Analys av skogarna i Dalarnas och Gävleborgs län

– prioriteringsstöd inför områdesskydd

LÄNSSTYRELSEN DALARNAS LÄN
Miljövårdsenheten
Rapport 2003:26

Länsstyrelsen Gävleborg
Rapport 2003:12

För innehåll och framförda åsikter svarar författarna.

Omslagsfoto Naturskog på Fregåsberget i Leksand, foto: Jemt Anna Eriksson

Karta publicerad med tillstånd av Lantmäteriverket, 96.0352.

Tryckning – Länsstyrelsens tryckeri, Falun, december 2003.

Upplaga: 200 ex.

ISSN 1101-3044 Länsstyrelsen Dalarna, Miljövårdsenheten

POSTADRESS	GATUADRESS	TELEFON	TELEFAX	POSTGIRO
791 84 FALUN	ÅSGATAN 38	023-810 00	023-813 86	6 88 19-2

FÖRORD

Länsstyrelserna har regeringens uppdrag att effektivt genomföra insatser för att bevara, skydda, och restaurera naturmiljön och den biologiska mångfalden. Utöver det direkta arbetet med bland annat bildande av naturreservat är kunskapsuppbyggnad och information till berörda aktörer prioriterade arbetsuppgifter.

I miljömålet ”Levande skogar" definieras delmål som rör långsiktigt skydd av skogsmark och förstärkt biologisk mångfald. En åtgärd för att nå dessa målsättningar är att utarbeta en regional bevarandestrategi som utgår från tillståndet i länens skogar.

I arbetet med kunskapsuppbyggnad har Länsstyrelserna sett det som angeläget att ta fram yttäckande tillståndsbeskrivningar av länens skogar och våtmarker, med en högre geografisk upplösning än vad som är möjligt med hjälp av riksskogstaxeringens material. Detta arbete har utförts inom det så kallade W-RESE-X-projektet, vilket ingår i det av MISTRA finansierade forskningsprogrammet RESE - Remote Sensing for the Environment. Forskare, bildtolkningsspecialister och personal från länsstyrelserna i Dalarna och Gävleborgs län har arbetat tillsammans för att genomföra de olika delprojekten.

Föreliggande rapport är slutrapportering av delprojektet rörande bevarandestrategi – den innehåller bristanalys, representativitetsanalys och rumsliga ekologiska analyser av regionens skogar. Rapporten är tänkt att utgöra ett underlag för Länsstyrelsernas strategiska ställningstaganden i naturskyddsarbetet, bland annat urval av vilka områden/naturtyper som långsiktigt ska skyddas, i olika delar av regionen, genom bildande av naturreservat. Arbetet har utförts under ledning av Per Angelstam och Grzegorz Mikusinski, institutionen för naturvetenskap, centrum för landskapsekologi, Örebro universitet.

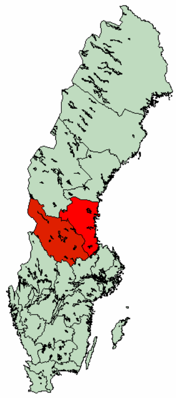
Vi är glada över att dessa naturvårdsbiologiska analyser har blivit utförda i våra län och vår förhoppning är att resultaten ska engagera länsaktörer och länsmedborgare!

Stig Hammarsten
Miljövårdsdirektör
Länsstyrelsen Gävleborg

Stig-Åke Svenson
Miljövårdsdirektör
Länsstyrelsen Dalarna

Gap analysis and planning of habitat networks for the maintenance of boreal forest biodiversity in Sweden

– a technical report from the RESE case study in the counties of Dalarna and Gävleborg



Final report to Mistra's research programme
Remote Sensing for the Environment (RESE)

The wRESEx project, part C

Per Angelstam[1,2], Grzegorz Mikusinski[1,2], Jemt Anna Eriksson[3], Peter Jaxgård[1], Olle Kellner[4], Anna Koffman[4], Bosse Ranneby[5], Jean-Michel Roberge[2], Mats Rosengren[6], Stefan Rystedt[3], Britt-Inger Rönnbäck[7], Jan Seibert[8]

1. Department of Natural Sciences, Centre for Landscape Ecology, Örebro University, SE-701 82 Örebro
2. Department of Conservation Biology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station; SE-730 91 Riddarhyttan
3. County administration board of Dalarna, SE-791 84 Falun
4. County administration board of Gävleborg, SE-801 70 Gävle
5. Department of Forest Resource Management and Geomatics, Swedish University of Agricultural Sciences, SE-901 83 Umeå
6. METRIA Miljöanalys, P.O. Box 24154, SE-104 51 Stockholm, Sweden
7. Department of Environmental Engineering, Geographical Information Technology, Luleå University of Technology, SE-971 87 Luleå, Sweden
8. Department of Environmental Assessment, Box 7050, Swedish University of Agricultural Sciences, SE-750 07 Uppsala

Centre for Landscape Ecology, Department of Natural Sciences,
Örebro University
and
Department of Conservation Biology, Forest Faculty,
Swedish University of Agricultural Sciences

LIST OF CONTENTS

Sammanfattning

Den svenska skogspolitiken innebär att biologisk mångfald ska bevaras, både i form av hållbara produktiva ekosystem och bevarande av livskraftiga populationer av alla naturligt förekommande arter. Givet en lång historia av intensivt nyttjande av skogarna för produktion av virke, och en konkurrens mellan arealer för produktion och naturvård, så är det angeläget att utveckla kostnadseffektiva och verksamma tekniker för strategisk och taktisk planering. Detta gäller såväl skydd av natur, men även skogsskötsel och återskapande av funktionella ekosystem.

Som en praktisk tillämpning av utvecklingsarbetet inom forskningsprogrammet ”Fjärranalys för miljön” genomfördes under 2002 en regional bristanalys för länen Dalarna och Gävleborg. Baserat på resultaten av denna analys presenteras sedan en rumslig analys av var trakter av speciellt intresse för bevarande av olika skogstyper ligger, i vilken grad är de skyddade och om de utgör fungerande nätverk av livsmiljöer för olika arter.

Inledningsvis presenteras en metodik för regional bristanalys (Angelstam och Andersson 1997, Angelstam och Mikusinski 2001). Vi använder metodiken för att uppskatta tillgången av olika skogstyper med höga naturvärden i relation till skogspolitikens mål i olika regioner liksom hur stor andel av dessa tillgångar är skyddade. Analysen innehåller följande olika steg: (A) uppskatta arealen av olika åldersklasser genom modellering med digitala höjdmodeller av den relativa fördelningen av olika naturliga skogliga störningsregimer och kunskaper om deras olika åldersfördelning; (B) uppskatta dagens mängder av olika skogstyper som definierats i (A) genom satellitbildsdata som kalibrerats med skogliga beståndsdata; C) uppskatta arealerna av olika representativa skogstyper som behövs för att bevara livskraftiga stammar av det mest krävande arterna och baserat på de nya kunskaperna om tröskelvärden för hur mycket biotop som är nog; (D) beräkna skillnaden mellan B och C där ett negativt värde innebär en brist i arealen av biotop, och därmed behov av restaurering och till och med återskapande av biotoper. För att illustrera skevheten i hur skogar på olika ståndorter påverkats gjordes beräkningarna både avseende den mark som är skogsmark idag och den mark som var skogsmark förr. Jämförelser mellan olika geografiska regioner ger därmed underlag för att bedöma hur representativ dagens sammansättning är jämfört med det ursprungliga landskapet. Slutligen (E) uppskattade vi hur mycket av olika representativa skogstyper med brist som är skyddade, och hur mycket som är inkluderat i planerna för framtida skydd för att nå kortsiktiga och långsiktiga mål. Vi diskuterar även behovet av återskapande av olika skogstyper.

I det andra avsnittet presenterar vi ett angreppssätt för att utvärdera funktionen av de arealer som det enligt den regionala bristanalysen är brist på. Detta baseras på kvalitativa och kvantitativa kunskaper om arter med olika landskapsekologiska krav som är specialiserade på olika skogstyper, och en kartering av olika skogstyper (åldersklasser och trädslagsblandningar) med satellitbilder som integrerats i GIS (geografiska informationssystem) (se Angelstam och Mikusinski 2003). För detta använde vi: (1) ett tematiskt relevanta digitala landtäckedata; (2) detaljerade kunskaper om ett urval av indikatorarter (paraplyarter) för att bygga habitatmodeller som identifierar trakter med goda, och dåliga, förutsättningar för att bevara lokala stammar av specialiserade arter av olika slag i olika regioner; (3) analyser av huruvida de arealer som finns som tillgångar enligt bristanalysen också utgör funktionella nätverk. Detta gjordes genom att kombinera of databasen för skogsvegetation av olika slag med arters kvalitativa och kvantitativa biotopkrav i Geografiska InformationsSystem; (4) Jämförelse av kartor som beskriver var lämpliga

trakter för arter som är specialiserade på olika skogstyper finns i relation till enskilda skogsbestånd som är föremål för beslut om skydd, skötsel eller restaurering.

I rapportens tredje del använder vi satellitbildsdata från olika tidsperioder för att dokumentera eventuella trender i förekomsten av bestånd med höga naturvärden som identifierats i nyckelbiotopsinventering hos både små privata markägare och skogsbolag av olika slag liksom trender i mängden stora sammanhängande skogsområden. Dessa analyser är av betydelse för att öka medvetenheten om problemen att vidmakthålla funktionella nätverk, och därmed behovet av regionala bristanalyser och planering med habitatmodeller.

Resultaten från den regionala bristanalysen avseende skogar äldre än 110 år visar en tydlig trend med brist i studieområdets sydöstra del till ett överskott i de inre nordvästra delarna av området. Det är dock viktigt att notera att satellitbilderna säger lite om de gamla skogarnas naturvårdskvaliteter. Ståndorter på fuktig och torr mark hade genomgående större brister än friska marker. Vi har inte studerat bristerna i andra för naturvården viktiga skogstyper som nyligen brända skogar, översvämmade skogar eller kulturpräglade skogar.

Habitatmodellerna för arter som specialiserat sig på olika skogstyper visade att trakter som tillgodoser krav på tillräckligt stora bestånd, och bestånd som inte ligger tillräckligt nära varandra för att tillåta att individer lätt kan röra sig mellan olika skogsområden, måste behandlas som separata ”gröna infrastrukturer”. Modelleringen kan alltså ses som en analys av skogsarealernas funktionalitet i två steg. Sammantaget visar analyserna att den regionala bristanalysen kraftigt överskattar den areal som kan bedömas som funktionell.

Den totala arealen skyddad skog i de två länen var 108,000 ha motsvarande 3,2% av skogsarealen. Variationen mellan olika naturgeografiska regioner var dock stor, från under 1 % i de största till 25 % i fjällskogen. Totalt fanns 56,000 ha nyckelbiotoper (både enskilda ägare och bolag), vilket motsvarar 1.7% av den totala skogsarealen. Andelen nyckelbiotoper varierade lite, från 1,3 % till 3,0 %.

Analyserna av de skogsbestånd som identifierats inom ramen för små privata markägares och stora skogsbolags inventering av nyckelbiotoper visar att andelen bestånd som i någon form bedöms ha påverkats av avverkningar, direkt eller indirekt, var större (29%) än den andel som skyddats i någon form (3%). I allmänhet hade små bestånd påverkats av avverkning mer (8% av arealen) oftare än större bestånd (5%). Omvänt så hade större bestånd skyddats i större mån (6%) än små bestånd (1%).

Läs mer i:

Angelstam, P., Andersson, L. 1997. I vilken omfattning behöver arealen skyddad skog i Sverige utökas för att biologisk mångfald skall bevaras? - SOU 1997:98, Bilaga 4, 75+ 71 sidor.

Angelstam, P., Mikusinski, G. 2001. Hur mycket skyddad skog kräver mångfalden? En svensk bristanalys. - WWF, Stockholm. 20 sidor.

Angelstam, P., Mikusinski, G. 2003. Paraplyarter och landskapsanalys med GIS-stöd underlättar planering för artbevarande i skogen. - SLU SkogsFakta 7.

Abstract

The Swedish official policies require that biodiversity should be maintained, both in the form of sustainable and productive ecosystems and of viable populations of all naturally occurring species. Given a long history of intensive use and management of forest landscapes for economic production, and competition for resources for biodiversity conservation, there is a need to develop cost-efficient and effective techniques for long-term management strategies and tactical planning. This applies to the set-aside of protected areas, but also the selection and design with regard to both contemporary forest management and to rehabilitation and even re-creation of functional ecosystems.

This study presents a regional gap analysis for the counties of Dalarna and Gävleborg in central Sweden and, based on the results of that analysis, a spatially explicit evaluation of conservation area networks in relation to where forests of high conservation interest are located.

First, we present an approach for regional gap analysis. We use this to provide numerical estimates of the ecoregional gaps in the amount of existing as well as protected areas of forest types with high conservation value, the properties of which are incompatible with forest management. This part contains the following steps: (A) estimate the amount of potential forest vegetation based on modelling of the distribution of different natural forest disturbance regimes, and knowledge about the age distribution within these different disturbance regimes; (B) estimate today's amount of the naturally occurring forest types defined in (A) using remote sensing data calibrated with forest stand data; (C) estimate the minimum numerical amount of representative forest types needed to maintain populations of the most demanding species based on the appearing knowledge about population's non-linear responses to habitat loss; (D) estimate the difference between B and C, where a negative values implies a gap in habitat area (area gaps) and a need for habitat rehabilitation and/or re-creation. To illustrate the biased loss of forests on different site types the results will be divided into those caused by loss of forest cover by clearing of past forests, as well as loss of different forest types on today's forest land. Comparisons among ecoregions allow for analyses of differences in representivity. Finally, (E) we estimate how much of the existing different representative forest types with gaps that are protected today in nature reserves (protection gaps), and how much is included in current plans for future protection. We also discuss the need for habitat rehabilitation of mapped forest types, the quality of which needs to be restored to be fully functional.

Second, we present an approach for evaluating the functional connectivity of the network of different forest types with clear gaps in amounts. This is based on knowledge about the quantitative habitat requirements of specialised focal species for each forest type and complete mapping of the existing respective habitat networks using remote sensing and a Geographic Information System (GIS). We used: (1) A thematically relevant digital land cover data base; (2) A selection of appropriate focal species to derive Habitat Suitability Index (HSI) model parameters at the scale of individuals and local populations for the forest types with obvious gaps in the different ecoregions; (3) Analysis of the functional connectivity of the existing habitat networks by integrating land cover data and the quantitative requirements of the focal umbrella species in GIS-based HS models; (4) Comparisons of the probability maps from the HS-models and the spatially explicit information about patches of different forest types to allow for strategic planning for

acquisition of new protected areas, as well as management, rehabilitation and re-creation of the selected target habitats outside protected areas.

Third, we use remote sensing data from three time periods to document the spatial and temporal variation in functional connectivity of conservation areas related to the recent history of habitat loss and fragmentation for the forest types with apparent gaps within the study area. This is particularly important to reinforce the awareness about the problems related to the maintainance of viable populations, and hence the need for strategic forest conservation planning.

The results from the regional gap analysis regarding forests older than 110 years show a clear trend with gaps in the coastal regions to an apparent surplus the interior of the study area. Sites on wet and dry ground have clear deficits in ecoregions with a long history of land use. We have not studied gaps in other important habitats such as burned forest, flooded forest and windthrown forest.

The Habitat Suitability Index models show that tracts with suitable and sufficiently connected habitat patches can be identified, and different focal forest types need to be managed as separate "green infrastructures". The spatially explicit analyses also show that the regional gap analysis overestimates the amount of functional habitat, i.e. habitat that is sufficiently well connected.

Within the two counties the total area of legally protected forest was about 108,000 ha (i.e. 3.2% of total forest area). However, in the largest ecoregions the proportion of legally protected forest of all forest land was below 1%. On the other hand, in the ecoregion located in the north-westernmost part of the study area had as much as 25 % of the total forest area under legal protection. The area of Woodland Key Habitats (WKH) (both belonging to small private landowners and companies) was about 56,000 ha (1.7% of total forest area). The proportion of forest covered by WKH varied much less among the ecoregions: from 1.3% to 3.0% in ecoregion 32.

The analyses of the fate of WKH and larger old forest patches show that the proportion of individual WKH affected by logging is larger (29 %) than those that have been protected (3 %). In general small WKH have been affected by logging more (8 % of the area) often than the larger ones (5 % of the area). Conversely, large WKH have been protected to a larger extent (6 %) than small ones (1 %).

1. Introduction

Anthropogenic habitat loss and alteration are the two major factors behind the degradation of forest biodiversity in general and the extirpation of specialised species in particular. Hence, in the present managed landscapes, habitat networks representative of the naturally occurring forest types are not available with sufficient amount and connectivity. To mitigate these problems, the establishment of protected areas, as well as the use of environmentally friendly forest management regimes and habitat rehabilitation need to be combined (Lindenmayer and Franklin 2002, Angelstam 2002). Gap analysis (e.g. Scott et al. 1996, Jennings 2000) and systematic conservation planning (Margules and Pressey 2000) are two important tools to determine the relative need of these management approaches, and where they should be located.

In managed landscapes protected areas are usually restricted to securing the aspects of forest ecosystems within a particular ecoregion that cannot be secured within traditional management, such as large intact forest areas (Yaroshenko et al. 2001), old-growth forests and other types of high conservation value forests (Peterken 1996). To estimate the need of protected areas for biodiversity maintenance in different ecoregions one needs: 1. knowledge of the authentic dynamics of forests; 2. the requirements of different components of biodiversity expressed as quantitative targets for the amount of different forest habitat; and 3. an understanding of the extent to which managed landscapes can contribute to the maintenance of biodiversity (Angelstam and Andersson 1997, 2001).

Gap analysis can be defined as the identification of disproportionate scarcity of certain ecological features in a management unit, relative to the representation to a larger region surrounding the management unit (Perrera et al. 2000). The concept can also be extented to scarcity relative to how much habitat area is required for the maintenance of biodiversity (Angelstam and Andersson 2001). So far, however, the needs of protected areas have commonly been based on coarse estimates and often with clear political component. In Canada the endangered spaces programme advocated 12 % (Iacobelli et al. 1995). In Finland 10 % was proposed in the mid-1990s (Virkkala 1997), while Lõhmus et al. (2003) suggested 12 % in Estonia. Neither has it always been clear whether the targets represent ecologically founded long-term targets representing what the maintenance of biodiversity requires, or short-term targets based on political compromises such as negotiated in certification standards (Elliot and Schlaepfer 2001).

The development of protected areas in Sweden has followed a similar avenue. Swedish environmental policy aims at maintaining biodiversity. For forest environments the forest policy (SOU 1992) and environmental quality objectives (SOU 2000) state that naturally occurring species should be maintained in viable populations. In addition a goal for biodiversity is being developed (Nature conservation policy from 2002). Largely due to a long history of forest management with insufficient considerations to the maintenance of representative forest types, today about 2000 forest species are red-listed (Gärdenfors 2000). Analyses of the habitat requirements of red-listed species show that they require forest components, which are not typical for managed forests (cf. Berg et al. 1994, Larsson et al. 2001), such as old coniferous forests, late stages in the deciduou forest succession, dead wood and large deciduous trees. To maintain viable populations of such habitat specialists, it is essential to create reserves for the remaining areas of forest types, the structure and dynamics of which is incompatible with the managed forest.

In Sweden, Liljelund et al. (1992) made one of the first attempts to estimate the need of protected forest areas. Depending on the quality of the matrix surrounding protected areas their estimate was 15% reserves with a hostile matrix and half as much with a matrix with considerable nature conservation considerations. Later, based on the forest policy (SOU 1992) stating that of viable populations of all naturally occurring populations should be maintained, Angelstam and Andersson (1997, 2001) made an detailed analysis of the gaps in the present forest reserve network. Using the appearing knowledge about the dynamics of different forest types, forest and land use history, habitat loss thresholds of forest habitat specialists and current management practises they estimated the need for protected forest areas for different broad ecoregions in Sweden. They recommended that, depending on the ecoregion, there was a need to set aside all the existing forests with natural properties (about 5%), but also to start a restoration and re-creation corresponding to between 3 and 11 % of the landscape.

The investigation of the need to set aside forest in reserves (Angelstam and Andersson 1997) was followed by an increase in the amount of grants to protect forests of high conservation value in Sweden. In a first step the planned increase in protection of forests encompassed 800,000 ha. In the government's proposition 2000/01:130 another 320,000 ha of productive forest was proposed be set aside as nature reserves, 30,000 ha as biotope protection and 30,000 ha in the form of agreements with landowners for a limited time period. Additionally, the formerly privatised state-owned forest have become public again, partly with the aim to supply land to compensate private landowners for the potential loss of land for the establishment of protected areas. The county administrative boards have regional responsibility for the selection and establishment of reserve networks. The national forestry board is responsible for the set-aside of small areas, usually <5 ha, of high conservation value Woodland Key Habitats on private land. Moreover, the forest industry has set aside forest for protection within their landscape ecological plans (SUS 2001). It is currently estimated that the summed amount of forests set aside, with or without legal protection, will amount to 2,000,000 ha in year 2010. This figure corresponds to 9 % of the forest area with a growth rate of more than 1 cubic meter per ha and year, and to 7 % of the forest area as defined by FAO (2001).

However, for the practical implementation of these ambitious forest conservation plans, there is a need to make analyses of the gaps in the amount of habitat needed to maintain naturally occurring species also at a regional scale considering the specific conditions found in for example different natural regions (e.g., Angelstam and Mikusinski 1999). Additionally, to secure a favourable conservation status and function of the resulting network of forest reserves, spatially explicit planning techniques should be developed to aid decision-making process for the incorporation of new objects into the representative reserve networks of different forest types (e.g., Verner et al. 1986, Scott et al. 2002, Puumalainen et al. 2002). Depending on the regional situation, this strategic conservation planning should handle the establishment by authorities of new forest reserves of different types, as well as the need for landowners to select appropriate management activities for the maintenance, restoration and rehabilitation of different forest habitats outside reserves. If acting in concert in the whole landscape, such strategic planning could enhance the development of functional and cost-efficient representative networks of habitats for the long-term maintenance of viable populations of all naturally occurring species as stated in the policies.

Maintaining viable populations of species in the long term is a much more demanding task than providing habitat for individuals in the short term. Consequently, the step from planning for the set-aside of single Woodland Key Habitats (Hansson 2001), to planning and implementation of functional habitat networks in the whole landscape is large (Angelstam et al. 2001, Brunckhorst 2000). So far, gap analyses with a relevant ecoregional resolution, followed by a cost-efficient spatially explicit strategic planning that takes into account also representativity of the regional forest types and sufficient connectivity to maintain populations, is not at hand in Sweden. Apart from the incomplete ecological knowledge about the quantitative need of different forest types to maintain biodiversity, this kind of strategic conservation work has been hampered by the absence of thematically fully relevant spatially explicit data with a complete landscape cover for the entire ecoregions across ownership boundaries. Additionally, due the lack of spatially explicit relevant data necessary to give an overview of the negative effects of habitat loss and fragmentation on biodiversity, the understanding of the status and trends of different existing habitat networks is poorly understood. Finally, a successful implementation of strategic plans requires integration of efforts among all relevant managers in the region and therefore the identification of potential obstacles in this process is equally important. This implies challenges in a wide range of both scientific and applied fields.

Based on satellite remote sensing data, the research programme Remote Sensing for the Environment (RESE) provides for the first time land cover data suitable for application in both regional gap analysis and spatially explicit strategic planning for the maintenance of forest biodiversity in Sweden. The repeated mapping of landscapes by remote sensing during about two decades also provides opportunities for analyses of the trends in the amount of different land cover types over time as well as changes in connectivity of habitat networks.

Gap analysis may mean several things. Here we focus on the gaps in the amount of the different representative forest habitats that are needed in the long term to maintain viable populations of the naturally occurring species, which cannot survive in the regular managed landscape. Gap analysis thus aims at identifying the most endangered types of habitat in an ecoregion. What are the long-term needs of protected areas for different forest types? How much does exist of those today? How much of what exists is protected? Is there also a need for rehabilitation, and even re-creation of habitats?

Within a particular ecoregion, the forest types for which gaps have been identified also need to be evaluated as to the extent to which they actually fulfil the function of providing habitat networks for species, which are specialised on this kind of forest. This evaluation often result in the need of strategic planning for acquiring additional protected areas, as well as management and rehabilitation of forests areas to improve the selected green infrastructure in focus.

This study presents a regional gap analysis for the counties of Dalarna and Gävleborg in central Sweden and, based on the results of that, an approach for spatially explicit evaluation of conservation area networks in relation to where forests of high conservation interest are located. First we present an approach for regional gap analysis, and use it to provide numerical estimates of the ecoregional gaps in the amount of existing as well as protected areas of forest types with high conservation value, the properties of which are incompatible with forest management. This part contains the following steps:

- A: estimate the amount of potential forest vegetation based on modelling of the distribution of different natural forest disturbance regimes, and knowledge about the age distribution within these different disturbance regimes (Angelstam and Andersson 1997)
- B: estimate today's amount of the naturally occurring forest types defined in A using remote sensing data calibrated with forest stand data

- C: estimate the numerical amount of representative forest types needed to maintain viable populations of the most demanding species based on the appearing knowledge about population's non-linear responses to habitat loss (e.g., Fahrig 2001).
- D. estimate the difference between B and C, where a negative values implies a gap in habitat area and a need for habitat rehabilitation and/or re-creation. To illustrate the biased loss of forests on different site types the results will be divided into those caused by loss of forest cover by clearing of past forests, as well as loss of different forest types on today's forest land. Comparisons among ecoregions allow for analyses of differences in representivity.
- E. estimate how much of the existing different representative forest types with gaps are protected today in nature reserves (protection gaps), and how much is included in current plans for future protection. We also discuss the need for habitat rehabilitation of mapped forest types, the quality of which needs to be restored to be fully functional.

Second, we present an approach for evaluating the functional connectivity of the network of different forest types with clear gaps in amounts. This is based on knowledge about the quantitative habitat requirements of specialised area-demanding focal species for each forest type, as well as complete mapping of the existing respective habitat networks using remote sensing and GIS. This complex evaluation requires:

- 1. A thematically relevant and digital land cover data base.
- 2. The selection of appropriate focal species to derive Habitat Suitability (HS) model parameters at the scale of individuals and local populations for the forest types with obvious gaps in the different ecoregions (Angelstam et al. 2003 a).
- 3. Analysis of the functional connectivity of the existing habitat networks by integrating land cover data and the quantitative requirements of the focal umbrella species in GIS-based HS models.
- 4. Comparisons of the probability maps from the HS-models and the spatially explicit information about patches of different forest types to allow for strategic planning for acquisition of new protected areas, as well as management, rehabilitation and re-creation of the selected target habitats outside protected areas.

Third, we use remote sensing data from three periods to document the spatial and temporal variation in functional connectivity of conservation areas related to the recent history of habitat loss and fragmentation for the forest types with apparent gaps within the study area. This is particularly important to reinforce the awareness about the problems related to the maintainance of viable populations, and hence the need for strategic forest conservation planning.

2. Study area

2.1. The counties of Dalarna and Gävleborg

Biogeographically, Sweden ranges from the northernmost part of the European lowland temperate forest to tundra in the north. The most dominating forest types are different kinds of boreal and hemiboreal forests (Anonymous 1965). This study area encompasses the counties of Dalarna (county code W, covering 28,193 sq. km) and Gävleborg (county code X, covering 18,192 sq. km) located in the transition zone between these two main forest types (Figure 1). The total land area covered is 46,385 sq. km (SCB 2003), corresponding to 11 % of Sweden's land area. The corresponding figures for the forest land are 20,010 and 14,925 sq. km for the two counties and 15 % of the forest land in Sweden (SCB 2003).

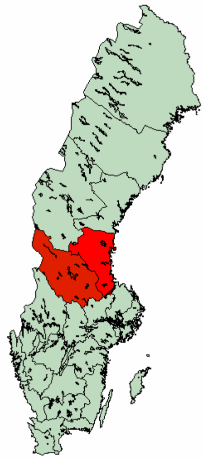


Figure 1
Location of the WX-region in Sweden.

2.2. Regional stratification systems

The WX-region ranges from hemiboreal forest in the SE, through three types of boreal forest, to mountains with alpine vegetation zones above the tree line in the NW. For the regional gap analysis three different stratification systems were used to present the data. The two first ones are based on natural features and the third is the distriction of the Regional Forestry Boards in the Dalarna-Gävleborg region.

2.2.1. Biogeographic regions of the Nordic Council of Ministers

The most commonly used classification of the representative types of nature in the Nordic countries was made by the Nordic Council of Ministers (1983). This ecoregional stratification was based on a survey of the natural conditions by means of a physical-geographical division of regions and the contemporary knowledge of the structuring vegetation types and land forms, with the aim of providing a stratification for the physical planning of the countryside (Table 1, Figure 2).

Table 1
The ecoregional division of the representative types of nature by Nordic Council of Ministers (1983).

Name of ecoregion	***Code***	***Ecoregion***	***Area (sq.km)***
Woodlands south of "Limes norrlandicus"	26	Hemiboreal	1031
Woodlands north of "Limes norrlandicus"	27	South boreal	6342
Hilly lands of the south boreal region	28a,b	South boreal	15322
Hilly middle boreal woodlands	30a	Middle boreal	16957
Coniferous woodlands of northernmost Sweden and Finland; very poor bedrock and large mires, 32a has a very high precipitation	32a,b	North boreal	4960
Premontane region; very poor bedrock	33d,f,g	Subalpine	4562
Southern mountain area	35	Alpine	865

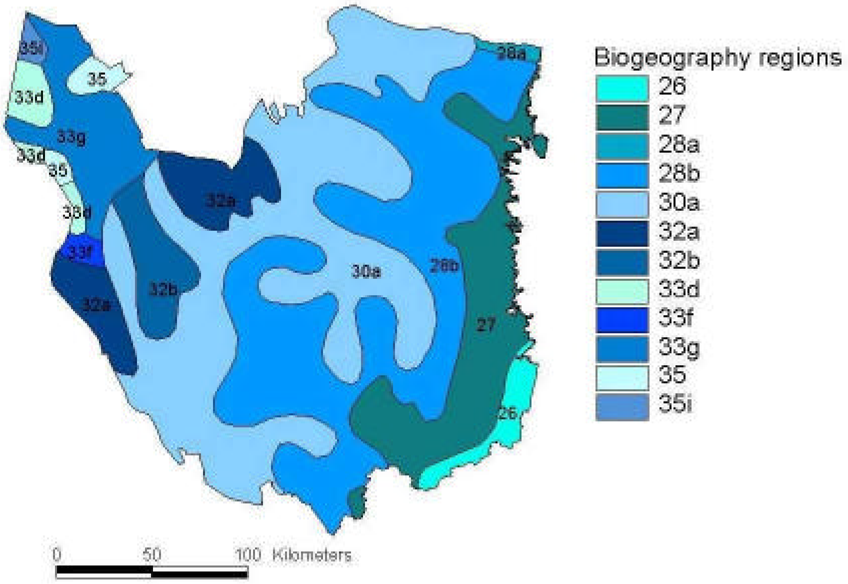


Figure 2
The division of the counties Dalarna and Gävleborg into ecoregions made by the Nordic Council of Ministers (1983). The alpine region is not a forest habitat and therefore not included in the analysis.

2.2.2. Stratification based on altitude and geology

In order to stratify the region into areas with relatively uniform natural conditions, a method that uses altitude and bedrock information for estimating weathering intensity was applied (Eriksson et al. 1996). As a source of altitude information, a GSD Terrain Elevation Bank from the National Land Survey was used (http://www.lm.se/english/gsd/e_hojd.pdf). This database contains elevation data for points in a regular 50-m grid. The elevations are in metres with one decimal place and the mean standard error is 2.5 metres. For the purpose of this study, point data were converted into a 50-m grid in ArcInfo. As a first source of geological information, county bedrock maps at the scale 1:200,000, 1:250,000 and 1:400,000 produced by the Swedish Geological Survey were used (Anonymous 1991). Second, according to Eriksson et al. (1996) the bedrock types were divided into classes that describe their potential for weathering and were given the following codes: low with below 1.2 kEq/(ha*year) – code 10, high from 1.2 to 6 kEq/(ha*year) – code 20, and very high above 6 kEq/(ha*year) – code 30. These maps provide a very generalised distribution of the geological conditions in the study area. In this study, a digitised version of these maps converted to regular 50-m grid was used. The first step in the stratification was based on the elevation information, which was divided into four intervals with the following codes: below 200 m.a.s.l. – code 1, from 200 to 500 m.a.s.l. – code 2, from 500 to 800 m.a.s.l. - code 3, and above 800 m.a.s.l. – code 4. Codes given to both altitude intervals and weathering classes illustrated relative weathering capacity, and were used to calculate final weathering intensity where both values were simply added in each 50 m pixel in ArcInfo. This resulted in a fine-grained weathering intensity database. Since bedrock maps used in this study had much lower geometric resolution in comparison to the elevation database, we finally generalised the weathering intensity database by removing polygons smaller than 1 km^2. The summary that describes final weathering intensity strata used in this study is presented in Table 2 and Figure 3.

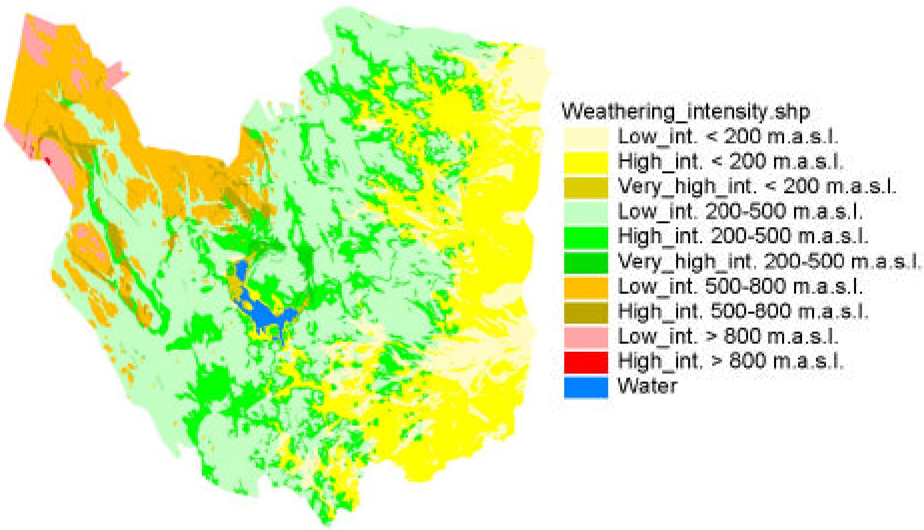


Figure 3
The regional stratification based on altitude and bedrock.

Table 2
Division of Dalarna (W) and Gävleborg (X) counties into weathering intensity strata – summary data.

Name of strata	***Code***	***Area (sq.km)***	***Proportion (%)***	***Number of patches***	***Mean patch size (sq. km)***
Low weathering intensity located below 200 m a.s.l.	11	4 952	9.6	188	26.3
Low weathering intensity located between 200 and 500 m a.s.l.	12	20 087	38.8	236	85.1
Low weathering intensity located between 500 and 800 m a.s.l.	13	5763	11.1	100	57.6
Low weathering intensity located above 800 m a.s.l.	14	996	1.9	36	27.7
High weathering intensity located below 200 m a.s.l.	21	10 789	20.8	101	106.8
High weathering intensity located between 200 and 500 m a.s.l.	22	7 509	14.5	342	22.0
High weathering intensity located between 500 and 800 m a.s.l.	23	850	1.6	67	12.7
High weathering intensity located above 800 m a.s.l.	24	15	0.0	6	2.5
Very high weathering intensity located below 200 m a.s.l.	31	195	0.4	11	17.7
Very high weathering intensity located between 200 and 500 m a.s.l.	32	301	0.6	11	27.4
Water	99	349	0.7	1	349.0

2.2.3. Administrative stratification based on National Board of Forestry subregions

The National Board Forestry is responsible for the implementation of the Swedish forest policy. Within the Dalarna/Gävleborg region there are seven districts (Figure 4).

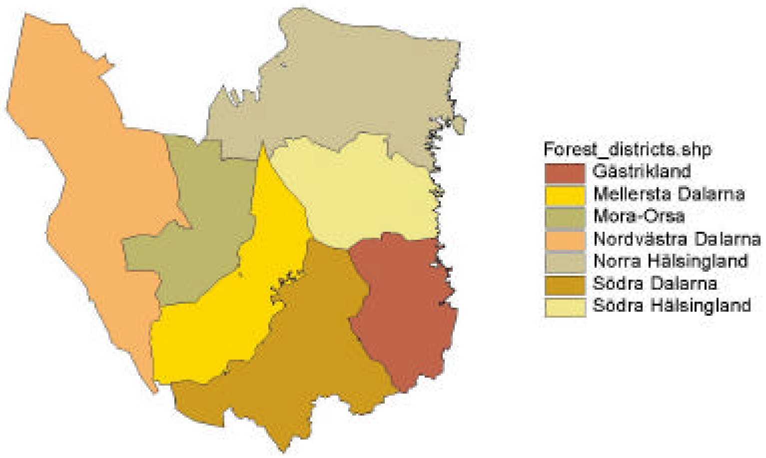


Figure 4
Map of the study area showing the location of the different forest administration districts of the national board of forestry.

2.3. The boreal forest: disturbance regimes and forest types

2.3.1. The ASIO-model and disturbance regimes

The boreal forest is the world's largest biome (Shugart et al. 1992). In Fennoscandia the structure and dynamics are relatively well studied and understood (e.g., Angelstam 1998a,b, Engelmark 1999, Engelmark and Hytteborn 1999, Niklasson and Granström 2000, Larsson and Danell 2001, Korpilahtli and Kuuluvainen 2002). There is a relationship between both site and regional conditions on the one hand and boreal forest dynamics on the other (Arnborg 1990, Angelstam 1998a,b, Yaroshenko et al. 2001, Jasinski and Angelstam 2002, Pennanen 2002).

Broadly speaking, the boreal forest disturbance regimes range from succession following large-scale disturbances such as fire and wind to small-scale dynamics associated with gaps in the canopy created by the loss of individual trees. The principal relationship between the main disturbance regimes and site conditions in the boreal forest is explained in the ASIO-model (Rülcker et al. 1994, Angelstam 1998b). The driving explanatory variable in the model is the occurrence and behaviour of wildfire in sites with different fuel characteristics and macroclimates found in boreal forest stands and landscapes. Four groups of average fire frequencies are assigned, being inversely related to the average fire intensity. These frequencies range from extremely low in some wet tall herb sites or at high altitude/latitude with a humid climate were fire is Absent or occurs Almost never to sites where fire occurs Seldom, to mesic sites with Infrequent fire and to dry lichen sites were fire occurs Often. Hence, the name of the model is ASIO. Based on the complex interactions between probabilistic (e.g. mean fire intervals in different site types) and random events (e.g. where and when a fire occurs), the interaction between fire and local as well as regional site conditions influencing fire behaviour was used to deduce three main disturbance regimes found in European boreal forest, viz.: 1. succession from young to old-growth mixed deciduous/coniferous; 2. multi-cohort Scots pine dynamics; and 3. gap-phase Norway spruce dynamics; (Angelstam 1998, 2002; see Table 3).

The ASIO-model was developed as a conceptual model to guide the maintenance and restoration of ecologically sustainable boreal forest ecosystems. The model is based on the hypothesis that if forest management can simulate the composition and structure found in boreal forest landscapes with naturally dynamic spatial and temporal patterns of forest regeneration after natural disturbances, then self-sustained forest ecosystems will be created, and biodiversity maintained (Hunter 1999).

2.3.2. Forest types and developmental stages

The boreal forest in Fennoscandia comprises two conifers and a few decidous tree species (Table 4). While gap-phase dynamics and multi-cohort Scots pine dynamics can be simplified to just a couple of types (Dyrenkov 1984), the succession from young to old-growth stands includes several more or less distinct stages. In addition the variation in the amount of deciduous and coniferous trees needs to be considered (Table 3).

