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Targets for boreal forest biodiversity conservation – a rationale for macroecological research and adaptive management

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The maintenance of biodiversity is one of several internationally recognised objectives of forest management. Empirical evidence from Europe suggests that forest management is responsible for the loss of biodiversity and that the extent of the loss is a function of the amount, duration, and intensity of resource extraction. The pattern of biodiversity impoverishment as a function of habitat alteration is not always linear, but rather it is likely to exhibit thresholds beyond which the long-term maintenance of the elements of biodiversity is threatened. Such thresholds could be used for establishing conservation targets in forest management.

We present a general procedure for identifying multiple thresholds to be used in the determination of conservation targets in forests. We suggest a six-step procedure: 1) Stratify the forests into broad cover types as a function of their natural disturbance regimes. 2) Describe the historical spread of different anthropogenic impacts in the boreal forest that moved the system away from naturalness. 3) Identify appropriate response variables (e.g. focal species, functional groups or ecosystem processes) that are affected by habitat loss and fragmentation. 4) For each forest type identified in step 1, combine steps 2 and 3 to look for the presence of non-linear responses and to identify zones of risk and uncertainty. 5) Identify the "currencies" (i.e. species, habitats, and processes) which are both relevant and possible to communicate to stakeholders. 6) Combine information from different indicators selected. A review of the historical development of forest use in eight boreal case studies illustrates the need for international collaboration to follow this procedure.

To put this procedure into action and to design management applications, we suggest the development of an international network of adaptive management teams consisting of managers, policy-makers, and scientists. This network should be charged with testing different approaches to the management of forests that will ensure that biodiversity is restored in areas where it has been lost and maintained where forestry intensification has yet to occur.

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The concept of sustainable development was created as a strategy to deal with human activities jeopardising the meeting of future needs. The concept has ancient roots (e.g. Hunter 1996, Williams 2003) and the term "sustainable forestry" dates back to 1713 when Hans Carl von Carlowitz in Germany in the very first forestry textbook addressed the problem of sustainable wood production in the context of the local industry's needs (Schuler 1998). In its modern sense, however, sustainable development as defined by the Brundtland Commission in 1987 can rather be viewed as a three-legged stool supported by economic, social, and environmental components or "legs" (e.g. Goodland and Daly 1996). The elements of biodiversity can be considered as being a part of the environmental "leg", although it may be argued that some components of biodiversity should be considered under the auspices of the social and economic "legs". The fact that biodiversity is sometimes defined, or perceived, as being limited to species richness has triggered the development of concepts such as ecosystem health (Rapport et al. 1998) and ecological integrity (Pimentel et al. 2000). The multitude and ambiguity of concepts is thus a continuous source of confusion for practitioners (Kaennel 1998, Franc et al. 2001), despite a clear definition being provided under the Convention on Biological Diversity (Anon. 1992). Following Noss (1990) and Larsson et al. (2001), we define biodiversity as having three main elements: ecosystem composition, structure, and function.

In spite of ubiquitous policies to promote the sustainable use of renewable resources, the clearing of forests for agriculture and human infrastructures together with the intensive management of forests for fibre production continues to challenge the long-term maintenance of forest sustainability globally (Williams 2003). In response to this, concepts such as sustainable forest management (Schlaepfer and Elliott 2000, Franc et al. 2001, Lindenmayer and Franklin 2002, Sverdrup and Stjernquist 2002, 2003, Rametsteiner and Mayer 2004) and ecosystem management (e.g. Meffe et al. 2002) have been advocated over the past 20 yr.

To determine the relative efficacy of biodiversity management tools such as protected areas on the one hand and different kinds of forest management and ecosystem restoration practices on the other, we need to assess the status and trends of biodiversity elements over multiple spatial scales. However, the efficacy of different strategies may vary among ecoregions as a function of the biophysical or geographic conditions and management history, resulting in different kinds of landscape mosaics (Lindenmayer and Franklin 2003, Angelstam and Kuuluvainen 2004). This requires monitoring in the form of repeated measurements of a range of biodiversity elements (e.g. Larsson et al. 2001), as well as mutual learning about experiences conducted under different conditions (Angelstam et al. 1997).

Principles such as sustainable forest management are made more explicit by breaking down the issues into different criteria, such as biodiversity, social issues, and economics. Each criterion is then accompanied by a number of indicators representing measurable variables (Higman et al. 1999). There have been a number of attempts to develop criteria and indicators for the sustainable management of forests (e.g. Duinker 2001, Rametsteiner and Mayer 2004). These include the Montreal Process, the Helsinki Process now termed the Ministerial Conference on the

Protection of Forests in Europe (MCPFE), and a variety of other regional initiatives. A common characteristic for all of these schemes is that the maintenance of biodiversity is identified as an important criterion of sustainable forest management.

According to Loyn and McAlpine (2001), the purpose of indicators is to assess and monitor whether forests are being managed in a sustainable fashion, and to provide information about processes in the forest and their management. Although a substantial number of indicators have been developed to monitor elements of biodiversity, it is important to recognise that most sets of indicators have been designed for regional or national scale reporting and not for use at an operational scale (but see Kneeshaw et al. 2000, Angelstam and Dönz-Breuss 2004). Consequently, the indicators may have relatively little value at the scale of the management unit, i.e. the actual landscape (Loyn and McAlpine 2001, Finegan et al. 2001, Kanowski et al. 2001). Furthermore, many indicators fail to provide a clear link between a given measurement and its relationship to the maintenance of biodiversity.

Ultimately an indicator is useful only if it can be compared with a target based on some kind of benchmark or reference (Higman et al. 1999, Puumalainen et al. 2002). Ecosystems often exhibit non-linearities, thresholds or "flips" corresponding to sudden changes in their properties (Muradian 2001, Gunderson and Pritchard 2002). Thus, a desired range of variation in these properties must be defined so that management goals can be set. For example, a small decrease in the area of forest in a region may result in little immediate concern. However, if that change involves the crossing of a critical threshold, then it may have serious implications for biodiversity. The formulation of targets is implicitly encouraged by the fact the long-term visions such as the conservation of native biodiversity have been incorporated into policy and international treaties (Duinker 2001). As an example, politically-negotiated, short-term targets based on long-term visions are an important part of the Swedish environmental policy (Anon. 2000). Some forms of forest certification, a kind of third-party market-driven mechanism aimed at sustainable forest management, can also be included within this context (Elliott and Schlaepfer 2001). Certification standards hence represent a set of targets at the scale of the forest management unit, and several certification schemes take into account the possibility of continuous improvement. It should, however, be noted that certification tends to focus on short-term political and economic goals, which are locally relevant and viewed as realistic to achieve within a short time frame, generally just a few years. The extent to which certification will prove effective in the long term will depend on the degree to which the resulting targets will actually evolve continuously to promote different aspects of sustainability in actual landscapes (Angelstam 2003).

Policy targets are thus not equivalent to ecologically based targets emerging from theoretical and empirical studies showing that environmental nonlinearities or thresholds exist (e.g. Angelstam et al. 2003a). Even though research on thresholds remain in its infancy, ecologically-based targets inspired from such thresholds could be used to postulate management and conservation strategies. The concept of critical load provides an example of such an approach (see Sverdrup and Stjernquist 2002). It was coined to define the amount of acidic deposition that the most sensitive elements in an ecosystem could tolerate without significant damage. For the maintenance of biodiversity, critical loss of, for example, habitat structures in relation to the range of natural variation, would be an analogous concept. We stress, however, the need for explicitly recognising uncertainty and, rather than proposing target numbers, there should be a focus on probabilistic targets defined using a variety of indicators, and on the associated "zones of risk" (e.g. Muradian 2001, Phillis and Andriantiatsaholiniana 2001, Angelstam et al. 2003a).

There is evidence for non-linear responses of species and ecosystem processes to gradients of habitat alteration (e.g. Andrén 1994, Jansson and Angelstam 1999, Muradian 2001, Cooper and Walters 2002, Benton 2003, Bütler et al. 2004a, b). Such non-linear responses may indicate thresholds, i.e. relatively narrow ranges in forest degradation (at local or landscape scales) over which the biological response changes abruptly. In spite of this, the practical application of objective quantitative targets at appropriate spatial scales has largely been neglected in the development of sustainable forest management (Lammerts van Buren and Blom 1997, Duinker 2001). There are several reasons for this. One is that research is usually restricted to a limited combination of temporal and spatial scales (Vogt et al. 2002). Another is that, until recently, little thought had been given to the theoretical and methodological aspects of threshold detection (Toms and Lesperance 2003, Guénette and Villard 2004). We need to address not only what we do within the framework of what is considered economically possible or socially acceptable at present, but also within a window encompassing the long-term ambition of policies advocating the maintenance of biodiversity. This can be challenging to scientists as it may be considered risky for their own funding and career (Mills and Clark 2001, Hanski 2002). Moreover, even though a considerable amount of knowledge exists, it is often poorly synthesised and communicated to policy-makers and managers (Lee 1993, Kinzig et al. 2003).

