Introductory Research Essay

Forest degradation, conservation and restoration in Sweden

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Abstract

Forest ecosystems in Sweden are dynamic, and many species rely on natural disturbance regimes. Today, most structurally complex forests have been converted into even-aged stands of predominantly coniferous trees. Attempts to conserve biodiversity and ecosystem services have mostly involved silvicultural precautions and forest protection, but habitat restoration is becoming increasingly important.

Before ecological restoration is attempted, researchers and conservation managers must try to understand the (1) site-history, (2) current state, and (3) natural variability of the ecosystem to be restored. Traditional approaches often focus on repairing specific habitat conditions, rather than on restoring landscape processes that form and sustain habitats. A potential short-cut in choosing the appropriate scales for restoration would be to restore habitats for so called 'umbrella species'. Umbrella species require large expanses of functionally intact habitat. Consequently, many other naturally co-occuring species would benefit from their protection.

Ecological restoration may also be the only way to relieve extinction debts in remnant habitats. Restoration methods have been developed to:

- Mimic natural conditions (disturbance regimes and substrate availability)
- Improve connectivity for species dispersal (create migration corridors)
- Enlarge habitats
- Minimize edge effects by creating buffer zones
- Enable species re-introductions
- Eradicate exotic species

Restoration success, however, is not only measured in terms of species recovery. Stakeholder involvement is also crucial. Ecological restoration is an inherently subjective process, i.e. people decide on what to restore and for what reasons. Restoration managers must therefore consider public opinion before attempting to bring about change. Change, however, is inevitable, whether it is anthropogenic or not, and ecological restoration will influence future trajectories either way. Long-term monitoring and evaluation must therefore become integrated parts of ecological restoration in Sweden and elsewhere.

Forest ecosystems

Biogeography

More than sixty percent of Sweden is covered by forest, but there are regional differences in forest composition. Deciduous elements in boreal and hemiboreal Sweden are largely comprised of birch (*Betula* spp.). Nemoral forests, however, are comprised of many additional species, e.g. ash (*Fráxinus excelsior*), elm (*Ulmus* spp.), lime (*Tilia* spp.) and oak (*Quercus* spp.). Still, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate both nemoral and boreal regions, much thanks to commercial forestry. Apart from a latitudinal gradient affecting temperature, precipitation is predetermined by an altitudinal east-to-west gradient. In addition, Sweden is under substantial oceanic influence from the Atlantic Ocean and Gulf current. Consequently, many plant species in Sweden persist at latitudes far beyond their range in e.g. Russia (Ahti et al. 1968).

Only 10,000 years ago, glaciation made boreal regions uninhabitable to many plants and animals in Sweden. Even to this day, most species are opportunistic rather than specialized (Esseen et al. 1997). Sweden's flora and fauna is largely comprised of forest species, and Hymenoptera, Diptera and Coleoptera are the largest contributors to overall biodiversity (Nilsson et al. 2001). Many fungi and vertebrate species are also common, but a markedly smaller proportion of vascular plants and bryophytes inhabit forests (Nilsson et al. 2001).

Temperature, habitat size, and deciduous tree cover, have all been positively associated with mammalian species richness (Danell et al. 1996). To a certain extent, variations in temperature are explained by latitude. Normally, declines in species richness are to be expected in a south-to-north gradient (e.g. Järvinen & Väisänen 1973, Virkkala 1987, Stokland 1994, Väisänen & Heliövaara 1994), but similar latitudinal patterns in abundance are not self-evident. Birds, for example, remain abundant towards the north in spruce forest, but decline in abundance towards the north in pine forest (Esseen et al. 1997). Such patterns are likely predetermined by other factors, e.g. forest admixture, as predicted by Danell et al. (1996).

Human activities have altered many plant and animal communities. Forestry has become a major threat to many forest dependent species, but others thrive under human influence, e.g. large mammalian browsers (Cederlund & Bergström 1996). It has even been shown that changes in human land use triggered an increase in bird species richness in Sweden between 1850 and 1970 (Järvinen & Ulfstrand 1980). Most birds, however, were habitat generalists in contrast to many red-listed species of today. In fact, fifty percent of Sweden's red-listed species inhabit nothing but forest (Anonymous 2007).

Natural disturbance

In boreal forests, natural disturbance regimes maintain biodiversity (Angelstam 1998). Fire can affect forest structure, species composition, and woody debris deposition (substrate availability). Fire return intervals and fire intensities also determine plant succession and bud/seed survival (Payette 1992, Schimmel & Granström 1996). In general, the plant species richness peaks at early or intermediate levels of succession, and early post-fire stands in coniferous forests are often characterized by deciduous trees, e.g. aspen and birch (Esseen et al. 1997). Early, intermediate, and late successional plant species support a variety of lichens, mosses and fungi. Woody debris created by fire will also provide food, shelter and breeding grounds for many invertebrate species.

In Sweden, disturbance regimes will have to be actively restored on a large scale to protect biodiversity (Angelstam & Mikusinski 2001). Attempts have been made to generalize the role of fire in boreal ecosystems. In forest management, one conceptual landscape model is called ASIO (Angelstam 1998). The acronym refers to four levels in fire frequency: Absent, Seldom, Infrequent and Often. The model was developed to help foresters assess local conditions, and mimic natural disturbance regimes by choosing appropriate forestry methods. ASIO allows generalizations to be made locally, and it assumes that fire frequency is inversely related to fire intensity. In areas naturally subjected to fire, forest managers might therefore choose to prescribe burns. In areas were natural fires are nonexistent, however, interventions might be ill advised. Accordingly, intermediate solutions might be in place where fires are rare or infrequent. For example, many forestry companies of today choose to burn clear cuts.

In areas with relatively few natural fires, small-scale dynamics become as important as large-scale disturbances (Nilsson et al. 2001). Gaps created by, for instance, windthrown trees alter light and nutrient conditions at the patch scale, and provide living space for many pioneer species. Although boreal species often have impressive dispersal abilities, many species are threatened. Unfortunately, very little is known about their abilities to re-colonize areas where disturbance regimes have been restored either at the patch scale or at the landscape level.

Coarse woody debris

Snags and fallen logs provide substrates, nutrients and nest sites for many plant and animal species (Esseen et al. 1997, Grove 2002). Snags are mainly utilized by fungi, lichen, and invertebrate species whereas downed logs host an additional array of bryophytes and vascular plants (Maser et al. 1979, Esseen et al. 1997). Decomposed logs (nurse-logs) may also play an important role in the regeneration of trees. In a study by Hofgaard (1993), fallen logs covered only six percent of the forest floor, but nursed 40 percent of the tree seedlings.

In boreal forests, bacteria, fungi and invertebrates are the main decomposers, but bryophytes and lichens contribute by adding moisture (Harmon et al. 1986, Stenlid 1993,

Esseen et al. 1997). Food webs are intricate and many invertebrates, e.g. beetles, depend on wood fungi, i.e. fungal mycelia and fruit bodies (Lawrence 1989). Peaks in invertebrate richness normally occur within two years on snags or before woodpeckers have removed residual bark (Esseen et al. 1997, Bull 1983). Sap- and heartwood, however, will keep providing substrates and nutrients for decades (Esseen et al. 1997).

Spruce logs generally support more bark and wood inhabiting fungi, and a larger variety of invertebrate species, than pine logs (Esseen et al. 1997). Many species are also associated with dead deciduous wood. Birch trees alone support more than 1200 species (Anonymous 2010a), and sixty percent of Sweden's red-listed species are associated with dead deciduous wood (Anonymous 2010a). In Sweden, dead deciduous wood is ~2.3 times more common in protected areas than in commercial forest stands (Anonymous 2010b).

Substrate quality is also important. Red-listed, saproxylic, species have been more closely linked to coarse woody debris than saproxylic species in general (Anonymous 2010a, Anders Dahlberg pers. comm.). Many red-listed cryptogams have also been associated with downed logs above specific diameters. Particularly demanding invertebrates and cryptogams are, normally, restricted to trunks wider than 20 centimeters (Kruys et al. 1999).

Large trunks remain standing for longer time periods, and their decomposition takes longer (Raphael & White 1984, Lindenmayer et al. 1997, Harmon et al 1986, Stone et al. 1998). Large trunks are also more likely to remain moist throughout prolonged droughts (Nilsson et al. 2001). In addition, large, standing, and hollow trees provide essential nesting and roosting sites for many birds and bats (Ahlén & Tjernberg 1996). Hence, coarse woody debris might be more crucial to biodiversity than the overall volumes of dead wood in a forest (Nilsson et al. 2001).

Finally, dead wood can be of outmost importance to animals in streams and rivers. Dead wood can trap sediment and organic materials, affect stream decomposition, and alter water flows. This will, in turn, create favorable conditions for benthic invertebrates and fish (Eriksson & Näslund 2002, Markusson 1998, Nyberg & Eriksson 2001). Tree decomposition rates in aquatic environments will vary between species. Inundated coniferous logs will subsist for longer time periods than more rapidly decaying deciduous logs (Dahlström et al. 2005, Christer Nilsson pers. comm.).