Table 3
Summary of the different natural forest disturbance regimes and subtypes found in boreal and temperate forests (based on Angelstam et al. 1993, Dyrenkov 1984, Oliver and Larsen 1996, Angelstam 1998a,b, 2002).

Disturbance regimes and subtypes	**Type of disturbance**
Successional dynamic (single-cohort or "even-aged" stands) • stand initiation • young • middle-aged • harvestable • ageing • old-growth	Non-biotic: • stand-replacing large-scale external disturbance such as severe high-intensity fire and windthrow Biotic: • stand-replacing external disturbance caused by: insects, fungal disease, beaver
Gap dynamic (all-aged or multiple-cohort stands with a wide range of tree diameters/ages) • even (gaps created mainly by removal of one or a few trees) • patchy (gaps created mainly by removal of tree groups)	Non-biotic: • local disturbance at the scale of trees or patches by windthrow and self-thinning Biotic: • local disturbance at the scale of trees or patches caused by insects, fungal disease
Cohort dynamic (uneven-aged stands with different relative amounts of two or more cohorts of younger and older trees) • regeneration (mainly young cohorts) • mixed cohorts • digression (mainly old cohorts)	Non-biotic: • low-intensity disturbance with partial loss of trees caused by low-intensity fire or windthrow Biotic: • low-intensity disturbance with partial loss of trees caused by large herbivores and insects

Table 4
Life history traits of boreal tree species (Nikolov and Helmisaari 1992).

Tree species	Scientific name	Response to shade	Site preference on mineral soil
Scots pine	*Pinus sylvestris*	Intolerant	mesic to dry
Norway spruce	*Picea abies*	Tolerant	wet to mesic
Silver birch	*Betula pendula*	Intolerant	mesic to dry
Downy birch	*Betula pubescens*	Intolerant	wet to mesic
Aspen	*Populus tremula*	Intolerant	wet to mesic

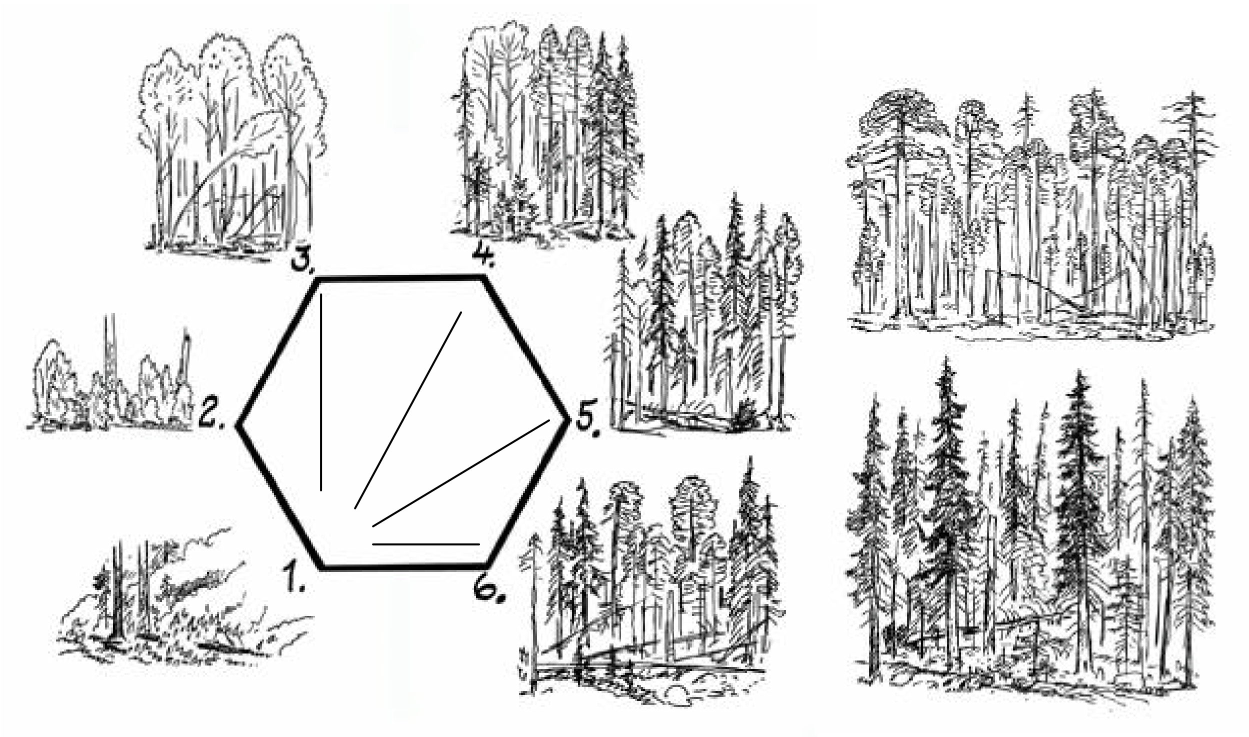


Figure 5
Drawing illustrating six successional stages after fire including an early deciduous and a late coniferous a phase and how these can develop through a multitude of successional pathways (left). Cohort dynamics in a dry Scots pine forest is shown in the upper righ corner and gap dynamics in a wet Norway spruce stand in the lower right corner (drawing by Martin Holmer).

Succession
A given set of trees of a single age class, or cohort, proceeds from life to death through a series of developmental stages (Oliver and Larsen 1996). Large-scale disturbances such as fire or wind initiate succession and allow forests to regenerate over large areas simultaneously. In boreal forest, examples of different successional stages are recent burns, young stands of mixed coniferous and/or deciduous trees, and old-growth forest stands (e.g. Furyaev and Kireev 1979, Furyaev 1996, Angelstam and Arnold 1993, Angelstam 1998b, Yaroshenko et al. 2001). Due to spatial and temporal heterogeneity of disturbances the structural complexity of age classes within a landscape increases with age (Johnson 1992). If viewed over longer time spans, successional stages are usually ephemeral at a particular site. To persist in the landscape, species specializing in a particular stage must be able to disperse from areas with suitable but degrading habitat in order to colonise new sites where the habitat conditions are good or improving. A critical requirement of many species is therefore the maintenance of a stable patch dynamics within the landscape (Pickett and White 1985).

Empirical data from boreal and temperate forest show that the maximum possible range of all the different steps in the succession usually exceeds well over 250 years (Jahn 1991, Johnson 1992). In a detailed study of boreal forest in Sweden, Niklasson and Granström (2000) showed that the range of age classes on mesic sites stands covers 300 years. Pennanen (2002) assumed maximum ages of 400 years for Scots Pine and 350 years for Norway spruce. The development of a single cohort of trees following a disturbance event can be divided into several distinct stages. Oliver and Larsen (1996) describe four stages of stand development.

However, both from a silvicultural and wild life (sensu Hunter 1990) point-of-view, more than these four stages are needed to capture the structural and compositional variation among different successional stages. In managed forest cutting classes, the terms harvested, young, thinning and final felling are useful as they link the development of the stand to the silvicultural operations (e.g. Smith et al. 1997). However, this division does not include later developmental stages of particular importance for forest biodiversity. Thomas' (1979) and Angelstam's (1999, 2002) distinction of six stages provides a compromise between simplicity and detail and is adopted here (Table 5 and Figure 5). In Table 5 we also suggest a thematic resolution with respect to the deciduous component in different age classes, which would be appropriate for succession.

<u>1. Stand initiation</u>
Just after extensive disturbances such as fire, wind-throw, large-scale insect outbreaks, or clear-cutting, the environmental conditions are often unique. As an example, many species of insects have adapted to this by using the burned dead wood as a substrate (Wikars 1992). Similarly, some plants require heat to germinate (Granström 1993). The specific conditions of the site and the surrounding matrix determining the further forest forming process are created at this stage.

<u>2. Young</u>
In this phase the typical herb, shrub and tree layers vegetation has recovered, often after a phase of herb-rich pioneer ground vegetation. After a natural disturbance, there are often still living trees and patches of trees as well as large amounts of coarse woody debris left from the previous stand. Remnants of the previous stand that died will start to decay. It should be noted that even a severe stand-replacing fire usually does not consume more than about 20 % of the standing biomass of the burned stand (Johnson 1992, Furyaev and Kireev 1979). Moreover, considerable proportions of the disturbed area are often left intact as groups and stands of trees (e.g. Pyne 1984, Johnson 1992, Eberhart and Woodard 1987).

<u>3. Middle-aged</u>
In this phase self-thinning and gradual replacement of light-demanding species (e.g. *Betula* and *Populus*) with shade-tolerant species (e.g. *Picea*) (see Table 4) take place. Towards the end of this stage trees start to compete with each other and some trees die from lack of light or soil moisture, a process called suppression, which leads to stem exclusion (Smith et al. 1997). In Table 5 we suggest a thematic resolution with respect to the deciduous component in different age classes, which would be appropriate for succession.

<u>4. Harvestable</u>
At this phase the light-demanding deciduous broad-leafed phase fades away and shade-tolerant *Picea* and *Abies* take over. The forest gradually acquires a multi-storey vegetation structure and the herb layer vegetation changes towards having more shade-tolerant species. Unless a new disturbance occurs, an ageing stand will gradually enter the understory re-initiation stage (Oliver and Larsen 1996). In this stage scattered trees that previously were successful become damaged or die due to insects, fungi, snow-break, wind, falling trees or other factors. These small gaps in the canopy allow more light and moisture to reach the forest floor. As a consequence, there is an advance regeneration of shade-tolerant species. These four first developmental stages in the succession will have their equivalents in most managed forests. However, due to various silvicultural practices both the tree species composition, the vertical and horizontal vegetation structure as well as the amount and types of dead wood are

being manipulated, usually with the aim to reduce unwanted and promote wanted forest components.

5. Ageing
In this phase, shade-tolerant species are becoming older and start to develop diameters of interest for the largest primary nest excavators, such as the black woodpecker (*Dryocopus martius*), bark texture suitable for different specialized lichens (Uliczka and Angelstam 1999), and canopies that can carry the nests of large raptors. Dead wood is accumulating and the vertical and horizontal vegetation structure is becoming more complex. This stage is usually not allowed to develop in a managed forest.

6. Old-growth
After well over a century or two without a completely or partially stand replacing disturbance the stand is gradually opening up with the formation of gaps in the canopy as large trees or groups of trees fall down. Coarse woody debris is abundant and vegetation structure is complex. As in the young forest, the tree age distribution is usually bimodal (e.g. Oliver and Larsen 1996), now dominated by old trees but with appearing young cohorts both in gaps and as an additional vegetation layer. The relationship between the size and the age of the trees is becoming less and less obvious.

Table 5
Categories of age classes and tree species mixes found in natural succession of large-scale disturbance, and which ideally ought to be mapped to assess the main components of the forest succession (Angelstam 1999). The categories necessary to satisfy the thematic resolution for conifer wood production, which is the by far most dominating reason for mapping different forest types, are denoted with the letter (W). Categories that should be covered for biodiversity assessment purposes are denoted with the letter (B).

Successional stages	Recently disturbed	Young	Middle-aged	Harvest-able	Ageing	Old-growth
Approximate age (years)	0-5	5-30	30-70	70-110	110-150	>150
Proportion deciduous (basal area)						
0-20 %	(W) (B)	(W) (B)	(W) (B)	(W) (B)	(B)	(B)
20-50 %	(B)	(B)	(B)	(B)	(B)	(B)
>50 %	(B)	(B)	(B)	(B)	(B)	(B)

Multiple successional pathways and their duration
The time that the successional development takes shows large variation. Although, as a rule, the full range of successional stages will take more than 200 years in boreal and temperate forests in Europe (Falinski 1986, Leibundgut 1993), it can take both much longer and much shorter time. In the Pacific Northwest region of North America, some types of old-growth stands may take several hundred years to develop (Kohm and Franklin 1997). By contrast the succession in riparian forest with willows (*Salix* spp.) and other deciduous trees may enter an old-growth phase in only 60 years (Oliver and Larsen 1996). Boreal broad-leafed deciduous tree species such as *Populus* and *Betula* may develop old-growth characteristics within similar time frames (Carlson and Stenberg 1995, Carlson 2000).

It is, however, rare that the development after a stand-replacing disturbance in an area is a linear sequence passing through each step in the successional development described above. Instead there are several pathways through which successions may proceed (Figure 5, left). In principle, the disturbance can be initiated in any of the different stages, albeit with different probabilities. In mesic boreal forest a new fire is unlikely to occur due to low fuel loads before a stand age of 20 years. During the first 3-5 decades after a disturbance episode the fire risk is increasing due to fuel accumulation (Schimmel 1993, Niklasson and Granström 2000). Similarly, all factors being equal, a stand's susceptibility to wind varies with age (Gardiner and Quine 2000).

Cohort dynamic

Several tree species show clear adaptations to low intensity disturbances. Scots pine and fire is a good example. In the boreal zone, natural Scots pine forests on dry sites are characterized by frequent low-intensity fires that produce stands with several age cohorts of trees (Sannikov and Goldammer 1996, Angelstam 1998b; Figure 5). Due to its thick bark, and to the long distance between the ground and the canopy, a Scots pine tree becomes less sensitive to fire damage with increasing age. As a consequence, a typical natural dry site Scots pine forest has several distinct age cohorts of living trees, standing snags, both of which eventually produce a continuous supply of dead wood on the ground in different stages of decay (e.g., Sannikov and Goldammer 1996). Such a forest has a park-like appearance. According to Leibundgut (1982), Dyrenkov (1984) and Fedorchuk et al. (1998) this type of disturbance regime occurs also in Norway spruce forests on mesic well-drained sites in association with wind-throw events that remove a portion of the canopy.

Dyrenkov (1984) distinguished three different types of uneven-aged cohort dynamics; viz. 1. regeneration (stands are dominated by younger trees but with an overstory of old and very old trees as well as snags and coarse woody debris); 2. intermediate (the different age cohorts are evenly distributed within the stand) and 3. digression (cohorts of old and very old trees dominate). In natural Scots pine forests on sediments there are typically 3-5 distinct cohorts that range over at least 200-300 years of age (e.g., Sannikov and Goldammer 1996). Sometimes, due to absence of fire for longer time, and to the associated accumulation of nutrients, the site type may develop towards a more productive one.

Gap dynamic

In the absence of large external disturbances, the death of single tree or groups of trees maintains the formation of gaps in which more or less shade tolerant trees can regenerate. A relatively even, both temporally and spatially, regeneration process determines the stand dynamics. The age/diameter distribution of trees within a stand is the inverse J-type (Kuuluvainen 1994) and a simple mean age conveys no information of the typical age structure. The internal age distribution can be characterized as all-aged or consisting of multiple cohorts (Figure 5). Note however that the relationship between the size and age of trees is often poor as small trees can be very old (e.g. Oliver and Larsen 1996). In naturally dynamic landscapes such stands often form corridors, networks or clusters in the wet and moist parts of the landscape. Typically, these forests have a relatively moist and stable microclimate and a continuous supply of dead decaying wood in different stages of decay. This type of dynamics occurs also in large extensive areas where the climate is moist and fires uncommon (Angelstam 1998b, Ohlson and Tryterud 1999). The tree species involved include Norway spruce and *Abies* spp. in boreal and montane forests. Dyrenkov (1994) distinguished two sub-types: with even and patchy spatial tree distribution within the stand, respectively. The first type is characterized by an even distribution of different tree ages in the stand. This is associated with smaller gap sizes including one or a few trees. The second type is characterized by a patchy distribution of different tree ages in the stand. This is associated with larger gap sizes.

2.3.3. The age distributions of stands in different disturbance regimes

Landscape patterns in naturally dynamic forests can be estimated using knowledge about past disturbance regimes. With fire as a once dominating large-scale disturbance, the age-class distribution of forests can be estimated using simple analytical models of equilibrium dynamics (e.g. Johnson and Van Wagner 1985). A distinction needs, however, to be made between time since fire and stand age. The reason is that both fire severity and the fire-adaptedness of different tree species, and hence site type, strongly affects the stand age distribution of of different forest types although the time since disturbance is the same.

<u>Succession</u>
Succession after more or less complete stand-replacing disturbance on mesic sites dominated by spruce and mixed coniferous forest was the dominating natural disturbance regime in the boreal forest. Thus the forest landscape was dominated by a mosaic of more or less even-aged stands with different times since they last burned or blew over. Both theoretical and empirical studies provide information about the quantitative distribution of stands in landscapes following fire. Imagine a checkerboard consisting of a collection of 1000 squares (=stands). If all stands would burn at an age of 100 years and if the stands are evenly distributed among the different age classes, just as if they were logged according to the normal forest paradigm, the result would be a rectangular distribution. Now let us assume that instead a constant proportion of each age class was burned. This would result in a negative exponential distribution (Johnson and Van Wagner 1985). Finally, if fires were confined to older stands with a certain fuel load, then a Weibull distribution (Van Wagner 1978) would result. Hence, the conclusion is that the manner in which stands burn results in a specific age distribution (Figure 6).

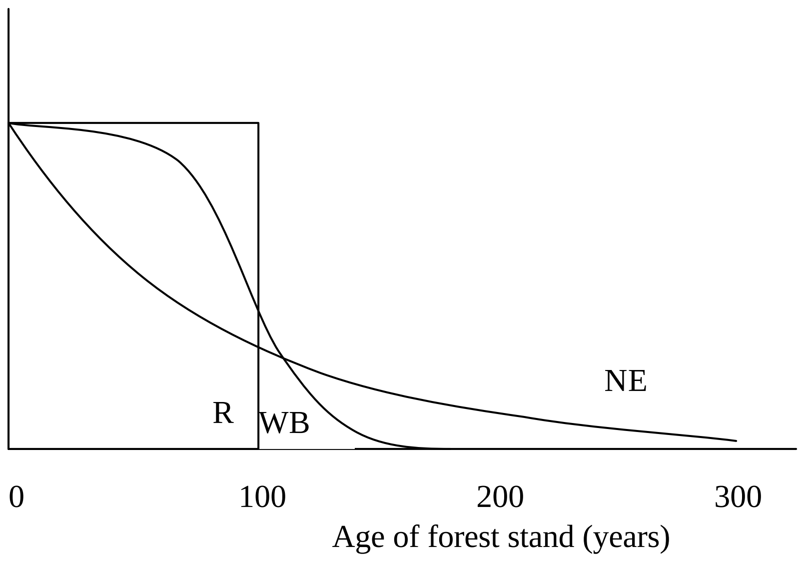


Figure 6
Time since fire distribution of forest successions for a rectangular distribution (R) corresponding to the ideal of sustainable and even timber supply, as well as negative exponential (NE) and Weibull (WB) distribution corresponding to different theoretical age distributions (from Johnson 1992). All distributions have the same average fire frequency. The y-axis denotes the relative amount.

To estimate the natural distribution of stands with different time since large-scale disturbance in boreal forest in their Swedish gap analysis, Angelstam and Andersson (1997, 2001) used the mean of negative exponential and Weibull distributions for an average fire frequency of 100 years. This corresponds to the age distribution of even-aged stands, but naturally with the once usually present remnants of pines, which survived the disturbance. Empirical data from the middle boreal forest on mesic and dry sites before the appearance of agriculture about 1650 (Niklasson and Granström 2000) show a distribution of time since disturbance, which was very similar to the mean between the negative exponential and Weibull distributions. For spruce-dominated forests on mesic sites, but not Scots pine forests (see below) this empirical information can be used as an estimate of the stand age distribution in the landscape (Niklasson pers. comm.).

The differences in the life history of trees in the boreal biome means that shade intolerant species will dominate in the early part of the natural succession and shade tolerant species in latter part. The result is that the deciduous birch and aspen would have dominated earlier part of the succession, and the shade tolerant spruce the latter part. However, the empirical knowledge of the quantitative distribution of deciduous trees in a natural succession is poor. For the purpose of illustrating the patterns of early dominance of deciduous trees and the gradual decline in the proportion of deciduous trees with age due to shade intolerance and the relatively shorter life span of deciduous trees compared with spruce in natural forest, Angelstam and Andersson (1997 page A-5, Table 6) subdivided the area under succession in different age classes into different types of deciduous admixture. However, even if the same procedure could be employed here (Table 7), considering the limited quantitative empirical information about the regional variation in the amount of deciduous trees in natural landscapes in our study area, we do not employ this estimate in the regional gap analysis, but rather discuss it in the results. Another limitation for doing gap analyses regarding the deciduous component is the absence of good information about the past and current amount of old deciduous trees in the cultural landscape.

Table 6

Estimate of the natural distribution of different proportions (in volume %) of deciduous trees in different age classes according to the Swedish gap analysis made by Angelstam and Andersson (1997 page A-5). The figures are based on distributing the sum of each class into different classes of deciduous admixture assuming that shade intolerant deciduous species decline in proportion with time.

percent decide	young (0-29 yrs)	middle-aged (30-69 yrs)	old (70-109 yrs)	ageing (110-149 yrs)	old-growth (>150 yrs)
0-19	8	8	7	3	8
20-49	10	12	8	3	0
50-	10	12	8	3	0
Sum	28	32	23	9	8

Table 7
Estimate of the distribution of different proportions (in volume %) of deciduous trees in different age classes according to the ideas of the Swedish gap analysis made by Angelstam and Andersson (1997 page A-5; see Table 6). Note that age class resolution in this study is determined by that of the remote sensing data while the former study had a thematic resolution based on a separation of ageing and old-growth forests.

percent decide	stand re-initation (0-9 yrs)	young (10-40 yrs)	middle-aged (40-70 yrs)	old (70-110 yrs)	ageing and old-growth (>110 yrs)
0-19		9	7	7	22
20-49		10	8	5	0
50-		10	8	5	0
Sum	10	29	23	17	22

Cohort dynamics
The fire-adapted life history of the Scots pine means that a distribution of time since disturbance such as reported by Niklasson and Granström (2000) cannot be used as an estimate of the stand age distribution in the landscape. Using the modelling approaches developed by Mladenoff and Baker (1999), Pennanen (2002) showed that on spruce sites the stand age distribution was similar to previous theoretical and empirical studies, while pine forests with a cohort dynamics had very high mean stand ages due to the almost continuous presence of old fire-resistent trees. Empirical data from Scots pine forest dominated forests with cohort dynamics show the same pattern (e.g., Kostamuksha, Yaksha).

Gap-phase dynamics
On wet spruce-dominated sites gap-phase dynamics is assumed to dominate. Such stands have moderate mean stand ages, but with a very high variance due to the presence of regeneration of trees in gaps and old trees. Most stands are consequently old, but due the shorter life expectancy of Norway spruce compared with Scots pine, the age distribution ought to be narrower.

2.3.4. Conclusions about age distributions

The principal differences between the age distributions in the three types of disturbance regimes is summarised in Figure 7 and our numerical estimates of the age distribution of stands of the three main disturbance regimes are presented in Table 8. Note that the theoretical estimates used by Angelstam and Andersson (1997) for succession is very close to the empirical information from Niklasson and Granström (2000). The large macroclimatic variation in the WX-region with a long gradient from high altitude western oceanic climate to low altitude eastern more continental climate (Ångström 1974) merits means that different age distributions must be used in different regions (Angelstam 1998b). For successsion at altitudes over 500 m we estimated the natural age distribution by calculating the arithmetic mean between succession and gap dynamics. For cohort we pushed the age distribution towards old forest (cf. Pennanen 2002) (for details see Table 8).

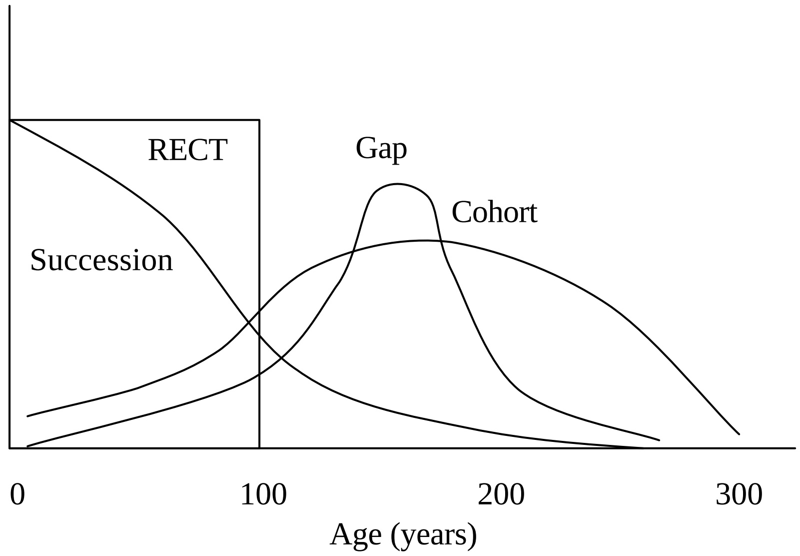


Figure 7
The relative distribution of stands with different mean ages in the three types of forest disturbance regimes. For pictures showing what the forests with the three types of disturbance regimes look like see Figure 5. The rectangular distribution is shown for comparison (cf. Figure 6).

Table 8
Estimated proportions of different age classes in naturally dynamic forests with different natural disturbance regimes (bold). For succession the theoretical rectangular (RECT), negative exponential (NE), Weibull (WB) and mean of negative exponential and Weibull (NE+WB) (see Angelstam and Andersson 1997, 2000), and the empirical data for naturally dynamic boreal forests (pre 1650) from Niklasson and Granström (2000: fig 14) are presented. For cohort and gap we use the same distribution as Angelstam and Andersson (1997, 2001). To account for the large climatic differences between different parts of the study area, we use for western and high altitude area stand age distributions, which have been skewed towards older age classes for succession and cohort dynamics. Due to the paucity of local empirical data, for succession these were derived by using the mean of the empirical succession data and the estimates for gap-phase dynamics, and for cohort by reducing the amount of middle-aged and harvestable age classes by 50 %. These "oceanic" age distributions are given within brackets and applied to the 500-800 m altitude interval in the stratification based on altitude/bedrock, to the north boreal (32ab) and subalpine (33) ecoregions and to the NW Dalarna national board of forestry regions.

Age class (yrs)	Succession					Cohort	Gap
	RECT	NE	WB	NE+ WB	Empiri-cal		
1. Stand initiation (0-9)	10	10	9	10	**10 (6)**	**5 (5)**	**1**
2. Young (10-39)	30	25	28	27	**29 (12)**	**5 (5)**	**1**
3. Middle-aged (40-69)	30	19	27	23	**23 (12)**	**10 (5)**	**1**
4. Harvestable (70-109)	30	17	28	23	**17 (10)**	**10 (5)**	**1**
5. Ageing and old-growth (110-)	0	28	7	17	**22 (60)**	**70 (80)**	**96**

2.3.5. Aggregating age classes across sites – an example

Biologically old forest is a type of forest that forestry has not aimed at maintaining. By contrast an average naturally dynamic coniferous forest landscape consists mainly of dry pine forests, wet spruce forests and different stages of succession after fire or other large-scale disturbance on mesic sites. To understand how much old forest of different types exists in the natural dynamic boreal forest the area of age classes with high stand ages must be added up. The first column (I) in Table 9 shows the approximate distribution of different stand types. About 70 % is assumed to be succession forest with forest in different age categories from a newly burnt area to old forest. About 20 % multi-layered pine forest, most of which can be considered as old forest because of the large fraction of old trees and dead wood of different types. Finally, about 10 % wet spruce forest with internal dynamic, which mainly can be counted as old forest (Rülcker et al. 1994). In the next column (II), distributions are calculated as average values for the most important forest types in coniferous forest landscapes according to Angelstam and Andersson (1997). This definition of biologically old forest corresponds to coniferous forest, which is considerably older than forest that is normally cut today (i.e. about 110 years), as well as younger forest that includes ageing deciduous trees. Both are forest types that normally do not exist in cultivated forests. The sum of these forest environments - which are denoted as B, C, D, F in Table 9 and which, in a sense, could be counted as biologically old forest – is thus 46 % of an average coniferous forest landscape with the site type distribution of the example. Without clearly stating the relative amount of different tree species/site types Pennanen (2002:222) estimated the proportion of old-growth forest in the landscape for different mean fire intervals and severity. The average of the 9 different modelling scenarios for a mean fire interval of 100 years ranges from about 20 to 80 %.

Table 9
A tentative example of the distribution of forest areas with different disturbance regimes and age classes in a fictive natural coniferous forest landscape. The bold numbers represent forest of high conservation value.

I. Type of forest dynamic and distribution in different forest environments in a natural forest landscape.	II. Ditto expressed in %
Succession forest (70 %) • A. Young and middle-aged trivial stands (approx. 2/3) • B. Older forest with considerable amount of deciduous trees (ca. 1/6) • C. Old or almost old forest (ca. 1/6)	 46 **12** **12**
Internal dynamic (10 %) (D)	**10**
Multilayered pine forest (20 %) • E. <110 years (ca. 4/10) • F. >110 years (ca. 6/10)	 8 **12**
SUM	100

According to Östlund et al. (1997) the amount of old forest in Lycksele 1913 was estimated at 83 %. Without knowing the distribution of different disturbance regimes and parameters describing fire frequency and intensity, these emprical estimates from a time period when forest fire regimes already had been altered are difficult to interpret. Moreover, there has been a gradual change in the age distribution of forests within certain site types due to the gradual transition from a naturally dynamic landscape before the advent of industrial use of forests. This includes both altered grazing regimes and human alteration of fire regimes. For the eastern part of Västerbotten's county this kind of landscape change commenced already around 1650 (Niklasson och Granström 2000). Already by the 19th century the age distribution had been considerably skewed towards younger age classes, as well as towards smaller average patch sizes (Niklasson and Granström 2000). There is nothing to suggest that this transition started later in our study area. Also in Finland there has been reported an increase of fires between the 17th and 19th century (see Pennanen 2002). Consequently, we feel that studies based on historical data from the latter part of the 19th century only (e.g., Linder and Östlund 1998, Axelsson et al. 2001, 2002) do not accurately represent the stand age structure of the naturally dynamic forest landscape to which species have adapted by evolution (Figure 8). To improve our benchmarks for biodiversity conservation in naturally dynamics systems more needs to be learned from biological archives and contemporary reference landscapes.

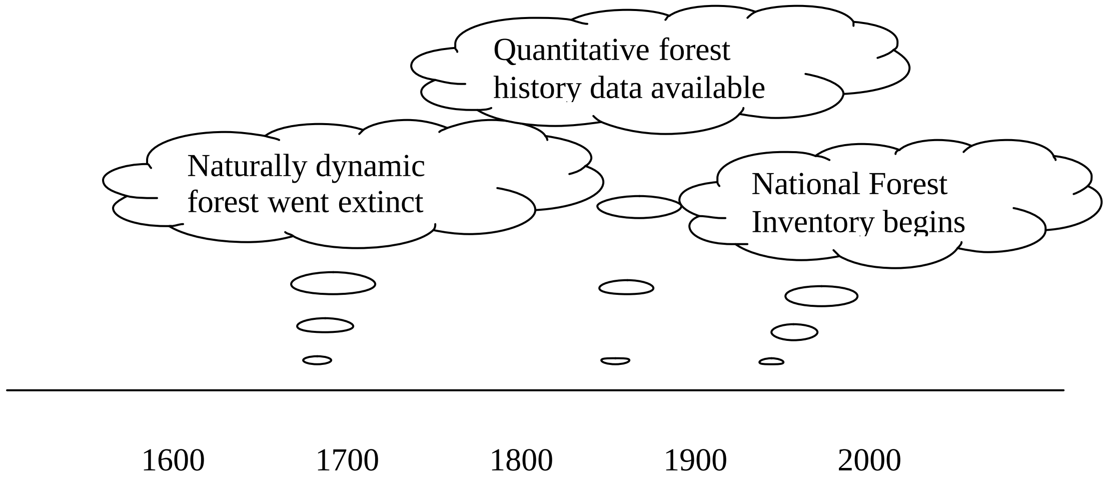


Figure 8
Generalised description of the phases in land use history and the different points-of-view presented by studies of naturally dynamic forests sensu Angelstam and Andersson (1997) and the pre-industrial forest landscape as revealed by forest history studies (e.g. Östlund et al. 1997, Axelsson et al. 2002). Note that that the National Forest Inventory did not start until 1923.

2.4. Forest types of conservation interest

Forests on certain site types and developmental stages occurring in Scandinavia have been identified as incompatible with modern forestry (e.g. Esseen et al. 1997). These are usually forests older than final age of logging, having more deciduous trees and/or located on undrained sites. The level of incompatibility of certain forest types with forestry may be discussed in the frame of natural disturbance regimes and different forms of forest management (Angelstam 2002). Even if quantitative gaps in the amount of these exposed forest types have not been evaluated, the national, regional and local set aside practices have been based on this general knowledge of how habitat loss driven by forestry affects biodiversity. Guided by the regional experience, the county administrative boards participating in this project have asked for a gap analysis with special emphasis on four types of forests perceived as having high conservation value (old coniferous, old pine, wet, old deciduous) (Table 10, 11).

Table 10
Relationships between the ASIO-model (=site types), disturbance regimes and four forest types of high conservation interest.

ASIO-class	A	S	I	O
Site type	wet sites	all other (mesic) sites		dry sites
Disturbance regime	Gap phase	Succession		Cohort dynamics
Forest types of conservation interest	wet coniferous forest	old deciduous old coniferous		old dry pine

Table 11
Differences in dynamics and management needs of different forest types of conservation interest. Some of them are suitable for 'natural development' within protected areas while other needs to be actively managed.

Forest type	Site type	Characteristics	Tentative mode of maintenance
wet coniferous forest	wet	assumed eternal gap dynamics; very long duration	no need of management
old deciduous	mesic and dry	moderate duration	need to consider the temporal dynamics in planning and may need management (remove spruce)
old coniferous	mesic	assumed old-growth; long duration	no need of management
old dry pine	dry	assumed old-growth; long duration if subject to low-intensity fire	requires management by fire

3. Regional gap analysis
3.1. Procedure for regional gap analysis

3.1.1. Area gaps

To do regional gap analysis we followed the general logic of Angelstam and Andersson (1997) (Table 12 a). Due to the problem of mapping forest types using remote sensing in the ecotone between agricultural land and forest, i.e. usually abandoned pastures and meadows (Mikusinski and Angelstam 1999), we focus on the natural disturbance paradigm. However, in the discussion we will discuss the contribution of deciduous trees found in forest edges. Below, we provide the sequence of steps in analysis presented in the introduction. The procedure is summarised for different forest age classes and site types in Table 12 a. In Table 12 b the same procedure is presented for forest with different tree species composition.

A: Estimate the amount of potential forest vegetation based on modelling of the distribution of different natural disturbance regimes, and knowledge about the age distribution within these different disturbance regimes. The analyses cover the entire land area, except for non-forested mires and alpine areas. We assume that the spatial extent of forest land has been constant. Then the following steps were carried out:

- A "TOPOINDEX" was calculated using a Digital Elevation Model;
- The landscape was divided into three types: wet/moist, mesic and dry;
- Wet/moist was associated to gap phase dynamics, mesic to succession, and dry to cohort dynamics;
- Different age distributions were applied for different disturbance regimes as well as different parts of the WX-region.

B: Estimate today's amount of the naturally occurring forest types defined in A. Remote sensing data was calibrated with stand data provided by forest companies for each satellite scene to map the age-class and tree species composition. We assume that no transitions of land from forest to mire and vice versa have occurred. For the site type classification based on the digital elevation model the pixel size was 50x50m. The analyses, however, were made at the same spatial resolution (25x25 m) as for the 33 forest types in Table 17.

C: Estimate the minimum numerical amount of representative forest types needed to maintain viable populations of the most demanding species based on the appearing knowledge about population's non-linear responses to habitat loss (e.g., Fahrig 2001). There is a large variation in this threshold depending on the life-history traits of species. However, empirical studies suggest that when habitat loss has proceeded so that 10 % remains there are usually problems for the long-term viability of the local population (Andrén 1994). Appearing empirical threshold values for focal species (Angelstam and Breuss 2001, Angelstam et al. 2003a, and several articles in Angelstam and Breuss 2003) confirm this general notion. As an example, the average threshold for landscape scale occurrence of 15 bird species was 19 % and for the beetle *Tragosoma depsarium* the threshold was about 25 %.

Spatially explicit simulation models have also been used to assess landscape thresholds. These models have indicated that the effects of habitat loss alone are far more important for the extinction risk of species than habitat configuration. Fahrig (1998, see also 2001) showed that changes in configuration causes population declines only under relatively limited conditions including factors concerning both landscape structure and species life-history characteristics. According to her simulations, species prone to fragmentation 1) have a limited dispersal ability, 2) prefer habitat, which covers less than 20 % of the area, 3) do not prefer ephemeral habitats, 4) are territorial and show strong site-fidelity and 5) have a clearly higher mortality rate in the landscape matrix than within the preferred habitat.

We therefore use the 20 % threshold value also suggested by Angelstam and Andersson (2001) as an estimate of the acceptable habitat loss. It should, however, be stressed that the issue of thresholds is far from being well understood as to the variation among species with different life history traits found in different forest types. The rationale for using birds and other potential focal/umbrella species is to follow the precautionary principle (Roberge and Angelstam in press).

D. Estimate the difference between B and C, where a negative value implies a gap in amount of area, and hence a need for habitat re-creation (see Figure 9). The losses will be divided into loss of forest cover in general as well as the loss of the focal forest types on today's forest land.

- Loss of forest on the different site types was made as GIS analyses and summarised for the three different stratifications.
- Loss of certain forest types was made by comparing the estimated amount of different forest types from step A and the remote sensing based land cover map. The estimates of the sufficient amount of habitat (A*C) was made using a C-value of 0.2.

The regional gap analysis focuses on the age class distribution within the three disturbance regimes (Table 12 a) but discusses also the tree species composition (Table 12 b). We have not studied gaps in other important habitats such as burned forest, flooded forest and windthrown forest.

In spite of the poor knowledge about reference values for the natural amount of deciduous stands, we attempt a procedure for making a gap analysis for the deciduous component for one of the disturbance regimes, namely succession. The estimation is based on the age distribution in Table 12 a, and on the estimates of the amount of three categories of deciduous tree admixtures presented in Table 7 (0-20 %, 20-50 % and >50 %) in succession. The results are presented for two age classes (40-69 years and >70 years, respectively).

To describe today's amount of deciduous trees, deciduous pixels both from mesic and dry sites are used. This is assumed reasonable because of the reduction of fires on dry sites as derived by TOPOINDEX modelling, which consequently should have made dry sites more mesic due the the accumulation of organic matter.

E: Making a tentative gap analysis for tree species admixtures at mesic and dry sites (Table 12 b). This gap analysis goes through the same principal steps as for the forest age classes (A – D above). However, the results must be taken with much more caution, since the model for tree species admixtures is much less well-founded than that for stand age. Still, the difference between tree species admixture classes is an important aspect of today's forests, and the results of this step are therefore relevant for nature conservation strategies. Tree species admixtures of wet sites were, however, not analysed, since there is no available model for this.

- DEC_1: Estimate the amount of different tree species classes in the natural landscape (analogous to step A). Combining the distribution of disturbance regimes and age classes (obtained in step A above) with the distribution of three categories of deciduous tree admixtures did this for succession forests (presented in Table 7). Succession forests with less than 20 % deciduous trees were assumed to be either spruce dominated or mixed coniferous, because pure pine stands occur mainly on dry sites. Forests with cohort dynamics (dry sites) were all assumed to be pure pine stands (>70 % pine).

DEC_2: Describing today's amount of tree species admixture classes (analogous to step B). For describing today's amount of tree species admixture classes, mesic and dry sites were joined into one unit. The forest at mesic and dry sites was classified into four classes of tree species admixture, corresponding to the four classes in the modelled natural distribution (DEC_1). Joining mesic and dry sites in step E2 is reasonable, because there is no overlap between forests with succession dynamics and cohort dynamics as regards natural tree species admixtures (DEC_1). Thus, without losing information, we could avoid the extra uncertainty that is usually the consequence when combining two spatial data sets, each with a certain stochastic error. In addition, the border between sites with succession forest dynamics and sites with cohort dynamics is rather diffuse in the field, and many sites having mesic soil moisture have had cohort dynamics and vice versa.

