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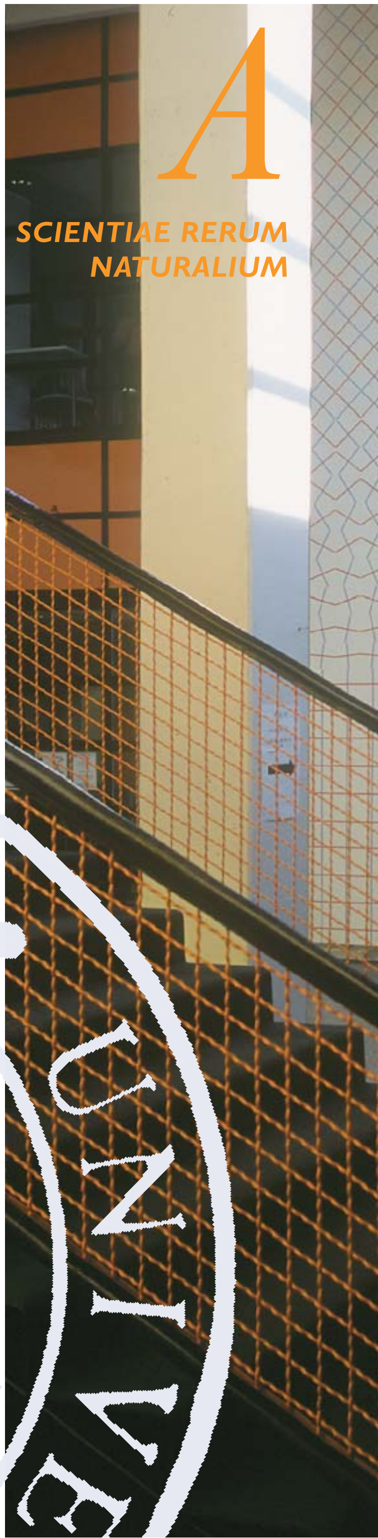

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SCIENTIAE RERUM NATURALIUM

*Eija Hurme*

# ECOLOGICAL KNOWLEDGE TOWARDS SUSTAINABLE FOREST MANAGEMENT

## *HABITAT REQUIREMENTS OF THE SIBERIAN FLYING SQUIRREL IN FINLAND*

*FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU*

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A Scientiae Rerum Naturalium 515

*EIJA HURME*

# ECOLOGICAL KNOWLEDGE TOWARDS SUSTAINABLE FOREST MANAGEMENT

Habitat requirements of the Siberian flying squirrel in Finland

Academic dissertation to be presented, with the assent of the Faculty of Science of the University of Oulu, for public defence in Kuusamonsali (Auditorium YB210), Linnanmaa, on November 28th, 2008, at 12 noon

OULUN YLIOPISTO, OULU 2008

Acta Univ. Oul. A 515, 2008

Supervised by
Professor Mikko Mönkkönen

Reviewed by
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ISBN 978-951-42-8938-5 (Paperback)
ISBN 978-951-42-8939-2 (PDF)
http://herkules.oulu.fi/isbn9789514289392/
ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)
http://herkules.oulu.fi/issn03553191/

Cover design
Raimo Ahonen

OULU UNIVERSITY PRESS
OULU 2008

**Hurme, Eija, Ecological knowledge towards sustainable forest management. Habitat requirements of the Siberian flying squirrel in Finland**
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*Acta Univ. Oul. A 515, 2008*
Oulu, Finland

## *Abstract*

Maintaining biodiversity in boreal forest landscapes in conjunction with forestry is a challenging task. This requires ecological understanding that is based on empirical research. In this thesis, I examined spatial and temporal occupancy patterns as well as predictability of the occurrence of the Siberian flying squirrel (*Pteromys volans* L.) in Finland. I used thematic maps which matched habitat requirements of the flying squirrel in forested landscapes and data on species presence and absence, which were gathered in suitable forest habitats.

The results of this thesis provide applications for landscape management. First, the preferred habitat characteristics of the flying squirrel were linked to available forest data. In addition, some predictive habitat models could be used to estimate the distribution of the flying squirrel within a region. Second, based on a five year study the forests were classified as continuously occupied, continuously unoccupied and variable-occupancy patches. The dynamic occupancy pattern emphasizes the need for repeated surveys to also locate the seldom-used suitable habitats in a landscape. Third, a comparison of simulated future scenarios in long-term forest planning suggested that flying squirrel habitat might be maintained without considerable loss of timber in a landscape. Thus, a combination of ecological and economic goals in forestry planning is an encouraging alternative. Fourth, there were more polypore species in forests occupied by the flying squirrel. This suggests that conservation of the flying squirrel habitats would protect other naturally co-occurring species, and thus the flying squirrel could be assigned as an umbrella species in mature spruce-dominated forests.

Based on these findings, I suggest that the flying squirrel could be used as one of the target species for forest management in boreal forest landscapes. Further research challenges are related to the examination of habitat thresholds and to the projection of future scenarios where ecological, economic and social aspects are combined to assist in complex decision making processes.

*Keywords:* boreal forest, forest planning, future scenario, habitat model, landscape management, occupancy dynamics, presence-absence, species distribution, umbrella species

***To my family***

# Acknowledgements

This work was based on the co-operation of many skilled persons, and I feel privileged that I was able to be a part of this. I am thankful for all the people who have helped me in various ways during these years.