Human impacts

Wood extraction

In Sweden, logging activities can be traced back to the Neolithic period (Esseen et al. 1997). At first, forests were cleared for cattle grazing and agriculture, but by the 17th and 18th century charcoal became equally important. Charcoal fueled the mining industry and goods were often overexploited locally. Other major exports were potash and tar, also created from forest products. Large-scale alternations, however, began only 150 years ago (Axelsson 2001). To begin with, trees (mainly pine trees) were cut selectively to fit specific dimensions in sawmills. Later, in the late 19th century, came the industrial revolution with further demands for spruce and smaller trees used in pulp factories. Selective logging was even banned in the 1950's and replaced by clear cutting (Ebeling 1959).

Approximately one percent of Sweden's forests (230,000 hectares) are clear-cut annually, and large areas (320,000 hectares) are subjected to thinning (Anonymous 2007). The average stand area for final felling is ~3.7 hectares, and commercial forests cover 22.9 million hectares (Anonymous 2007). Rotation periods vary, but normally forests are harvested within 80-130 years. Generally, forest stands in southern Sweden have shorter rotation periods than commercial forests in the north.

Three methods dominate silviculture in Europe and North America: cut-to-length logging, full-tree logging and tree-length logging. In Sweden, the primary method is cut-to-length logging. It is a mechanized harvesting system in which trees are delimbed and cut to length directly at the stump. Harvesting is typically followed by soil scarification and re-planting of coniferous trees.

For many years deciduous trees were considered a nuisance in forestry, and their elimination was often advocated. In southern Sweden, deciduous trees were actively replaced by spruce, and in the north herbicides caused rapid declines in deciduous tree cover (Anonymous 2009). Today bigger profits are to be expected from deciduous trees in forestry. Stakeholders are also more environmentally aware. Revised practices in stand level management have begun to reverse the trend for nemoral Sweden, but it is still unclear to what extent the improvements benefit biodiversity (Anonymous 2009, Davis et al. 2008). In order to address such problems more resources have to be put towards quantitative assessments.

Wood extraction affects biodiversity at several spatial and temporal scales. Detrimental effects include:

- **Habitat loss.** Effects of habitat loss are predetermined by e.g. species resilience (survival mechanisms and dispersal abilities). Habitat predictability governs the evolution of dispersal strategies (Southwood 1977). Continuity is important to many species with specific habitat, food, and microclimate preferences. However, natural disturbance will not necessarily break continuity. Forest fires, for instance, maintain multi-cohort pine forests in Sweden (Nilsson et al. 2001).

- **Habitat alternation.** Environmental change will affect many plant and animal species both positively and negatively. Commercial and pristine forests, however, are significantly different from each other in terms of both stand structure and disturbance frequency (Esseen 1992, Johnson et al. 1998). Similarities between artificially created environments and natural successions, e.g. clear cuts and burned stands are often superficial. Complexity is much greater in pristine forests than in relatively uniform and managed stands.

- **Fragmentation.** Forests are often divided into isolated fragments by forestry. Many sessile species are eradicated locally in deforested patches. Mobile species, however, can crowd in remnant patches or move between fragments. Smaller populations are more prone to extinction, and in crowded patches competition is intense. Small fragments are also more susceptible to edge effects, e.g. predation and changes in microclimate. Even mobile populations in increasingly isolated patches are less likely to migrate successfully, and to mix with other metapopulations.

Diminished dead wood supplies add a further dimension. Old-growth forests typically contain 30-90 m^3 of coarse woody debris (CWD) per hectare, but commercial forests contain only ~6 m^3 per hectare (Clark et al. 1998, Fridman & Walheim 2000, Siitonen et al. 2000, Stenbacka et al. 2010). Large quantities of dead wood are also destroyed during harvesting (Hautala et al. 2004). Before commercial forestry, snags used to constitute twenty percent of the forest biomass in Sweden (Nilsson 1933). No such records are available for downed logs (Angelstam & Mikusinski 1994), but Angelstam (unpublished data) has argued that fallen logs in pristine forests in Russia are 46 times as common. Increasing biofuel demands may also instigate stump harvesting (Caruso et al. 2008).

Fire elimination

Wildfires are random but frequent events in nature and play an important role in maintaining biodiversity. Fires create large volumes of dead wood and allow deciduous trees to colonize areas otherwise dominated by conifers. Mosaic landscapes created by fire also sustain many other plant and animal species with specific microclimate and substrate requirements. Historically, humans have employed fire for many purposes, e.g. hunting and improved cattle grazing. Today forest fires are largely suppressed in order to protect people and economic values (timber). By implementing control systems, humans have altered wildfire frequency, scale and severity. At present, 300-5000 forest hectares burn annually in Sweden, but historically forest fires covered much larger areas (~200,000 hectares), (Esseen et al. 1997, Granström 2001).

Ecological effects of fire vary tremendously with fuel quantity, condition and distribution. In some forests, in e.g. North America, fire suppression will allow surface fuels to accumulate, and trees to develop in the understory. Inadvertent fires in such areas can develop into high-intensity burns that spread from the forest floor via the understory to the canopy (Kimmins 1997, Cooper 1961). In Sweden, fuel accumulation is less of a problem since fuel loads never exceed natural levels. In fact, the fuel accumulation is offset by the fuel decomposition within 50 years (pers. comm. Anders Granström). Structural complexity, however, is also maintained by fire in Sweden. Monocultures rarely resemble multi-cohort stands (even after fire) because of differences in tree mortality (pers. comm. Anders Granström). In even-aged stands, forest fuels are either consumed entirely or not at all, and intermediate results are therefore rare.

Fire elimination can affect the species richness and abundance negatively. Hundreds of fire-dependent species are red-listed in Sweden, and many are threatened (Anonymous 2006). Some species have even gone extinct, e.g. *Sericoda bogemannii* and *Corticaria planula* (Anonymous 2006). Many beetles rely on newly burned forest stands, and many others rely on subsequent plant successions. Several species of fungi and vascular plants have been closely linked to post-fire sites (Anonymous 2006), e.g. *Pulstilla vernalis*, *Care pilulifer*, *Chimaphilia umbellate*, *Geranium bohemicum* and *Geranium lanuginosum* (Anonymous 2006). So far, no vascular plants have gone extinct, but declines in species abundance have been observed (Esseen et al. 1997).

Individuals of an endangered species, left in an environment with an altered disturbance regime, may survive for several decades before going extinct. Hence, presence/absence estimates can be deceptive in areas with extinction debts. Frequencies are less deceptive, but do not solve the underlying problems with altered habitats. Restoration attempts, however, might stabilize conditions and re-create suitable habitats for many organisms. In recent years, prescribed fires have been employed by forest managers to safeguard biodiversity in Sweden. According to the Swedish Environmental Protection Agency (SEPA) positive trends in abundance and distribution have been confirmed for several fire-dependent insect species (Anonymous 2006).

Alternations in forest structure and species composition

Forestry affects biodiversity at several spatial and temporal scales. Declines in species richness have been associated with e.g. habitat loss (e.g. Esseen et al. 1992), fragmentation (e.g. Komonen et al. 2000, Mladenoff et al. 1993), stand-level complexity (e.g. Axelsson & Östlund 2001), disturbance (e.g. Attiwill 1994, Kuuluvainen 2002), coarse woody debris (e.g. Fridman & Walheim 2000), and deciduous tree cover (e.g. Uotila et al. 2001). Substantial parts of boreal Sweden have been clear-cut and turned into even-aged coniferous stands, and natural dynamics have been replaced by cut-to-length logging, soil scarification, monocultures, and pre-commercial thinning. Official statistics confirm the pattern and show a steady increase in tree growth, height, and total volume (Anonymous 2009a).

Deciduous trees have been eliminated both directly and indirectly. Immediate, silvicultural, measures to eradicate deciduous trees have involved thinning/logging and/or herbicide treatments. Indirectly, deciduous trees have been negatively affected by herbivores, water abstraction, and/or fire suppression. Windthrown and diseased trees have also been removed efficiently, preventing gap-dynamics at the patch scale.

Comparative studies by e.g. Angelstam (unpublished data) support deciduous tree assessments made in Sweden by e.g. Axelsson et al. (2002). In an open letter to the Swedish Environmental Protection Agency (SEPA), Angelstam argued that forestry measures had reduced deciduous tree cover with 94 percent (Mild & Stighäll 2005). His conclusion was made from data collected in similar, but pristine, habitats in Russia. He continued by conveying similar declines in old trees. Only two percent of Sweden's spruce and pine trees exceed 45 centimeters in diameter (Anonymous 1989). Pine trees, in particular, have been disproportionally affected by past selective logging (Essen et al. 1997).

Changes in the composition of tree species, and their effects on biodiversity, are poorly understood. In a study by Palmgren (1932), branches from birch, spruce and pine trees were compared in terms of invertebrate abundance, and results revealed that invertebrates were more numerous on branches of birch. Bird densities have also been positively associated with deciduous tree cover in boreal forests (Andersson et al. 1967). Some bird species even disappear below certain old-growth and deciduous threshold values. The capercaillie (*Tetrao urogallus*), for example, is likely to go extinct in areas with less than 30 percent old-growth forest (Wegge & Rolstad 1986). Another species that relies heavily on vast expanses of mixed coniferous-deciduous forest is the endangered white-backed woodpecker (*Dendrocopos leucotos*), (Carlson & Stenberg 1995).

