sustain viable populations or natural disturbance and successional dynamics (see Fig. 2b). Forest 3 could represent a case where the natural process has been introduced but the structures and species have not yet been rehabilitated (see Fig. 2c). Forest 4 is an artificial forest with very low degree of naturalness on any of the axis (see Fig. 2d).

Fig. 2. Examples of states and combinations of forest naturalness in the structure-species-processes –space (see Fig. 1). (a). Pristine taiga forest in the Dvina-Pinega natural forest massif in the Archangelsk region; this is one of the largest intact boreal forest areas in northern Europe. All natural processes, structures and species are intact and present. Corresponds to forest 1 in Fig. 1. (b). Susimäki is a small (50 hectares) protected forest fragment in southern Finland. Many of the natural structures are still present, but the species pool has deteriorated and the full range of natural disturbance and successional dynamics cannot take place in such a small area. Corresponds to forest 2 in Fig. 1. (c). An example of forest where the process has been introduced (fire and post-fire succession with deciduous trees), but where the structures and species do not yet correspond to a natural state. A restored site using cuttings and fire in the Evo area in southern Finland (for details see Vanha-Majamaa et al. 2007). Corresponds to forest 3 in Fig. 1. (d). A planted and thinned young pine forest in southern Finland scores low in all three dimensions of forest naturalness (see forest 4 in Fig. 1). (Photos by Timo Kuuluvainen).

forests that rank highest on the processes dimension, as they likely have a higher capacity to improve on the naturalness scale over a longer period. Both of those aims should involve management targets (e.g. amounts of CWD and large diameter trees) at stand and landscape scales. In the northern boreal region, where there are still large expanses of forest with minimal human disturbance, the aim of management could be to maintain natural disturbance regimes over large landscapes. In regions with less impact from industrial forestry, the aims can thereby be more ambitious and at a larger scale (Angelstam et al. 2004b).

Table 1. Assessment of naturalness based on components of structures, species and processes.

Degree of naturalness of component	Structures	Species	Processes
3	Abundant* dead wood, all age classes represented, large trees* and the full spectrum of typical tree species for the habitat represented	All typical species occurring in viable populations	Original hydrology, natural levels of herbivory, signs of natural disturbances (fire, windthrow etc)
2	Loss of one of the components	Decline in several* species and loss of single species, habitat specialists	Loss of some process
1	Loss of several* of the components above but a well established stand of native tree species	Decline among many* common species and loss of most habitat specialists	Loss of several* processes for extended time periods
0	Clearcut area, or even-aged forest planted with exotic tree species	Many* common species missing and occurrence (dominance) of non-typical and invasive species	Completely transformed ecosystem with human controlled cultivation

* To be defined in relation to natural baseline for the forest ecosystem at hand.

Quantitative criteria for ranking of degrees of naturalness (Table 1) are clearly needed. Criteria related to specific quantitative variables such as amounts of dead wood and presence of indicator species are promising. However, these barely cover the conceptual framework that is required to sufficiently address the naturalness that encompasses several aspects in forest ecosystems. As shown above (Fig. 1), evaluating and ranking of the structures, species and processes components separately, as opposed to a summed score, can be used to set more specific and representative priorities in practical conservation. This should enable the use of limited resources of conservation more cost-effectively. A generally applicable method for the whole boreal region seems an unattainable goal at the moment. Due to inherent differences in forest ecosystems in different regions any quantitative criteria and indicators need to be elaborated for individual biogeographic regions at landscape and stand scales, and also for different forest types. Acknowledging this diversity would allow setting conservation performance targets at long-term, regional and management levels, which will differ depending on ambition and the past history of forest use (Angelstam et al. 2004b).

Acknowledgements

This paper builds on discussions during several meetings of the Prifor-network. Financial support was obtained from the Nordic Forest Research Cooperation (SNS). We are grateful to both SNS and all participants at these meeting for providing opportunity to explore different facets of North European forests. The comments of two anonymous reviews and the associate editor helped to improve the manuscript.

