

**BIODIVERSITY CONSERVATION
IN FORESTRY: ESSAYS ON THE
ECONOMICS OF SITE SELECTION**

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OULU 2005



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Academic Dissertation to be presented with the assent of
the Faculty of Economics and Business Administration,
University of Oulu, for public discussion in Auditorium
TA105, Linnanmaa, on December 2nd, 2005, at 12 noon

OULUN YLIOPISTO, OULU 2005

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ISBN 951-42-7918-2 (nid.)
ISBN 951-42-7919-0 (PDF) <http://herkules.oulu.fi/isbn9514279190/>
ISSN 1455-2647 <http://herkules.oulu.fi/issn14552647/>

OULU UNIVERSITY PRESS
OULU 2005

Juutinen, Artti, Biodiversity conservation in forestry: essays on the economics of site selection

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2005
Oulu, Finland

Abstract

The purpose of this thesis is to investigate the economics of biodiversity maintenance in boreal forests. From the many tasks available in forest management to improve biodiversity maintenance, the focus is on the lengthening of forest rotation and strict protection, i.e., protected areas. Accordingly, the analysis basis on two different models named forest rotation model and site selection model. Moreover, both socially optimal and cost-effective conservation are considered. The data consists of 32 old-growth stands from northern Finland.

The four studies of this dissertation provide evidence of the non-negligible economic consequences of taking biodiversity services into account along with timber production in the forest management. Study I shows that theoretically the optimal management of initial stands involves three alternatives: immediate clear cutting, delayed harvesting, and protection. Moreover, the numerical analysis reveals that taking into account the biodiversity services along with timber production results in considerably longer optimal rotation than in pure timber production management. Delayed harvesting is the most common option for socially optimal management of old-growth forests. However, the integrated approach results also in strict protection of some stands.

Study II compares alternative approaches, named integrated, ecological and penny pincher selection, for selecting forest reserves. It suggests the integrated selection leads to 9–19% higher conservation cost-efficiency than the other selections. The integrated selection takes into account both the economic value and ecological features of the stands as the other selections focus only on one of these aspects. It seems also that the xeric forest type may be under-represented in the current old-growth forest preservation network in the studied region.

Study III analyses the performance of alternative biodiversity indicators used in the selection of protected areas. It shows that the use of indicators likely results in a loss of species and, therefore, a complete species inventory is necessary if the goal is to maintain all species in the landscape. However, the use of indicators seems to be an economically more efficient practice than to execute a large species survey for habitat protection.

Study IV examines the relative merits of alternative biodiversity conservation targets for forestry, which give different weights to species according to their conservation status and assumed population persistence. Also, socially optimal conservation is solved as a benchmark by maximizing the benefits from timber production and biodiversity services. According the results it is optimal to protect 16 out of 32 stands. Alternative conservation goals give different characters in terms of benefit-cost tradeoffs. More specifically goals relying on complementarity between protected stands result in great marginal costs at a high conservation level.

Keywords: cost-efficiency, environmental economics, forest management, integer programming, socially optimal conservation

Acknowledgement

I am indebted to my advisors, Professor Markku Ollikainen (University of Helsinki) and Professor Rauli Svento (University of Oulu) who supervised my work with good spirit and encouragement. Their support and comments are gratefully acknowledged. In particular, Markku was always willing to read, comment and discuss my ongoing work, regardless his own busy schedule, and I greatly benefited from his ample expertise in the fields of forestry economics and environmental economics.

I like to express my gratitude to the co-authors of the articles for their valuable collaboration. Professor Mikko Mönkkönen (University of Jyväskylä) guided me with intensive discussion to understand the ecological principles of biodiversity. The daily discussions with Erkki Mäntymaa (University of Oulu) encouraged me to continue the work at moments when I was frustrated and the research seemed fruitless. Juha Salmi (Metsähallitus, Rovaniemi) did valuable work by calculating the MELA-simulations for this research. I thank Metsähallitus for fruitful co-operation.

I also want to express my gratitude to the referees of my dissertation work, Professor Erkki Koskela and Professor Jari Kuuluvainen (University of Helsinki). Their comments and criticisms were helpful in refining the draft version of the dissertation to its final form. Their also give me many valuable suggestions for future work.

My thanks are extended to Professor Mikko Puhakka (University of Oulu) and many other colloquies at the Department of Economics for their encouragement and comments. I warmly thank Seppo Eriksson, Leena Ervasti and Seija Hurskainen (University of Oulu) for helping me with many practical and administrative problems during this process. In addition I am grateful for my father and friends for their endless support.

This dissertation has mainly been carried out under the auspices of the Finnish Biodiversity Research Programme (FIBRE). From March 2000 to 2003, I have had the opportunity to participate in the FIBRE project named “Managing boreal forest landscapes for biodiversity: ecological tools and economic implications”. The project was led by Mikko Mönkkönen. Taking part in the work of the multidisciplinary and multi-skilled research team has been an excellent and educative experience. Funding for this research came from the Academy of Finland, the Maj and Tor Nessling Foundation, and the Finnish Forest Industries Federation. Also, I have had funding from the Eemil Aaltonen Foundation, the Finnish Cultural Foundation, the Finnish Society for Forest

Science, the Tauno Tönning Foundation, University of Oulu, and the Yrjö Jahnsso Foundation. The Department of Economics at University of Oulu has provided the practical working conditions to undertake this dissertation. These arrangements have provided me good conditions for completing this dissertation and this support is gratefully acknowledged.

And finally, my deepest gratitude goes to my family, Jaana, Atte and Aapo, who have given me joy and love through the many years of this project.

Oulu, October 2005

Artti Juutinen

List of original articles

The thesis includes the following separate studies, which are referred to in text by means of Roman numerals.

- I Juutinen A (2005) Socially Optimal Biodiversity Conservation in Forestry: An Application of the Hartman Rotation Model. Manuscript.
- II Juutinen A, Mäntymaa E, Mönkkönen M & Salmi J (2004) A Cost-Efficient Approach to Selecting Forest Stands for Conserving Species: A Case Study from Northern Fennoscandia. *Forest Science* 50: 527–539.
- III Juutinen A & Mönkkönen M (2004) Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. *Ecological Economics* 50:35–48.
- IV Juutinen A & Mönkkönen M (2005) Comparing Strategies to Select Protected Areas for Species Conservation in Boreal Forests. Manuscript.

Artti Juutinen is the corresponding author of all articles in the thesis and he participated throughout all stages in studies I–IV. Study II was originally planned by Erkki Mäntymaa and Mikko Mönkkönen. Artti Juutinen implemented the plan and carried out all the calculations, except the MELA-calculations for the study II were done by Juha Salmi. Juutinen was also the main writer of the research report II. Studies III and IV were planned by Artti Juutinen and Mikko Mönkkönen; Artti Juutinen carried out all the calculations and was the main writer of the reports.

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1 Introduction

Forests have a variety of ecological functions and provide a multitude of commodities and services to human beings, such as timber and amenity services. Their production always entails a trade-off. This trade-off is taken into account in optimal forest management by balancing harvest revenue with the marginal amenity benefits. The most current and urgent challenge to forest management is conserving forest biodiversity along with timber production. In boreal forests, biodiversity maintenance is usually thought to require a network of totally preserved forest areas surrounded by forests under restricted management and commercial forests.¹ In this dissertation we focus on biodiversity maintenance and ask: what does this imply for forest management in terms of socially optimal rotation and strict protection?