Recent positive trends in deciduous tree cover have been regional in Sweden, and no improvements have been confirmed for the northern boreal (Anonymous 2009a). Relatively old forests have become more common, but are still comparatively scarce (Anonymous 2009b). Pre-industrial forests were generally much older than commercial forests of today although intervals between events of natural disturbance are much longer now (Esseen et al. 1997, Granström 2001). Many forest species, e.g. epiphytic lichens,

are sensitive to negative trends in forest age (Esseen et al. 1997). Habitat protection alone, however, will not protect deciduous trees from being outcompeted by commercially planted spruce trees. Instead, forest managers will have to mimic or reinforce former disturbance regimes (succession orders) to prolong the deciduous phase and maintain biodiversity.

Conservation

Forest legislation, protection and management in Sweden

A first version of the Swedish Forestry Act was passed by the Swedish parliament in 1903 (Barklund et al. 2009). It declared that harvested forests had to be replanted. Much later, in 1974, environmental concerns were addressed in its first paragraph (de Jong et al. 1999). Prior to 1974, large areas had been clear-cut without any environmental restrictions (Andersson 2009). In 1980, however, extensive legislation made forest management plans mandatory (Barklund et al. 2009). Today's timber stock is much larger than it was originally, yet very few pristine forests remain (Anonymous 2009a). Consequently, many forest species are threatened, but there are also other species that depend on habitats created and maintained by humans (Barklund et al. 2009).

Nowadays, production (timber harvesting) and conservation goals are given equal importance. Today's Forestry Act came into effect in 1994, but 15 quality objectives were also released by parliament in 1999. The forest objectives were expressed in Chapter 12 entitled "Sustainable Forests". Among other things the Forestry Act (Barklund et al. 2009) stresses that:

- reforestation is mandatory
- sensitive habitats must be left undamaged
- deciduous and upland forests require special attention

Forest owners are assigned "freedom under responsibility", but they must show general conservation considerations in day-to-day forestry practices, and engage in policy updates. In clear-cuts, for example, snags, valuable deciduous trees, and eternity trees must be retained. Small-scale measures are applied everywhere to meet landscape requirements although minimum threshold values are unknown for most species. The general assumption is that protected areas alone cannot sustain biodiversity.

Ownership patterns in Sweden make forest protection difficult, and this is clearly reflected in conservation statistics. Only 3.3 percent (Anonymous 2008b) of Sweden's forests are protected, and less than 5 percent of those forests are found in productive lands (Anonymous 2007). Legally, government agencies can confiscate valuable forests, yet most protected areas are restricted to government property. In order to solve this matter, several legal instruments have been developed:

- **National parks** – Large areas with strong legal protection. Mostly pristine or semi-natural areas on state land with long-term protection.

- **Nature reserves** – Small, intermediate, or large areas with long-term legal protection. State property, or privately owned land, with environmental, recreational and/or scientific values.

- **Habitat protection areas** – Small areas with disproportionately high conservation values.

- **Nature conservation agreements** – 50 year commitments made by forest owners and the state. Forest owners normally receive economic compensation.

- **Voluntary set asides** – Areas protected without any compensation from the state.

- **Wildlife sanctuaries** – Restricted areas intended for animals sensitive to seasonal disturbances.

- **Natural monuments** – Areas with extraordinary landscape features.

Most protected areas (83 %) are nature reserves and, therefore, long-term commitments made by the state.

Many government agencies and industry organizations influence forestry. Chief responsibilities are vested in the Ministry of Agriculture, but most decisions are implemented by the Swedish Forest Agency. State forests outside the national parks are managed by Sveaskog – a commercial forest company owned by the state. Fifty percent of Sweden's forests are privately owned (Anonymous 2007), and many private associations belong to the Swedish Federation of Forest Owners. Commercial companies own 24 percent, and are normally members of the Swedish Forest Industries Association (Anonymous 2007). Additional forests are owned either by the state or other public organizations.

In recent years, certification systems have been developed by e.g. the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) as marketing tools for sustainably grown forest products. Most forestry companies in Sweden are certified either by FSC or PEFC (Andersson 2009). FSC and PEFC standards are very similar to Swedish Forestry Act standards (Andersson 2009). Forest companies join FSC and PEFC voluntarily, and have done so since 1993, but stated environmental objectives are rarely fulfilled. An evaluation made by the Swedish Forest Agency revealed success rates below 65 percent in sites subjected to regeneration felling

(Andersson 2009). Especially red-listed species were neglected in clear-cuts with percentages for "complete consideration" below 50 percent (Andersson 2009).

Research findings are constantly setting new objectives for forestry, and programs for landscape management have been initiated by e.g. Sveaskog (see "Ecoparks" at www.sveaskog.se). Among other things, researchers in ecology have pointed out the importance of (reviewed in Esseen et al. 1997):

- **Habitat protection** – to identify and protect key habitats for biodiversity
- **Natural disturbance** – to identify and facilitate natural disturbance regimes
- **Coarse woody debris** – to maintain natural or critical substrate levels
- **Deciduous trees** – to increase deciduous tree cover in previously mixed forests
- **Forest age** – to preserve and expand old-growth forests
- **Connectivity** – to preserve and create functional networks

Habitat restoration is becoming increasingly important. In many forests, natural dynamics are suppressed, and extinction debts are likely to be extensive. A first step would be to retain critical threshold levels. Thresholds are easily underestimated in areas where large forests have already disappeared (Angelstam & Mikusinski 2001). In Sweden, for example, large expanses of previously mixed coniferous-deciduous forest have been restored for the endangered white-backed woodpecker without it recovering.

Ecological restoration

Ecological restoration is not easily defined. Several attempts have been made by e.g. the Society for Ecological Restoration International (SER). SER's most recent definition (SER 2004) has been widely cited and states that "ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". SER continue by listing attributes of restored ecosystems in a "Primer on Ecological Restoration". The primer states that:

- Species assemblages must be intact
- Indigenous species must be present
- Functional groups must provide long-term stability
- Habitats must be capable of supporting viable populations
- There must be functional performance at every developmental stage
- Ecosystems must be resilient and self-sustainable
- All potential threats must be eliminated

Restoration success, however, is not necessarily determined by the full expression of all listed SER attributes. Attributes are only expected to "demonstrate an appropriate trajectory of ecosystem development towards the intended goals of reference". Public opinion and stakeholder involvement will also influence restoration outcome. Generally, successful projects involve many participants with slightly different objectives (Emily

Bernhardt pers. comm.). Scientific, educational, recreational, aesthetic and economic values are sometimes equally important to people involved in conservation work - and since people decide on what to restore, and for what reasons, ecological restoration can be a subjective process.

An extended version of the SER primer would probably include guidelines like those presented by Palmer et al. (2005). They argue that project leaders must:

- Provide detailed and realistic guiding images
- Provide improvements that can be quantified
- Avoid harmful methods to the extent possible
- Make monitoring data publicly available

Research and monitoring must become integrated parts of ecological restoration. Managers depend on reliable information from researchers in order to address matters such as the (Figure 1, Kuuluvainen et al. 2002):

- Site-history of the ecosystem to be restored
- Current state of the ecosystem to be restored
- Natural variability of the ecosystem to be restored

In turn, science would benefit significantly from pre- and post-monitoring by conservation managers. To provide useful information, monitoring should follow a sampling design that allows for statistical analysis.
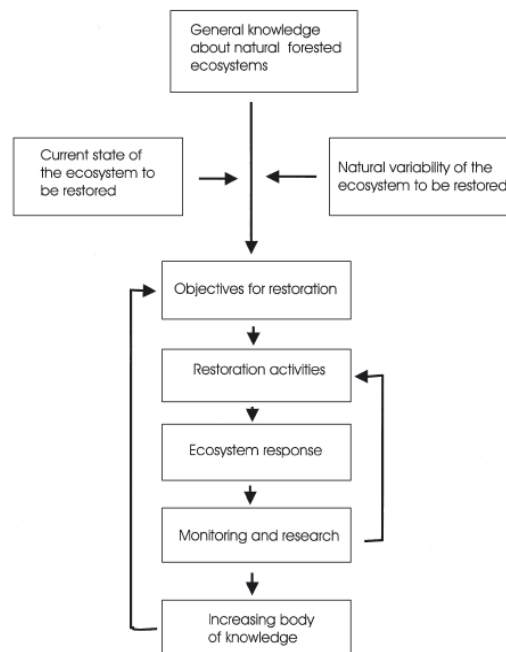
Figure 1. Input essential to successful restoration projects, and feedback loops made possible by monitoring. Figure published by Kuuluvainen et al. 2002.

It can be difficult to determine conservation targets in a dynamic ecosystem largely influenced by forestry. To address such problems researchers have compared (i) historic conditions with present day conditions, (ii) degraded environments with pristine environments, and (iii) conceptual models with reality (Kuuluvainen et al. 2002). It may also make sense to compare degraded habitats with restored habitats to isolate and quantify determinants of e.g. biodiversity.

Another problem in nature conservation is that protected areas, sometimes, only sustain biodiversity temporally at the patch scale. Protected areas can be too small for sufficient, large-scale, disturbance regimes to be implemented (Niklasson & Granström 2000). Threatened species with poor dispersal abilities might, therefore, suffer substantially from unexpected, negative, events in isolated patches. Hence, it might be better to restore areas adjacent to existing source populations (Tilman et al. 1997, Huxell & Hastings 1999, Hanski 2000).

