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Biodiversity in young versus old forest

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Abstract

This introductory essay has been written with the purpose to form a foundation for my PhD-study. My research task is to analyze how optimal selections of forest reserves can be made, considering biodiversity as well as economy. I cover several different areas which are of importance to my studies.

The essay starts with a description of the biodiversity concept and what characterizes biodiversity in the boreal forest. It continues with an overview of concepts relating to succession, such as disturbance and resilience. This theoretical opening is followed by a chapter covering the importance for biodiversity of both young and old boreal forest and later it describes the complex problem of reserve establishment. A section on the Swedish national forest inventory (NFI) is motivated by the planned use of data from this source. An overview on what an NFI is and how it has been used in previous studies related to biodiversity is given. The essay finishes with a chapter in which interesting research approaches on how to make the establishment of new reserves more efficient are discussed.

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Introduction

The purpose of this introductory essay is to form a foundation for my PhD-study which will focus on how to make optimal selections of forest reserves; more specifically on how to find the most cost efficient distribution of forest ages to achieve the highest biodiversity value. The importance of young forest for the total biodiversity on a landscape scale has often been neglected when establishing reserves in the past. The unique species composition combined with a lower acquisition value and the potential biodiversity value in the future old forest should make young forest worth focusing on when establishing new reserves.

I have chosen to cover several different areas associated with biodiversity in young and old boreal forests in this essay, with main emphasis on ecological differences between these age classes, how to measure biodiversity, concepts relating to succession, and how National Forest inventory data have been used in ecological analyses.

Biodiversity in boreal forest

Biodiversity

The concept of biodiversity is spanning over many spatial scales; the diversity of ecosystems, the diversity of species in the system and the genetic diversity within the species are all included. In the Rio Convention on biological diversity (Anon 1992), a definition of the word “biological diversity” was established: “Biological diversity means the variability among living organisms from all sources including, *inter alia*, terrestrial marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems”. The positive outcome for human welfare from the different systems has also become imbedded in the concept, for example photosynthesis and the ability to purify the air and soil. Diversity can also be divided into three types: compositional, structural and functional (figure 1). Composition is what a system consist of i.e. diversity of species and diversity of genes. A system’s structure is how the species and other components are organized. Function is how the components of a system are working together and the processes that the system performs. Nutrient cycling and disturbances are kinds of functional traits. The function concept is vague (Puumalainen et al. 2003) and depends on the other two types (structure and composition) (Bengtsson et al. 2000). Since function is hard to define, and indirectly captured in the preservation of structures and composition, it is rarely used in biodiversity measurement (Ferris & Humphrey 1999).

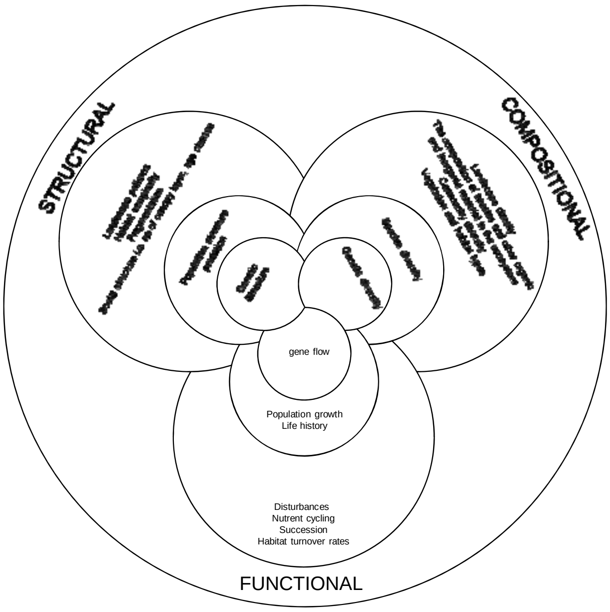

Figure 1 A modified version of Noss' (1990) model of biodiversity organization when combining types and levels of biodiversity. In order to coincide with the biodiversity definition from the Rio Convention (Anon 1992) it is only three circles deep (instead of Noss' original four), and the characteristics of the spheres have been complemented with information from Ferris and Humphrey (1999) and Spanos and Feest (2007)

How to measure biodiversity

It is impossible to measure all components of biodiversity; instead an estimate of the value of different key factors often is used as an indicator of the real biodiversity. It is important to find measurable indicators to be able to estimate the biodiversity status (Noss 1990). A good indicator is characterized as being (1) sensitive enough in order to notice a change early, (2) widely distributed, (3) able to give a continual assessment over a wide range of stress factors, (4) common enough not to be affected by sample size, (5) easy and cost effective to measure and collect, (6) able to differ between natural fluctuations and anthropogenic impact, and (7) ecologically meaningful (Cook 1976; Ferris & Humphrey 1999; Munn 1989; Noss 1990)

There are different ways to assess biodiversity depending on spatial level, and there is no need to look at the entire scale if the focus is on one specific level (Noss 1990). The most common level to measure is the species level. An accepted approach then is to select key species or structures and draw conclusions from the diversity and abundance of those (Spanos & Feest 2007). Several studies have focused on the correlation between species, with varying outcomes. One study points to a correlation between species richness of vascular plants and species richness of liverworts and mosses in boreal forest (Dynesius & Zinko 2006). If this is a general phenomenon, it indicates that if you have an estimate of the species richness of one of the groups, you could assume that the other follows the same pattern. A problem when using indicator species is the possibility of relict populations. If the population size is too small or if there is not enough suitable habitat, the population in due time is doomed to extinction (Nilsson et al. 2001) There is also a risk of missing biodiversity when just focusing on species due to the fact that a large part of species diversity is composed by small microscopic species that we know little about. In order to avoid this problem it might be better to focus on preserving a variety of ecosystems and landscapes instead (Franklin 1993). Dead wood is often used as an indicator of high biodiversity in the boreal forest, but thresholds of quantities and qualities are hard to identify (Gibb et al. 2006). The abundance of broad leaved trees is also used as an indicator but with the same threshold problem.