Historically, in forests economics the focus has largely been on efficient timber management. A classical analytical approach for efficient timber production in terms of optimal forest rotation is the Faustmann model, in which forest owners are assumed to maximize the present value of net harvesting revenue (Faustmann 1849). Reed (1986) provides a survey, for example.

A framework suitable to analyzing biodiversity maintenance as an integral part of forest management dates back to Hartman's (1976) seminal work, which included amenity services in the classical forest rotation model by assuming that forest land's present value depends on the forest stock along with net incomes from harvesting. He showed that if the amenity benefits are increasing with the rotation age, then the optimal rotation age for the forest will exceed the Faustmann rotation age thereby delaying the

¹ Forest management is the major cause for species loss and endangerment in the Fennoscandian forests (Esseen *et al.* 1997, Rassi *et al.* 2001). At landscape level, the key features include habitat loss and fragmentation, which are important in particular regarding old-growth forests and species indigenous to these forest types. Due to forestry most natural forest has been lost, patch sizes have decreased and the isolation of stands has increased. At stand level, mono-cultural harvesting practices have resulted in homogenous even-age stands lacking structures, such as existence of decaying wood and deciduous trees that are important features for many forest dwelling species. As Hanski (2000) pointed out, the exact ecological requirements of most species harbouring in boreal forests remain unknown, but a large number of species have become adapted to live under conditions that are rarely found in intensively managed forest landscapes. Consequently, 566 forest species are currently classified as threatened in Finland, out of the ca 20 000 species for which sufficient knowledge is available to allow the classification (Rassi *et al.* 2001). Moreover, the extinction debt of boreal forest species is estimated to be of the order of 1000 species in Finland (Hanski 2000).

harvest (see also Strang 1983). If environmental values are high enough, the forest will not be harvested at all, i.e., the forest is strictly protected.

Hartman's approach is relevant for biodiversity maintenance, because maintaining biodiversity yields benefits in a similar fashion as a forest provides, e.g. recreational services. Delayed harvesting and strict protection can be seen as means for biodiversity maintenance. However, the concept of amenity value is too broad for a precise analysis of efficient biodiversity maintenance in forests and therefore this framework has to be tailored to reflect a more specific description of biodiversity. Importantly, this modification should be based on biological knowledge on different aspects of biodiversity.

As far as we know there exist only two studies which are based on Hartman's approach which have considered explicitly biodiversity services.² Koskela *et al.* (2004) examined the economics of biodiversity conservation at the stand level by extending the Hartman model to take into account green tree retention. Moreover, they assessed empirically the optimal volume of retention trees and optimal rotation ages in a simulation model calibrated to Finnish pine forestry. They found that biodiversity conservation may increase the socially optimal rotation age far beyond the Faustmann rotation age. Koskela *et al.* (2005) extended the analysis of green tree retention by defining analytically the first-best instruments to induce the Faustmannian or Hartmanian private landowners to behave in a socially optimal manner. They provided also numerical simulations for optimal biodiversity policies.

So far we have considered forest management at stand level. Typically, biodiversity management requires, however, a wider perspective. A forest area, comprising of many stands, sustains a given ecosystem, so that harvesting a stand would have a considerable impact on the whole ecosystem (Koskela and Ollikainen 2001). Thus, harvesting a stand cannot be done independently of other adjacent stands, because there is spatial interdependence between stands in a forest area in terms of biodiversity services. There exist only a few analytical studies of the economic problem behind stand interdependence (Bowes and Krutila 1985, 1989, Swallow and Wear 1993, Swallow *et al.* 1997, Koskela and Ollikainen 2001, Amacher *et al.* 2004). So far, the stand interdependence has not been analysed analytically with a specific description for biodiversity, although Koskela and Ollikainen (2001) using the Hartman model provided a thorough analytical treatment of alternative time paths for non-timber benefits.

² There are also other related studies devoted to the economic potential, costs and benefits of ecological forest management (e.g., Montgomery *et al.* 1994, Haight 1995, Bevers and Hof 1999, Calkin *et al.* 2002). These studies integrate timber production and species viability for forest management. The viability is based on species population dynamics (growth and dispersal), which is affected by harvesting. Montgomery *et al.* (1999) used a site-selection approach which integrates species viability and the opportunity costs of conservation, but their study included also other land uses than forest management (see also Haight *et al.* 2002). Typically, only single species or taxonomic group has been considered in these type studies. Lichtenstein and Montgomery (2003) attempted to bridge the gap between studies that model cost-effective land management for single species and studies that model large set of species or biodiversity. Nalle *et al.* (2004) developed a method that combines economic and ecological models in a dynamic and spatial analysis to evaluate land use decisions and find cost-effective land use alternatives. They demonstrated the method by using two species with different habitat preferences to illustrate tradeoffs among ecological objectives as well as the more commonly recognized tradeoffs between economic and ecological objectives. They compared also the dynamic approach with a static reserve approach and found that the former is substantially more efficient than the latter.

There exist, however, an extensive literature on spatial interdependence in the context of site selection models. These empirical studies have focused on strict protection and applied numeric optimization models to find out the most efficient conservation networks given the goals and restrictions of the conservation. The site selection approach, where a land manager has to decide whether to harvest or protect a stand, is particularly useful when considering the protection of old-growth forests, since clear cutting combined with regeneration is the dominant silvicultural method in Fennoscandia.³

Site selection models have widely been used in the biodiversity conservation literature (e.g., Kershaw *et al.* 1995, Hacker *et al.* 1998, Snyder *et al.* 1999, Polasky *et al.* 2000), but in most cases, economical aspects have not been adequately taken into account since sites are assumed to have equal value. This unjustified assumption may severely impede cost-efficient conservation planning. For example, using county-level data for the United States, Ando *et al.* (1998) showed that accounting for heterogeneity in land prices results in a notable increase in efficiency in terms of either the cost of achieving a fixed coverage of species or the coverage attained from a fixed budget. Similar results were also demonstrated by Balmford *et al.* (2000) in a global context and by Polasky *et al.* (2001) for the state of Oregon, USA. However, these studies, which we will call integrated site selection models, operated on far larger level than most forest management planning and operations are conducted. From a practical point of view, it is necessary to address cost-efficiency at the scale which is relevant for forest managers, e.g., landscape scale (see, e.g., Mönkkönen 1999).

Applications of the integrated site selection approach to protection of forest are few (see footnote 2). To our knowledge, only Stokland (1997) has compared the efficiency of alternative selection strategies, with an aim at maximizing the number of species and also including the opportunity costs of conservation. Nonetheless, generalizing his results is difficult since opportunity costs were not measured directly and only a narrow selection of taxa were used in the analysis.

