

# RESERVE NETWORK DESIGN IN FRAGMENTED FOREST LANDSCAPES

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Academic dissertation

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Helsinki 2003

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ISBN 952-91-6380-0 (paperback)  
ISBN 952-10-1395-8 (PDF)  
<http://ethesis.helsinki.fi>

Yliopistopaino  
Helsinki 2003

# Reserve network design in fragmented forest landscapes

Paula Siitonen

The thesis is based on the following original articles, which are referred to in the text by the Roman numbers I–IV:

- I Siitonen, P., Järveläinen, T., Laurinharju, E. , Mannerkoski, I., Pajunen T., Siitonen, M., Tanskanen, A., and Tukka, H. 2003. Species richness correlations and complementary of ten different taxa in boreal forests (submitted)
- II Siitonen, P., Lehtinen, A. and Siitonen, 2003. M. Effects of forest edges on wood-rotting fungi. (submitted)
- III Siitonen, P. Tanskanen, A. and Lehtinen, A. 2002. Method for selection of old forest reserves. *Conservation Biology* 16. 1398–1408.
- IV Siitonen, P., Tanskanen, A. and Lehtinen A. 2003. Continuity or connectivity ? Cost-efficient selection of forest reserves with a multiobjective spatial algorithm (submitted).

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*To my family*

## Contributions

The following table shows the major contributions of authors to the original articles.

	I	II	III	IV
Original idea	PS	PS	PS	PS
Materials	TJ,EL,IM, TP, MS, PS, HT	PS, MS	Metsähallitus GIS- data	Tornator GIS-data
Analysis	PS, AT	PS, AL	PS, AT, AL	PS, AT, AL
Manuscript preparation	PS	PS	PS	PS

TJ: Tapani Järveläinen, EL: Erkki Laurinharju, AL: Antti Lehtinen, IM: Ilpo Mannerkoski, TP: Timo Pajunen, MS: Mikko Siitonen, PS: Paula Siitonen, AT: Antti Tanskanen, HT: Harri Tukia. In addition, several field workers assisted in the field, (specifically Taisto Pulkkinen in manuscript II), and staff of Metsähallitus and StoraEnso(Tornator) gave valuable comments for the articles and manuscripts III–IV.

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# Contents

Summary	7
1 Introduction	7
1.1 Indicators of biodiversity	8
1.2 Site selection methods	9
1.3 Spatial reserve network design	10
2 Objectives of the thesis	11
3 Material and methods	12
3.1 Study areas	12
3.2 Forest stand databases in geographic information systems	12
3.3 Field inventories	12
3.4 Statistical analyses	13
3.5 Edge-core area model	13
3.6 Reserve selection model and algorithm	14
3.7 Definition of the conservation goals and objectives for reserve selection	15
4 Main results and discussion	16
4.1 Species groups and environmental variables as indicators	16
4.2 The edge type and age affect the spatial pattern of fungi within old forest edges	17
4.3 With spatial functions, more clustered solutions can be achieved without extra cost	18
4.4 Weighting and definition of the objectives affects the balance between quality, spatial arrangement and representativeness of the reserve network	19
4.5 More clustered solutions can be obtained at the cost of present day quality	19
4.6 Relative weights of spatial objectives regulate spatial arrangement of the results	20
4.7 Pre-specified inter-reserve target distances affect spatial arrangement of the solution	21
4.8 Biased and insufficient data biases results	22

5	Reserve design in a changing world – managing within the unmanageable	23
5.1	Gap between overall goals and specific objectives	23
5.2	Changing goals	23
5.3	Practical considerations	25
5.4	Availability of land for conservation	25
5.5	Combination rather than competition between different strategies	25
	Acknowledgements	26
	Literature cited	26
I	Siitonen, P., Järveläinen, T., Laurinharju, E. , Mannerkoski, I., Pajunen T., Siitonen, M., Tanskanen, A. and Tukia, H., Species richness correlations and complementary of ten different taxa in boreal forests	33
II	Siitonen, P., Lehtinen, A. and Siitonen, M., Effects of forest edges on wood-rotting fungi	55
III	Siitonen, P. Tanskanen, A. and Lehtinen, A., Method for selection of old forest reserves	75
IV	Siitonen, P., Tanskanen, A. and Lehtinen A., Continuity or connectivity? Cost-efficient selection of forest reserves with a multiobjective spatial algorithm	89

# Summary

## 1 Introduction

Intensive management has altered the structure of forest stands and landscapes (Esseen et al. 1997). Fragmentation and loss of habitats, or even their total discontinuation are major threats to forest biodiversity (Saunders et al. 1991; Andrén 1997). Extinction rates are high in the tropics, but fragmentation and loss of habitats due to intensive forest management also threatens species adapted to natural forests in boreal ecosystems (Andrén 1997; Esseen et al. 1997; Rassi et al. 2000). Consequently, large numbers of forest-dwelling plant and animal species have declined (Haila 1994; Esseen et al. 1997; Rassi et al. 2000). It is probable that existing reserves will be insufficient to represent and maintain the full variety of the biodiversity of boreal forests in the long term (Haila 1994; Angelstam and Pettersson 1997; Virkkala and Toivonen 1999; Prendergast et al. 1999; Hanski 2000). Consequently, they should be complemented with new conservation and restoration areas (Margules and Pressey 2000).

Designing reserve network is a crucial part of forest conservation planning (Noss 1999; Shafer 1999; Margules and Pressey 2000). Systematic reserve network design includes 1) problem identification and structuring (e.g. definition of goals, their specification by concrete objectives and constraints) 2) modeling and generation of candidate solutions (e.g. by optimizing methods or algorithms), 3) their critical evaluation (e.g. by sensitivity analysis of parameters) and 4) determination of action plans (see also Margules and Pressey 2000; Belton and Steward 2002). A reserve network should represent the full variety of biodiversity and ensure long term persistence of species, habitats and natural processes characteristic to a given region (Pressey et al. 1997; Margules

and Pressey 2000). These overall conservation goals are usually specified by a set of objectives for the number, area and spatiotemporal distribution of features (species, populations, habitat characteristics) (Csuti et al. 1997; Pressey et al. 1997; Margules and Pressey 2000). From the perspective of biodiversity conservation alone, the efficiency of a reserve network means achievement of these long term conservation goals and specific conservation objectives (Pressey et al. 1997; Possingham et al. 2000; Rodrigues et al. 2000). However, in real life, conservation competes with other land use practices, and land available for conservation is limited by political (e.g. borders), economic (e.g. land price, wood and agricultural production and building), and social constraints (e.g. land-ownership) (Rothey 1999; Prendergast et al. 1999; Kurttila et al. 2002; Peterson et al. 2003). Hence, in real-life reserve design, a cost-efficient reserve network achieves goals set for biodiversity conservation best and at minimum cost (e.g. economic expenditure, area, number of sites, loss of biodiversity) by considering constraints set by other land use practices and values (Pimm and Lawton 1998; Prendergast et al. 1999; McDonnell et al. 2002; Hughey et al. 2003).

Changes in conservation legislation and practices, conservation targets, economic needs, land ownership and societal values increase the complexity and uncertainty of conservation design. Conservation and management planners need tools to evaluate alternative conservation plans and candidate reserves in terms of achievement of conservation goals measured against costs, to identify priority areas for conservation and for relevant and cost-efficient conservation decisions in an increasingly uncertain, unmanageable and dynamic world (Angelstam and Pettersson 1997; Pressey et al. 1997; Prendergast et al. 1999; Possingham et al. 2000;

Peterson et al. 2003; see also Hof and Bevers 2002).

Concerning the overall goals – representativeness and persistence – of biodiversity conservation, the most reliable reserve design approach would evidently be to model the best arrangement of habitat patches separately for each species using population viability analysis (Soulé 1987; Hanski 1999; Possingham et al. 2000; Cabeza and Moilanen 2001; McCarthy et al. 2003). This technique analyses the dynamics of populations and has been applied to rank different landscapes in terms of their capacity to maintain viable (meta)populations, and to the planning reserve systems where the extinction probability of particular well-studied species is acceptably low (Soulé 1987; Hanski and Ovaskainen 2002; Moilanen and Cabeza 2002). However, evaluation of such umbrella or flagship species has shown that conservation of viable populations of one species does not automatically ensure the persistence of others (Simberloff 1998; Andelman and Fagan 2000; Williams et al. 2000). Although it is technically possible to consider conservation targets for several species at the same time (Moilanen and Cabeza 2002), insufficient data on spatiotemporal dynamics of species and their habitats makes it practically impossible to define concrete conservation objectives and to model a habitat network which would be appropriate for all species (Possingham et al. 2000). Moreover, there will never be enough time, funding or taxonomic knowledge to survey the biodiversity of all species (Noss 1999; Prendergast et al. 1999). Despite insufficient ecological knowledge, conservation decisions are constantly made. To overcome this problem, a wide range of indicators and decision support tools has been developed.

## 1.1 Indicators of biodiversity

An important question in conservation design is whether certain well-known and eas-

ily surveyed species, taxa or environmental variables can be used to predict overall biodiversity, and to select a subset of areas which would well maintain or at least represent other species or conservation goals (Prendergast et al. 1993; Noss 1999; Vessby et al. 2002; Lawler et al. 2003). Several studies published on co-variation of species groups have shown that patterns of richness or rarity of different taxa often do not coincide (Prendergast et al. 1993, 1997; Niemelä and Bauer 1998; Simberloff 1998; Jonsson and Jonsell 1999; Andelman and Fagan 2000; Lawton et al. 1998; Similä et al. 2002), but other studies supported success of certain species (e.g. Nilsson et al. 1995), or taxonomic group (Vessby et al. 2002; Saetersdal et al. 2003) as indicators.