A Marie Curie Incoming Fellowship within the 7th European Framework Programme (236030) to Ekaterina Shorohova is greatly appreciated.

All authors contributed equally to writing this publication. Guntis Brūmelis also coordinated the collaborative process.

References

Aksenov, D., Dobrynin, D., Dubinin, M., Egorov, A., Isaiev, A., Karpachevskiy, M., Laestadius, L., Potapov, P., Purekhovskiy, A., Turubanova, S. & Yaroshenko. 2002. Atlas of Russia's intact forest landscapes. Global Forest Watch, Moscow. 32 p. Available at: http://www.globalforestwatch.org/common/russia/Atlas_report_pdfs/Cover-032.pdf. [Cited 21 Oct 2010].

Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9(4): 593–602.

— 2004. Habitat thresholds and effects of forest landscape change on the distribution and abundance of black grouse and capercaillie. Ecological Bulletins 51: 173–187.

— & Andersson, L. 2001. Estimates of the needs for forest reserves in Sweden. Scandinavian Journal of Forest Research Supplement 3: 38–51.

— & Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: A European perspective. Ecological Bulletins, 51: 117–136.

— , Bütler, R., Lazdinis, M., Mikusiński, G. & Roberge, J.-M. 2003. Habitat thereseholds for focal species at multiple scales and forest biodiversity conservation – dead wood as an example. Annales Zoologici Fennici 40(6): 473–482.

— , Boutin, S., Schmiegelow, F., Villard, M-A., Drapeau, P., Host, G., Innes, J., Isachenko, G., Kuuluvainen, T., Mönkkönen, M., Niemelä, J., Niemi, G., Roberge, J-M., Spence, J., & Stone, D. 2004a. Targets for forest biodiversity conservation – a rationale for macroecological research and adaptive management. Ecological Bulletins 51: 487–509.

— , Dönz-Breuss, M. & Roberge, J.-M. 2004b. Targets and tools for the maintenance of forest biodiversity – an introduction. Ecological Bulletins 51: 11–24.

Auvinen, A.-P., Hildén, M., Toivonen, H., Primmer, E., Niemelä, J., Aapala, K., Bäck, S., Härmä, P., Ikävalko, J., Järvenpää, E., Kaipiainen, H., Korhonen, K.T., Kumela, H., Kärkkäinen, L., Lankoski, J., Laukkanen, M., Mannerkoski, I., Nuutinen, T., Nöjd, A., Punttila, P., Salminen, O., Söderman, G., Törmä, M. & Virkkala, R. 2007. Evaluation of the Finnish national biodiversity action plan 1997–2005. Monographs of Boreal Environmental Research 29. 54 p.

Auziņš, R. & Ek, T. 2001. Woodland key habitats in Latvia. Tools in Preserving biodiversity in nemoral and boreonemoral biomes of Europe. NACONEX. Available at: http://www.pro-natura.net/naconex/news5/naco-rep.htm#E1. [Cited 17 Nov 2010].

Bergeron, Y. & Harper, K.A. 2009. Old-growth forests in the Canadian Boreal: thre exception rather than the rule. In: Wirth C., Gleixner G. & Heimann M. (eds.). Old-growth forests: function, fate and value. Ecological Studies 207. Springer New York, Berlin, Heidelberg. p. 285–300.

Berglund, H., Hottola, J., Penttilä, R. & Siitonen, J. 2011. Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. Ecography. (In press).

Bogushevsky, V. 1912. [Apropos of article by Rozhkov "Forest inventory in the northern forests"]. Po povodu statyi Rozhkova "K ustroystvu severnykh lesov". Lesnoy Journal 2–3: 299–310. (In Russian).

Bormann, F.H. & Likens G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag New York Inc. 253 p.

Brūmelis, G., Dauškane, I., Ikauniece, S., Javoiša, B., Kalviškis, K., Madžule, L., Matisons, R., Strazdiņa, L., Tabors, G., & Vimba, E. 2011. Dynamics of natural hemiboreal woodland in the Moricsala Reserve, Latvia. The studies of K.R. Kupffer revisited. Scandinavian Journal of Forest Research 26(S10): 54–64.