Ecological research is seldom designed to provide answers directly applicable to management issues, and planning tools are often not designed to incorporate ecological knowledge as such. In addition, there is insufficient understanding about how policies could be implemented within a given social-ecological system or type of institutions (Angelstam et al. 2003b, Berkes et al. 2003, Lazdinis and Angelstam 2004, Sandström et al. 2004). In other words the active adaptive ecosystem management feed-back loop from research to policy and management and back again often does not take place (Lee 1993, Ludwig et al. 1993). Finally, due to logistic and economic constraints as well as the scientific challenges involved in measuring high-quality biological response variables such as fitness parameters, the traditional ways of doing natural science often do not lend themselves to studies at the scale of landscapes and regions (e.g. Balée 1998, Egan and Howell 2001, Boutin et al. 2001, Kohler 2002, Kinzig et al. 2003). Addressing the issue of landscape-scale conservation targets can be seen as big holistic science, or macroecology (Brown 1995), and, while there has been some progress (e.g. Gunderson et al. 1995, Gunderson and Pritchard 2002), it remains an area in which little work has been done.

Our experiences come from the World's boreal forests, commonly used as the woodshed of regions of economic growth. The boreal forests are relatively simple ecosystems compared to, for example, tropical forests. For this very reason they are also relatively well known (e.g. Shugart et al. 1992, Hansson 1997, Burton et al. 2003). BorNet (<www.bornet.org>), a network of scientists and managers interested in promoting research on conservation targets (Angelstam et al. 2004a), has organised a number of workshops to identify knowledge gaps (Whittaker and Innes 2001a, b, c, Leech et al. 2002). The project identified knowledge gaps associated with the following questions (Leech et al. 2002, Whittaker et al. 2004): How much and where should forests be fully protected in reserves? How can management effectively re-create, restore, or maintain important features required to conserve biodiversity? How can we determine the effectiveness of these biodiversity conservation efforts? The workshops identified a surprising number of knowledge gaps, and revealed just how scanty our knowledge of biodiversity in boreal forests really is.

The questions posed by BorNet reflect the typical questions asked by managers: How much forest do we need to set aside in reserves to meet biodiversity goals? How much unharvested woodland do we need to leave in the matrix surrounding the forest reserves? How many trees should be left when a stand is cut? What are the important forest features to restore and how much is required? Hence, there are clear indications from forest managers but also policy-makers (Rametsteiner and Mayer 2004), the industry (Hebert 2004) and forest-product retailers (Djurberg et al. 2004) that there is a need for landscape-scale research to address the question "How much habitat is enough?".

The aim of this paper is two-folded. First we suggest a scientific approach that would contribute to filling the knowledge gaps identified in order to develop concrete quantitative targets for conservation at the scale of forest management units. Second, we propose strategies for the efficient international co-operation amongst scientists, managers, and policy-makers that is needed to apply approaches for the implementation of ecologically-based targets for the sustainable use of boreal forest resources. Although the focus is on the boreal forest, we also include hemiboreal and mountain forests because they share similar components, structures and processes (e.g. Mayer 1984, Shugart et al. 1992).

Targets and levels of ambition

The deceptively simple question "How much forest is enough?" does not have a straightforward answer. Forest ecosystems constitute a gradient from "natural" forests, which maintain all components, structures and functions of forests (e.g. Peterken 1996), to fibre crops such as poplar plantations on former agricultural land. All human activities, at least with an historical perspective, probably move forest landscapes along such gradients (Williams 2003), even when the management aims are designed to maintain "natural forests", as in British Columbia, Canada. In fact, all forests on Earth have, to some extent, been affected by various human activities for many centuries, often without apparent negative effects on biodiversity (e.g. Balée 1998). In remote areas, these activities take the form of hunting, reindeer herding, local floodplain clearance, and harvesting of hay along small streams. In North America, aboriginal populations have cleared forests and used fire as a management tool for thousands of years (e.g. Pyne 1984, Williams 1989). The period of industrial exploitation of the majority of European forests has lasted several centuries, starting with high-grading and the removal of large trees and followed by large-scale clear-felling and the gradual development of silvicultural systems aimed at sustainable timber production (Angelstam et al. 1995).

Currently, however, the concept of sustainable forest management is in the process of being redefined both in policy and practice. Hence, from a long-lasting focus on classic sustainable timber management (Schlaepfer and Elliot 2000), there is an ongoing transition toward multi-functional ecosystem management (Meffe et al. 2002), ecological sustainability (Goodland and Daly 1996) and, ultimately, sustainable resilient social-ecological systems (e.g. Berkes et al. 2003). Depending on the country and region this transition results in the consideration of new ecological products and processes such as the maintenance of viable populations, biodiversity, or protective functions (Kräuchi et al. 2000, Larsson et al. 2001, Lindenmayer and Franklin 2003, Angelstam et al. 2004b).

As a consequence, one can formulate at least four different target levels for the conservation of biodiversity (Table 1). An obvious first level is that the compositional elements of biodiversity are maintained. This is represented by occupancy of one of several species in a given landscape. Occupancy is often the only information available for conservation areas such as the Swedish Woodland Key Habitats (Hansson 2001) and other protected areas. However, many national and regional policies (e.g. Boyce 1992,

Table 1. The focal spatial scale of management increases with the level of ambition of conservation targets.

Level of ambition	0.01 km^2	1 km^2	100 km^2	10000 km^2	1000000 km^2
occupancy	vascular plants	small birds	most mammals		
population viability		a plant population	a songbird population		
ecosystem integrity				minimum dynamic area in boreal forest	wolf/caribou interaction
ecological resilience					movements of ecoregions under climatic change

Schmiegelow and Hannon 1993, Mönkkönen 1999, Angelstam and Andersson 2001) are explicit about the fact that occupancy is insufficient, and indicate that "all naturally occurring species should maintain viable populations". A second target level is therefore to ensure population viability over long time (e.g. Sjögren-Gulve and Ebenhard 2000). An increase in the threshold amount of habitat needed for probability of occupancy vs probability of breeding (Angelstam 2004) suggests higher conservation costs of this increased target level. The word "all" in such policies makes it almost imperative to define thresholds for a suite of efficient focal or umbrella species (Lambeck 1997, Mönkkönen and Reunanen 1999, Roberge and Angelstam 2004). As ecosystems are open and dynamic, the total area needed to ensure the persistence of species increases with the time period associated with the term "viability". Hence, a third level is to ensure ecosystem integrity and health (e.g. Pimentel et al. 2000). To achieve this, minimum dynamic areas (Pickett and White 1985) are needed that continuously provide habitat for many viable populations over multiple spatial scales, as well as for the interactions among them (e.g. Bengtsson et al. 2003, Angelstam et al. 2004c). Finally, a fourth target level may be to ensure long-term ecological sustainability, or ecological resilience (Gunderson et al. 1995, Gunderson and Pritchard 2002). Resilience is measured as the magnitude of disturbance that can be absorbed before the system is unable to recover to its previous state, resulting in a restructuring of the ecosystem with different controlling variables and processes. For each of these target levels for the maintenance of biodiversity, there is a continuous gradient with increasing spatial dimensions including specific thresholds for the composition, structure and function of biodiversity. There is thus a suite of targets that can be specified for the maintenance of biodiversity in an area, each target representing an increasing probability of maintaining a functional ecosystem.

A procedure for establishing and communicating conservation targets

Here we present an approach for formulating scientifically-based conservation targets at different spatial scales. We elaborate six basic steps for formulating occupancy targets for conservation, as suggested by Angelstam (2001), which aim at combining management regimes with biodiversity requirements into assessment systems.

Step 1. Stratifying forests based on their natural dynamics

The presence of different disturbance regimes in a forest implies different selection pressures on species, different habitats and a diversity of processes. It is therefore necessary to stratify the broad cover types of the boreal forest into different baseline disturbance regimes such as succession after large-scale disturbance, gap-phase dynamics in the absence of large-scale disturbance and cohort dynamics with frequent, low-intensity fires (e.g. Angelstam 1998), but also the different characteristic developmental stages after disturbance (e.g. Haapanen 1965, Thomas 1979, Angelstam 2002, Angelstam and Kuuluvainen 2004). Disturbance regimes vary according to the complex and regionally varying interaction between biogeophysical and macroclimatic conditions (Pyne 1984, Agee 1993, Angelstam 1998, Haeussler and Kneeshaw 2003) and result in forests with different structure in terms of tree species and age class distributions, both within stands and among stands in landscapes. This step provides insight into the selection of species and functional groups of species as response variables. As a consequence this may also be very relevant to determining the scale upon which the indicator should be maintained as large disturbance events means maintenance is only possible over large regions.