The key person behind this thesis is my excellent supervisor Mikko Mönkkönen. He originally suggested a topic related to flying squirrels for my master's thesis in 1999, and here I am now. It is hard to imagine a better supervisor, or scientist. Mikko seems to always be in a good mood, enthusiastic to experiment with something new, keen for any questions and problems, and trusting that something interesting will always be found behind the numbers. He has also been extremely fast to give precise comments on my various manuscripts. These characters have encouraged me a lot. Thank you, Mikko.

I basically inherited this "flying squirrel work" from Pasi Reunanen. He introduced me to the flying squirrel forests in the spring of 1999, and after that we have spent weeks and weeks searching for pellets in various forests, discussing various topics. Pasi also turned out to be an encouraging unofficial supervisor that I highly appreciate. Besides a great deal of numbers, I have received thorough advice from the fine gentlemen Ari Nikula and Vesa Nivala. I admire their expertise in GIS and deep understanding of the MS-NFI data. In addition, Ari has never forgotten to wish me good luck after what ever problem we just had.

Mikko Kurttila's knowledge made it possible to even think the idea of estimating the future forests, and luckily Mikko patiently explained so many things also to me. Tero Heinonen and Timo Pukkala helped considerably with calculations and ideas about future forests, too. I received excellent and much needed advice from Anna-Liisa Sippola about polypores and from Jari Oksanen about statistics. Skilful and enthusiastic master's students Taru Heikkinen, Mikko Pentinsaari, Maarit Ukkola and Hanna Ylinen did a great deal of high quality work in their shares. I am glad that I had some time for an interesting co-operation with a historian Anne-Ruuttula-Vasari, and the possibility to become amazed by the beauty of the old maps. I also thank the staff of the Zoo and the Zoological Museum of Oulu for their help with traps and beetles.

I thank Metla and Erkki Tomppo for access to MS-NFI data. I got forest stand data from state owned forests with the help of Maarit Kaukonen and Kari Louhisalmi from Metsähallitus. Thanks to Maarit, and Tupuna Kovanen from the Environmental Centre of Northern Ostrobothnia, I could use existing data on the flying squirrel occurrence. Irmeli Hanka kindly made it possible to use forest stand data from the City of Kajaani.

Professor Per Angelstam and Doctor Jeff Bowman carefully examined my thesis with wise remarks. The language of this summary was kindly checked by Mikael Mökkönen. My work was financed by the University of Oulu (Centre of Excellence), the Academy of Finland (Sunare-project, no 52772), the Ministry of Agriculture and Forestry of Finland (Mosse-project, no 25058) and the EnviroNet, joint graduate school of the University of Oulu and NorNet. The Department of Biology offered working facilities and friendly service in the office.

I have been lucky with my room mates. Five years with Robert Thomson made the working days very cosy. During the past couple of years, Pauliina Louhi has also been an excellent companion. Thank you, Robert and Pauliina. Moreover, I have spent time with colleagues Angeliina Alopaeus, Lotta Jaakkola, Katja Kangas, Marja Kuosa, Satu and Petri Lampila, Tuija Liukkonen, Ahti Putaala, Vitali Reif, Claudia Siffczyk, Louise Sørensen, and Anne Törn. They, along with many others, have joined the "nine o'clock coffee group", helped to brake up the long afternoons in a cafeteria or were otherwise good company. Thank you all.

In the end, I am grateful to my parents Kaisa and Heikki and sister Tuija for their existence and support. I have also been very fortunate to have a few good friends, including those with hoofs and fins, who have really coloured my days. My spouse Esa Vuoppola was excellent it-support at home, and while I sat by the computer during the past year, Esa, Leena Vuoppola, Eero Vuoppola and Maarit Ukkola kept our son Juho company. Thank you for helping me to finish this work. I owe my deepest gratitude to my family – the shining lights Esa and Juho – for love and sharing the life with me.

Oulu, October 2008 Eija Hurme

# List of original articles

This thesis is based on the following articles, which will be referred to in the text by their Roman numerals:

I Hurme E, Reunanen P, Mönkkönen M, Nikula A, Nivala V & Oksanen J (2007) Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. Ecography 30: 277–287.

II Hurme E, Mönkkönen M, Reunanen P, Nikula A & Nivala V (2008) Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape. Ecography 31: 469–476.

III Hurme E, Mönkkönen M, Nikula A, Nivala V, Reunanen P, Heikkinen T & Ukkola M (2005) Building and evaluating predictive occupancy models for the Siberian flying squirrel using forest planning data. Forest Ecology and Management 216: 241–256.

IV Hurme E, Kurttila M, Mönkkönen M, Heinonen T & Pukkala T (2007) Maintenance of flying squirrel habitat and timber harvest: a site-specific spatial model in forest planning calculations. Landscape Ecology 22: 243–256.

V Hurme E, Mönkkönen M, Sippola A-L, Ylinen H & Pentinsaari M (2008) Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. Ecological Indicators 8: 246–255.

I have actively participated and partly been responsible in the study design, gathering and analyzing the data, and especially in the manuscript preparation of each paper in this collaborative research process.