It is costly to make field inventories and measure biodiversity. Therefore land managers use surrogate measures that are easily available in the forest management and biodiversity protection. This practise results in inefficient conservation if the indicator does not reflect overall biodiversity accurately. Using site selection models it is possible to test systematically how well a particular indicator reflects overall biodiversity (e.g., Virolainen *et al.* 2000). However, previous studies have not tested indicators adequately from economic viewpoint because they have assumed that sites have equal value and inventory costs have not taken into account in the test (see Flather *et al.* 1997, and McGeoch 1998, for reviews on indicator studies). Balmford and Gaston (1999) have,

³ Forest protection can largely be considered as following a site selection problem: how is one to choose the best targets given that conservation is costly and the funds for conservation are limited? For example, a new type of management, called landscape ecological forest management, has been implemented in Finland for state owned forests (Halman *et al.* 1996). Under this paradigm, forest stands are not managed in isolation from the surrounding landscape, but entire landscapes, usually consisting of some tens of thousands of hectares, are considered a planning unit (Mönkkönen 1999). The main tools used in this management planning system include mimicking natural disturbance regimes in harvesting, enhancing possibilities for species to move among habitat patches through increasing connectivity by designing movement corridors and stepping stones, and setting some stands aside from commercial harvesting (i.e., buffer and restoration zones) either temporarily or permanently.

however, assessed the benefits of high quality biodiversity inventories and found them valuable.

Site selection models are flexible and many alternative measures for biodiversity have been used in the analysis (e.g., Margules *et al.* 1988, Kershaw *et al.* 1995, Church *et al.* 1996, Pressey *et al.* 1997, Hacker *et al.* 1998, Howard *et al.* 1998, Williams 1998, Arthur *et al.* 2002). The most common measure has been the number of species. Another widely used practice has been to favour threatened or rare species to common species. Site selection models have also been used in the context of habitat diversity (Snyder *et al.* 1999). Recently, species viability and uncertainty have got lot of attention in these studies (Church *et al.* 2000, Haight *et al.* 2000, Polasky *et al.* 2000, Rodrigues *et al.* 2000, Williams and Araújo 2000, Haight *et al.* 2002, Lichtenstein and Montgomery 2003). However, these alternative aspects of biodiversity have not been analysed in the economic context taking into account the costs of conservation and the value of biodiversity.

To investigate efficient biodiversity maintenance one needs to determine precisely what is meant by biodiversity and how it is measured. The term biodiversity – a contraction of ‘biological diversity’ or ‘biotic diversity’ – refers to the diversity of life at all levels of the biological hierarchy. Biodiversity is commonly considered at the genetic, species and ecosystems levels (Noss 1990), but it is important to note that it embodies linkages between these different levels. Thus, biodiversity is a very complex and manifold concept, which can be interpreted and analysed on a number of levels and scales (see, e.g., Pearce and Moran 1994 or Gaston 1996 for more detailed discussion of the meaning of biodiversity). Moreover, it is important to note that biodiversity conservation reflects two aspects: representativeness and persistence (Margules and Pressey 2000). The former indicates that due to the conservation efforts the forests should represent as widely as possible the ecological characteristics that are typical for a given region. The latter reflects the ecosystem integrity and species viability. Thus, it is not enough to secure that those biological features which are considered important are represented in a given area today, but they must also be maintained in the long run.

We focus on species diversity and use the number of species as a metric of biodiversity. Species richness is a simple and transparent measure and it is often positively correlated with many other (genetic, taxonomic, functional, etc.) measures of biodiversity (Gaston 1996, Gaston and Spicer 1998). Moreover, by using the number of species as a measure for biodiversity at landscape level it is possible to take into account, how well the areas supplement each other regarding their biological features in the analysis.

We contribute to the literature by consider two different approaches. In the first approach (study I) we use the classical forest rotation model (Faustmann 1849) extended with amenity services (Hartman 1976). In the second approach (studies II–IV) we use site selection models. In all these studies we use empirical data from 32 old-growth forests stands from northern Finland.

More precisely, in the first approach, we specify the amenity services for biodiversity conservation using species presence function and link this biodiversity metrics to the economic value of biodiversity conservation, for the first time in the literature to our knowledge. We execute an analysis and demonstrate theoretically that the optimal management of initial stands involves three alternatives: immediate clear cutting, delayed

harvesting, and protection (Hartman 1976, Strang 1983). We present also an empirical application for this approach. Our parametric model shows that taking into account the biodiversity services along with timber production results in considerably longer optimal rotation than in pure timber production management (Koskela *et al.* 2004). Delayed harvesting is the most common option for socially optimal management of old-growth forests. However, the integrated approach results also in strict protection of some stands.

In the second approach (studies II–IV) we use static site selection models in conjunction with empirical applications. In study II, we integrate timber production and biodiversity conservation by developing budget-constrained models that result in cost-effective selection of protected areas (Stokland 1997, Ando *et al.* 1998, Balmford *et al.* 2000, Polasky *et al.* 2001). These models maximize species diversity under a given budget constraint, which ensures that the opportunity costs of conservation do not exceed the allowable funds for conservation. In contrast to previous studies, we consider a wide variety of forest species. We also measure the opportunity costs accurately as forgone timber revenues defined in an optimal rotation solution. Further, we make the empirical analysis at the spatial level, where the decision making take place in practise. Using alternative variants of site selection models we found that the integrated model leads to 9–19% higher conservation cost-efficiency than the other models. Moreover, the current old-growth forest preservation network in this region may not represent accurately the given forest types.

It may be difficult to apply integrated site selection using number of species as biodiversity metric in practice, because this requires expensive species inventories. Therefore it is important to find cost-effective indicators for species richness. We address this issue in study III by developing a method for testing indicators in economic context while the previous literature has focused on the ecological aspect. We show that the use of indicators likely results in a loss of species and, therefore, a complete species inventory is necessary if the goal is to maintain all species in the landscape (Flather *et al.* 1997, Oliver *et al.* 1998, van Jaarsvelt *et al.* 1998, Chase *et al.* 2000, Reyers *et al.* 2000). However, the use of indicators seems to be an economically more efficient practice than to execute a large species survey for habitat protection in our case study.

To select protected areas cost-efficiently, land managers should set explicit conservation goals. There are, however, multiple aspects in determining species diversity, and these may have different economical implications. To address this problem, we formulated a benchmark model, which maximizes the benefits from timber production and biodiversity services representing socially optimal conservation in study IV. We also developed an optimisation framework for choosing the habitat-protection strategy that maximizes the number of species subject to an upper bound on funding. We used the framework to compare six alternative strategies based on the different conservation goals with respect to the trade-off between biodiversity protection and opportunity costs of conservation. The strategies differed given unequal weight to species according to their conservation status, and assumed population persistence. We found that it is optimal to protect 16 out of 32 stands. Moreover, the alternative strategies have different characters in terms of benefit-cost tradeoffs. Particularly, the strategies taking into account the complementarity among protected stands result in large marginal costs at high conservation level.

The rest of this thesis is organized as follows. In the next section, we present the data. Section 3 includes the summaries of studies I–IV. Finally, in the appendix we present the original articles.

2 Data

In this section we briefly describe the data used in studies I–IV. The main focus is on highlighting the differences in how the data was applied in separate studies. A more detailed description can be found in the original articles (see appendix).

The data for empirical applications originate from 32 forests stands in northern Finland within two landscape ecological forest management areas, Puhos and Siikavaara (Fig. 1). The forests in the study area are not totally intact old-growth stands, because the most valuable timber was removed during the 19th and early 20th century by selective harvesting. However, these stands were considered to be the best targets for the complementation of the Finnish old forest conservation network (Ministry of the Environment 1996). The age of the stands varied between 116–176 years (Table 1).

Four forest site types were chosen and eight stands of each type were surveyed: xeric coniferous forests, mesic spruce forests, spruce mires, and herb-rich spruce dominated heath forests. These site types cover the whole gradient of forests in the region and represent a fertility gradient ranging from barren pine heaths to herb-rich forests. Accordingly, the timber volume of the stands varied between 75–397 m³/ha (Table 1).