Boreal forest

The boreal forest is a homogeneous circumpolar vegetation belt that covers over 14.7 million km^2 or 11 % of the terrestrial land on earth (Bonan & Shugart 1989) which makes it the largest forest ecosystem on the planet (Kuusela 1992). The Fennoscandian boreal forest is characterized by a relatively homogenous structure dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* (Essen et al. 1997*)*. The main broad-leaved trees are birch and aspen (Gustafsson & Ahlén 1996).

Sweden is an oblong country that extends over several vegetation zones, but where the boreal zone is dominating (figure 2). Boreal forests cover almost 14 million ha, or 63% of the forest land, the distribution of standing volume is 45% Scots pine, 41% Norway spruce, 12% birch and 2% other broad-leaved trees (statistics from the counties of Dalarna, Gästrikland, and northwards, which almost coincide with the vegetation zone border) (Linder 1998). The other vegetation zones are nemoral, hemi boreal and alpine (Gustafsson & Ahlén 1996). The boreal zone can be subdivided into the southern, middle and northern boreal zones (Ahti et al. 1968) (figure 2). In the southern boreal zone, a variety of broad-leaved trees like oak, elm, and lime could occur in the conifer forests alongside birch and aspen (Essen et al. 1997). The middle and northern boreal zones are separated by a difference in understory vegetation (Essen et al. 1997) and a more sparse forest in the northern boreal zone (Gustafsson & Ahlén 1996)

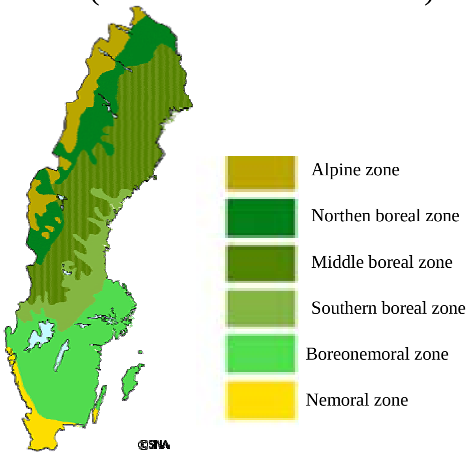

Figure 2. Vegetation zones in Sweden from the National atlas of Sweden (www.sna.se 2008).

Biodiversity in the boreal forest is mainly depending on: (1) Fire disturbance, since a majority of the species in the boreal forest is depending on fire, or the event following a fire (Essen et al. 1997). (2) Deciduous trees, which are characteristic of the first successional stages after a perturbation. A deciduous forest is one of the most species rich types in the boreal zone, consisting of both early and late successional species (Essen et al. 1997). Many species in the boreal forest are depending on deciduous trees even in late successional stages when conifer trees are dominating (Hagar 2007). (3) Gap disturbance from tree fall, which is important in forests that are not influenced by large scale disturbances (Essen et al. 1997). It gives a variation of patches in different successional stages (Kuuluvainen 1994) (4) Forest continuity, i.e., the extent in time of tree cover, but also of other structures like dead wood. The importance of long forest continuity for biodiversity in boreal forest is not always obvious though (Ohlson et al. 1997), since a lot of the species are adapted to large disturbances and therefore have a high dispersal capacity (Essen et al. 1997). (5) Dead wood, i.e. standing and lying dead trees or tree parts. The total volume of dead trees is important for associated species (Sippola & Renvall 1999), but also the number of dead trees over a certain diameter (Nilsson et al. 2001). A variety of decay stages and tree species are also important for the total diversity since there are specialist species adapted to different types and states of dead wood (Kaila et al. 1994)

Concepts relating to succession

Holling introduced the concept of **resilience** to ecology over thirty years ago (Holling 1973). Despite this, there still exist different interpretations of this term (Neubert & Caswell 1997), much due to the fact that it is complex and wide and can be regarded at multiple levels (Carpenter et al. 2001). Holling distinguished between **engineering resilience,** a systems ability to return to a stabile state after a disturbance and **ecological resilience,** the amount of disturbance a system can absorb before it changes to an alternative stable state. The ecological resilience is, according to Holling, more interesting in natural systems because it does not assume that the system is near equilibrium, which is often not the case, while engineering resilience makes that assumption. (Holling 1996). Pimm (1991) represents a different view; he considers resilience as a systems ability to withstand disturbance and the time it takes to return to equilibrium, corresponding to the engineering resilience. This view assumes that multiple stabile states do not exist. A pedagogic way to illustrate those different ways to interpret resilience is the ball and cup model (figure 4).

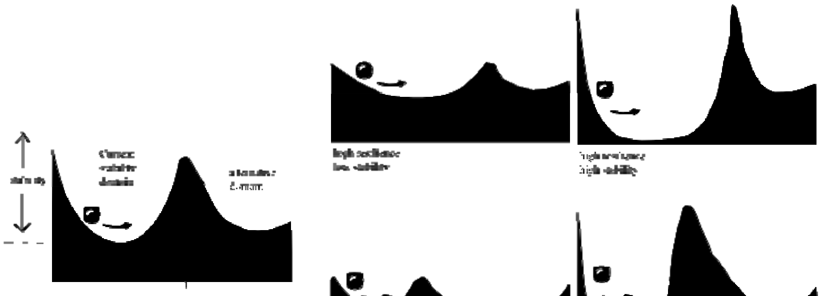

Figure 4. Modified ball and cup model from (Gunderson 2000; Hamilton & Haeussler 2008) of system stability and resilience. The cups represent a stability state, the balls represent the system and the arrows represent disturbances. The depths of the cup represent stability (or engineering resilience), the slopes represent the return time and the width on top of the cup represent (ecological) resilience (the amount of disturbance that can be absorbed before the ball roles over to an alternative stabile state). Equilibrium is on the bottom of the cup. Adaptive capacity is the system's ability to remain in the same stable state if the shape of the cup changes.

When measuring resilience in a system using Hollings view, three things have to be considered (1) the amount of change the system can undergo without switching to another stabile state (2) the ability to recover after a disturbance (Carpenter et al. 2001) and (3) **adaptive capacity,** how a system can learn and adjust to new conditions (a systems robustness) (Gunderson 2000). A high resilience on one scale does not necessary mean high resilience if the system is viewed on another scale and resilience could also change over time (Carpenter et al. 2001). High resilience in a system is not always desirable, polluted water systems for example could be very resilient (Carpenter et al. 2001).