# Contents

# 1 Introduction

## 1.1 Integration of ecological knowledge to forest planning

Maintenance of necessary patterns and processes in ecological systems is a central goal in conservation biology (Soulé 1985, Muradian 2001). This is easy to understand since habitat availability, for example, is typically a prerequisite for species existence. Therefore, the highest threats to species existence, habitat loss, change and degradation (Saunders *et al.* 1991, Fahrig 1997), are related to habitat availability. Often species or ecosystem protection and maintenance of biodiversity have been based on conservation areas. Specific conservation areas however, do not necessarily cover all the important habitats. In forests, for example, many threatened forest-associated species live outside the protected areas (Lindenmayer & Franklin 2002). The surroundings of the conservation areas are also modified by land use, which may affect the habitat availability through degraded movement areas between the conservation areas. This calls for managing the conservation areas and their surroundings simultaneously (Lindenmayer & Franklin 2002).

Land use in general is a complex decision making process which combines different perspectives into a compromise. Today, ecological, economic and social aspects are an integral part of land management. In a perfect decision making situation, competing and even conflicting goals can be united to produce an accepted outcome (Keeney 1982). A good example of a multi-objective land use activity in forested landscapes is forestry. Goals in forestry and conservation are often complex to combine and may be open to conflicts: forestry is dependent on an even flow of timber and ecological concern typically focuses on threatened species or habitats, which need protected areas. Maintenance of the specific ecological values or the biodiversity of forests in conjunction with continuous timber production is thus a challenging task.

Maintenance of biodiversity and sustainable use of natural resources also have strong support from the legislation. Implementation of conservation and sustainable use of biodiversity into national decision making was stated in the Convention of Biological Diversity in 1992, Rio de Janeiro. Therefore, the aim of the Finnish Forest Act is to promote economically, ecologically and socially sustainable use of forests so that the forests are sustainably productive while their biological diversity is maintained (Anon. 1997).

In order to maintain biodiversity, a broader view for forest management includes the definition of ecological values and their incorporation into practice. Therefore, conservation planning and management in forested landscapes need ecological understanding based on sound applied research. Consideration and definition of multiple objectives on appropriate spatial and temporal scales are also needed. This may require a variety of approaches and methods. Carignan & Villard (2002) suggest that the integration of species-oriented approaches (*e.g.* Landres *et al.* 1988) and ecosystem approaches (*e.g.* Walker 1995) would probably be the most useful strategy to integrate biodiversity values into landscape management planning.

In a species oriented approach the focus is on a single species or on a certain group of species. Ecological research on species habitat preferences has recently enlarged into niche-based habitat models (Guisan & Zimmermann 2000, Scott *et al.* 2002, Guisan & Thuiller 2005), which aim to understand and predict the species distribution using attributes of its environment. Distribution models may be very useful, but they are also always compromises between model precision and transferability of the model to other areas (Araújo & Guisan 2006, Randin *et al.* 2006). Spatial characteristics may differ and also temporal aspects such as population patterns can make a difference to the outcome. The model may explain the species distribution perfectly in one area but not be suitable for use in other areas (*e.g.* Randin *et al.* 2006). This may limit the transferability of the model.

The species-oriented approach also includes indirect methods. They are built on the assumption that a certain species indicates the existence or the condition of the environment or of some other species (Landres *et al.* 1988, Simberloff 1998, Lambeck 1997). Hence, some species might work as shortcuts to describe biodiversity values and as such, support landscape management (Noss 1990, Ricketts *et al.* 1999, Andelman & Fagan 2000, MacNally *et al.* 2002, Roberge 2006). Conservation of an umbrella species, for example, would protect simultaneously other co-occurring species (Fleishman *et al.* 2000). An umbrella species can be defined as relatively demanding or sensitive for a certain habitat type as well as the size of its habitat (Fleishman *et al.* 2000, Roberge & Angelstam 2004). Thus, conservation areas for an umbrella species would simultaneously include habitats also for other species having similar but smaller habitat demands (Simberloff 1998, Caro & O'Doherty 1999, Roberge & Angelstam 2004).

The ecosystem approach focuses on whole ecosystems. Application of separate demands of many different species into landscape planning is complicated, so ecosystem protection can be a straightforward alternative because it automatically covers the species living in it. Numerous large areas of native habitats or otherwise important areas have been protected world wide (Lindenmayer & Franklin 2002). This approach can also be applied for smaller areas. In Finland, for example, small sites important for forest biodiversity such as rich groves or small wells are protected via forest legislation (Anon. 1997).

Both approaches naturally have their problems. The species-oriented approach is impeded by the lack of knowledge since only a fraction of the species can be studied in detail. Limited financial resources may only allow for partial ecosystem protection. Ecologically important patterns may also be difficult to define. At times, the existing ecological information needed for management practices may be too complicated for generalization. On the other hand, the practices in landscape planning may not be flexible or designed to incorporate the available ecological information.

A better understanding of the ecological systems and ways to apply this understanding to landscape planning practices and current situations is needed. Simultaneous consideration of different approaches is potentially the solution for the maintenance of biodiversity (Carignan & Villard 2002, Lindenmayer & Franklin 2002). Multi-objective landscape planning requires tools to simultaneously handle and understand ecological, economic and sociological aspects (Opdam *et al.* 2002). The comprehensive examination of the problem requires identification and structuring of the problem, determination of the preferences of different stake-holders as well as alternative scenarios relating to the problem, and finally, estimation and comparison of the alternatives (Keeney 1982).