In some regions taxonomic indicators appear to coincide rather well when tested with the complementarity concept, the idea of which is that areas selected to include indicator species would also include other species (Howard et al. 1998; Lawler et al. 2003). However, results of coincidence tests appear to vary among regions and scales (Flather et al. 1997). Moreover, complementarity areas have usually been selected to cover at least one representation of focal species, although such a minimum set appears to fail to maintain viable populations in the long term (Pressey et al. 1994; Cabeza and Moilanen 2001). Long-term persistence of species can be improved by preferring large populations; large habitat patches close together and sites with high population density (Nicholls 1998; Margules and Pressey 2000; Moilanen and Cabeza 2002). Coincidence of complementarity areas selected to include certain proportions of individuals or several representations of species belonging to different taxa have rarely been examined, specifically in boreal forests (Nicholls 1998). The first paper of this thesis (I) addresses particularly this question.



## 1.2 Site selection methods

Several methods have been developed to select priority areas for conservation. The earliest methods scored sites on the basis of species richness or rarity or other features considered important for conservation (Usher 1986). These approaches failed even to represent all the species or other target features because they simply maximized numbers of features without considering their identity (Pressey and Nicholls 1989; Williams et al. 1996). Thus, some species or other features were unnecessarily repeated in selected subsets of sites, whereas others (specifically those occurring in species-poor sites) were lacking (Williams et al. 1996).

Kirkpatrick (1983) first presented a simple heuristic algorithm to select complementary conservation areas, and since then a wide range of heuristic and linear mathematical programming methods has been developed and applied to various reserve design problems (see Margules et al. 1988; Saetersdal et al. 1993; Church et al. 1996; Csuti et al. 1997; Pressey et al. 1997; Rothley 1999; Church et al. 2000; Rodrigues et al. 2000; Hof and Bevers 2002; Rodrigues and Gaston 2002). These methods were usually applied to select a complementary subset of sites (e.g. stands, grid cells, or other planning units) which together would fulfill conservation targets defined by the number, area or proportion of features (e.g. species, environmental variables) at minimum cost (e.g. economic expenditure, area, number of selection units) (Pressey et al. 1993; Underhill 1994). Alternatively, methods have been applied to satisfy objectives best when number of sites or area that may be chosen is restricted (maximal coverage location problem e.g. Church et al. 1996).

The linear programming techniques (such as the branch and bound algorithm promoted by Underhill (1994) and other optimizing algorithms (Cocks and Bair 1989; Church et al. 1996) can guarantee an optimal solution, but they usually fail to solve

complex real-life planning problems with several non-linear objectives for proportions and spatial arrangement of features in landscape areas of thousands of selection units (Pressey et al. 1997; McDonnell et al. 2000; Briers 2002; Önal 2003). Heuristic algorithms can not ensure optimality, but they usually find a slightly sub-optimal solution to complex problems with several non-spatial and spatial objectives and planning units across wide areas (Pressey et al. 1996; Csuti et al. 1997; Pressey et al. 1997). Two main approaches of heuristic algorithms have been used (Csuti et al. 1997; Pressey et al. 1997; Williams 1998). Richness-based "greedy" heuristic algorithms (e.g. Kirkpatrick 1983) begin with a site, which fulfills the unfulfilled objectives the best, and then adds site one at a time according to which satisfies the remaining unfulfilled objectives with the best cost-benefit ratio. Rarity algorithms (e.g. Margules et al. 1988; Csuti et al. 1997; Williams 1998) starts with a site containing most unique features, and selects in every cycle site which contains rarest unselected feature.

In real life conservation, it is usually more important than absolute optimality to screen from large numbers of possible solutions a few good ones (Pressey et al. 1996; Williams 1998). There can be several alternative sets of areas that can reach conservation goals as well (Ferrier et al. 2000) Therefore, it is often necessary to run the models several times to find alternative solutions. Some methods, such as simulated annealing and random search techniques (Possingham et al. 2000; Öhman and Erikson 2002), produce usually several good solutions instead of a single optimal one, which is useful for real-life conservation design. Information of irreplaceability; optional areas for conservation and numbers of replacements of certain area are considered useful information for conservation planners (Ferrier et al. 2000; Noss et al. 2002). Hence, practicability and flexibility are usually considered more important characteristics of a system than its absolute optimality (Margules and Pressey 2000).

### 1.3 Spatial reserve network design

The spatial location of reserves was long neglected, although sizes and inter-area distances are critical for the persistence of many poorly dispersing species with discrete habitat requirements in fragmented landscapes (Hanski 1999; King and With 2000; Briers 2002; Cabeza and Moilanen 2001; Moilanen and Cabeza 2002). Species living in metapopulations may persist in fragmented landscapes over time by establishing themselves in new empty suitable habitat patches to replace local extinctions (Hanski 1999). Fragmentation of habitats decreases the sizes of distinct habitat patches and increase inter-patch distances (Saunders et al. 1991). If reserve network is highly fragmented, this restricts opportunities for dispersal between sites leading to poor capacity of reserves to maintain species in the long term (Hanski and Ovaskainen 2002; Rodrigues et al. 2000). Since reserve networks are often designed specifically for poorly dispersing species with discrete habitat requirements and threatened by habitat fragmentation, it is imperative to consider spatial relationships in reserve design. To fulfill the objective for species persistence, reserves should be large enough to maintain entire population of species in long term, or they should be located so close to each other that species can efficiently re-colonize locally extinct habitat patches to ensure persistence of a metapopulation (Shafer 1999; Hanski 1999; Possingham et al. 2000; Cabeza and Moilanen 2001; Hanski and Ovaskainen 2002; Briers 2002).

Disconnected reserve systems or long and thin reserves may consist mainly of edge habitats particularly if the surrounding habitat differs considerably from the protected one (Saunders et al. 1991; Fagan et al. 1999; McDonnell et al. 2002). Fragmentation of old forests increases area exposed to edge-effects within remaining old forests (Saunders et al. 1991; Murcia 1995). The effects of

man-made forest edges are complex, including changes in microclimate, elevated wind-throw and alteration of species interactions (Matlack 1994; Chen et al. 1995; Murcia 1995; Andr n 1997; Esseen and Rehnhorn 1998; Fagan et al. 1999; Laurance et al. 2001).

The depth of area exposed to physical edge effect depends on orientation, topography and physiognomy of edges, and species responses to physical and ecological changes occurring in forest edges differ considerably (Murcia 1995; Sih et al. 2000). Species responses to edge-effect over time is unclear. On the basis of the few available studies, edge effect appears to be strongly dynamic over time (Matlack 1994; Murcia 1995; Rehnhorn and Esseen 1998, II). The proportion of the total area of a forest fragment subject to edge effect is regulated by the size, shape and position of the fragment in the landscape, and is greatest in small and irregularly shaped fragments (Laurance and Yensen 1991; Saunders et al. 1991). Increased proportion of area exposed to edge effect decreases the efficiency of reserves to maintain species dwelling on original habitat and thereby the achievement of overall conservation goals (Saunders et al. 1991). Furthermore, maintenance costs of reserves depend generally more on boundary length than on area (Shafer 1999; Possingham et al. 2000). Hence, clustered reserves are more preferable for both economic and ecological reasons (Saunders et al. 1991; Possingham et al. 2000). The examination of the effects of different aged edges to wood-rotting fungi, and demonstration of a spatially explicit model to assess edge-core area relationships in landscape scale are tasks of the paper II.

Nicholas and Margules (1993) presented an upgraded heuristic algorithm with adjacency constraints, which supported selection of sites nearest to already selected ones. Rothery (1999) applied a multicriteria reserve selection procedure to maximize connectivity, reserve area and rare species representations. Moreover, Possingham et al. (2000) used simulated annealing and minimized

boundary length in relation to reserve area in order to obtain a more compact reserve network, and Briers (2002) applied negative exponent of inter-area distance to weight strongly sites close to already selected ones (see also Ömal and Briers 2002).

A problem similar to clustering of reserves is the clustering of harvest sites (it is more expensive to harvest and maintain dispersed than clustered stands), and several spatial optimization methods have been developed and applied to forestry and other natural resource planning (see e.g. Hof and Joyce 1992; Church et al. 2000; Murray and Snyder 2000; Falcão and Borges 2001; Bettinger et al. 2002; Öhman and Eriksson 2002; Öhman and Lämås 2003; Jumppanen et al. 2003). For example, Öhman and Eriksson (2002) integrated linear programming with simulated annealing to obtain continuous areas of old forests in long term forest planning.

However, relying only one large reserve can have disadvantages; natural catastrophes can cause local extinctions by destroying entire populations, and one large reserve will probably not represent all of the habitats occurring in the target region (Saunders et al. 1991; Balbin 1993; Possingahm et al. 2000). Hence, it is less risky to have at least a few separate representations of target features. However, few methods consider the tension between achieving the objectives for larger continuous reserves, increasing connectivity (decreasing inter-reserve distances and area of a cluster, defined here as the sum of the area of reserves separated from each other by an inter-reserve distance of certain maximum length), and ensuring spatial and non-spatial representativeness of reserve networks (Prendergast et al. 1999; Briers 2002; Siitonen et al. 2003; III). Furthermore, the methods have only rarely been applied to solve complex real-life forest conservation planning problems where several non-spatial and spatial objectives for number, area, proportion and spatial distribution of features must be satisfied at minimum

economic expenditure over wide areas with numerous potential stands (Prendergast et al. 1999; Kurttila 2001; Store and Kangas 2001; Kurttila et al. 2002; Siitonen et al. 2003; Öhman and Eriksson 2002). In addition, wide landscape areas are usually divided into several operational sub-regions with their own forestry and conservation targets. The two last papers (III, IV) of this thesis demonstrate applications of a new heuristic multiobjective algorithm in real-life reserve design problems in eastern and northern Finland.

## 2 Objectives of the thesis

This thesis focuses on multicriteria reserve network design in fragmented forest landscapes, and demonstrates some new reserve design methods to address non-spatial and spatial conservation problems including their applications in real-life conservation planning.

The aims of the first (I) paper were to examine 1) whether certain species group can be used to predict number of species in other taxa, and 2) to select a subset of areas which would well maintain or at least include other species. Thus, species richness correlations and coincidence of complementary areas of vascular plants, mosses, liverworts, epiphytic lichens, ground lichens, polypores, carabids, saproxylic beetles, other beetles, spiders and land snails were examined. In addition relationships between species richness of different taxa and environmental variables were analyzed.