Succession is a wide concept that can be regarded at many different levels (McCook 1994), like the biodiversity and the resilience concepts it is all a question of scale, both spatial and temporal. Succession in the forest is a change in species composition and structure over time, the change is regulated by disturbances of various sizes and magnitudes (Uotila & Kouki 2005). An ecosystem is never in a fixed state, it is rather in a dynamic, constantly changing state. Holling (1995) has made a model of ecosystem function that describes an ecosystem over time (figure 5). According to the model, an ecosystem is in one of four different phases, exploitation, conservation, release or reorganization. A system passes through all phases and is constantly moving forward in the loop although the time in each phase differs. The release phase is very short in time but large in effect, it could be the effect of e.g. a fire or a storm. After this impact the system has to reorganize and prepare for new exploitation, for example bind nutrients. This reorganization phase is also short in time and it is during this period that the system is most vulnerable. If the ecosystem is weakened in any way, for example by loss of species due to human impact, it may jump out of the cycle, and a new system will start to develop (Bengtsson et al. 2000). The next phase, exploitation, is longer in time and this is when pioneer and opportunistic species establish. The fourth and longest phase, conservation, is when the connectedness between species increase and the more competitive species take over. As time passes, ecosystems in this stage accumulate nutrients and biomass and become more and more connected. At first the connectedness makes the system stabile, but with too strong connections the system gets fragile because of the strong effect that a small change can have on the whole system. When a disturbance occurs the system is back in the release phase. (Holling et al. 1995).

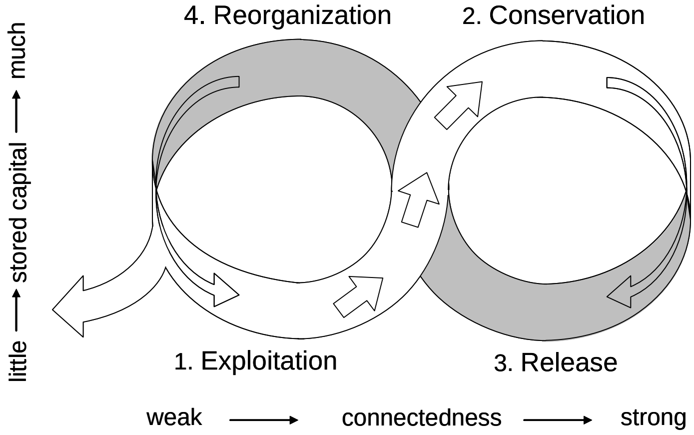

Figure 5: Hollings renewal cycle (Holling et al. 1995). The four stages of an ecosystem over time: exploitation, where new opportunistic species colonize, conservation, when stronger more competitive species take over and nutrients and biomass accumulate, release, when the more or less stabile ecosystem is exposed to an altering situation e.g. a fire and nutrients and biomass are released, finally reorganization, when the ecosystem is reorganizing e.g. binding nutrients. The x-axis shows the connectedness between organisms and the y-axis shows the change in amount of stored biomass and nutrients. The arrows indicate the time in each phase, where one long arrow is a short time. An ecosystem could jump out of the cycle between the reorganization phase and the exploitation phase and start a fundamentally different ecosystem cycle.

Species that are adapted to early stages of succession affect the species that follow during later parts in the cycle. These effects could be positive, meaning that the early species **facilitate** for the subsequent species, or they could be negative, if the early species make it more difficult for the subsequent species to establish, an **inhibitory** effect. The early species could also be insignificant for the oncoming species, i.e. they are **tolerant** (Connell & Slatyer 1977). After a disturbance, the first species to colonize are the ones with high dispersal abilities and rapid growth rate but they are often shade intolerant and have low maximum height and age (**r-selected**). Species which have less rapid dispersal and growth tend to be more tolerant to shade, grow higher and become older (**K-selected**). (McCook 1994)

Succession in a historical perspective

One of the pioneers in the field was **Clements** who saw succession as "the growth or development and the reproduction of a complex organism" (Clements 1928). This idea of an ecosystem as an organism striving to a climax stage (Clements 1936) was questioned by **Gleason** who saw succession as more random, depending on the species present, with each succession being unique (Gleason 1927). **Egler** agreed with Gleason and meant that the reason for succession was the difference in growth rate of the species present, where the fast growing species dominate early and later more slow growing species equipped with other life history traits like long life-span and large size take over. All species are present in the beginning according to this theory. (Egler 1954). **Drury and Nisbet** had a similar view, they stated that "most of the phenomena of succession can be understood as consequences of differential growth, differential survival (and perhaps differential colonizing ability) of species adapted to growth at different points on environmental gradients."(Druy & Nisbet 1973). An ecologist that agreed more with Clements was **Odum,** whose view of succession can be summarized into three parts (I) the orderly process of community changes, the changes are directional and this make them predictable (II) it is a result of modifications by the community on the physical environment and (III) it culminates in the establishment of a stabile ecosystem (as stabile as is biologically possible at the site in question) (Odum 1969). The attempts among scientists to explain the patterns of succession continued with, among many others, **Grime** (1974) who divided environments into categories according to a triangle where the rate of disturbance competition and resources present interacts. He stressed that different species are adapted to different levels of disturbance and cope with limiting resources in various ways. Changes during succession alter the environment between the different categories which in turn favors the species specialized in the specific environment.

In the attempt to understand and predict succession, a number of other models and views have been created e.g. **Botkin** (Botkin 1981), **Huston and Smith** (Huston & Smith 1987), **Tilman's** (Tilman 1985) and **Horn** (Horn 1981)

Succession in the boreal forest

The **natural disturbance regime** in an area shapes the vegetation structure. Fire used to be the major natural disturbance regime in the boreal forest but has more or less disappeared due to suppression by humans (Zackrisson 1977). This has lead to a substantial change of the ecological dynamics of the forest. Species depending on fire differ in their ecological characteristics, some spread easily over large areas and can survive on small spots after fires distributed randomly. Small and fragmented fires are often the case today due to efficient fire prevention. Other species need fires to return to the same spot, i.e. fire depending seeds in the seed bank (Granström 2001). Other natural disturbance regimes in the boreal forest are wind, insect outbreaks, flooding and drought.