Table 12 a
Summary of the procedure for making gap analysis for different ecoregions based on the natural disturbance paradigm, habitat loss thresholds, and data from remote sensing. Past and present amounts were calculated separately for five different age classes for each of the three site types and for the 6 ecoregions, the 10 strata of the altitude and bedrock stratficiation and the 7 national board of forestry districts.

Step in the gap analysis	Estimates in ha and proportion of the three natural disturbance regimes based on topoindex (see Table 3) (ha and %)														
	Gap-phase					Succes-sion					Cohort				
A1. Potential distribution of the three forest disturbance regimes within the original forest cover assuming all land except mires and alpine areas was forested															
A2. Loss to non-forest habitats of each disturbance regime calculated by subtracting from A1 the area now being agriculture, urban or infrastructure according to the topographic map															
A3. Estimate of the past amount of the three forest disturbance regimes on the land that is forested today (=A1-A2)															
Age classes (see Table 8)	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
A4. Estimation of the natural amounts of the different age classes on today's forest land (A3) made by subdividing the different disturbance regimes according to a natural age-class distribution with the same resolution as used in the description of today's forests															
A5. As A4 but for the original forest (A1) cover assuming all land except mires and alpine areas was forested															
B1. Today's amounts of the five age classes on the three disturbance regimes based on remote sensing															
B2. Proportion of potential amount on today's forest land existing today (i.e. B 1/A4).															
B3. Proportion of potential amount on original forest existing today (i.e. B 1/A5)															
C. Long-term goal based on A5 and habitat loss threshold ranges															
D. Gaps in existing amount (=re-creation) (B-C)															

Table 12 b
Summary of the procedure for making gap analysis for distribution of tree species admixture classes for mesic and dry sites. The natural distribution of tree species admixture classes were modelled based on the natural disturbance paradigm and a topographic model. Today's amount of tree species admixture classes was estimated from remote sensing data. The results are presented for age classes older than 40 years. For deciduous and mixed coniferous-deciduous forests the two oldest classes are put together into one class (>70 years old). Succession forests with <20 % deciduous trees were assumed to be either spruce dominated or mixed coniferous, because pure pine stands occur mainly on dry sites. Forests with cohort dynamics (dry sites) are assumed to be pure pine stands (>70 % pine).

Step in the gap analysis	Estimates in ha									
Main disturbance regimes	Succession/mesic							Cohort/dry		
Generalised tree species admixtures in two of the disturbance regimes	Spruce and mixed coniferous (<20 % decid., <70 % pine)			Mixed conif.-decid. (20-50 % deciduous)		Deciduous (>50 % deciduous)		Pine (>70 % pine)		
Age classes (see Table 8)	3	4	5	3	4 +5	3	4+5	3	4	5
DEC_1. Estimation of the natural amounts of the different tree species admixture classes in the three oldest age classes on today's forest land. Made by subdividing the natural amounts of different age classes on today's forest land in the Succession (mesic) disturbance regime (Table 12 a, line A4) according to the estimates in Table 7, of natural distribution of different deciduous-conifer admixtures. For the Cohort (dry) regime it is the same amounts as in Table 12 a, line A4, since all forests there are assumed to be pine forests.										
When classifying today's forest into tree species admixture classes from remote sensing data, mesic and dry sites are treated together. Still, the four tree species classes correspond to the four classes describing the natural landscape above.	Mesic sites and dry sites according to satellite data									
	Spruce and mixed coniferous (<20 % decid., <70 % pine)			Mixed conif.-decid. (20-50 % deciduous)		Deciduous (>50 % deciduous)		Pine (>70 % pine)		
Age classes (see Table 8)	3	4	5	3	4 +5	3	4+5	3	4	5
DEC_2. Today's amount based on remote sensing.										
DEC_3. Proportion of potential amount on todays forest land existing today (i.e. E2/E1) (corresponds to Table 12 a, line B2)										
DEC_4. Long-term goal based on E1 and habitat loss threshold ranges (corresponds to Table 12 a, line C).										
DEC_5. Gaps in existing amount (E2-E4) (corresponds to Table 12 a, line D).										

3.1.2. Protection gaps

As described in Table 13 there are several types of conservation areas, which have different legal protection (see also Figure 9). According to the Natura 2000 handbook, European Community directives should be implemented in the national legislation. In Sweden this has been made in several steps. On July 1, 2001 a new legislation was made to clarify the meaning of the Habitat Directive and the Birds Directive (see Prop. 2000/01:111, Skyddet för vissa djur- och växtarter och deras livsmiljöer). These changes imply a need to apply for permission according to 7 kap 28 a § miljöbalken. Permission is needed to carry out management and action, which can have a negative effect on areas as decribed in 7 kap 27 § miljöbalken. All the forest areas appointed as Natura 2000 areas have from July 1, 2001 been assigned a status of national interest. In addition the aim is to let plans become encompassed by the Habitat Directive. Therefore changes have been made in 4 kap 1 and 8 §§ miljöbalken. The new rules implement article 6.2-4 in the Habitat Directive. In our analysis only Natura 2000 area located within existing nature reserves are included.

Table 13
Instruments for the protection of forest areas with high conservation value.

<table>
<tr><td>Type of conservation area</td><td>Protection institute</td><td>Legal ground</td><td>Implementing body</td></tr>
<tr><td rowspan="2">Protected areas</td><td>• national park
• nature reserves (both established and soon to be gazetted)
• biotope protection areas</td><td>• The Environmental Code</td><td>• Swedish Environmental Protection Agency
• County administrative board
• National Board of Forestry</td></tr>
<tr><td>• nature conservation agreements [1]</td><td>• The Land Code Law</td><td>• National Board of Forestry</td></tr>
<tr><td>Woodland Key Habitats of two types</td><td>• Not protected. It is a result of the Woodland Key Habitats inventory. However, Woodland Key Habitats on certain holding have voluntary protection</td><td>• Forest policy</td><td>• National Board of Forestry by advicing landowners and the big forest companies</td></tr>
<tr><td>Variable retention</td><td>• Certification</td><td>• None</td><td>• Certified companies</td></tr>
</table>

1. Conservation agreements last for up to 49 years and focus on securing forests with conservation values related to, for example, a certain phase in forest succession.

In this step we estimated how much of the existing different forest types of high conservation value with area gaps is secured by different kinds of protection. The logic for summing up the results by ecoregions is shown in Table 14a. Tables 14a,b summarise how the analyses of protection gaps for different forest age classes and tree species combinations were made.

Table 14 a
Principle for presenting the amount of existing old forest (over 110 yr) with different levels of protection within ecoregions.

	Ecoregion					
Subdivision of B in Table 12 a	26	27	28ab	30a	32ab	33dfg
E1. Amount of old forest with legal protection[1]						
E2. Amount of old forest where the forestry assumes responsibility for protection[2]						
E3. Areas under consideration[3]						
E4. Amount of old forest not encompassed by E1, E2 and E3						

1. Forests considered to be legally protected are those where logging is prohibited within areas protected under 7 chapter in the environmetal code, i.e. national parks, nature reserves (both established and soon to be gazetted), biotope protection areas. Nature conservation agreements, which are established under the land code law are also included in the statistics.
2. Includes both forests owned by small private land owners and companies.
3. Areas under consideration are areas with documented nature values that are proposed to be legally protected, but where the County Administration Boards have not yet decided which ones to protect.

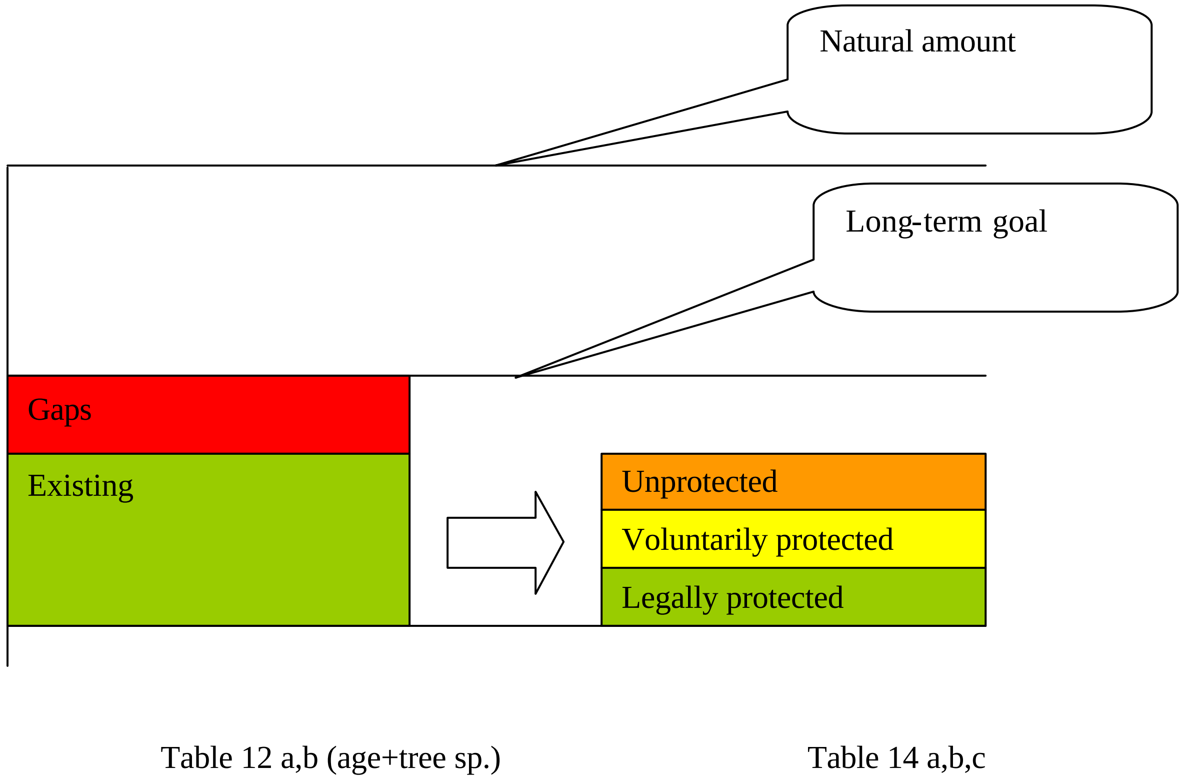


Figure 9
Example for a habitat rarely found in today's managed landscape with its natural amount, long-term goal, gap in amount (D) and protection gaps (E2 and E3). Compare with tables 12a,b and 14a,b,c). For forest types highly compatible with modern forestry there are no gaps, but a surplus.

Table 14 b
Procedure for estimating the amount of protected areas based on spatially explicit analysis of forest in different age classes in the three disturbance regimes.

	Areas in ha														
	Gap-phase					Succession					Cohort				
Age classes	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
P1. Amount of existing forest of the five age classes with legal protection1															
P2. Amount of the five age classes within existing forests where the forestry assumes responsibility for protection2															
P3. Amount of five age classes being considered for protection															
P4. Amount of forest not encompassed by P1, P2, and P3															
Sum (=Table 12 a, line B1)															

1. Forests considered to be legally protected are those where logging is prohibited within areas protected under 7 kap. Miljöbalken, i.e. national parks, nature reserves (both established and to be gazetted), nature conservation agreements and biotope protection areas.
2. Forestry is assumed to take responsibility for leaving Woodland Key Habitats.

Table 14 c
Procedure for estimating the amount of protected areas based on spatially explicit analysis of forest in different forest types and age classes in the three disturbance regimes.

	Areas in ha																					
	Gap-phase[3]											Succession and cohort										
	Spruce and mixed conif. (<20 % decid., <70 % pine)			Mixed conif.-decid. (20-50% deciduous)			Decid. (>50 % deciduous)		Pine (>70 % pine)			Spruce and mixed conif. (<20 % decid., <70 % pine)			Mixed conif.-decid. (20-50 % deciduous)			Decid. (>50 % deciduous)		Pine (>70 % pine)		
Age classes	3	4	5	3	4	5	3	4+5	3	4	5	3	4	5	3	4	5	3	4+5	3	4	5
P1. Amount of existing forest of the respective class with legal protection1																						
P2. Amount of existing forest of the respective class where the forestry assumes responsibility for protection																						
P3. Amount of existing forest of the respective class being considered for protection																						
P4. Amount of forest not encompassed by P1, P2, and P3																						
Sum (=Table 12 b, line E2) 3																						

1. Forests considered to be legally protected are those where logging is prohibited within areas protected under 7 kap. Miljöbalken, i.e. national parks, nature reserves (both established and to be gazetted), nature conservation agreements and biotope protection areas.
2. Forestry is assumed to take responsibility for leaving Woodland Key Habitats.
3. Gap-phase forests (wet sites) were not analysed with respect to tree species admixture in the gap analysis (Table 12 b).

3.2. Data sources used in the analyses

In this section we list the data used for all the three groups of analyses made within the project (Table 15).

Table 15
List of different digital data sets both prepared internally and available from elsewhere. Each row is described with respect to the data needed for the different groups of analyses. All data layers cover the entire WX region.

Type of information	***Section 3 Regional gap analysis***	***Section 4 Description of functionality using HSI-modelling***	***Section 5 Trends in high conservation value forests***
Stratification into regions • Ecoregions • Altitude/weathering • Forest management districts	 x x x		 x
Distribution of forest disturbance regimes based on modelling based on DEM	x	x	
Land cover map for the forest today • 2001	 x	 x	 x
Habitat Suitability model maps • old dry pine (2 for each) • old coniferous (2 for each) • deciduous (2 for each) • wet		 x x x x	
Forest reserve network • National Parks/Nature Reserves/Biotop protection • Woodland Key Habitats	 x x		survival and functionality of Woodland Key Habitats
Clear-felled areas for three time periods: Late 1970s (MSS) Late 1980s (TM) About 2000 (TM)			trend and difference maps based on the available data

3.2.1. Regions

The results were presented using three regional stratifications. We used digital versions of the two types ecoregions (physical geography and altitude/bedrock) described in the study area section and the division into the regions of the National Board of Forestry. The discussion of representativity is made by ecoregions and the other results presented only as raw data in the appendices.

3.2.2. Coarse site type classification for disturbance regime stratification

Topography is a suitable surrogate for the spatial variations of hydrological processes and conditions across the landscape (Moore et al. 1991). A simple way to capture the control of topography on hydrology is the use of topographic indices. In this study topographic indices were calculated from a digital elevation model (DEM) with a grid resolution of 50 m. The idea was to be able to divide the landscape according to its wetness status as indicated by the values of the topographic indices.

The TOPMODEL index ln(a/tanß) (Beven and Kirkby 1979), which had been calculated from digital elevation data using a new algorithm (Seibert, in prep.) as described below, was tested and evaluated concerning its ability to detect the topographical prerequisites for the occurrence of three types of disturbance regimes in the boreal forest zone, namely found in wet, mesic and dry site types.

The TOPMODEL index is one of the most frequently used indices to estimate spatial wetness distributions. It is computed from the upslope area per unit contour length (*a*), which indicates the amount of the water flowing towards a certain location, and the local slope (tanß), which is a measure of the drainage from a place. This index can be calculated from gridded elevation data using various algorithms, which differ mainly in the way the upslope area is computed (Quinn et al. 1995, Wolock and McCabe 1995, Tarboton, 1997).

Multiple-flow-direction algorithms tend to give more realistic looking spatial pattern (Quinn et al. 1991, 1995) than single-direction algorithms where the flow is concentrated to distinct lines. One problem of a single-flow-direction algorithm, where all area from one cell is routed into the steepest of its eight neighbouring cells, is that the steepest gradient actually might fall between two of the eight cardinal and diagonal directions. Tarboton (1997) tackled this problem by using of triangular facets, which remove the limitation to only eight possible directions. The method used in this study combines the advantages of the multi-flow-direction algorithm as proposed by Quinn et al. (1991) with the use of triangular facets (Seibert, in prep.).

Around the midpoint, M, of any pixel eight planar triangular facets were constructed with the midpoints, P_1 and P_2, of two adjacent neighbouring pixels. For each of these local planes the direction of the steepest gradient was computed. If this steepest direction was outside the 45^o (p/4 radian) angle range of the triangular facet, the direction with the steeper gradient of the two directions towards the two neighbouring cells was used as steepest directions. After computing the steepest direction for all eight triangular facets, those directions were determined which had a steeper gradient than both of their adjacent facets (local outflows). The flow was then distributed to these local outflows using a weighing based on the gradients. The flow algorithm we used differed in two other points from other algorithms. Firstly, streams were assumed to start when the accumulated area exceeded a certain threshold area (typically set to ~15,000 m^2). The accumulated area of a ‘stream cell’ was routed downslope as ‘stream area’ and not considered in the calculation of *a* in any downslope cell, because the basic assumptions, which underlie the TOPMODEL index, do not hold when there is a stream. Secondly, we treated cells without any adjacent downslope cell, i.e. depressions, differently than in most algorithms, where these so called ‘sinks’ are ‘filled’ before the index is calculated. Instead we considered depressions as real topographic features and continued the search for downslope cells using all cells which were located 2, 3, ... cells away, until at least one downslope cell was found and the area was routed to this/these cell(s) (Rodhe and Seibert 1999).

When the topographic index is computed over larger areas, regional variations of the recharge have to be considered. Weighing the area depending on the relative recharge can do this. Here we used the pattern of the annual mean runoff to compute a map of these weights. It should be noted that overland flow is rarely observed in these parts of Sweden, and runoff originates mainly from groundwater. Thus, the mean runoff is a suitable measure of long-term mean recharge. The annual runoff (Raab and Vedin 1995; digital map version of annual runoff) was divided by the minimum value within the region. Then the area was multiplied with these factors before it was routed downhill. The area coming form a cell with twice as high runoff as the minimum, for instance, was 'worth' 5000 m^2 (= 2*50*50) instead of only 2500 m^2. The threshold for stream initiation for these weighted areas was set to 20,000 m^2.

For computational reasons the DEM had to be divided into smaller units (rectangles). Frames of 50 cells were used around each such rectangle to ensure that 'cutting' the DEM into pieces did not influence results. In that way, the accumulated area (*a*) equalled to that which had been computed if the calculations were done on the entire DEM. The frames were clipped before the rectangles with the computed index values were put together for the entire area (i.e. index values computed for frame cells were not used).

The national inventories of woodland key habitats and wet forests as well as data from the national forest inventory (NFI) and forest companies were used to divide the resulting grid data into three classes of the wetness gradient that reflect the disturbance regimes mentioned above. The final GIS processing took into consideration the individual pixel value and the minimum and maximum value within a defined neighbourhood. The ability of the index to predict disturbance regimes was evaluated using forest classification of satellite images, digital vegetation data and field surveys. The NFI data about the site type distribution for each ecoregion is presented in Table 16.

Table 16
The distribution of site moisture types according to the national Forest Inventory data.

Name of ecoregion	Code	Ecoregion	Dry % (1)	Mesic % (2)	Moist % (3)	Wet % (4+5)	sample size
Woodlands south of "Limes norrlandicus"	26	Hemiboreal	3.3	55.5	33.8	7.4	337
Woodlands north of "Limes norrlandicus"	27	South boreal	8.1	50.1	26.8	15.1	631
Hilly lands of the south boreal region	28a,b	South boreal	3.9	57.4	27.9	10.8	1852
Hilly middle boreal woodlands	30a	Middle boreal	3.6	49.8	31.3	15.3	3036
Coniferous woodlands of northernmost Sweden and Finland; very poor bedrock and large mires, 32a has a very high precipitation	32a,b	North boreal	3.3	43.2	31.0	22.5	688
Premontane region; very poor bedrock	33d,f,g	Subalpine	6.1	45.5	26.7	21.7	644

3.2.3. Topographic maps

To estimate the loss of forest we used the digital version of GSD Road Map (blå kartan) in the 1:100,000 scale (http://www.lm.se/english/gsd/e_bla_98.pdf). This database provides the total coverage of the study area and contains broad thematic information in the form of polygons, lines, and point features. In order to estimate today's total forest cover as well as the historic loss of forest to other land-use types, we used following classes of GSD Road Map: forest, mountain forest, built-up area and open area. To estimate additional loss of forest to infrastructure, also linear features like roads and power lines were used. In this case, linear features were buffered according to a special scheme (Table 17) and converted afterwards to raster format with 25x25 m resolution. In addition, information from GSD Road Map was used to estimate amount of edge habitats in the study area. Besides the land use classes listed above, also bogs, water and mires were included in this part of analysis.

Table 17
Rules for buffering linear features.

Linear feature	Code in GSD Road Map	Buffer size
Motorways	5011, 5016	30 m
National roads	5012, 5017,	20 m
Other major roads	5022, 5021	15 m
Intermediate roads	5025, 5024, 5029, 5028, 5014, 5018, 5033, 5036	10 m
Small roads	5061, 5060, 5071, 5070	6 m
Other small roads	5082, 5091	3 m
Normal railroads	273, 272, 271, 276, 275, 274	20 m
Industrial railroads	279	15 m
Major single powerlines	2611, 2612, 2614	25 m
Major double powerlines	2618	30 m

3.2.4. Forest classification

To describe today's land cover types the digital topographic maps were combined with remote sensing data (Ranneby et al. unpubl.). The final product was a grid based GIS database that classifies each 25 x 25 m pixel into a certain land cover class. The highest thematic resolution has been provided for forest and mire types. A total of 33 forest types were described under the forest mask from the 1:100,000 scale topographic map using remote sensing classification (Table 18). The remote sensing classification of this type of objects is complicated and reported correct classification rates are usually poor. For several reasons traditional methods will not give satisfactory results. To overcome these problems, we used a non-parametric approach (Ranneby et al 2003). The Landsat TM images were de-noised using wavelet-transformations. With this method the information from neighbouring pixels is utilised without any requirements of parameter estimation. The feature vector is then extended using difference images both over time and seasons. However, before the extended feature vector can be used the components have to be re-scaled. The size of the re-scaling factor is a function of the dependence between the studied objects and the component. Usually, more than one variable defines the classes. Then there will not exist any natural order relation between the classes so conventional dependence measures, as the correlation coefficient cannot be used. Instead measures with the origin in the information theory are used. From this a suitable metric can be developed and class prototypes defined. Measures for quality assessment of both the method and the classified image have been developed and applied. The tree species percentages correspond to basal area measurements and the stand ages are weighted by the basal area. For each satellite scene stand age and tree species composition from local forest stand data were used to calibrate area estimates. In order to account for the error in forest classification at the pixel level, indicated by the confusion matrices separately for each satellite scene, the areas used in gap analysis were calibrated values from these matrices.

Initially a total of 33 classes of forest types/age classes were produced (Table 18). Depending on the purpose of the respective analysis, these were then reduced to 25 classes (Table 18). Because pixels are summed for a large area, this thematic resolution is judged to be acceptable for the regional gap analysis. However, for the habitat suitability modelling the habitat needs to be combined by several classes. It should be noted that the thematic resolution is insufficient to separate between ageing and old-growth as well as for low (0-20 %) proportions of deciduous trees (Mats Rosengren unpubl.).

Table 18
Matrix with the criteria describing the 33 classes of remotely sensed forest types, forested bog and clear-felled areas. The classification by letters into 14 types (a-n) plus clear-felled areas (o,p) and forested bogs (q) denote the simplification needed to improve the accuracy for the regional gap analysis. Note that due to the requirements of sufficient spatial resolution for habitat suitability modelling several of the 33 classes need to be merged in different combinations.

Forest type	***percent decid***	***other criteria***	***clear-felled areas***	***10-40 yrs (young)***	***40-70 yrs (middle-aged)***	***70-110 yrs (old)***	***>110 yrs (ageing and old-growth)***
Pine	0-19	>70 % pine		1 a	9 a	17 d	25 i
Spruce	0-19	>70 % spruce		2 a	10 a	18 e	26 j
Coniferous (=rest)	0-19	20-69 % pine or 20-69 % spruce		3 a	11 a	19 f	27 k
Condecmix	20-49	-		4, 5, 6 b	12, 13, 14 b	20, 21, 22 g	28, 29, 30 l
Deciduous A	50-69	-		7 c	15 c	23 h	31 m
Deciduous B	70-	-		8 c	16 c	24 h	32 n
Other open	-	low basal area	33 o				
Clear-felled areas			34 p				
Forested bog			35 q				
No data							

3.2.5. *Forested mires*

The classification of mires was made for all areas on the topographic 1:50,000 map (GSD Terrängkartan) denoted as open mire. This was achieved by combining the layers for mires and forest. Areas having both forest and mire were then classified as forested mire. The resulting map is available only as a raster image with 5-m pixels and is of highly variable quality. In general the GSD 1:50,000 is of better quality in the southern and eastern part of the region. Because the forest classification has been made under the mask of the 1:100,000 scale GSD Vägkartan inconsistences are created when the information layers are combined. The data set with the better geometric resolution (1:50,000 Terrängkartan) was used in the final product. All data sets had 25-m pixels. The mire classification in three parts was merged to one grid. All the six classes were expanded with 3 pixels and the mire mask was used so that the forest mire class would fill all the area up to the open mire. To achieve a complete forest cover classification the 33 classes in Table 18 the classification of clear-felled areas for 1986-2001 was added. Any areas missed with this procedure were filled with forest from the 1:50,000 scale GSD Terrängkartan and other land cover types listed below.

10 Forest (Gröna kartan)
11 Forest in mountain areas (Gröna kartan)
12 Mountain forest (Gröna kartan)
15 Clear-felled area (Gröna kartan)
20 Fen (blå myr) (Gröna kartan)
21 Bog (brun myr) (Gröna kartan)
25 Forested mire (Gröna kartan)
31 Wet/poor mire
32 Wet/rich mire
33 Other/poor mire
34 Other/rich mire
101 - 133 forest class 1-33 (cf. Table 18)
211 - 229 type of clear-felled area 11-29
301 Water (Blå kartan)
302 Settlement (Blå kartan)
303 Forest (Blå kartan)
307 Open ground (Blå kartan)
308 Tree-less mountain (Blå kartan)
310 Mountain forest (Blå kartan)
313 Wet areas (Blå kartan)

3.2.6. *Clear-felled areas*

Mapping of clear-felled areas within the wRESEx area was done from satellite data covering the years 1975 to 2001. The time period covered for a specific area varies due to the availability of individual cloud free scenes covering different parts of the area. In total 20 individual satellite scenes were used. The methods are described in detail by Rosengren et al. (2003).

Mapping of clear-felled areas was performed with a multitemporal technique based on pair-wise image differences and interactive thresholding. The classification was performed only within the area defined by a forest mask from digital maps. Pixel classification of a multi source data set requires that each sample must represent a measurement in each data layer from the same position on ground. For the wRESEx project the 25-m sample distance between pixels were chosen with pixel alignment (pixel corner) with the corners of the topographic map sheets in the Swedish National Grid. All data were geocorrected and re-sampled according to this. Pixel interpolation with cubic convolution was used for the re-sampling of satellite data, while the 25-m raster versions of map masks were generated directly from vector maps.

Masks from the topographic maps were used for mapping the clear-felled areas. The forest area was defined by the forest mask from the 1:100,000 scale “blue map” (Blå kartan) which was the only homogeneous data covering the whole area. For the wetland classification, 5-m raster masks from a mixture of digital maps and scanned 1:50,000 topographic maps (Gröna kartan) were used to separate wetland without forest (to be further classified from satellite data) from forested wetlands (not covered by the forest mask in Blå kartan). This 5-m raster mask was reduced to 25-m pixel size for combination with the satellite data for the wetland classification. This means that the forested wetlands were not classified within the classification of forest and clear-felled areas.

Satellite data

Landsat satellites registered all the images used in this study. Landsat-1 was launched already in 1972 with the MSS sensor (Multi Spectral Scanner) being the main instrument. Landsat 1-3, all with MSS sensors, were operated between 1972 and 1982. The MSS sensor has 4 spectral bands in visible and near infrared, with 80 m ground resolution (57x 80 m pixel sampling distance). These bands were oddly numbered and called MSS bands 4,5,6 and 7.

The next generation Landsat satellites were introduced with the launch of Landsat-4 in 1982, with a new TM sensor (Thematic Mapper) as the principal instrument. The TM sensor has 7 spectral bands in visible, near infrared, mid infrared and thermal infrared with 30 m ground resolution.

Most of the satellite data were geometric corrected with ortho-correction methods, using the digital elevation model to remove image parallaxes. The geometric accuracy requirement for multitemporal data classification is to aim for less than one pixel RMS error. This quality was not reached for all scenes used, leading to local misalignments between scenes in some cases. The main reason for this has been the deteriorated geometric quality of the ageing Landsat-5 TM sensor, which was launched already in 1984 and could not be replaced completely until 2000 by Landsat-7. Both the Thematic Mapper and the MSS data were resampled to 25-m pixel size for the continued processing. The image data is stored as 8 bit integer data in each band, corresponding to digital numbers from 0 – 255.

All scenes were manually interpreted for cloud cover and other image data errors. Areas covered by clouds, haze and shadows from clouds were digitised on the screen. Other pixels having erroneous measurements for different other reasons were also marked and included in the "cloud mask", which in reality is a mask defining pixels not to be used for classification. Examples of this are data dropouts, resampling effects at the scene edges and "no data" pixels outside the imaged area.

For the mapping of clear-felled areas, only one spectral band was utilised for each scene pair. The best spectral band, both when considering maximum correlation to timber volume (for conifers) and concerning the image contrast or signal to noise ratio, is the middle infrared (MIR) band TM5. For the change detection between two TM scenes, TM5 was always used. As there were no MIR band present in the old MSS-data, the best band available in MSS-data had to be used. This is the red spectral band TM3 corresponding to the MSS band MSS5. Single band difference images were produced between scene-pairs from different years.

3.2.7. Mires

In the wRESEx project, the classification of treeless mires has been done with a help of satellite images and climatic data. Taking into account productivity and hydrological, four types of mires were distinguished (wet poor, dry poor, wet rich, dry rich). This data set is not used in this study.

3.2.8. Forest ecotones

To estimate the amount of forest edge habitats in different parts of the study area we used the digital version of GSD Road Map in the scale 1:100,000 (http://www.lm.se/english/gsd/e_bla_98.pdf). In all cases forest and mountain forest were treated as one category. Four different types of edges were considered: between forest and bog, between forest and water, between forest and open areas, and finally between forest and moorland. The results were reported as the forest edge density for each of account units.

Analyses of the edge between forest and agricultural land were made by calculating for each 5x5 km area the length of the circumference of the open area theme polygons in 1:100,000 topographic map. The results are presented in Figure 26.

3.3. Results of the regional gap analysis

The results of the regional gap analysis are presented here for each of the six ecoregions described in section 2.2.1 (Table 1). Results for the other two stratifications (see section 2.2.) are presented in the appendeces but not discussed in the text. The letters following after the headings refer to the different steps in the gap analysis regarding old forest (see Table 12 a,b).

3.3.1. Regional area gaps

3.3.1.1. The natural amount of three disturbance regimes

The amounts of the three site types wet, mesic and dry corresponding to the disturbance regimes gap dynamics, succession and cohort dynamics, respectively, are given in Appendix 1 and summarised for the six ecoregions in Figure 10. Except for the small ecoregion 26, mesic site types dominated. In ecoregions 28-33 mesic site types are as common as wet and dry together. There is also a very clear trend with an increasing proportion of mesic sites and decreasing amount of wet and dry sites from the southern ecoregions at lower altitude and the northern ecoregions at higher altitude.

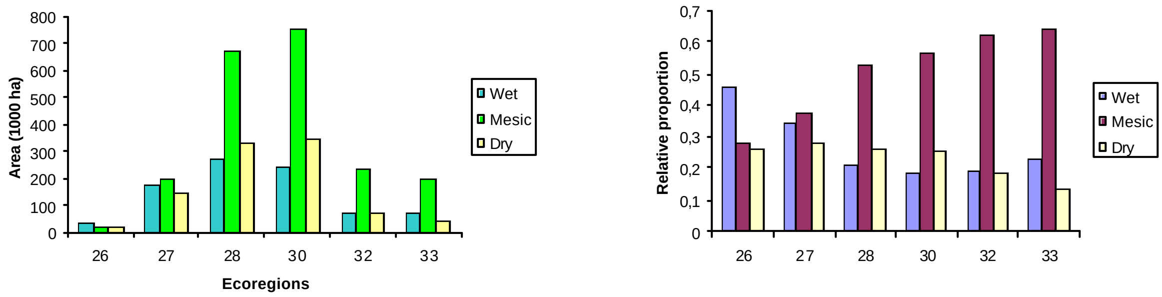


Figure 10
The area (left) and proportion (right) of the three main different site conditions wet, mesic and dry in the six ecoregions of the Dalarna-Gävleborg study area.

3.3.1.2. Loss of forest to agricultural land, urban areas and infrastructure

Except for mires and land above the tree line the natural potential vegetation in the region is assumed to be forest. Hence, all transformation of forest land to other land cover types is considered as forest loss. On average, 9 % of the potential forest cover in the Dalarna-

Gävleborg region has been converted to other land use. As shown in Figure 11 the largest losses are in ecoregions 27 and 28.

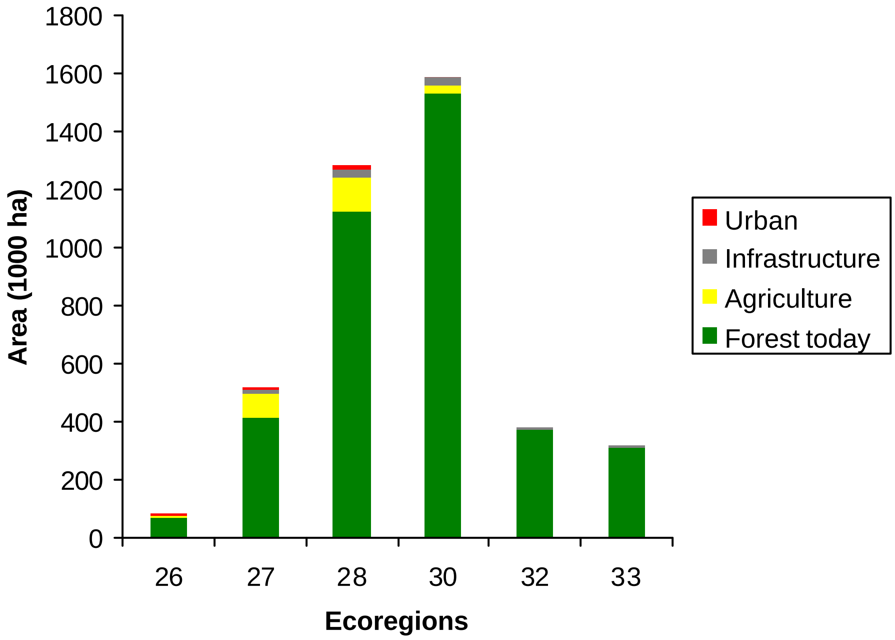


Figure 11
Loss of forest land in different ecoregions.

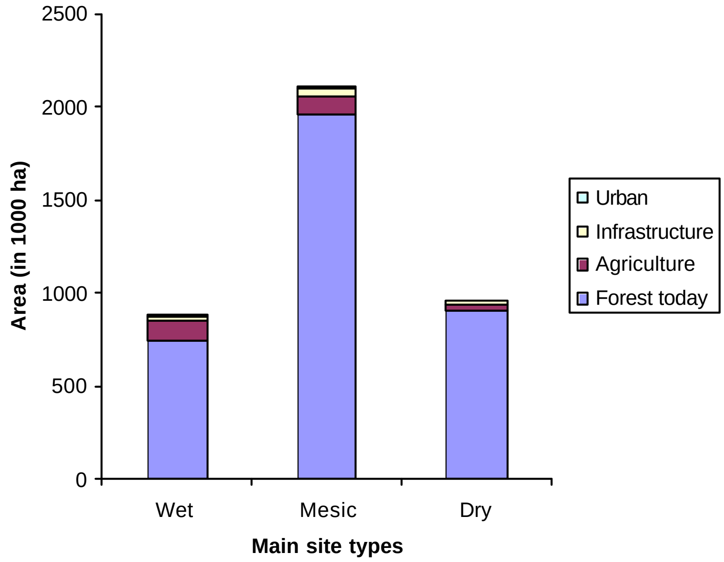


Figure 12
Loss of forest on different site types due to various reasons in the Dalarna-Gävleborg study area.

The loss of forest is highest on wet and mesic sites and lowest on dry sites (Figure 12). However, when using the more precise stratification based on altitude and local soil conditions, the differences among different strata are much larger. As shown in Figure 13, there is a clear difference between land, which is suitable for agricultural development (i.e. below the Marine Limit at about 200 m a.s.l. and having the richest calcareous soils) on the one hand, and the upland poorer areas on the other hand. In the former group the loss is 15-40 % while in the latter is generally below 5-10 %. Except for the rich usually calcareous soils there is a clear tendency towards a declining rate of forest loss from wet via mesic to dry soils. To summarise, the long land use history has produced a clearly biased distribution of site types with forest cover compared with the natural situation.

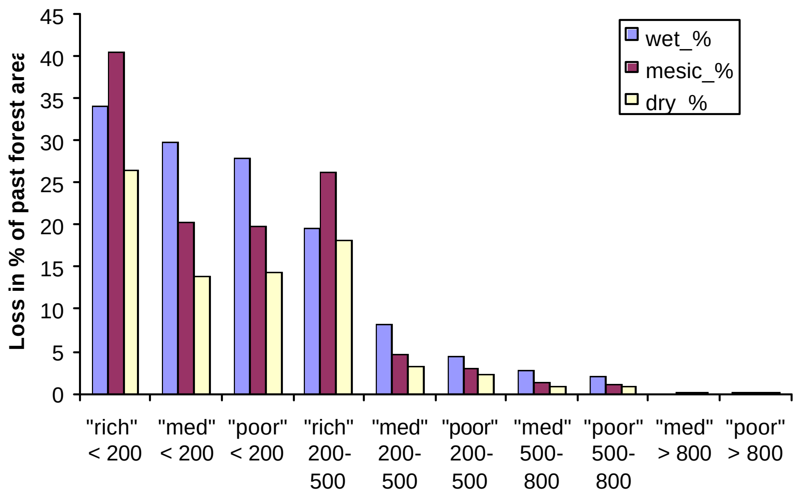


Figure 13
Proportion of former forest land that has been lost due clearing for agriculture, urban areas and infrastructure on site types at different altitude and with different nutrient conditions based on the rate of weathering of the bedrock parent material (see section 2.2.2).

3.3.1.3. Estimate of the natural age class distributions on today's forest land

By applying the estimated natural distribution of age-classes to the amount the three natural disturbance regimes using the TOPOINDEX model we estimated the natural age class distribution in the Dalarna-Gävleborg region (Figure 14). As can be seen, forests older than 110 years should have dominated the naturally dynamic landscape on all site types. In fact, due to remnant old trees that survived fires and storms, this age class probably had a mean stand age of more than 150 years. Among the three disturbance regimes, forest on wet sites would have had the highest proportion of old forest.

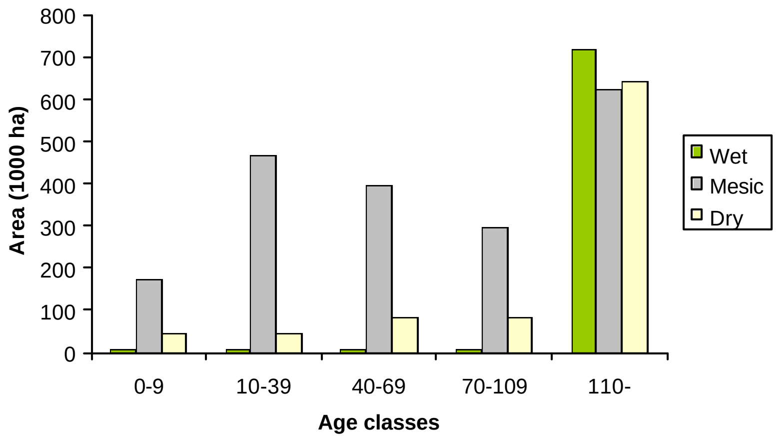


Figure 14
Estimated natural age-class distribution in the three main site types in the Dalarna-Gävleborg study area.