Designing of reserves requires data on species responses to edges. The second paper (II) addresses the effects of different aged edges on the spatial distribution of wood-rotting fungi in old forest fragments. The aims were: 1) to estimate the depth of the edge effect within old forest fragments, 2) to assess the impact of time since edge formation, 3) to analyze effects of the spatial

patterns of suitable substrates and species on occurrences of target species, and 4) to apply a new GIS-based edge-core area model to compare effects of different edge widths on the proportion of interior area of old forests in a wide landscape area in eastern Finland.

In papers III and IV a new multiobjective heuristic algorithm is described and applied to support selection of forest reserves in real life planning situations in two forest landscapes in northern and eastern Finland. The aims were, in particular to examine the effects of four spatial functions on the level of achievement of the pre-specified non-spatial and spatial conservation objectives, the total area selected and its economic expenditures (III and IV). Moreover, the algorithm was applied to select areas to fulfill objectives defined for one sub-region and the whole region separately (III). Paper IV focuses on the effects of the different maximum inter-area target distances and a proximity function (giving more weight to stands which are close to already selected stands) on spatial arrangement and cost-efficiency of the solutions.

## 3 Material and methods

### 3.1 Study areas

Indicator taxa analyses (I) were carried out in two state-owned forest areas, belonging to southern (Lohikoski) and northern (Kuhmo) boreal vegetation zones (Ahti et al. 1968). The regions include gradients from intensively managed forests to near-primary old growth forests. Field inventories to assess edge effects on wood-rotting fungi (II) were carried out partly in the same old forest fragments in Kuhmo as in the indicator taxa study. The assessment of edge core area relationships (II) was calculated from a 185 00 ha forest landscape in the Kuhmo and Nurmes communes in eastern Finland.

In paper III, a multiobjective heuristic algorithm was applied to the state-owned planning region (96 000 ha; 10 162 forest stands) in Taivalkoski commune, northern Finland. The Taivalkoski planning region belonged to the northern boreal vegetation zone (Ahti et al. 1968), and included conservation areas, the Kylmäluoma recreational area where forest management was limited, and managed forests. One fifth of the forests were > 140 years old. In paper IV, the algorithm was applied to a planning region (ca. 10 000 ha; 5 600 forest stands) owned by Tornator (former by StoraEnso) in eastern Finland. The planning region belongs to the southern boreal vegetation zone. The forests were intensively managed and only 2 % were >120 years of age.

### 3.2 Forest stand databases in geographic information systems

Data on volume of living trees of different tree species, forest canopy height, forest age, forest type and particularly valuable key biotopes were mapped in the field by staff of the Forest and Park Service (II, III) or Tornator (IV), and were available in the geographic information system for all forest stands. The volume of dead trees was available for all stands in the study region in paper (IV) and from all old forest stands in Taivalkoski (III). In Taivalkoski, staff of the Forest and Park service mapped data on old forest indicator fungi from old forests in the Kyläluoma recreational area and managed forests with plenty of dead wood. In protected areas, data on indicator fungi was incomplete.

### 3.3 Field inventories

To examine whether certain species groups or environmental variables can be used to predict richness and complementary areas

of other species, both species and environmental variables were surveyed from a total of 194 sample plots, each 300 m<sup>2</sup> in size in a gradient from old growth forests through different-aged managed forests to clear cuts in the Kuhmo and Lohikoski study areas (I). In each sample plot, number and abundance of vascular plants, mosses, liverworts, epiphytic lichens, ground lichens, polypores, beetles, carabids, other beetles, spiders and land snails were surveyed and environmental variables (volume of dead and living tree species and key habitats) were mapped in the field (see I for details of the methods).

To examine species responses to edges, fifteen edges between old-growth spruce-dominated forests and young and old man made clear cuts and natural peatlands was surveyed in Kuhmo (II). All fallen spruce logs (> 10 cm diameter, 10 679 logs) in three old growth forest fragments were located by the global positioning system (GPS), and environmental variables and the occurrence of four old forest indicator fungi, a light adapted fungus and a pathogenic and saprophyte fungus were investigated in each log.

### 3.4 Statistical analyses

Total numbers of species and individuals were used as a measure of species richness and abundance in sample plots when analyzing coincidence of different taxa (I). Frequency sums of Coleoptera in Finland were used as a measure of national scale rarity (Rassi et al. 1993; 2000). Mean numbers of species and individuals in sample plots belonging to the same successional classes were compared, and species turnover along the successional gradient was compared by the Czekanowski index of percentage similarity (I). Spearman correlation analysis was used to examine whether species richness between different taxa and the frequency value of Coleoptera co-vary. Moreover, a greedy heuristic algorithm (described in paper III) was applied to select a complemen-

tary subset of sites that contains 5 % of the total number of the individuals (population) of each animal species, and 5 % of the total number of occurrences of each plant or fungal species (I). Complementary subsets of sites were selected separately for each taxa. The coincidence of complementary sites of different taxa was compared by calculating the proportion of other species captured by a subset of sites chosen on the basis of certain species group. Relationships between numbers of species and environmental variables were analyzed by Spearman rank correlation analysis, and the Mann-Whitney U-test was applied to test differences of species richness in the sites with and without key biotopes (I).

The relationship of the edge type to the depth of the edge effect was first analyzed by nonparametric tests comparing frequencies of species and log variables at different distances to edges (II). Secondly, descriptive statistics of the logs with and without target species were compared by univariate analysis in order to assess the relationship of the explanatory variables to occurrence of the target species. Next, a multiple logistic regression procedure (Quinn and Keough 2002) was used to analyze the effects of the explanatory variables on the occurrences of fungal species. Both forward selection and backward elimination of variables with the criterion  $P < 0.05$  for their inclusion or exclusion were used in model building. The analyses were made with SYSTAT 8.0.

### 3.5 Edge-core area model

To estimate the area exposed to edge-effect at landscape scale, we used ArcInfo to calculate, on the basis of a forestry inventory GIS-database, the interior and edge areas of all >120 years-old spruce-dominated forest fragments in the target region of ca. 185 000 ha in Kuhmo, eastern Finland (II). The edge width (d) was buffered from each border of each fragment, and the buffer zones were

intersected. The edge width for each different edge type was computed separately on the basis of the difference of the canopy height between focal old forest fragment and adjacent forest. Thus, it was assumed that the depth of edge effect declines with diminishing physical differences (reduced canopy height difference) between adjacent forest stands during maturation of the edge (Matlack 1993, Chen et al. 1995). The width of the edge effect ( $d_j$ ) of adjacent habitat ( $i$ ) inside the old forest fragment  $j$  was  $d_i = h_j - h_i$ , where  $h_j$  was the canopy height of the old forest fragment  $j$  and  $h_i$  was the canopy height of adjacent forest  $i$ . The efficiencies of the scenarios with different edge widths to maintain old forest interior area were compared by the edge–core area relationships, by the numbers of core areas, and by the numbers of disappeared core areas.

### 3.6 Reserve selection model and algorithm

A multiobjective greedy heuristic algorithm was applied to select a set of forest stands that best fulfills several non-spatial (area, number, and proportion of the features) and spatial (spatial arrangement of the features) objectives assigned to a given region (I, III, IV). To run the algorithm, attribute and geometric data of the forest stands were needed, and objectives and a cost function (e.g. area, economic expenditure or any mathematical statement) had to be prespecified. The algorithm selects stands on the basis of their cost-benefit ratios. The cost-benefit ratio of a candidate stand is the sum of the quality value and the spatial value of the stand divided by its cost. The quality value of the stand measures the degree of achievement of the unfulfilled non-spatial objectives, and the spatial value describes how well it satisfies the spatial objectives. The greater the quality value, the better the stand fulfills one or more objectives. In every cycle, the cost-benefit ratios are recalculated on the basis

of the current degree of fulfillment of the objectives. The unfulfilled part of the objective is used to weight objectives and the speed with which they are achieved.

The spatial value of a stand is the weighted sum of the values of three functions: continuous area ( $f_a$ ), connectivity ( $f_c$ ), isolation ( $f_i$ ) and proximity ( $f_p$ ).

The continuous area ( $a_j$ ) is the total area of selected stands adjacent to each other (III). The continuous area of a candidate stand is the size of the continuous area to which this stand would belong if it were selected. The continuous area value  $f_a(a_i)$  of stand  $i$  is  $f_a(a_i) = f_a(a_{ia}) - f_a(a_{ib})$ , where  $a_{ia}$  is the continuous area after and  $a_{ib}$  is the largest distinct continuous area in  $a_{ia}$  before the selection of stand  $i$  (III).

A cluster is a group of selected stands separated from each other by a certain maximum interstand (edge-to-edge) distance ( $m$ ), and the size of a cluster is the total area of these stands (III). The connectivity value  $f_c(c_i)$  of the stand  $i$  is a function of the difference between the cluster size before and after the candidate stand has been selected. The connectivity ( $c_i$ ) of stand  $i$  is  $c_i = ca_i - \max(cb_{i1} \dots cb_{ik})$ , where  $ca_i$  is the cluster size after selecting stand  $i$ ,  $cb_{i1} \dots cb_{ik}$  are the sizes of the existing clusters that stand  $i$  would connect if it were selected, and  $\max(cb_{i1} \dots cb_{ik})$  is the size of the largest existing cluster before selecting stand  $i$ . To calculate the connectivity of a stand, a maximum inter-stand distance ( $m$ ), must be defined (III). The isolation value of the stand  $i$  is a function of the distance  $d_i$  between a candidate stand  $i$  and the nearest stand already selected (III). The proximity value  $f_p$  of the stand  $i$  is a decreasing function of the distance  $d_i$  between a candidate stand  $i$  and the nearest stand already selected (IV).