A guideline for forestry and reserve management developed in Sweden is the ASIO model. It divides the forest land into four “fire tendency” groups based on disturbance regime, geographical location and site features such as water and nutrient recourses. The fire frequency can be: **A**bsent, **S**eldom, **I**nfrequent or **O**ften. Vegetation structure in the boreal forest can be affected by disturbance regimes in three different ways: (1) gap phase dynamics in spruce forest, a moist and stabile microclimate with a continuity of dead wood in different decay stages and a continuity in tree cover (2) succession, which leads to even age stands, from deciduous forest in the early stages to conifer forest in later stages (3) multi cohort in pine forest, a dry environment with a high frequency of low intense fires, which leads to an uneven age distribution due to the surviving trees after every disturbance. The idea is to mimic those three natural disturbance regimes using different techniques on the four different types of forest land. A forest that never burns should be left unmanaged, in an S-forest a clear cut, possibly with shelter wood system can be used, in mesic I-forest a larger area has to be considered in order to ensure that a full range of successional stages is present at all times and dry sites should be managed in a way that a forest with different tree age cohorts is maintained. The model can be used as a tool when trying to understand the dynamics in the boreal forest and when monitoring biodiversity on a landscape level. (Angelstam 1998)

If the goal is to get the highest biodiversity on a landscape level it is important to try to have forest of different types and of all successional stages present. Different species are adapted to different forest ages and some species need several successional stages in an area to maintain viable populations (Fuller & DeStefano 2003). Several bird species for example are adapted to a variety of forest types and/or forest ages in different parts of their life-cycle. Numerous both plant and animal species in the boreal forest are depending on disturbances. One specific but yet informative example is the lichen *Ramalina sinensis,* which grows on living aspen stems. The lichen is weakened by a parasitic fungus and the impact increases as the aspen grows older. The lichen is adapted to and depend on large scale disturbances which create aspen regeneration, and the opportunity to colonise new, younger trees (Hedenås et al. 2006).

The **intermediate disturbance theory** states that moderate disturbance is needed to keep competitive strong species from dominating (Connell 1978) and that the highest diversity of species occur after an intermediate time span since the disturbance (Collins et al. 1995). The importance of disturbance for the preservation of biodiversity needs to be considered in reserve management (Angelstam 1998; Berglind 2004; Fries et al. 1997; Granström 2001)

Differences between young and old forests

Age distribution

The age distribution in managed forest differs from the age distribution in protected forest, with a higher proportion of old forest in reserves and higher proportion of young forest in managed areas (figure 6). The difference is more distinct in the northern part of the country where 80% of protected forest is over 120 years compared to 15% in the managed forest. In the southern part, the age of the protected areas are more evenly distributed. Only approximately 7 % of forest over 120 years is protected in the southern part while approximately 25% of forest over 160 years is protected in the northern part. (Anon 2006)

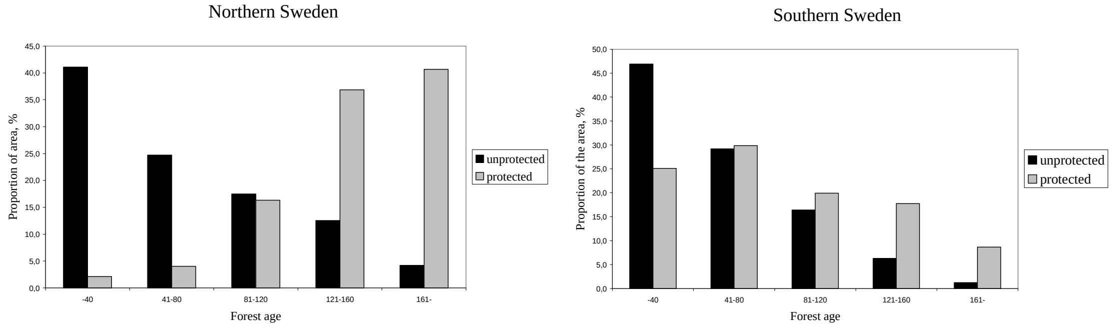

Figure 6. Modified figures of age distribution 2003-2005 of protected and unprotected forest (Anon 2006). The northern part embodies the majority of the boreal forest in Sweden

Dead wood and understory vegetation

The main reason for variation in species and structures in a particular forest type in the boreal forest is differences in naturalness and stage of succession (Junninen et al. 2006). The amount of dead wood is one feature that varies depending on forestry impact and age of the forest. The natural pattern of dead wood densities is “u-shaped” with the lowest amount in a intermediate aged forest (Sturtevant et al. 1997). It is a different relationship in managed forest. In a Finish study from 2001 the lowest densities of dead wood existed in the first stage (on a clear cut), and then increased (not linearly, it oscillated during succession), with the largest amount in managed old growth stands (Uotila et al. 2001). There was also a larger total supply of coarse woody debris in pristine forests compared to managed forests. These patterns are similar in Sweden, but the density of coarse woody debris is increasing in managed forests, due to new forestry guidelines (Ekbom et al. 2006) and there will be a substantial increase in coarse woody debris in newly cut stands, and eventually in all age classes if the forestry follows these new guidelines (Ranius & Kindvall 2003).

Natural disturbances create open areas with plenty of sun exposed dead wood (Kaila et al. 1997). There is generally less dead wood in the boreal forest today, and especially sun exposed dead wood, due to management activities such as suppression of fire and removal of damaged and dead trees (Sverdrup-Thygeson & Ims 2002). Many red-listed wood-living invertebrates in Sweden depend on dead wood in different decay stages (Essen et al. 1997). In a study from the late 1990s (Jonsell et al. 1998) found that there were about 550 red listed wood living invertebrates in Sweden whence about 25% preferred sun exposed dead wood and only about 10 % preferred shaded wood. Aspen is an important tree species for the saproxylic beetle fauna in the boreal forest (Sverdrup-Thygeson & Ims 2002) and many of the insects species using aspen as a resource are threatened. A majority of those threatened species could survive on a clear cut if both dead and alive aspen trees are left after the felling (Martikainen 2001).