Step 2. Understanding a landscape's historical position (position on x-axis)

Different kinds of sociopolitical and economic systems in particular regional contexts often result in different effects on the biosphere (Balée 1998). The second step is therefore to understand the relationship between economic development and the degree of deviation from the benchmark provided by natural dynamics. This requires an understanding of the historical spread of different waves of anthropogenic impacts on the forest (e.g. Williams 2003). Several studies have identified characteristic steps in the historic development of forest use (see Angelstam et al. 2004b). A common division of phases of forest use is 1) large intact areas with benchmark conditions, not necessarily without people (Balée 1998, Stevenson and Webb 2004), but essentially without any major changes in the composition, structure or function of the forests; 2) high-grading or selective harvesting of the most desirable timber species; 3) large-scale unsustainable exploitation, in the form of "tree-mining", typical for most remote parts of the boreal forest today; 4) economically sustainable sustained timber yield being typical for parts of northern Europe; and 5) the current efforts to include new values such as the maintenance of biodiversity (e.g. Raivio et al. 2001). Active adaptive management of forest ecosystems in the form of sustainable ecosystem management (e.g. Duinker and Trevisan 2003, Burton et al. 2003) can be viewed as a future aim, and thus a sixth phase. This means that a wider array of forest values besides timber must be maintained including biodiversity and ecosystem services, which is beginning to be introduced in some jurisdictions, such as some National Forests within the USA (e.g. Lee 1993). When drawn on a series of maps, the gradual expansion of these historical phases form isolines (e.g. Angelstam 1998, Imbeau et al. 2001) facilitating the identification of landscape replicates in regions with different baseline disturbance regimes (Isachenko and Reznikov 1996).

From a management perspective, these five stages can be translated into semi-quantitative indicators of degree of human intervention. Examples are time since anthropogenic transformation of a particular forest type began in the area (e.g. Williams 2003), management intensity measured as transport infrastructure (Angelstam et al. 2004d), tenure system, match between silvicultural practices (including harvesting, regeneration, and management methods) and forest disturbance regimes (e.g. Angelstam 2002), number of management rotations (Angelstam and Dönz-Breuss 2004), and length of rotation (Thomas 1979). It is important to have the ability to place stages of human development on a long time continuum because although forest management attempts to maintain wood supply over multiple forest rotations, maintenance of biodiversity tends to be considered over the short-term. This can lead to a "shifting baseline" syndrome whereby local management history affects our perception of what is "natural" or possible. For example, a forest manager in Sweden finds it hard to believe that Swedish forests ever had the proportion of old deciduous trees seen in boreal forests with a short management history such as in Canada and Russia. Similarly, forest managers in Canada and Russia find it hard to believe that their practices could lead to the paucity of downed woody material so evident in Scandinavian managed forests despite the fact that the harvesting practices are similar in the two countries. The difference is one of duration of human activity.

Natural forest components which change in relation to these forest history phases include snags, coarse woody material, certain tree species and large trees at the stand scale (e.g. Angelstam and Dönz-Breuss 2004, Shorohova and Tetioukhin 2004), and the proportion of old-growth forest and large unbroken areas at the landscape scale (Yaroshenko et al. 2001). These components can then be related to the steps in the history of forest use. Siitonen (2001), Yaroshenko et al. (2001) and Angelstam and Dönz-Breuss (2004) show how forest history can determine forest structure at multiple spatial scales. Forest structures closely associated with the meta-species and being the most time- and cost-efficient to measure could be density of large trees with bark (for epiphytic lichens), dead/dying trees with bark (for most woodpeckers and saproxylic insects), decayed logs (for certain bryophytes and the regeneration of certain tree species) and proportion of mature old, closed-canopy forest and the landscape scale (for certain birds, litter invertebrates etc.).

Step 3. Finding representative response variables (y-axis)

In this step, response variables – such as species or ecosys tem processes – that are likely to be affected by loss of natural forest structures should be identified (Table 2). For species, we suggest the use of "metaspecies", i.e. groups of species classified according to specific combinations of habitat requirements for reproduction and feeding. This is analogous to Haapanen's (1965) approach used with birds in Finland, to the life form concept used by Thomas (1979) and Gillingham and Parker (2001), and to the concept of "functional types" (Wiens et al. 2002). We thus agree with Copolillo et al. (2004) who argued for clear justification and that selection criteria should accompany any focal species strategy. Such metaspecies or functional groups thus allow 1) conducting macroecological analyses spanning several biogeographical regions, and 2) ensuring that the range of habitat variation covers the full spectrum from intact benchmark areas to extensively altered landscapes, and not only habitat configuration. We recommend that research on the topic should be conducted at the landscape scale and over several years (Stephens et al. 2003).

Table 2. Examples of elements of biodiversity at different spatial scales.

Biodiversity component:	Tree scale	Stand scale	Landscape scale
Composition (species)	Saproxylic invertebrates and fungi	Cyanolichens, invertebrates and small birds	Large birds and mammals
Structure (habitats)	Dead wood, old large trees	Tree species and age classes	Amount of different stand types and their spatial and size distribution
Function (processes)	Mycorrhizal symbiosis	Fire, nutrient cycling	Dispersal, browsing and predation

The following groups are provided as examples of metaspecies with habitat requirements that include the landscape scale and that have evolved to fill the different patch types of the boreal forest biome: 1) guilds of species with particular physiological adaptations that have evolved to cope with certain environmental conditions (e.g. cyanobacterial epiphytic lichens); 2) guilds of species or circumpolar species or genera that require habitats that are not compatible with intensive forest management (e.g. species requiring coarse woody debris of different decay stages and diameter classes, large or old trees, slowly growing wood, very old interior forest conditions, burned forest, certain tree species, or combinations thereof); 3) guilds of species that are sensitive to the loss of large, relatively unbroken woodland (e.g. species with very large area requirements due to large body size or to a predominantly carnivorous diet).

It is also important that the functional elements of biodiversity are maintained. Thus, one could use certain ecological processes as dependent variables. Altered fire frequencies (Niklasson and Granström 2000) and hydrologic regimes (see Degerman et al. 2004) are examples in boreal forest. Less obvious examples are disruption of predator-prey relationships such as factors favouring generalist predators that have reduced the breeding success of species associated with extensively forested landscapes (Kurki et al. 2000) or introduced predators (Nordström et al. 2003), and browsing by superabundant wild herbivores on certain trees species that changes forest composition (Angelstam et al. 2000, Ripple and Beschta 2003). Additionally, air pollution is causing leaching of nutrients such as nitrogen from sensitive soils and changing vegetation in some regions (Sverdrup and Stjernquist 2002). Socio-economic changes in rural communities followed by land abandonment constitute another example (Angelstam et al. 2003c, Mikusiński et al. 2003).

Step 4. Analysing biological response to gradient in forest degradation

This step involves testing hypotheses about non-linear responses to habitat gradients by establishing relationships between steps 2 and 3 for each forest type defined in step 1 (Fig. 1). This could be done by relating response variables (e.g. abundance, fitness, or population viability) of the selected metaspecies ensemble to the position along historical continuum of forest use, or to a surrogate measure for that position (e.g. proportion of pristine forest area, amount of snags or dead wood). We argue that rather than finding an exact threshold, the idea should be to establish intervals along the resource axis that represent the three zones of risk for the conservation of metaspecies of target ecological processes: clearly inadequate, marginal, or clearly suitable conditions (cf. Phillis and Andriantiatsaholiniaina 2001, Angelstam et al. 2003a).

Such analyses can be made in either of the following two main streams. The first involves the collection and analysis of original data. Analyses can hence be conducted using both traditional empirical approaches and by exploring the effects of different levels of habitat loss on species with certain combinations of life history traits using modelling and simulation. In both cases the x-axis (independent variables) would represent forest structures at spatial scales which are relevant for the hypothesis that these affect species, or ecosystem functions, on the y-axis (dependent variables). This is analogous to the dose-response type relationships commonly used in ecotoxicology (Connell et al. 1999). Special efforts are, however, needed to ensure that the dose varies sufficiently for a response to be expected. Such analyses can be done at several levels of scientific scrutiny. Systematic collection of observations and their analytical description leads to more precise and testable hypotheses, which can then be evaluated using mensurative (comparative) or manipulative experimental approach (see Krebs 1999, Haila 2002). Kohler (2002: 212) uses the concept "practices of place" whereby it is "…the arrangement of spatial elements that provides critical evidence of relations between creatures and their environment…". Places are thus to the field ecologist what experimental setups are to laboratories. "Practices of place" are alleviated by co-ordinated co-operation among case studies made in replicated forest and land use history gradients. This means that studies are designed based on the idea that temporal gradients, such as the decline of dead wood over time with the historic development of forest management (e.g. Linder and Östlund 1998), can be replaced with spatial gradients (e.g. Rouvinen et al. 2002, Angelstam and

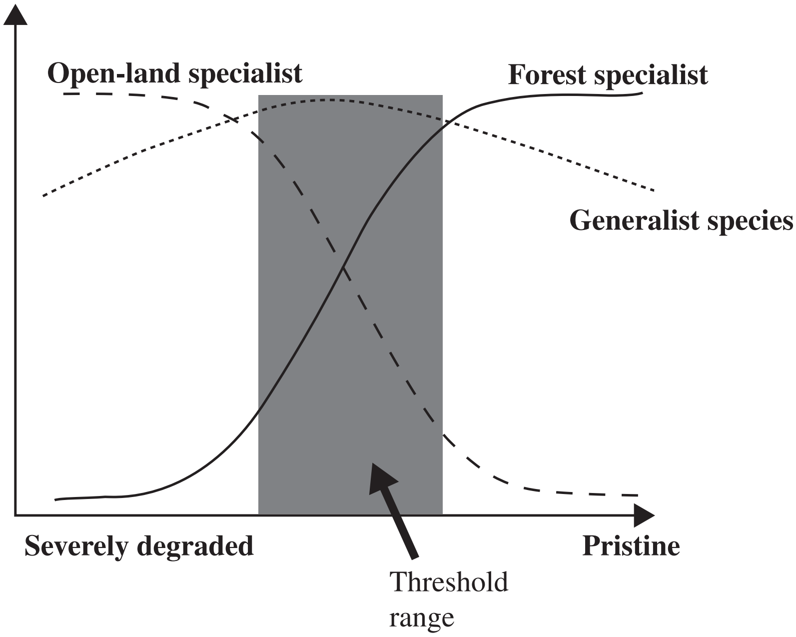

Fig. 1. Responses of three hypothetical species (or metaspecies – see text) to a gradient from intensive harvesting and ecological degradation to pristine forest mosaics. Response curves are dramatically different, but some of these patterns may have been undetected if sampling had been restricted to a short portion of this gradient. Sampling portions where responses change most suddenly (threshold range) is particularly critical to learn from these responses and to make relevant adjustments to management regimes.