Recently, research on modeling future scenarios of landscape structure under different landscape management plans, mainly forestry, has begun (Boutin & Hebert 2002). A selection of tools to handle complex spatial problems has started to become available especially for forest planning (Kurttila 2001) and for understanding forested ecosystems as such (Scheller & Mladenoff 2007). Some recent studies have already focused on multi-species studies and overall land use (Schumaker *et al.* 2004, Polasky *et al.* 2005). It seems that producing future scenarios under different landscape management plans would increase our understanding of underlying patterns and processes (Boutin & Hebert 2002), and help decision making in land management planning.

## 1.2 Landscape ecological perspective

The maintenance of biodiversity calls for a landscape ecological perspective into the whole planning process and realization of conservation goals. This requires simultaneous planning and management of entire landscapes (Margules & Pressey 2000). The underlying idea of landscape ecology is that landscapes are heterogeneous mosaics of different landscape elements in space and time, so this heterogeneity has effects on the ecosystem (Forman & Godron 1986, Wiens 1995). The questions focus on patterns of structure, function and change in a landscape. Landscape ecological thinking addresses the spatial heterogeneity of landscapes, and interactions between the organisms and their environment within the landscape. Replicated experiments are rare because they are very complicated or even impossible to carry out over large landscapes. Thus, landscape ecological research rests mainly on descriptive research as well as on simulations of spatial patterns.

Complex landscape heterogeneity is also dependent on spatial and temporal scales (Levin 1992). Determination of the right scale for the question is essential for understanding the problem at hand, although it is not necessarily apparent immediately (Wiens 1989). Each species likely has unique responses to the structure of patches and landscapes (Hokit *et al.* 1999); humans do not necessarily perceive the important landscape patterns in the same way as other organisms such as birds or beetles do. The temporal scale is also important in landscape ecological research because it allows for a better understanding of variation in ecological patterns and processes in time.

Landscapes are often classified by the habitat patches and matrix surrounding them (Forman & Godron 1986). Landscape ecology is partly based on the MacArthur and Wilson (1967) theory of island biogeography, which describes the relationships between sizes of separate islands and their distances from the mainland. However, in terrestrial environments the landscape can rarely be categorized in a two-fold way to habitat islands and the matrix between them, although the two-fold landscape classification is still often used because of its simplicity. Landscape structure can further be defined by composition, configuration and connectivity (Taylor *et al.* 1993, Merriam 1995). Composition refers to different elements in the landscape, whereas configuration refers to their arrangement within it. Connectivity is originally termed as an interaction of the species with the landscape structure and movement among habitat patches (Merriam 1984), and as such it is a very species- and landscape-specific character

(Taylor *et al.* 1993, With *et al.* 1997, Tischendorf & Fahrig 2000). In general, our understanding of inter-patch movements of individuals and spatio-temporal dynamics of populations is limited (Bowne & Bowers 2004). Therefore, even though connectivity would be a very important landscape character for management purposes, its definition and estimation is difficult.

In forested environments, landscape ecological research has mainly focused on fragmentation issues and landscape projection models (Boutin & Hebert 2002). Fragmentation is a character of a landscape, when habitats become smaller in size and more isolated from each other. If individuals are unable to move from a habitat patch to another because of the isolation of habitat patches, a landscape may be so fragmented from the species perspective that it increases the negative effects of pure habitat loss on species existence (Bender *et al.* 1998, Harrison & Bruna 1999). Different species perceive the landscape structure according to their specific responses; therefore the prediction of fragmentation effects requires a proper understanding of the biology for the species in question (Wiegand *et al.* 2005). Configuration effects should also be distinguished from the effects of habitat loss, which has been found to be the most important factor for species existence (Fahrig 2002, 2003).

Among landscape projection models, a patch-matrix-corridor approach (Forman 1995) and patch-matrix approaches are traditional ways to categorize the landscape from a certain perspective. Landscape classification into patches and matrix is also the basis for ecological population models and metapopulation studies (Hanski 1999). A landscape continuum approach (McIntyre & Hobbs 1999) suggests an application of a degree of habitat destruction for landscape categorization. This includes research on habitat thresholds, for example by exploring minimum requirements for how much habitat is needed by a population to persist or how much disturbance a population can tolerate.

Projection of future scenarios for alternative management plans may help to understand characteristics and production possibilities of certain landscapes. Scenarios are useful tools for landscape managers since they help in decision making, especially when the underlying uncertainties are taken into account. Research on habitat thresholds as well as simulations of future scenarios would, besides increasing our knowledge, promote the partnership of landscape ecological research and forest management planning (Boutin & Hebert 2002).

## 1.3 Objectives of the thesis

This thesis is based on five research articles which address the occurrence of the Siberian flying squirrel (*Pteromys volans* L.; hereafter flying squirrel) in a boreal forest landscape. I used statistical models to explain and predict the occurrence of the species based on the preferred habitat characteristics in northern Finland. The models took advantage of the existing knowledge of the habitat preferences of the flying squirrel and available forest data. I used thematic maps which matched habitat requirements of the flying squirrel. The first 2 papers examine spatial and temporal patterns of the flying squirrel's occupancy in a landscape and the following 3 papers address the concept of suitable habitats for the flying squirrel in light of conservation and sustainable forest planning.