Bryant, D., Nielsen, D. & Tangley, L. 1997. The last frontier forests: ecosystems & economies on the edge. World Resources Institute. 42 p.

Burnett, C., Fall, A., Tomppo, E. & Kalliola, R. 2003. Monitoring current status and trends in boreal forest land use in Russian Karelia. Conservation Ecology 7(2): 8. [Online document]. Available at: http://www.consecol.org/vol7/iss2/art8/. [Cited 11 Nov 2010].

Bütler, R., Angelstam, P. & Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woodpecker Picoides tridactylus. Ecological Bulletins 51: 219–232.

Clements, F.E. 1932. Nature and structure of the climax. Journal of Ecology 24: 252–284.

Dyrenkov, S.A. 1984. [Structure and dynamics of taiga spruce forests]. Struktura i dinamika tayezhnykh el'nikov. Nauka Publ., Leningrad. 176 p. (In Russian).

Edenius, L., Brodin, T. & White, N. 2004. Occurrence of Siberian jay Perisoreus infaustus in relation to amount of old forest at landscape and home range scales. Ecological Bulletins 51: 241–247.

Ericsson, T.S., Berglund, H. & Östlund, L. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biological Conservation 122(2): 289–303.

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

EU. 2003. Natural old boreal and hemiboreal forests; The interpretation manual of European Union habitats – EUR25. Available at: http://www.forestbiota.org/docs/eee_HabitatClassificationForestBIOTA.pdf. [Cited 21 Oct 2010].

EEA. 2004. CSI specification – species diversity. Available at: http://www.eea.europa.eu/data-and-maps/indicators/species-diversity. [Cited 17 Nov 2010].

Hanski, I. 1991. Single species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42(1–2): 17–38.

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

Hottola, J., Penttilä, R., Siitonen, J., Tomppo, E. & Ovaskainen, O. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented forests. Manuscript.

Hytteborn, H. & Verwijst, T. 2011. The importance of gaps and dwarf trees in the regeneration of Swedish spruce forests, the origin and content of Sernander's (1936) gap dynamics theory. Scandinavian Journal of Forest Research 26(S10): 3–16.

Hyvärinen, E., Kouki, J., Martikainen, P. & Lappalainen, H. 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. Forest Ecology and Management 212: 315–332.

— , Kouki, J. & Martikainen, P. 2006. Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. Conservation Biology 20: 1711–1719.

Ivashkevich, B.A. 1915. [Manchurian forest. Description for the Eastern forest concession of the community of Chinese-Eastern Railway with the plan of economy]. Manchzhurskiy les. Opisaniye Vostochnoy lesnoy kontsessii obschestva Kitaisko-Vostochnoy zheleznoy dorogi i plan khozyaistva na neyo. Issue 1. Harbin. (In Russian).

Jansson, G., Angelstam, P., Åberg, J. & Swenson, J.E. 2004. Management targets for the conservation of hazel grouse in boreal landscapes. Ecological Bulletins 51: 259–264.

Jonsson, B.G. & Hofgaard, A. The structure and regeneration of high altitude Norway spruce forests – a review of Arnborg (1942, 1943). Scandinavian Journal of Forest Research 26(S10): 17–24.

— , Kruys, N. & Ranius, T. 2005. Lessons from species ecology for dead wood management at a landscape scale. Silva Fennica 39(2): 289–309

Jonsson, M., Ranius, T., Ekvall, H., Bostedt, G., Dahlberg, A., Ehnström, B., Nordén, B., Stokland, J.N. 2006. Cost-effectiveness of silvicultural measures to increase substrate availability for red-listed wood-living organisms in Norway spruce forests. Biological Conservation 127(4): 443–462.

Jönsson, M.T., Fraver, S. & Jonsson, B.G. 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. Journal of Vegetation Science 20(1): 91–106.