Dönz-Breuss 2004). This approach has also been called the ergodic hypothesis.

The second method is to assess a hypothesis by synthesis of the available information, whereby the results of a series of published studies are evaluated in relation to a particular hypothesis. Given that there are a sufficient number of published studies, quantitative syntheses from a series of comparative and experimental studies can be conducted to assess how general the threshold levels are. A quantitative synthesis that analyses a set of analyses is called a meta-analysis (Hunt 1997). Major methodological advances occurred in the 1970s, enabling not only the determination of whether or not an effect was present in a set of studies, but also the estimation of the magnitude of that effect (Rosenberg et al. 2000).

Step 5. Communication between science, practise and policy

Finally, when results from the first four stages are available, there is a need to identify biodiversity "currencies" to communicate the status of biodiversity across different spatial scales. When doing this it is important to consider the wide range of different systems of property rights and management cultures found in the boreal forest. As an example, Uliczka et al. (2004) suggest that sufficiently well-known species should be preferred as "messengers" to communicate the results to managers and other stakeholders. The more managers and other stakeholders can relate to such species, the more effective they are. For example, game species such as the capercaillie *Tetrao urogallus* have widespread appeal in Europe (e.g. Suchant and Braunisch 2004). Hence, at least some of the response variables identified in Step 3 should assess the status of sufficiently charismatic and/or appealing to stakeholders to be used in communicating results to managers and other interest groups. Such an approach was adopted successfully by the Royal Society for the Protection of Birds when the osprey *Pandion heliaetus* was used to communicate the success of their fine-filter conservation strategy to the British public. That being said, such "messengers" must act as umbrellas for less charismatic species to be included in conservation strategies, i.e. their habitat and spatial requirements should be such that their protection should in turn allow maintaining viable populations of many other species (see Roberge and Angelstam 2004).

Step 6. Combining information from different indicators selected

Because several currencies may be relevant to biodiversity conservation in a given area, the final step is to determine how to combine or to choose among these various "currencies" to set conservation targets. This is where ecological data and biodiversity values must be confronted with other, potentially conflicting forest values. No matter how good the science is behind conservation targets, land-owners and land managers determine the ultimate fate of conservation strategies.

Too often, researchers accomplish most of the preceding steps in isolation and then present their results to decision-makers. Another model, which we propose here, is to form adaptive management teams (Boutin et al. 2002) whereby researchers, land managers and policy-makers share decisions and responsibilities toward the success or failure of the strategy they jointly adopted.

Discussion

The boreal forest as a time machine

The boreal forest provides a unique resource for the gradual development of performance targets to promote sustainable forest ecosystem management as outlined above. It is the only forest biome on the Northern Hemisphere where the full gradient of alteration, from large intact benchmark areas to altered forest in need of restoration exists (Hannah et al. 1995, Angelstam et al. 1997, Yaroshenko et al. 2001, Aksenov et al. 2002, Drushka 2003, Burton et al. 2003, Lee et al. 2003). The reason is the steep gradient in land use history whereby the gradual exploitation and intensive management of boreal forest resources has spread like a tidal wave from areas of high demand to more and more remote regions, and with clear effects on biodiversity (Mikusiński and Angelstam 1998, Angelstam et al. 2004e).

These northern forests hence represent a unique research opportunity (sensu Kohler 2002), enabling retrospective studies that substitute space for time. The boreal forest biome is, however, huge, and within some regions or countries the variation is insufficient to allow for such an approach. Using this natural laboratory as a "time machine" to understand the effects of the human footprint on forests therefore requires international co-operation (Table 3; for a more detailed description of different boreal case studies, see Appendix).

Scientific approaches – methods and pitfalls

Traditional ecological studies are usually reductionist and specialised providing high precision at fine scales but limited value for inference over broader scales such as landscapes and regions (Kohler 2000). Brown (1995) argued that to address regional and global problems of environmental change and decreasing biological diversity, macroscopic studies that trade off the precision of small-scale experimental science to seek robust solutions to big problems are required. The loss of habitat in general and of large forest patches with natural composition, structure and function in particular, is a good example of such a problem. However, the cost and logistical challenges associated with replicated, large-scale experiments limit the spatial and temporal range of application (Carpenter et al. 1995). For example, Boutin et al. (2001) acknowledged that the Achilles heel of the Kluane project (Krebs et al. 2001) was the absence of replication.

Additionally, in regions with a long and intensive history of forest use, or in regions where the history of exploitation is relatively recent, certain parts of the axis representing the gradient from altered landscapes to benchmark areas simply do not exist. For example, when determining the number of habitat patches sufficiently large for forest specialist species in Finnish managed forest landscapes, Mykrä et al. (2000) found that their availability was limited for most species, and hence also for experimentation. The same is true for landscapes with different amounts of dead wood, unless conscious efforts are made to obtain a broad and continuous gradient (Bütler et al. 2004a, b). Given the relatively high number of circumpolar species or genera in the boreal forest, there are major opportunities to compare forest processes along extensive gradients in anthropogenic disturbance.

Table 3. The approximate temporal progression of different forest history phases from the perspective of biodiversity in boreal and hemiboreal forest. Benchmark conditions are defined as a landscape with only local human use of resources (e.g. Yaroshenko 2001). Selective harvest is defined as high-grading of certain species or dimensions of trees and exploitation means that all dimensions are used. Sustainable yield timber production is defined as the use of harvesting, regeneration and stand treatment methods ensuring maximum sustainable yield. For details about the 8 case studies mentioned in the table, see Appendix.

Case study	Benchmark	Selective harvest	Exploitation	Sustained yield	Rehabilitation and re-creation
Scotland	Pre-Roman	Medieval	18th century	20th century	Present
Central Sweden	Pre-Medieval	Medieval	ca 1750	Present	Present
Finnish-Russian border	Present	Late 1800s	Present	Present	Present
Quebec	Variable depending on forest type	19th century	Present	Present	
New Brunswick	Pre-1800s	Early 1900s	Present	Present	
Great Lakes	Pre-1800s	19th century	1850s to present	Present	
Alberta	Pre-1950s	Logging of white spruce in 1950s	Present		
Pechora-Ilych strict reserve	Present				

Sampling suitable response variables along gradients of relevant length can be viewed as establishing dose-response curves (Connell et al. 1999). This means that thresholds are considered as zones of low/high risk, or uncertainty, along the axis describing the independent variable. Rather than showing discrete shifts at a certain value, there is a region on the habitat axis in which the rate of change is accelerated in relation to points away from this threshold interval (Wiens et al. 2002, Angelstam et al. 2003a; Fig. 1). It is the challenge of finding opportunities of sampling the full the gradient in habitat change that requires further attention from researchers, managers, and policy-makers.

A coarse-filter approach to derive management targets would be to use the "historical range of variability" (HRV) (e.g. Egan and Howell 2001: 7, Davis et al. 2001: 30) as determined by natural disturbance regimes. The procedure would be to run a series of forest projections based on a stochastic disturbance regime and tabulate the range of values observed for an attribute of interest, say old forest. We could then establish that our target for old forest is somewhere in that range and companies must show long-term forest projections that meet or exceed this target in order for their forestry activities to be considered sustainable, and a monitoring program should be used to determine if they are meeting the target. Like Davis et al. (2001), we view the HRV approach as a goal to be satisfied on a large regional scale. All local management may not be within HRV but desired future conditions for the region can use HRV as a broad target for management. This notion also applies to fine-filter (i.e. species) targets.

Extinction debts and the direction of change

Nonlinear response to habitat loss is not the only ecological surprise that managers may have to face. The extinction of a local population may not occur immediately following habitat loss or fragmentation, and is also strongly influenced by stochastic processes. The time period during which a species persists after habitat destruction is called the time delay or the extinction timelag. Theoretical models show that this time delay is greatest for species for which the environmental condition is near the threshold for persistence (Hanski 2000). The time delay also depends on species-specific factors. These time delays often result in underestimates of the risk of extinction. Following the deterioration of habitat in a region, there may be a number of species that survive but which will inevitably be extirpated as stochastic processes take effect. The number of species that are expected to become extinct due to past adverse environmental changes is called "extinction debt" (Tilman et al. 1994), although this often reflects extirpation rather than extinction. Before the extinction debt is paid by actual extinction, the relative proportion of rare species in the total number of species will increase.