Grasses are very abundant after a clearcutting whereas natural forests which regenerate after disturbance, e.g. a fire, often lacks grasses. The total number of species seems to change similarly along succession regardless if the forest is natural or managed, with a peak at intermediate ages (Uotila & Kouki 2005). In Finland a decrease in dwarf shrubs and an increase in bryophytes have been observed in managed forests. It is thought to be due to lack of fire, which has a negative effect on e.g. *Vaccinium vitis-idaea* and *Vaccinium myrtillus* (Uotila & Kouki 2005).

A study from Canada (Botting & Fredeen 2006) on the diversity and abundance of terrestrial lichens, mosses and liverworts in sub boreal spruce forests showed a difference in species composition between old growth and young second growth forests. 30% of the species were unique for old growth forest and 21% were only found in second growth. Twice as many species of liverworts where unique for old forest whereas an equal amount of lichen species were uniquely found in the two forest ages. In a study from Finland, liverworts were more diverse in semi-natural forest in most of the successional stages compared to a managed forest, possible due to a greater supply of dead wood in pristine forest. In older forest liverworts are outcompeted by mosses. A young forest had higher total species richness of vascular plants, bryophytes and lichens than an old forest regardless of naturalness (Uotila & Kouki 2005). As a general pattern, the diversity of the understory vegetation increases after a fire and continues to increase until it reaches a peak and then it starts declining indefinitely (Hart & Chen 2006). The velocity of the decrease depends on the site type and geographical position (Tonteri 1994).

Epiphytic lichens

Lichens are often used as indicators of long forest continuity (Gauslaa 1995), a quality that is regarded as important for the biodiversity in boreal forest (Essen et al. 1997), see section “Boreal forest“. In today’s landscape, where the area of old pristine forests decreases and the remaining patches are isolated in protected areas, it has become a priority to try to create suitable habitats for lichens depending on long continuity (Essen et al. 1997). A study in Norway on colonization of lichens in young forests shows that a main reason that some lichen species are confined to old growth forest is their poor dispersal ability, and not the characters of the young forest in itself (Hilmo & Såstad 2001). Another Norwegian lichen study compared how different epiphytic lichens respond to light stress in old and young forest. It seems like species that are indicators of long forest continuity, and therefore sensitive to changes, are negatively affected by a sudden increase of light. The strength of the effect and the ability to recover differed between species (Gauslaa & Solhaug 1996). These studies imply that a majority of the indicator species have a possibility to survive in managed forests if old trees are left on clear cuts and if alternative logging methods are used.

Conservation aspects

A forest management more in harmony with the natural disturbance regimes and succession would be desirable (Similä et al. 2002) if biodiversity is to be preserved. In areas adapted to fire disturbances, natural early succession stages could be more rare than old growth forest, and therefore under more urgent need of protection (Hansen et al. 1991). A natural distribution of forest ages would also be desirable from a conservation viewpoint, but it is difficult to know how much young forest habitat and early successional habitat that would naturally exist in a landscape, man has manipulated the structure and composition for a long time (Thompson &

DeGraaf 2001). An idea for biodiversity conservation would be to guarantee sufficient amounts of different young forest habitat in the landscape that will support viable populations of all native species (Askins 2001). But, it might not be enough to establish new reserves in young forests in order to preserve all species adapted to early stages of succession; biodiversity has to be considered in the managed forest as well. Fire-favored species could for example benefit from a clear-cut, as a substitute for a post fire forest, if there are substrates present that would naturally occur after a fire, i.e. dead wood (Gibb et al. 2006).

In forestry today the use of tree plantation and fertilization leads to homogenous, fast growing young forests. This environment is far from what species associated with early successional habitat are adapted to (Askins 2001). Many species do not survive in these heavily managed forests, and instead they need young forests with the characteristic structures of natural early successional stages, for example several tree layers and a large supply of dead wood (Uotila & Kouki 2005). Wood associated fungi is one example of a species group which would benefit from the protection of natural young forest because early successional forest inhabit more wood associated fungi than any of the subsequent stages. Young forest characteristics can be created by allowing disturbances in existing reserves or by leaving and creating dead wood on clear cuts (Junninen et al. 2006).

Several authors stress that the present prevailing policy to protect forest in late successional stages has to be reconsidered, and that naturally regenerated young successional stages should be given more attention when establishing new reserves (Berglind 2004; Junninen et al. 2006; Linder 1998; Similä et al. 2002). A young natural forest consists of unique species, structures and functions that may be lost if the focus on protecting old-growth forest continues (Spies & Franklin 1991).

Protected areas

The reason for establishing protected areas is to maintain environments that are of special value for animal, plants and humans. The idea is to keep the variety in nature for generations to come (Miljöbalken 1998). There has been a debate among ecologists (the SLOSS debate) about whether it is better to have a **S**ingle **L**arge **O**r **S**everal **S**mall reserves, if the goal is to preserve as much biodiversity as possible. The origin of this debate is based on two theories, one about the species-area relationship and one about species distribution, called island biogeography theory (MacArtur & Wilson 1967) The relationship between species richness and area is not linear; a small area has few species and the species richness increases rapidly with increasing size, until a point when size no longer control species richness, and the relationship fades (figure 3).

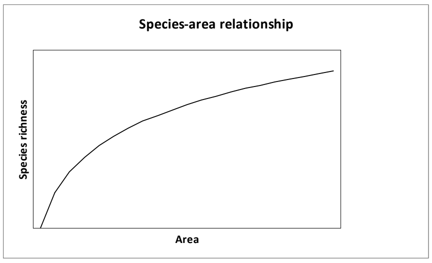

Figure 3: The relationship between area and species richness

The island biogeography theory is based on the assumption that large islands have more species than small ones. The reason for this is, according to the theory, that the probability of extinction is bigger on a small island and the probability of colonization is bigger on a large island. The distances between the islands is also a factor that influences the colonization (and indirect extinction) rate. The species richness on the islands is decided by the equilibrium between the extinction and colonization rate. The relationship is more complicated when trying to use the same theory on habitat islands in a fragmented landscape, since there is a lack of a clear distinction between the habitat “islands” and the surrounding “water” landscape (Ås 1993).