The spatial and non-spatial objectives, spatial value functions and their weights are user-defined, and depend on planning goals. The objectives for preferred sizes of distinct continuous areas or clusters can be defined by adjusting the functions  $f_a$  and  $f_c$ , respec-

tively. The tension between achieving non-spatial and spatial objectives is resolved by relative weightings of the objectives (III, IV).

The system was implemented with a CA-Visual Objects developing tool for Windows 95/NT operating systems. Inter-stand edge-to-edge distances were calculated and adjacent stands identified with ArcInfo.

### 3.7 Definition of the conservation goals and objectives for reserve selection

The algorithm was used to support the design of reserve network particularly to enhance maintenance of habitats and species characteristics of old-growth forests in the target regions by establishment of additional forest reserves (III, IV). This overall conservation goal was specified by definition of conservation objectives for preferred quality, area, and spatial distribution of forests in cooperation with foresters and conservation planners of the regions (III, IV). In paper III, the goal of reserve selection was to select additional conservation areas from unreserved old forests for conservation, whereas in paper IV the focus was in the selection of a subset of present old forests and restoration areas to achieve in long term sustainable solution. In both regions, the planning goal was to select a subset of forest stands that best complements of existing reserves in terms of achievement of these objectives while minimizing economic expenditure. Two different cost-functions were used: 1) economic value of forest land (III) and 2) real economic price of the forest land and timber volume (IV).

In each region, existing reserves, including key biotopes protected by law, were preselected. Non-spatial objectives for the proportions of protected old forests were defined separately for pine-, spruce- and birch-dominated forests, in order to ensure representativeness of the reserve network. Several alternative scenarios were built with

different proportions, reflecting conservation needs and constraints specific for each region. In addition, sub-objectives were used to define the preferred selection order of old forests. These objectives were related to the characteristics of old-growth forests considered important for species specialized to them, such as the volume of decaying wood, the volume of old aspen, goat willow and rowan, the number of key habitats not protected by law and the area of forests along shore lines of lakes and rivers. Because the total areas of old birch-dominated forests were in all regions insufficient to reach the objectives, an additional objective was set for the proportion of younger mixed forest, which could be most easily restored to old deciduous tree-dominated forests. In paper III, more protection-oriented objectives were defined for one sub-region, the Kylmäluoma recreational area, where forest management was limited.

New reserves should also decrease fragmentation of old forests by increasing areas of individual reserves and decreasing inter-reserve distances to facilitate species persistence: large old forest areas situated close together are considered to maintain viable populations of species adapted to them better than small and isolated old forest fragments (Saunders et al. 1991; Andrén 1997; Hanski 1999). However, reliance on only one large reserve may have some disadvantages (e.g. storms and diseases may cause local extinctions) and a single area will probably not represent adequately those habitats occurring in a target region (Balbin 1993; Possingham et al. 2000). Therefore, it may be less risky to have at least a few separate reserves. The spatial objective were (1) to increase the area of individual reserves within certain limits (III, IV), (2) to decrease inter-reserve distances and to increase the area of clusters in order to facilitate species dispersal (III, IV), and (3) to ensure the spatial evenness of the reserve network (III).

Several different target sizes of continuous reserves were defined and different maxi-

imum inter –area distances were used to calculate the connectivity of each stand, and to define a cluster (IV). In paper III, calculations were made with and without spatial objectives and with and without pre-selection of existing reserves. An isolation function to ensure evenness was applied only in paper III, and a proximity function in paper IV. The solutions were compared with the state of achievement of non-spatial and spatial objectives, area needed, costs, and the state of fragmentation of the selected areas.

## 4 Main results and discussion

### 4.1 Species groups and environmental variables as indicators

The crucial question in conservation planning is whether certain species, taxa or environmental variables could be used to predict overall biodiversity of other groups, and to identify sites which would also cover conservation targets set for other species. In the first paper (I), we examined whether species richness and complementary areas of vascular plants, mosses, liverworts, epiphytic lichens, ground lichens, polypores, carabids, other beetles, spiders and land snails in Finnish boreal forests co-vary.

The rather weak correlations among different taxa indicated that it is difficult to identify a single species group that could be used as an indicator of overall biodiversity in boreal forests in Finland. No single species group correlated significantly with all the other species groups. This result supports observations of studies in tropical forests (Lawton et al. 1998), in Britain (Prendergast et al. 1993; 1997), and in boreal ecosystems (Saetersdal et al. 1993; Niemelä et al. 1996; Niemelä and Bauer 1998; Jonsson and Jonsson 1999; Similä et al. 2002). Indeed, it is very likely that species with different habitat re-

quirements and niches will have dissimilar responses to habitat modification.

Despite the rather few correlations in species numbers among taxa, the species groups associated with similar kinds of habitat characteristics appeared to co-vary. Specifically, liverworts and polypores (dwelling on the volume and diversity of dead wood and sensitive to microclimatic conditions) were positively associated with each other. Moreover, numbers of vascular plant, polypore, moss and liverwort species were positively associated with the number of all other species, although e.g. vascular plants (in Kuhmo) and polypores (in Lohikoski) did not correlate significantly with any single species group. The high number of vascular plants (including several broad-leaved tree species) in, e.g. fertile soils and moist depressions increased the total number of species through their effect on microhabitats and litter (see Ryti 1992). Thus, richness of vascular plants and mosses could possibly be used as indicators of other species groups associated with soil fertility, litter quality, soil moisture or minor water bodies, but are more expensive or difficult to identify in the field (e.g. land snails and beetles living on the ground). Correspondingly, polypores could serve as indicators of richness of liverworts associated with dead wood or dependent on a moist microclimate. Vascular plants, bryophytes and polypores have often been used as indicators of forest conservation value and specifically for the identification of key biotopes (Karström 1992; Esseen et al. 1997; Kotiranta and Niemelä 1996; Renvall 1995; Söderström 1988; Sverdrup-Thygeson and Lindenmayer 2002; Saetersdal et al. 2003).

A complementary subset of sites selected with certain taxonomic groups can include a large percentage of other species (I). Sample plots selected to include 5 % of the total number of individuals (populations) of each animal species, or 5 % of the total number of representations of each plant or fungal species of certain taxa, included 37–



83 % of all other species in Kuhmo and 41–85 % in Lohikoski. However, the proportion of sample plots needed to fulfill these selection objectives varied considerably (5–48 %) among taxa. In Kuhmo, 70 % of sites (90 % for mature forests) and in Lohikoski 83 % of sites (93 % for mature forests) were required to include 5 % of individuals or occurrences of all species. The comparison of the number of other species captured by the top five sites selected on the basis of different species groups showed that beetles captured most other species (45–49 %) in both areas. When only mature forests were considered, sites selected to meet objectives for liverworts (in Kuhmo) and for carabids (in Lohikoski) included most other species (49 % in Kuhmo and 55 % in Lohikoski, respectively). This finding is consistent with observations made in some other studies (e.g. Howard et al. 1998; Lawler et al. 2003) showing that complementary areas can coincide even though richness or rarity hotspots do not overlap. However, beetles, liverworts and carabids are not very easy to identify on the field, which limits their usefulness as indicators. The varying conclusions of studies testing biodiversity indicators is partly due to differences in the indicator groups tested, the methods used to measure biodiversity (e.g. richness, rarity, complementarity) and test indicators, the scales of studies and the areas where the analyses were made (Williams 1998; Noss 1999; Howard et al. 1998; Lawer et al. 2003).

The assessment of the structural elements of a forest stand is much faster and easier than species inventories, and therefore structural elements have widely been used to indicate the conservation value of forests (Noss 1990; 1999; Lindenmayer et al. 2000). The significantly higher number of all species, vascular plants and mosses in the sites with minor water bodies or moist depressions (I) supported the conservation value of these key habitats (Esseen et al. 1997). Key biotopes were also often included in the complementary sites selected on the

basis on several different taxa. Furthermore, positive and significant correlation between total number of species and volume of living aspens supports the importance of aspen as a host for lichens, bryophytes (Nilsson et al. 1995, Kuusinen 1996), and beetles (Siitonen and Martikainen 1994) observed in several earlier studies (see also Esseen et al. 1997). In addition, our results show that simply the volume of dead trees indicates richness of species associated with dead trees rather well. Our finding that the volume of dead fallen trees and snags appeared to reflect richness of polypores, liverworts and epiphytic lichens supported the results of several earlier studies (Söderström 1988; Bader et al. 1995; Renvall 1995; Esseen et al. 1997).

#### **4.2 The edge type and age affect the spatial pattern of fungi within old forest edges**

The edge type (natural peatland or man-made forest edge) and time since edge formation appeared to affect the depth of edge effect and the spatial pattern of fungi within old forest edges (II). The frequency of light-adapted *G. sepiarium* increased substantially near young clear-cut edges, but declined to the same level as in old-forest interior when the edge matured. By contrast, frequencies of indicator fungi were slightly reduced < 25 m distance from young and < 10 m from old and peatland edges, and increased substantially 10–25 m from old and natural edges. Moreover, the preceding pathogenic fungus *F. pinicola* decreased significantly near young and old edges.

These results support studies showing that edge effects are complex and change with time, due to complex interactions between several factors (Matlack 1994; Murcia 1995; Esseen and Renhorn 1998). First, changes in microclimate – increased solar radiation and decreased moisture – within old forest edges affect species composition

directly and indirectly (Murcia 1995). Reduced moisture of the microclimate may decrease colonization of interior orientated indicator fungi in logs near young edges because of several factors including spore production and germination, dispersal lengths, lifetime of the spores, and spatial distribution of suitable habitats and target species.

Second, some fungi respond to changes in physical environment with a time lag, and do not disappear immediately after the habitat has temporarily become unsuitable for them (Renvall 1995; Niemelä et al. 1995). Drying out of microclimate may reduce colonization of new trunks and production of new fruit bodies of moisture-sensitive species, but does not necessarily kill a fungus which has already colonized a trunk. When the microclimate again becomes suitable for these species as a result of e.g. maturation of edge, fungi may start to produce fruit bodies again. This kind of quiet life inside a trunk may partly explain a strong peak of some indicator fungi of old forest near old clear cut edges. Because some individuals may live inside a trunk without producing fruit bodies, bacidiocarps do not necessarily indicate real distribution of fungi. Considerable annual variation in fruit body patterns of *P. centrifuga*, *A. lapponica* and *F. rosea* result from several interacting factors affecting their bacidiocarp production and colonization.