Thus, after deterioration of a habitat patch network there are a number of species that are likely to go extinct, although they have not yet done so. Within community ecology, this phenomenon was earliest described as faunal collapse or relaxation (Brown 1971), and has been elaborated both theoretically and empirically with respect to loss of species from reserve systems isolated by conversion of surrounding habitats (e.g. Miller 1978, Glenn and Nudds 1989). While a strict island analogy is overly simplistic for most forest management applications, for species reliant on habitats particularly vulnerable to traditional forestry practices, such patterns may still be expected.

On the other hand, boreal forest organisms may be a selected group of species where good dispersal abilities are characteristic of many if not all taxa because of the dynamic nature of the boreal biome. For example, only 20000 yr ago today's Canada was devoid of boreal forests (Delcourt and Delcourt 1991) and all species that presently occur in the northern forests must have been able to re-colonise their current ranges from glacial refugia further south. This provides some hope that re-colonisation is possible in degraded landscapes if species persist elsewhere.

The critical need for reference areas

Targets need to be defined in relation to a benchmark or reference point. Within the boreal forest there are at least two visions for biodiversity. The naturalness concept (Peterken 1996) represents one. Here, the "natural" state refers to areas without large anthropogenic impacts and this vision is often referred to as the natural disturbance regime paradigm, whereby the nature of the ecosystems in a region are determined by the natural range of variability of disturbances and their consequences (e.g. Angelstam 1998, Bergeron et al. 2001, 2002, Kuuluvainen et al. 2002, Angelstam and Kuuluvainen 2004). The second vision is represented by pre-industrial cultural landscapes (e.g. Kirby and Watkins 1998), and the pre-contact North American landscapes with aboriginal human populations (Stevenson and Webb 2004).

Without benchmarks found in reference areas it is virtually impossible to formulate ecologically based targets. How should a benchmark landscape be selected? Even in the immense boreal forest biome, benchmark areas are not present in each ecoregion (Aksenov et al. 2002, Lee et al. 2003). As each region or country usually represents a narrow range of natural variation, co-operation among regions with different biodiversity status and land use history is needed (Angelstam et al. 1997). Indeed, researchers from extensively altered boreal forest regions need to find appropriate benchmark areas and thus, to collaborate with researchers working in such regions. Finland and Russian Karelia have long established such a relationship. Conversely, regions with a long history of intensive forestry provide an invaluable source of information for researchers working in less altered regions (e.g. portions of Canada and Russia – Aksenov et al. 2002, Lee et al. 2003).

At first glance, the boreal forest may seem huge and without threats to its biodiversity as a whole. However, it is estimated that the remaining proportion of more or less intact boreal forests is only 20% while for the hemiboreal the figure is 2% and for the nemoral, only 0.2% remains (Hannah et al. 1995). Recent studies (e.g. Yaroshenko et al. 2001) show that even in European Russia a surprisingly small area (13%) of what could be called intact natural forest landscapes remains today. Further west in Europe such intact productive areas no longer exist. Even when considering all the productive boreal forest in Sweden, only ca 5% can be considered to have a high conservation value (Angelstam and Andersson 2001). In southern Finland, the proportion of old-growth forest is 0.5% of the total land area (Hanski 2000). In Scotland, the original forest cover has largely been lost, with only ca 1% left and many of the characteristic species, such as wolf and beaver, extirpated. The maintenance of boreal forest biodiversity is therefore evidently a matter that concerns the European boreal forest as a whole.

Given what has happened in the centres of economic development, such as in western Europe and southern Canada, it is important that people from both the economic centre and the periphery share the biological knowledge gained from these large-scale changes in boreal forest biodiversity (Fig. 2). In the former, the maintenance of biological diversity requires the restoration of habitats to reach the requirement for the full restoration of species in the future. In the latter, forest management should not be intensified to the point that important forest components fall below the threshold and species start to be lost.

A vision for the future – the Boreal Atlas

For the maintenance of boreal forest biodiversity, it is crucial to make sure that what we know is widely communicated. Effective communication and mutual learning can mitigate the frequently occurring gap between policy and practice. Maps are efficient in this respect; they can delineate and describe different properties, allow integration of complex information, show data gaps, are trans-cultural, and have heuristic value. A simple way of communicating biodiversity status and trends is to discuss the fate of particular species, for examples by presenting maps of past and present distributions. Presenting the amount of certain habitat structures in relation to thresholds is another effective tool for communicating biodiversity status in terms that the general public finds easy to understand.

An obvious starting point would be to illustrate indicators suggested by the MCPFE such as dead wood or landscape-level spatial pattern of forest cover (Rametsteiner and Mayer 2004). As an example Stokland et al. (2003) reported the status of a number of MCPFE indicators for Norway, Sweden, and Finland. The recently published data of large intact boreal forest areas based on remote sensing illustrates the potential for beginning to do maps for the whole boreal forest.

Reactive or proactive conservation planning?

With an international perspective, depending on the regional history of land use, it is in principle possible to work with different combinations of forest management, protected areas, and habitat re-creation to maintain forest bio-

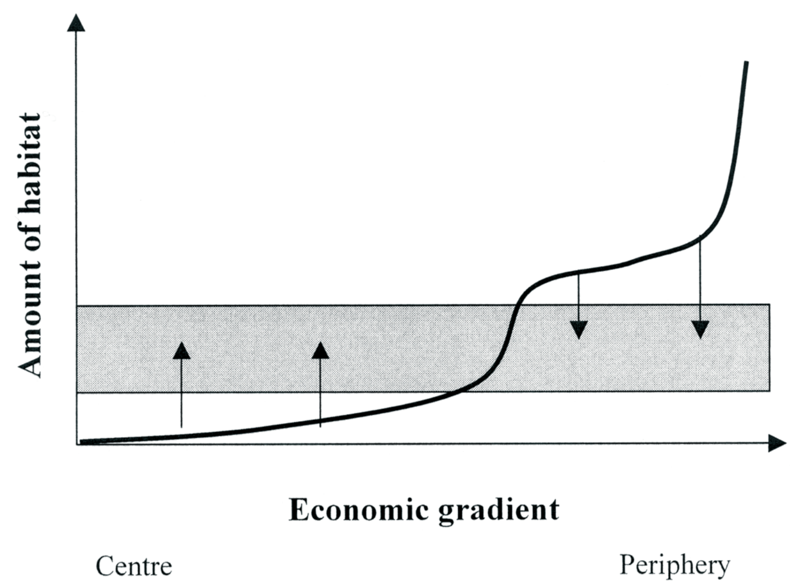

Fig. 2. Illustration of the problem of trying to strike the balance between forest use and nature conservation in boreal forests from the centre to the periphery of economic development. The black line illustrates the range of remaining amounts of authentic habitat along this gradient. The darker interval represents the tentative range of threshold values to be exceeded for the maintenance of viable populations of forest specialists with large area requirements. Finally, the arrows represent the need for restoration in the areas with a long history of intensive land use, and the need for pro-active planning to avoid repeating mistakes as the economic "frontier" spreads to the periphery.

diversity. However, the probability of success, and degree of freedom to choose among different combinations, is considerably higher when the land-use history is short. It is thus vital to realise that some regions may be limited in the range of possible tools for biodiversity conservation due to a long history of land use. This is particularly evident in Europe when contrasting forestry in western and eastern Europe, and should be considered as forestry is rapidly becoming more intensive in the Baltic States and Russia (e.g. Lopina et al. 2003, Kurlavicius et al. 2004). We have to realise that the goals that are discussed in relation to mechanisms, such as in forest certification standards, are political and not ecological. If we do not realise this, there is a considerable risk that even more near-natural forests in eastern Europe will be transformed and biodiversity lost in a very near future, as has happened in Sweden and other countries in western Europe in the past.

The recent mapping of the World's last intact forest areas (e.g. Bryant et al. 1997, Aksenov et al. 2002, Lee et al. 2003) shows that the boreal forest is one of the few ecosystems still having areas of large seemingly intact forests. Unlike the situation in northwestern Europe, where no such forests remain (Yaroshenko et al. 2001), conservation planning could, and should, be undertaken before commencing logging and other forms of resource extraction.

The obvious first step is to ensure ecosystem representation at the landscape scale within a particular ecoregion (e.g. Margules and Pressey 2000). Second, the appropriate structure, species composition and ecological processes with indicators and targets should be formulated at the landscape scale. Finally, at the scale of stands and riparian zones, there is a need to identify the nature and types of forest structures that should be retained. Thresholds for how much retention should take place at multiple scales are thus needed (Hebert 2004), as well information on the spatial configuration of forest that is needed to maintain the functionality of habitat networks.