A term used in the debate is **minimum dynamic area**, referring to the smallest area that can be recolonised using internal sources after a natural disturbance, maintaining the same biodiversity (Pickett & Thompson 1978). There is no clear right or wrong in the SLOSS debate. Different species and ecosystems have different needs (Margules et al. 1982). For example, movable species that depend on the access of suitable habitat on a landscape scale (Okland et al. 1996), may not be negatively affected by fragmentation if suitable habitats exist within their moving range. Applications of the basic theories behind the debate have resulted in patch design recommendations for reserve establishment regarding size, shape and position. Among recommendations are that large, circular and aggregated areas are better than small, oblong and scattered ones. (Diamond 1975). Another advice is to concentrate protected areas near valuable forests rather than to spread them all over the landscape when making new reserves (Hanski 2000) since it makes it easier for species to emigrate from the valuable forest to the new reserve. It has also been proposed to protect natural young forests adjacent to natural old forest for the same reason since they can host some of the structures that old forest specialist species are depending on (Hanski 2000).

A recommendation of suitable reserve area based on just species-area relationship and island biogeography theory, as Diamond (1975) suggests, may not be enough (Margules et al. 1982). Pickett and Thompson (1978) have stated five criteria, based on the minimum dynamic area concept, which should be fulfilled by a nature reserve in addition to the considerations regarding size, shape and position. A protected area should (1) be considerably larger than the largest disturbance patch size (2) include internal recolonisation sources (3) include patches of different ages since disturbance (4) cover enough area to support large consumer populations in habitat not made unsuitable by disturbance and (5) contain separate minimum dynamic areas of each included habitat type. The reserves in Sweden today are not likely to fulfill all those conditions, especially if the large scale and long term dynamics are going to be implicated (Bengtsson et al. 2003). A change in climate will lead to an alteration of forest composition and a forest with high biodiversity is more likely to cope with a change and adapt to the new conditions (Naeem 1998). It might not be enough to protect small patches of reserves in a heavily managed landscape if the purpose is to lower the impact of large scale disturbances (Hansen et al. 1991). To keep the dynamics in a landscape, biodiversity values in the managed forests have to be considered as well (Bengtsson et al. 2003). In order to preserve biodiversity in managed boreal forests a heterogeneity of ages on a landscape level is desirable (Niemelä et al. 1996) as well as a heterogeneity of structures and composition.

National Forest Inventory – what it is and how it is used in previous studies regarding biodiversity

The forest in Sweden has been surveyed since 1923 by the Swedish National Forest Inventory (Anon 1932); one of the longest permanent monitoring programs in the world. Norway and Finland have similar inventories, also started in the 1920's (www.metla.fi 2008; www.skogoglandskap.no 2008). The main purpose of the Swedish NFI, which was initiated by the Swedish government, was to measure growing stock, growth and other variables important for the commercial use of the forest, but now the aim has widened to also include variables important for biodiversity. The data are unique because they give information about the state of the forest in the whole country over a long period of time. The information is used for general statistics, monitoring, regional and national planning, science, education and for international data support, e.g. the EU monitoring program ICP (International Co-operative Programme on Assessment and Monitoring of Air pollution Effects on Forests), FRA (Forest Resource Assessment of the UN) and, for the IPCC (Intergovernmental Panel for Climate Change). The long continuous information is a goldmine when analyzing the change of different features that we now know are important for biodiversity, such as the amount of dead wood, the proportion of broad-leaved trees or changes in species composition (Mäkipää & Heikkinen 2003). The data have been used for biodiversity assessment during the last few years, but there have been some problems with the analyses due to changes in inventory design and changes in variables measured over the years.

One example of use of the NFI-data for conservation-related purposes is a study by Fridman (2000) who made a comparison of the state of the forest between reserves and the forestland outside them. The intention was that this kind of information could be of help when new protected areas are established. Bergstedt and Milberg (2001) used the data to analyse the effects of different logging intensities on the ground vegetation, which might be of interest when new strategies for forestry are evaluated. There have also been studies on the supply of dead wood (Fridman & Walheim 2000) and on the regeneration of broadleaved trees in conifer forest (Götmark et al. 2005).

The data from Finland's NFI have been used by Tonteri (1990) in a study where the Cajander classification system of forest types (from poor to productive sites), using indicator species, was evaluated. The study showed that there is a gradient in species abundances between forest types, i.e. no species is clearly characteristic for one type. Forest age and geographical aspects for example are important as well when describing species abundances. In another study by Tonteri (1994) the factors explaining species richness were analyzed. The result was that site quality is most important, as compared to succession and crown coverage. But succession is affecting the species richness as well with a decrease in richness as the forest grows older.

Reflections on future research on efficient reserve establishment

In order to study the complicated concept of biodiversity it is important to reflect over what it is and how to measure it. We do not yet fully understand the complexity of nature and in order to keep as much of its treats as feasible, a preservation of all biodiversity is desirable. When establishing new reserves the idea is to preserve as much biodiversity as possible, and since money is a limiting resource, there is a will to minimize the cost as well. There has been a tendency to disregard young forests and its special characteristics when establishing reserves. It is important to preserve old forest since they have structures and a species composition that takes long time to develop. They are also attractive to forestry and need to be protected from felling. But the boreal forest is dynamic, and adapted to large scale disturbances. These disturbances and the following successions are very important for the biodiversity and the entire range of successional stages needs protection.

Dynamic reserves have been proposed in recent years as a complement to the static ones that we have today (Bengtsson et al. 2003). A dynamic reserve is only protected for a limited time. It would be very interesting to make a future scenario and try to optimize the locations of such moving reserves over time on a regional or national level. This could also be a good way to overcome the unwillingness among landowners to give up their land. If it is not forever and they keep the ownership, it might be easier to have a positive communication between owners and agencies.

There is a skew distribution of forest reserves in Sweden today, with most of the protected areas located in the northern parts (Fridman 2000). I think it would be better for the biodiversity in the country as a whole if the reserves were more evenly distributed geographically, especially since there is a more diverse flora and fauna in the southern parts of Sweden. A model with more areas of young forest protected in a more evenly spread pattern over the country would be interesting to analyze, both at present, and in a future scenario. Studies have shown that it is better to establish reserves near other valuable forests (Hanski 2000) and thus that it might be better to concentrate reserve areas. I still believe that a more even distribution over the country would be good on a national scale but that an aggregated distribution could be a good option on a landscape scale. The evaluation of the efficiency of such scenarios would be well suited for future research.