Third, changes in microclimate may improve the competitiveness of light-adapted species at the cost of species requiring logs with high water content (Bader et al. 1995; Renvall 1995; II). Moreover, changes of microclimate near edges may also affect species composition indirectly through changes in successional pathways (Niemelä et al. 1995). The studied indicator fungi were specialized according to the tree species, diameter, decay stage and moisture of the surrounding biotope (Bader et al. 1995; Renvall 1995; Kotiranta and Niemelä 1996; II); but they can also be dependent on the way the

tree dies and on pioneer decayers, which determine successors (Niemelä et al. 1995).

Fungi appeared to occur closer to logs colonized by the same species than to unoccupied logs, suggesting limited dispersal and aggregation of suitable logs (Bader et al. 1995; Edman and Jonsson 2001; II). Although the number of spruce logs in a suitable stage of decay was not higher near colonized logs, the suitability is affected by other factors such as diameter not considered in this analysis. However, logs next to colonized logs are likely to receive more spores, and consequently have a higher colonization probability than distant logs (Nordén and Larsson 1999; King and With 2002; Edman 2003). Consequently, poorly dispersing species with discrete habitat requirements colonize new habitats less efficiently than well dispersing species and are therefore more sensitive to rapid habitat changes (Hanski 1999).

On a landscape scale, the edge effect appeared to reduce the efficient old forest area considerably (II). Assuming, on the basis of an empirical study with fungi, that edge effect penetrates approximately two times the canopy height difference (0–40 m) into old forest from the clear cut edges, 29 % of old forest area was exposed to edge effect, and the interiors of numerous small fragments completely disappeared. Consequently, old forest area exposed to edge effect can be substantially regulated by sizes and shapes of old forest fragments, and by management of adjacent forests, which sets a great challenge to forestry, conservation and restoration planning around old forest reserves.

### **4.3 With spatial functions, more clustered solutions can be achieved without extra cost**

The use of the spatial functions and the weighting of the non-spatial and spatial objectives altered markedly the spatial ar-

rangement of the subset of selected stands, but did not affect substantially the total area needed, the economic expenditure or the achievement of the non spatial objectives (III, IV). Thus, different ecological benefits in the terms of spatial arrangement of the reserves can be achieved with approximately the same area or economic expenditure. The solutions depend, of course, on the spatial pattern, area and number of features in the target region as well as on the objectives, their weights and cost-functions (Nicholls and Margules 1993; Possingham et al. 2000). For example, numerous small distinct reserves were caused mainly by preselection of small key habitats protected by law. The algorithm selected new stands adjacent to existing reserves in order to increase the size of individual reserves within target limits, and selected new small stands close together and between the clusters to decrease inter-reserve distances and to create larger clusters. The balance between increasing area of individual reserves and decreasing inter reserve distances was regulated by adjusting the weights of spatial functions.

#### **4.4 Weighting and definition of the objectives affects the balance between quality, spatial arrangement and representativeness of the reserve network**

Weighting and definition of the non-spatial and spatial objectives regulate the balance between quality and spatial arrangement of the selected reserves. When the goal is to select areas which satisfy quality and area objectives well at present, the weight of non-spatial objectives should be set high in relation to spatial objectives (III). When spatial arrangement of the reserves is more important than their present quality, the spatial objectives should be weighted more (IV). Real-life reserve design wanders between these two goals.

However, ambitious and strongly weighted non-spatial objectives – in relation to the number of available features which fulfills these objectives in the target region – means that several stands become irreplaceable, which decreases the number of alternative solutions (Ferrier et al. 2000). For example, in paper IV (see also Siitonen et al. 2003), small differences between solutions with differently weighted spatial objectives were partly caused by rather ambitious (in relation to the available resource which fulfilled some of the non-spatial objectives) and strongly weighted non-spatial objectives for the proportions of old forests. The algorithm used the unfulfilled part of the objectives to weight the speed with which they are achieved (III), as a consequence of which the algorithm preferred to first select stands which supported achievement of the unfulfilled and strongly weighted objectives for old forests. Since rather few old forests were left in the whole area, tight non-spatial objectives forced the algorithm to select nearly all of them (Siitonen et al. 2003; IV).

#### **4.5 More clustered solutions can be obtained at the cost of present day quality**

The long-term planning goal was to complement the network of old forest reserves by creation of larger continuous areas, but the total area of old forests in the study region in eastern Finland was scattered and insufficient (IV). Therefore, selecting only those remaining old forests which fulfill strict criteria for age and quality would lead to fragmented and in the long term perhaps not the most cost efficient solution in terms of representativeness of the habitats and persistence of old-forest adapted species at minimum economic expenditure (Hanski 1999; 2000). Therefore, it was necessary to consider also younger forests to obtain more compact solutions in the long term.

To provide alternative solutions for com-

parison, the weight of the spatial objectives was substantially increased in relation to non-spatial objectives (Siitonen et al. 2003; IV). As a result, the number of alternative solutions in terms of non-spatial objectives increased, and the spatial arrangement of the solutions was regulated more by spatial functions and spatial objectives (IV). Thus, more compact spatial arrangement of the reserves was obtained at the cost of the present quality of reserves, while economic expenditure did not change markedly. In the long term, larger reserves closer together may support persistence of species that require wide and continuous old forest areas (Hanski 2000), are sensitive to edge-effects (Esseen and Renhorn 1998; Fagan et al. 1999) or disperse poorly (King and With 2002; Edman 2003) more efficiently than presently well qualified but small and scattered fragments. In regions, e.g. in southern Finland, where the remaining few old forest fragments are small and isolated, restoration may be the only possibility to maintain species adapted to old forest in the long term (Hanski 2000; Westphal and Possingham 2003).

Balancing of weight between non-spatial and spatial objectives is thus an efficient tool for restoration planning. The algorithm can be applied sequentially, and the weight of the objectives can be adjusted on each cycle. For example, areas protected by law and all > 120 years old forests were first preselected for the conservation core areas (IV). After that the weight of the spatial objectives was increased to complement these core areas to increase their areas and connectivity by selecting stands adjacent to and between already selected areas (IV). Moreover, even when the weight of the non-spatial objectives was decreased in relation to spatial objectives, the algorithm preferred to select the remaining unprotected oldest forest stands which fulfilled several non-spatial objectives (IV). For example, 110 years old forest with a lot of dead wood was likely to be selected because it supported achievement of the objectives for both > 80 and >

100 years old forests and volume of dead wood, if these objectives were not yet fulfilled.

It is imperative to note that the objective is not wrong even if it cannot be fulfilled, which is usually the case in reserve selection, and the objectives should not be fit to meet available resources. Therefore, for instance, the non-spatial objectives for the total areas of pine-, spruce- and birch-dominated forests were defined as proportions of their assumed original rather than remaining extent (III, IV). Consequently, the objectives for old birch-dominated forests were not fulfilled in any regions simply because there were not enough such forests left (III, IV). Instead of adjusting the weight of the objective, an additional sub-objective was defined to obtain younger mixed forests that would eventually fulfill targets for old deciduous-tree dominated forests (III).

The idea of changing the weight of the objectives is to provide alternative scenarios for decision makers (see also Ferrier et al. 2000; Possingham et al. 2000; Store and Kangas 2001; Peterson et al. 2003). It is also informative to screen the benefits and costs of "impossible" solutions such as protection of almost everything or almost nothing, in order to determine the limits of the realistic alternatives (Peterson et al. 2003). Moreover, scenario building provides information on the price of the fulfillment of different conservation objectives. The method (III, IV) allows the decision maker to compare several alternative scenarios in relation to the achievement of non spatial and spatial objectives and costs.

#### **4.6 Relative weights of spatial objectives regulate spatial arrangement of the results**

Spatial functions address the critical question of whether conservation efforts should focus on one large or several small reserves (Saunders et al. 1991; Shafer 1999). To evalu-

ate the tension between continuous area and connectivity objectives, the algorithm was applied giving different weights to these objectives (Siitonen et al. 2003; IV). Siitonen et al. 2003 observed that use of the spatial objectives increased the number of small individual reserves and size of the cluster most when the connectivity objective was weighted but also to some extent when the continuous area objective was weighted. The non-spatial objectives and their weights, target size of individual reserves and maximum inter-reserve (edge-to-edge) distances were the same in this calculation (Siitonen et al. 2003). Thus weighting of the continuous area objective did not markedly increase the area of individual reserves only because there were only a few large enough continuous old forest areas that would also meet some non-spatial objectives, but also because the maximum inter-area distance to create a cluster was rather long (500 m) (IV). Moreover, the target size of individual reserves (50–100 ha) did not support the selection of reserves larger than 100 ha (Siitonen et al. 2003). Consequently, it was much easier for the algorithm to find stands which in addition to non-spatial objectives, also fulfill the connectivity objective, than to increase the area of the individual reserve (IV). In addition to weighting of the objectives, the tension between the increasing size of continuous area and increasing connectivity appeared to be strongly regulated by definition of target sizes for continuous area and maximum inter-area target distances of stands belonging to the same cluster (IV).

#### **4.7 Pre-specified inter-reserve target distances affect spatial arrangement of the solution**

To evaluate the tension between spatial objectives the algorithm was applied with different maximum inter-stand distances (100–500 m) with and without a proximity function (IV). The proximity function, which gives

more weight to stands close to already selected stands, was used particularly to regulate the selection order of stands which were located closer to already selected stands than the maximum inter-area target distance defined for the formation of a cluster. The continuous area objective (defined without any upper limit), non-spatial objectives and their weights were the same in all scenarios. However, the weights of the non-spatial objectives were substantially reduced (IV).