3.3.1.4. The age class distribution today based on remote sensing data

Compared with the estimated natural age-class distribution, today's forest landscape is dominated by young and middle-aged forests (Figure 14 and 15). The largest shift in this respect was found for forests on wet sites.

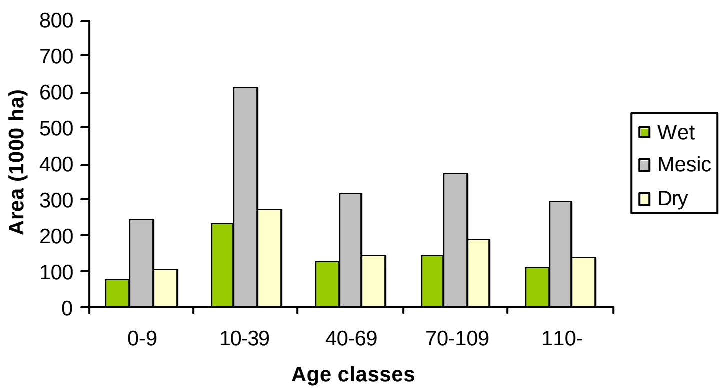


Figure 15
Today's age-class distribution as revealed by remote sensing in the three main site types in the Dalarna-Gävleborg study area.

3.3.1.5. Existing proportion of natural amount of the age classes

In Figure 16 the generalised age-distribution in the whole Dalarna-Gävleborg study area in the past and at present (see Figures 14 and 15) are presented for each of the six ecoregions.

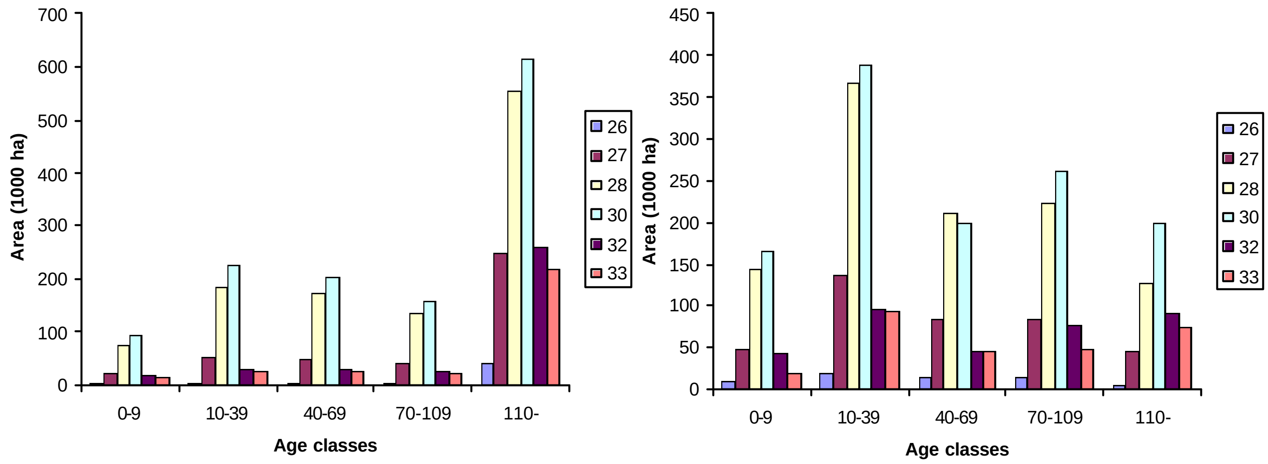


Figure 16
Comparison of the age-class distribution in a naturally dynamic landscape (left) and as revealed by remote sensing at present (right) in six ecoregions of the Dalarna-Gävleborg study area.

3.3.1.6. Past, present and threshold amounts for old forest in WX-region

As shown in Figure 17 the amount of old (>110 years) forest has declined considerably from the estimated past naturally dynamic situation to the estimated present amount. The regional gap analysis also suggests that on average the amount of old forest is higher than the estimated threshold amount in regions 30-33 and lower than the threshold amount in regions 26-28. Note, however, that the regional gap analysis does not take into account the quality of the stands, or the functionality of the existing forest areas in a landscape context.

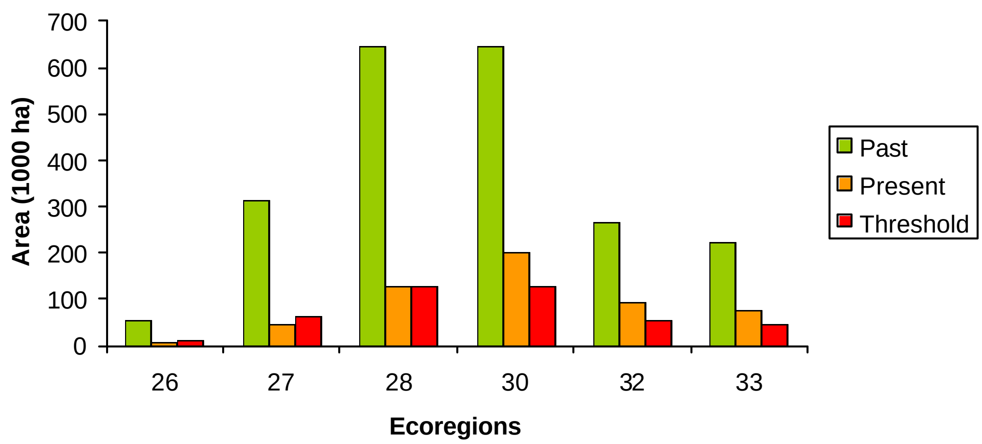


Figure 17
Past, present and thresholds amounts of forest older than 110 years by ecoregion.

3.3.1.7. Gaps in existing amount of old forest

In all but one forest type in one ecoregion (mesic in ecoregion 30) less that a half of the natural amounts of old forest is left. Compared with the overall gap analysis presented in Figure 17, the pattern of gap/surplus of old forest using a threshold value of 20 % differs considerably among the different site types (Figure 18). While the regional gap analysis suggests no gaps for old forest on mesic sites, there are considerable gaps for wet sites in ecoregions 26-30 and gaps for dry sites in ecoregions 26-28.

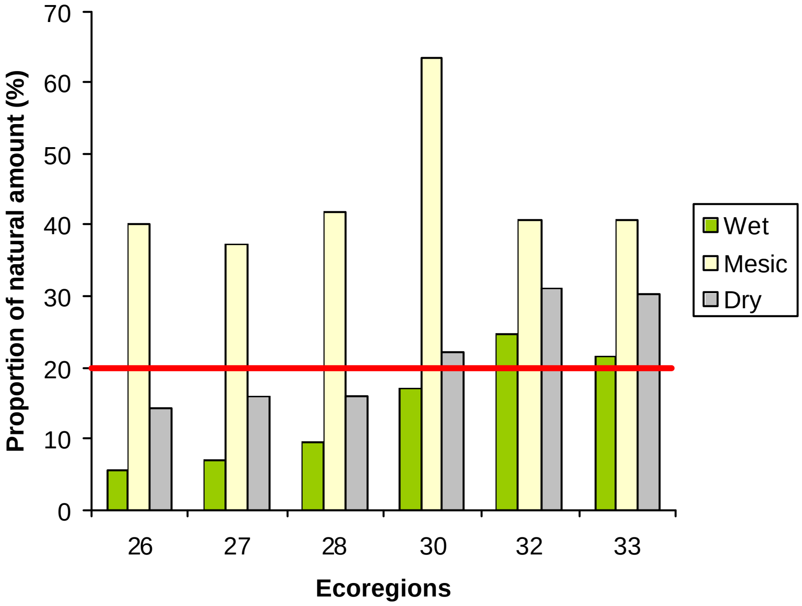


Figure 18
Estimated gaps and surpluses of forest older than 110 years in different ecoregions and on different site types. A habitat threshold value of 20 % is indicated by the red line.

3.3.1.8. The amount of four forest types with high conservation value

Pine cohort forests had the highest amount of forest older than 110 years (10 % of all dry and mesic forest sites as an average over the whole study area). The amount of spruce and mixed coniferous forests older than 110 years was 4 %. Mixed coniferous-deciduous forests had a low proportion of forest older than 110 years (1 %), and deciduous forests only insignificant amounts (0.1 %). In forests older than 70 years, there were more mixed coniferous-deciduous forests (4 % of all dry and mesic forest sites) and also some deciduous forests (1 %).

There was a geographic trend with an increasing amount old coniferous forest from the SE to the NW part of the study area, with 2-3 times higher proportion old coniferous forest in the latter. For old deciduous forest, the trend was reversed: the coastal regions have 2-3 times higher proportion than the upland regions (Figure 19).

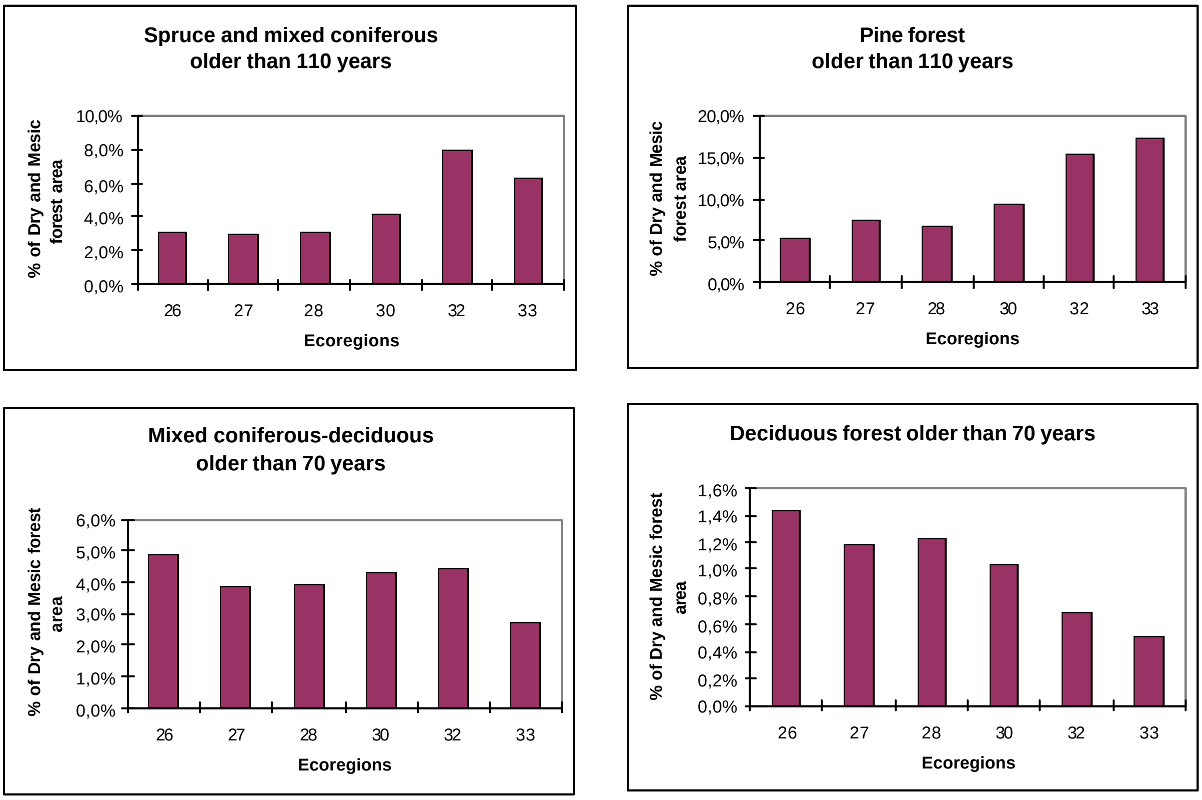


Figure 19
Present proportions of different tree species combinations on dry and mesic sites according to modelling using Topoindex/DEM, which are covered by old forests (>110 yrs for pine and spruce and >70 yrs for deciduous) in different ecoregions.

3.3.2. Regional protection gaps

3.3.2.1. How much forest is protected today within the different ecoregions?

Within the counties of Dalarna and Gävleborg, the total area of legally protected forest was about 108,000 ha (i.e. 3.2% of total forest area). In the largest, centrally located ecoregions (ecoregions number 28 and 30) the proportion of legally protected forest of all forest land was below 1%. On the other hand, ecoregion 33 located at higher altitudes in the north-western part of the study area had as much as 25 % of the total forest area under legal protection. The area of Woodland Key Habitat (both belonging to small private landowners and companies) was about 56,000 ha (1.7% of total forest area). The proportion of forest covered by Woodland Key Habitats varied between ecoregions from 1.3% in ecoregions 27 and 28 to 3.0% in ecoregion 32 (see Table 19a and Figure 20a).

Table 19 a
Proportion of forest land protected in different ecoregions in the counties Dalarna and Gävleborg.

	Ecoregion						
Subdivision of B in Table 12 a	26	27	28ab	30a	32ab	33dfg	Total
E1. Legal protection (%) *	4.8	1.0	0.6	0.9	4.1	24.8	3.2
E2. Woodland Key Habitats (%) **	1.9	1.3	1.3	1.7	3.0	1.5	1.7
E3. Areas under consideration (%) ***	0.0	1.7	0.5	1.5	0.5	1.0	1.0
E4. Other (%)	93.3	95.9	97.6	95.9	92.4	72.7	94.1
Total area x 1000 ha	60.8	400	1071	1211	350	282	3375

** Forests considered to be legally protected are those where logging is prohibited within areas protected under 7 chapter in the environmetal code, i.e. national parks, nature reserves (both established and soon to be gazetted), biotope protection areas. Nature conservation agreements, which are established under the land code law are also included in the statistics.*
*** Includes both forests owned by small private landowners and companies.*
**** Areas under consideration are areas with documented nature values that are proposed to be legally protected, but where the County Administration Boards have not yet decided which ones to protect.*

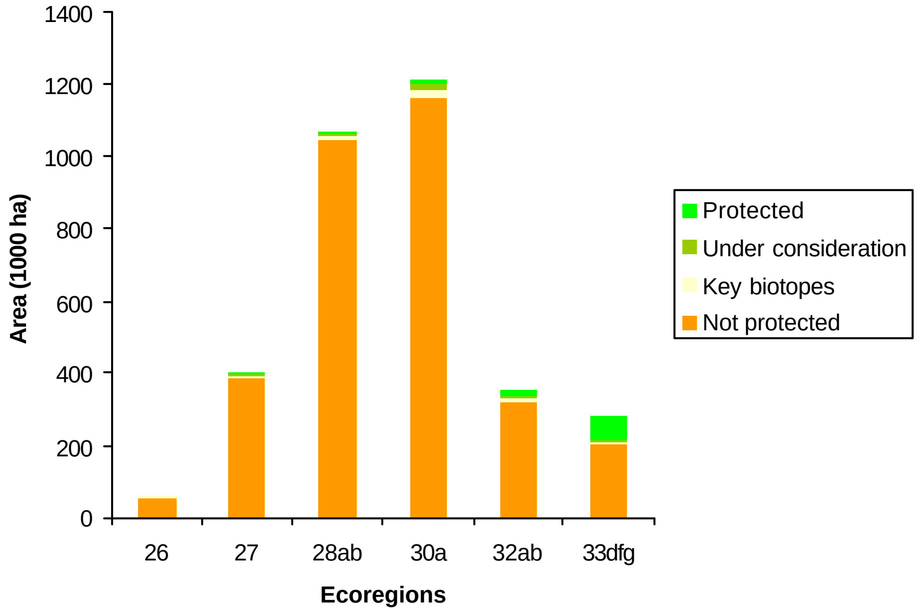


Figure 20 a
Amount of forest with different protection status in Dalarna and Gävleborg.

3.3.2.2. How much of the existing old forest is protected today

Within the counties of Dalarna and Gävleborg the total amount of legally protected old forest as mapped with remote sensing is about 37,000 ha (see row E1 in Table 19b). The amount of Woodland Key Habitats (small private landowners and companies) was about 20,000 ha (see row E2 in Table 18). The amount of old forest (>110 yrs according to the remote sensing data) with different protection status in the different ecoregions is presented in Figure 20 b,c,d.

Table 19 b

Amount of existing old forest (over 110 yrs for coniferous forests and over 70 yrs for deciduous rich forests) in 1000 ha with different levels of protection within ecoregions. Legal protection areas were updated 2003-04-01, whereas Woodland Key Habitat data are from March 2002. The category "legal protection" also includes areas where the administrative process towards legal protection has started, but is not yet completed (see also Table 19 a)

	Ecoregion					
Subdivision of B in Table 12 a	26	27	28ab	30a	32ab	33dfg
E1. Amount of old forest with legal protection [1]	0.7	1.1	1.6	3.6	6.5	21.0
E2. Amount of old forest where the forestry assumes responsibility for protection [2]	0.3	1.3	3.8	6.7	4.4	1.6
E3. Amount of old forest under consideration [3]	0.0	1.8	1.4	5.6	0.7	0.8
E4. Amount of old forest not encompassed by E1, E2 and E3	8.5	59.3	168.4	239.3	92.6	56.8
Sum (1000 ha)	9.4	63.4	175.2	255.3	104.2	80.2
Proportion of protected (E1+E2+E3) (%)	9.9	6.5	3.9	6.3	11.1	29.1

1. Forests considered to be legally protected are those where logging is prohibited within areas protected under 7 chapter in the environmetal code, i.e. national parks, nature reserves (both established and soon to be gazetted), biotope protection areas. Nature conservation agreements, which are established under the land code law are also included in the statistics.
2. Includes both forests owned by small private landowners and companies.
3. Areas under consideration are areas with documented nature values that are proposed to be legally protected, but where the County Administration Boards have not yet decided which ones to protect.

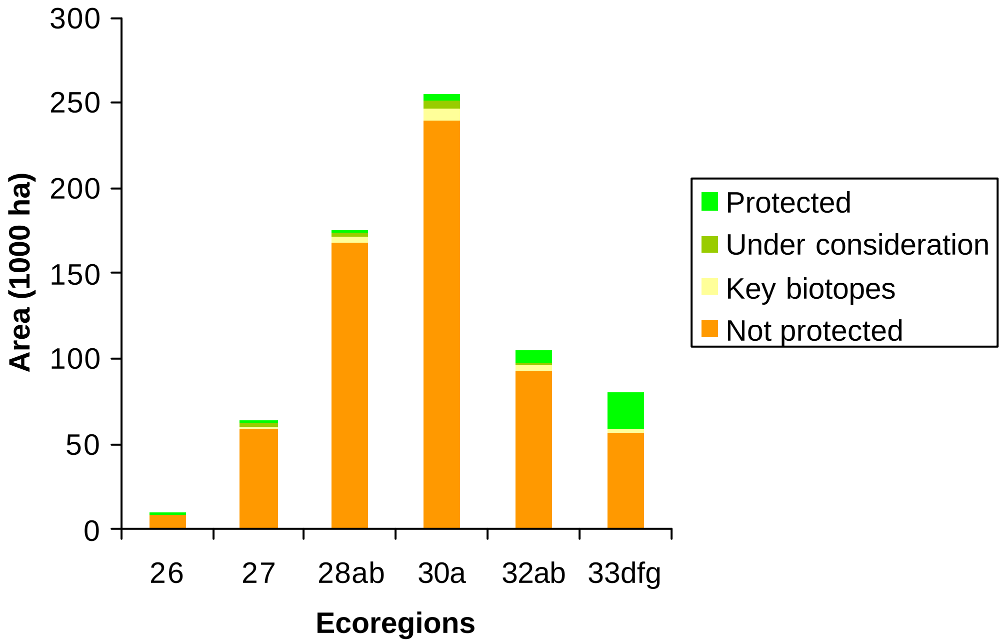


Figure 20 b
Amount of old forest according to the remote sensing data with different protection status. Note that Woodland Key Habitats have no formal protection.

Table 19 c.
Existing amount (in 1000 ha) of four forest types with high conservation value, subdivided according to level of protection within physical geographic regions and counties.

	Physical geographic region							County	
	26	27	28ab	30a	32ab	33dfg		Dalarna	Gävleborg
Old spruce and mixed coniferous (<20 % deciduous, <70 % pine) >110 years:									
E1. Legal protection	0.1	0.2	0.4	0.9	2.5	6.2		10.9	1.0
E2. Woodland Key Habitats	0.0	0.3	0.9	1.9	1.8	0.5		4.1	1.5
E3. Areas under consideration	0.0	0.3	0.3	1.4	0.2	0.2		1.2	1.2
E4. Other	1.7	11.4	32.8	50.3	24.2	12.0		89.3	44.1
Sum	1.9	12.2	34.4	54.5	28.7	19.0		105.5	47.8
Old mixed coniferous-deciduous (20-50 % deciduous) >70 years:									
E1. Legal protection	0.3	0.3	0.5	0.9	1.2	2.4		5.0	1.3
E2. Woodland Key Habitats	0.1	0.4	1.2	2.0	0.8	0.2		2.6	2.2
E3. Areas under consideration	0.0	0.5	0.3	1.3	0.1	0.1		0.8	1.5
E4. Other	3.1	16.4	45.2	54.3	13.8	5.5		77.9	60.9
Sum	3.5	17.6	47.3	58.5	15.9	8.1		86.2	65.9
Old deciduous (>50 % deciduous) >70 years:									
E1. Legal protection	0.2	0.1	0.1	0.2	0.1	0.5		1.0	0.4
E2. Woodland Key Habitats	0.0	0.1	0.3	0.4	0.1	0.0		0.5	0.5
E3. Areas under consideration	0.0	0.1	0.1	0.2	0.0	0.0		0.2	0.3
E4. Other	0.9	5.5	15.2	14.3	2.3	1.0		21.9	17.5
Sum	1.1	5.8	15.7	15.1	2.6	1.6		23.5	18.6
Old pine (>70 % pine) >110 years:									
E1. Legal protection	0.1	0.5	0.6	1.7	2.7	11.9		17.6	1.7
E2. Woodland Key Habitats	0.1	0.4	1.4	2.4	1.7	0.8		5.0	1.9
E3. Areas under consideration	0.0	0.9	0.7	2.7	0.3	0.5		2.2	3.0
E4. Other	2.8	26.0	75.1	120.4	52.3	38.3		222.1	94.6
Sum	2.9	27.9	77.8	127.2	57.0	51.5		247.0	101.2

In region 26 (hemiboreal region), old deciduous forest dominates in the legally protected areas (Figure 20 c). This region covers only a small area in the two studied counties, and the Färnebofjärden National Park covers significant areas of alluvial forest, rich in deciduous trees. Regions 27, 28 and 30 all have a very low fraction protected forest, but rather equally distributed between forest types. In region 32 and 33, old pine forests are underrepresented in protected areas compared to unprotected, despite that larger areas of pine forest are protected here than elsewhere in the two counties. Also old deciduous forests are underrepresented in region 32.

In Woodland Key Habitats, old pine forests are underrepresented in all physical geographic regions (Figure 20 d). In the large ”central” regions 28 and 30, and in region 32, also old deciduous forests are underrepresented.

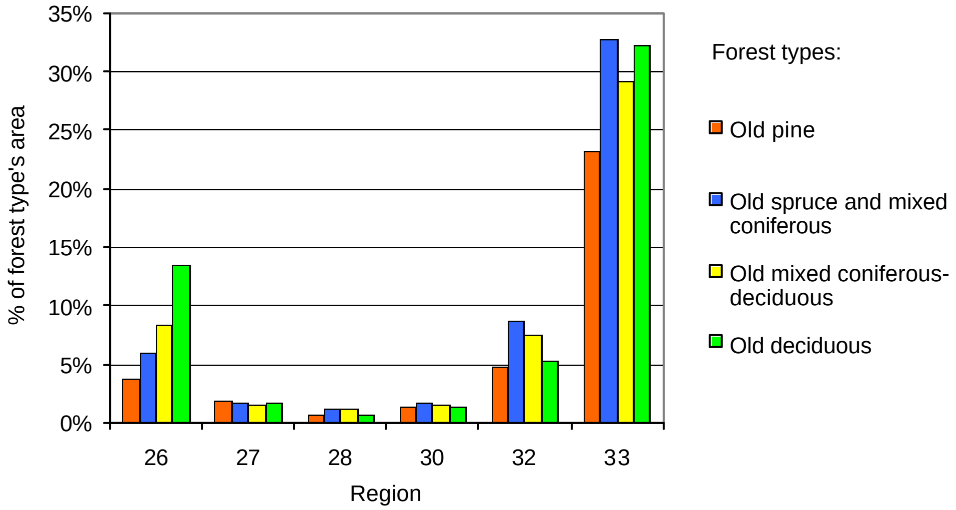


Figure 20 c
The proportion of legally protected areas of the existing area of four forest types with high conservation value.

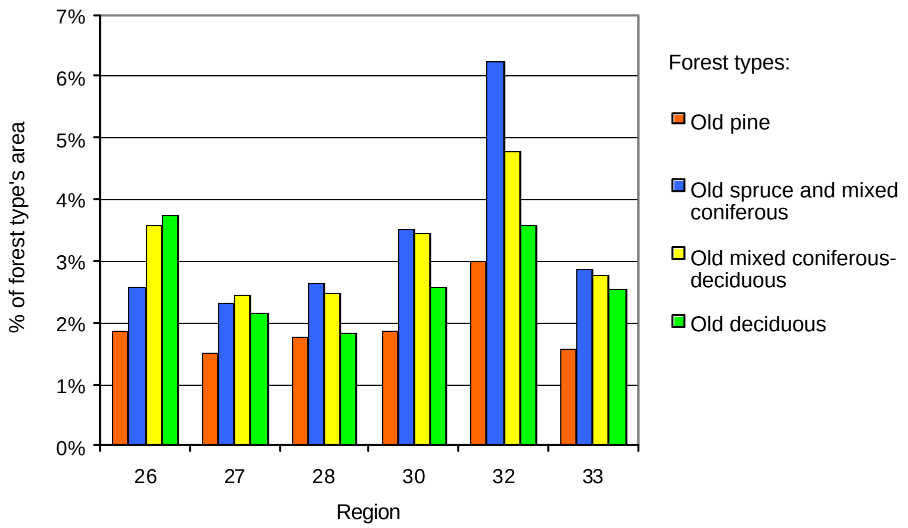


Figure 20 d
Fraction of the existing area of four forest types with high conservation value located within Woodland Key Habitats.

3.4. Quality evaluation of regional area gap analysis

Gap analysis as a strategic, and habitat modelling as a tactical planning tool involve the use of both verbal and mathematical models. As such, errors and uncertainties enter at various stages into the models and may have an influence on the final results (Table 20). Because the choice of habitats to model is based on the results of the analysis of gaps in the amount of habitat, it is important to evaluate whether the gap analysis results are suitable for use in the decision-making process concerning the protection, management and/or restoration of habitats (Rönnbäck and Angelstam 2003).

Table 20
Types of input data and variables used in the gap analysis and habitat modelling (see Table 15). The quality evaluation focuses on the abiotic and biotic/ecological variables.

Abiotic	**Biotic/ecological**	**Technical**
Resolution and quality of DEM	Forest ecology and natural disturbance regimes	Type and quality of satellite image sensors
Choice of Topoindex algorithm	Evolutionary adaptations (=choosing the "right" species for using thresholds)	Correction of scenes (=cause of inconsistencies at scene borders)
Geographical area over which the analysis is made	Quantitative habitat selection (=empirical knowledge about variables and parameters)	Choice of algorithm for segmentation of the satellite image into different land cover classes
	Critical threshold values	Ground thruthing

Two important methods for assessing uncertainty propagation are sensitivity analysis and uncertainty analysis. The latter refers to the propagation of uncertainties in source data sets and model parameters to the analysis results, whereas sensitivity analysis refers to the relative importance that each source of uncertainty has on the analysis results (Crosetto and Tarantola 2001). In Hunsaker et al. (2001) various aspects of spatial uncertainty in ecology are discussed, and the need for handling uncertainty is stressed. In particular, the application of ecological research to legislatively driven environmental problems such as biodiversity maintenance has increased the need for quantification of uncertainties about spatial dynamics (Goodchild and Case 2001, Sklar and Hunsaker 2001).

Rönnbäck and Angelstam (2003) evaluated the results from the gap analysis made in the counties Dalarna and Gävleborg. The first purpose was to study how errors and uncertainties affect the results of the numerical estimates of ecoregional gaps in the amount of forest habitats of different kinds needed to maintain viable populations of naturally occurring species. Both sensitivity analysis and uncertainty analysis were performed. Because the source data sets for the gap analysis contained no explicit information about its quality, the prototype for identification and quantification of uncertainties developed by Rönnbäck (2003) was used to obtain that information. The second purpose of the study was to test whether or not this prototype could be used for assessing unspecified quality in another case study having other kinds of source data sets. The data sets were then varied according to these quantifications, and the numerical estimates of the ecoregional gaps were recalculated.

The gap analysis contained the following steps (for details see section 3.1):

(A1) estimation of the amount of different kinds of forest vegetation based on modelling of the distribution of different natural forest disturbance regimes based on a Topoindex approach using digital elevation models, and
(A2) models and empirical information about the age distribution and tree species composition within these different disturbance regimes;
(B) estimation of today's amount of the naturally occurring forest types defined in A2 using remote sensing data calibrated with forest stand data;
(C) estimation of the proportion of representative forest types needed to maintain viable populations of the most demanding species based on the appearing knowledge about focal species population's non-linear responses to habitat loss;
(D) estimation of the difference between B and C, where a negative values implies a gap in habitat area and a need for habitat rehabilitation and/or re-creation.

The estimations for forest older than 110 years were considered particularly important because they are the most important forest type for maintaining viable populations of naturally occurring specialised forest species. Hence, the studies concerning uncertainty and its effect on the numerical estimates of ecoregional gaps focussed on forest older than 110 years.

Based on the complex interactions between probabilistic (e.g. mean fire intervals in different site types) and random events (e.g. where and when a fire occurs), the interaction between fire and local as well as regional site conditions influencing fire behaviour was used to deduce three main disturbance regimes found in European boreal forest (Table 21), viz.:

1. succession from young to old-growth mixed deciduous/coniferous on mesic sites (MESIC-SUCC);
2. multi-cohort Scots pine dynamics on dry sites (DRY-COHORT); and
3. gap-phase Norway spruce dynamics on wet sites (WET-GAP)..

Since the used data sets had no documented information of its quality, the producers of each data set were contacted and interviewed in accordance with the questionnaire developed by Rönnbäck (2003). The interviews resulted in Table 21.

Table 21
Variables for which uncertainties were estimated, the step in the gap analysis where it was applied, the proportion of old (>110 yrs) used and the estimated range of variation.

Variable	***Step***	***Proportion of old (>110 yrs) forest***	***Estimated range of variation (%)***
Abiotic			
Based on Topoindex algorithm and DEM (estimation of the amount of forest with different disturbance regimes)	A1		About +/- 20 % of the estimated value
Biotic/ecological			
Forest ecology and natural disturbance regimes (estimated amount of old forest below 500 m a.s.l.)	A2	Mesic-Succession (22%)	14-30
		Dry-Cohort (70%)	50-90
		Wet-Gap phase (96%)	50-100
ditto at 500-800 m a.s.l.	A2	Mesic-Succession (60%)	40-80
		Dry-Cohort (80%)	60-100
		Wet-Gap phase (96%)	92-100
Critical threshold values			
(20% was used as an average).	C	Mesic-Succession (20%)	15-25
		Dry-Cohort (5%)	1-9
		Wet-Gap phase (35%)	25-45

In the original gap analysis the threshold value was set to 20% for the different forest types. Since the quality assessment gave separate values for the individual forest types, these new threshold values were used before any simulation was made (Table 21). All variables suffering from uncertainties were varied simultaneously and independently, since the influence of each single variable was of less interest in this study. A total of 1000 Monte Carlo simulations were made, each using the modified original Excel workbook as source data, and each producing an equally likely numerical estimate of the regional gaps. The results were reported for the different ecoregions (Table 1).

Changing the threshold values for each site type results in estimates that differs considerably compared with the original estimates when using a threshold value of 20% for each forest disturbance regime. The original estimates and the estimates when changing the threshold values for each site type are compared in Figure 21. The simulations were performed using the new threshold values for each site type and randomly varying the other variables suffering from uncertainties. Hence, the numerical estimates of gaps and surpluses resulting from the new threshold values were used as a modified original. The mean values and the standard deviations for the estimated gaps and surpluses from the simulation are shown in Figure 22. The histogram bars represent the modified original, the lines represent the standard deviations and the dots represent the mean values.

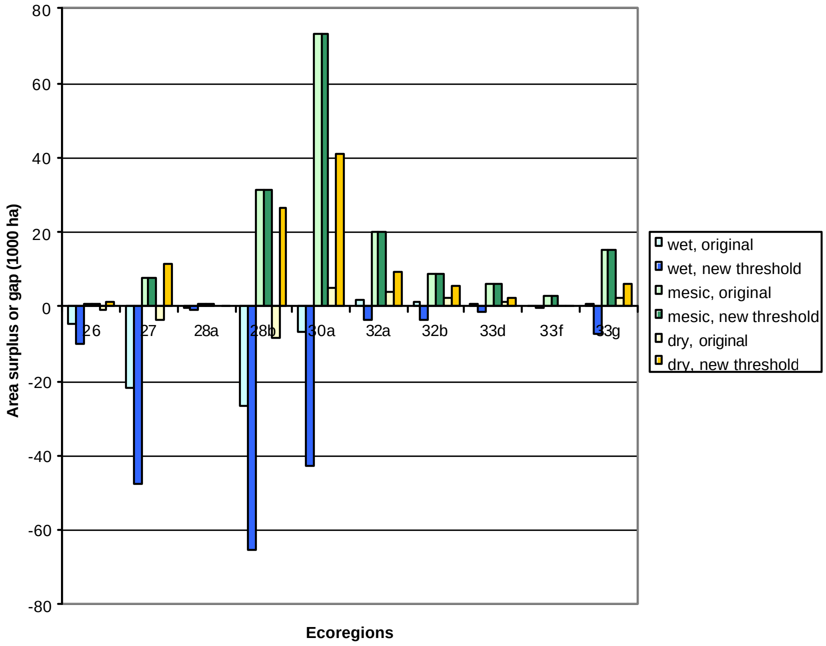


Figure 21

Comparison of the original estimated gaps and surpluses of old forest and the estimates when the threshold values are changed as shown in Table 21.

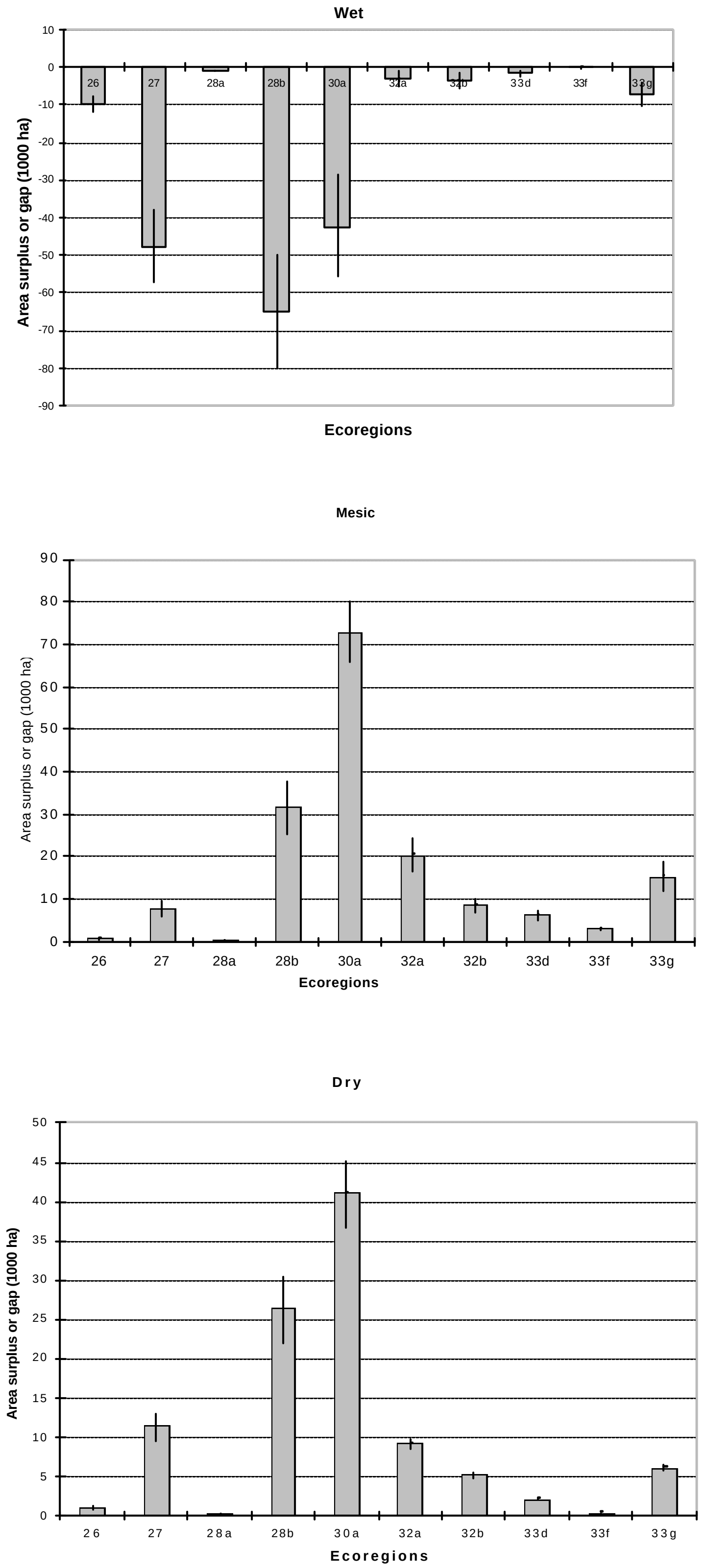


Figure 22
Error bars from the uncertainty analysis assuming the range of variation defined in Table 21, column 3.

The study performed by Rönnbäck and Angelstam (2003) showed a useful method for the overall evaluation of how sensitive the numerical estimates of a regional gap analysis are to errors and uncertainties in data sets. However, special attention must be given to the results of the uncertainty analysis and the sensitivity analysis. The simulations indicated that the numerical estimates of the regional gaps have uncertainties, particularly regarding the threshold values, which need to be considered when interpreting the gap-analysis results.

It should be noted that, because only the numerical estimates of ecoregional gaps were of interest this study, it disregards the spatial variation. For example, because not all forest areas of a given type are sufficiently large or too far apart, without spatially explicit evaluation, the assets in the gap analyses will be overestimated (see section 4.5; Angelstam et al. 2003b).

4. Conservation planning with the use of specialised species

In this section, we present an approach for evaluating the functional connectivity of the network of different forest types. Using GIS-modelling we integrate knowledge about the quantitative habitat requirements of specialised and demanding specialised species for each forest type and a spatially explicit data base with complete mapping of the existing respective habitat networks. This complex evaluation requires:

- 1. A thematically relevant and digital land cover database derived using remote sensing.
- 2. The selection of appropriate focal species to derive Habitat Suitability Index (HSI) model parameters at the scale of individuals and local populations for the forest types with apparent gaps in the different ecoregions (Angelstam et al. 2003a).
- 3. Analysis of the functional connectivity of the existing habitat networks by integrating land cover data and the quantitative requirements of the focal umbrella species in GIS-based Habitat Suitability models.
- 4. Comparisons of the maps from the HSI-models and the spatially explicit information about patches of different forest types to allow for strategic planning for acquisition of new protected areas, as well as management, rehabilitation and re-creation of the selected target habitats outside protected areas.

The resulting maps show the relative potential for hosting the focal species, and not the actual occurrence. For simplicity in the report we present the maps with cut-off values representing higher and lower probabilities as defined by occurrence thresholds at multiple scales. To denote that different species have different requirements, two species are modelled for each focal forest type. Note that to address the issue of viable populations, the number of size of suitable tracts from the maps have to be known (see section 6.12).