Only a fraction of the total forest area is protected in natural reserves or national parks. It is therefore unrealistic to think that all the forest biodiversity can be preserved in protected areas alone. A better consideration regarding biodiversity needs to be taken into account in managed forests as well. It would be interesting to model the cost-efficiency of joint planning with protected areas and managed forest on a landscape scale.

References

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici **5**:169-211.

Angelstam, P. K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science **9**:593-602.

Anon. 1932. Uppskattning av Sveriges skogstillgångar. Jordbruksdepartementet, Stockholm.

Anon. 1992. Convention on Biological Diversity, RIO.

Anon. 2006. Skogsdata 2006. Institutionen för skoglig resurshushållning och geomatik. Sveriges Lantbruksuniversitet, Umeå.

Askins, R. A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin **29**:407-412.

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

Bengtsson, J., S. G. Nilsson, A. Franc, and P. Menozzi. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management **132**:39-50.

Berglind, S. A. 2004. Area-sensitivity of the sand lizard and spider wasps in sandy pine heath forests - umbrella species for early successional biodiversity conservation? Ecological Bulletins **51**:189-207.

Bergstedt, J., and P. Milberg. 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. Forest Ecology and Management **154**:105-115.

Bonan, G. B., and H. H. Shugart. 1989. Environmental-Factors and Ecological Processes in Boreal Forests. Annual Review of Ecology and Systematics **20**:1-28.

Botkin, D. B. 1981. Causality and Succession. Pages 36-55 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer-Verlag, New York.

Botting, R. S., and A. L. Fredeen. 2006. Contrasting terrestrial lichen, liverwort, and moss diversity between old-growth and young second-growth forest on two soil textures in central British Columbia. Canadian Journal of Botany-Revue Canadienne De Botanique **84**:120-132.

Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems **4**:765-781.

Clements, F. E. 1928. Plant Succession and Indicators: A definitive edition of Plant Succession and Plant Indicators. The H. W. Wilson Company, New York.

Clements, F. E. 1936. Nature and Structure of the Climax. The Journal of Ecology **24**:252-284.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental-Analysis of Intermediate Disturbance and Initial Floristic Composition - Decoupling Cause and Effect. Ecology **76**:486-492.

Connell, J. H. 1978. Diversity in Tropical Rain Forests and Coral Reefs - High Diversity of Trees and Corals Is Maintained Only in a Non-Equilibrium State. Science **199**:1302-1310.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of Succession in Natural Communities and their Role in Community Stability and Organisation. The American Naturalist **111**:1119-1144.

Cook, S. E. K. 1976. Quest for an Index of Community Structure Sensitive to Water-Pollution. Environmental Pollution **11**:269-288.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation **7**:129-146.

Druy, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum **54**:331-368.

Dynesius, M., and U. Zinko. 2006. Species richness correlations among primary producers in boreal forests. Diversity and Distributions **12**:703-713.

Egler, F. E. 1954. Vegetation Science Concepts I. Initial Floristic Composition, A Factor in Old-Field Vegetation Development. Vegetatio **4**:412-417.

Ekbom, B., L. M. Schroeder, and S. Larsson. 2006. Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. Forest Ecology and Management **221**:2-12.

Essen, P.-A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal forests. Ecological Bulletins **46**:16-47.

Ferris, R., and J. W. Humphrey. 1999. A review of potential biodiversity indicators for application in British forests. Forestry **72**:313-328.

Franklin, J. F. 1993. Preserving Biodiversity - Species, Ecosystems, or Landscapes. Ecological Applications **3**:202-205.

Fridman, J. 2000. Conservation of Forest in Sweden: a strategic ecological analysis. Biological Conservation **96**:95-103.

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

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

Fuller, T. K., and S. DeStefano. 2003. Relative importance of early-successional forests and shrubland habitats to mammals in the northeastern United States. Forest Ecology and Management **185**:75-79.

Gauslaa, Y. 1995. The Lobarion, an Epiphytic Community of Ancient Forests Threatened by Acid-Rain. Lichenologist **27**:59-76.

Gauslaa, Y., and K. A. Solhaug. 1996. Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. Functional Ecology **10**:344-354.

Gibb, H., R. B. Pettersson, J. Hjälten, J. Hilszczanski, J. P. Ball, T. Johansson, O. Atlegrim, and K. Danell. 2006. Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. Biological Conservation **129**:437-450.

Gleason, H. A. 1927. Further Views on the Succession Concept. Ecology **8**:299-326.

Granström, A. 2001. Fire management for biodiversity in the European boreal forest. Scandinavian Journal of Forest Research **16**:62-69.

Grime, J. P. 1974. Vegetation Classification by Reference to Strategies. Nature **250**:26-31.

Gunderson, L. H. 2000. Ecological resilience - in theory and application. Annual Review of Ecology and Systematics **31**:425-439.

Gustafsson, L., and I. Ahlén 1996. National Atlas of Sweden. Geography of Plants and Animals. SNA, Stockholm.

Götmark, F., J. Fridman, G. Kempe, and B. Norden. 2005. Broadleaved tree species in conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden. Forest Ecology and Management **214**:142-157.

Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: A review. Forest Ecology and Management **246**:108-122.

Hamilton, E. H., and S. Haeussler. 2008. Modeling stability and resilience after slashburning across a sub-boreal to subalpine forest gradient in British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **38**:304-316.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving Biodiversity in Managed Forests - Lessons from Natural Forests. Bioscience **41**:382-392.

Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici **37**:271-280.

Hart, S. A., and H. Y. H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences **25**:381-397.

Hedenås, H., K. Lundin, and L. Ericson. 2006. Interaction between a lichen and a fungal parasite in a successional community: Implications for conservation. Journal of Vegetation Science **17**:207-216.