Beetles, birds, wood-inhabiting fungi and vascular plants were sampled in each stand. These taxa were selected to cover a wide array of dispersal potential and life forms in order to yield general results. The data consists of 103 vascular plants, 30 forest birds, 64 wood-inhabiting fungi, and 435 beetle species, making a total number of species of 632. The number of species varied from 124 to 202 species at stand level (Table 1). The species were typically treated as having equal importance in the analysis, but in study IV weights for these species were assigned according to their threatened status and rarity.

For studies II–IV the opportunity costs were measured as forgone timber revenues defined in an optimal rotation solution for stand management, thus including both the land value and the value of standing timber. Finnish forestry planning model, called MELA, was used to calculate the site value for each stand (Siitonen *et al.* 1996). MELA approximates the Faustmann approach taking into account several alternative forest treatment schedules and timber assortments. The same MELA-results were used for study I, but the site values for each stand were calculated strictly according to the classical Faustmann approach, which includes only one timber assortment and focus on final felling omitting, e.g., thinning. More precisely, we picked certain MELA-simulations and used them as data to construct timber growth functions for each stand. These single

variable time-dependent functions are by far simpler than the growth functions used in MELA.

For study III we calculated the inventory costs for the alternative species group, which were considered as potential indicators for overall diversity. The inventory costs are based on the actual time and effort spent to collect the data for that particular group including the travel costs, materials, and working hours for field work and species identification. These costs cannot be calculated for each stand separately because all 32 stands should have been inventoried anyway. Likewise, it is not reasonable to express these costs per hectare because each stand irrespective of its size was sampled with equal effort.



Fig. 1. Location of the study areas. The vegetation zones are based on Kalliola (1973).

For studies I and IV empirical results on Finnish households willingness to pay for increased biodiversity conservation (Mäntymaa *et al.* 2002) were used to value biodiversity benefits and investigate the socially optimal conservation. This social value of biodiversity includes all sources of value, such as use values, existence values and option values. In study I, the value from biodiversity based on the annual willingness to pay. More precisely, we used an average figure calculated over the different conservation

programs that were presented in the questionnaire. In contrast, the figures of the total willingness to pay at different levels of conservation were used in study IV. To calculate the total willingness to pay we applied 30-year payment schedule, as was told to respondents in the questionnaire, and used a four percent discount rate.

Table 1. Forest type, age, timber volume, and total number of species of the studied stands.

Stand	Forest type	Age, years	Timber volume, m ³ /ha	Number of species
1	xeric	117	86	151
2	xeric	116	186	158
3	xeric	136	147	158
4	xeric	135	171	137
5	xeric	122	203	166
6	xeric	138	135	156
7	xeric	136	178	136
8	xeric	127	188	161
9	mesic	119	196	157
10	mesic	143	186	137
11	mesic	143	186	124
12	mesic	162	75	158
13	mesic	138	241	144
14	mesic	156	128	148
15	mesic	120	124	131
16	mesic	135	150	139
17	spruce mires	123	140	179
18	spruce mires	115	162	146
19	spruce mires	142	99	177
20	spruce mires	144	147	168
21	spruce mires	117	177	148
22	spruce mires	176	127	150
23	spruce mires	135	114	181
24	spruce mires	145	178	173
25	herb-rich	143	196	163
26	herb-rich	116	288	149
27	herb-rich	122	397	153
28	herb-rich	176	133	202
29	herb-rich	176	133	148
30	herb-rich	176	133	169
31	herb-rich	130	123	152
32	herb-rich	143	212	165

3 Summary of the articles

3.1 Socially Optimal Biodiversity Conservation in Forestry: An Application of the Hartman Rotation Model (study I)

Study I analyzes socially optimal forest management in terms of the rotation period and strict protection of stands when society values biodiversity services and harvest revenue. A framework suitable to analyzing biodiversity maintenance as an integral part of forest management dates back to Hartman's work (1976), which included amenity services into the classical forest rotation model (see also Strang 1983). We tailor this approach to reflect a more specific description of biodiversity.

Recognizing that biodiversity has multiple facets and can be defined and measured in different ways at various levels of biological hierarchy (Noss 1990), we focus on species richness (cf. Weitzman 1993 and Solow *et al.* 1993). The next relevant question is how the stand and species are linked together in time? This linkage provides in fact a rather complex process from which we take into account only two general properties. First, forest stands have different ecological characteristics, and therefore, they provide habitats for different species. Second, these characteristics change due to forest succession. This implies that the number of species found in a given stand differs between stands and it depends positively on the age of the stand (Siitonen *et al.* 2000, Siitonen 2001). Following these simplified principles, we formulate a species presence function and incorporate it into the Hartman model.

After determining the biodiversity metric, we will link the number of species to the value of biodiversity services assuming that the biodiversity valuation is a function of the number of species found in a given stand. This can be justified by noting that the biodiversity value of a given stand evidently depends on its ecological characteristics, such as the species prevailing there (see Lehtonen *et al.* 2003). Since the number of species is an increasing function of the age of the stand, also the value of biodiversity will increase with the age of the stand.

Reflecting the actual conservation situation, we assume that the social planner has an initial old-growth stand as these are the most threatened forest habitat types needing strict protection. As is well known, the presence of the initial stand implies that the rotation

problem can most conveniently be studied in two phases (Johansson and Löfgren 1985, p. 86). First, the social planner decides upon the use of the initial stand. Then, from that point onwards the choice reduces to a conventional steady-state choice of rotation age. Our focus is on the stand level management, which can be seen as a starting point for an extended analysis at the landscape level.

After developing a general biodiversity model, we examine the properties of efficient forest management and biodiversity maintenance. We demonstrate theoretically that the optimal management of initial stands involves three alternatives: immediate clear cutting, delayed harvesting, and protection. We also consider the qualitative properties of the optimal rotation age of the initial forest. It turned out that a higher species presence will increase the rotation age. The interpretation of this result is straightforward. The more suitable environment a stand provides for species, the longer a landowner who values also biodiversity services will wait for the first harvesting

We then present a parametric application of this approach using site-specific empirical data. We select specific functional forms for timber production, species presence, and biodiversity valuation and calibrate the exogenous parameters. Our parametric model shows that taking into account the biodiversity services along with timber production results in considerably longer optimal rotation than in pure timber production management (Koskela *et al.* 2004). Delayed harvesting is the most common option for socially optimal management of old-growth forests. However, the integrated approach results also in strict protection of seven out of 32 old-growth forests. Recall that our sample includes four forest types, having eight stands of each type. The protected stands were spruce mires (5 stands) and xeric (2 stands) forests. Mesic spruce forests and herb-rich forests were all harvested. Thus the protected forests did not represent all the available habitat types in our case study.

We examined also how the results, i.e. the number of protected stands, change as the parameter values which were used in original analysis change and considered how the results depend on selected functional forms. Interestingly, the impacts of change in parameter values were asymmetric. The effect which lengthens the optimal rotation age increased the number of protected stands more than they were reduced due the effect which shortens the optimal rotation age. Moreover, it turned out that all the initial forests, except one, would be protected if the forests would not grow but rather stay at the initial timber volume level. Based on MELA simulations all the forests were still growing, although we are dealing with old-growth forests. Thus, the prerequisite for these outcomes appears to be the growth of the timber volume.