In areas where natural disturbance regimes have been suppressed for a long time even protected areas can be degraded (Kuuluvainen et al. 2002). Restoration measures can fill many purposes in both exploited and protected forests. Principles of ecological restoration are often referred to when forest managers want to (Kuuluvainen et al. 2002):

- **Mimic natural (historic) conditions (disturbance regimes)** – the forest structure is altered to improve/increase substrate quality/quantity for forest species.

- **Improve connectivity** – corridors are created for species dispersal between forest patches.

- **Enlarge habitats** – habitats are extended to maintain viable populations, facilitate plant succession, and endorse natural disturbance.

- **Protect core areas with focal species** – buffer zones are created to minimize edge effects.

In a sense restoration ecology combines two disciplines: habitat rehabilitation and risk management. Risk management is becoming increasingly important in times of climate change. Many ideas on how to deal with uncertainty have been presented, and implementing several ideas simultaneously might in fact be the best solution. An "indeterministic approach" (Miller et al. 2007) would at least improve our chances of finding a sufficient method. Already, researchers have revealed many restoration myths (Hilderbrand et al. 2005):

(1) **The myth of the carbon copy** – A single end-point exists.

(2) **The myth of the field of dreams** – Build it (restore physical structures) and they (the desired species) will come.

(3) **The myth of fast-forwarding** – All recovery processes can be shortened.

(4) **The myth of the cookbook** – Standard methods can be successfully implemented everywhere.

(5) **The myth of command and control** – Humans can control nature.

(6) **The Sisyphus complex** – Underlying problems can be solved by treating symptoms.

Naturally, an indeterminstic approach has inherent conflicts. A hands-off approach might be against public opinion, but then again; hasty interventions can bring about unforeseen failures. Some researchers, however, are advocating an active involvement despite future uncertainties. Dunwiddie et al. (2009), for example, outlined three strategies in light of climate change:

- **The Boeing Approach (Component Redundancy)** – Large populations will ensure that some individuals/metapopulations persist. Genetic diversity will promote adaptation.

- **The Microsoft Approach (Functional Redundancy)** – Introduced genotypes will better future odds. Diversity will ensure functional attributes in an ever changing world, and some non-native species will be better equipped for future conditions. Diversity will yield viable adaptations among functional groups.

- **The Starbucks Approach (Increased Connectivity)** – Migration corridors will facilitate movement and inter-population breeding. Populations can re-colonize previously degraded habitats.

Some researchers even support the idea of "neo-native" environments where non-native species replace less resilient, indigenous, species with similar functional traits (Miller et al. 2007). By excluding non-native species, restoration managers ensure historical fidelity, but run the risk of creating "forest museums" rather than adaptable ecosystems. Needless to say, climate change could bring about catastrophic failure under such conditions (Figure 2, Harris et al. 2006).
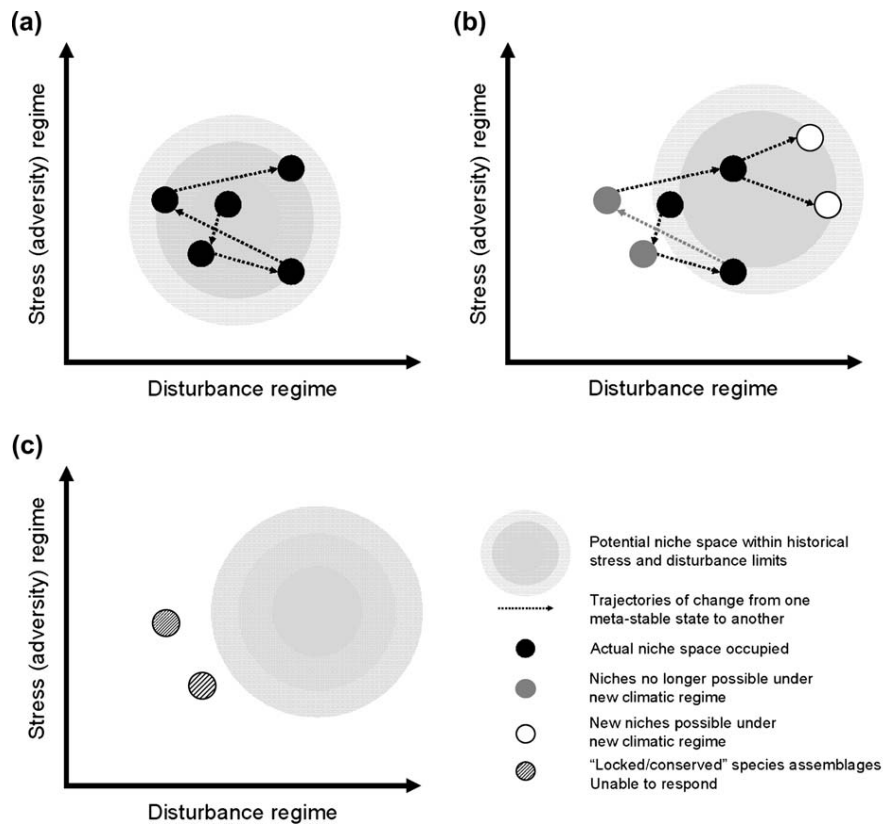
Figure 2. (a) Impact of normal climatic shifts on available niche space; (b) change in available niche space in response to changing climate; (c) "locked" assemblages unable to change in response to changing climate. Model published by Harris et al. 2006.

In Sweden, attempts to set objectives and goals for restoration have been made by e.g. Angelstam and Andersson (2001). Their underlying assumption was that at least 20 percent of a particular habitat must be preserved at the landscape level for a species to subsist. Many birds and mammals require vast expanses of habitat, and many studies have revealed minimum requirements, i.e. landscape threshold values, around 10-30 percent (Andrén 1994). Angelstam and Andersson (2001) concluded that current forestry practices are insufficient in Sweden (failure rate 8-16 percent), and that 3-11 percent of forests will have to be actively restored for long-term goals (set by the Swedish parliament) to be fulfilled. It was also concluded that restoration needs were greater in the south of Sweden. Regional differences would have been even larger, however, if protected mountain regions had not been excluded beforehand.

In Sweden, most restoration challenges are undertaken at the patch scale. However, ecological restoration, as defined by SER (2004), should be a holistic endeavour. A landscape matrix is normally comprised of several interacting ecosystems. Stream and forest ecosystems, for example, are interconnected and exchange lateral subsidies (nutrients and energy), (Baxter et al. 2005). Cascading effects in both directions must therefore be investigated before a proper evaluation of restoration success can be performed.
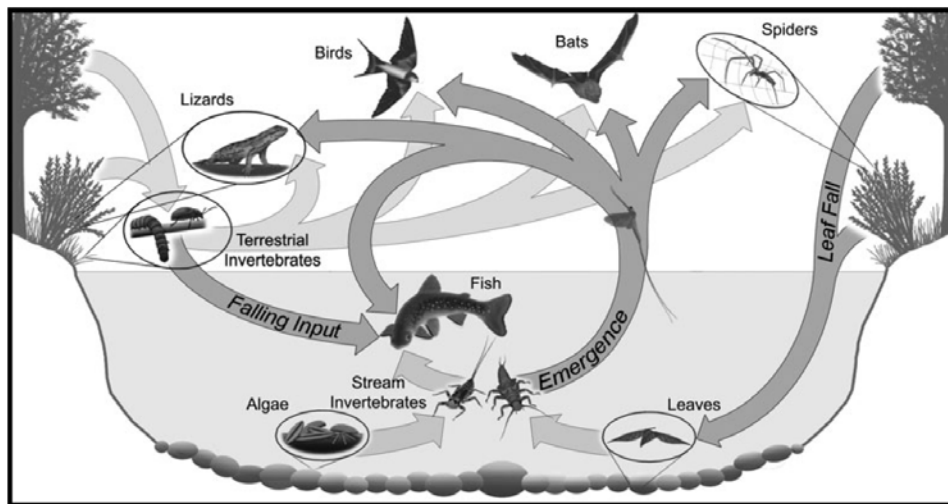
Lateral subsidies: terrestrial aquatic interdependence

Riparian habitats and streams are closely linked and exchange lateral subsidies (energy and nutrients). Instream habitats may obtain 99 % of their energy from terrestrial environments, and leaf litter alone can provide ~29 % (Fisher & Likens 1973). Microorganisms initiate the leaf degradation, and are later fed upon by macroinvertebrates (shredders) that disintegrate coarse particulate organic matter (CPOM). Fine particulate organic matter (FPOM) is created from CPOM either by shredders or stream exposure whereby it is collected by filter feeders. Lastly, predators (e.g. odonates and salmonids) consume shredders and filter feeders. Benthic production alone, however, cannot sustain drift-feeding fishes, e.g. salmonids (Allen 1951). Instead, many fish species rely on terrestrial subsidies, i.e. invertebrate prey (Baxter et al. 2005).

Terrestrial predators, e.g. bats, birds, lizards and spiders, also depend on allochtonous prey, i.e. stream-derived insects (Figure 3, Baxter et al. 2005). The net flux of invertebrate prey can shift seasonally across the aquatic-terrestrial interface. In a study by Nakano and Murakami (2001), the aquatic insect emergence peaked in spring when the terrestrial biomass was low. Otherwise, terrestrial inputs were maintained throughout the whole summer. The patterns were explained by a peak in riparian plant productivity in summer – the plant cover above streams lowered instream productivity whereas defoliation enhanced it.