Josefsson, T., Hörnberg, G. & Östlund, L. 2009. Long-term human impact and vegetation changes in a boreal reserve: implications for the use of protected areas as ecological references. Ecosystems 12(6): 1017–1036.

Junninen, K. & Komonen, A. 2011. Conservation ecology of boreal polypores: a review. Biological Conservation 144 (1): 11–20.

Keane, R.E., Hessburg, P.F., Landres, P.B. & Swanson, F.J. 2009. The use of historical range and variability (HRV) in landscape management. Forest Ecology and Management 258(7): 1025–1037.

Kitnæs, K. & Forfang, A.-S. 2001. Two woodland habitat mapping methods and their applications. Tools in Preserving biodiversity in nemoral and boreonemoral biomes of Europe. NACONEX. Available at: http://www.pro-natura.net/naconex/news5/naco-rep.htm#E1. [Cited 17 Nov 2010].

Kontula, T. & Raunio, A. 2009. New method and criteria for national assessments of threatened habitat types. Biodiversity and Conservation 18(14): 3861–3876.

Korpilahti, E. & Kuuluvainen, T. (eds.). 2002. Disturbance dynamics in boreal forests: defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36(1). 447 p.

Kotiranta, H. & Niemelä, T. 1996. Uhanalaiset käävät Suomessa. Summary: Threatened polypores in Finland. 2nd revised edition. Suomen Ympäristökeskus & Edita, Helsinki. 184 p.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research Supplement. 3: 27–37.

— , Arnold, K. & Martikainen, P. 2004. Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. Journal for Nature Conservation 12(1): 41–52.

Kriteerityöryhmä. [Working group on the conservation biological criteria for forest protection in southern Finland]. 2003. Etelä-Suomen metsien monimuotoisuusohjelman luonnonsuojelubiologiset kriteerit. [Conservation biological criteria for forest protection in southern Finland]. Suomen ympäristö 634: 1–72. (In Finnish).

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.

— 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. Ambio 38(6): 309–315.

— , Mäki, J., Karjalainen, L. & Lehtonen, H. 2002. Tree age distributions in old-growth forest sites in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 169–184.

Lande, R., Engen, S. & Sæther, B.-E. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press. Oxford. 212 p.

Landres, P.B., Morgan, P. & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9(4): 1179–1188.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget C. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11(5): 1027–1039.

Lilja, S. & Kuuluvainen, T. 2005. Structure of old Pinus sylvestris dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Silva Fennica 39(3): 407–428.

Lindholm, T. 2003. Method of old-growth forest inventory in Finland. The Finnish Environment 485. p. 50–53.

Lloyd, S. (ed.). 1999. The last of the last: the old-growth forests of boreal Europe. Taiga Rescue Network. Jokkmokk, Sweden. 67 p. + maps.

Löfman, S. & Kouki, J. 2001. Fifty years of landscape transformation in managed forests of southern Finland. Scandinavian Journal of Forest Research 16(1): 44–53.

Lõhmus, A., Lõhmus, P., Remm, J. & Vellak, K. 2005. Old-growth structural elements in a strict reserve and commercial forest in Estonia. Forest Ecology and Management 216(1–3): 201–215.

Lommi, S., Berglund, H., Kuusinen, M. & Kuuluvainen, T. 2009. Epiphytic lichen diversity in late-successional Pinus sylvestris forests along local and regional forest utilization gradients in eastern boreal Fennoscandia. Forest Ecology and Management 259(5): 883–892.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ. 224 p.

MCPFE. 2007. State of Europe's forests 2006. The MCPFE report on sustainable forest management in Europe. Jointly prepared by the MCPFE Liason Unit Warsaw, UNEC for Europe and FAO. 263 p. Available at: http://www.foresteurope.org/filestore/foresteurope/Publications/pdf/state_of_europes_forests_2007.pdf. [Cited 22 Oct 2010].

Metsäntutkimuslaitos. 2009. Valtakunnan metsien 11. inventointi (VMI11). Maastotyön ohjeet 2009. Koko Suomi. Moniste. 120 s. (In Finnish).