3.2 A Cost-Efficient Approach to Selecting Forest Stands for Conserving Species: A Case Study from Northern Fennoscandia (study II)

Study II analyzes cost-efficient conservation of boreal old-growth forests using site selection framework. We integrate economic and ecological aspects to construct alternative forest preservation networks that would maintain a maximum amount of

diversity of species prevalent in old-growth forests under a given budget constraint (Ando *et al.* 1998, Balmford *et al.* 2000, Polasky *et al.* 2001). The objective of the study is, first, to compare alternative conservation models in terms of selected species, forest types, and associated costs, i.e., assess the relative performance of these methods. Second, we relate the ideal solution provided by these models to the current conservation network to make recommendations how to supplement the existing network in a cost-efficient way.

For this purpose, we develop three models, and solve them numerically. The first model is the integrated model, which we use as a benchmark. The second is the traditional ecological model, which represents recently adopted practices in landscape ecological forest management, and is based on ecological arguments for reserve site selection (Mönkkönen 1999). Our third model is called “penny-pincher selection” where the conservation network is established beginning with low-cost sites in order to get as large an area as possible under conservation and to avoid conflicts among land uses. For instance, conserved areas in Fennoscandia are located mainly on low productivity lands (Nilsson and Götmarm 1992, Virkkala 1996, Stokland 1997).

We first examined how the species representation in the selected conservation network varies as a function of opportunity costs for all three models by varying the budget or the site constraint. It turned out that the target functions of the models are growing and discontinuous and their shapes depend on the level of the opportunity costs. Interestingly, we found that there is a critical threshold value for the budget size in the integrated model. Below the budget size of 17 000 USD, it is optimal to select the stands with the lowest opportunity costs and to establish as large a network as possible, since any increase in the number of stands rapidly increases the species representation. Above this threshold and given that the network includes eight stands, the complementarity of selected stands becomes more important than the size of the network as such. It is no longer optimal to select the nine cheapest stands, for example, because with this budget there is a combination of eight stands available covering a larger number of species.

We also examined the cost differences between the models. It turned out that, when only few stands are selected into conservation network, the ecological selection is clearly more expensive than the integrated selection. In contrast, the penny-pincher selection costs as much as integrated selection at this low level of conservation. The cost difference between ecological and integrated selection reduces as the number of protected stands and species coverage increases while the opposite occurs between penny-pincher and integrated selection. We also calculated the mean values of cost differences over the whole range of species represented (168–632). Penny-pincher selection costs, on average, 9% more than integrated selection. The respective figure for ecological selection varies between 15–19% depending on whether the minimum or the maximum cost solutions are considered.⁴ Thus, the integrated selection method saves considerable amounts of money relative to the other two selections. Interestingly, penny-pincher selection can provide the same number of species as ecological selection but with lower average costs.

Next we analyzed how different forest types are represented in the selected conservation network. The spruce mire is the dominant forest type in the integrated

⁴ Ecological models usually have multiple optimal solutions (with several sets of stands all containing the same number of species). When this happens we represent them with the minimum and maximum opportunity costs to show the variation in the results. The cases are named minimum and maximum cost solutions.

selection, particularly at low budget levels, because spruce mires have, on average, the lowest forest value. The proportions of the other types vary rather widely, at low budget levels. Above the opportunity costs of about 17 000 USD, it is optimal to initially include at least one stand of each type in the network. As funds increase, the share of xeric and herb-rich forests increases, while that of spruce mires decreases. From practical viewpoint, the result indicates that the xeric forest types may be an important target for conservation along with spruce mires and herb-rich forests. Thus, these types may be under-represented in the current conservation network in the study area. Forest type selection is rather different in the ecological model. The most important forest types for biodiversity conservation are the herb-rich forests and the spruce mires. Also xeric forests contribute rather much to the optimal conservation network, with mesic forests clearly showing the lowest contribution. Mesic forests become selected only when about half of the total conservation budget is used. Interestingly, in ecological selection, all forest types do not become represented in the optimal network until conservation efforts were at a high level.

Our material includes four taxonomic groups representing a wide array of taxa inhabiting boreal old forests. It appears that our results depend on the selected groups. Obviously, taxa with a relatively high number of species, such as beetles, have a strong effect on the results. However, the size of the taxa is not the only factor contributing to the results. Another crucial factor is the level of habitat specialization of various taxa. For instance, there are less wood-inhabiting fungi species than vascular plants, but still complete conservation of fungi incurs higher costs than the full coverage of vascular plants.

Maximizing just the number of species subject to a budget constraint may result in a network of areas that cannot support species persistence in the long run (Virolainen *et al.* 1999, Rodrigues *et al.* 2000). In order to assess the validity of our previous results, we executed an optimization aiming to maximize the abundance of each species in the selected network subject to a budget constraint. It turned out that the difference between species richness and abundance method was minor. Therefore, it seems that the representation approach based on presence-absence data effectively controls also for species abundance. This may stem from the pattern that species richness often correlates with species abundance (e.g., Rosenzweig 1995). The two methods, however, differed with respect to the cost differences among the three selection models. When abundance was included as a goal in selection, the difference between integrated and ecological selection increased to an average of 25% from 15–19% in the original approach, but the penny-pincher model was almost as cost-effective as the integrated model, the difference being only 3% on average (9% in the original approach).

3.3 A Testing Alternative Indicators for Biodiversity Conservation in Old-Growth Boreal Forests: Ecology and Economics (study III)

The protection of regional biodiversity requires that priority for the protection of individual areas be based on the contribution, which the area can make to represent overall biodiversity. However, it may be extremely costly to measure this contribution for all potential sites. Therefore, area selection procedures have to rely on surrogate measures of biodiversity (Faith and Walker 1996). As a result, choosing the best possible indicators becomes a crucial step in biodiversity maintenance.

We search for indicators for species conservation. We first study whether taxonomic groups, beetles, birds, vascular plants, and wood-inhabiting fungi, can be used as indicators. We test, for example, whether birds can be used as indicators for other taxa. We also test whether or not a specified sub-group of species (including species of birds, beetles and fungi; hereafter named as the old-growth forest indicator species), which earlier studies suggest to indicate old-growth forest conditions, cover the variation in overall species richness of old-growth forests.

To test these indicators, we develop the following method by using site selection models. First, we run the site selection procedures using optimisation algorithms separately for different potential indicators. Second, we execute the optimisation for benchmark selection by using information of all species. Thus, the benchmark selection represents, by assumption, the maximum level of biodiversity in the region at given resources devoted to conservation. Third, we compare the results from indicator-based area selection with the results from site selection based on information of all species to study how well biodiversity become conserved when using information of indicators only. Based on this comparison, we end up with a ranking of potential indicators. However, we execute the ranking by using two alternative site selection procedures, the ecological and integrated model. The ecological model uses information on species presence/absence only by maximising species richness under a given upper limit for a number of protected sites (Howard *et al.* 1998, van Jaarsveld *et al.* 1998, Reyers *et al.* 2000, Virolainen *et al.* 2000), whereas the integrated model explicitly takes into account both economic and ecological aspects of biodiversity by maximising species richness under a given budget constraint (Ando *et al.* 1998, Balmford *et al.* 2000, Polasky *et al.* 2001). Comparisons between integrated and ecological selections allow us to see if the ranking remains the same when the costs of biodiversity surveys as well as the opportunity costs of conservation are incorporated into the procedure.