Increasing inter-area target distances decreased the sizes of distinct continuous areas, because formation of clusters by selecting stands between already selected stands was easier with long than short inter-area distances. Moreover, the algorithm also created smaller continuous areas when using the proximity function, because use of the proximity function decreased the relative weight of the continuous area function (IV). The proximity value of a candidate stand was higher the closer it was to the nearest already selected stands, whereas a candidate stand received more connectivity value the more its selection increased the area of a cluster. Furthermore, stands adjacent to already selected stands received value from each spatial function, because they increased the continuous area, were located close to already selected stands, and increased the area of a cluster at least by their own size. However, usually they did not support the formation of larger clusters as efficiently as interconnecting “stepping stones” between two distinct clusters.

The longer the inter-area target distance, the more the proximity function regulated the selection order of stands which were located within the pre-specified maximum inter-area target distance. This was indicated by e.g. strings of small stands (IV). Thus, the proximity and connectivity functions together can lead to the selection of reserve networks which consider certain maximum dispersal lengths of target species (maximum inter-area target distance) and simultaneously give more value to stands closer to

already selected stands. Weights of the functions can be adjusted on the basis of data from e.g. species dispersal (e.g. Nordén and Larsson 1999; King and With 2000; Edman 2003).

In real life conservation area design, only certain parts of the large stands are often protected, e.g. to connect two distinct areas to each other. When the interconnecting stand is large and expensive, the algorithm does not always consider it. Therefore, transformation of the vector format stand database to raster (grid) data would increase flexibility of the systems specifically in terms of spatial arrangement of the reserves. The algorithm could then select only those parts of the stands that best fulfill the non-spatial and spatial objectives.

The size of the target region and particularly the number of candidate stands (selection units) affected the result (Siitonen et al. 2003; III; IV). Siitonen et al. 2003 observed that the solution in one sub-region was more clustered when the algorithm was applied to the whole region than when the stands were selected only from that sub-region. Thus, consideration of a larger landscape area surrounding the target region can result in a spatially more desirable solution (Siitonen et al. 2003). The larger the planning region and the number of selection units, the more alternative solutions exist and the more cost efficient solution can be found. The large number of candidate stands is particularly important when the target region has several landowners, and availability of land for conservation is limited (see Kurttila et al. 2002). When planning region consist of several sub-region belonging to different landowners or otherwise having different land use goals, the algorithm can be applied to select stands to fulfill the objectives set for each subregion in addition to planning targets for the whole area (III; Kurttila et al. 2002; Siitonen et al. 2003).

## 4.8 Biased and insufficient data biases results

Inadequate data can bias and complicate the reserve selection independently of the selection methods used (Prendergast et al. 1999). For example, missing data of indicator fungi from existing reserves in the Taivalkoski planning region systematically biased the results, particularly when the existing conservation areas were not preselected (III). Because indicator fungi in the Kylmäluoma recreational area and managed forests had been inventoried more closely than in existing reserves, the algorithm preferred selection of stands outside reserves to satisfy these objectives (III). Although the algorithm itself would provide an optimal or good solution, the accuracy of the results is affected by the quality of the data.

Systematically collected data on spatial and specifically temporal distribution of species and habitat characteristics is scarce (Margules and Pressey 2000; Possingham et al. 2000). Typically, data is biased towards charismatic species and specific areas, independently their real indicator or conservation value (Gaston and Rodrigues 2002). In Finland, characteristics of old forests and indicator species in many old existing reserves have been more poorly studied than in unprotected old forests, which were inventoried recently to select complementary areas for protection. However, inadequate data of existing reserves made it difficult to set realistic conservation objectives and to assess how well conservation needs were already achieved. On the basis of such data well studied regions appear to be more valuable than poorly studied regions. Conservation decisions must be made despite deficient data, but it is imperative to note that reserve selection systems are sensitive to both the quality and quantity of input data (Prendergast et al. 1999; Margules and Pressey 2000; Possingham et al. 2000).

## 5 Reserve design in a changing world – managing within the unmanageable

Reserve network design consists of several interacting dynamic systems, and its management requires understanding of the systems and their uncertainties. These uncertainties are related to every phase of reserve selection: to definition and specification of the overall goals by the objectives and cost-functions, sensitivity of algorithms to deficient data and biased objectives, ability of the algorithms to solve the planning problems and interpretation of the results.

### 5.1 Gap between overall goals and specific objectives

Overall conservation goals – representativeness and long term persistence of viable populations of species, their habitats and processes – include requirements for dynamic reserve design approach because nature is not static. First, the populations which should be maintained are dynamic over time, with local extinctions and colonization of new habitats (Hanski 1999). Second, the habitat patch network is dynamic since patch sizes, inter-area distances and suitability for target species all change due to e.g. natural succession and disturbances and human activities (Esseen et al. 1997; Saunders et al. 1991; Hanski 1999). In reserve selection, a crucial goal is to allocate reserves in such a way that they will also fulfill the conservation targets in future even if surrounding habitat drastically changes (Hanski 2000; Possingham et al. 2000).

However, insufficient ecological knowledge makes it difficult to define conservation objectives and their weights in order to accurately reflect real long term conservation goals for representation and persistence of species and habitats (Prendergast et al. 1999; Margules and Pressey 2000; Possing-

ham et al. 2000; III). Moreover, testing of shortcuts such as indicator species, taxa and environmental variables gives varying results on their ability to indicate overall biodiversity, particularly its persistence (Pressey et al., 1994; Howard et al. 1998; Wilson 1998; An-delman and Fagan 2000; Lawler et al. 2003; I). The least risky strategy might be combination of several different approaches in goal and objective setting. This might include definition of objectives on the basis of the population viability analysis of certain well known species with different responses to habitat modification (a shopping basket approach see e.g., Niemelä and Bauer 1998), and definition of the objectives for preferred spatiotemporal arrangement of the features on the basis of requirements of several different species and natural forest dynamics (Noss 1990; 1999; Lindenmayer et al. 2000; Williams 1998). However, it is important to note that in complex multicriteria planning problems such as real life reserve selection, there is always an uncertainty as to whether specific conservation objectives accurately reflect real conservation goals (Margules and Pressey 2000; III). Therefore, fulfillment of the conservation objectives does not necessarily mean that a species would persist; this can be assessed afterwards by species specific population viability analyses, if sufficient data is available (Cabeza and Moilanen 2001).

### 5.2 Changing goals

Third, conservation, economic and social objectives and constraints set for a given region vary, reflecting values of the human society and impacting the availability of the land for conservation (Hughes et al. 2003; Peterson et al. 2003). For example, existing reserve networks appear to be biased in relation to present conservation goals partly because they were established originally for other reasons (e.g. scenic beauty) (Shafer 1999). It is rather evident that increasing

ecological knowledge will constantly update conservation needs, whereas e.g. marketing forces such as changes in wood and land price and changes in landownership alter economic, social and political constraints.

Fourth, the reserve network itself is dynamic, since every new conservation area changes the degree to which reserve networks achieve changing conservation targets. The ability of conservation areas to represent and maintain biodiversity in the long term may drastically decline e.g. by climatic change through its effects on species ranges (Shafer 1999). Indeed, our present conservation goals and planning usually ignore climatic change simply because it is too difficult to predict its possible effects. Finally, new conservation practices such as temporary conservation areas, increasing the characteristics of natural ecosystems in managed areas, and restoration smooth the traditionally sharp border between preserved and managed areas (see e.g. Esseen et al. 1997; Angelstam and Pettersson 1997; Prendergast et al. 1999). Conservation areas are not isolated from their surroundings; thus improvement or decrease in the capacity of the managed forests to maintain species also affects the efficiency of reserve network (e.g. due to reduced edge effects) (Saunders et al. 1991; Murcia 1995; Shafer 1999; II).

Management of dynamic reserve design systems requires understanding of the complex interaction of these interconnected dynamic systems, and acceptance of the partial unmanageability and uncertainty of the whole system (Peterson et al. 2003). The solution of such a planning problem would require combination of dynamic population models and algorithms which can dynamically solve multicriteria spatial problems over long time periods in constantly changing forest landscape (Prendergast et al. 1999; Possingham et al. 2000; Noss et al. 2002). It is important to understand that because of these changing forces there will perhaps never be "enough" conservation areas, and attempts to find final solutions for fitting

together conservation and economic targets will obviously fail. Adaptive management, in which conservation strategies are constantly updated through interactive screening of different development scenarios might be a cost-efficient management strategy in the unpredictable future.

Scenario planning is a potential framework for conservation planning and policy making in an uncertain and changing world (Peterson et al. 2003, III,IV). The central idea of scenario planning is to consider a variety of possible futures that include many of the important uncertainties in the system, rather than to focus on a single outcome (Peterson et al. 2003; Westphal and Possingham 2003). Several conflicting or alternative scenarios are used to explore the uncertainty of the future consequences of a decision. Participation of several interest groups in goal setting, analyzing and interpreting of scenarios appeared in many cases to build shared understanding, which facilitated the generation of conservation decisions accepted by different instances (Store and Kangas 2001). In conservation design, scenario planning appears to increase understanding of key uncertainties, incorporates alternative perspectives, and increases the resilience of decisions to surprise (Prendergast et al. 1999; Peterson et al. 2003). Foresters and conservation planners of the forest and park service (III) and Tornator (IV) participating in the reserve selection efforts presented in this thesis, reported that specification of concrete conservation objectives and evaluation of the solutions opened partially the black box of overall biodiversity conservation goals and increased their (and our) awareness of the uncertainties of reserve design. Correspondingly, our capacity to understand economic and social constraints was improved. Moreover, close co-operation between different interest groups is also important because it helped us to understand and focus on finding solutions to real-life conservation problems (see also Prendergast et al. 1999).