Figure 3. Exchange of lateral subsidies between aquatic and terrestrial environments. Published by Baxter et al. (2005).

Terrestrial food webs are also intricate and allochtonous prey can drive behavioral, numerical and growth responses among many of its consumers (Sabo & Power 2002ab). Aquatic prey subsidies can even have bottom-up effects on terrestrial predators that, in turn, lower effects of herbivory on land (top-down control). In Germany, for example,

emerging midges were shown to support an abundance of spiders capable of depressing leafhopper populations (Henschel et al. 2001). Spiders are polyphagous and adjust rapidly to changes in prey availability, e.g. numerically by increasing their reproductive rate (Wise 1979, Wise 1993).

Ecologists have long recognized that instream communities rely on commodities and services provided by riparian habitats. Among other things, riparian habitats provide (Palik et al. 2000):

- Coarse woody debris
- Particulate and dissolved organic matter
- Temperature and light regulation
- Erosion control
- Sediment traps

More recently, researchers have begun to realize the effects of different water regimes on terrestrial communities. Riparian zones form important habitats for many terrestrial plants and animals. Some species require moist soils or water directly, and others rely on stream-derived subsidies. Buffer strips alongside water might also provide important migration corridors for many species in an otherwise fragmented landscape.

Terrestrial environments can suffer substantially from water level manipulations by humans, e.g. hydropower development (Renöfält et al. 2010). Dams will not only divide channels into fragments, but also alter water regimes and sediment dynamics. Reservoirs create new habitats, and water regulation can reduce e.g. rapids, floodplains and wetlands. Detrimental impacts are therefore to be expected well beyond aquatic boundaries (Nilsson et al. 1997). Recovery processes are also evident in some channels subjected to dam removal (Bednarek 2001). However, dam removal in itself will not ensure species recovery. In many places, anthropogenic effects on water levels have even older origins. For instance, many channels in northern Sweden have been manipulated to facilitate timber floating.

In Sweden, large scale timber floating began in the early 19th century and continued until the 1980's (Nilsson et al. 2005). Rapids, waterfalls and boulders made log floating difficult and work treacherous. Obstacles were either removed with black powder, dynamite, hoisting cranes and bulldozers, or circumvented via assembled floatway structures, e.g. flumes (Nilsson et al. 2005). Dams and stone piers were also erected to cut of tributaries and to regulate/redirect water flows. Most streams and rivers in Sweden have been altered, and sometimes river beds were bulldozed multiple times (Christer Nilsson pers. comm.).

Channelization for timber floating purposes typically reduces the (Nilsson et al. 2005):

- Watercourse complexity
- Stream sinuosity
- Variation in water depth
- Channel roughness
- Bank length
- Flooding frequency
- Hyporheic exchange
- Floodplain connectivity

Channelization alters the timing, magnitude and duration of peak flows (Nilsson et al. 2005). Generally, channelized streams move at higher velocities, and inflict more injury during flooding (Nilsson et al. 2005). Infrequent but severe floods can even remove riparian plants entirely or cover them with sediment (Bendix 1999) thereby causing anaerobic conditions (Blom & Voesenek 1996, Friedman & Auble 1999). Plants may also be less nutritious in riparian zones where the hyporheic exchange and sediment deposition has been reduced by channelization (Harner & Stanford 2003). Frequent and less severe floods, on the other hand, add nutrients and facilitate plant dispersal (Nilsson et al. 1991, Nilsson et al. 2010).

Riparian herbivores may be affected by changes in plant palatability caused by channelization. Remember also, that riparian predators can affect plants indirectly via top-down effects on terrestrial herbivores caused by aquatic prey subsidies (Henschel et al. 2001). Results from Finland, support the assumption that channelization affects the invertebrate emergence negatively by causing less retention of allochtonous detritus (Muotka et al. 2002). It has also been hypothesized, that natural channels have more standing water (pools), and larger surface areas for semi-aquatic invertebrates to emerge from (Iwata et al. 2003). In addition, floatway structures have reduced the length of riparian corridors (Nilsson et al. 2005). Iwata, Nakano and Murakami (2003) showed that both benthic invertebrates and insectivorous birds were more abundant in riparian habitats where meandering created longer streams.

Researchers have also identified shifts in species composition between pristine (semi-natural) and channelized streams. Müller (1962), for example, showed that channelization favored blackfly larvae with a preference for fast currents. However, it is uncertain to what extent channelization affects the species richness in streams. Liljaniemi et al. (2002) found no differences in invertebrate richness between degraded streams in Finland and pristine streams in Russia. Muotka et al. (2002), however, reported that channel reconfiguration enhanced the invertebrate richness in what used to be degraded streams.

If all regulated (dammed) and channelized streams were to be restored in Sweden it is likely that at least some lotic and riparian ecosystems would move toward a better functional state. In Sweden, such improvements are evident in riparian habitats where channelized streams have been restored, and many plant species have recovered (Helfield et al. 2007). This is not to say, that all stream environments can be restored. Large

boulders cannot be recreated from gravel left by explosives, and many species might have gone locally extinct. Furthermore, climate change might alter species assemblages, precipitation and winter conditions (Harris et al. 2006). Hence, it is more difficult than ever for restoration managers to identify target conditions, choose appropriate indicators (focal species), and to set time scales for evaluation.

Many species inhabit riparian zones in Sweden, and their protection is of great biodiversity concern. History has witnessed the depletion of many riparian forests, but functional attributes have been altered even in consistent habitats. Laeser et al. (2005) showed that riparian spiders were much less abundant in re-vegetated, channelized, stretches than in their natural counterparts. This suggests that not only riparian habitats will have to be restored for terrestrial communities to recover, but also streams and rivers.

Temporal dynamics: deciduous forest succession

Today, coniferous trees excel in both nemoral and boreal regions where they dispose a lot of seeds. Especially spruce trees produce large amounts of seed every 3-4 years. Since spruce seedlings can develop in densely packed forests with limited sunlight, spruce trees can become serious contenders to already established pioneer tree species, e.g. oak and birch. Before commercial forestry, fire suppression, and water abstraction; shade-intolerant species, e.g. birch, aspen and sallow, thrived in naturally disturbed, boreal, forests. Natural disturbance regimes were equally important in nemoral Sweden, but there were also several deciduous (understory) contenders to spruce, e.g. beech, ash and lime. Nowadays, forest managers are trying to re-establish former coniferous-deciduous relationships by removing spruce and by prescribing fire.

Dead wood creation has also become an integral part of spruce removal (selective logging). Directions from SEPA (Wikars 2008) state that dead wood enrichment should be conducted in gaps (or in close proximity to gaps) created from spruce removal. SEPA wants coarse woody debris to be closely deposited in sunlit positions facing north. Further recommendations involve mechanical conversions of live trees into snags. Snags created from deciduous trees are believed to enhance vegetative regeneration in gaps of sufficient size (Wikars 2008).

In Sweden, mature forests with large deciduous components (≥ 30 %) have been monitored since 1953. In nemoral Sweden, commercial forests are considered to be mature at an age of 60 years. In boreal and hemiboreal Sweden, the equivalent age is 80 years. Many older trees (35 %) were harvested between 1953 and 2000. The figures are somewhat deceptive, however, in that the negative trends for hemiboreal and boreal Sweden disguise positive trends for the south (de Jong 2002). Regardless of age, the most recent trend for deciduous trees in Sweden is positive, but young successions (3-10 years old) form the largest part (de Jong 2002). Young deciduous successions may include anything from neglected industrial forests, not yet subjected to commercial thinning, to barren areas largely comprised of birch trees (Götmark 2010).

Nemoral Sweden is likely to have suffered substantially from hardwood depletion long before 1953, and its species pool is probably largely distorted. For that reason, some scientists, e.g. Angelstam and Andersson (2001), have argued that more nemoral than boreal forests will have to be restored. A majority of Sweden's red-listed species are found in the south, but most species of European concern (species with 10 % of their European population in Sweden) inhabit the north (de Jong 2002). Researchers must therefore predict both past and future trajectories (for species in Sweden and elsewhere) so that forest managers will know what to prioritize.

Clearly, dense stands of deciduous forest can emerge in post-fire sites (De Chantal & Granström 2007). However, natural fires are generally more intense than prescribed burns since most forests burn naturally after prolonged droughts (Wikars 2004). Another problem is that large-scale, high-intensity, burns are difficult to emulate within the present structure of predominately tiny forest reserves (Granström 2007). Forest managers are therefore looking into alternative ways of benefitting deciduous trees in previously mixed coniferous-deciduous forests. In Sweden, three methods have been widely used:

- **Selective logging** – The selective harvest of e.g. spruce trees in previously mixed coniferous-deciduous forests (Lundberg 2010).

- **Gap creation** – The creation of openings in dense forest to enhance stand-level complexity and to benefit species that depend on sun exposed substrates (Lundberg 2010).

- **Conservation thinning** – The removal of competitive trees around individuals of particular conservation concern for enhanced growth and prolonged life expectancy (Lundberg 2010).