More precisely we use two different types of site selection models named DIV and NUM in the analysis. The name DIV refers to species diversity, i.e., one selects stands that supplement each other from the viewpoint of species richness (the complementarity model). The DIV model, which incorporates information on all species, is the benchmark model with which all the other models are compared. NUM indicates that, in this model type, a given species is counted numerous times in the target function, if it is present on several protected stands. Thus, the NUM model resembles a scoring procedure, i.e., stands are given some conservation value which does not depend on the selected

conservation network. If species number in an indicator species group is small, all species may become included into the network after just a few stands are selected. In such cases, the DIV models can no longer be used to select the remaining stands according to their conservation value, i.e. the operative range of DIV models is limited.⁵ By using the NUM type model, stands can be ranked even though all species are already covered by the existing conservation area network. If the DIV and NUM models include the budget or area constraint, they are named as integrated (IDIV and INUM) or ecological models (EDIV and ENUM), respectively.

We first test indicators from a purely ecological perspective. In general, areas selected by using the indicator species criteria cover less species in total than the areas picked by the benchmark selection. Beetles and vascular plants seem to be the best indicators when protected areas are picked by the EDIV model. Understandably, beetles cannot be a poor indicator group, when economic costs are ignored, since about 68% of the species are beetles in our sample and the aim is to maximize species richness. Vascular plants are a good indicator group, because spruce mires and herb rich forests are the most important forest types in ecological optimisation for all species, and these types have a high diversity of vascular plants (see study II). Birds and the old-growth forest indicator species seem to perform the worst as overall indicators of total species richness when protected areas are picked by the EDIV model. The ENUM models result in same ranking of the indicator species as the EDIV models. Interestingly, the scoring model outperforms the complementarity model for birds and old-growth forest indicator species, the groups in which the number of species are the smallest.

The ecological test does not consider the differences in the inventory and opportunity costs between alternative indicators, thus we next incorporate these into the analysis. Because the inventory costs are independent of the level of conservation, at low levels of conservation in terms of species representation, the share of inventory costs from total costs is high, and they may dominate the cost pattern. This is clearly the case when we consider the benchmark or the costs of using beetles or old-growth forest indicator species as an indicator group, because their inventory costs are the highest. It is typical for all the models that the opportunity costs increase exponentially as the species coverage increases, i.e., the marginal costs of conservation are increasing. If a particular species group is a poor indicator, its use will increase the opportunity costs of conservation relative to better indicators.

In order to rank the indicators, we calculated the relative cost differences between indicator models (IDIV) and the benchmark. Vascular plants seem to be the best indicator group. The mean cost difference between the benchmark and vascular plants is bigger than the differences for other groups at every particular level of species represented. However, a general pattern in these results is that the wider the operative range of an indicator, the smaller is the total average cost difference (calculated over the whole operative range of an indicator) because of fixed inventory costs. The operative range of vascular plants is larger than birds, for example. Therefore, the total average cost difference of birds is the highest 79%, but birds are, however, an inferior indicator group

⁵ The operative range of an indicator is the range of conservation costs or number of sites, in which the indicator species are not all represented in the selected conservation network. After the indicator species are fully represented, the remaining unprotected stands cannot be selected by using the indicator.

relative to vascular plants at its operative range. Thus, it is not straightforward to rank the indicators by using IDIV models, because the operative ranges of indicators vary.

We calculated also the relative cost differences between the INUM models and the benchmark. In the INUM models, the operative ranges of the indicators are same. Interestingly, the scoring procedure seems to be more effective than the complementarity models in representing all species. Only for beetles, where the number of species is rather high, the INUM model is poorer than the IDIV model. According to the INUM optimisations, birds are the best indicators, and vascular plants are almost as good as birds. Beetles and old-forest indicators are the poorest indicators.

3.4 Comparing Strategies to Select Protected Areas for Species Conservation in Boreal Forests (study IV)

Forest protection can largely be considered as the following site selection problem: how to choose the best forest areas given that conservation is costly and the funds for conservation are limited? To solve this problem, a land manager has to define explicit goals for conservation. This is difficult, however, because biodiversity has multiple facets and can be measured at different levels of biological hierarchy (Noss 1990). It is not so easy to define a precise diversity measure either (Weitzman 1992). This indicates that several alternative strategies, addressing the range of interests and objectives, can be used to guide decision makers towards those choices which society would be willing to accept (Williams and ReVelle 2002). To shed light on this issue, we compare alternative site selection models, which aim to efficient forest biodiversity maintenance.

More precisely, we ask how alternative conservation goals perform in terms of their biological features and economic properties when the site selection is made subject to a binding budget constraint. We organize this assessment in two phases as follows. First, we develop a benchmark model which reflects the socially optimal conservation obtained by maximizing the sum of harvest revenue and biodiversity benefits. Second, from this optimal solution we infer the “optimal” conservation budget, which we then use to solve the cost-effective site selection for other conservation goals. We use six budget-constrained models which differ in terms of their more specific goals giving unequal weight to species according to three criteria: conservation status, abundance and assumed population persistence. We compare these budget-constrained solutions with the socially optimal solution and analyse pros and cons of achieving these alternative goals.

Our budget-constrained models can be described as follows. Model 1 (Species richness) maximizes the number of species in the selected conservation network. Model 2 (Red-listed species) maximizes also species richness, but the species are assigned a weight according to their threatened status. In model 3 (Rare species) we give weights to the species according to their rarity. Model 4 (Multiple representation) maximizes the number of species at stand level. Model 5 (Red-listed species + abundance) is similar to model 2, but it maximizes species abundance in addition to the number of species weighted by species threatened status. Model 6 (Rare species + abundance) maximizes species abundance and the number of species weighted by species rarity.

It is socially optimal to protect 16 out of 32 stands. The sensitivity analysis showed, however, that the optimal number of protected stands depends strongly on the value of biodiversity services. The original result is more sensitive to scaling-down biodiversity values than scaling-up. A 20% reduction in the level of biodiversity value, for example, reduces the optimal number of protected stands by 25%, but a 20% increase in the level of biodiversity value increases the optimal number of protected stands only by 12.5%.

We start our discussion of alternative site selection specification by studying how the size of conservation budget affects the achievement of these ecological goals. These results for model 1 have been described in the section 3.2, thus here we consider only the results of the other models. In model 2 the red-listed species are protected first, if it is possible under the given budget, and they contribute strongly to the biodiversity because their weight is high. Therefore the object function achieves a high value even with relatively low budget size in model 2. It turned out that vulnerable species ($n = 9$ and weight = 100) are all represented in the selected network when six stands are protected and the opportunity costs are about 18 000 €. Instead, 28 stands (about 108 000 €) are needed to cover all near-threatened species ($n = 9$ and weight = 10).

It seems that rare species are rather evenly distributed among stands. Therefore, the differences between the best and the worst conservation targets are not very large when the aim is to maximize the representation of rare species (model 3). Similarly the conservation target of maximizing species count is attained relatively slowly in model 4 as the budget size increases. Thus, the variation in number of species between stands is not as large as the variation in species composition. Also species abundance is quite evenly distributed among stands, and therefore, the targets in models 5 and 6 are attained relatively more slowly than in models 2 and 3 as the budget size increases.