### 5.3 Practical considerations

Efficiency in conservation planning means that objectives are met readily and at minimum cost. The kind of heuristic algorithms presented in this thesis can not guarantee how near to the optimum the solution is (Pressey et al. 1997). However, the method succeeded in solving a complex planning problem with several spatial and non-spatial objectives across wide areas (III,IV,V). In real-life planning, practicability and flexibility are possibly more important requirements of a reserve design tool than absolute optimality (Pressey et al 1997; Ferrier et al. 2000, Margules and Pressey 2000). Decision makers need explicit statements to support harvesting or conservation decisions of certain stands; on how harvesting or conservation of a stand would affect the fulfillment of the conservation and economic objectives and at what cost (Ferrier et al. 2000; Church et al. 2000). Because conservation and management needs and resources (candidate stands) constantly change, the alternative scenarios must be updated almost interactively. Therefore objectives, their weights and planning regions must be easily changed, and the results should be understandable.

### 5.4 Availability of land for conservation

One rarely addressed planning problem is availability of land for conservation (Prendergast et al. 1999). In real life, conservation areas are selected from a landscape divided into several operational sub-regions, which belong to several landowners with their own land use and conservation targets (Prendergast et al. 1999; Kurttila 2001; Kurttila et al. 2002; Siitonen et al. 2003). The landowners may provide their lands for conservation, but the order in which they do so is not necessarily the priority order of provided areas for conservation. Decision makers then must assess whether the land provided satisfies

unfulfilled conservation objectives well enough in relation to other areas which are not available for conservation now, or will perhaps never be. Thus, in addition to direct costs and benefits, a decision maker should also consider the risk that better land may never be available, and if they do not select the land offered for conservation now, it will possibly not be available in the future (e.g. because it will be harvested). This kind of problem exists presently e.g. in southern Finland, where existing reserves are inadequate to maintain species, and new conservation and restoration areas are recruited from privately owned lands through e.g. voluntarily protection. The method presented in this thesis can be applied to solve such a planning problem by assessing how well offered candidate reserve achieves objectives defined for the whole target region considering risk that better land will not be available. Decision analysis techniques, which can consider several decision makers might provide useful information for conservation design in regions with several landowners (see e.g. Belton and Stewart 2002)

### 5.5 Combination rather than competition between different strategies

In reserve selection, an objective has usually been to minimize the costs needed to achieve ecological benefits or objectives (e.g. certain proportions of population of species or desired spatial arrangements of habitats) (Possingham et al. 2000). However, in forestry planning objectives are usually defined in order to maximize wood production (economic benefits), whereas ecological, recreational and landscape values including the legislation which regulates harvesting are constraints which limit the economic use of forests (Kurttila et al. 2002; Church et al. 2000). However, simplification of conservation objectives as constraints may lead to a fragmented and ecologically inefficient so-

lution, particularly if the spatial objectives are not considered (Prendergast et al. 1999; Briers 2002; Öhmal and Eriksson 2002; III, IV). On the other hand, a simple economic cost function based on land and wood price does not consider real harvestings costs (such as transportation and storing costs) and social constraints (e.g. landownership), and may result in an economically inefficient solution, respectively (Church et al. 2000).

An alternative would be to integrate these different approaches into one problem. The most efficient solution would possibly be obtained by defining objectives for both timber production and conservation while minimizing production and conservation costs. To solve such a multiobjective dynamic reserve and harvesting area selection problem, the method should calculate dynamically spatiotemporal relationships between candidate sites. One of the main problems is that although forest growth can be predicted, the exact locations of natural disturbances and harvesting (e.g. because of changes in wood market and landownership) can usually not be predicted in advance. Consequently, temporal dynamics of the forest landscape (pool of potential sites) can only be partly simulated, and therefore effects of habitat fragmentation caused by forestry to particular sites can not be predicted, only restricted (IV). Combination of economic, ecological and recreation criteria to one planning problem is challenge for the development of the future decision support system tools for cost-efficient reserve design in uncertain and changing world.

## Acknowledgements

This thesis was financed by the Ministry for Forestry and Agriculture, Metsähallitus (Finnish Forest and Park Service) and Tornator (former StoraEnso Forest) in Finland and it is part of Biodiversity in Boreal Forest- project of Academy of Finland. I thank the Forestry and Nature Service Units of the Forest and

Park Service in Kuhmo and Savonlinna, and the Research Station of the Friendship Park in Kuhmo, specifically Dr. Raimo Heikkilä, for valuable aid in practical organization of the field work (I, II). Field assistant Taisto Pulkkinen made great work in the field for the studies in paper II. I extend special thanks to E. Keränen, K. Louhisalmi, A. Tyni, and P. Virnes from the Finnish Forest and Park Service, and to Juha-Veli Hyttiäinen, Tuija Luukkanen, and Jukka Pekkarinen from Tornator for their intensive participation in goal setting and interpretation of the results in papers III–IV. Specifically, I thank my supervisor professor Jari Niemelä who always had time to answer my questions and read my manuscripts. Warm thanks to professor Ilkka Hanski, professor Raimo P. Hämäläinen, members of Biodiversity in Boreal Forest- project and several other persons for their excellent comments to my work in strategic moments. I thank all the authors of the papers of this thesis for their valuable work and interesting time we have spend to carry out these studies. Finally, I would like to warmly thank my family and friends, who all have one way or other supported achievement of one stepping stone in my life: this thesis.

## Literature sited

- Ahti, T., Hämet-Ahti, L., Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botannici Fennici* 5:169–211.
- Andelman, S. J., Fagan, W. F. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of national Academy of Science of the USA* 97:5954–5959.
- Andrén, H. 1997. Habitat fragmentation and changes in biodiversity. *Ecological Bulletins* 46: 171–181.
- Angelstam, P., Pettersson, B. 1997. Principles of present Swedish forest biodiversity management. *Ecological Bulletins* 46:191–203.
- Bader, P., Jansson, S., Jonsson, B. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce

- forests. *Biological Conservation* 72:255–262.
- Balbin, L. 1993. Environmental representativeness: regional partitioning and reserve selection. *Biological Conservation* 66: 223–230.
- Belton, V., Steward, T. J. 2002. Multiple criteria decision analysis. An integrated approach. Kluwer Academic Publishers, Boston.
- Bettinger, P., Graetz, D., Boston, K., Sessions, J., Chung, W. 2002. Eight heuristic planning techniques applied to three increasingly difficult wildlife planning problems. *Silva Fennica* 36:561–584.
- Briers, R. A. 2002. Incorporating connectivity into reserve selection procedures. *Biological Conservation* 103:77–83.
- Cabeza, M., Moilanen, A. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology and Evolution* 16:242–247.
- Chen, J., Franklin, J. F., Spies, T. A. 1995. Growing season microclimatic gradients from clear cut edges into old-growth Douglas -fir forests. *Ecological Applications* 5:74–86.
- Church, R. L., Stoms, D. M., Davis, F. W. 1996. Reserve selection as a maximal covering location problem. *Biological Conservation* 76:105–112.
- Church, R. L., Murray, A. T., Figueroa, M., Barber, K.H. 2000. Support system development for forest ecosystem management. *European Journal of Operational Research* 121:247–258.
- Cocks, K. D., Baird, I. A. 1989. Using mathematical programming to address the multiple reserve selection problem: an example from the Eyre Peninsula, South Australia. *Biological Conservation* 49:113–130.
- Csuti, B., Polasky, S., Williams, P. H., Pressey, R. L., Camm, J. D., Kereshaw, M., Kiester, A. R., Downs, B., Hamilton, R., Huso, M., Sahr, K. 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80:83–97.
- Edman, M., Jonsson, B.-G. 2001. Spatial pattern of downed logs and wood decaying fungi old-growth *Picea abies* forest, *Journal of Vegetation Science* 12:609–620.
- Edman, M. 2003. Dispersal ecology of wood-decaying fungi – implications for conservation. Department of Ecology and Environmental Science. Umeå University. Doctoral Dissertation.
- Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46:16–47.
- Esseen, P., Renhorn, K. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* 12: 1307–1317.
- Fagan, W. F., Cantrell, R. S., Cosner, C. 1999. How habitat edges change species interactions. *American naturalist* 153:165–182.
- Falcão, A. O., Borges, J. G. 2001. Combining random and systematic search heuristic procedures for solving spatially constrained forest management scheduling problems. *Forest Science* 48:608–621.
- Flather, C. H., Wilson, K. R., Dean, D. J., McComb, W. C. 1997. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecological Applications* 7:531–542.
- Ferrier, S., Pressey, R.L., Barrett, T. W. 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biological Conservation* 93:303–325.
- Gaston, K. J., Rodrigues, A.S. L. 2002. Reserve selection in regions with poor biological data. *Conservation Biology* 17:188–195.
- Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Annales Zoologici Fennici* 31:203–217.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: modeling the consequences of different approaches to biodiversity conservation *Annales Zoologici Fennici* 37:271–281.
- Hanski, I., Ovaskainen, O. 2002. Extinction debt and extinction threshold. *Conservation Biology* 16:666–673.
- Hof, J. G., Joyce, L. A. 1992. Spatial Optimization for Wildlife and Timber in Managed Forest Ecosystems. *Forest Science* 38:489–508.
- Hof, J., Bevers, M. 2002. *Spatial optimization in ecological applications*. Columbia University Press.
- Hughey, K. F. D., Cullen, R., Moran, E. 2003. Integrating economics into priority setting and evaluation in conservation management. *Conservation Biology* 17:93–103.
- Howard, P. C., Viscanic, P., Davenport, T. R. B., Kigney, F. W., Baltzer, M., Dickinson, C. J., Lwanga, J. S., Matthews, R. A., Balmford, A. 1998. Complementarity and the use of