Adaptive management teams and international co-operation

Active adaptive management can be defined as a systematic approach to adaptive management that involves the deliberate designation of control areas that enable results of management actions to be better interpreted. Ideally, an active adaptive management approach with iterated assessment and corrective action should be applied through continuous mutual learning by scientists, policymakers, managers and other actors until the targets are reached (Gunderson et al. 1995, Meffe et al. 2002). In reality, however, we are usually far away from this ideal situation (Pimentel et al. 2000, Duinker and Trevisan 2003, Trauger et al. 2003). While adaptive management is frequently advocated, it is frustrated by a number of factors. These include insufficient care in the experimental design associated with active adaptive management, and a disconnection in the adaptive management cycle. This may be due to lack of knowledge, resources or will, such that management actions may not be modified, in spite of emerging knowledge (Gunderson et al. 1995). Active adaptive management must take place within the ecosystems of interest for a particular manager or owner. For forest ecosystems, this usually means at the scale of villages actual landscapes, forest management units or river watersheds. Such physical landscape units can be viewed as replicates within an ecoregion. To actually assess the components of biodiversity, one needs to conduct empirical assessments using repeated measurements of relevant indicators, which should link to the management tools and be based on quantitative targets at multiple scales within the forest management unit or landscape.

Where do scientists fit here? Naess (1974) distinguished between the understanding of science within itself and in connection with the development of societies. Traditionally, the philosophy of science deals with the former, discussing theoretical, logical and methodological problems. However, particularly in applied sciences, there is a need to understand the role of science as a part of the ongoing debate in society. Naess (1974: 136) argues that scientists may both "…be a formidable agitator and a responsible and intellectually sound researcher." Lee (1993) elaborates further on this and argues that science provides a navigational aid to practise adaptive management or deliberate long-term experimentation with the economic uses of ecological systems to learn what works and what does not. This aid he calls the "compass" that points in the right direction by applying the rigor of analysis, verification and correction to our public policies. The other is the "gyroscope" of continual democratic debate, or bounded conflict. Together, the "compass" of adaptive management and the "gyroscope" of bounded conflict can bring about social learning in large ecosystems over the decades-long times needed to move towards sustainability. There are, however, many obstacles (e.g. Lee 1993, Gunderson et al. 1995, Mills and Clark 2001, Berkes et al. 2003). Kinzig et al. (2003) offer a number of recommendations, including restructuring of science curricula and establishment of science-policy forums with leaders from both arenas, and specifically constituted to address problems of uncertainty.

Turning science into practice requires collaboration at all steps, time to build mutual understanding, willingness to change, and a clear presentation of tradeoffs. There is also a need to provide leadership, inspiration, and co-ordination. Adaptive management teams focused on a particular case study are an efficient approach, because they provide a forum for the involvement of a variety of stakeholders including ecosystem managers, the public and policy makers.

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Appendix

To illustrate the range of conditions with respect to the maintenance of biodiversity in the boreal forest we review a number of ongoing landscape-scale studies in both the Old and the New World. For each case study we briefly describe the biome, its history, as well as the current management regime and related biodiversity conservation issues. We used this information to illustrate the predictability, in a broad sense, through which landscapes are gradually altered. For detailed analyses of species' responses it is, however, also important to take into account other kinds of gradients such as those related to macroclimatic and biogeographic differences.

The Old World

Scotland

The native forests of northern Scotland form the westernmost boreal forests in the Old World. The boreal forests are typically dominated by Scots pine *Pinus sylvestris*, with small quantities of birch *Betula pubescens* and juniper *Juniperus communis*. The principal boreal forest vegetation type is Scots pine – *Hylocomium splendens* woodland (Rodwell 1991). In warmer humid areas along the west coast, oakwoods predominate, with both sessile and pedunculate oak being present *Quercus petraea*, *Q. robur*, respectively. Alder *Alnus glutinosa* may be locally common, especially on wetter sites. In addition there are far larger areas of plantations of exotic conifers, mainly Sitka spruce *Picea sitchensis*, but including Douglas fir *Pseudotsuga menziesii*, larch *Larix* spp. and lodgepole pine *Pinus contorta*.

The forests of Scotland have had a long history of degradation. The pine-dominated Caledonian forest previously covered > 1.5 million ha of the Scottish Highlands (Anon. undated) but, today, they cover ca 16000 ha, over half of which consists of very open pine woodland. Much of this remaining resource is heavily grazed by deer, preventing any recruitment of young trees. Clearance of the Caledonian forest started in Neolithic times. The broadleaved woodlands of the lowlands were largely gone by the time of Agricola's Roman invasion of 82 BC. It progressed slowly until the 17th century, when large-scale harvesting began (Steven and Carlisle 1959, Aldhous 1995). The timber was used for ship-building, manufacture of wooden pipes and as fuel for iron-smelting and glass making. Replanting sometimes followed harvesting, with records of selected pine seed being used as early as 1613 (Steven and Carlisle 1959). Planting and forest restoration occurred at some of the estates seized after the 1745 uprising – with variable actual success. However, in many cases, the land was converted to sheep range. In the 19th century, the advent of refrigerated transport combined with an increase in sporting interests resulted in many areas being converted to what has become known as "deer forests", where management was focussed on providing trophy stags from open hill habitats. As a result, by the 1913, British-grown timber could only supply 7% of the nation's needs (Wonders 1991). This reliance on overseas (particularly Canadian and Baltic) timber was disrupted by both World Wars, resulting in the heavy exploitation of the remaining forests, primarily by specially recruited Canadian lumbermen (the Canadian Forestry Corps). Following the two World Wars, a major state project to restore timber resources saw many remaining forest areas converted to plantations of exotic species, as well as massive afforestation programme in open unwooded hill areas. This process largely ended in the 1990s, to be replaced with an increasingly biodiversity-focussed effort to restore and expand native and boreal woodlands.

Maintenance of biodiversity in the boreal forests of Scotland must thus pursue a twin approach. Firstly, our relict native forests are too small and fragmented to maintain the boreal biodiversity – indeed our current concerns over capercaillie *Tetrao urogallus* may reflect a fragmentation-induced extinction debt being paid off (Moss 2001). So major efforts are being made to restore and expand the forest area, which paradoxically can bring conflict with open ground biodiversity, also rare in a European context. Understanding the thresholds of species area requirements is vital in planning the balance between functioning woodland and open ground ecosystems.

Secondly, we must find a way of understanding and improving our large plantation areas, which may in time develop large trees, deadwood habitats, structural diversity and transitional edge habitats. The difficulty in terms of the macroecological research proposed in this paper is that the y-axis – the species group response variable – does not use exotic forests in a consistent way. For example deer have readily colonised the plantations, and in the small areas of old plantations bird diversity can be quite high. Lower plants on the other hand can be very poorly represented within plantations, especially where site conditions prevent long term stability of larger trees. Essentially we have a forest which is more boreal-like for some species groups than for others.

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Bergslagen, central Sweden

This region is located in the transition zone between hemiboreal and boreal ecoregions. The forests are dominated by Norway spruce *Picea abies* and Scots pine. The deciduous forest component consists mostly of birches *Betula* spp. and aspen *Populus tremula*. Broad-leaved trees are very rare except near settlements and as remnant of wooded grassland with oak *Quercus robur* and also ash *Fraxinus excelsior* on moist sites.

In Sweden the first local industrial use of the forest was for mining and the production of copper and iron in the

Bergslagen area of central Sweden. Local iron production started > 2000 yr ago, but became a major regional industry during the early Middle Ages. From the 17th to the 20th century, this entailed an extensive exploitation of the forest (Wieslander 1936, Arpi 1951, 1959). At this time the forest landscape was settled throughout, and the local economy was based on iron and charcoal production, as well as low intensity agriculture. Domestic grazing animals and extensive grazing in the forest were an important part of the economy (Angelstam 2002). The consumption of charcoal peaked towards the end of the 19th century, and in 1885 it was estimated that 20–25% of the cut timber volume was used for charcoal production (Arpi 1959). The remaining steel industry, which also owned the forestland, was hit by economic problems that peaked between 1975 and 1985. The last iron mines were closed in 1991. While only minor parts of the forest land have been cleared for agricultural purposes, the composition and structure of forests have been severely altered (Angelstam 1997, Mikusiński et al. 2003).

The long economic history of mining and forest use in the Bergslagen region has affected the environment. The four large predators, brown bear *Ursus arctos*, wolf *Canis lupus*, lynx *Lynx lynx* and wolverine *Gulo gulo* were gradually exterminated during the 19th century (Angelstam 2002). After a long period of forest harvesting for the production of charcoal, the timber itself became an important source of income for these industries and they gradually evolved into large forest industries. Due to large areas of forests ready for harvesting in the middle of the 19th century, and to compensate for the reduced incomes of companies owning both industry and forest, the logging rates increased and forest management became intensive including the use of herbicides and pre-commercial and commercial thinning. As a consequence a number of specialised species have become extirpated (e.g. Angelstam and Mikusiński 1994, Enoksson et al. 1995). From the point of view of sustained timber yield, however, this region is still highly productive. This combined effects of lack of top predators and a large cohort of young forest in the landscape provided the base for a strong increase of the population of moose *Alces alces* (Angelstam et al. 2000). The intensive browsing pressure now hampers the attempts to restore the amount of deciduous forest, which is needed to maintain viable species requiring old deciduous forest (Mikusiński et al. 2003).