The results of budget-constrained models can also be presented in terms of marginal costs. The marginal costs are increasing in all models indicating that conserving an extra unit of biodiversity will constantly cost more than the previous unit. However, the speed of this increase differs between the models. In particular, in the models based on complementarity between stands (i.e., maximizing species richness), marginal costs are minor at a low conservation level (in terms of relative biodiversity, i.e. actual conservation level/conservation when all stands are protected) but start to rise rapidly with the increasing conservation level. Therefore, it is very costly to protect the last remaining species. In the models that take into account the assumed population persistence the marginal costs rise less sharply with an increasing conservation level, but they start to rise earlier compared with models ignoring the persistence aspect. Thus, it may not be economically efficient to establish a large conservation network to protect all species in given area. In contrast, a large conservation network is more likely justified, when the habitat-protection strategy focuses on species persistence.

It is interesting to compare how effective the models are in terms of achieving the alternative goals under the budget constraint (39 304 €), which corresponds to the socially optimal conservation level in terms of the benchmark model. The maximum species richness is achieved by using model 1, but the conservation network picked by using the other models usually covers almost as many species as model 1. Therefore, it seems that the species abundance and population persistence aspects effectively control also for species richness.

It is likely that red-listed species are not totally covered in the conservation network if this aspect is omitted from the area selection method. In our analysis, only one vulnerable species and a few near-threatened species were typically not covered by the area selection methods that do not give any special attention to the red-listed species compared with the outcome of model 2 at the socially optimal conservation level. Model 5 is the second most effective model in terms of covering red-listed species, of course, because it explicitly includes this aspect of biodiversity.

Also, the rare species are not totally covered in the conservation network if this aspect is not included in the area selection method although the differences between the models are not as large as in the case of covering the red-listed species. Interestingly, model 6 results in the same outcome as model 3 implying, that the species abundance is not an important aspect in model 6 at 39 304 € budget level.

The models support quite poorly the multiple representations of species, except model 4, of course. The outcome of model 5 implies, however, that the species abundance and multiple-representation operate similarly in the area selection methods. The multi-objective models (models 5 and 6) as well as model 4 seems to be quite effective in terms of considering all the studied aspects of biodiversity simultaneously.

References

- Amacher G, Koskela E & Ollikainen M (2004) Forest rotations and stand interdependency: ownership structure and timing of decisions. *Nat Res Model* 17: 1–45.
- Ando A, Camm J, Polasky S & Solow A (1998) Species distributions, land values, and efficient conservation. *Science* 279: 2126–2128.
- Arthur JL, Haight RG, Montgomery CA & Polasky S (2002) Analysis of the threshold and expected coverage approaches to the probabilistic reserve site selection problem. *Environ Model Asses* 7: 81–89.
- Balmford A & Gaston K (1999) Why biodiversity surveys are good value. *Nature*, 398: 204–205.
- Balmford A, Gaston KJ, Rodrigues ASL & James A (2000) Integrating costs of conservation into international priority setting. *Conserv Biol* 14: 597–605.
- Bevers M & Hof J (1999) Spatially optimizing wildlife habitat edge effects in forest management linear and mixed-integer programs. *For Sci* 45: 249–258.
- Bowes M & Krutilla J (1985) Multiple-use management of public forestlands. P. 531–569 in *Handbook of Natural Resource and Energy Economics*, Vol. II, Kneese A & Sweeney J (eds.). North-Holland, Amsterdam.
- Bowes M & Krutilla J (1989) Multiple-use management: the economics of public forestlands. *Resources for the Future*, Washington, D.C., pp. 353.
- Calish S, Fight R & Teeguarden D (1978) How do nontimber values affect Douglas-fir rotations? *J For* 76: 217–221.
- Calkin D, Montgomery C, Schumaker N, Polasky S, Arthur J & Nalle J (2002) *Can J For Res* 32: 1329–1342.
- Chase MK, Kristian III WB, Lynam AJ, Price MV & Rottenberry JT (2000) Single Species as Indicators of Species Richness and Composition in California Coastal Sage Scrub Birds and Small Mammals. *Conserv Biol* 14: 474–487
- Church RL, Stoms DM & Davis FW (1996) Reserve selection as a maximal covering location problem. *Biol Conserv* 76: 105–112.
- Church R, Gerrard R, Hollander A & Stoms D (2000) Understanding the tradeoffs between site quality and species presence in reserve site selection. *For Sci* 46: 157–167.
- Esseen P-A, Ehnström B, Ericson L & Sjöberg K (1997) Boreal forests. *Ecol Bull* 46: 16–47.
- Faith DP & Walker PA (1996) Environmental diversity: On the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv Conserv* 5: 399–415.
- Faustmann M (1849) Berechnung des Wertes welchen Waldboden sowie noch nicht haubare Holzbestände für die Waldwirtschaft besitzen. *Allgemeine Forst- und Jagd-Zeitung*, vol. 15. Republished in 1995 with the title “Calculation of the value which forest land and immature stands possess for forestry”. *J For Econ* 1: 7–44.

- Flather CH, Wilson KR, Dean DJ & McComb WC (1997) Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol Applic* 7: 531–542.
- Gaston KJ & Spicer JI (1998) *Biodiversity: an introduction*. Blackwell Science, Oxford, United Kindom. 113 p.
- Gaston KJ (ed.) (1996) *Biodiversity: a biology of numbers and difference*. Blackwell Science, Oxford, United Kindom. 369 p.
- Hacker J, Cowlshaw G & Williams P (1998) Pattern of African primate diversity and their evaluation for the selection of conservation areas. *Biol Conserv* 84: 251–262.
- Haight RG (1995) Comparing extinction risk and economic cost in wildlife conservation planning. *Ecol Applic* 5: 767–775.
- Haight RG, Revelle C & Snyder S (2000) An integer optimization approach to a probabilistic reserve site selection problem. *Oper Res* 48: 697–708.
- Haight RG, Cypher B, Kelly PA, Phillips S, Possingham HP, Ralls K, Starfield AM, White PJ & Williams D (2002) Optimizing habitat protection using demographic models of population viability. *Conserv Biol* 16: 1386–1397.
- Halman E, Hokkanen M, Juntunen H, Korhonen K-M, Raivio S, Savela O, Siitonen P, Tolonen A & Vainio M (1996) Alue-ekologinen suunnittelu. Metsähallitus, Metsätalouden julkaisu 3, Vantaa. 59 p.
- Hartman R (1976) The harvesting decision where a standing forest has value. *Econ Inquiry* 14: 52–58.
- Hanski I (2000) Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann Zool Fennici* 37: 271–280.
- Howard PC, Viskanic P, Davenport TRB, Kigenyi FW, Balzer M, Dickinson CJ, Lwanga JS, Matthews RA & Balmford A (1998) Complementarity and the Use of Indicator Groups for Reserve Selection in Uganda. *Nature* 394: 472–475.
- Johansson P-O & Löfgren K-G (1985) *The economics of forestry & natural resources*. Basil Blackwell. Oxford, UK. 292 p.
- Kalliola R (1973) *Suomen kasvimaantiede*. WSOY, Porvoo, Finland.
- Kershaw M, Mace G & Williams P (1995) Threatened status, rarity, and diversity as alternative selection measures for protected areas: A test using afro-tropical antelopes. *Conserv Biol* 9: 324–334.
- Koskela E & Ollikainen M (2001) Optimal private and public harvesting under spatial and temporal interdependence. *For Sci* 47: 484–496.
- Koskela E, Ollikainen M & Pukkala T (2004) Biodiversity conservation in boreal forests: optimal rotation age and volume of retention trees. HECER, Discussion paper No. 2, Helsinki, Finland.
- Koskela E, Ollikainen M & Pukkala T (2005) Biodiversity policies in commercial boreal forests: optimal design of subsidy and tax combination. HECER, Discussion paper No. 41, Helsinki, Finland.
- Lehtonen E, Kuuluvainen J, Pouta E, Rekola M & Li C-Z (2003) Non-market benefits of forest conservation in Southern-Finland. *Environ Sci Policy* 6: 195–204.
- Lichtenstein M & Montgomery C (2003) Biodiversity and timber in the coast range of Oregon: inside the production possibility frontier. *Land Econ* 79: 56–73.
- Margules CR, Nicholls AO & Pressey RL (1988) Selecting networks of reserves to maximise biological diversity. *Biol Conserv* 43: 63–76.
- Margules CR & Pressey RL (2000) Systematic conservation planning. *Nature* 405: 243–253.
- McGeoch MA (1998) The selection, testing and application of terrestrial insects as bioindicators. *Biol Rev* 73: 181–201.
- Ministry of the Environment (1996) Protection of old-growth forests in northern Finland; report III by the working group for protection of old-growth forests (in Finnish). 1996. The Finnish Environment 30, Nature and natural resources, Helsinki, Finland. 111 p.