4.1. Umbrella and focal species

Two types of approaches have been proposed in order to conserve biodiversity within the constraints of limited funding and knowledge: ecosystem approaches (Franklin 1993, Walker 1995) and species-oriented approaches (Tracy and Brussard 1994, Caro and O'Doherty 1999). The former is based on the application of general ecological principles, while the latter rests on the selection of appropriate species that could be used as surrogates. As put forward by Wilcove (1994) both of these approaches should be considered as part of a continuum of necessary steps for conservation planning. Indeed, while general knowledge on ecosystem processes and structures is essential, it remains crucial to also refer to the requirements of the species in order to design concrete criteria for conservation in real-world landscapes (Hansen et al. 1993, Lambeck 1997, 1999). Hence, in our approach for regional gap analysis, we used both the available information about natural disturbance regimes and forest types, as well as information on habitat loss threshold ranges for forest species. When it comes to spatially explicit conservation planning, species' requirements represent once again an essential tool.

The umbrella species concept is one promising way to use species requirements to assist conservation planning. Its main assumption is that the requirements of demanding species would encapsulate those of other, co-occurring species that have lower requirements (Lambeck 1997). By directing management effort towards the requirements of the most exigent or sensitive species, one should theoretically provide enough also for cohabitants dependent on the same habitats. This concept is intuitively appealing and offers a simple, ecologically based shortcut for conservation planning. The term "umbrella species" has been defined in a variety of ways that emphasise different uses and properties. This has resulted in some confusion about the meaning of the term. Here we adopt the following definition: an umbrella species is a species whose conservation confers protection to a large number of naturally co-occurring species (Roberge and Angelstam in press).

Traditionally the umbrella species concept has been proposed as a tool for determining the minimum size of conservation areas (Wilcox 1984). Here the main assumption is that providing large enough areas for wide-ranging species will also protect most species with smaller home ranges. Because of the relationship between body size and home range size (McNab 1963), large vertebrates have been favoured (Shafer 1990, Wallis de Vries 1995, Berger 1997, Carroll et al. 2001). Another use of umbrella species is to assist in the selection of habitat remnants to be included in a reserve network. The general methodology consists in setting aside for protection the sites where the umbrella species occur(s) or where species diversity for the umbrella taxon is high (Ryti 1992, Launer and Murphy 1994, Kerr 1997, Fleishman et al. 2000, Fleishman et al. 2001).

Umbrella species approaches have been criticised on the grounds that it is improbable that the requirements of one species would encapsulate those of all other species (Noss et al. 1997, Carroll et al. 1998, Basset et al. 2001, Hess and King 2002). Moreover centres of biodiversity do not necessarily coincide among taxa and some endemic species may not be protected by a site-selection umbrella (Kerr 1997, Lawton et al. 1998, Oliver et al. 1998). This suggests that management for a single umbrella species would not be sufficient for maintenance of biodiversity in a landscape. Therefore we stress the need for using multiple species as umbrellas (Launer and Murphy 1994, Lambeck 1997, Noss et al. 1997, Carroll et al. 1998, Miller et al. 1998, Fleishman et al. 2000, Basset et al. 2001, Bonn and Schröder 2001, Carroll et al. 2001, Hess and King 2002, Roberge and Angelstam in press).

The focal-species approach (Lambeck 1997) is a type of umbrella species scheme that deals elegantly with the need for using multiple species. This approach extends the umbrella species concept to the whole range of processes that threaten species persistence in managed landscapes. Lambeck (1997) proposed to identify a suite of "focal species" that would be used to define the spatial, compositional, and functional attributes that must be present in a landscape. The species with the most demanding requirements for each relevant landscape attribute would determine its minimum acceptable value and the appropriate management regime. This way, all other less demanding species should theoretically be conserved.

Our approach builds to a large extent on Lambeck's (1997) focal-species concept. We propose to select a few focal species for each forest type of high conservation interest identified in the gap analysis, based on their high requirements regarding different attributes of the landscape (Angelstam et al. 2003a, Roberge and Angelstam in press). These focal species for each forest type could be arranged in a hierarchical manner with the most sensitive at the top of a conceptual scale, or ladder (cf. Karström 1992). The suite of focal species would cover a range of requirements regarding spatial needs, habitat types, resources, and microclimatic conditions.

In addition to its role as an ecological conservation tool, such a suite of species is expected to have a tangible value as a communication and pedagogic tool that facilitates exchanges between scientists, managers, and the public. This is an asset of species-based approaches that should not be neglected, since applying science is an endeavour that involves many social aspects in addition to ecological knowledge.

4.2. Habitat modelling and spatially explicit planning

With new objectives such as the maintenance of biodiversity, land managers are faced with the challenge of using their data for partly new purposes. For example, in forestry the development of landscape ecological plans (e.g., Angelstam and Pettersson 1997), means that forest management data are being used to assess the conservation value of forests based on tree species composition, age classes and patch sizes of forest stands in the landscape. To evaluate the extent to which existing habitat networks also are functional there is a need to develop procedures for assessing networks of conservation areas, and subsequently use that as a basis for planning of conservation and restoration measures. There are a multitude of factors that affect the distribution and abundance of a species. For operational spatially explicit planning purposes, however, one needs to simplify. Habitat suitability index (HSI) modelling consists of combining spatially explicit land cover data with quantitative knowledge about the requirements of specialised species and building spatially explicit maps describing the probability that a species is found in a landscape (Verner et al. 1986, Brooks 1997, Scott et al. 2002). With adequate quantitative data on a suite of particular focal species, a series of predictive landscape models for the different vegetation types in a landscape can be built. This requires quantitative information on the habitat requirements of the species at least three spatial scales.

First, the landcover of vegetation for a particular focal species (LANDCOVTYPE) must be mapped with sufficient detail to match the operational scale of individuals. The habitat for a given species is often composed of a combination of such landcover types. Secondly, the necessary amount of patches of suitable landcover types must be defined for an individual (HAB_PATCH). To define the patches clearly, the species chosen for HSI modelling should have a high degree of specialisation on certain types of vegetation cover. The species' occurrence is affected mainly by the extent and spatial distribution of natural or anthropogenic disturbances, which either create or destroy the habitat. In managed forest landscapes, such disturbances are mostly a result of silvicultural systems, ownership pattern (large/small) and socio-economic situation. Thirdly, species have requirements at the population level. The number of patches and their spatial distribution make up connectivity (Forman 1995). Several studies have investigated the relative importance of habitat amount and configuration for animal populations. Simulation studies have predicted varying effects of habitat fragmentation on extinction thresholds, depending on the mechanisms assumed by the different models (Fahrig 1997, Fahrig 2002). Simulations by Fahrig (1997, 2001) have predicted that habitat loss is more important than habitat configuration. Additionally, almost all empirical studies from North America have shown that forest cover had a main effect on the distribution and abundance of breeding birds, while configuration did not explain much more (McGarigal and McComb 1995, Drolet et al. 1999, Trzcinski et al. 1999; but see Villard et al. 1999). This suggests that the total amount of sufficiently large habitat patches in a landscape (HAB_PROP) could be used as a single measurement of landscape suitability, and thus as a surrogate for connectivity, at the population scale (Fahrig 2001, Scott et al. 2002). Moreover, if patches are ephemeral, for example a certain successional stage lasting only a few years or decades (HAB_DUR), the landscape must be large enough to contain a stable patch dynamic of this particular stage (Pickett and White 1985). In summary, a HSI model for a given species (HSI_SP) is made up of all the variables described above and pictures the relative suitability for the species across a given landscape.

HSI_SP = *f*[(LANDCOVTYPE); (HAB_PATCH); (HAB_PROP); (HAB_DUR)]

Note that this is not a mathematical expression, but rather a summarised description of the information needed for assessing the suitability of the landscape using neighbourhood analysis techniques in GIS. With this approach the maintenance of local populations of all "focal" species, and their associated species, will require the integration (i.e. not the sum) of the habitats of all focal species' HSI_SP. In order words, the network of each representative habitat (one or several land cover types) often must be analysed and managed as a separate infrastructure. Technically, the HSI modelling and its involvement in planning involves the following two steps:

1. GIS modelling using focal species parameters
Using the land cover map with different forest environments and site types, thematic maps for different focal species were made. To stress that the connectivity concept is probabilistic we used two different focal species for each forest theme (wet, old deciduous, old spruce/mixed, old pine) with different quantitative requirements. GIS and parameters for the quantitative requirements of the selected focal species at different spatial scales corresponding to the levels of individuals and populations were then used to produce Habitat Suitability maps (Figure 23).

2. The planning phase
The HSI map and the associated land cover theme on which the model is built, were combined to classify patches of the theme into those that are poorly as well as well connected. Poorly connected patches are located outside the area suggested as suitable habitat by the HSI model. Using the habitat suitability model as a guide, the existing patches of the relevant theme can be divided into three categories:
a. Outside the network suggested by the HSI model
b. Inside and protected for 2 species with different demands
c. Inside not protected for 2 species with different demands

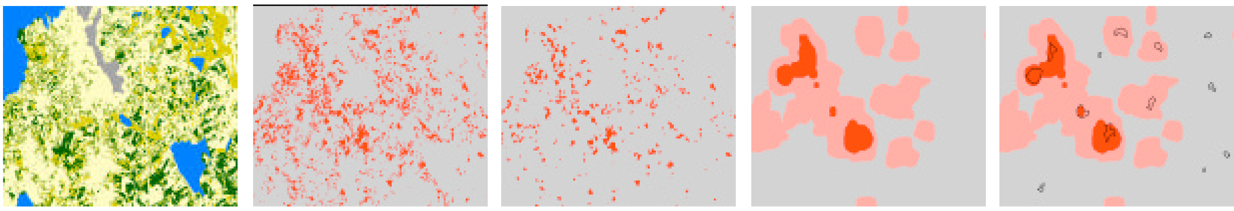


Figure 23
Steps in the HSI modelling approach for spatially explicit evaluation of the conservation area network and strategic planning. From left to right the modelling procedure is described from the land cover data base to the final model with potential areas to be protected, managed or restored.

4.3. Parameters for habitat modelling

Angelstam et al. (2003a) reviewed the quantitative information about birds' requirements at the level of individuals and populations and found that for a number of specialised and demanding species the parameters needed for building spatially explicit habitat models are at hand. In addition to birds, species from other taxa can also be linked to different forest types (Wikars 2003). In the following, we present two species - one less and one more demanding in terms of area requirements and/or the degree of connectivity - for each of the four forest types of the highest conservation interest for the creation of protected areas. The habitat variables (land cover themes from Table 18) and parameters are listed in Table 22. Because different forest classes may provide different amounts of resources for the focal species, we introduced the term "resource density", which is an estimation of the relative value of particular forest class for each species.

Although the selected species are among the most demanding for their respective forest types, we acknowledge that the selected species may not be <u>the</u> absolute most demanding species. Indeed, knowledge on the requirements of some organism groups such as insects is still imperfect and it may turn out in the future that some other species are most demanding than the ones we used. However, we prefer to adopt an adaptive strategy by which one begins with the currently selected species and adjusts in consequence if new knowledge shows that the initial choice of species was not optimal.

4.3.1. Old deciduous forest

The different phases in the succession after stand-replacing disturbance are ephemeral, lasting only a few decades at a particular locality. As focal species for this type of habitat we chose two bird species, the lesser spotted woodpecker (*Dendrocopos minor*) and the long-tailed tit (*Aegithalos caudatus*). Both species depend on a higher proportion of deciduous trees than is usually found in managed forests (Jansson and Angelstam 1999, Wiktander et al. 1992), the former also dependent on a higher amount of dead wood than regularly found in managed forests (Olsson et al. 1992, Olsson 1998). Our study area is well within the distribution range of both species (Lönnberg 1927, SOF 1990).

Pixels of the themes defining long-tailed tit habitat were selected, and a 25-m buffer was added. The resulting mask was use to identify pixel clusters that satisfy the minimum effective patch size requirement of 7 ha. Using the remaining sufficiently large patches we assessed their degree of connectivity from this species' point-of-view using neighourhood analys in a 1 sq. km window.

It should be noted that the deciduous theme appeared inconsistent among the different satellite scenes. There is hence a need to calibrate the scenes in order to make them comparable. This was not done in the forest classification database. One approach could be to find areas of overlap between scenes and to correlate the amount of selected theme (patches) according to HSI-model within 1-km grid (compare slope with 1:1 slope). Yet another approach is to do the entire analyses scene by scene.

Pixels of the themes defining lesser spotted woodpecker habitat were selected, and a 25-m buffer was added. The resulting mask was used to identify pixel clusters that satisfy the minimum effective patch size requirement for a fine-grained habitat selection in 1 ha patches. Due to assumed qualitative difference among subsets of the selected themes, the resource density was adjusted with a coefficient (see Table 22). Using the remaining sufficiently large patches we assessed their degree of connectivity from this species' point-of-view using neighourhood analys in a 2 sq. km window.

4.3.2. Old spruce forest

In the absence of stand-replacing disturbance by fire or storm, stands on all site types will develop old-growth characteristics with old stand age, multiple vegetation layers, high volumes of dying and dead trees as well as coarse woody debris. Being dependent of insects living in old, dying and dead trees, the three-toed woodpecker (*Picoides tridactylus*) is a characteristic species in such forests (e.g., Pakkala et al. 2002, Bütler et al. 2003). Similarly, although less demanding, due to its feeding and breeding habits the complete *Parus* guild with treecreeper (*Certhia familiaris*) is confined to older forest (Uliczka and Angelstam 2000, Jansson and Andrén in press). Modelling was performed using a neighbourhood analysis in GIS and with parameter values listed in Table 22.

Pixels of the themes defining the complete *Parus* guild including coniferous tit species and treecreeper habitat were selected, and a 25-m buffer was added. The resulting mask was use to identify pixel clusters that satisfy the minimum effective patch size requirement of 20 ha. Using the remaining sufficiently large patches we assessed their degree of connectivity from this species' point-of-view using neighourhood analysis in a 1 sq. km window. For this focal forest type two sets of themes were used, one representing only the old forest with little modern forestry impact (>70 years), and one representing also the old forest that has regenerated after more modern forestry (>40 years).

Pixels of the themes defining three-toed woodpecker habitat were selected, and a 25-m buffer was added. The resulting mask was use to identify pixel clusters that satisfy the minimum effective patch size requirement for a fine-grained habitat selection in 10 ha patches. Using the remaining sufficiently large patches we assessed their degree of connectivity from this species' point-of-view using neighourhood analys in a 4 sq. km window.

4.3.3. Old pine forest

The natural disturbance with low-intensity fire and regeneration of Scots pine cohorts after fire usually results in open stands with multiple cohorts of trees and large amounts of snags and coarse woody debris (Siitonen 2001). If found in sufficiently large patches, such pine forest is suitable habitat for the capercaillie (*Tetrao urogallus*) (Storch 2000, 2001, Hjeljord et al. 2000).

Pixels of the themes defining the capercaillie habitat were selected, and a 100-m buffer was added. Because the habitat selection is coarse-grained (Rolstad and Wegge 1987) the resulting mask was use to identify pixel clusters that satisfy the minimum effective patch size requirement of 200 ha. Using the remaining sufficiently large patches we assessed their degree of connectivity from this species' point-of-view using neighourhood analys in a 16 sq. km window. For this focal forest two sets of themes were used, one representing only the old forest with little modern forestry impact (>70 years), and one representing also the old forest that has regenerated after more modern forestry (>40 years).

The habitat of the beetle *Tragosoma depsarium* is sun-exposed logs with an origin as pine trees often having had a retarded growth with a high proportion of rot-resistant heartwood, caused by repeated fires (Gärdenfors et al. 2002). Wikars (2003) studied the habitat requirements of *Tragosoma depsarium* at three spatial scales. At the scale of logs the species prefers bark-free, sun-exposed large downed logs with a core of slowly grown heartwood. In today's relatively closed forests such logs are found mainly on clear-felled areas and where Scots pine seed trees have been retained, and in south-facing forest edges. In fact Tragosoma depsarium was never observed within the forest reserves studied. In landscapes with naturally dynamic and open Scots pine forests the species is common. Finally, at the landscape scale *Tragosoma depsarium* required that more than 25 % (or 30-35 % of the forest area) of 5x5 km large landscapes was older than 120 years. First a theme representing the scales of logs and stands was established by selecting clear-felled areas and forest with low basal area larger than 10 ha on mesic and dry sites. Second, a theme with more than 25 % old pine and coniferous forest in 25 sq. km grid cells using neighbourhood analysis was made. Third, observations of *Tragosoma* are uncommon at altitudes over 400 m a.s.l.. Suitable habitat was then defined as the combination of the three themes.

4.3.4. Wet old forest

In naturally dynamic boreal landscapes, forests on wet sites have a longer continuity of forest cover than other site types (Jasinski and Angelstam 2002, Gandhi et al. 2002). For species requiring a moist and relatively stable microclimate, wet sites with mature forest provide conditions that favour certain specialised lichen species. The removal of forest cover, or reduction in patch size has been observed to result in local extinction of the lichen *Evernia divaricata* over a 16-year period (Sjöberg and Ericson 1992). In a study in Russia *Ramalina thrausta* was confined to wet spruce forests in gullies (T. Ek and P. Angelstam unpubl.). When surrounded by dry to mesic sites, the probability of occurrence was significantly lower 5-10 m from the edge compared to the interior of the wet spruce stand. Andersson (2000) and Wallén (2001) found similar results for this species as well as for *Evernia divaricata*. However, in the absence of good empirical knowledge, we follow the approach of Aune and Jonsson (unpublished) and use local microclimatic requirements as a proxy. This is modelled by considering both the risk of blowdown (Esseen 1994), securing a core of old stands on wet sites by removing 50 and 100 m buffer zones, respectively. In addition we consider all old forest above 500 m a.s.l. as generally suitable.

Table 22

Variables and parameters for HSI-modelling as outlined in section 4.2. Forest types identified as having gaps in the amount needed to maintain local populations, representative focal species with higher and lower quantitative requirements, type of GIS analysis and parameters at the scales of habitat patches and landscapes.

Forest type	Focal species	Theme (cf Table 18) LANDCOVTYPE	Resource density	Patch requirements HAB_PATCH	Required proportion of patches in the neighbourhood and neighbourhood window size (km^2) HAB_PROP	Reference
Old deciduous	Aegithalos caudatus	12-16, 20-24, 28-32	1	7 ha patch; using 25 m buffer	15 % (1)	Jansson and Angelstam (1999)
	Dendrocopos minor	20-22 23-24, 28-32	0.5 1	1 ha patch using 25 m buffer	20 % (2)	Wiktander et al. (1992) Wiktander (pers. comm.)
Old coniferous	Parus/Certhia guild (2 variants)	18-24, 26-32 and with 10-16	1 0.5	20 ha patch; using 25 m buffer	60 % (1)	Jansson and Andrén (in press) Uliczka and Angelstam (2000)
	Picoides tridactylus	18-24 26-32	1 1	10 ha patch using 25 m buffer	25 % (4)	Angelstam et al. (2003 a), Bütler et al. (2003) Amcoff and Eriksson (1996)
Old pine	Tetrao urogallus (2 variants)	17+35, 25+35 19+35, 27+35 and with 9+35, 11+35 forest bog (note 1 and 2)	1 0.8 0.5	200 ha patch; using 100 m buffer	25 % (16)	Storch 2001 Angelstam (unpubl. EB51)
	Tragosoma depsarium	33, 34 located in landscapes with 25 % forest older than 70 years	1	10 ha patch	25 % (25) <400 m a.s.l.	Wikars (2003)
Wet	Less demanding lichens	17-32 on wet site	1	Core without 50 m buffer	or terrain over 500 a.s.l.	BG Jonsson/Aune Sjöberg and Ericson 1992 Ek 1995
	More demanding lichens	17-32 on wet site	1	Core without 100 m buffer	or terrain over 500 a.s.l.	ditto

1. The addition of 100 to the forest class code (Table 18) in the HSI model log means that the version made by Stefan Rystedt was used.
2. The addition of 300 relates to wet site on the complete land cover map made by Stefan Rystedt.

4.4. Identification of important forest tracts using habitat modelling

4.4.1. Old deciduous

Inspection of the HSI-modelling map for the long-tailed tit (Figure 24) and lesser spotted woodpecker (Figure 25) shows clear differerences in the occurrence of important forest tracts at the borders between different satellite scenes (e.g. the SE part of the region). This shows that habitat model outcomes (for deciduous forest) are not directly comparable among scenes. We therefore describe the results scene-wise for the three major scenes covering Hälsingland, NW Dalarna and SE Dalarna, respectively.

Within the satellite scene covering the landcape of Hälsingland:

- Long-tailed tit habitat appears common except in the western upland areas. However, the comparisons with field data suggest that the amount of deciduous forest has been overestimated. One example is the Digerberg area adjascent to the Korpmäki nature reserve. Similarly, parts of Orsa Finnmark turn out as having much deciduous forest areas while in reality this appears to be other types of land cover (see also discussion).
- A concentration of lesser spotted woodpecker habitat is found along the northern border. Nature reserves with old deciduous forest patches with high conservation value such as Brassberget and the unprotected Nortjärnsberget near Hennan, Ysberget-Laxtjärnsberget, Gåsberget, Lövsalen on Hornslandet are clearly delineated. Hästmyrberget with mixed spruce and deciduous forest at the border to Medelpad also showed up in this habitat model. The unprotected areas Bastjärnsrönningen and the old forest east of Hagåsens Nature Reserve contain productive spruce forest with significant admixture of deciduous trees and were marked as lesser spotted woodpecker habitat. The soon established nature reserve Älvåsen was compared with the forest stand data. Of the stands within the landcover types for lesser spotted woodpecker habitat 5 stands had <20 % deciduous admixture and 7 stands with >20 % deciduous.

Within the satellite scene in SE Dalarna/Gästrikland:

- Concentrations of lesser spotted woodpecker habitat are found in the abandoned cultural landscape between Leksand and Furudal in association with the Siljansringen area, which provides good conditions for deciduous trees demanding better soils, on Sollerön and in lower part of the Dalälven river (such as the Båtfors area). In the southern part of this scene deciduous forest patches are found NW of Ludvika (Hästberg and Laxsjön) and at Högbyn SE of Fagersta.
- At the border between satellite images in Gästrikland there is a sharp difference in the amount of deciduous forest.
- We suggest that the obvious lack of old deciduous forest i St Tunaslätten can be attributed to the presence of deciduous trees in forest/field edges and in the agricultural landscape itself. Previous studies suggest that the deciduous component in this edge habitat is being seriously underestimated because the deciduous cover has only been estimated in areas under the forest mask of the topographic map (Mikusinski, Arnberg, Angelstam in prep.). Inspection of the areas with the highest amount of edge between agricultural land and other habitats (Figure 26) shows that there is a good match between the absence of deciduous forest tracts and the most evident concentration of a high density of edge habitats. These are known to have large amount of deciduous trees (Mikusinski and Angelstam 1999, Mikusinski et al. in prep.).

Within the satellite scene in NW Dalarna:

- Suitable habitat for lesser spotted woodpecker is virtually absent and long-tailed tit habitat occurs as small patches only.

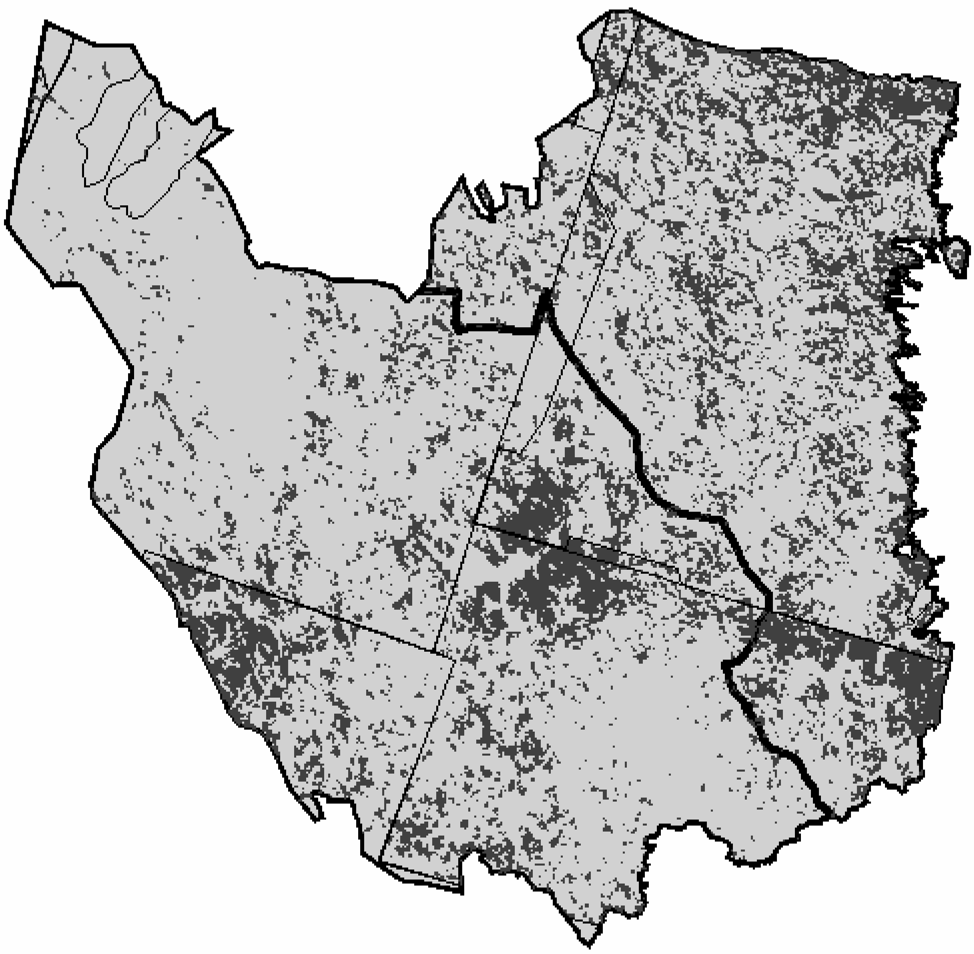


Figure 24
Map showing the tracts of suitable habitat for long-tailed tit in the counties of Dalarna and Gävleborg. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.

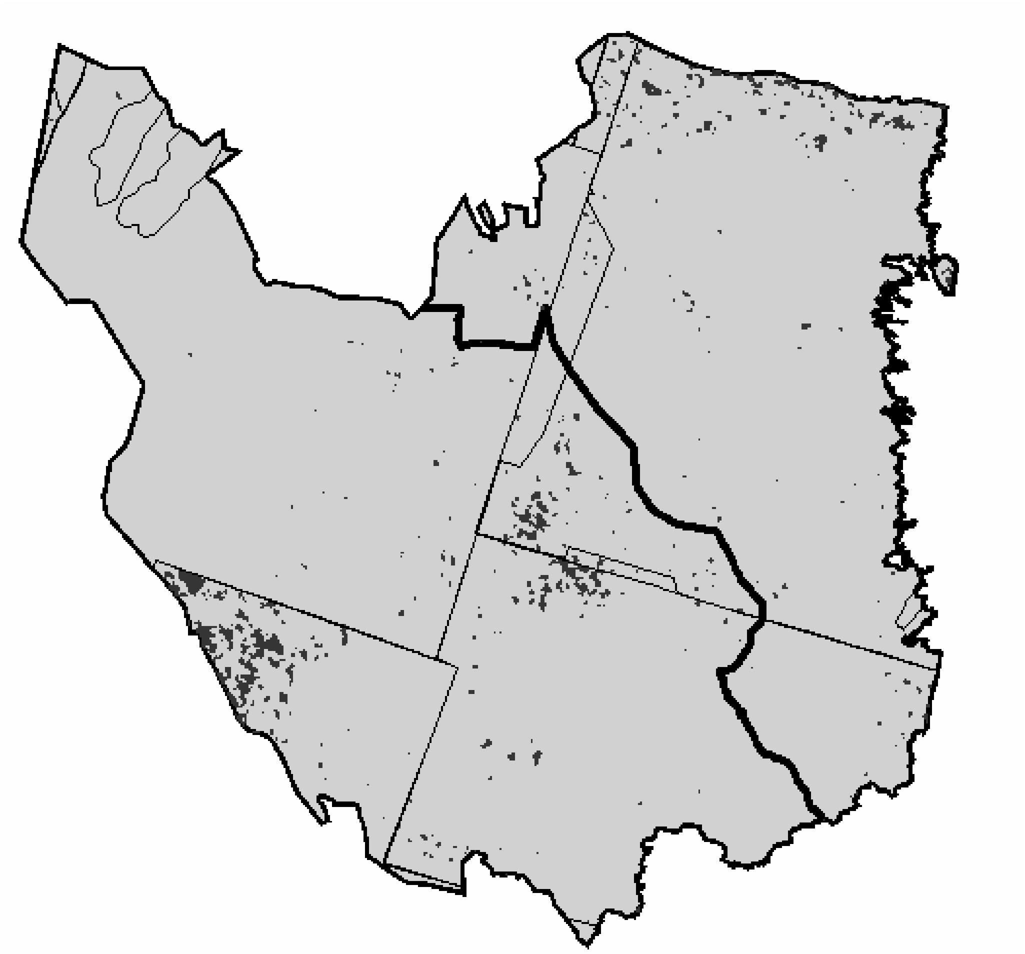


Figure 25
Map showing the tracts of suitable habitat for lesser spotted woodpecker in the counties of Dalarna and Gävleborg. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.

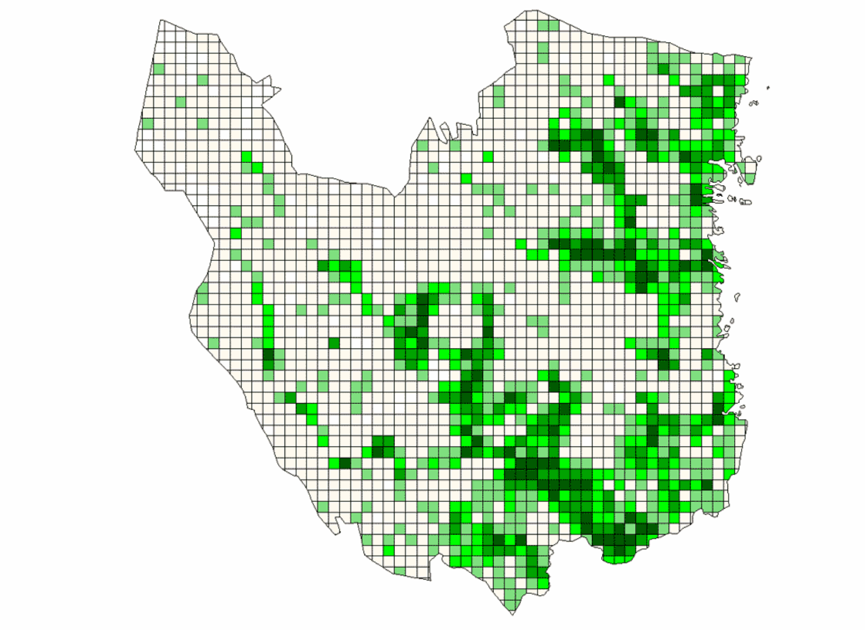


Figure 26
Map of the counties Dalarna and Gävleborg showing the density of openland edge in 5x5 km grid cells. The intensity of the green colour denotes the relative amount of edge habitat. This map can also be viewed as simple habitat model för species found in agricultural landscapes.

4.4.2. Old coniferous forest

For old coniferous forest (mixed pine/spruce and spruce) the *Parus*/tree creeper guild (Figure 27) and the three-toed woodpecker (Figure 28) were used to model the distribution of high conservation value forest tracts. The three-toed woodpecker habitat showed clear concentrations in upland areas in the southwestern part of the WX-region, north of Älvdalen and Orsa, in northern Hälsingland, but also in areas away from the agricultural areas and the Baltic Sea coast.

Habitat tracts for the complete *Parus*/tree creeper guild were nested within three-toed woodpecker habitat. The reason is that three-toed woodpecker has a fine-grained habitat selection and can therefore use smaller patches being further apart while the *Parus*/tree creeper guild has a coarse-grained habitat selection. This habitat is concentrated in the remote areas of the WX-region; in the subalpine forest near Transtrandsfjällen and Fulufjället, as well as the upland areas north of Älvdalen and Orsa. In addition, small patches are found in the northern periphery of the landscape Hälsingland.

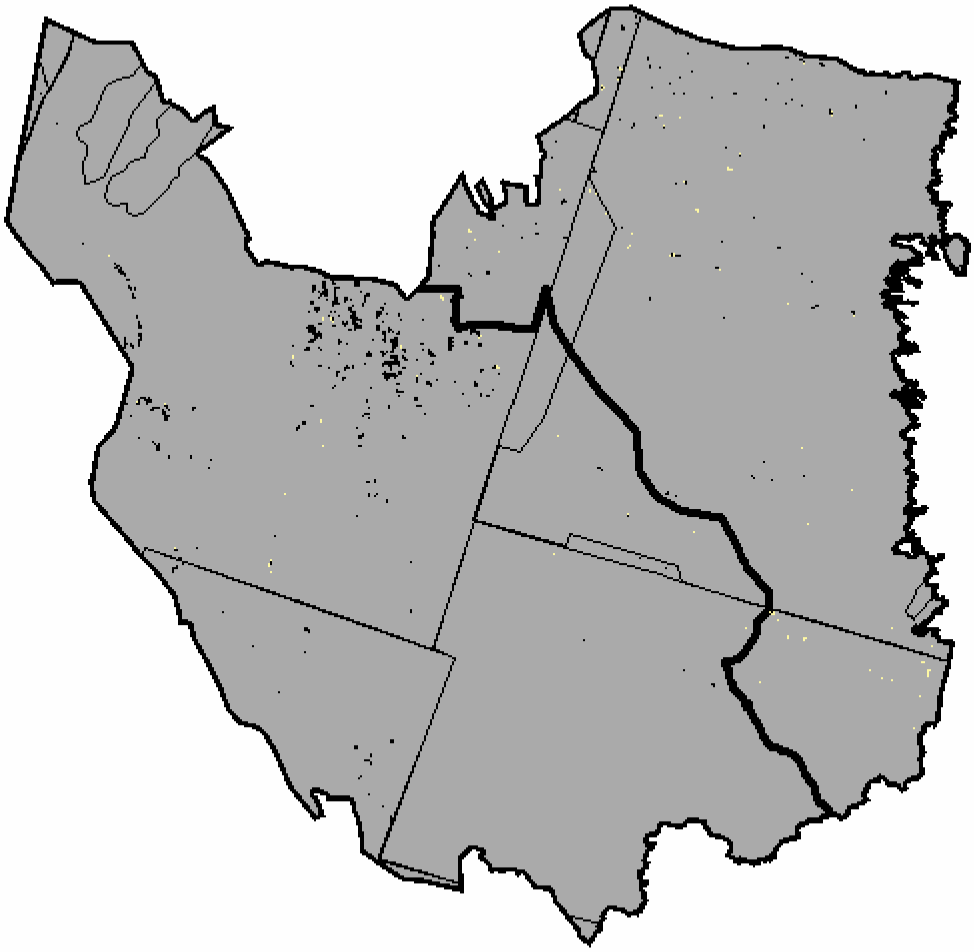


Figure 27
Map showing the tracts of suitable habitat for the complete Parus*/tree creeper guild in the counties of Dalarna and Gävleborg. The darker areas are based on forests older than 70 years and the lighter areas on forests between 40 and 70 years of age. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.*

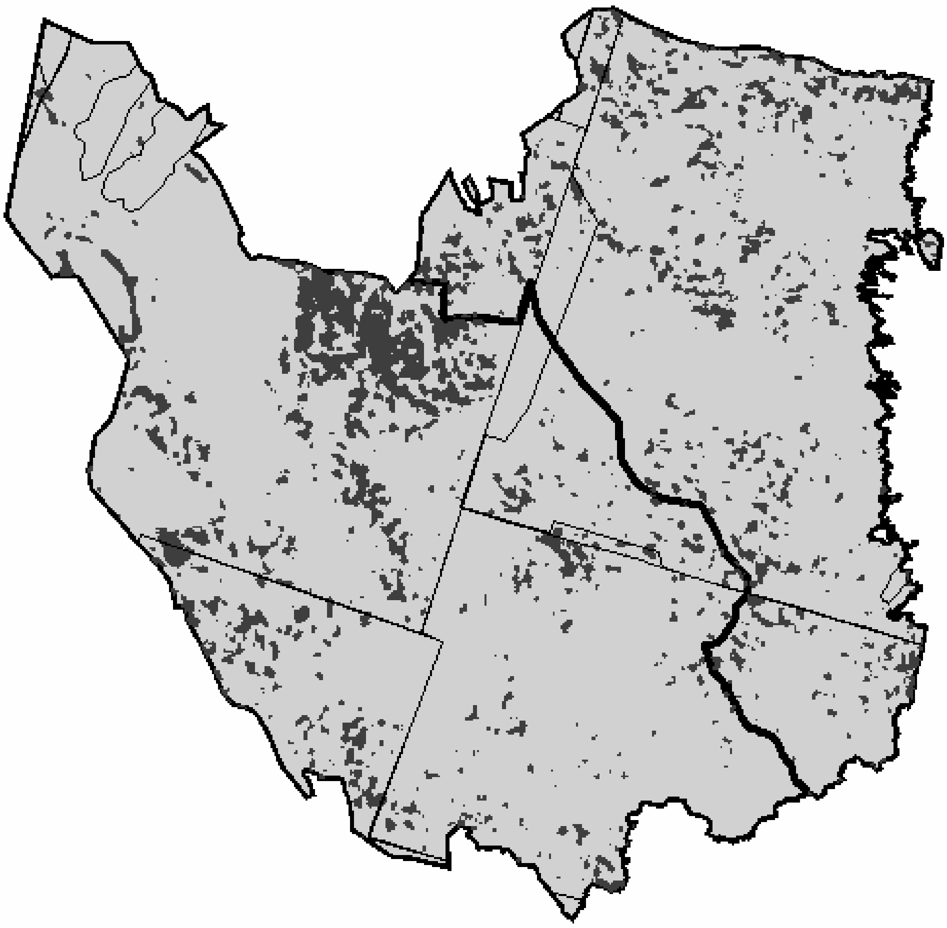


Figure 28
Map showing the tracts of suitable habitat for three-toed woodpecker in the counties of Dalarna and Gävleborg. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.

4.4.3. Old pine forest

For old pine forest two focal species - namely capercaillie (Figure 29) and *Tragosoma depsarium* (Figure 30) - were used to identify forest tracts with potentially high conservation value. Because of the more restrictive parameters for *Tragosoma depsarium* than for capercaillie (only forest below 400 a.s.l., and both clear-felled areas and a high proportion of old forest in the landscape), the tracts of *Tragosoma* became a subset of the tracts representing traditional capercaillie leks in old pine forest.

The HSI-modelling suggests several interesting patterns with both presence and absence of tracts. The southern, southeastern and eastern as well central agriculture dominated parts of the WX-region have few or no tracts for these two focal species. These areas have had the longest history of intensive forest management in the region. Three areas with high concentrations of old pine forest are the northwestern part of Dalarna along the mountains, the central part of Österdalälven NW of Mora and Orsa Finnmark. In the latter area both focal species co-occur. A well-known area called Sandviksmoarna, which connects the valley of Hennan and the valley of river Svågan, is clearly delinated as capercaillie and *Tragosoma depsarium* habitats. Here about 3000 hectares were recently covered by field inventories of the county adminstrative board. The area contains old and ageing pine forest and some spruce forest. Many stands have high conservation value with old-growth structure. In addition there are smaller tracts along the Baltic Sea north of Söderhamn. The areas of capercallie habitat in younger forest are confined to the eastern part of the study area.

It should be noted that the capercaillie model used here is made for large leks. Using the habitat patch requirement for small leks, the suitable area will be considerably larger.

4.4.4. Wet old forest

Detailed parameter values used for the animal species are not at hand for lichens requiring a generally moist microclimate within the wet old forest stands. Using buffers of 0, 50 and 100 m we estimated the amount of suitable habitat for more and less demanding species of lichens found in wet old forests below 500 a.s.l. Above this altitude all old forest patches were considered having a suitable microclimate due to the generally moist macroclimate. The results (Figure 31) show that suitable tracts for lichens specialising on wet old forest habitats are very uncommon except at high latitude where the macroclimate is assumed to be more favourable.