During the 1990s the natural disturbance regime concept became a widely accepted approach to argue for applying an increased range of silvicultural methods. Still, however, clear-felling with variable retention is the norm. The current Swedish forest policy defines the biodiversity maintenance objective as that "all naturally occurring species should maintain viable populations". Given the region's very long history of forest use and management, this is an ambitious goal. Consequently, in the absence of a well-developed system of protected areas, the main tool to achieve the biodiversity goal is to attempt proactive forest management and restoration.

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Eastern Finland and Russian Karelia

In the European boreal forest zone one of the most important areas for maintaining forest biodiversity is the border zone between Finland and Russia, stretching 1250 km from the Baltic Sea to the north. This zone still contains large areas of boreal forest in their natural or near-natural state. To protect the uniqueness and biodiversity of the forests along the Finnish-Russian border, an initiative has emerged to form a network of protected areas on both sides of the border – the so-called "Green belt of Fennoscandia". These large unmanaged forest areas are not only important for maintaining forest biodiversity, but also indispensable as natural benchmark areas providing templates of natural variability for developing ecologically sustainable forest management in Fennoscandia (Korpilahti and Kuuluvainen 2002). This is because in areas like southern Finland the often small forest protection areas do not provide useful benchmark areas because their structure and dynamics have been affected by both past utilisation and the surrounding managed forest matrix, where for example fire is excluded.

The "Green Belt" encompasses all three main boreal forest zones: the southern, middle and northern boreal zones, and represents a wide spectrum of variation in ecological conditions. The landscapes are characterised by a mosaic of peatlands, especially in the north. Although the natural conditions on both sides of the border are similar, the land use history is different. On the Finnish side, intensive forest management has strongly shaped the structure of forests during recent decades, and only relatively small fragments of natural forest are left untouched. Moreover, dense network of forestry roads and efficient fire suppression do not allow any large scale natural disturbances. On the other side of the border, in Russian Karelia, large areas of natural forest still exist, although cuttings are advancing continuously. Forest fires are still rather common in Russian Karelia. This situation has created interesting possibilities for research on how forest utilization at different spatial scales affects forest structure and biodiversity (Kouki and Väänänen 2000, Rouvinen et al. 2002, Brotons et al. 2003).

A fundamental question is what will happen in this area in the future. Protected areas comprise a low proportion of total forest area on both sides of the border, although it increases northward. It is evident that protected areas alone will not be sufficient to maintain the full diversity of the area. The crucial question is what will happen in the managed forests (Burnett et al. 2003). State owned forests in Finland are now being managed with the so-called landscape ecological forest management practices, which aim at ensuring all aspects of sustainability. On private and company owned land, forest certification schemes are used. In spite of more environmentally friendly forestry practices that have been implemented during the past years, the area of old-growth forest will still decrease during the current forestry management plans. On the Russian side, although progress has been made in forest protection, the harvesting of forest will continue and the area of old-growth forests is expected to diminish rapidly (Burnett et al. 2003). The most urgent task is to develop and apply management methods that would allow the maintenance of biodiversity. In Russia the situation is similar to northern Canada where natural forest is being logged. On the other hand, in the intensively managed forests of Finland, the question is more how to restore the biologically impoverished ecosystems (Kuuluvainen et al. 2002).

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Pechora-Ilych strict nature reserve, Russia

In northern Europe, the forests from Scandinavia to the Ural Mountains are similar regarding climate (Tukhanen 1980, 1984) and tree species composition (Kuusela 1990). They differ, however, distinctly from the forests of Siberia in the east (Kuusela 1990). Scots pine and Norway spruce form 98 to 100% of the conifers in the east and the west of Europe, respectively. Birches and aspen dominate in early- and mid-successional stages, which are common features of naturally dynamic boreal forests due to large-scale disturbances. Siberian elements (*Larix sibirica*, *Pinus sibirica*, *Abies sibirica*), occur east of the Fennoscandian shield but constitute only a minor proportion of the timber volume (Kuusela 1990).

The largest remaining tracts of the natural boreal forest in Europe are found in the most remote parts of European Russia (Yaroshenko et al. 2001). In the remote Komi Republic 10.7% of its area of 416000 km^2 is protected (Taskaev and Timonin 1993). To this should be added the forests in protective zones along water, roads and urban areas as well as buffer zones near reserves which comprise 13% of the forests (Kuusela 1990). In some remote regions, such as the 40700 km^2 Troitsko-Pechorsk region in the south-eastern part of the Komi Republic, 40% of the forests are protected. The Pechoro-Ilych Strict Nature Reserve with its buffer zone is situated in this region. Along with the adjacent Yugyd-Va National Park this is the very last naturally dynamic forest system in Europe and covers an area of > 30000 km^2, almost the size of the Netherlands. In the reserve all main northern and middle boreal forest landscape types are present, from fire-prone pine plains, to undulating hills with all stand types and to mountain forests (Lavrenko et al. 1995). The Pechoro-Ilych reserve, which was proposed in 1915, and founded in 1930, has been used for nature protection, monitoring research and education in Russia for > 50 yr.

Although unaffected by logging and exploitation of gas and oil, it has been sparsely settled and exposed to clearing for agriculture along the rivers for centuries (Saveleva 1997). In spite of this, the Pechoro-Ilych reserve and the surrounding buffer zones is one of the very few remaining large intact boreal forest areas in Europe (Kuuluvainen et al. 1998, Yaroshenko et al. 2001, Jasinski and Angelstam 2002, Angelstam et al. 2004).

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The New World

New Brunswick, Canada

New Brunswick has the longest history of intensive forest management among Canadian provinces (Baskerville 1995). Large-scale, industrial harvesting started in the early 1950s but this was preceded by decades of "high-grading" of the forest, during which the best specimens of white pine *Pinus strobus*, red spruce *Picea rubens* and yellow birch *Betula alleghaniensis* were selectively cut.

New Brunswick's forest is dominated by mixed stands with a dominance of conifers (*Picea* spp., *Abies balsamea*). Broad-leaved stands co-dominated by sugar maple *Acer saccharum*, American beech *Fagus grandifolia*, and yellow birch occupy rich, well-drained sites, whereas wet areas and bogs are dominated by black spruce *Picea mariana*. Following the high-grading phase affecting white pine, then yellow birch and red spruce, large-scale clearcutting took place in conifer-dominated stands and spruce plantation started as early as 1957. Since the mid 1980s, large-scale uneven-aged management of broad-leaved stands was undertaken to remove low-quality specimens and gradually increase the quality of sawtimber. Intensive forestry, including spruce budworm *Choristoneura fumiferana* control and fire suppression, has resulted in the virtual disappearance of stands that could be considered as old growth. Forest composition and structure have thus been substantially altered, with unknown effects on forest biodiversity. Among higher vertebrates, however, the only well-documented casualties are the grey wolf and the woodland caribou *Rangifer tarandus*, which were extirpated at the turn of the 20th century. In both cases, however, excessive trapping and hunting rather than habitat loss are probably to blame.

Public lands represent 50% of the forest lands in the province. Conifer-dominated stands are treated through clearcutting with variable retention, replanted with conifers, and treated with herbicides. Deciduous-dominated stands are managed using various uneven-aged systems. The policy for biodiversity conservation on public lands is based on the concept of mobile reserves and targets higher vertebrate species associated with all combinations of stand age classes and tree species composition (Anon. 1995). Companies holding timber licenses must meet quantitative targets expressed as areas of specific wildlife habitat types. Each wildlife habitat type includes specific structural elements defined according to the corresponding list of typical species (e.g. snags of a minimum size, minimum canopy closure). Some of these structural criteria are being reconsidered in the light of recent data on forest birds from Guénette and Villard (unpubl.), which suggest that current threshold values are too low. However, a recent report from a Finnish consulting firm (Anon. 2002) suggests that the province could double its supply of softwood from public lands through an intensification of silviculture while meeting its current biodiversity objectives. This and related proposals are currently being examined through public consultations.

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The Western Great Lakes region, USA

The western Great Lakes region (Minnesota, Michigan and Wisconsin) was settled by Europeans relatively late, and widespread land-clearing did not occur until the mid 1800s in the southern regions and the late 1880s to early 1900s in the more boreal northern areas (Frelich 2002). Historically, the northern regions of Minnesota had high frequency of intense forest fires (Heinselman 1973, Clark 1988). Some large areas (150000 ha) representing all of the important forest types were even set aside as reserves (Heinselman 1996). Even if affected by native Americans there is a valuable forest history gradient from centres of economic development northward to the US and Canadian border. Pollen studies show that on a century basis the overall rate of change in the spectrum of forest types during the past 8000 yr was less than half of that during the last century (Jacobson and Grimm 1986).