The Swedish Forest Agency (Götmark 2010) lists five situations where selective logging, gap creation, and conservation thinning can be valid:

1. Birch and aspen forests threatened by competition from spruce.
2. Riparian and wetland habitats rich in deciduous trees, but threatened from competition with spruce after water abstraction.
3. Multi-cohort pine forests where natural fires have been suppressed.
4. Oak forests threatened by tree species associated with late successions, e.g. spruce and beech.
5. Forests where cattle grazing previously supported diverse plant communities.

Methods like selective logging, gap creation, and conservation thinning have many benefits, especially if combined with dead wood enrichment. To begin with, managers avoid hazards from dealing with fire. Another benefit in not using fire, is that valuable assets of older trees are kept intact. Older pine and oak trees are built to withstand fire, but uncontrolled burns always put valuable individuals at risk. Some coleopteran species

with limited dispersal abilities rely heavily on remnant trees for their survival (Eriksson & Jonsell 2001), and continuity at the patch scale can be vital since there is no immediate substitute for old trees. Trees older than 250 years are particularly important, not only to beetles, but also to many nesting birds (Ranius et al. 2009). In addition, many tree crowns grow wider with age and thereby expose understory species (many which are threatened) to direct sunlight (Nock et al. 2008).

Mechanical conversions of live trees into snags and downed logs might help fulfill the demands of saproxylic species otherwise provided for by wildfires and/or gap dynamics. Some species, however, are strictly pyrophilous and require charred wood. Hence, forest managers will have to balance the interests of pyrophilous species against the continuity demands of late successional species. A potential solution would be to burn adjacent and less valuable forests, but it is still unclear to what extent burns in degraded habitats can substitute fires in pristine environments. In general, commercial forests are relatively uniform and densely packed (Granström 2007). Consequently, prescribed burns often kill either everything or nothing at all (Granström 2007). An understory of densely packed spruce can also fuel stand-replacing fires (Granström 2007).

In Sweden, selective logging (spruce removal) has been an essential part of the conservation program, i.e. action plan, for the white-backed woodpecker (Mild & Stighäll 2005). The white-backed woodpecker is considered to be an umbrella species since it is highly restricted to large tracts of mixed coniferous-deciduous forest with large quantities of dead deciduous wood. The program was initiated in 2005, but the white-backed woodpecker is yet to recover. This is not to say that it never will, but it does illustrate why evaluation is important. Especially, since methods such as selective logging have received even less attention than prescribed burns.

Much of what used to be mixed coniferous-deciduous forest in hemiboreal Sweden has lost its value to the white-backed woodpecker. Large areas are therefore being restored. Restoration measures have been implemented under the assumption that spruce removal, dead wood enrichment, and prescribed burns will (Mild & Stighäll 2005):

- prolong the deciduous phase
- enhance deciduous tree growth
- increase deciduous tree regeneration
- diversify stand structures
- provide substrates of different quality
- expose more substrates to sunlight
- benefit biodiversity

With that being said, spruce trees are still scarce in protected broadleaf forests. One explanation could be that spruce trees have understory contenders, e.g. beech trees, in broadleaf forests. However, spruce trees have also become less prominent, proportionally, in mixed coniferous-deciduous forests (Götmark 2010). Spruce volumes may have increased with as much as 3.3 percent since 1993, but deciduous volumes have increased even faster (+27.7 %), (Götmark 2010).

Spruce removal and dead wood enrichment may benefit threatened species associated with mixed coniferous-deciduous forests, but what about threatened species associated with current forest conditions? Will the methods depress populations associated with late successions of spruce, and thereby overall biodiversity? Many coniferous forests support threatened species, and some conservationists might even argue that spruce forests in nemoral Sweden have been neglected. Large coniferous volumes have been protected, but proportionally the volumes represent less than two percent (Götmark 2010). Moreover, some researchers predict that climate change will affect spruce forests negatively (Bernadzki et al. 1998, Bolte et al. 2009).

Larger volumes of beech than spruce (14 % versus 2 %) have been protected in nemoral Sweden, but only proportionally. Consequently, this is not to say that the current situation is satisfactory for either species. There are also other deciduous tree species, apart from beech, with limitations in terms of legal protection, e.g. the aspen (Götmark 2010). In Sweden, seventy percent of the aspen trees grow in nemoral regions, yet only one percent enjoys legal protection (Götmark 2010). Many threatened species have been associated with aspen, but existent forest reserves are unlikely to safeguard all naturally co-occurring species.

Even in forest reserves, only semi-natural forests persist, and without pristine environments (target conditions to aim for), conservation managers are blindfolded. Mixed coniferous-deciduous forests will inevitably change. Desired goals must therefore be achieved at the landscape level where natural disturbance regimes no longer fit spatial and temporal scales.

Conclusions

Substantial parts of Sweden are still covered in forest, but human land use has severely altered forest structure, age and composition. Today, disturbance regimes are manipulated for human protection and financial gain. Fires, for example, are suppressed, and water levels are kept low for increased productivity in commercial forests. In addition, silvicultural practices favor coniferous trees on behalf of deciduous trees. Large areas have been converted into coniferous monocultures even where forests used to be comprised of mostly deciduous and broadleaved species.

Forestry companies now see commercial gain in sustainably grown forest products. Requirements must be fulfilled, however, for standards to become more than marketing tools. Today, many companies fail to meet the standards set by the FSC, much to the detriment of biodiversity (Andersson 2009). In Sweden, degraded forest support less species than pristine environments, and some species have even gone extinct (Anonymous 2006). Others, like the white-backed woodpecker, are likely to go extinct without precautionary measures (Mild & Stighäll 2005). Ecological restoration might, in fact, be the only way to relieve extinction debts. Many areas across Sweden are likely to benefit from successful interventions, and restoration needs are said to be largest in the south (Angelstam & Andersson 2001).

It is also important to consider the response time and duration of a given restoration action. Traditional approaches to habitat management often focus on repairing specific habitat conditions, rather than on restoring landscape processes that form and sustain habitats. Ecological restoration is expensive, however, and sometimes there are many stakeholders involved. The easiest way out is, therefore, to start by choosing methods with little variation in restoration outcome between projects, and treatments that require little maintenance over time. A perfect example would be the efforts to reconnect channelized streams with their former floodplains in northern Sweden. Results from riparian zones adjacent to such streams have revealed significant increases in plant species richness, probably for the long-term (Figure 4).
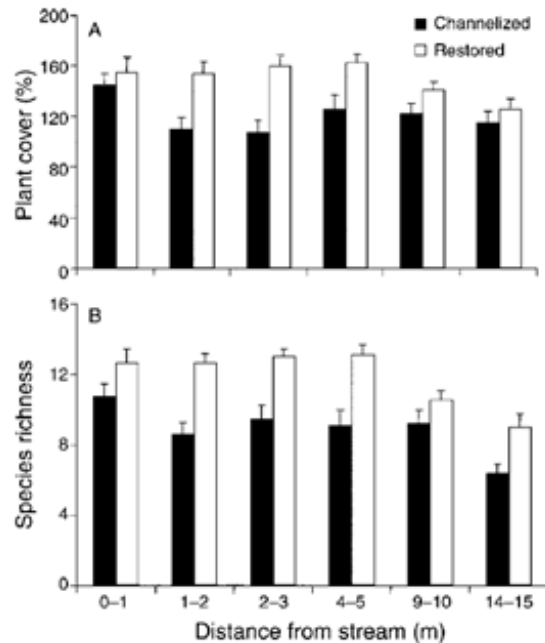
Figure 4. Plant cover and plant species richness at different distances to channelized and restored streams (Helfield et al. 2007).

More importantly, however, ecological restoration is an inherently subjective process. People decide on what to restore, and for what reasons. For example, riparian plants are rarely part of the equation when streams are to be restored in Sweden. In fact, restoration objectives rarely encompass other species than salmon (*Salmo salar*) and trout (*Salmo trutta*). Stream restoration for salmonid species will, however, bring back former disturbance regimes (Figure 5) and thereby riparian plants (Figure 4). In effect, stream restoration for salmonid species might ensure the subsistence of many non-target species. Protected species with such influences are often referred to as 'umbrella species', and the concept appears to be gaining ground among restoration practitioners in Sweden. For instance, a lot of resources have been put towards habitat restoration for the white-backed woodpecker – a potential umbrella species in mixed coniferous-deciduous forest. However, the concept has received little scientific attention in a restoration context.
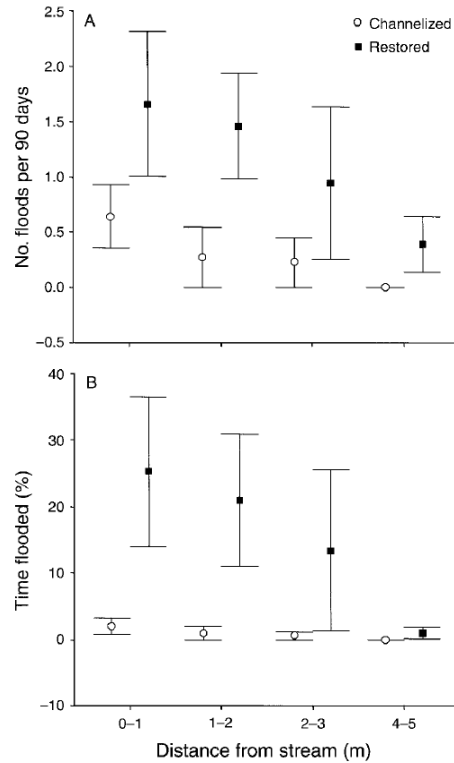
Figure 5. Frequency and duration of floods at different, perpendicular, distances to channelized and restored streams (Helfield et al. 2007).