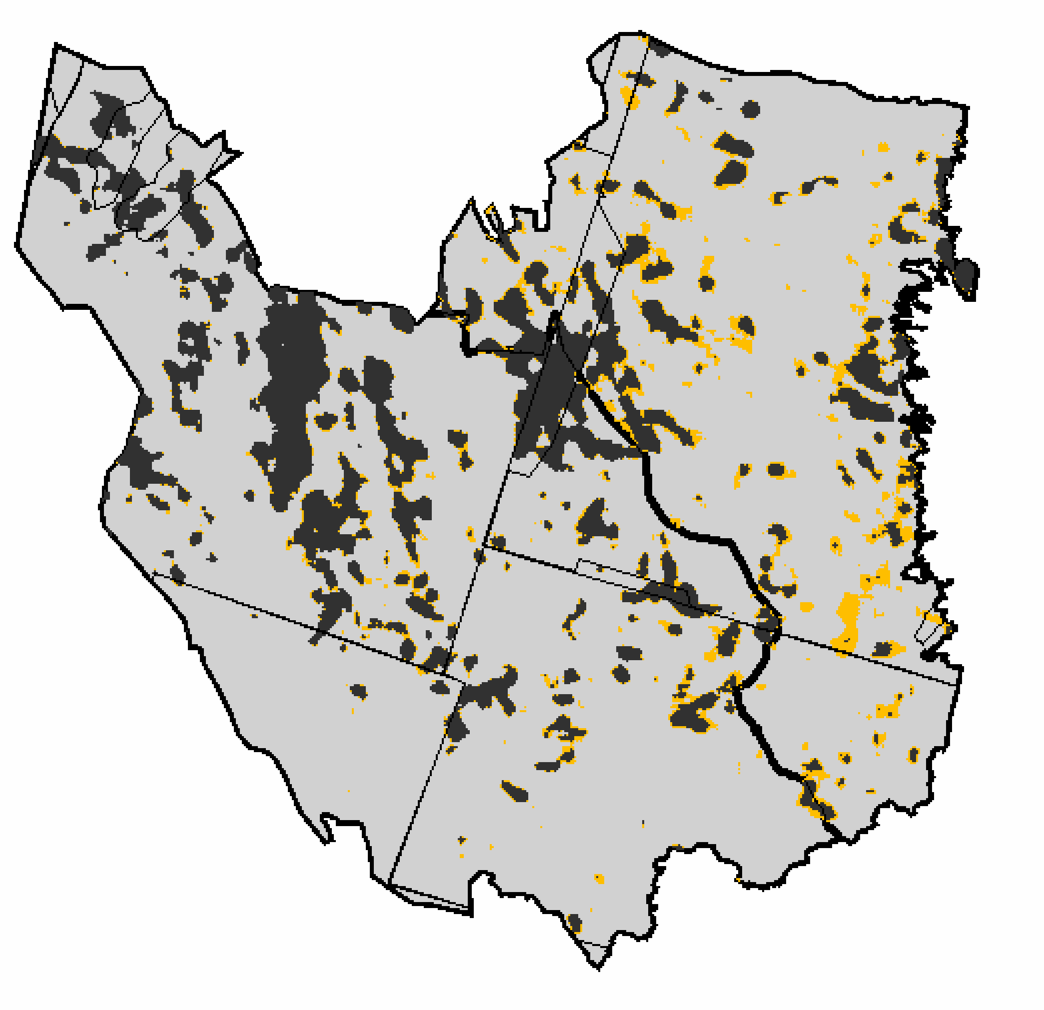


Figure 29
Map showing the tracts of suitable habitat for large capercaillie leks in the counties of Dalarna and Gävleborg. The darker areas are based on forests older than 70 years and the lighter areas on forests between 40 and 70 years of age. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.

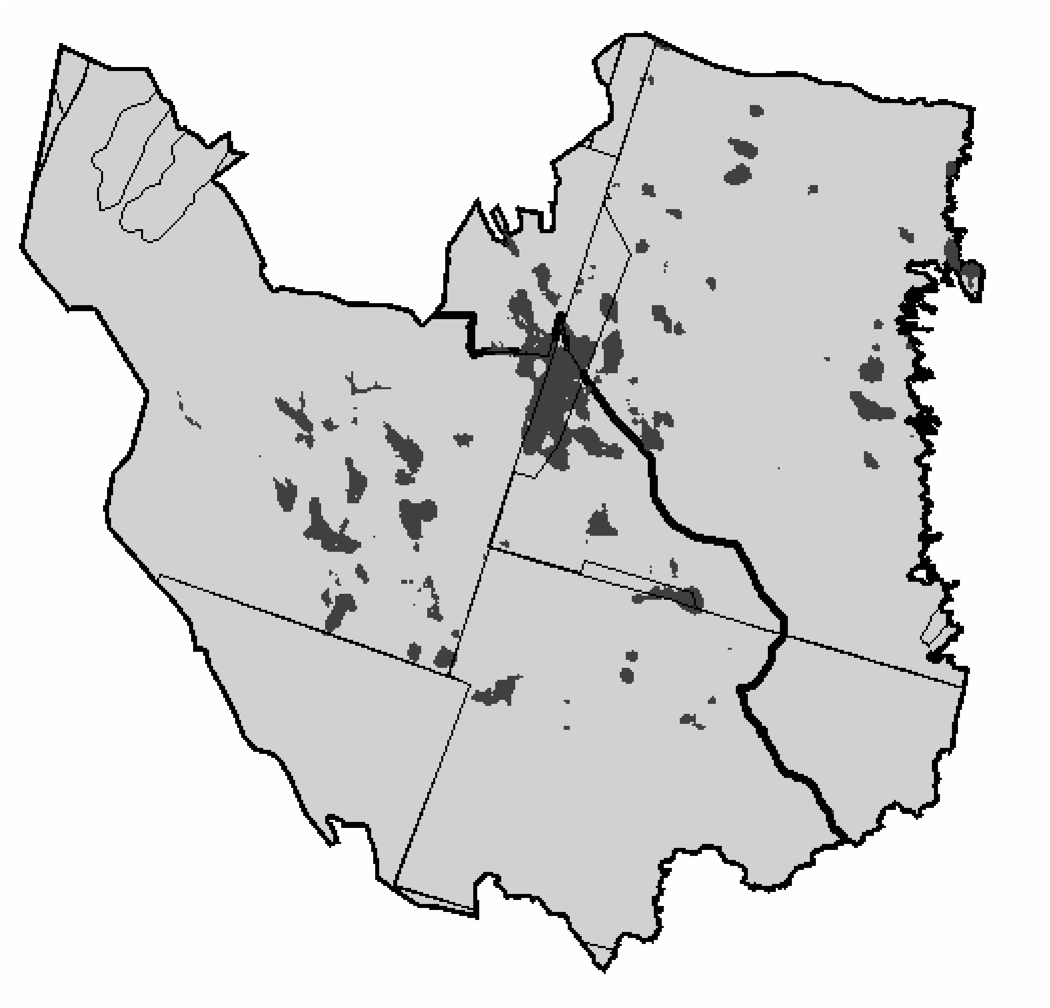


Figure 30
Map showing the tracts of suitable habitat for the beetle Tragosoma depsarium *in the counties of Dalarna and Gävleborg. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.*

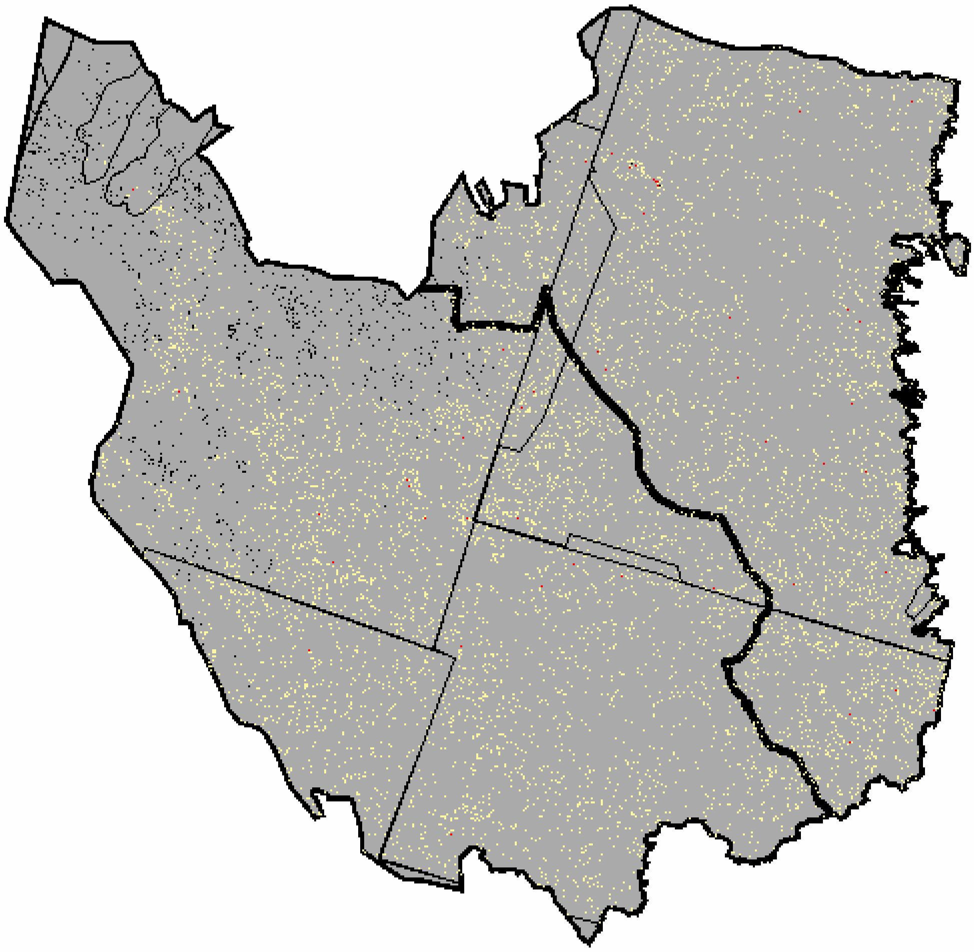


Figure 31
Map showing the tracts of suitable habitat for lichens preferring wet old forest in the counties of Dalarna and Gävleborg. The darkest areas represent the most demanding species, the red areas with less demanding species. The light yellow patches represent all old (>110 years) forest on wet sites as determined by Topoindex modelling. The lines denote borders between the different satellite scenes used to map the amount and distribution of different forest types, which were used in the regional gap analysis and the HSI-modelling.

4.5. Comparison of the amount of existing and functional forest areas

The HSI-modelling procedure can be described using species-specific occurrence thresholds to estimate the gradual removal of unsuitable patches of a particular focal forest type until only sufficiently large and connected patches from the target species' point-of-view remain. Using the different steps in the HSI-modelling procedure we compared the amount the four different focal forest types considered important in the regional gap analysis with the amount of forest patches, which can be considered as fully functional to maintain local populations in the short term. Additionally, because the satellite data is poor at identifying forests with high conservation value forests, the habitat quality needs to be assessed in the field. Finally, to assure the long-term viability of populations, the issue of habitat renewal needs to be addressed.

Based on the results from the habitat models shown in Table 23 and Figure 32, the level of overestimation was considerable. Depending on the species, 10-80% of the amount of habitat available in the regional gap analysis can be considered as functional based on the HSI-models.

Table 23
Area of forest patches for a given focal habitat in sq. km and focal species with the WX region in three steps in the HSI-modelling procedure described in Table 22 (see also Figure 23).

Forest type	Focal species	Amount according to regional gap analyis	Amount remaining after too small patches have been removed	Remaining amount of functional habitat patches
Old deciduous	Aegithalos caudatus	6659	5217	3417
	Dendrocopos minor	3944	3123	436
Old coniferous	Parus/Certhia guild (whole HSI-model)	13176	6758	369
	Picoides tridactylus (whole HSI-model)	8993	7020	2528
Old pine	Tetrao urogallus	13653	13465	3429
	Tragosoma depsarium	8115	4615	306
Wet old		No buffer	50 m buffer (less demanding lichens)	100 m buffer (more demanding lichens)
	All of Dalarna and Gävleborg	3309	376	359
	<500 m a.s.l.	2950	17.4	0.6

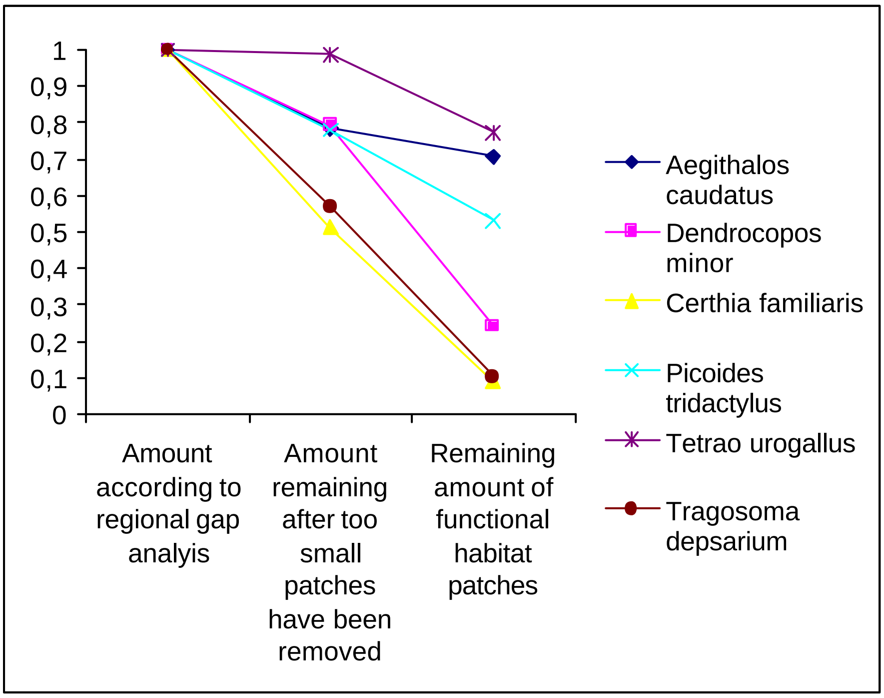


Figure 32
Illustration of how the regional gap analyses overestimates the amount of functional habitat for individuals and local populations of the 6 focal species for which HSI-models were developed, and for wet forest lichens. The declining trend from left to right should be interpreted as the (1) the removal of too small patches for the model "species" leaving only good stands and (2) the removal of patches located to far from each other to provide functional connectivity for the focal species. What remain are the good tracts shown in Figures 24-25 and 27-31.

4.6. Misclassification rates for different generalised forest classes

In this section we have tabulated misclassification rates for the generalised forest classes that are used in the spatially explicit analyses. For each generalised class we present the area in the respective satellite images, which is classified into that class, as well as the fraction of that class which is misclassified. This corresponds to the fraction of image pixels in the class for which the corresponding spot on the ground is actually not in that class. We also report the real area for the class in question (this differs more or less from the image area). Finally, we give the fraction of the class in the real world, not classified into the right class in the image. Below an example in the form of forest older than 110 years is presented.

A total area of 189,000 ha was classified as old forest, i.e. older than 110 years, in the Hälsingland satellite scene image (194/17). Assuming that we would make field checks at each single pixel, we would find that 71 % of this area was covered by forest belonging to other classes (younger than 110 years). On the other hand, if we would map all the 135,000 ha (unbiased estimate) old forest that actually exists in the field, only 40 % of that area would be covered by old forest pixels in the scene images, and 60 % is classified into other classes.

As can be seen in Table 24, several of the generalised classes suffer from high misclassification rates. This may be a major problem, but the problem may also be less serious than it seems. If most of the misclassification is made close to the limit of the class, the problem is much less serious than if most misclassified pixels are completely different from the class in question. The magnitude of the problem also depends on the spatial arrangement of the misclassified pixels in relation to the correctly classified ones. The problem for spatially explicit analyses is less serious if the misclassified pixels occur mostly in mosaics together with correctly classified pixels, than if the misclassified pixels are clustered so that whole stands are systematically misclassified.

The sensitivity of the spatial analyses to the respective misclassification rates must therefore be examined in a study of its own. We have, though, made preliminary evaluations, by visual inspection of the different classifications in areas where we have other information sources on stand properties. These inspections indicated that the misclassification of forest older than 110 years really is a problem for the spatial analyses. More intensively managed stands tended to be classified as >110 years whereas more natural stands (among them the really old stands) tended to be classified as younger, probably because they had a less dense canopy due to self-thinning. Thus, there was a systematic bias towards stands of less conservation value. On the other hand, the misclassification of deciduous stands appeared to be more of the kind that pixels close to the class limit where misclassified. Preliminary, we therefore believe that the spatial analyses based on classification of deciduous forest are better than would be judged from the misclassification rates. Note, however, the differences among individual satellite scenes.

Table 24
Misclassification rates for different generalised forest classes

Scene	Total forest area (1000 ha)	Image area classified as >110 years (1000 ha)	Fraction of image area misclassi-fied (%)	Real area older than 110 years (1000 ha)	Fraction of real area "missed" by the image classifi-cation (%)
All forest older than 110 years					
194/17 ("Hälsingland")	1121	189	71	135	60
194/18 ("Södra Dalarna")	721	97	69	82	63
196/17 ("Norra Dalarna")	938	224	46	253	52
All forest older than 70 years					
194/17 ("Hälsingland")	1121	434	29	390	21
194/18 ("Södra Dalarna")	721	274	33	245	25
196/17 ("Norra Dalarna")	938	454	17	466	19
Old deciduous forest fulfilling the requirements for* Aegithalos caudatus *(Table 22)					
194/17 ("Hälsingland")	1121	221	59	157	42
194/18 ("Södra Dalarna")	721	140	54	105	39
196/17 ("Norra Dalarna")	938	114	71	86	62
Old deciduous forest fulfilling the requirements for* Dendrocopos minor *(Table 22).					
194/17 ("Hälsingland")	1121	123	72	70	52
194/18 ("Södra Dalarna")	721	82	69	49	48
196/17 ("Norra Dalarna")	938	62	81	48	75
Old coniferous forest fulfilling the requirements for* Certhia familiaris *(model a) (Table 22)					
194/17 ("Hälsingland")	1121	249	46	199	32
194/18 ("Södra Dalarna")	721	160	50	134	40
196/17 ("Norra Dalarna")	938	219	42	193	34
Old pine forest fulfilling the requirements for* Tetrao urogallus *(Table 22)					
194/17 ("Hälsingland")	1121	234	35	246	38
194/18 ("Södra Dalarna")	721	127	39	145	47
196/17 ("Norra Dalarna")	938	275	25	333	38

When using only two age classes, ”old” and ”young”, classification accuracy is considerably higher if the age limit is set to 70 years, compared to a limit at 110 years. With a limit at 70 years, there is 71 % classification accuracy of ”old” forest in the north-east scene (194/17) and 83 % in the north-west scene (196/17). With a limit at 110 years, there is only 29 % classification accuracy in in the north-east scene and 54 % in the north-west scene (196/17). Especially for the north-east scene, the misclassification rate for forest older than 110 years is too high to be useful in spatially explicit models (Table 25 and 26).

Table 25
Age class classification accuracy of scene 194/17 from 2001.

Area (1000 ha)						
Age class on ground	Age class in image					
	10-40yrs	40-70yrs	70-110 yrs	>110yrs	low BA	Sum
10-40yrs	259.6	73.6	11.7	24.3	47.3	416.5
40-70yrs	55.7	107.0	50.3	34.8	0.8	248.6
70-110 yrs	9.3	50.7	122.3	71.9	0.1	254.2
>110yrs	3.4	18.1	59.5	54.5	0.0	135.5
low BA	42.0	3.0	1.2	4.0	15.9	66.0
Sum	370.0	252.3	245.1	189.3	64.1	1120.8

Table 26
Age class classification accuracy of scene 196/17 from 1999.

Area (1000 ha)						
Age class on ground	Age class in image					
	10-40yrs	40-70yrs	70-110 yrs	>110yrs	low BA	Sum
10-40yrs	208.0	31.2	5.2	17.1	27.9	289.4
40-70yrs	39.0	44.7	27.0	19.6	1.7	132.0
70-110 yrs	8.7	30.7	111.0	61.4	0.3	212.1
>110yrs	16.8	29.2	85.5	121.1	0.8	253.4
low BA	35.6	2.2	1.7	4.6	6.9	51.0
Sum	308.1	138.0	230.3	223.9	37.6	937.9

5. Losses of forests with high conservation value

5.1. Survival of stands found in the woodland key habitat (WKH) inventory

A woodland key habitat stand (WKH) is an area of forest, which has been identified as having a high value for the maintenance of forest biodiversity. The designation criteria include the presence of natural forest structures, species, and signs of past management. In Sweden more than 40,000 individual objects with different qualities have been identified on land owned by small private landowners. Here objects smaller than 10 ha make up 95 %. These objects have been identified, but do not have any legal protection. However, if the forest owner is certified through the schemes offered by Forest Stewardship Council (FSC) and Pan-European Forest Certification (PEFC), logging is not supposed to occur.

In this analysis we obtained data (polygons as shape-files) about (1) the Woodland Key Habitats on land owned by small private landowners from the National Board of Forestry and for the land owned by companies from the companies owning forest in the Dalarna/Gävleborg region, (2) the areas logged as revealed by comparison of satellite images from period between 1988 and 2001, and (3) the polygons describing protected areas in 2002 (Dalarna 2002-09-30, Gävleborg 2002-02-14; for the forms of legal protection see Table 14a) .

Viewing the Woodland Key Habitats in the WX-region as a population, individuals have three potential fates: (1) become a protected area; (2) being left as a Woodland Key Habitat stand; and (3) having been logged. By combining the databases for Woodland Key Habitats with remotely sensed data on the creation of clear-felled areas, we were able to estimate the fate of Woodland Key Habitats (Figure 33). Our analysis revealed some regional differences. In the southeastern regions 26 to 30 the proportion protected and affected by logging are very similar, while in the upland northwestern regions 32 and 33 the the Woodland Key Habitats were more often protected and less often logged.

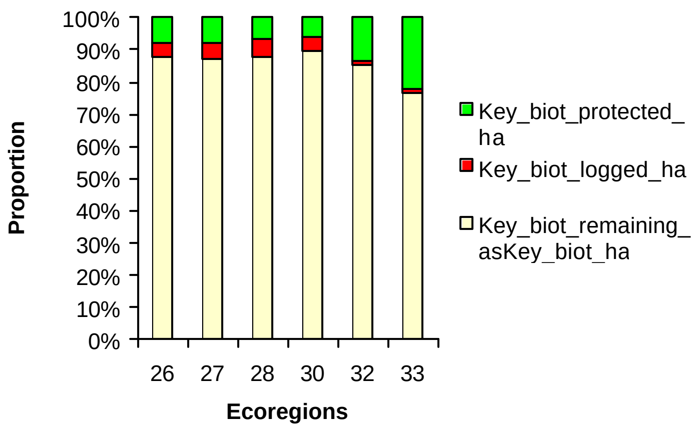


Figure 33
Fate of WKH stands in different ecoregions in the WX study area.

5.1.1. *Protection of WKH stands in detail*

Within the WX-region a total of 11,663 WKH polygons larger than 0.5 ha were registered in the digital data bases. The analyses show that 3.8 % of all the polygons partially or totally overlapped with the database showing the protected areas as in March 2002. The proportion of Woodland Key Habitats, with complete overlap with protected areas was 1.3 % and the proportion with some overlap was 2.5 % (Figure 34).

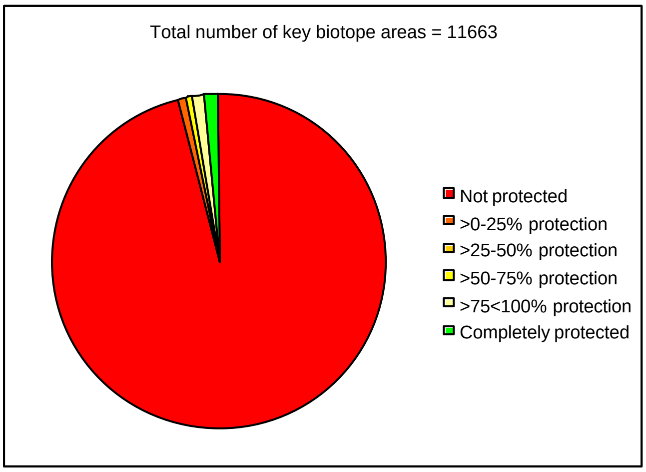


Figure 34
Relative distribution of different categories of overlap between the WKH stands and protected areas.

5.1.2. *Logging and WKH stands in detail*

The proportion of Woodland Key Habitats, which were affected by logging was analysed in three ways. First, after having removed all polygons smaller than 0.5 ha being too sensitive for digitising errors, we analysed the WKH polygons as reported in the databases delivered to us. In this category the complete overlap with logged areas was only 0.5 %. However, another 28.5 % showed partial overlap with the clear-felled areas mapped using satellite data suggesting either that the WKH stand has been partly logged, or if interpreted as a digitising error, logged up to the border of the WKH stand (Figure 35).

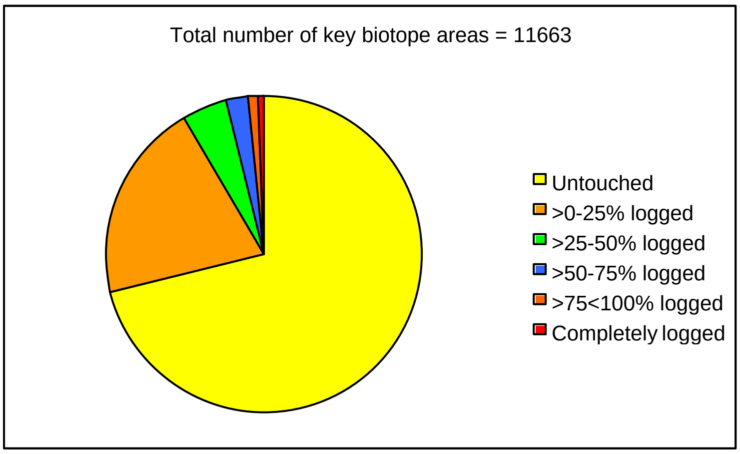


Figure 35
Relative distribution of different categories of overlap between the WKH stands and logged areas.

WKH are designated to contribute to the maintenance of biodiversity by securing habitat for red-listed species. Esseen (1994) showed that strong winds blow down trees in forest edges. Assuming that a 50-m wide buffer of forest would protect the WKH stand from blowdown, logging in such a buffer zone would have long-term deleterious effects on the local habitat quality. Therefore, in a second analysis, we added a 50-m buffer to each of all the 11,663 Woodland Key Habitats and repeated the analysis above. In this category the complete overlap with logged areas was virtually none (0.03 %) (Figure 36). However, another 48 % showed partial overlap with the clear-felled areas mapped using satellite data suggesting that the WKH stand's buffer zone has been partly logged.

To maintain a favourable conservation status in the long term, Woodland Key Habitats may also be dependent on maintaining a microclimatic typical for forest interior stands. Assuming a buffer zone of 50 m of intact forest surrounding the WKH stand, and allowing for a 50-m blowdown zone. Therefore we also analysed the occurrence of logging with the WKH stand itself and the 100-m wide buffer zone. This operation resulted in some Woodland Key Habitats becoming merged and the total sample size was reduced to 11,654. In this category the complete overlap with logged areas was virtually none (0.02 %). However, another 63 % of the WKH polygons showed partial overlap with the clear-felled areas mapped using satellite data suggesting that the majority of WKH's buffer zones for blowdown and microclimate have been partly logged (Figure 36).

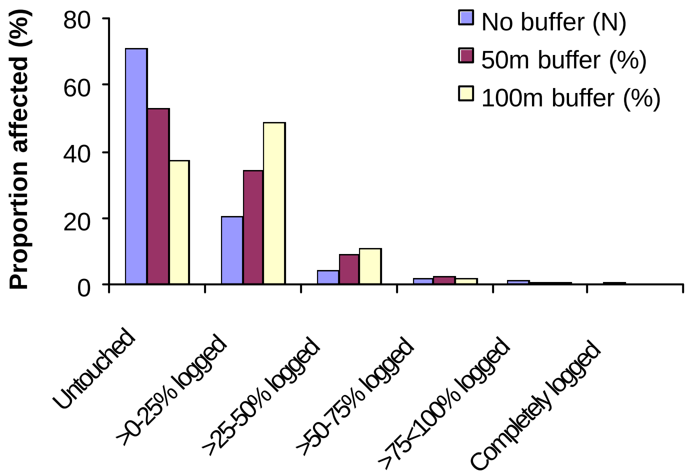


Figure 36
The distribution of different proportion of the WKH stands that have been affected by logging using buffers around the polygon of 0, 50 and 100 m around them.

5.1.3. Relationships between the size and fate of WKH stands

The proportion of WKH stands affected by logging and having been protected was clearly related to their size (Figure 37). While the mean proportion of WKH stands logged declined with increasing size, the mean proportion of area protected increased with size. In other words, a clear tendency toward logging of smaller Woodland Key Habitats and conservation of the larger was observed.

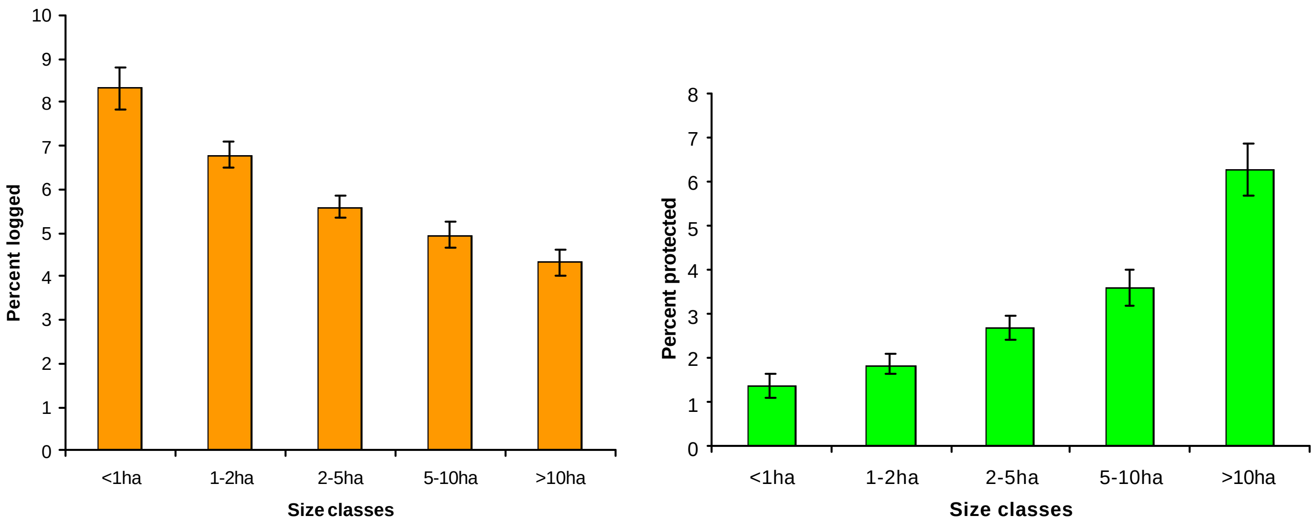


Figure 37
The proportion of WKH stands affected by logging and protected in relation to their size. The vertical error bars represent the standard error.

5.2. Fragmentation of old forest tracts

5.2.1. Rationale

Small and isolated forest patches are not suitable habitat for many species specialising on old forest. The spatial configuration of the old forest is consequently of importance for the population viability of such species. Hence, as shown in section 4.5, it is not sufficient to analyse the amount of pixels with old forest without considering their spatial configuration (Angelstam et al. 2003b). The aim of this analysis was to estimate the amount of forest interior, which could be considered as functional old forest patches, and how this changed over the past two decades.

5.2.2. Methods

5.2.2.1. Satellite data used

We analysed the changes of the forest landscape between the late 1970s and the late 1980s, and between the late 1980s and around 2000, respectively. We also did one analysis on data describing the current state. This analysis is only presented as a map without statistics, see figure 43. The study area was the two counties within the satellite scene covering northern Hälsingland (eastern scene 194/17) and northern Dalarna (western scene 196/17), see Figure 38 and Table 27.

Figure 38
Map showing the location of the two satellite scenes covering northern Hälsingland (eastern scene 194/17) and northern Dalarna (western scene 196/17) in the counties Dalarna (dark) and Hälsingland (light).

Table 27
Description of the satellite data used in the analysis of changes in the amount of larger old forest tracts.

Scene area 194_17 Hälsingland	**Description**
33cl_t0_ejmoln	Forest classification for 1988, 33 forest classes.
33cl_t0_moln	Same as above but classification for areas covered by clouds in the main scene.
33class_t2	Forest classification for 2001, 33 forest classes.
33class_t2 (moln)	Same as above but classification for areas covered by clouds in the main scene.
Tm-hyggen	Clear-felled areas mapped from Landsat TM between 1988-2001 (a few are from 1986-) (See also section 3.2.6.)
MSS-hyggen	Clear-felled areas mapped from MSS satellites between 1975-1988 (a small area in Hälsingland have cuts from 1979-1992) (See also section 3.2.6.)
Scene area 196_17 Northern Dalarna	
33cl_t0_ejmoln	Forest classification for 1986, 33 forest classes.
33cl_t0_moln	Same as above but classification for areas covered by clouds in the main scene
33class_t2	Forest classification for 2000, 33 forest classes.
33class_t2	Same as above but classification for areas covered by clouds in the main scene
Tm-hyggen	Clear-felled areas mapped from Landsat TM between 1988-2001 (a few are from 1986-) (See also section 3.2.6.)
MSS-hyggen	Clear-felled areas mapped from MSS satellites between 1975-1988 (a small area in Hälsingland have cuts from 1979-1992) (See also section 3.2.6.)

5.2.2.2. Choice of age classes

The spatial analyses were done using ArcInfo 8.2 and the area distributions were calculated in Arcview 3.2 with the function "tabulate areas". In order to reconstruct the forest landscape in the oldest time period we combined forest classification with the mapping of clear-felled areas. The confusion matrices treat corrections of forest classification but not the mapping of clear-felled areas. Therefore the area figures cannot be corrected in the confusion matrices. Hence, the absolute figures should not be used in interpretations of the data, but the relative changes in the results. Also the figures on the amounts of forest older than 70 years, which are presented in the results, are not corrected in confusion matrices.

5.2.2.3. Defining old forest

For the comparison between "late 1980s" and "2000", old forest was defined as all forest older than 70 years selected from the "late 1980s" and "2000". For the comparison between "late 1970s" and "late 1980s" a combination of data had to be used as there is no forest classification for the time period "late 1970s". Therefore the old forest had to be reconstructed by merging clear-felled areas with back-transformed forest data.

Clear-felled areas made during the period 1975-1988, and mapped using MSS, were considered to be old forest in the late 1970s. These clear-felled areas were merged with the grid layer with forest older than 70 years in the classification for late 1980s. The merged grid layer was considered to represent forest older than about 60 years in the late 1970s. In other words, the forest older than 70 years in the late 1980s was transformed back in time about 10 years and merged with the clear-felled areas.

Next, the "late 1970s" was compared with the late "late 1980s". Forest older than 60 years in the 1970s should be compared with forest older than 60 years in the 1980s and not with forest older than 70 years. Forest older than 70 years around the year 2000 was merged with clear-felled areas from the period late 1980s to around 2000 (using Landsat TM satellite data). In other words the forest older than 70 years at "2000" was back transformed 13-14 years and merged with the clear-felled areas, which were considered as old forest in the "late 1980s". That grid layer represents forest older than about 60 year in the "late 1980s".

5.2.2.4. Defining old forest interior

Old forest pixels closer than 50 m from a clear-felled area or young forest were considered as being affected by edge effects from the surrounding matrix. Such pixels were removed. First an influence grid layer for each time section was calculated. The influence grid layers for the comparison between the "late 1980s" and "2000" consisted of forest younger than 40 years and all clear-felled areas carried out before the time period in question. For the comparison between the "late 1970s" and "late 1980s", the influence grid layer matching to "late 1970s" corresponds to the grid layer with forest younger than 40 years in the "late 1980s". The influence grid layer matching to "late 1980s" consisted of forest younger than 40 years at the late 1980s and all clear-felled areas made between the "late 1970s" and "late 1980s". Finally, we calculated a buffer of 50 m around the influence grid layer.

A neighbourhood analysis was then used to estimate the amount of connected old forest pixels. The method was focal mean counting on the surrounding 5x5 pixels. Connected old forest was then defined as old forest pixels, which were surrounded by the same kind of pixels to at least 50 %. In this way small isolated patches and forest edges were masked away. The remaining forest patches were considered as old forest interior.

5.2.2.5. Creation of individual forest patches

Using a grouping operation, old forest interior pixels forming a continuous forest patch were transformed to a grid layer consisting of patches with unique identity. Pixel neighbours with the side towards each other were counted as connected in the grouping operation while pixels with only diagonal contacts were not counted as connected. Thanks to the unique identity, the area for each individual patch could be calculated.

In the neighbourhood analyses not every pixel in the old forest interior was >70 years because small gaps have been artificially been converted to old forest. To estimate the true amount of old forest interior, we wanted to include only real old forest pixels. Therefore the amount of old forest within the old forest interior patches was calculated. This amount was slightly smaller than the area of the patches. In the sections below the expression core areas refers to old forest pixels located within the old forest interior.

The total core area of old forest interior patches for each time period was presented for each of five size classes: 0-20 ha, 20-50 ha, 50-100 ha, 100-500 ha, >500 ha. The area for each size class was calculated as well as the total core area. The proportion of core area of old forest interior of the total forest land is presented for the two satellite scenes.

5.2.3. Results

5.2.3.1. The satellite scene 194/17 “Hälsingland”

The amount of old forest interior in 1988 and 2001 turned out to be similar in most comparisons. In the scene, 34 % of the forest land was older than 70 years in both years and 19 % of the forest land was located within old forest interior patches in both years. Of the forest older than 70 years in 2001, 46 % consisted of forest that had aged during the period 1988-2001 (the forest was younger than 70 years 1988 and older than 70 years 2001). The size class distribution is also similar when the two years are compared. The size class >500 hectares has slightly decreased from 1.80 % to 1.66 % of all forest land. In both years the majority of the old forest interior is located in small patches, < 20 hectare, it is 6.5 % of the forest land (Figure 39).

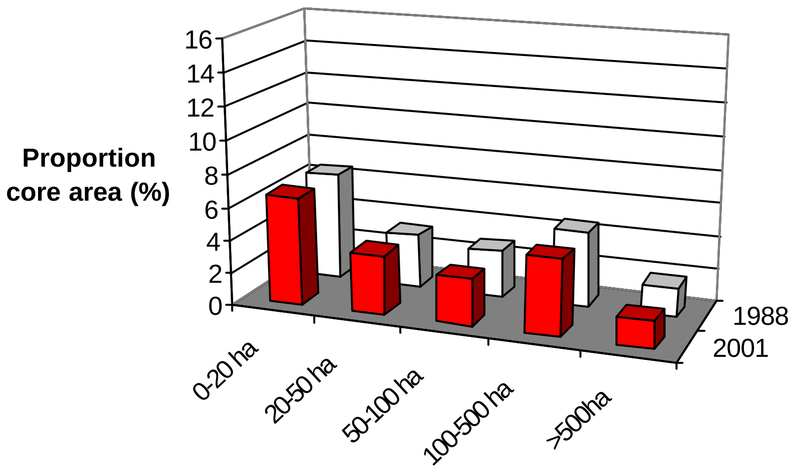


Figure 39
The estimated amount of old forest core area in 1988 and 2001 within the satellite scene covering northern Hälsingland (194/17).