In the first paper I examined the habitat patch pattern of the flying squirrel in the landscape (I). All habitat patches within the study area were surveyed, and the aim was to understand how forest attributes, distances between habitat patches and occupancy of a neighboring habitat patch explain and predict the occupancy of the focal patch. The models built in this study were mainly descriptive. In paper II, I studied the flying squirrel occupancy in a landscape across a time period of seven years. This paper continued the research set-up in the first paper by addressing temporal variation in the habitat patch occupancy, possible changes in the landscape structure and applicability of predictive models among years. These models were based on the existing ecological information of habitat preferences and kept as simple as possible. In the third paper, I addressed spatial transferability of predictive models (III). I built predictive models specifically for applied use in forest management, and evaluated the models using data from geographically different areas. The fourth paper examined possibilities to link ecological information directly to forest planning (IV). I assessed the outcome of five future forest management scenarios in one large landscape and studied how information about flying squirrel habitats can be integrated into long-term forest management planning calculations. Finally, I addressed one possible indirect method within the species-oriented approach and tested the concept of an umbrella species (V). If other rare and endangered species co-exist with flying squirrels in similar habitats, forests protected for the flying squirrel would benefit other species as well. Thus, the flying squirrel could be used as a shortcut tool to help in site-selection problems in northern boreal forests. As such, it could be a small step towards a combination of species-oriented and ecosystem approaches.

# 2 Material and methods

## 2.1 The Siberian flying squirrel

The single species approach is a way to start understanding the complex ecosystem (Opdam *et al.* 2002). I selected an arboreal Siberian flying squirrel for this work since it has been found to be a good example species for landscape ecological studies (Reunanen 2001, Selonen 2002). In addition, intensive ecological research has focused on the flying squirrel in Finland during the last decade; hence there is a relatively good amount of knowledge of its ecology. Therefore, it is an excellent species for applied case studies.

The global range of the flying squirrel covers the Eurasian taiga zone from Japan (Hokkaido) in the east to Finland and Estonia in the west (Ognev 1940). Flying squirrels prefer mature, Norway spruce (*Picea abies*) dominated forests, which have a mixture of deciduous trees (Mönkkönen *et al.* 1997, Hanski 1998, Reunanen *et al.* 2000). In particular, aspen (*Populus tremula*) is an important tree species for the flying squirrel because of nesting cavities and food (Hanski 1998). In northern Finland, flying squirrels seem to prefer continuously forested areas (Reunanen *et al.* 2000). The individuals use several nests such as cavities, twig dens or nest boxes year round (Hanski 1998). Flying squirrels move relatively well in forested landscapes by gliding from tree to tree (Selonen & Hanski 2003). They prefer closed canopy forests for moving, but can also traverse areas that are characterized by scattered trees or bushes (Selonen *et al.* 2001, Selonen & Hanski 2003, 2004). Therefore, flying squirrels can inhabit relatively large forested areas: home ranges average eight hectares for females and 60 hectares for males (Hanski *et al.* 2000). Most of the juveniles will disperse from their natal forest (Selonen & Hanski 2004), but the adult flying squirrels, especially females, seem to be very site-tenacious (Hanski *et al.* 2000).

The flying squirrel was first protected by the Nature Conservation Act in Finland in 1923 (Rassi *et al.* 2001). During 1950–1980, signs of a population decline were detected (Hokkanen *et al.* 1982), and after Finland became a member of the European Union (EU) in 1995, the flying squirrel was defined as a strictly protected species (included in Annex IVa of the Habitat Directive [Council Directive 92/43/EEC]). A recent national survey estimated the population size to be approximately 140000 female flying squirrels in Finland (Hanski 2006). The flying squirrel is classified as vulnerable (VU) according to the IUCN criteria in the national red-list (Rassi *et al.* 2001).

Concern over the well being of the flying squirrel in Finland has led to guidelines for forestry practices (Anon. 2003) and other land uses (Anon. 2005). Occupied sites of the species are strictly protected in Annex IVa. Typical habitats of the species are often economically valuable, and as a result, several conflicts between conservation of the flying squirrel and forestry practices have occurred during past years. Flying squirrels may also live close to human settlements, which have led to conflicts in land use planning in cities (*e.g.* Jokinen *et al.* 2007).

### *2.1.1 Presence and absence of the flying squirrel*

The flying squirrel is a nocturnal rodent that silently moves within the forest canopy during the dim times of the day. Since direct observations of the species are difficult to make and field surveys in this thesis were carried out in broad areas, indirect signs for the species presence were needed. I based the observations of the flying squirrel on its fecal pellets. Flying squirrels have distinctive yellowish pellets about the size of rice grains, which can be found at the bases of large spruce and deciduous trees within the mostly used forest sites (Skarén 1978, Reunanen *et al.* 2000). Currently, the pellets are routinely used in surveys to assign the presence of the flying squirrel within a forest, for example for forestry or other landscape planning purposes (*e.g.* Heikkinen 2003, Pimenoff & Vuorinen 2005). For an experienced person the pellets are relatively easy to find and unlikely to be misinterpreted with those of other species.