There is no such thing as passive environmental decisions. Choosing to do nothing is only an option among many, especially in times of climate change. For that reason, long-term monitoring and evaluation (adaptive management) must become integrated parts of both nature conservation and ecological restoration. If conditions were to change considerably (and rapidly) because of climate change, it might even become necessary to think beyond conventional ideas of historical fidelity. Until then, however, it might be a good idea to manage risks by means of ecological restoration.

References

Ahlén, I. and Tjernberg, M. 1996. Rödlistade ryggradsdjur i Sverige – Artfakta. ArtDatabanken, Sveriges lantbruksuniversitet, Uppsala.

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

Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. New Zeeland Department of Fisheries Bulletin, 10.

Andersson, G., Gerell, R., Källander, H. and Larsson, T. 1967. The density of birds in some forest habitats in Stora Sjöfallet National Park, Swedish Lapland. Acta Univ. Lund, Sect. II., No. 17.

Andersson, J. 2009. Past and future effects of forest management in the Swedish boreal forest, bio fuel harvesting and goals for sustainable management. Introductory Research Essay. Department of Wildlife, Fish, and Environmental Studies. Swedish University of Agricultural Sciences.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-366.

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

Angelstam, P. and Andersson, L. 2001. Estimates of the Needs for Forest Reserves in Sweden. Scandinavian Journal of Forest Research 16 (2): 38-51.

Angelstam, P. and Mikusinski, G. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. Annales Zoologici Fennici 31: 157-172.

Angelstam, P. and Mikusinski, G. 2001. Hur mycket skog kräver mångfalden? En svensk bristanalys. Världsnaturfonden (WWF).

Anonymous 1989. Skogsstatistik årsbok (1989). Skogsstyrelsen Jönköping.

Anonymous 2006. Åtgärdsprogram för bevarande av brandinsekter i boreal skog. Naturvårdsverket, ISBN: 91-620-5610-7.

Anonymous 2007. The Swedish forest. A compilation of facts on forests, forestry and the forest industries in Sweden. Swedish Forest Agency.

Anonymous 2008b. Skogsstatistisk årsbok 2008. Sveriges officiella statistik. Tabergs Tryckeri AB, Taberg.

Anonymous 2009a. Forestry statistics 2009. Official Statistics of Sweden. Swedish University of Agricultural Sciences.

Anonymous 2009b. Swedish Statistical Yearbook of Forestry 2009. Swedish Forest Agency, ISBN: 978-91-88462879.

Anonymous 2010a. http://www-miljo.slu.se/dokument/notiser/ma8_02.pdf (2010-11-29).

Anonymous 2010b. Skogsdata 2010 tabeller. Riksskogstaxeringen. http://www.slu.se/sv/webbtjanster-miljoanalys/statistik-om-skog/skogsdata/ (2010-11-29).

Attiwill, P. M. 1994. The disturbance dynamics of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Axelsson, A. 2001. Forest Landscape Change in Boreal Sweden 1850-2000 – a multi-scale approach. Doctoral Thesis, Swedish University of Agricultural Sciences.

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

Axelsson, A., Östlund, L. and Hellberg, E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866–1999 based on interpretation of historical records. Landscape Ecology 17: 403–418.

Barklund, Å., Lundgren, B. and Ingemarson, F. 2009. The Swedish Forestry Model. Royal Swedish Academy of Agriculture and Forestry.

Baxter, C. V., Fausch, K. D., and Saunders, W. C. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Bednarek, A. T. 2001. Undamming rivers: A review of the ecological impacts of dam removal. Environmental Management 27: 803-814.

Bendix, J. 1999. Stream power influence on southern Californian riparian vegetation. Journal of Vegetation Science 10: 243-252.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J. and Zybura, H. 1998. Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. Journal of Vegetation Science 9: 229–238.

Blom, C. and Voesenek, L. 1996. Flooding: the survival strategies of plants. TREE 11: 290-295.

Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J. and Roloff, A. 2009. Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. European Journal of Forest Research 129 (3): 261-276.

Bull, E. L. 1983. Longevity of snags and their use by woodpeckers. Snag habitat management. Rocky mountain For. Range Exp. Stat., Fort Collins, pp. 66-67.

Carlson, A. and Stenberg, I. 1995. Vitryggig hackspett (Dendrocopus leucotos). Biotopval och sårbarhetsanalys. Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Uppsala. Rapport 27, ISBN 91-576-4932-4.

Caruso, A., Rudolphi, J. and Thor G. 2008. Lichen species diversity and substrate amounts in young planted boreal forests: A comparison between slash and stumps of *Picea abies*. Biological Conservation 141: 47-55.

Cederlund, G. and Bergström, R. 1996. Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. Conservation of faunal diversity in forested landscapes. Chapman and Hall, pp. 265-281.

Clark, D. F., Kneeshaw, D. D., Burton, P. J. and Antos, J. A. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Canadian Journal of Forest Research 28: 284-290.

Cooper, C. F. 1961. The ecology of fire. Scientific American 204: 150-160.

Dahlström, N., Jönsson, K. and Nilsson C. 2005. Long-term dynamics of large woody debris in a managed boreal forest stream. Forest Ecology and Management 210: 363-373.

Danell, K., Lundberg, P. and Niemelä, P. 1996. Species richness in mammalian herbivores: patterns in the boreal zone. Ecography 19: 404-409.

Davies, Z. G., Tyler C., Stewart, G. B. and Pullin A. S. 2008. Are current management recommendations for saproxylic invertebrates effective? A systematic review. Biodiversity and conservation 17: 209-234.

De Chantal, M. and Granström, A. 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. Forest Ecology and Management 250: 3-8.

de Jong, J. 2002. Populationsförändringar hos skogslevande arter i relation till landskapets utveckling. CBM: s skriftserie 7. Centrum för biologisk mångfald, Uppsala.

de Jong, J., Larson-Stern, M. and Liedholm, H. 1999. Grönare skog. Halls Offset AB, Växsjö.

Dunwiddie, P. W., Hall, S. A., Ingraham, M. W., Bakker, J. D., Nelson, K. S., Fuller, R. and Gray, E. 2009. Rethinking Conservation Practice in Light of Climate Change. Ecological Restoration 27: 320-329.

Ebeling, F. 1959. Sveriges skogar under 100 år: En sammanfattande redogörelse över det svenska skogsbruket 1859-1959. Domänverket och Norrlandsfrågorna.

Eriksson, P. and Jonsell, M. 2001. Inventering av trädinsekter vid nedre Dalälven 1997-99. Upplandsstiftelsen, Naturvård & Friluftsliv, stencil nr. 20.

Eriksson, T. and Näslund, I. 2002. Improving freshwater stream habitats: Importance of instream structures and large woody debris – Sweden. Kungliga Skogs- och Lantbruksakademiens tidsskrift 141: 77-82.

Esseen, P.A., Ehnström, B., Ericson, L. and Sjöberg, K. 1992. Boreal forest – the focal habitats of Fennoscandia. Ecological principles of nature conservation, pp. 252-325.

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

Fisher, S.G. and Likens, G.E. (1973). Energy flow in Bear brook, New Hampshire: An alternative approach to stream ecosystem metabolism. Ecological Monographs 43: 421-439.

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

Friedman, J. M. and Auble, G. T. 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. Regulated Rivers: Research and Management 15: 463-476.

Granström, A. 2001. Fire management for biodiversity in the European boreal forest. Scandinavian Journal of Forest Research Supplement 3: 62-69.

Granström, A. 2007. The Research Base for Fire Management in Fennoscandian Forest Reserves. Fire and Forest. The International Forest Fire Symposium in Kajaani 13.-14.11.2007. Nature Protection Publications of Metsähallitus (Series A 175) 12: 48-54.

Grove, S. J. Saproxylic insect ecology and the sustainable management of forests. Annual review of ecology and systematics 33: 1-23.

Götmark, F. 2010. Skötsel av skogar med höga naturvärden – en kunskapsöversikt. Svensk Botanisk Tidsskrift 104 (S1): 1-88.

Hanski, I. 2000. Extinction debt and species credit in boreal forests: modeling the consequences of different patterns of forest restoration. Annales Zoologici Fennici 37: 271-280.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Andersson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Harner, M. J. and Stanford, J. A. 2003. Differences in cottonwood growth between a losing and a gaining reach of an alluvial floodplain. Ecology 84: 1453-1458.

Harris, J. A., Hobbs, R. J., Higgs, E. and Aronson, J. 2006. Ecological Restoration and Global Climate Change. Restoration Ecology 14: 170-176.

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

Helfield, J., Capon, S. J., Nilsson, C., Jansson, R., and Palm, D. 2007. Restoration of rivers used for timber floating: effects on riparian plant diversity. Ecological Applications, 17: 840–851.

Henschel, J. R., Mahsberg, D., and Stumpf, H. 2001. Allochthonous Aquatic Insects Increase Predation and Decrease Herbivory in River Shore Food Webs. Oikos 93: 429-438.

Hilderbrand, R. H., Watts, A. C. and Randle, A. M. 2005. The Myths of Restoration Ecology. Ecology and Society 10 (1): 19.