Mikusiński, G., Gromadzki, M. & Chylarecki, P. 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology 15(1): 208–217.

Mladenoff, D.J., White, M.A. & Pastor, J. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3(2): 294–306.

Møller, P.F. 2000. The Danish strategy for natural forests – background, realisation and perspectives. Eesti Metsakaitsealade Võrgustiku Rajamine. University of Tartu, Estland. p. 6–12. Available at: http://www.geus.dk/departments/quaternary-marine-geol/research-themes/env-cli-res-gr-forest-def-uk.htm. [Cited 4 July 2011].

Morozov, G.F. 1912. [The doctrine about forest]. Ucheniye o lese. Saint Petersburg. 83 p. (In Russian).

Müller, J. & Bütler, R. 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129(6): 981–992.

Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31: 109–121.

Nitare, J. (ed.). 2000. Signalarter. Skogsstyrelsen, Jön-

köping. (In Swedish).
Norén, M., Nitare, J., Larsson, A., Hultgren, B. & Bergengren, I. 2002. Handbok för inventering av nyckelbiotoper. Skogsstyrelsen, Jönköping. (In Swedish).
Paltto, H., Nordén, B., Götmark, F. & Franc, N. 2006. At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? Biological Conservation 133(4): 442–454.
PEFC. Finland. 2009. Criteria for group certification; level of a forestry centre or forest management association, PEFC FI 1002: 20092009. Available at: http://www.pefc.fi/media/Standardit%202008_09/PEFC%20FI%201002_2009%2009112009.pdf. [Cited 13 Sept 2010].
Pennanen, J. & Kuuluvainen, T. 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. Forest Ecology and Management 164(1–3): 157–175.
Penttilä, R., Siitonen, J. & Kuusinen, M. 2004. Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. Biological Conservation 117(3): 271–283.
Peterken, G.F. 1996. Natural woodland: ecology and conservation in northern tmeperate regions. Cambridge University Press, Cambridge. 522 p.
Pykälä, J. 2007. Implementation of Forest Act habitats in Finland: Does it protect the right habitats for threatened species? Forest Ecology and Management 242(2–3): 281–287.
Ranius, T. & Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation 119(1): 51–59.
Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. (eds.). The 2010 Red List of Finnish species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki. 685 p.
Remmert, H. 1991. The mosaic-cycle concept of ecosystems. An overview. In: Remmert, H. (ed.). The mosaic-cycle concept of ecosystems. Ecological Studies 85. Springer Verlag, Berlin, Heidelberg, New York. p. 1–21.
Reunanen, P., Mönkkönen, M., Nikula, A., Hurme, E. & Nivala, V. 2004. Assessing landscape thresholds for the Siberian flying squirrel. Ecological Bulletins 51: 277–286.
Roberge, J-M. & Angelstam, P. 2006. Indicator species among resident forest birds – a cross-regional evaluation in northern Europe. Biological Conservation 130(1): 134–147.
Rouvinen, S. & Kouki, J. 2008. The natural northern European boreal forests: unifying the concepts, terminologies, and their application. Silva Fennica 42(1): 135–146.
Sernander, R. 1936. [The primitive forests of Granskär and Fiby]. Granskär och Fiby urskog: en studie över stormluckornas och marbuskarnas betydelse i den svenska granskogens regeneration. Acta Phytogeographica Suecica 8: 1–232. (In Swedish).
Shorohova, E., Kuuluvainen, T., Kangur, A. & Jõgiste, K. 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. Annals of Forest Science 66(2): article 201.
Shorohova, E.V. & Soloviev, V.A. 2002 Living and dead wood carbon dynamics in pristine boreal Norway spruce forests subjected to windthrow disturbances. In: Shaw S. & Apps M. (eds.). The role of boreal forests and forestry in the global carbon budget. 8–12 May, 2000. Edmonton, Alberta, Canada. p. 179–194.
Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.
Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.L. & Huhta, E. 2006. Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? Ecological Indicators 6(4): 686–700.
Sjörs, H. 1963. Amphi-Atlantic zonation, nemoral to Arctic. In: Löve, Á. & Löve, D. (eds.). North Atlantic biota and their history. The Macmillan Company, New York. p. 109–125.
Smirnova, O.V. 2004. (ed.). [Eastern-European forests: the history in Holocene and modern state]. Vostochno–Evropejskiye lesa: Istoria v golotsene i sovremennost'. Volume 1. Nauka publ., Moscow. 479 p. (In Russian).
Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins 49: 71–83.
Suchant, R. & Braunisch, V. 2004. Multidimensional habitat modelling in forest management – a case study using capercaillie in the Black Forest, Germany. Ecological Bulletins 51: 455–469.

Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annales Zoologici Fennici 43(4): 373–383.

— , Heinonen, T., Kouki, J. & Matero, J. 2007. Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: Cost-effective measures for multi-species conservation. Biological Conservation 140(3–4): 359–372.

— , Punttila, P. & Heikkilä, R. 2009. Species-area relationships of red-listed species in old boreal forests: a large scale data analysis. Diversity and Distributions 15(5): 852–862.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. & Mönkkönen, M. 2010. Woodland key habitats in northern Europe: concepts, inventory and protection. Scandinavian Journal of Forest Research 25(4): 309–324.

Tonteri, T., Ahlroth, P., Hokkanen, M., Lehtelä, M., Alanen, A., Hakalisto, S., Kuuluvainen, T., Soininen, T. & Virkkala, R. 2008a. [Assessment of threatened habitat types in Finland – Part 1: Results and basis of assessment]. Metsät. In: Raunio, A. & Kontula, T. (eds.). Suomen luontotyyppien uhanalaisuus – osa 1: Tulokset ja arvioinnin perusteet. p. 111–132.

— , Ahlroth, P., Hokkanen, M., Lehtelä, M., Alanen, A., Hakalisto, S., Kuuluvainen, T., Soininen, T. & Virkkala, R. 2008b. [Assessment of threatened habitat types in Finland – Part 2: Habitat type descriptions]. Metsät. In: Raunio, A. & Kontula, T. (eds.). Suomen luontotyyppien uhanalaisuus – Osa 2: Luontotyyppien kuvaukset. p. 257–334.

Trass, H., Vellak, K. & Ingerpuu, N. 1999. Floristical and ecological properties for identifying of primeval forests in Estonia. Annales Botanici Fennici 36(1): 67–80.

Uotila, A., Kouki, J., Kontkanen, H. & Pulkkinen, P. 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecology and Management 161(1–3): 257–277.

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T & Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. Forest Ecology and Management 250(1–2): 77–88.

Villard, M.-A. & Jonsson, B.G. (eds.). 2009. Setting conservation targets for managed forest landscapes. Conservation Biology Series, Cambridge University Press. 411 p.

Virkkala, R. & Rajasärkkä, A. 2007. Uneven regional distribution of protected areas in Finland: consequences for boreal forest bird populations. Biological Conservation 134(3): 361–371.

Volkov, A.D. 2003. [The bio-ecological basics of exploitation of spruce forests in the north-west of taiga zone of Russia]. Bioekologicheskye osnovi ekspluatatsii el'nikov severo-zapada taezhnoy zony Rossii. Petrozavodsk, Karelian Science Centre, Russian Academy of Sciences. 250 p. (In Russian).

Wallenius, T., Niskanen, L., Virtanen, T., Hottola, J., Brūmelis, G, Angervuori, A., Julkunen J. & Pihlström, M. 2010. Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. Ecological Indicators 10(6): 1093–1101.

Wirth, C., Messier, C., Bergeron, Y., Frank, D. & Fankhänel, A. 2009. Old-growth forest definitions: a pragmatic view. In: Wirth C., Gleixner G. & Heimann M. (eds.). Old-growth forests: function, fate and value. Ecological Studies 207. Springer New York, Berlin, Heidelberg, p. 11–33.

Total of 105 references