In this thesis, I categorized the occurrence of the flying squirrel into two classes: presence and absence. Absence is difficult to assign since animals may not always leave visible signs of their stay (Putman 1984). Due to possible errors in observations and sampling, MacKenzie (2005) recommended the use of terms detection and non-detection. In this study, the whole forest was surveyed without time limits to confirm the absence of the species (*i.e.* the lack of pellets). The surveys were carried out in the late spring and early summer when the pellets that had accumulated during the late winter to early spring time had not yet decomposed (personal observation). The pellets assign the use of forest sites during the last few months, although site-specific variation in decay rates may exist (Putman 1984). This accuracy was relevant for the research questions and time scale used in this study. Therefore, I use the terms of presence and absence throughout this thesis.

However, no exact knowledge of the decay rate of pellets or true estimate for the detection probability exists. Based on yearly censuses of same forest sites in southern Finland (Pimenoff & Vuorinen 2005), occupied sites did not necessarily have pellets the next year, and an unoccupied site could have pellets the next year. This suggests that in general the pellets will decompose within a year. Even though the field personnel of this research project were very experienced and trained to detect flying squirrel pellets if present, I cannot completely rule out the possibility that a fraction of sites were falsely assigned as unoccupied. Thus, occupancy estimates (*e.g.* proportion of patches occupied) are minimum values.

In addition, the possible use of areas outside the habitats classified as suitable was not surveyed. The earlier ecological work on habitat preferences of the flying squirrel is rather comprehensive, and relatively precise knowledge of the basic habitat requirements is available (*e.g.* Mönkkönen *et al.* 1997, Hanski 1998, Selonen *et al.* 2001, Reunanen *et al.* 2002a). In my study area, flying squirrels require mature spruce dominated mixed forests. It is known that in the late summer and autumn, dispersing juvenile flying squirrels may use a wider spectrum of habitats (Selonen & Hanski 2004, Selonen *et al.* 2007). The aim of this study was to locate and predict forest structures that fill the known habitat preferences of adult flying squirrels as well as possible, focusing especially on the typical breeding habitat characteristics in early summer. Therefore, surveying only habitats known to be important for the species persistence is reasonable. Consequently, my results only apply to the reproducing part of the population.

## 2.2 Study areas

These studies were carried out in Finland (Fig. 1.) in the north-westernmost part of the geographical range of the flying squirrel (Reunanen *et al.* 2002b). The transition zone between the middle and northern boreal vegetation zones is roughly located through the study region (Ahti *et al.* 1968). Topography varies from 120–190 m above sea level (a.s.l.) in Kajaani to 180–380 m a.s.l. for the more hilly regions in Taivalkoski. Landscapes are characterized by forested hills between low lands, small water courses and bogs. Forests are dominated by the conifers Scots pine (*Pinus sylvestris*) and Norway spruce, and mixed with deciduous trees such as birch (*Betula* ssp.), aspen and alder (*Alnus incana*).

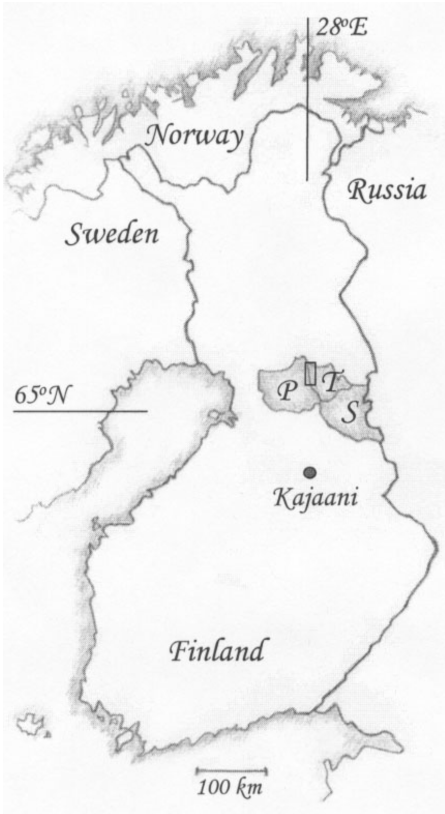


**Fig. 1. Location of the study areas. Studies (I–V) were carried out within an area denoted by a rectangle. In study III, data from municipalities Pudasjärvi (P), Taivalkoski (T), Suomussalmi (S), and the city of Kajaani were also used.**

## 2.3 Forest data

To categorize the landscapes from the perspective of the flying squirrel, I used two available forest data sources that are widely used in forestry planning. The multi-source national forest inventory data (MS-NFI) are based on classified satellite images (papers I, II). Forest stand data are derived from the measurements of the forest structure in the field (papers III, IV and V). These data suited my questions well since MS-NFI data allow for the examination of large landscapes, whereas forest stand data include accurate information from separate forest stands.

The MS-NFI data were provided by the Finnish Forest Research Institute. MS-NFI data are based on Landsat TM 5 satellite images, consisting of 25-m pixels, which are further combined with multi-source (MS) data on other landscape structures (Tomppo 1993). Estimates for tree species, age and volume are available from the forests per each pixel, and classification of the MS-NFI data is verified using field plots. These data are mainly used for nation-wide forest inventories and regional planning.