- indicator groups for reserve selection in Uganda. *Nature* 394:472–475.
- Jonsson, B. G., Jonsell, M. 1999. Exploring potential biodiversity indicators in boreal forests. *Biodiversity and Conservation* 8:1417–1433.
- Jumppanen, J., Kurttila, M., Pukkala, T., Uutera, J. 2003. Spatial harvest scheduling approach for areas involving multiple ownership. *Forest Policy and Economics* 5: 27–38.
- Karström M. 1992. The project one step ahead – a presentation. *Svensk Botanisk Tidskrift* 86:103–114.
- King, A. W., With, K. A. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23–39.
- Kirkpatrick, J., B. 1983. An iterative method for establishing priorities for selection of nature reserves: an example from Tasmania. *Biological Conservation* 25:127–134.
- Kotiranta, H., Niemelä, T. 1996. Threatened polypores in Finland. Environmental guide 10. Finnish Environment Institute, Edita, Helsinki.
- Kurttila, M. 2001. The spatial structure of forests in the optimization calculations of forest planning – a landscape ecological perspective. *Forest Ecology and Management* 142: 129–142.
- Kurttila, M., Uutera, J., Mykrä, S., Kurki, S., Pukkala, T. 2002. Decreasing the fragmentation of old forests in landscapes involving multiple ownership in Finland: economic, social and ecological consequences. *Forest Ecology and Management* 166:69–84.
- Kuusinen, M. 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist* 28:443–463.
- Laurance, W. F., Yensen Y. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77–92.
- Laurance, W. F., Didham, R. K., Power, M. E. 2001. Ecological boundaries: a search for synthesis. *Trends in Ecology and Evolution* 16:70–71.
- Lawler, J. J., White, D., Sifneos, J. C., Master L.L. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17:875–882.
- Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdsley, N. A., Strok, N. E., Srivastava, D. S., Watt, A. D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391:72–76.
- Lindenmayer, D. B., Margules, C. R., Botkin, D. B. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14: 941–950.
- Margules, C. R., Nicholls, A. O., Pressey, R. L. 1988. Selecting networks of reserves to maximize biological diversity. *Biological Conservation* 43:663–676.
- Margules, C. R., Pressey, R. L. 2000. Systematic conservation planning. *Nature* 405: 243–253.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge – trends in space and time. *Journal of Ecology* 82, 113–123.
- McCarthy, M. A., Andelman, S. J., Possingham, H. 2003. Reliability of relative predictions in population viability analysis. *Conservation Biology* 17:982–989.
- McDonnell, M. D., Possingham, H. P., Ball, I. R., Cousins, E. A. 2002. Mathematical methods for spatially cohesive reserve design. *Environmental Modeling and Assessment* 7:107–114.
- Moilanen, A., Cabeza, M. 2002. Single-species dynamic site selection. *Ecological Applications* 12:913–926.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- Murray, A. T., Snyder, S. 2000. Spatial modeling in forest management and natural resource planning. *Forest Science* 46:153–156.
- Nicholls, A. O., Margules, C. R. 1993. An upgraded reserve selection algorithm. *Biological Conservation* 64:165–169.
- Nicholls, A. O. 1998. Integrating population abundance, dynamics and distribution into broad-scale priority setting. In: Mace, G. M., A. Balmford, and J. R. Ginsberg (eds). *Conservation in Changing world*. Cambridge University Press, Cambridge, UK, pp. 251–272.
- Niemelä, J., Haila, Y., Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352–368.
- Niemelä, J., Bauer, B. 1998. Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in Swiss Jura mountains. *Biodiversity and Conservation* 7:1407–1416.

- Niemelä, T., Renvall, P., Penttilä, R. 1995. Interactions of fungi at late stages of wood decomposition. *Annales Botannici Fennici* 32:141–152.
- Nilsson, S. G., Arup, U., Baranowski, R., Ekman, S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* 9:1208–1215.
- Nordén, B., Larsson, K.– H. 1999. Basidiospore dispersal in the old-growth forest fungus *Phlebia centrifuga* (Basidiomycetes). *Nordic Journal of Botany* 20:215–219.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355–364.
- Noss, R. F. 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. *Forest ecology and management* 115:135–146.
- Noss, R. F., Carroll, C., Vance-Borland, K., Wuertner, G. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the greater Yellowstone ecosystems. *Conservation Biology* 16:895–908.
- Peterson, G. D., Cumming, G. S., Carpenter, S. R. 2003. Scenario planning: a tool for conservation in an uncertain world. *Conservation Biology* 17: 358–366.
- Pimm, S. L., Lawton, J. H. 1998. Planning for biodiversity. *Science* 279:2068–2069.
- Possingham, H., Ball, I., Andelman, S. 2000. Mathematical methods for identifying representative reserve network. Pages 291–306 in S. Ferson, and M. Burgman, editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D.W. Gibbon 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335–337.
- Prendergast, J. R., Eversham, B. C. 1997. Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. *Ecography* 20:210–215.
- Prendergast, J. R., Quinn, R.M., Lawton, J.H. 1999. The gaps between theory and practice in selecting nature reserves. *Conservation Biology* 13:484–492.
- Pressey, R. L., Nicholls, A. O. 1989. Efficiency in conservation evaluation: scoring versus iterative approaches. *Biological Conservation* 50:199–218.
- Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright R. I., Williams, P. H. 1993. Beyond opportunism: key principles for systematic reserve selection. *TREE* 8:124–128.
- Pressey, R. L. 1994. *Ad hoc* reservations: forward or backward steps in developing representative reserve systems? *Conservation Biology* 8:662–668.
- Pressey, R. L., Ferrier, S., Hager, T. C., Woods, C. A., Tully, S.L., Weinman, K.M. 1996. How well protected are the forests of north-eastern New South Wales? — Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. *Forest Ecology and Management* 85:311–333.
- Pressey, R. L., Possingham, H. P., Day, J. R. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biological Conservation* 80:201–219.
- Quinn, G. P., Keough, M. J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- Rassi, P. 1993. Frequency score of Coleoptera in Finland 1.1960–1.1990 (Report no. 6). WWF Finland, Helsinki.
- Rassi, P., Mannerkoski, I., Peltonen, S.-L. Alanen, A. 2000. 2<sup>nd</sup> red data book of Finland. Ministry of Environment, Helsinki.
- Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35:1–51.
- Rodrigues, A. S., Cerdeira, J. O., Gaston, K. J. 2000. Flexibility, efficiency, and accountability: adaptive reserve selection algorithm to more complex conservation problems. *Ecography* 23: 565–574.
- Rodrigues, A. S. L., Gaston, K. J. 2002. Optimisation in reserve selection procedures – why not? *Biological Conservation* 107: 123–129.
- Rothley, K. D. 1999. Designing bioreserve networks to satisfy multiple, conflicting demands. *Ecological Applications* 9:741–750.
- Ryti, R. R. 1992. Effect of the focal taxon on the selection of nature reserves. *Ecological Applications* 2:404–410.
- Saetersdal, M., Line, J. M., Birks H. J. 1993. How to maximize biological diversity in nature reserve selection: vascular plants and breeding birds in deciduous woodlands, Western Norway. *Biological Conservation* 66:131–138.
- Saetersdal, M., Gerda, I., Blom, H., Ihlen, P., Myrseth, E., Pommeresche, R., Skartveit, I.,

- Solhøy, T., Aas, O. 2003. Vascular plants as a surrogate species group in complementary site selection of bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biological Conservation* 115:21–31.
- Saunders, D. A., Hobbs, R. J., Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.
- Shafer, G. L. 1999. National park and reserve planning to protect biological diversity: some basic elements. *Landscape and Urban Planning* 44:123–153.
- Sih, A., Jonsson, B. G., Luikar, G. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* 15:134–135.
- Siitonen, J., Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scandinavian Journal of Forest Research* 9:185–191.
- Siitonen, P., Tanskanen, A., Lehtinen, A. 2003. Selecting forest reserves with a multiobjective spatial algorithm. *Environmental Science and Policy* 6:301–309.
- Simberloff, D. 1998. Flagships, umbrellas and keystones: is a single species management passé in the landscape era? *Biological Conservation* 83:247–257.
- Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L., Huhta E. 2002. Co-variation and indicators of species diversity: can richness of forest dwelling species be predicted in boreal forests? *Ecological Applications* (In press).
- Soulé, M. E. 1987. *Viable populations for conservation*. Cambridge University Press, Cambridge, UK.
- Store, R., Kangas, J. 2001. Integrating spatial multi-criteria evaluation and expert knowledge for GIS-based habitat suitability modelling. *Landscape and Urban Planning* 55:73–93.
- Sverdrup-Thygeson, A., Lindenmayer, D. B. 2002. Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix 2002. *Forest Ecology and management* 5903:1–11.
- Söderström, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in Northeast Sweden. *Biological Conservation* 45:169–178.
- Underhill, L. G. 1994. Optimal and suboptimal reserve selection algorithms. *Biological Conservation* 70:85–87.
- Usher, M. B. 1986. Wildlife conservation evaluation: Attributes, criteria and values. In *Wildlife Conservation Evaluation*, ed. M. B. Usher. Chapman and Hall, London, pp. 3–44.
- Westphal, M., Possingham, H. 2003. Applying a decision-theory framework to landscape planning for biodiversity: Follow-up to Watson et al. *Conservation Biology* 17:327–329.
- Vessby, K., B. Söderström, A. Glimskär, and B. Svensson 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* 16:430–439.
- Virkkala, R., Toivonen, H. 1999. Maintaining biological diversity in Finnish forests. *The Finnish environment* 278. The Finnish Environment Institute, Helsinki.
- Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humpries, C., Pressey, R. 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology* 9:1518–1527.
- Williams, P. H. 1998. Key sites for conservation: area selection methods for biodiversity. In: Mace, G. M., A. Balmford, and J. R. Ginsberg (eds). *Conservation in Changing world*. Cambridge University Press, Cambridge, UK, pp. 211–249.
- Williams, P. H., N. D. Burgess, and C. Rahbek 2000. Flagship species, ecological complementarity, and conservation the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation* 3:249–260.
- Öhman, K., Eriksson, L. O. 2002. Allowing for spatial consideration in long term forest planning by linking linear programming with simulated annealing. *Forest Ecology and Management* 161:221–230.
- Öhman, K., Lämås, T. 2003. Clustering of harvest activities in multi-objective long-term forest planning. *Forest Ecology and Management* 176:161–171
- Önal, H., Briers, R. 2002. Incorporating spatial criteria in optimum reserve network design. *Proceedings of the Royal Society in London* 269:2437–2441.
- Önal, H. 2003. First-best, second best, and heuristic solutions in conservation reserve site selection. *Biological Conservation* (in press).