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

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Holling, C. S. 1996. Engineering resilience vs. ecological resilience. Pages 31-43 in P. C. Schulze, editor. Engineering Within Ecological Constraints. National Academies Press, Washington DC.

Holling, C. S., D. W. Schindler, B. W. Walker, and J. Roughgarden. 1995. Biodiversity in the functioning of ecosystems: an ecological synthesis. Pages 44-83 in C. Charles Perrings, K. G. Mäler, C. Folke, C. S. Holling, and B.-O. Jansson, editors. Biodiversity loss. Economic and Ecological Issues. Cambridge University Press, Cambridge.

Horn, H. 1981. Some Causes of Variety in Patterns of Secondary Succession. Pages 24-35 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer-Verlag, New York.

Huston, M., and T. Smith. 1987. Plant Succession - Life-History and Competition. American Naturalist **130**:168-198.

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

Junninen, K., M. Simila, J. Kouki, and H. Kotiranta. 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography **29**:75-83.

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

Kaila, L., P. Martikainen, P. Punttila, and E. Yakovlev. 1994. Saproxylic Beetles (Coleoptera) on Dead Birch Trunks Decayed by Different Polypore Species. Annales Zoologici Fennici **31**:97-107.

Kuuluvainen, T. 1994. Gap Disturbance, Ground Microtopography, and the Regeneration Dynamics of Boreal Coniferous Forests in Finland - a Review. Annales Zoologici Fennici **31**:35-51.

Kuusela, K. 1992. The boreal forests: an overview. Unasylva **43**:3-13.

Linder, P. 1998. Stand Structure and Successional Trends in Forest Reserves in Boreal Sweden. Pages 7-36. Department of forest Vegetation Ecology. Swedish University of Agricultural Sciences, Umeå.

MacArtur, R. H., and E. O. Wilson 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N. Y.

Margules, C., A. J. Higgs, and R. W. Rafe. 1982. Modern Biogeographic Theory - Are There Any Lessons for Nature Reserve Design. Biological Conservation **24**:115-128.

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

McCook, L. J. 1994. Understanding Ecological Community Succession - Causal-Models and Theories, a Review. Vegetatio **110**:115-147.

Miljöbalken 1998. Svensk Författningssamling. 1998:808, Stockholm.

Munn, R. E. 1989. The Design of Integrated Monitoring Systems to Provide Early Indications of Environmental Ecological Changes. Environmental Monitoring and Assessment **11**:203-217.

Mäkipää, R., and J. Heikkinen. 2003. Large-scale changes in abundance of terricolous bryophytes and macrolichens in Finland. Journal of Vegetation Science **14**:497-508.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology **12**:39-45.

Neubert, M. G., and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology **78**:653-665.

Niemelä, J., Y. Haila, and P. Punttila. 1996. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. Ecography **19**:352-368.

Nilsson, S. G., J. Hedin, and M. Niklasson. 2001. Biodiversity and its assessment in boreal and nemoral forests. Scandinavian Journal of Forest Research **16**:10-26.

Noss, R. F. 1990. Indicators for Monitoring Biodiversity - a Hierarchical Approach. Conservation Biology **4**:355-364.

Odum, E. P. 1969. The Strategy of Ecosystem Development. Science **164**:262-270.

Ohlson, M., L. Söderström, G. Hörnberg, O. Zackrisson, and J. Hermansson. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation **81**:221-231.

Okland, B., A. Bakke, S. Hagvar, and T. Kvamme. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation **5**:75-100.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation **13**:27-37.

Pimm, S. L. 1991. The Balance of Nature? University of Chicago Press, Chicago.

Puumalainen, J., P. Kennedy, and S. Folving. 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. Journal of Environmental Management **67**:5-14.

Ranius, T., and O. Kindvall. 2003. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biological Conservation **119**:51-59.

Similä, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation **106**:19-27.

Sippola, A. L., and P. Renvall. 1999. Wood-decomposing fungi and seed-tree cutting: A 40-year perspective. Forest Ecology and Management **115**:183-201.

Spanos, K. A., and A. Feest. 2007. A review of the assessment of biodiversity in forest ecosystem. Management of Environmental Quality: An International Journal **18**:475-486.

Spies, T. A., and J. F. Franklin 1991. The structure of natural young, mature and old-growth Doglas-fir forests in Oregon and Washington. U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Sturtevant, B. R., J. A. Bissonette, J. N. Long, and D. W. Roberts. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications **7**:702-712.

Sverdrup-Thygeson, A., and R. A. Ims. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation **106**:347-357.

Thompson, F. R., and R. M. DeGraaf. 2001. Conservation approaches for woody, early successional communities in the eastern United States. Wildlife Society Bulletin **29**:483-494.

Tilman, D. 1985. The Resource-Ratio Hypothesis of Plant Succession. American Naturalist **125**:827-852.

Tonteri, T. 1994. Species Richness of Boreal Understorey Forest Vegetation in Relation to Site Type and Successional Factors. Annales Zoologici Fennici **31**:53-60.

Tonteri, T., K. Mikkola, and T. Lahti. 1990. Compositional Gradients in the Forest Vegetation of Finland. Journal of Vegetation Science **1**:691-698.

Uotila, A., and J. Kouki. 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: Successional patterns after anthropogenic and natural disturbances. Forest Ecology and Management **215**:113-137.

Uotila, A., M. Maltamo, J. Uuttera, and A. Isomäki. 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. Ecological Bulletins **49**:149-158.

www.metla.fi. 2008. http://www.metla.fi/metla/index-en.htm. The Finnish Forest Research Institute (Metla).

www.skogoglandskap.no. 2008. http://www.skogoglandskap.no/english/index.html. Norwegian Forest and Landscape Institute.

www.sna.se. 2008. http://www.sna.se/webbatlas/kartor/vilka.cgi?temaband=S&lang=SE&karta=vegetationszoner_i_sverige&vt1=OK. Sveriges Nationalatlas.

Zackrisson, O. 1977. Influence of Forest Fires on North Swedish Boreal Forest. Oikos **29**:22-32.

Ås, S. 1993. Are Habitat Islands Islands - Woodliving Beetles (Coleoptera) in Deciduous Forest Fragments in Boreal Forest. Ecography **16**:219-228.