The northern portions of Minnesota, Michigan, and Wisconsin contain significant representation of the boreal or sub-boreal forests. In presettlement times, these forests were dominated by the spruce-fir-birch, or red *Pinus resinosa* and white pine forest types, with jack pine *Pinus banksiana* on xeric sites and swamp conifers in lowlands (Stearns and Guntenspergen 1987, Host et al. 1996, White and Host 2000). These forests are transitional with the northern hardwood forest type, which includes sugar maple, basswood *Tilia americana*, and yellow birch in the west, and maple-hemlock *Tsuga canadensis* in Michigan's Upper Peninsula and northwestern Wisconsin (Pastor and Mladenoff 1992). The extensive logging at the turn of the century successively removed the pines, hemlocks and hardwoods (Whitney 1987) and led to the widespread development of the seral aspen-birch type, currently the dominant forest type of the Lake States.

Biodiversity management has received considerable attention recently in the Western Great Lakes Region. For example, Minnesota completed a monumental Generic Environmental Impact Statement (GEIS) study on "Timber Harvesting and Forest Management in Minnesota" (Anon. 1994). Among the foci of the study included forest health, plant and animal diversity, and forest wildlife. Major concerns were identified with respect to soil sustainability, landscape patterns, and biological diversity of forest birds (Anon. 1994). The latter is among the most well-known group of animals in the forests and serves as a primary surrogate for overall biodiversity conservation in the region today (Niemi et al. 1998; <http://nrri.umn.edu/mnbirds>). Moreover, society realised that the forest resource is not infinite and a heated debate ensued on sustainable forest cutting levels that continues today. The study resulted in new legislation on forest management practices, policies, and renewed consideration of forest biodiversity values. Most recently, the natural historical disturbance patterns (1870s) and current forest cutting patterns have been examined (Host and White 2003) as well as the potential effects on biodiversity (Manolis 2003).

The northern portions of Minnesota, Wisconsin, and Michigan have a majority of the forests found in the region and a majority of the forest ownership is in the public domain. The Boundary Waters Canoe Area Wilderness (BWCAW) is over 400000 ha and is off-limits to logging and other human development. The federal Chippewa and Superior National Forests have recently completed forest plans that have explicit consideration of biodiversity values as part of their forest scenario planning. The previously mentioned natural range of variability concepts have been employed by federal, state, and other landowners in the western Great Lakes (Host and White 2001).

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Alberta, Canada

The boreal forests of northern Alberta have only a recent history of large-scale industrial development (Schneider 2002). Whereas harvesting has occurred since the early 1900s, it was essentially restricted to the high-grading of large conifer trees (primarily white spruce *Picea glauca*) by small, localised mills. This pattern began to shift in the 1940s, with a greater demand for timber resources. At this time, a regulatory and management body was established in the province, with the primary objective of ensuring sustainable timber yields. The most dramatic changes in forest management have occurred in the past few decades, with the advent of technologies and markets for deciduous pulpwood, and the rapid expansion of the forest industry through the granting of huge leases of public land (e.g. Schmiegelow and Hannon 1993). While the forest is now considered fully allocated from a timber standpoint, there nevertheless remain large areas of forest in a relatively pristine state.

Alberta's boreal forest consists primarily of mixed forest. Trembling aspen *Populus tremuloides*, balsam poplar *Populus balsamifera* and white spruce are the most abundant upland species, with lesser amounts of white birch *Betula papyrifera*, balsam and jack pine, whereas black spruce characterises wetter sites. Roughly one third of the forested landbase is considered merchantable with the remainder consisting of treed peatlands, bogs, and fens. Forest tenure systems have resulted in a divided landbase (Cumming and Armstrong 2001), whereby the deciduous and coniferous components of the forest are often allocated to separate companies, and subsequently managed for different objectives. In addition to the rate and extent of forest development activities, this raises further concerns for biodiversity conservation, as older, mixed forests support the highest levels of species richness, and highest abundance of many species. Most harvesting is through clearcutting, with site preparation and re-planting of conifer sites, and natural regeneration of deciduous sites. Efforts at ecologically sustainable forest management by industry leaders have resulted in some retention (ca 5% average) of merchantable material within harvest blocks. However, while commitments have been made to biodiversity conservation, a comprehensive set of management objectives at the provincial level is lacking, and no quantitative targets are specified. Compounding this problem are the often competing interests or other resource sectors on forest land. Continued agricultural expansion and conversion of forest is a serious concern (Hobson et al. 2002), as are the widespread exploration and development activities associated with gas and oil industries. The disturbance rates of the latter approximate that of the forest industry in some areas (Schneider et al. 2003).

In response to the expansion of industrial forestry activities in the early 1990s, substantial research programs have been developed to address sustainable forest management. The focus on biodiversity issues has, however, been largely reactive, rather than proactive to date, and there exists an urgent need to identify and secure benchmark areas for continuing ecological study, and as part of an active adaptive management framework (Boutin et al. 2002). The challenges for biodiversity conservation in this region are somewhat futuristic as the vast majority of species, including large carnivores such as wolves, have large tracts of available habitat remaining. Woodland caribou are an exception. Current industrial activity will lead to a substantial reduction in the habitats and forest structures most affected by forest harvesting (old growth, unsalvaged recent burns, large snags, downed woody material). The challenge is to establish targets for these attributes that must be met in long-term forest projections in a fashion similar to the need to maintain timber supply over the long-term.

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Quebec, Canada

A wide range of forest ecoregions is found in the province of Quebec. The St. Lawrence valley is dominated by temperate hardwood forests and bordered by hemiboreal forest types characterised by admixtures of balsam fir, yellow birch, and associated species. Further to the north and at higher altitudes, the forest is truly boreal. The southern part of the boreal zone is dominated by balsam fir, trembling aspen and paper birch. In the north, black spruce becomes the dominating species, but jack pine, balsam fir, trembling aspen, and paper birch occur in varying proportions depending on site characteristics and stand age. Natural disturbances in Quebec's boreal forests include stand-replacing forest fires (Bergeron et al. 2001, 2002), cyclic epidemics of the spruce budworm (Morin et al. 1993), and windthrow (Ruel 2000). Public lands represent 89% of the productive forest of Quebec. The remaining 11% in private tenure is mostly located in the St. Lawrence valley.

Large-scale forest exploitation in Quebec started in the second half of the 19th century and was concentrated in the St. Lawrence valley, where white pine was selectively harvested for ship construction under the British Empire.

In the boreal forests, however, extensive harvesting by clearcutting started much later, between the 1930s and the early 1950s in its southern parts and later in more remote areas. This northern advance of forestry is still ongoing, virgin forest being harvested further north every year. At the present, an east-west band of untouched forest – varying in width from 100 km to 400 km – is still found between the front of forest operations and the southern edge of non-commercial, open taiga forest. New forest roads are rapidly stretching into this zone, which has almost been totally allocated to forest companies by the provincial government in the form of forest management contracts. Nowadays, almost all harvesting is done through clearcutting, special care being given to the protection of soils and regeneration. Besides final felling, silviculture during stand development is rather minimal, except perhaps the intensive use of pre-commercial thinning in some regions.

Although recent, the intensive use of an even-aged management system throughout this portion of the boreal forest is changing deeply the composition and structure of landscape mosaics, which are considerably more complex under natural disturbance regimes. Studies on fire history regimes of Quebec and north-eastern Ontario's boreal forest show that short fire cycles generally described for boreal ecosystems do not appear to be universal. Rather, important spatial and temporal variations have been observed (Bergeron et al. 2001). Hence, variations in the fire cycle have an important influence on forest composition and structure at both the landscape and regional levels. In northwestern Quebec, Harper et al. (2002) have shown that large proportions of the land base are composed of overmature and old-growth stand types under natural disturbance regimes. The extensive use of even-aged management systems based on clear-cutting practices in these forests is thus likely to truncate their natural age-class distribution, eliminating overmature and old-growth stages (Bergeron et al. 2001, 2002). This will in turn affect the biodiversity that is associated with these stand types (Boudreault et al. 2002, Drapeau et al. 2003). In Quebec's forest act, the only regulation that may refer to the maintenance of biodiversity as a whole refers to the maintenance of 30% of the productive land base into forest cover types of > 7 m height in forest management units. Otherwise regulations concern specific habitats of game and non-game species based on a species by species approach. Such regulations partly address the issue of biodiversity maintenance but do not set management objectives that could address simultaneously all levels biological diversity. Development of forest management planning approaches at the strategic level and diversified use of silvicultural techniques designed to maintain a spectrum of forest compositions and structures at different scales in the land base are coarse-filter avenues that are currently proposed to maintain the variability of stand types and hence, species diversity in such ecosystems (Bergeron et al. 2002). Additionally, the presence of large tracts of untouched natural forests in the North offer opportunities for the development of a functional network of protected areas.

Finally, with the northern expansion of forestry in areas where fire cycles are shorter, it is likely that forestry companies will have to deal more and more with the reality of wildfires in the near future. The salvage logging of burned forests, a practice rarely used in the past, has increased in recent years (Nappi et al. 2004). The Quebec Forest Act of 1986 and its recent modifications have provided several incentives to intensify salvage logging (Quebec Government 2003) with no management guidelines to maintain biodiversity in these habitats. This raises serious concerns given the major contribution of recently burned forests both as a key habitat for wildlife species and as the main source of recruitment for standing dead wood, particularly in the black spruce forest of eastern Canada (Drapeau et al. 2002, Nappi et al. 2003).

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