Hoofgaard, A. 1993. Structure and regeneration patterns in a virgin Picea abies forest in northern Sweden. Journal of Vegetation Science 4: 601-608.

Huxell, G. R. and Hastings, A. 1999. Habitat loss, fragmentation and restoration. Restoration Ecology 7: 309-315.

Iwata, T., Nakano, S., and Murakami, M. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. Ecography 26: 325-337.

Johnson, E.A., Miyanishi, K. and Weir, J. M. H. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. Journal of Vegetation Science 9: 603-610.

Järvinen, O. and Ulfstrand, S. 1980. Species turnover of a continental bird fauna: Northern Europe, 1850-1970. Oecologia 46: 186-195.

Järvinen, O. and Väisänen, R. A. 1973. Species diversity of Finnish birds, I: Zoogeographical zonation based on land birds. Ornis Fennica 50: 93-125.

Kimmins, J. P. 1997. Fire. A pervasive and Powerful Environmental Factor. Forest Ecology. A foundation for sustainable management. Prentice hall, pp. 296-313.

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

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

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J. and Tukia, H. 2002. Principles of Ecological Restoration of Boreal Forested Ecosystems: Finland as an Example. Silva Fennica 36 (1) discussion papers.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 26: 97-125.

Laeser, S. R., Baxter, C. V., Fausch, K. D. 2005. Riparian vegetation loss, stream channelization, and web-weaving spiders in northern Japan. Ecological Research 20: 646-651.

Lawrence, J. F. 1989. Mycophagy in the Coleoptera: feeding strategies and morphological adaptations. Insect-fungus interactions. Academic Press, pp. 1-23.

Liljaniemi, P. Vuori, K. M., Ilyashuk, B., and Luotonen, H. 2002. Habitat characteristics and macroinvertebrate assemblages in boreal forest streams: relations to catchment silvicultural activities. Hydrobiologia 474: 239-251.

Lindenmayer, D. B., Cunningham, R. B. and Donelly, C. F. 1997. Decay and collapse of trees with hollows in eastern Australian forests: Impact on arboreal marsupials. Ecological Applications 7: 625-641.

Lundberg, K. 2010. Hotade arter i tallmiljöer på Sveaskogs mark i Västerbotten och Norrbotten. Skötselförslag och analys av potentiell habitatutbredning. Examensarbete i biologi, 30 hp. Sveriges lantbruksuniversitet (SLU).

Markusson, K. 1998. Omgivande skog och skogsbrukets betydelse för fiskfaunan i små skogsbäckar. Skogsstyrelsen, Jönköping.

Maser, C., Anderson, R. G., Cromack, K., Williams, J. T. and Martin, R. E. 1979. Dead and down woody material. Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. Agricult. Handbook 553, USDA For. Serv., Portland, pp. 78-95.

Mild, K. and Stighäll, K. 2005. Åtgärdsprogram för bevarande av vitryggig hackspett (*Dendrocopos leucotos*) och dess livsmiljöer. Naturvårdsverket, rapport 5486.

Millar, C. I., Stephenson, N. L. and Stephens, S. L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145–2151.

Mladenoff, D. J., White, M. A., Pastor, J. and Crow, T. R. 1993. Comparing spatial patterns in unaltered old-growth and disturbed forest landscapes. Ecological applications 3: 294-306.

Müller, K. 1962. Flottningens inverkan på fisket. Schiltz (Germany): H. Guntrum II.

Muotka, T., Paavola, R., Haapala, A., Novikmec, M., and Laasonen, P. 2002. Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration. Biological Conservation 105: 243-53.

Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic Interdependence between Terrestrial and Aquatic Food Webs. Proceedings of the National Academy of Sciences of the United States of America 98 (1): 166-170.

Niklasson, M. and Granström, A. 2000. Number and sizes of fire: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81: 1489-1499.

Nilsson, C., Brown, R. L., Jansson, R., Merritt, D. M. 2010. The role of hydrochory in structuring riparian and wetland vegetation. Biological Reviews 85: 837-858.

Nilsson, C., Gardfjell, M. and Grelsson, G. 1991. Importance of hydrochory in structuring plant communities along rivers. Canadian Journal of Botany 69: 2631-2633.

Nilsson, C., Jansson, C. and Zinko, U. 1997. Long-term responses of river-margin vegetation to water-level regulation. Science 276: 798-800.

Nilsson, C., Lepori, F., Malmquist, B., Törnlund, E., Hjerdt, N., Helfield, J. M., Palm, D., Östergren, J., Jansson, R., Brännäs, E., and Lundqvist, H. 2005. Forecasting Environmental Responses to Restoration of Rivers Used as Log Floatways: An Interdisciplinary Challenge. Ecosystems 8: 779-800.

Nilsson, J. E. 1933. [Short history of the Hamra State Forest for years 1884-1930]. Norrlands Skogsvårdsförbunds Tidskrift 1933: 321-348.

Nilsson, S. G., Hedin, J., Niklasson, M. 2001. Biodiversity and its Assessment in Boreal and Nemoral Forests. Scandinavian Journal of Forest Research 3: 10-26.

Nock, C. A., Caspersen, J. P. & Thomas, S. C. 2008. Large ontogenetic declines in intra-crown leaf area index in two temperate deciduous tree species. Ecology 89: 744–753.

Nyberg, P. and Eriksson, T. 2001. Skyddsridåer längs vattendrag (SILVA). Fiskeriverket, Göteborg.

Palik, B. J., Zasada, J. C., and Hedman, C. W. 2000. Riparian Management in Forests of the Continental Eastern United States. Edited by Verry, E. S., Hornbeck, J. W., and Dolloff, C. A. Lewis Publishers.

Palmer, M. A., Bernhardt, E. S., Allan, J. D., Lake, P. S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C. N., Follstad Shah, J., Galat, D. L., Loss, S. G., Goodwin, P., Hart, D. D., Hassett, B., Jenkinson, R., Kondolf, G. M., Lave, R., Meyer, J. L., O'Donnell, T. K., Pagano, L. and Sudduth, E. 2005. Standards for ecologically successful river restoration. Journal of applied Ecology 42: 208-217.

Palmgren, P. 1932. Zur Biologie von *Regulus r. regulus* (L.) und *Parus atricapillus borealis* Selys. Eine vergleichendökologische Untersuschung. Acta Zoologica Fennica 14: 1-13.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. A systems analysis of the global boreal forest. Cambridge University Press, pp. 144-169.

Ranius, T., Niklasson, M. and Berg, N. 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). Forest Ecology and Management 257: 303–310.

Raphael, M. G. and White, M. 1984. Use of snags by cavity nesting birds in Sierra Nevada. Wildlife Monograms 86: 1-66.

Renöfält, B. M., Jansson, R. and Nilsson, C. 2010. Effects of hydropower generation and opportunities for environmental flow management in Swedish riverine ecosystems. Freshwater Biology 55: 49-67.

Sabo, J. L. and Power, M.E. 2002a. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83: 3023-3036.

Sabo, J.L. and Power, M.E. 2002b. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83: 1860-1869.

Schimmel, J. and Granström, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77: 1436-1450.

SER 2004. The SER International Primer on Ecological Restoration. Society for Ecological Restoration. Science & Policy Working Group (www.ser.org).

Siitonen, J., Martikainen, P., Punttila, P. and Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management 128: 211-225.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Stenbacka F., Hjältén, J., Hilszczanski J. and Dynesius, M. 2010. Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. Ecological Applications 20: 2310-2321.

Stenlid, J. 1993. Community and population biology of boreal decay fungi. Fungi of Europe: Investigation, recording and conservation. Royal Botanic Gardens, pp. 171-180.

Stokland, J. N. 1994. Biological diversity and conservation strategies in Scandinavian boreal forests. PhD thesis. Department of Biology. University of Oslo, Norway.

Stone, J. N., MacKinnon, A., Parminter, J. V. and Lertzman, K. P. 1998. Coarse Woody debris decomposition documented over 65 years on southern Vancouver Island. Canadian Journal for Forest Research 28: 788-793.

Tilman, D., Lehman, C.L. and Kareiva, P. 1997. Population dynamics in spatial habitats. In: Tilman, D. and Kareiva, P. (eds.). Spatial ecology. The role of space in population dynamics and interspecific interactions. Monographs in Population Biology 30: 3-20.

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

Virkkala, R. 1987. Effects of management on birds breeding in northern Finland. Annales Zoologici Fennici 24: 281-294.

Väisänen, R. and Heliövaara, K. 1994. Assessment of insect occurrence in boreal forests based on satellite imagery and field measurements. Acta Forestalia Fenica 243.

Wegge, P. and Rolstad, J. 1986. The spacing of capercaillie leaks in relation to habitat and social organization. Behavioral Ecology and Sociobiology 19: 401-408.

Wikars, L. 2004. Brandberoende insekter − respons på tio års naturvårdsbränningar. Fauna & flora 99 (2): 28-34.

Wikars, L. 2008. Åtgärdsprogram för björklevande vedskalbaggar i Norrland 2008-2012. Naturvårdsverket, rapport 5843.

Wise, D. H. 1979. Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae: Araneidae). Oecologia 41: 289-300.

Wise, D. H. 1993. Spiders in ecological webs. Cambridge University Press.