The forest stand data were given by Metsähallitus (III, IV, V) and by the City of Kajaani (III). The forest stand data are typically gathered by conducting forest inventories in the field and are then used in forest planning practices. Delineation of forest stands is based on soil type as well as tree species and age composition. Forests are first roughly delineated from aerial photographs, and the work is continued by visiting the forests. The borders of a stand in a forest are checked and basic measurements such as basal area and height for every tree species are determined in study plots (*e.g.* Uuttera & Hyppänen 1997). The volumes ($m^3 ha^{-1}$) of tree species in a study plot are calculated by the basic measurements of trees, and volumes from plots are further averaged for the whole stand.

MS-NFI data and forest stand data have their differences, but also many similarities since in the end, they are based on the same field measurements. Early comparisons between these two information sources show that the basic forest structures can be located using both types of data (Nikula *et al.* 2005). Therefore, comparison of the research results among studies in this thesis was possible.

## 2.4 Research methods

### *2.4.1 Patterns in the habitat patch occupancy (I)*

Availability of suitable habitats is important for species survival and reproduction. Therefore, the examination of large landscapes where populations operate is appropriate. In the first paper, I examined landscape characteristics that explained the occurrence of the flying squirrel. I used MS-NFI data to classify the study area of 374.6 $km^2$ into potential habitat patches, potential dispersal areas and areas incapable of being inhabited.

The habitat classification in papers I and II is the same as used in earlier studies of the landscape responses of the flying squirrel in northern Finland by Reunanen *et al.* (2002c, 2004; see paper I for further details). Habitat patches consisted of mature spruce-dominated forests, which had deciduous trees in the mixture. In core pixels (*i.e.* habitat considered suitable for reproduction), the first criterion was > 80% of spruce or > 80% of spruce and deciduous trees together in the total timber volume. The second criterion was that the total timber volume was ≥ 100 $m^3ha^{-1}$. The core pixels were further buffered by 50 m, and united as a potential habitat patch if their buffers overlapped or adjoined. The properties of buffer pixels were not specified since flying squirrels cross forest gaps of 20–70 m in one glide and thus, could easily reach neighboring core pixels if not separated more than this. In this paper, potential dispersal areas reflected pixels having ≥ 75 $m^3ha^{-1}$ of the total timber volume, and were connected if their buffers of 25 m were overlapped or adjoined. This represented all other forests approximately ≥ 10 m in height. Other habitats such as open areas, saplings and young forests were classified as areas incapable of being inhabited. The occurrence of the flying squirrel was surveyed from every potential habitat patch (n = 136) within the study area in the year 2000.

I compared the habitat and landscape variables between occupied and unoccupied habitat patches. Variables described the characteristics of habitat patches, the landscape surrounding the patches within 500 m of a habitat patch and the distances between the habitat patches. To take the amount of habitat in a landscape into account I used a variable reflecting the available suitable habitat within 500 m of a focal patch (*i.e.* the habitat that was easily accessible for an individual squirrel). This was the way to estimate the effect of habitat availability and loss in the landscape. The shortest inter-patch distances were measured as straight distances and also as least-cost distances, which were measured via a forested route. The vicinity of an occupied site may increase the probability of the occupancy of a neighboring site, so the distances were also measured to the nearest patch and separately to the nearest occupied patch.

I further used principal component analysis to produce new independent variables, and used them in explaining the occurrence of the flying squirrel in a habitat patch. In this way, I was able to use most of the patch and landscape information to describe the occurrence patterns. I ran a logistic regression analysis (Hosmer & Lemeshow 2000) backwards starting with all principal components and their two-way interactions and then removing non-significant effects step by step. The most parsimonious model was selected based on Akaike's Information Criterion. AIC is a function of the model deviance and the number of variables in a model (AIC; Burnham & Andersson 2003). The most parsimonious model was evaluated by randomly dividing the data into five groups of equal size, and repeating the modeling using four groups of the data each time. This produced five sub-models. I examined the variability in the model's accuracy by comparing the sub-models.

### *2.4.2 Temporal variation in the patch occupancy (II)*

Distribution models often assume that the habitat responses are similar in time (Randin *et al.* 2006). Due to changes in population density, for example, this is not necessarily the case. It would be important to know if a survey from a single year provides as accurate information about the habitat responses of the species as repeated surveys do. I addressed this problem by repeating surveys of the habitat patches within the same study landscape as in paper I during a seven year period. The surveys were carried out every second year, in 2000, 2002 and 2004. Part of the habitat patches were also surveyed in 2006. Using logistic regression and AIC in model selection, I built habitat models for each year. Having already gained results from paper I, I kept the variables and analyses simpler here. Based on the ecological hierarchy and existing knowledge of habitat preferences for the flying squirrel, I included patch area, patch quality, amount of good habitat in the vicinity of a patch and distance to the nearest occupied patch, respectively, to the models.

I evaluated the temporal consistency of the most parsimonious model from the year 2000 by testing its predictions for the year 2004. Based on the data on occupancy during 2000–2004, I also classified the habitat patches into three classes: continuously occupied, continuously unoccupied and variable-occupancy patches. I analyzed the response of these three occupancy classes to habitat variables. In addition, the possible effects of forest cuttings on the three occupancy classes as well as on occupancy events in patches (stable presence, stable absence, colonization and abandonment) were analyzed.