In the entire scene area, the total amount of forest older than 60 years were 46 % in 1988 and 42 % in the late 1970s, the amount of old forest interior was 34 % of forest land in 1988 and only 25 % in late 1970s. The amount of small (< 20 ha) patches of old forest interior decreased from the late 1970s to 1988. The amount of different size classes of old forest interior in the Hälsingland scene in 2001 is shown in Figure 40.

There might be an artefact in the mapping of clear-felled areas in the MSS-data, which covers the period 1976-1988. The area of clear-felled areas in the MSS data is half the area of the clear-felled areas mapped in the TM-data, which covers the period 1988-2001. If these differences in cutting rate is not real there might be an serious error in the data, MSS-clear felled areas which affects the spatial analyses as the clear-felled areas were used to reconstruct the area of 60 years old forest in time section late 1970s. For the scene 196017, Northern Dalarna, the amount of clear-felled areas in the MSS-data set and the TM-data set is about the same but we decided not to analyses that scene for the comparison late 1970:s and 1988.

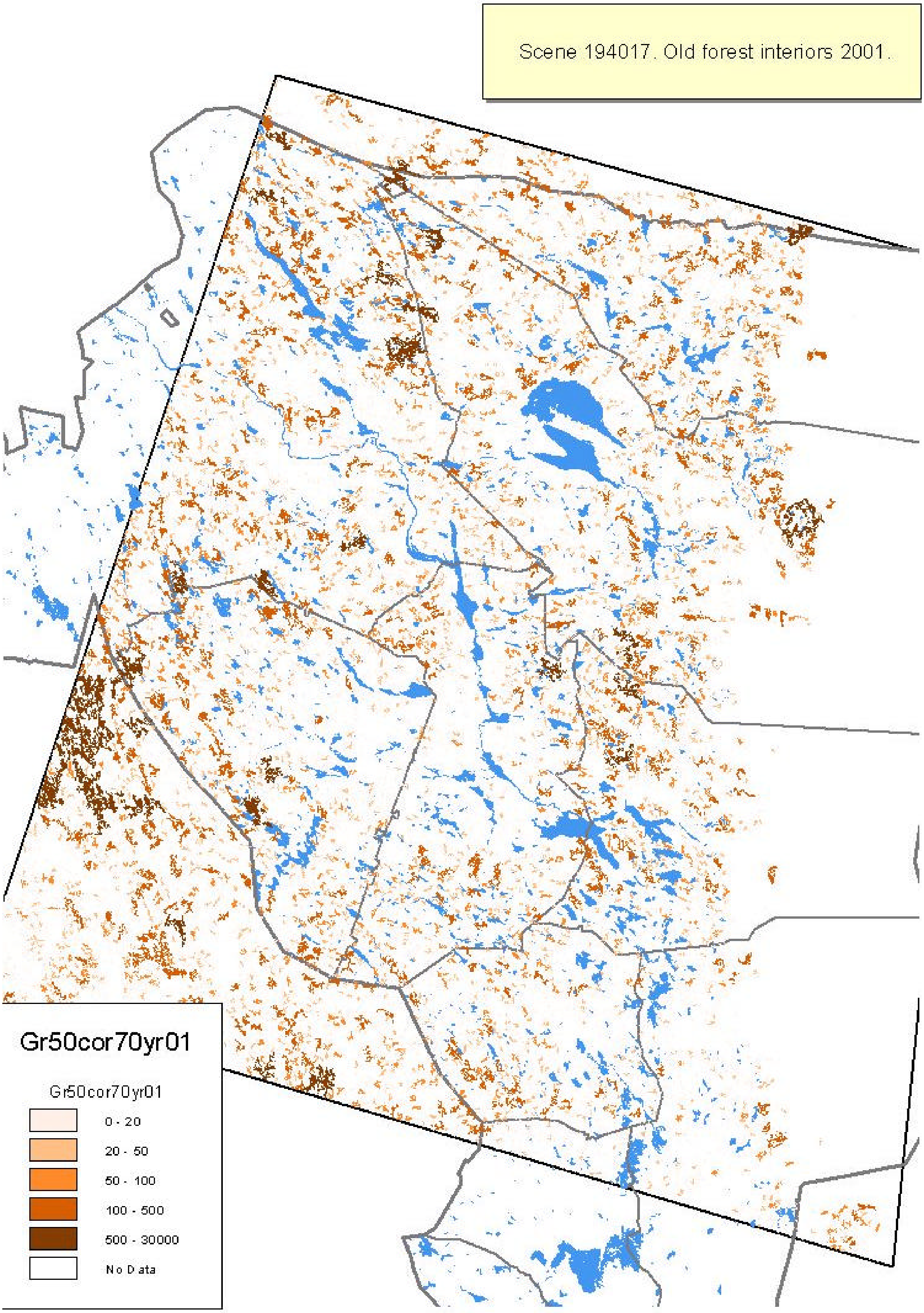


Figure 40
Patches of old forest interior in scene 194017 year 2001. Size classes > 20ha, 20-50 ha, 50-100ha, 100-500 and >500 are presented from light to darker colours.

5.2.3.2. The satellite scene 196/17 “Northern Dalarna”

The total amount of forest located within old forest interior patches declined slightly from 30 % in 1986 to 28 % in 1999. Of the forest older than 70 years in 1999, 29 % consisted of forest that had aged during the period 1986-1999. The size class distribution differed between the two period and showed a clear decrease from 15 % to 11 % in the amount of forest patches >500 ha (Figure 41). In both years there is a concentration of large patches of forest interiors in the upland areas in Dalarna (Figure 42). This concentration is unique in the study area.

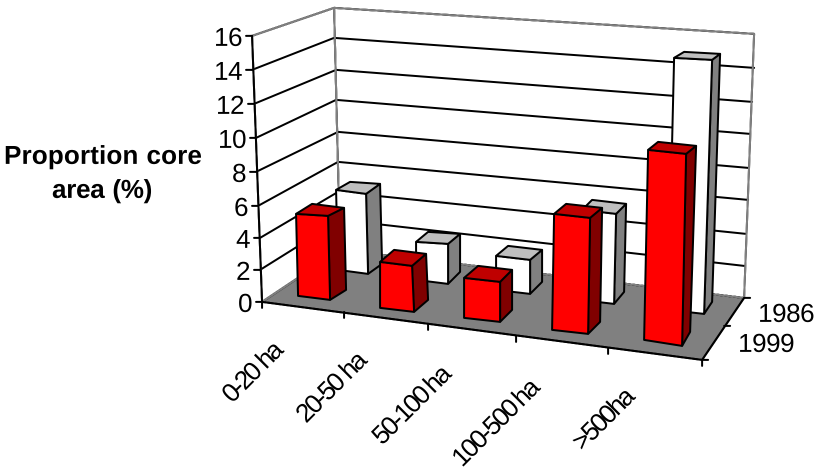


Figure 41
The estimated amount of old forest core area in 1986 and 1999 within the satellite scene covering northern Dalarna (196/17).

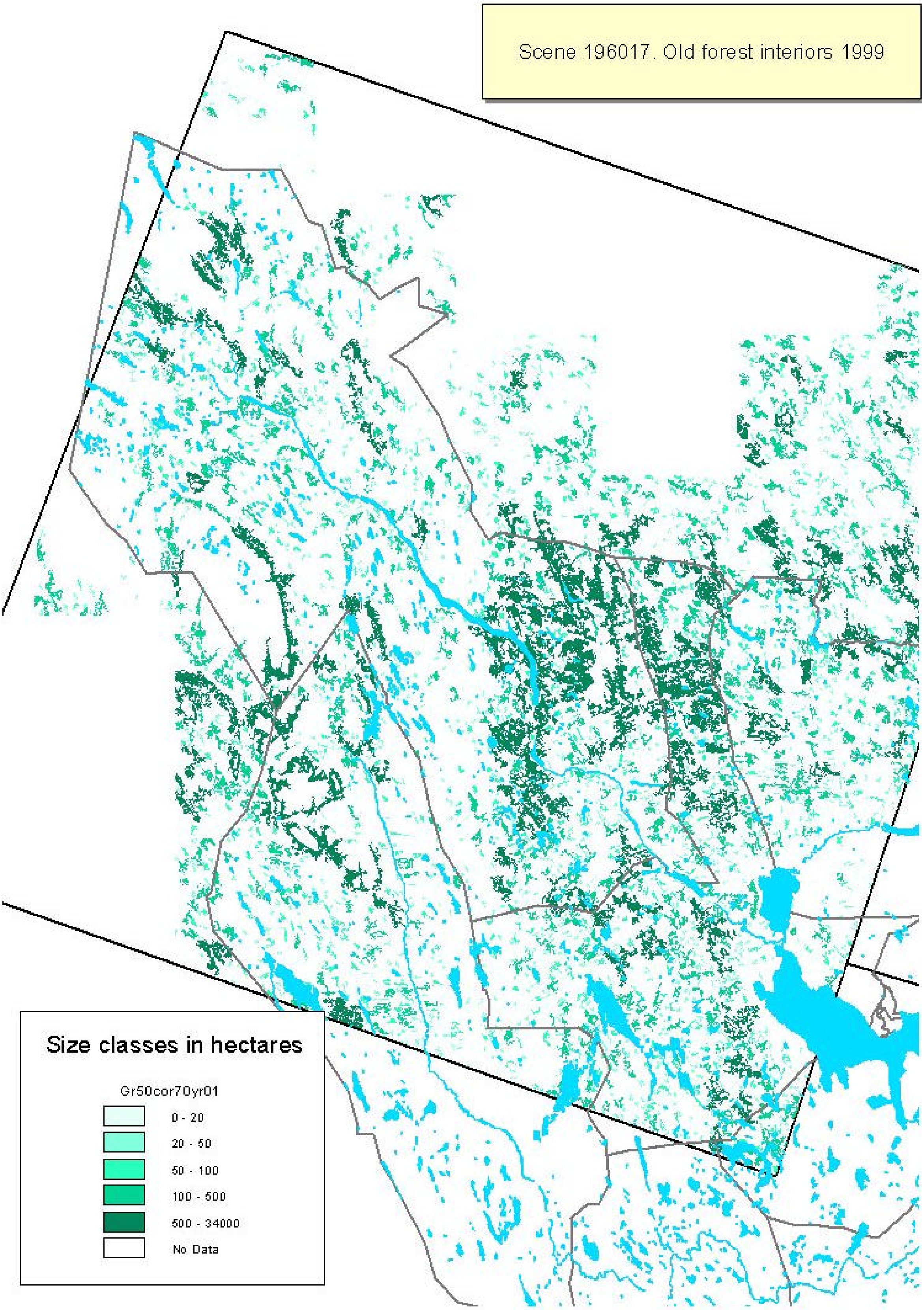


Figure 42
Patches of old forest interiors in scene 196017 year 1999. Size classes > 20ha, 20-50 ha, 50-100ha, 100-500 and >500 are presented from light to darker colours.

5.2.3.3. The amount of old forest in the counties Dalarna and Gävleborg

The two satellite images analysed cover regions with both longer (Hälsingland) and shorter (northern Dalarna) histories of forest management. In accordance to this the remaining amount of old forest interior was also generally higher in northern Dalarna than in Hälsingland (see Figure 43). In the Hälsingland scene 1.7 % of forest land is located in patches of forest interiors that are > 500 ha and and 6.5 % is located in patches < 20 ha. The corresponding figures for the Dalarna scene was 11 % and 5.2 %. According to statistical data received from National Board of Forestry the mean annual cutting rate of productive forest during the period 1978-2001 was 1.1 % in Dalarna and 1.0 % in Hälsingland. This explains well the decline of large old forest interior patches in Dalarna from the late 1980s to present. Within ecoregion 30 in the satellite scene covering northern Dalarna the amount of forest older than 70 years decreased from 50 % to 43 % and the amount of old forest interior from 34 % to 28 %. The size class >500 ha was reduced from 19.4 % to 9.9 %. By contrast, in Hälsingland the amount of such patches was already very low a decade or more ago.

It should be stressed that one should be careful when comparing different scenes as they were classified separately and have different data quality. However, such obvious differences as the size class distribution of forest interiors between scene Hälsingland/194017 and Dalarna/196017 are probably true and reflect a gradient in the forest history. The apparent concentration of large patches of forest interiors in the upland areas in north-eastern Dalarna is unique in the study area. These patches are mainly situated on community forests (Allmänningsskogar), which have not been intensively logged. This type of ownership coincides to certain degree with low productive ground. Another area within the concentration is located on a military training area where there had been no ordinary forestry.

Originally we thought it would be possibile to go back as far in time as the late 1970s using the data for clear felled areas mapped from the 1975 - 1988 (MSS-data). We assumed that the forest was old before it was felled and reconstructed the forest landscape. Nevertheless we noted that for the scene covering Hälsingland there was a much smaller amount of clear-felled areas than we could expect when we compared with statistics from National Board of Forestry, Region Gävle-Dala. We suspect that the low amount of old forest in the grid layer for the late 1970s for Dalarna is an artefact due to errors in the mapping of clear-felled areas using MSS-satellite images.

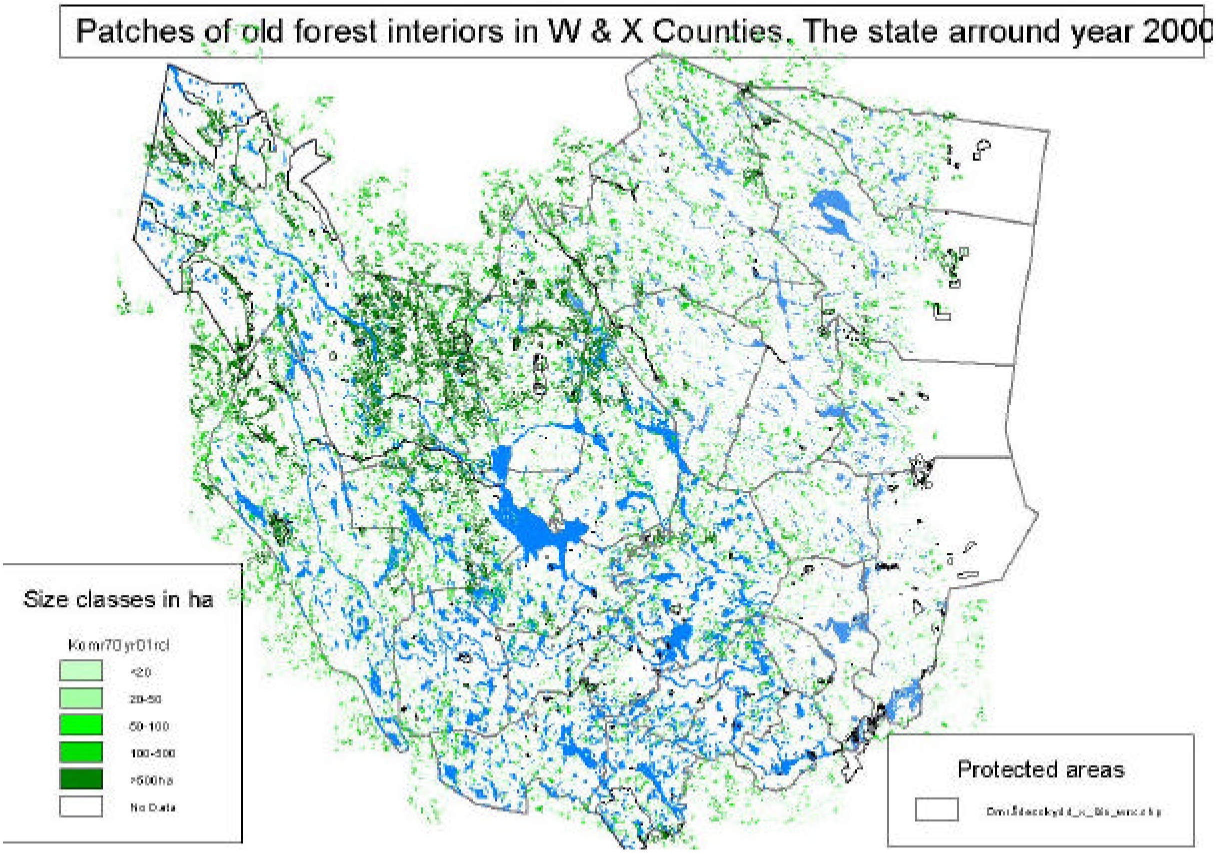


Figure 43
Patches of old forest interiors. Size classes > 20ha, 20-50 ha, 50-100ha, 100-500 and >500 are presented from light to darker colours. The state is from arround year 2000.

6. Discussion

6.1. Regional gap analysis - results

The regional gap analysis for the Dalarna/Gävleborg region presented here is founded on the current Swedish policies related to the maintenance of biodiversity in forest (SOU 1992, SOU 2000). These policies focus on the compositional component of biodiversity, explicitly expressed as the maintenance of viable populations of all naturally occurring species. As a consequence, the strategy for the set-aside of conservation areas presented in this study is guided by the ecological principles of connectivity of habitat patch networks (e.g., Forman 1995) and representation (e.g., Pressey et al. 1996) within an ecoregion.

It can, however, be debated at what scale biodiversity should be maintained. Following Larsson et al. (2001), we argue that the ecoregional approach is reasonable as it reflects nature rather than arbitrary administrative borders. Ideally, priorities for conservation within ecoregions should be based on intact natural forest remnants at multiple scales ranging from large to small (e.g. Yaroshenko et al. 2001, Hansson 2001, Angelstam et al. submitted). Naturally, strategies for the design of conservation area networks can be formulated using other principles, such as aesthetics (Lucas 1990) or recreational interests. But this lies beyond the field of natural sciences, which we as authors represent, and is a part of the society's general decision-making processes to attain the approved policies within the framework of sustainable development. Our contribution should thus be considered by decision-makers in concert with other studies representing other policies and values.

This study focuses on biodiversity in forests rather than forest biodiversity, which is found in both forests and the ancient cultural landscape with woodland pastures and meadows (Ihse 1995, Angelstam et al. 2001). Therefore the principles for doing the analyses are based on the paradigm of natural disturbance (e.g., Angelstam 1998a,b, 2002, Kuuluvainen 2002) rather than cultural landscape paradigm (e.g., Peterken 1996, Kirby and Watkins 1997). This restriction should be kept in mind in particular when it comes to the deciduous component (Mikusinski and Angelstam 1999, Mikusinski et al. submitted).

6.1.1. Differences in the distribution of different site types/disturbance regimes

The Dalarna/Gävleborg region spans a wide range of ecoregions, climatic conditions and altitudes. Consequently there are clear differences among regions in the distribution of different site types, and hence disturbance regimes. This reinforces the general idea that local conditions have to be considered on a case by case basis when setting priorities for conservation and restoration of functional habitat networks. In the absence of a forest site type map we therefore used modelling using digital elevation data to estimate the ecoregional variation in site type distribution.

6.1.2. Differences in representativity among regions

There was an evident bias towards higher losses of productive rather than poor sites in all regions. Moreover, the absolute losses were higher in regions with a longer land use history (in the SE and E) than a shorter one (in the NW). The stratification based on altitude and geology appears particularly effective in separating areas below the marine limit at around 200 m a.s.l., or at higher altitude if having high quality soils, from land at higher altitudes where there has not occurred any deposition of fine particles providing soils of interest for land clearing and agriculture.

6.1.3. Differences in area gaps among regions

It is vital to interprete the results from the regional gap analysis with great caution. The following example explains why. The results from the gap analysis suggest that, for the study area as a whole, there is enough old forest of the different site type combinations for long term persistance of most species confined to old forests. However, for spruce forests older than 110 years and deciduous forests older than 70 years, the quantities are just on the threshold, as for old pine forests in the lowland.

However, it is vital to realise that much of the ”old” forest measured by the remote sensing technique has been fairly intensely managed during the last decades. Consequently, most probably sufficient amounts of within-stand old-growth structures such as dead trees, large living trees and multi-layered stands are not at hand in many of those stands. The area, which is actually available for old-growth species, is therefore probably lower than the gross area measured here. Of the forest older than 70 years in 2001 for the Hälsingland scene, 46 % consisted of forest that had aged during the period 1988-2001 (the forest was younger than 70 years 1988 and older than 70 years 2001). The insufficient thematic resolution with respect to stand age and structure should therefore be kept in mind.

The estimated gaps/surplus of forest in a particular region depends thus both on the amount of the area of forest sites hosting different natural disturbance regime and the amount of high conservation value forest that remains after anthropogenic transformation. This has been shown in an earlier study based on National Forest Inventory data (Anonymous 1999).

Probably there is an underestimation of the natural amount of pine forest with cohort dynamics in the inland regions, reflected in a similar underestimation of the required minimum amount of old pine forests in these regions. This is because the topoindex model only considered soil moisture, whereas other components also affect the fire regime of a site. Site fertility is such an important additional factor. Because trees grow slower on poor sites, such stands become more open, which allows more sunlight to reach the ground. This in turn, should make the ground layer vegetation more fire-prone both because lichens and other kinds of fine fuels would be more common, and any vegetion more dry. There is a geographic trend in site fertility within the study area, with lower site fertility at higher altitude. The cooler climate at higher altitudes affects tree growth both directly and through decreased rate of humus mineralisation and weathering. In addition, parts of northwestern Dalarna have extremely nutrient-poor bedrock.

While soil moisture, modelled by the Topoindex method in this study, is the most important factor determining which disturbance regime is governing at a site, also other factors may contribute. Examples of such factors are slope and aspect (S and W slopes burn more often than N and E slopes), physical and chemical properties of the soil (sites with coarse grained soils and/or poor soils burn more often), and stand history (intensive fire leads to thin humus layer and a drier appearance whereas reduction of fires make dry sites more mesic due to accumulation of organic matter). Additionally the long absence of natural forest fire events and draining of wet site has made the site type distribution more narrow with lowered amounts of dry and wet sites.

The habitat models, finally, also stress that a very cautious interpretation of the results from the gap analysis should be made. By analysing the difference between the total amount of habitat area available according to the regional gap analysis and the area which satisfies the requirements of area-demanding habitat specialists at the scale of patches and landscapes, the regional gap analysis presents up to a 5-fold overestimate of the amount functional habitat (Angelstam et al. 2003b). By functional we mean that both patch size and connectivity requirement are satisfied.

6.1.4. Differences in protection gaps among regions

In central Sweden's lowland areas generally less than 1 % of the forest area is protected (Angelstam and Andersson 1997). As has been shown in several previous studies, a higher proportion of forest on poor inaccessible sites have been protected than on rich accessible sites (Götmark and Nilsson 1992). This is true also in this study area. Today less than 1 % is protected in most of the two counties (Table 19a). However, in the subalpine forests with low productivity the proportion of protected forest was 25 %. Angelstam and Andersson (1997, 2001) estimated that the long-term goal for protected areas in boreal forest, providing that the managed matrix is managed in a nature-friendly way, is about 8 % of the forest area. There is hence an area gap of about 5 %. According to Anonymous (1999) a total of about 5% of the productive forest below the subalpine region was judged to have a high conservation value. Consequently, in principle all the remaining forests of high conservation value ought to be protected. For the hemiboreal zone, which is found in the south-westernmost corner of the study area, the corresponding long-term goal was 12 %.

Lõhmus et al. (2003) estimated the minimum area of strictly protected forests, which could maintain species of 'management-incompatible forests' (i.e. not surviving in timber production areas), in Estonia (within the hemiboreal zone). The theoretical minimum need for strictly protected forests was estimated at 9–11% of current forest land. However, if current reserves retain their status, filling the gaps for underrepresented forest site types yielded a total coverage of 10–13%. Their model was robust to possible errors in the used values of fire frequency. Changing all used fire intervals by ±10% changed the estimate of long-term aim by only ±4 to ±5%, which means uncertainty about ±0.5% of forest land.

To reduce the gap between the desired level of protected areas and the current state, the Environmental Protection Board is developing a conservation planning strategy. Additionally, the county administrative boards will adapt the general guidelines locally. The counties Dalarna och Gävleborg will then use the results and experiences from this project.

6.2. Regional gap analysis – the procedure

Modelling is a way of simplifying the real world (Starfield et al. 1994). Our approach to regional gap analysis contains several steps and variables with different parameters, each of which having different levels of uncertainty. Lõhmus et al. (2003) repeated the procedure proposed by Angelstam and Andersson (1997) in Estonia and discussed these uncertainties. Below follows a first selection of items, which need to be considered in a sensitivity analysis (Rönnbäck and Angelstam in prep.):

- the classification into disturbance regime/forest type (Europe: Yaroshenko et al. 2001, Kuuluvainen 2002, Pennanen 2002; North America: Agee 1993a,b, 1999a,b)
- the relationship between site and disturbance regimes and resulting forest type (Angelstam et al. 1993, Angelstam 1998, Yaroshenko et al. 2001) Similarly, Quine et al. (2002) used abiotic factors to predict the distribution of different forest types in Scotland.
- the modelling of different site types using Digital Elevation Models and the Topoindex approach (Mackey et al. 1999, Bryan Lee pers. comm.).

- limitations of remote sensing as a method for mapping the conservation value of today's forest. For example, the oldest age class (>110 yrs) derived from the satellite images contains an unknown mixture of both old-growth forests of high value from a conservation perspective (from the demanding species' perspective), and old managed managed forests. An important further development is therefore needed to increase the thematic resolution in oldest age class, for example by using ancillary proxy data such as distance to roads, slope and ownership structure. Another issue is to what extent does remote sensing capture the quality of middle-aged forest (thinned or not; vertical layering, Åberg et al. 2003) and the amount of variable retention after clear-felling.
- the assumption that all land was forest and that only loss has occurred, could forest land have been gained from drained peatland?
- the gap for species requiring habitats that can be satisfied in the cultural/urban landscape outside the forest mask, which was underestimated (Mikusinski et al. submitted) may be overestimated
- the need for rehabilitation and restoration for improved quality of protected areas. Some examples are lack of fire due to the effective fire protection with the consequence that some pine forest need to burned , thereby reducing the amount of spruce in old-growth stands, riparian forests lack dead wood on the ground as well as in the water
- the use of topoindex modelling need to be evaluated. The validation is, however, difficult because most wet sites have already been affected by draining and ditching. Apparent overestimates of the present amount of wet forest should therefore be interpreted with caution
- the non-linear threshold responses of populations to habitat loss need further elaboration; variation among taxa and different forest disturbance regimes forest types is not even close to being fully understood for more than a handfull studies (Angelstam and Breuss 2003). Similarly, the differences between thresholds for habitat occupancy, population viability, ecosystem function and integrity are not well studied.
- the amount of natural forest structures satisfied by appropriate forestry methods (Angelstam and Andersson 2001)

6.3. Assessment of functional connectivity – the results

Any regional gap analysis based on area alone is likely to overestimate the amount of functional habitat networks (Angelstam et al. 2003 b). If for example a given amount of habitat is subdivided into many small and isolated patches, the function of the habitat network will be different as opposed to if the patches are large and close to other (Scott et al. 2002). Our analyses suggest that, depending on the species, only 10-80 % of the area considered as an assett for the most demanding species of different forest types can actually be considered as functional.

A major determinant of such landscape patterns is the ownership patterns and the associated past and present management regimes of the landscape. With digital ownership maps any variation among ownership categories could be understood. Another use of ownership maps would be to find opportunities for setting priorities not only for establishing conservation areas, but also for habitat rehabilition and even re-creation through easements, creation of protected areas or restoration management.

The analyses of focal species within and among particular forest types strongly suggest that each "green infrastructure" should be considered separately and that the fulfilment of the forest policy actually would require careful tactical planning. The HSI-models clearly illustrate the need for concentrating the protected areas to clusters where populations of species can survive in the long term, rather than establishing conservation areas across the whole landscape. We thus argue that the HSI-model maps can be most useful when setting priorities both locally and regionally. A good example is the rule in forest certification stating that 5 % of the forest area should be set aside as conservation areas. While the tradition is that the 5 % are equally distributed among the different landscape ecological plans, so that in some areas areas forests with high conservation value can not be set aside, in other areas fairly ordinary forests are set aside.

The HSI-modelling results thus suggest that one could question whether or not the so called “Swedish model” with general consideration and few reserves (Angelstam 2003) is the most optimal for all forest environments when trying to achieve a functional network of habitats. A triad approach with effective conservation area networks, multiple use management and intensive forest management in the vicinity of the mills appear more effective. Setting aside forest in landscape plans could nevertheless be useful in the short-term by satisfying the market demands as defined in certification standards.

6.4. Assessment of functional connectivity – the procedure and its validation

As well as the regional gap analysis is sensitive to different parameter values, also the habitat modelling has several sources of uncertainty. The stresses the need for thorough validation of the models by independent data collection (Angelstam et al. 2003 b). This project made new kinds of remote sensing available the land cover classes had improved thematic resolution. Different classification methods of remote sensing data may provide different quantitative and qualitative description of forest classes. Since the county administrative boards use also in their planning the so-called kNN classification (Mats Nilsson, Olle Hagner pers. comm.). Hence, there is a need to examine the sensitivity of our habitat modelling analysis to potential differences between kNN-classification, pixelwise classification with maximal likelihood as well as other classifications. The GIS analyses approaches also provide sources of variation in the final absolute amount of habitat, which is proposed as functional. Finally, the parameters for HSI models need to be refined (for details see also Angelstam et al. 2003 b). The non-linear threshold responses of populations to habitat loss need further elaboration; variation among taxa and different forest disturbance regimes forest types is understood only for a handfull of species (Angelstam and Breuss 2003). Similarly, the differences between thresholds for habitat occupancy, population viability, ecosystem function and integrity are not well studied. Finally, validation is of the models are needed, for example by making field studies of the presence of the target species in relation to the modelling results.

6.5. Temporal trends in connectivity

The analysis of the satellite data from the late 1980s and 1990s show that the area of large old forest patches defined as more than 500 ha large is very low compared with naturally dynamic landscapes (Yaroshenko et al. 2001, Aksenov et al. 2002). This can be interpreted as a past and present general decline for area-demanding species. Similarly, one could compare HSI-models for different focal species during different time periods. We argue that such analyses are of great importance to improve the awareness about the status and trends of forest biodiversity. These past losses of larger areas of old forest interior put the considerable efforts by land managers to improve the situation for specialised species by means of variable retention and landscape planning in perspective. Thus, the total sum of these opposing trends (deterioating old forest forest and improved young forest) must be interpreted not as a general improvement, but rather a decreased rate of decline in the favourable conditions for specialised species (Angelstam 2002).

6.6. How useful are satellite images in the mapping of high conservation value forests?

The classification of forest land into different forest types based on for example age class, tree species composition and stand structure based on satellite images is not perfect (Holmgren and Thuresson 1998, Kilpeläinen and Tokola 1999). In the case of forest with a high conservation value, we often deal with characteristics that are particularly difficult to be detected by remote sensing data in the form of satellite images. Two good examples are old-growth forest stands and stands with a high amount of dead wood. Correction of area estimates of different forest types using independent data makes the estimates unbiased, but there is still a stochastic error (Hagner 1989, Nilsson 1997). Integrating over larger areas, such as in the ecoregional gap analysis, this error becomes smaller (cf. Reese and Nilsson 1999, Katila and Tomppo 2001). However, when doing spatially explicit analyses, such as in the HSI-models, the pixelwise error is important also in analyses covering large areas. Another problem is that the confusion matrices can not be used to correct areas analysed with neighbourhood analysis used in the HSI-models. Thus, the total class areas are biased. This stresses further the need to validate models in the field.

Another problem is the mapping of stands with an admixture or dominance of deciduous tree species. Deciduous trees have been identified as particularly valuable for the presence and maintenance of species (Berg et al. 1994). In boreal forest deciduous trees are regularly mixed with conifers, and an estimation of the volume of deciduous trees in such forest may not be very precise (Katila and Tomppo 2001). Since our study area is located in regions with a generally very low proportion of deciduous tree species in the forest, the stand age and tree species composition from the forest companies' forest stand data used to calibrate area estimates was poorly represented by stands having a high proportion of deciduous trees. Therefore, the relative uncertainty of estimates was higher for deciduous trees than for conifers.

It has been demonstrated that in Swedish boreal landscapes stands dominated by deciduous trees are often concentrated around present and historic human settlements (Mikusinski et al., submitted). In central Sweden, Mikusinski and Angelstam (1999) found a decline in deciduous component from 15% to less than 2% with a distance to agricultural farms. The decline was especially dramatic in respect to trees and stand older that 110 years. As we pointed out in section 4.4.1, the amount of the deciduous component used in our study may therefore be locally seriously underestimated because the deciduous cover has only been described in areas under the "forest mask of the topographic map. In other words, groups of old deciduous trees, tree alleys, narrow strips of deciduous stands at the forest edge, and recent succession on former agricultural land have been disregarded in our study. An analysis made with another satellite-based data covering the entire landscape showed that deciduous trees and stands located outside "forest mask" can make up a substantial part of its total amount in the landscape (Mikusinski et al., submitted). We suspect that the error in the estimation of deciduous component caused by the above insufficiency of the presently used data would increase with declining forest cover. Therefore, we argue that future planning and management of deciduous forest shall aim at including data that cover the entire landscape.

6.7. Implementing conservation plans – a complex decision-making process

Making decisions about which forest areas should be set aside within conservation area networks in the form of national parks and nature reserves, as well as the rehabilitation and restoration of habitats is a complex activity. This report focuses on components and arguments based on conservation biology and landscape ecology. Examples of data sets, which were used this application project are:

- The history of landscape change measured as loss of forest area
- The regional gap situation with respect to representativity of different forest types
- Habitat Suitability Index models for specialised species and guilds
- The threat to existing forests with potentially high conservation value (Woodland Key Habitats and larger areas of old forest)

Altough it would be important to do so, we have not estimated future changes in the landscape (i.e., future distribution and abundance of deciduous forest patches).

Other factors not related to natural sciences, which also ought to be studied, include:

- The actors' understanding, willingness and ability to implement policies (cf. National Audit 1999)
- Conflicts within the forest biodiversity policies as well as other environmental goals (e.g., carbon sinks)
- Trade-offs with other uses of forests and their biodiversity

6.8. How the conservation tools could be used

Satellite images describing different forest types, Natura 2000 areas and Woodland Key Habitat databases are data, which can be used to map high conservation value forests of different types. Regional gap analysis and HSI-modelling are two analytic conservation planning tools. The former is strategic in nature and paints the big picture among regions with the area under study, such as the two counties in this study. The latter should be viewed as a decision support system to guide the tactical planning for management by creating protected areas, management and restoration of habitats.

We envision that, for example when contacting landowners, the actual operational work to identify important tracts using habitat models for different focal forest types should include the following steps:

- First, the ecology and dynamics of different forest disturbance regimes should be explained, and related to the local and regional land use history.
- Second, the contents of forest and other policies should be explained. This means that we need to maintain populations in the long-term and not only individuals in the short term.
- Third, the recently appearing insights from conservation biology and landscape ecology concerning critical thresholds levels for the amount of forest structures (e.g. dead wood, large and old trees, certain forest stand age classes and patch sizes) should be explained.
- Fourth, the results from the regional gap analysis should be presented to provide the big picture regarding the loss of forest on different types and of age classes in different regions.
- Fifth, the county-wide maps with the results from the HSI model showing the location of important forest tracts for different focal habitats being identified as having gaps in the regional gap analyses should be introduced by using small-scale maps (e.g., 1:250,000). It is, however, vital that the probalistic nature of the HSI-model maps is fully understood. Therefore, when presented the models should be presented using graduated colours and not "black and white" images suggest sharp borders between high and low habitat suitability.

- Sixth, forest owner's stand maps on paper or in a GIS (e.g. with a 1:10,000 scale) should be used to discuss the role of stands within forest tracts with potentially high conservation value.

6.9. Strategic restoration planning

In the same way as HSI-models can be used to guide the set-aside of existing forest of high conservation value to protected areas, these models can be used to indicate localities where restoration would efficiently improve the future functional connectivity of forest with high conservation value. This also requires the development of user-friendly models to present forecasts of the future forest landscape.

6.10. Analyses of threats to the existing green infrastructure

Throughout this report our point of departure is the Swedish forest policy with its focus on the maintenance of viable populations of all naturally occurring species. Our approach is to use the status of the habitat structures used by these species as a proxy. The analyses of the effects of logging and protection, respectively, of Woodland Key Habitats (WKH) suggest that the conservation status cannot be considered as completely favourable. We see a need for making more detailed analyses of how WKHs are affected by logging in the vicinity of them. It should also be noted that the control inventory of WKH stands suggests that only about a fifth (20 %) of forest stands with the quality of a WKH have been found. An important issue is to know what happens to such still unidentified stands with high conservation value.

However, assessing biodiversity is more than securing individual habitat patches (Larsson et al. 2001, Angelstam et al. 2003). In this section we focus on the processes that affect the future conservation status, or functionality, of the existing habitat structures and their renewal. A first important factor to take into consideration is the present or future threats to the target forest types of the existing green infrastructure (e.g., forest being located close to the road network). The simple reason is that these forests are the most accessible ones, and therefore the ones most likely to be logged. The anthropogenic infrastructure may also pose indirect threats to the green infrastructure. Areas with high conservation values located close to roads may be subject to intensive human disturbance through recreational or other activities. Road network with intense traffic may also create barriers that for certain species affect negatively the functional connectivity of habitat patches. On the other hand, a long distance to road network may be good indicator of forest quality (remote areas are usually much less affected by human action and remind more of the primeval stage).

The analyses of satellite images from the 1980s and 1990s in Hälsingland and Dalarna showed the remaining amount of old forest interior was generally higher where the history short than where is was short. In the Hälsingland scene only 2 % of forest land was located in patches of forest interiors that are > 500 ha while in Dalarna scene was 11 %. Unless these larger tracts of forests area protected we suspect that the higher figure in Dalarna will continue to decline.

6.11. Cultural woodland

Forest biodiversity is not only found in forest. Clearing, grazing and cultivation of forested land, a major impact on forests for millennia, has caused a dramatic reduction and fragmentation of the once naturally dynamic primeval forests (Mayer 1984, Hannah et al. 1994). Nevertheless, in some regions, forest biodiversity has to some extent been rescued by management methods practiced in the old cultural landscape (Tucker and Evans 1997, Kirby and Watkins 1998). To maintain summer and winter fodder for cows, sheep and other domestic animals, land was managed using fire, mowing, clearing, tree and water management. This range of cultural disturbances often resulted in forest biodiversity being maintained because of the presence of large and special trees in a landscape dominated by grazing and/or agriculture (e.g. Tucker and Evans 1997, Kirby and Watkins 1998). Today such habitats usually remain as small isolated patches in a managed matrix. Nevetheless in some parts of Europe the old management regimes are still in use. This applies to remote valleys in mountainous areas, as well as in regions, which have not yet been reached by the agricultural revolution with intensive management. The ancient practice of pollarding and lopping whereby branches of trees are cut but the tree is not, does maintain large trees that are growing slowly. Coarse woody debris on the ground was often limited but dead wood was available in the crowns of large trees, which were left to shade the ground. As a consequence suitable substrate both on the outside of the trees, as well as inside if hollow, will provide habitat for many forest species ranging from shade-intolerant vascular plants, lichens and insects to large birds (Mikusinski and Angelstam 1998, Nilsson et al. 2001).

However, for technical reasons we have not been able to include the forest at the edge between forest and agricultural land. To somehow correct for the underestimation of the deciduous component in forest/field edges the area of forest/field edges in each region could be used (see Figure 26).

6.12. How many local tracts are needed?

In this report we present an example of how systematic studies of habitat loss thresholds for of focal species can be used for assessing the functionality of habitat networks. The different steps are: 1) carefully select a suite of species representing each land cover type; 2) use quantitative targets based on the minimum habitat requirements defined by extinction thresholds of the focal species; 3) make regional gap analysis for the different land cover types; 4) use habitat modelling using occurrence thresholds at multiple scales to build spatially explicit maps describing the probability that existing habitat patches really contribute to the functional connectivity of that theme in the landscape. The latter is important, since gap analyses alone neglect aspects like the quality, size, duration and configuration of land cover patches, and therefore overestimate the amount of functional habitats. The presence of thresholds at different scales suggests that the conservation management should be planned in a spatially explicit way.