- Montgomery C, Brown G & Adams D (1994) The marginal costs of species preservation: The northern spotted owl. *J Environ Econ Managem* 26: 111–128.
- Montgomery C, Pollak R, Freemark K & White D (1999) Pricing biodiversity. *J Environ Econ Managem* 38: 1–19.
- Mäntymaa E, Mönkkönen M, Siikamäki J & Svento R (2002) Estimating the Demand for Biodiversity - Vagueness Band and Open Questions. In van Ierland E, Weikard H & Wesseler J (eds.). *Proceedings: Risk and Uncertainty in Environmental and Resource Economics, International Conference, June, 5-7 2002, Wageningen, The Netherlands*. Publisher: Environmental Economics and Natural Resources Group, Wageningen University.
- Mönkkönen M (1999) Managing boreal forest landscapes for biodiversity: Ecological and Economic Perspectives. *Biodiv Conserv* 8: 85–99.
- Nalle D, Montgomery AC, Arthur J, Polasky S & Schumaker N (2004) Modelling joint production of wildlife and timber. *J Environ Econ Managem* 48: 997–1017.
- Nilsson C & Götmark F (1992) Protected areas in Sweden: Is natural variety adequately represented? *Conserv Biol* 6: 232–242.
- Noss RF (1990) Indicators for monitoring biodiversity: A hierarchical approach. *Conserv Biol* 4: 355–364.
- Oliver I, Beattie A & York A (1998) Spatial Fidelity of Plant, Vertebrate, and Invertebrate Assemblages in Multiple-Use Forest in Eastern Australia. *Conserv Biol* 12: 822–835.
- Pearce D & Moran D (1994) *The economic value of biodiversity*. Earthscan Publications Ltd., London, United Kingdom. 172 p.
- Polasky S, Camm J, Solow A, Csuti B, White D & Ding R (2000) Choosing reserve networks with incomplete species information. *Biol Conserv* 94: 1–10.
- Polasky S, Camm J & Garber-Yonts B (2001) Selecting biological reserves cost-effectively: An application to terrestrial vertebrate conservation in Oregon. *Land Econ* 77: 68–78.
- Pressey RL, Possingham H & Day R (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol Conserv* 80: 207–219.
- Rassi P, Alanen A, Kanerva T & Mannerkoski I (eds.) (2001) *The 2000 red list of Finnish species (in Finnish)*. Ministry of the Environment, Helsinki, Finland. 432 p.
- Reed WJ (1986) Optimal harvesting models in forest management – A survey. *Nat Res Model*: 55–79.
- Reyers B, van Jaarsveld AS, Krüger M (2000) Complementarity as a biodiversity indicator strategy. *Proc Royal Soc Lond Ser B* 267: 505–513.
- Rodrigues ASL, Gregory RD & Gaston KJ (2000) Robustness of reserve selection procedures under temporal species turnover. *Proc Royal Soc Lond Ser B* 267: 49–55.
- Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge Univ Press 436 p.
- Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol Bull* 49: 1–31.
- Siitonen J, Martikainen P, Punttila P & Rauh J (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For Ecol Managem* 128: 211–225.
- Siitonen M, Härkönen K, Hirvelä H, Jämsä J, Kilpeläinen H, Salminen O & Teuri M (1996) *MELA Handbook, 1996 Edition*. The Finnish Forest Research Institute. Research Papers 622, Helsinki, Finland. 452 p.
- Snyder SA, Tyrrell LE & Haight RG (1999) An optimization approach to selecting research natural areas in national forests. *For Sci* 45: 458–468.
- Solow A, Polasky P & Broadus J (1993) On the measurement of biological diversity. *J Environ Econ Managem* 24: 60–68.

- Stokland JN (1997) Representativeness and efficiency of bird and insect conservation in Norwegian boreal forest reserves. *Conserv Biol* 11: 101–111.
- Strang W (1983) On the optimal forest harvesting. *Econ Inquiry* XXI: 576–583.
- Swallow S & Wear D (1993) Spatial interactions in multiple-use forestry and substitution and wealth effects for the single stand. *J Environ Econ Managem* 25: 103–120.
- Swallow S, Talukdar P & Wear D (1997) Spatial and temporal specialization in forest ecosystem management under sole ownership. *Am J Agr Econ* 79: 311–326.
- van Jaarsveld AS, Freitag S, Chown S, Muller C, Koch S, Hull H, Bellamy C, Krüger M, Endröby-Younga S, Mansell M & Scholtz C (1998) Biodiversity Assessment and Conservation Strategies. *Science*, 279: 2106–2108.
- Virkkala R (1996) Reserve network of forests in Finland and the need for developing the network: an ecological approach (in Finnish). Finnish Environment Institute, The Finnish Environment 16, Helsinki, Finland. 53 p.
- Virolainen KM, Virola T, Suhonen J, Kuitunen M, Lammi AI & Siikamäki P (1999) Selecting networks of nature reserves: Methods do affect the long-term outcome. *Proc Royal Soc Lond Ser B* 266: 1141–1146.
- Virolainen KM, Ahlroth P, Hyvärinen E, Korkeamäki E, Mattila J, Päivinen J, Rintala T, Suomi T & Suhonen J (2000) Hot spot, indicator taxa, complementarity and optimal networks of taiga. *Proc Royal Soc Lond Ser B* 267: 1143–1147.
- Weitzman M (1992) On diversity. *Q J Econ* 107: 363–406.
- Weitzman M (1993) What to preserve? An application of diversity theory to crane conservation. *Q J Econ* 108: 157–183.
- Williams JC & ReVelle CS (2002) Introduction to the Special Issue. *Environ Model Asses* 7: 57–59.
- Williams PH (1998) Key sites for conservation: area-selection methods for biodiversity. In: Mace GM, Balmford A & Ginsberg JR *Conservation in a Changing World*, pp. 211–240.
- Williams PH & Araújo MB (2000) Using probability of persistence to identify areas for biodiversity conservation. *Proc Royal Soc Lond Ser B* 267: 1959–1966.