How large is a landscape? Using 15 species of specialised birds Angelstam et al. (2003a) estimated the size of an area with ideal habitat that would be able to host 100 females of a species over long time to about 50,000 ha. With a size of over 5,000,000 ha and 6 ecoregions the Dalarna/Gävleborg region would thus have approximately 15-20 “landscapes” in each ecoregion.

Because the history of research on habitat thresholds is very recent, the empirical knowledge is limited. This applies in particular to extinction thresholds describing how large and many tracts of habitat are needed to maintain viable populations. Additionally, the dynamics of the landscape has to be included. A species using a 20-year period in a succession of 100 years there need an area, which is at least five time as large for long-term presence compared with a being present for the nearest decade. For potential focal bird species Angelstam et al. (2003 a) estimated that with the minimum occurrence thresholds at multiple scales the minimum area needed for 100 females was 250,000 ha for a dynamic managed landscape.

However, we do not know how many local tracts are needed within, say, an ecoregion to maintain viable populations. Assuming that viable populations would need to encompass an effective population of 500 females (Meffe and Carroll 1994), the area needed for viable populations would exceed 1,000,000 ha. With an average size of the local forest companies' ecological landscape plans ranging from 10,000 to 30,000 ha, this would mean that about 50 landscape ought to be included. This corresponds to the size of large ecoregions in the Dalarna-Gävleborg region. For species with large area requirements such as raptors and large carnivores this means that the appropriate management unit would be the whole of Sweden.

6.13. Bridging the gap between science and practise

From the scientists' point of view the wRESEx project has and will be an excellent and unique opportunity to implement landscape ecological models in practise. It has also provided an opportunity to learn about problems and possibilities concerning policy implementation. The large number of components involved and the complicated chain of events has, however, relied on an efficient leadership.

From the managers' point of view a vegetation description with complete cover of the region has been achieved in this research project through application of ecological science. For the first time, all parties in the county concerned are presented with a basis to jointly draw up a strategy for nature conservation. The users who participated in the project have clearly improved their competence in remote sensing, data quality assurance, interdisciplinary work and use of tools for landscape ecological analyses.

The Swedish environmental agency has requested all county administrative boards to work out nature conservation strategies till 2004. At the same time The Swedish environmental agency works on a national strategy. The wRESEx-project, part C, gives the county administrative boards of Dalarna and Gävleborg extraordinary good bases to work out a nature conservation strategy.

The 8th of April 2003 a seminar was arranged for conservationists and directors at the county administrative boards of Dalarna and Gävleborg where the results from part C was presented by researchers and user participants and afterwards there was an work shop. Below we summarise reflections from the workshop and other discussions among users.

- The regional gap analysis confirmed previous analyses made both nationally and regionally, and did therefore not provide much additional guidance for the operational conservation planning. To improve the regional resolution in the gap analysis the topoindex classification of different forest site type need to be validated. Based on the satellite images there is more old forest in the inland areas than close to the coast, where the history of forest use is longer. However, we consider the satellite image's ability to identify old forest too poor and comparisons with threshold values too uncertain to claim that there is a surplus of old forest. On the other hand the high amount of old forest suggest that to build functional networks of conservation areas, these should be concentrated to landscapes where conservation efforts have the best chance to be successful in the long term. Finally, rather than comparing today's amount of old forest with thresholds, we argue that the estimated base lines for the amount of old forest in naturally dynamic landscapes should be used to understand the conservation status of today's landscapes.

- Spatially explicit habitat models, however, is a good approach to use the concept of connectivity for evaluting different types of habitats and thus be used to derive guidelines as to where to locate protected areas. The county administrative board has the latest years made nature inventories in order to find forest objects to protect which is a step to full fill the environmental objective sustainable forests. There is currently a bank of forest objects, which have been nature assessed and at the stand level have acceptable to very high conservation values. Further there are objects which still are not visited in field. Might the identification of important forest tracts using habitat suitability modelling serve as a strategic tool in the decision making process, when one has to prioritise? Though we at the moment are not absolutely sure how to interpret the results from the spatial analyses; the tracts from habitat suitability modelling provide additional and important new information. However, validation in field, measuring occurrence of the species populations is of course urgent. Despite the uncertainty we have the intention to use the habitat suitability modelling when planning the network of protected areas. It should, however, be underlined that habitat suitability modelling is one tool of several others, such as the occurrence of threatened species (which might differ in their ecology from the umbrella species) and other values as recreation. Finally, the habitat suitability models highlight that different stakeholders as county administrative boards, National Boards of Forestry, FSC-certified forest companies, private landowners and NGOs must co-operate on the conservation issues. We knew that before, but now we have the tool to convince others.

- The county administrative boards have the obligation to explain and inform why the state buys land and establishes nature reserves. We think that the wRESEx-project part C has given us very useful presentation materials and possibilities to inform about the state of the forests in our counties and about nature conservation.

7. Acknowledgements

This project could not have been performed without the active and generous support of both the large land owners who provided their forest data (forest management data bases and Woodland Key Habitat data from StoraEnso, Sveaskog, Korsnäs, Västerås stift), and the National Board of Forestry in Dalarna and Gävleborg.

We also thank our colleagues Tommy Ek, Mats Niklasson, Colby Loucks, Kerstin Nordström, Russell Graham and Fiona Schmiegelow as well our our students Mikael Djupström, Peter Ekelund, Gunn-Mari Fransson, Cecilia Journath-Pettersson, Crister Lind, Micheal Manton, Jean Niyongabo, Merle Plassmann, Ylva Schlüter, Annika Sohlman-Wiessing, Kristoffer Stighäll and Bettina Wagner for detailed and constructive comments. Several important points needing clarification have also been raised during the senior author's presentations of parts or the content in this report at seminars held in Tartu (Ülo Mander), Bratislava (Marcus Walsh, Szabolc Nagy), Bialowieza (Petri Heinonen), Washington DC (Hans Djurberg, Bryan Lee), Brussels (Alan Belward, Stefan Leiner), Riga (Otto Zvagins, Normunds Prieditis, Maris Strazds, Maris Laivins, Martins Lukins), Tukums (Signe Rotberga) and Kaunas (Marius Lazdinis, Silvija Saudyte, Gediminas Brazaitis).

Financial support was provided by Mistra, the Swedish University of Agricultural Sciences, and WWF.

8. References

Åberg, J., Swenson, J. E. and Angelstam, P. 2003. The habitat requirements of hazel grouse (Bonasa bonasia) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. - Forest Ecology and Management 175: 437-444.

Agee, J. K. 1993a. Fire and weather disturbances in terrestrial ecosystems of the eastern Cascades. - Gen. Tech. Rep. PNW-320. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland,OR, U.S. 52 pp.

Agee, J. K. 1993b. Fire ecology of Pacific Northwest forests. - Island Press, Washington DC, 493 pp.

Agee, J.K. 1999a. Fire effects on landscape fragmentation in interior west forests. - In: Rochelle, J.A., Lehmann, L.A., Wisniewski, J. Forest fragmentation - wildlife and management implications. Brill, Leiden, pp. 43-60.

Agee, J. K. 1999b. A coarse-filter strategy. - Forum for Applied Research and Public Policy 14 (1): 15-19.

Amcoff, M. and Eriksson, P. 1996. Occurrence of three-toed woodpecker Picoides tridactylus at the scales of forest stand and landscape. - Ornis Svecica 6: 107-119.

Andersson, D. 2000. Grandominerande lokaler med ringlav i Norrbotten. - Institutionen för skoglig vegetationsekologi. SLU. (Examination project supervised by Per Linder)

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

Angelstam, P. 1998a. Towards a logic for assessing biodiversity in boreal forests. - In Bachmann, P. Köhl, M.and Päivinen, R. (eds.). Proceedings of the conference on the assessment of biodiversity for improved forest planning, held in Monte Verità, Switzerland. European Forest Institute Proceedings No. 18. Kluwer Academic Publishers, Netherlands, pp. 301-313.

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

Angelstam, P. 1999. Reference areas as a tool for sustaining forest biodiversity in managed landscapes. - Naturschutz report 16: 96-121. Landesanstalt für Umweltschutz, Thuringia, Germany.

Angelstam, P. 2002. Reconciling land management with natural disturbance regimes for the maintenance of forest biodiversity in Europe. - In: Bissonette, J. and Storch, I. (eds.), Landscape ecology and resource management: making the match, Island Press, pp 193-226.

Angelstam, P. 2003. Forest biodiversity management - the Swedish model. - In: Lindenmayer, D. B., Franklin, J.F. (eds.) Towards Forest Sustainability, CSIRO Publishing, Canberra, and Island Press, Washington, pp. 143-166.

Angelstam, P. and Andersson, L. 1997. I vilken omfattning behöver arealen skyddad skog i Sverige utökas för att biologisk mångfald skall bevaras? - SOU 1997:98, Bilaga 4, 75+ 71 sidor.

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

Angelstam, P. and Arnold, G.. 1993. Contrasting roles of remnants in old and newly cleared landscapes - lessons from Scandinavia and Australia for restoration ecologists. - In: Reconstruction of fragmented ecosystems: global and regional perspectives. Saunders, D. A., Hobbs, R. J. and Ehrlich, P. (eds). Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia. pp. 109-125.

Angelstam, P. and Breuss, M. (eds.) 2001: Critical habitat thresholds and monitoring tools for the practical assessment of forest biodiversity in boreal forest. - Report to MISTRA. Available at http://iufro.boku.ac.at/iufro/iufronet/d8/hp80206.htm
Angelstam, P. and Breuss, M. (eds.) 2003: Targets and tools for the maintenance of forest biodiversity. - Ecological Bulletins 51 in press.
Angelstam, P., Breuss, M. and Mikusinski, G. 2001. Toward the assessment of forest biodiversity of forest management units - a European perspective. - In: Franc, A., Laroussinie, O. and Karjalainen, T. (eds.). Criteria and indicators for sustainable forest management at the forest management unit level. European Forest Institute Proceedings 38:59-74. Gummerus printing, Saarijärvi, Finland.
Angelstam, P., Bütler, R., Lazdinis, M., Mikusinski, G. and Roberge, J. M. 2003b. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation – dead wood as an example. - Annales Zoologici Fennici 41 in press
Angelstam, P. and Mikusinski, G. 1999: Strategier för skydd av skog i Värmland - en pilotstudie baserad på nyckelbiotopsinventeringen. - Länsstyrelsen i Värmland. Rapport 1999: 16. (In Swedish)
Angelstam, P. and Pettersson, B. 1997. Principles of present Swedish forest biodiversity management. - Ecological Bulletins 46: 191-203.
Angelstam, P., Roberge, J.M., Lõhmus, A., Bergmanis, M., Brazaitis, G., Breuss, M., Edenius, L., Kosinski, Z., Kurlavicius, P., Larmanis, V., Lukins, M., Mikusinski, G., Racinskis, E., Strazds, M. & Tryjanowski, P. 2003a. Habitat suitability index modelling as a tool for landscape-scale conservation – a review of parameters for focal forest birds. - Ecological Bulletins 51 in press.
Angelstam, P., Rosenberg, P. and Rülcker, C. 1993. Aldrig, sällan, ibland, ofta. - Skog och forskning 93(1): 34-41. (In Swedish)
Anonymous. 1991. Berggrundskarta över Kopparbergs län, 1:250 000. - Sveriges Geologiska Undersökning Ser. Ah nr 18.
Anonymous. 1999. Naturvårdsanalys av skogarna i Dalarna-Gävleborg. - Skogsvårdsstyrelsen i Dalarna-Gävleborg i samarbete med länsstyrelserna i Dalarna och Gävleborg.
Arnborg, T. 1990. Forest types of northern Sweden. - Vegetatio 90: 1-13.
Axelsson, A. L., and L. Östlund. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. - Journal of Forest Ecology and Management 147: 109-122.
Axelsson, A-L, Östlund, L. & Hellberg, E. 2002. Changes in mixed deciduous forests of boreal Sweden 1866-1999 based on interpretation of historical records. - Landscape Ecology 17 (5): 403-418.
Aksenov, D., Dobrynin, D., Dubinin, M., Egorov, A., Isaev, A., Karpachevskiy, M., Laestadius, L., Potapov, P., Purekhovskiy, A., Turubanova, S., Yaroshenko, A. 2002. Atlas of Russia's intact forest landscapes. - Global Forest Watch Russia, Moscow. 184 pp.
Basset, Y., E. Charles, D. S. Hammond, and V. K. Brown. 2001. Short-term effects of canopy openness on insect herbivores in rain forest in Guyana. - Journal of Applied Ecology 38: 1045-1058.
Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests—distribution and habitat associations. Conservation Biology 8: 718–731.
Berger, J. 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. - Conservation Biology 11: 69-78.
Beven, K. J. and Kirkby, M. J. 1979. A physically based, variable contributing area model of basin hydrology. Hydrological Sciences - Bulletin des Sciences Hydrologiques 24: 43-69.

Bonn, A., and Schröder, B. 2001. Habitat models and their transfer for single and multi species groups: a case study of carabids in an alluvial forest. - Ecography 24: 483-496.
Brooks. R. P. 1997. Improving habitat suitability index models. - Wildlife Society Bulletin 25(1): 163-167.
Brunckhorst, D. J. 2000. Bioregional planning. Resource management beyond the new millenium. - Harwood Academic Publishers, Singapore.
Bütler, R., Angelstam, P. and Schlaepfer, R. 2003: Quantitative snag targets for the three-toed woodpecker, Picoides tridactylus. - Ecological Bulletins 51 in press.
Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (Dendrocopos leucotos). - Forest Ecology and Management 131: 215-221.
Carlson, A. and I. Stenberg. 1995. Vitryggig hackspett (Dendrocopos leucotos) - biotopval och sårbarhetsanalys. - Department of Wildlife Ecology, Report 27. Swedish University of Agricultural Sciences, Uppsala. (In Swedish).
Caro, T. M. and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. - Conservation Biology 13: 805-814.
Carroll, C., Noss, R. and Slauson K. 1998. The Klamath-Siskiyou ecoregion: case study for focal species analysis. - Wild Earth 1998/99:86-87.
Carroll, C., Noss, R. F. and Paquet, P. C. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. - Ecological Applications 11: 961-980.
Crosetto, M. and Tarantola, S. 2001. Uncertainty and sensitivity analysis: tools for GIS-based model implementation. - International Journal of Geographical Information Science 15(5): 415-437.
Drolet, B., Desrochers, A. and Fortin, M.-J. 1999. Effects of landscape structure on nesting songbird distribution in a harvested boreal forest. - Condor 101: 699-704.
Dyrenkov S. A. 1984. Structure and dynamics of taiga spruce forest. - Leningrad, Nauka Publ. 174 pp. (in Russian)
Eberhart, K. E. and Woodard, P. M. 1987. Distribution of residual vegetation associated with large fires in Alberta. - Canadian Journal of Forest Research 17:1207-1212.
Elliott, C. and Schlaepfer, R. 2001: Understanding forest certification using the advocacy coalition framework. - Forest Policy and Economics 2: 257–266.
Engelmark, O. 1999. Boreal forest disturbances. - In: Walker, L.R. (ed.), Ecosystems of Disturbed Ground: Ecosystems of the World, Vol. 16. Elsevier, Amsterdam, pp. 161–186.
Engelmark, O. and Hytteborn, H. 1999. Coniferous forests. - Acta Phytogeographica Suecica 84:55-74.
Eriksson , Hedlund, L. Johansson, S. and Nordström, K. 1996. Markens och det ytliga grundvattnets försurningskänslighet i Kopparbergs län. - Länsstyrelsen Dalarna Miljövårdsenheten.Rapport nr 1996:3 Länsstyrelsen Dalarna.
Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. – Biological Conservation 68: 19-28.
Esseen, P .A., Ehnström, B., Ericson, L. and Sjöberg, K. 1997. Boreal forests. - Ecological Bulletins 46: 16-47.
Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. - Journal of Wildlife Management 61(3): 603-610.
Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? - Ecological Modelling 105: 273–292.
Fahrig, L. 2001. How much habitat is enough? - Biological Conservation 100: 65-74.
Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. - Ecological Applications 12(2): 346-353.

Falinski, J. B. 1986. Vegetation dynamics in temperate lowland primeval forests. - Dr. W. Junk publishers. Dordrecht. 537 pp.
FAO. 2001. Global Forest Resources Assessment 2000: main report. - FAO Forestry Paper No. 140. Rome (also available at www.fao.org/forestry/fo/fra/main/index.jsp)
Fedorchuk V. N., M. L. Kuznetsova, A. A. Andreyeva and D. V. Moiseev. 1998. Forest reserve "Vepssky Les". - Forestry research. Saint-Petersburg, St.-P. Forestry Research Inst. 208 p. (in Russian)
Fleishman, E., Blair, R. B. and Murphy, D. D. 2001. Empirical validation of a method for umbrella species selection. - Ecological Applications 11: 1489-1501.
Fleishman, E., Murphy, D. D. and Brussard, P. F. 2000. A new method for selection of umbrella species for conservation planning. - Ecological Applications 10(2): 569-579.
Forman, R. T. T. 1995. Land mosaics - the ecology of landscapes and regions. - Cambridge University Press. Pp 632.
Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? - Ecological Applications 3: 202-205.
Furyaev, V. V. 1996. Pyrological regimes and dynamic of the southern taiga forests in Siberia. - In: Goldammer, J. and V.V. Furyaev (eds.). Fire in ecosystems of boreal Eurasia. Kluwer Academic Publishers, Dordrecht, pp 168-185.
Furyaev, V. V. and D. M. Kireev. 1979. A landscape approach in the study of post-fire forest dynamics. Nauka. Novosibirsk. (In Russian)
Gandhi, K,J.K., Spence, J.R., Langor, D.W., Morgantini, L.E. 2002. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). – Biological Conservation 102: 131-141.
Gardiner B. A. and C. P. Quine. 2000 Management of forests to reduce the risk of abiotic damage - a review with particular reference to the effects of strong. - In: Sannikov, S. N. and J.G. Goldammer. 1996. Fire ecology of pine forests of northern Eurasia. Fire in ecosystems of boreal Eurasia. Goldammer, J. & V. V. Furyaev (eds.). Kluwer Academic Publishers, Dordrecht, pp. 151-167.
Gärdenfors, U. (ed.) 2000. The 2000 Red List of Swedish species. - Artdatabanken, Uppsala. 397 pp.
Gärdenfors, U., Aasgaard, K. and Biström, O. 2002. Hundraelva nordiska evertebrater. – Nordiska ministerrådet, Köpenhamn och Artdatabanken, Uppsala. 288 pp.
Gärdenfors, U., Hilton-Taylor, C., Mace, G., and Rodríguez, J.P. 2001. The application of IUCN Red List Criteria at regional levels. - Conservation Biology 15: 1206-1212.
Götmark, F. and Nilsson, C. 1992. Criteria used for protection of natural areas in Sweden 1909-1986. - Conservation Biology 6: 220-231.
Granström, A. 1993. Spatial and temporal variation in lightning ignitions in Sweden. - Journal of Vegetation Science 4: 737-744.
Goodchild, M. F. and Case, T. J. 2001. Introduction. - In: C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case (eds.) Spatial Uncertainty in Ecology: Implications for Remote Sensing and GIS Applications, Springer-Verlag, pp. 3-10.
Hagner, O., 1989. Computer-aided Forest Mapping and Estimation of Stand Characteristics Using Satellite Remote Sensing. Work Report, Department of Biometry and Forest Management, Swedish University of Agricultural Science, Umeå, Sweden, 11 pp.
Hannah, L., Carr, J.L. and Lankerani, A.. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. - Biodiversity and Conservation 4: 128-155.
Hansen, A. J., Garman, S. L. Marks, B. and Urban, D. L. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. - Ecological Applications 3: 481-496.
Hansson, L. 2001. Key habitats in Swedish managed forests. - Scandinavian Journal of Forest Research Supplement 3: 52-61.

Hess, G. R., and King, T. J. 2002. Planning open spaces for wildlife. I. Selecting focal species using a Delphi survey approach. - Landscape and Urban Planning 58: 25-40.
Hjeljord, O., Wegge, P., Rolstad, J., Ivanova, M., Beshkarev, A.B. 2000. Spring-summer movements of male capercaillie Tetrao urogallus: a test of the landscape mosaic hypothesis. - Wildlife Biology 6(4): 251-256.
Holmgren, P. and Thuresson, T., 1998. Satellite remote sensing for forestry planning - a review. - Scand. J. For. Res. 13, pp. 90–110.
Hunsaker, C. T., Goodchild M. F., Friedl, M. A. and Case T. J. 2001. Spatial uncertainty in ecology: implications for remote rensing and GIS applications. - Springer-Verlag.
Hunter, M. L. 1990. Wildlife, forests and forestry. Principles of managing forests for biological diversity. Prentice-Hall. New Jersey. 370 pp.
Hunter, M, L. (ed.) 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press. 698 pp.
Iacobelli, T., Kavanagh, K. and Rowe, S. 1995. A protected areas gap analysis methodology. - WWF Canada. Toronto. Canada. 68 pp.
Ihse, M. 1995. Swedish agricultural landscapes - patterns and changes during the last 50 years, studied by aerial photos. - Landscape and urban planning 33: 21-37.
Jahn, G. 1991. Temperate deciduous forests of Europe. - In: Temperate deciduous forests. Röhrig, E. and B. Ulrich (eds.). 1991. Elsevier. pp. 377-402.
Jansson G. and Andrén H. In press. Habitat composition and bird diversity in managed boreal forests. - Scandinavian Journal of Forest Research.
Jansson, G. and Angelstam, P. 1999. Thresholds of landscape composition for the presence of the long-tailed tit in a boreal landscape. - Landscape Ecology 14: 283-290.
Jasinski, K. and Angelstam, P. 2002. Long-term differences in the dynamics within a natural forest landscape—consequences for management. - Forest Ecology and Management 161: 1-11.
Jennings, M.D. 2000. Gap analysis: concepts, methods, and recent results. - Landscape Ecology 15:5-20.
Johnson, E. A. 1992. Fire and vegetation dynamics; studies from the North American boreal forest. - Cambridge University Press. Cambridge. 129 pp.
Johnson, E. A. and van Wagner, C. E. 1985. The theory and use of two fire history models. – Canadian J. Forest Research 15: 214–220.
Karström M. 1992. Steget före - en presentation. - Svensk Botanisk Tidskrift 86: 103-114.
Katila, M. and Tomppo, E. 2001. Selecting estimation parameters for the Finnish multisource National Forest Inventory. Remote Sensing of Environment 76: 16-32.
Kerr, J. T. 1997. Species richness, endemism, and the choice of areas for conservation. - Conservation Biology 11: 1094-1100.
Kilpeläinen, P. and Tokola, T., 1999. Gain to be achieved from stand delineation in Landsat TM image-based estimates of stand volume. - Forest Ecology and Management 124, pp. 105–111.
Kirby, K.J. and C. Watkins. 1998. The ecological history of European forests. - CAB International, Wallingford, UK. 373 pp.
Kohm, K. A. and Franklin, J. F. 1997. Creating a forestry for the 21st century. - Island Press, Covelo, California.
Korpilahti, E. and Kuuluvainen, T. 2002. Disturbance dynamics in boreal forests: defining the ecological basis of restoration and management of biodiversity. - Silva Fennica 36(1). 447 pp.
Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. - Annales Zoologici Fennici 31:35-51.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. - Silva Fennica 36(1): 97-125.
Lambeck, R. J. 1997. Focal species define landscape requirements for nature conservation. - Conservation Biology 11: 849-856.
Lambeck, R. J. 1999. Landscape planning for biodiversity conservation in agricultural regions: a case study from the Wheatbelt of Western Australia. - Biodiversity Technical paper 2. Environment Australia, Canberra, Australia.
Larsson, S. and Danell, K. 2001. Science and management of boreal forest biodiversity. - Scandinavian Journal of Forest Research, Supplement 3. 123 pp.
Larsson, T.-B., Angelstam, P., Balent, G., Barbati, A., Bijlsma, R.-J., Boncina, A., Bradshaw, R., Bücking, W., Ciancio, O., Corona, P., Diaci, J., Dias, S., Ellenberg, H., Manuel Fernandes, F, Fernandez-Gonzalez, F., Ferris, R., Frank, G., Friis Møller, P., Giller, P.S., Gustafsson, L., Halbritter, K., Hall, S., Hansson, L., Innes, J., Jactel, H., Keannel Dobbertin, M., Klein, M., Marchetti, M., Mohren, F., Niemelä, P., O'Halloran, J., Rametsteiner, E., Rego, F., Scheidegger, C., Scotti, R., Sjöberg, K., Spanos, I., Spanos, K., Standovar, T., Svensson, L., Tømmerås, B.Å., Trakolis, D., Uuttera, J., VanDenMeerschaut, D., Vanderkerkhove, K., Walsh, P.M. and Watt, A.D. 2001. Biodiversity evaluation tools for European forests. - Ecological Bulletins 50. 236 pp.
Launer, A. E. and Murphy, D. D. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. - Biological Conservation 69: 145-153.
Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. - Nature 391:72-76.
Leibundgut, H. 1982. Europäische Urwälder der Bergstufe. - Verlag Paul Haupt, Bern, Stuttgart.
Leibundgut, H. 1993. Europeische Urwälder: wegweiser zur naturnahen Waldwirtschaft. - Verlag Paul Haupt, Bern, Stuttgart, Wien.
Liljelund, L.-E., Pettersson, B., Zackrisson, O. 1992. Skogsbruk och biologisk mångfald. - Svensk Botanisk Tidskrift 86(3): 227-232.
Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. - Island press, Washington, D.C.
Linder, P. and Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. - Biological Conservation 85: 9-19.
Lõhmus, A., Kohv, K., Palo, A. and Viilma, K. 2003. Loss of old-growth, and the minimum need for strictly protected forests in Estonia. - Ecological Bulletins 51 in press.
Lönnberg, E. 1927. Svenska fåglar. - A. Börtzells tryckeri AB, Stockholm.
Mackey, B.G., Mullen, I.C., Sims, R., Baldwin, K., Gallant, J., McKenney, D.W., 1999. Toward a spatial model of boreal forest ecosystems: the role of digital terrain analysis. In: Wilson, J., Gallant, J. (Eds.). Digital Terrain Analysis: Theory and Applications
Margules, C. R. and Pressey, R. L. 2000. Systematic conservation planning. - Nature 405: 243-253.
Mayer, H. 1984. Die Wälder Europas. - Gustav Fischer Verlag, Stuttgart. 691 pp. (In German)
McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. - Ecological Monographs 65(3): 235-260.
McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97: 130-140.
Meffe, G.K., Carroll, C.R. 1994. Principles of conservation biology. - Sinauer Associates, Inc. Publishers, Sunderland, Massachesetts, USA.

Mikusinski, G. and P. Angelstam. 1998. Economic geography, forest distribution, and woodpecker diversity in Central Europe. - Conservation Biology 12: 200-208.
Mikusinski, G. and Angelstam, P. 1999. Man and deciduous trees in boreal landscape. - In: Kovar P. [ed]: Nature and Culture in Landscape Ecology. Experience for the 3rd Millenium. The Karolinum Press, Prague, p. 220-224.
Mikusinski, G., Angelstam, P. and Sporrong, U. Manuscript. Distribution of deciduous forest and villages in Swedish forest landscapes. - Submitted Ambio.
Miller, B., R. Reading, J. Strittholt, C. Carroll, R. Noss, M. Soulé, O. Sánchez, J. Terborgh, D. Brightsmith, T. Cheeseman, and D. Foreman. 1998. Using focal species in the design of nature reserve networks. - Wild Earth 1998/99:81-92.
Mladenoff, D. J. and W. L. Baker (Eds.) 1999. Spatial Modeling of Forest Landscape Change: Approaches and Applications. - Cambridge University Press, 352 pp.
Moore, I. D., Grayson, R. B. and Ladson, A. R., 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. - Hydrological Processes5: 3-30.
Niklasson, M. and Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. - Ecology 81: 1484-1499.
Nikolov, N. and Helmisaari, H., 1992. Silvics of the circumpolar boreal forest tree species. - In: Shugart, H. H., Leemans, R., Bonan, G. B. A. (eds.) Systems Analysis of the Global Boreal Forest. Cambridge University Press, New York, pp. 13-84.
Nilsson, M., 1997. Estimation of Forest Variables Using Satellite Image Data and Air-borne Lidar. Silvestria 17, Swedish University of Agricultural Science, Umeå, Sweden.
Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., Ljungberg, H., Mikusinski, G. and Ranius, T. 2002: Densities of large living and dead trees in old-growth temperate and boreal forests. - Forest Ecology and Management 161: 189-204.
Nordic Council of Ministers. 1983. Representative types of nature in the Nordic countries. - Nordic Council of Ministers, Berlings, Arlöv. 60 pp + map.
Noss, R. F., O'Connell, M. A. and Murphy, D. D. 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. - Island Press, Washington, D.C.
Ohlson, M. and Tryterud, E. 1999. Long-term spruce forest continuity - a challenge for sustainable Scandinavian forestry. - Forest Ecology and Management 124: 27-34.
Oliver, C. D. and Larsen, B. C. 1996. Forest stand dynamics. - McGraw-Hill, New York. 518 pp.
Oliver, I., A. J. Beattie, and A. York. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. - Conservation Biology 12: 822-835.
Olsson, O. 1998. Through the eyes of a woodpecker: understanding habitat selection, territory quality and reproductive decisions from individual behaviour. - Doctoral thesis. Dept of Ecology, Lund University, Sweden.
Olsson, O., Nilsson, I. N., Nilsson, S. G., Pettersson, B., Stagen, A. and Wiktander, U. 1992. Habitat preferences of the lesser spotted woodpecker (Dendrocopos minor). - Ornis Fennica 69: 119-125.
Östlund, L., O. Zackrisson and A. L. Axelsson. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. - Canadian Journal of Forest Research 27: 1198-1206.
Pakkala, T., Hanski, I. and Tomppo, E. 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. - Silva Fennica 36: 279-288.
Pennanen, J. 2002. Forest age distribution under mixed-severity fire regimes - a simulation-based analysis for middle boreal Fennoscandia. Silva Fennica 36(1): 213-231.

Perrera, A. H., Euler, D. L. and Thompson, I. D. 2000. Ecology of a managed terrestrial landscape. Patterns and processes of forest landscapes in Ontario. - UBC Press, Vancouver. 336 pp.
Peterken, G. 1996. Natural woodland. Ecology and conservation in northern temperate regions. - Cambridge University Press, Cambridge. 522 pp.
Pickett, S. T. A. and White, P. S. 1985. The Ecology of Natural Disturbance and Patch Dynamics. - Academic Press, Inc. New York.
Pressey, R.L., S. Ferrier, T.C. Hager, C.A. Woods, S.L. Tully and K.M. Weinman. 1996. How well protected are the forests of north-eastern New South Wales? Analyses of forest environments in relation to formal protection measurements, land tenure, and vulnerability to clearing. - Forest Ecology and Management 85: 311-333.
Puumalainen, J., Angelstam, P., Banko, G., Brandt, J., Caldeira, M., Estreguil, C., Folving, S.,Garcia del Barrio, J. M., Keller, M., Kennedy, P., Köhl, M., Marchetti, M., Neville, P., Olsson, H., Parviainen, J., Pretzsch, H., Ravn, H. P., Ståhl, G., Tomppo, E., Uuttera, J., Watt, A., Winkler, B., Wrbka, T. 2002: Forest Biodiversity Assessment Approaches for Europe. - EUR Report 20423. Joint Resarch Centre, Ispra, European Commission, 128 pp.
Pyne, S. J. 1984. Introduction to wildland fire. - John Wiley and Sons, New York.
Quinn, P., Beven, P., Chevalier, P. and Planchon, O. 1991. The prediction of hillslope flow paths for distributed hydrological modelling using digital terrain models. - Hydrol. Processes 5: 59–79.
Quinn, P., Beven, K. and Lamb, R. 1995. The ln(a/tan B) index: how to calculate it and how to use is within the TOPMODEL framework. - Hydrological Processes 9: 161–182.
Quine, C.P., Humphrey, J.W., Purdy, K., Ray, D. 2002. An approach to predicting the potential forest composition and disturbance regime for a highly modified landscape: a pilot study of Strathdon in the Scottish Higlands. - Silva Fennica 36(1): 233-247.
Raab, B. and Vedin, H. (Editors) 1995. Climate, Lakes and Rivers. - The National Atlas of Sweden, SNA Förlag, Stockholm.
Reese, H., Nilsson, M. 1999. Using Landsat TM and NFI data to estimate wood volume, tree biomass and stand age in Dalarna. Working paper 53. Swedish university of agricultural sciences. Umeå. ISSN 1401-1204
Roberge. J. M. and Angelstam, P. 2003: Umbrella species as a tool for conservation: how strong is the evidence? - Conservation Biology (in press).
Rodhe, A., and Seibert, J. 1999. Wetland occurrence in relation to topography - a test of topographic indices as moisture indicators. - Agricultural and Forest Meteorology 98-99: 325-340.
Rolstad, J., and Wegge, P. 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. - Oecologia 72: 389-394.
Rönnbäck, I. 2003. Facilitating quality assessment in spatial epidemiological analysis. PhD thesis. Luleå University of Technology.
Rönnbäck, I. and Angelstam, P. Manuscript. Quality evaluation of regional gaps analysis concerning forest protection for biodiversity conservation. In: Rönnbäck, I. 2003. Facilitating quality assessment in spatial epidemiological analysis. PhD thesis. Luleå University of Technology.
Rülcker, C. P., Angelstam, P. and Rosenberg, P. 1994. Ecological forestry planning: a proposed model based on the natural landscape. - The Forestry Research Institute of Sweden. Report 8. (In Swedish with English summary)
Ryti, R. T. 1992. Effect of the focal taxon on the selection of nature reserves. - Ecological Applications 2: 404-410.

Sannikov, S. N. and J.G. Goldammer. 1996. Fire ecology of pine forests of northern Eurasia. - In: Fire in ecosystems of boreal Eurasia. Goldammer, J. & V. V. Furyaev (eds.). Kluwer Academic Publishers, Dordrecht, pp. 151-167.
SCB 2003. Statistical yearbook of Sweden 2003. - Statistiska Centralbyrån, SCB, Stockholm, Sweden.
Schimmel, J. 1993. Fire behavior, fuel succession and vegetation response to fire in Swedish boreal forest. - Dissertations in forest vegetation ecology 5. Swedish University of Agricultural Sciences, Umeå.
Scott, J.M., Heglund, P. J., Morrison, M., Raphael, M. G., Haufler, J. B. and Wall, B. (eds.). 2002. Predicting species occurrences: issues of scale and accuracy. - Island Press, Covello, CA, USA. 868 pp.
Scott, J. M., Tear, T. H., and Davis, F. W. (eds.) 1996. Gap Analysis; A landscape approach to biodiversity planning. - ASPRS Distribution Center. Annapolis Junction, MD.
Shafer, C. L. 1990. Nature reserves: island theory and conservation practice. - Smithsonian Institution Press, Washington.
Shugart, H. H., Leemans, R. and Bonan, G. B. 1992. A system analysis of the global boreal forests. - Cambridge University Press. Cambridge, 565 pp.
Siitonen, J. 2001: Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. - Ecological Bulletins 49: 11–41.
Sjöberg, K. and Ericsson, L. 1992. Forested and open wetland complexes. - In: Hansson. L. Ecological principles of landscape conservation. applications in temperate and boreal environments. Elsevier Applied Science. London and New York. Pp. 326-351.
Sklar F. H. and Hunsaker C. T. 2001. The use and uncertainties of spatial data for landscape models: an overview with examples from the Florida Everglades. - In: C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case (eds.). Spatial Uncertainty in Ecology: Implications for Remote Sensing and GIS Applications, Springer-Verlag, pp. 15-46.
Smith, D. M., B.C. Larson, M. J. Kelty and P. M. S. Ashton. 1997. The practise of silviculture: applied forest ecology. - John Wiley & Sons, Inc. New York.
SOF. 1990. Sveriges fåglar. 2:a upplagan. Stockholm.
SOU. 1992:76. Skogspolitiken inför 2000-talet. Huvudbetänkande 1990 års skogspolitiska kommitté. Allmänna förlaget, Stockholm.
SOU. 2000:52. Framtidens miljö – allas vårt ansvar. Slutbetänkande från miljömålskommittén. Fritzes offentliga publikationer, Stockholm.
Starfield, A., Smith, K.A. and Bleloch, A. L. 1994. How to model it. Problem solving for the computer age. Burgess Publishing, Edina, Minnesota. 206 pp.
Storch, I. 2000. Grouse. Status Survey and Conservation Action Plan 2000-2004. – IUCN, The World Conservation Union.
Storch, I. 2001. Capercaillie. BWP Update. - Journal of Birds of the Western Palearctic 3:1-24.
SUS 2001. 2002. Skogsvårdsstyrelsens utvärdering av skogspolitikens effekter. - Skogsstyrelsens Meddelande 2002:1.
Tarboton, D. G. 1997. A new method for the determination of flow directions and upslope areas in grid digital elevation models. - Water Resources Research. 33(2): 309-319.
Thomas, J.W. 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. - USDA Agr. Hdbk 553.
Tracy, C. R. and Brussard, P. F. 1994. Preserving biodiversity: species in landscapes. - Ecological Applications 4: 205-207.
Trzcinski, M. K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. - Ecological Applications 9(2): 586-593.

Tucker, G.M. and M.I. Evans. 1997. Habitats for birds in Europe. - BirdLife International, Cambridge.
Uliczka, H. and Angelstam, P. 1999. Occurrence of epiphytic lichens in relation to tree species and age in managed boreal forest. - Ecography 22: 396-405.
Uliczka, H. and Angelstam, P. 2000. Assessing conservation values of forest stands based on specialised lichens and birds. - Biological Conservation 95: 343-351.
Van Wagner, C. E. 1978. Age-class distribution and the forest fire-cycle. - Canadian J. Forest Research 8: 220–227.
Verner, J., Morrison, M.L. and Ralph, C.J. (eds.) 1986. Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates. - The University of Wisconsin Press.
Villard, M.-A., Trzcinski, M.K. and Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. - Conservation Biology 13: 774-783.
Virkkala, R. 1997. The significance of a reserve network in preserving the biodiversity of forests. - Suomen Riista 43: 38-47. (In Finnish with English summary).
Walker, B. 1995. Conserving biological diversity through ecosystem resilience. - Conservation Biology 9: 747-752.
Wallén, P. 2001. Habitat ecology of the pendulous lichens Alectoria sarmentosa, Bryoria fremontii and Ramalina thrausta. Department of Biology and Environmental Science, Umeå University. (examination project supervised by PA Esseen)
Wallis de Vries, M. F. 1995. Large herbivores and the design of large-scale nature reserves in western Europe. - Conservation Biology 9: 25-33.
Wikars, L. O. 1992. Forest fires and insects. - Entomologisk Tidskrift 13 (4): 1-12.
Wikars, L.-O. 2003. Habitat requirements of the pine wood-living beetle Tragosoma depsarium (Coleoptera: Cerambycidae) at log, stand, and landscape scale. - Ecological Bulletins 51 in press.
Wiktander, U., Nilsson, I.N., Nilsson, S.G., Olsson, O., Pettersson, B. and Stagen, A. 1992. Occurrence of the lesser spotted woodpecker Dendrocopos minor in relation to area of deciduous forest. - Ornis Fennica 69: 113-118.
Wilcove, D. S. 1994. Preserving biodiversity: species in landscapes. Response to Tracy and Brussard. - Ecological Applications 4: 207-208.
Wilcox, B. A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. - In J. A. McNeely and K. R. Miller, editors. National parks, conservation and development: the role of protected areas in sustaining society. Smithsonian Institution Press, Washington, D.C, pp. 639-647.
Wolock, D. M. and McCabe, G. J. 1995. Comparison of single and multiple flow direction algorithms for computing topographic parameters in TOPMODEL. - Water Resources Research 31(5): 1315-1324.
Yaroshenko, A. Yu., P.V. Potapov and S. A. Turubanova. 2001. The intact forest landscapes of Northern European Russia. - Greenpeace Russia and the Global Forest Watch. Moscow.