### *2.4.3 Spatial transferability of the habitat models (III)*

Defining and locating suitable habitats is essential from the perspectives of species conservation and landscape management. However, problems arise when characteristics of the suitable habitat should match practical planning procedures. There can be relatively good models that explain the characteristics of suitable habitats of a certain species (Guisan & Zimmermann 2000, Scott *et al.* 2002). However, the connections between the models and the planning practices may still remain weak because of incompatibility between data used in modelling and in planning. Expressing habitat requirements of a species in terms of the forest stand data (forest stand characteristics) used in forest management practices would provide a link between conservation and forestry planning. Model predictions are still not necessarily accurate with other areas. Therefore, variability in the model accuracy should be known before concerning model applications, and thus models should always be evaluated (Araújo & Guisan 2006, Randin *et al.* 2006).

My aim was to study the applicability of forest stand data to predict the occurrence of the flying squirrel in northern Finland, and to evaluate the models by using independent data from geographically different areas. I examined the forest and landscape related attributes explaining the occurrence of the flying squirrel in a forest stand. Flying squirrel occupancy in mature spruce-dominated forest stands in the year 2002 was determined from two study areas: in Taivalkoski (Lakusuo area; 91 stands) and in Kajaani (98 stands). The surveyed stands in Taivalkoski had ≥ 50% of total volume spruce and were ≥ 80 years old. In Kajaani, all the stands that had a volume of spruce ≥ 35 $m^3ha^{-1}$ were surveyed. These criteria were rather broad to ensure that all potentially suitable habitats were included to the study.

I built as parsimonious and interpretable models as possible, based on logistic regression and AIC. The variables entered to models were based on habitat preferences of the flying squirrel: stand size (ha), volumes ($m^3ha^{-1}$) of spruce and birch in the stand, and to the area (ha) of, and distances (m) to good quality stands within the 500 m radius around a focal stand. The quality of a stand was determined by the probability of the occupancy of a flying squirrel. I evaluated the predictive models by using presence-absence data from the other study area and compared the predicted probabilities with the observed occupancy. In addition, I tested transferability of two of the models with presence-only data from the three municipalities of Taivalkoski (n = 83), Pudasjärvi (n = 34) and Suomussalmi (n = 130).

### *2.4.4 Ecological habitat model in forest planning scenarios (IV)*

The central idea in landscape ecology is to examine patterns and processes at multiple spatial and temporal scales in dynamic heterogeneous environments. In long-term forest planning, both spatial and temporal scales are typically present together with ecological and economic aspects. I examined if suitable habitat for the flying squirrel can be maintained while ensuring timber production in the same planning area (ca. 10 000 ha). A stand was assigned as flying squirrel habitat (FSH) if it had a predicted probability of occupancy that was over 50%, which was calculated using the flying squirrel habitat model built in paper III. Mazerolle & Villard (1999) suggest that both patch and landscape characteristics should be included in the models when examining the distribution of animals. The habitat model used here included characteristics of a stand (stand size and volumes of spruce and birch) and the availability of good habitat within a 500 m radius around the stands.

Five alternative forestry plans, two having only an ecological or economic objective and three having a combination of both objectives were worked out. The ecological objective was to maximize the amount of suitable habitat for the flying squirrel and the economic objective was to maximize timber production in cubic meters within the planning area. The "Max FSH" plan maximized flying squirrel habitat, and the "Max NPV" plan maximized the net present value of timber. The "Forest Service" plan represented the present forest management strategy, the "FSH & Timber" plan had concerned both flying squirrel habitat and timber production, and finally the "Less Limits" plan was similar to "FSH & Timber" but had fewer restrictions such as protection for stand use. Future area-specific scenarios were simulated over 60 years in time for each alternative.

The MONSU forest planning software (Pukkala 2004) was used to simulate the scenarios. Optimizations were used to find the best combination of stand treatments under the specified objectives in the planning area (Pukkala & Kangas 1993), and a combination of three different heuristic techniques (Michalewicz & Fogel 2004) was used in the optimization to find as the most optimal solution for each scenario. I compared the outcomes of the plans with each other as well as with a theoretical production possibility frontier (Mas-Colell *et al.* 1983). The theoretical production possibility frontier in this study demonstrated a trade-off between ecological and economic objectives. The frontier shows the relationship between the objectives, which can be used to estimate how to increase one objective value without decreasing the other. In addition, I illustrated the spatial arrangement of suitable habitat in the planning area by thematic maps and defined habitat configuration patterns at the end of the planning period.

### *2.4.5 Test for an umbrella species concept (V)*

Indirect shortcut methods are suggested to improve the effectiveness of biodiversity conservation (Noss 1990, Ricketts *et al.* 1999). One of these indirect methods, an umbrella species concept, is especially related to the conservation perspective. Protection of the umbrella species will also conserve a number of naturally co-occurring species (Fleishman *et al.* 2000). Umbrella species may also be relatively demanding or sensitive for the habitat type and size of the habitat (Roberge & Angelstam 2004). Therefore, it may have a considerable spatial aspect in landscape planning. I addressed the role of the flying squirrel as an umbrella species here since there are higher amounts of dead wood found in the occupied forests in northern Finland than in other forest sites (Reunanen *et al.* 2002a). In Finland, about a quarter of forest-associated species are dependent on coarse woody debris (CWD) (Siitonen 2001). These species have become prominent among red-listed species (Rassi *et al.* 2001).

I studied the relationship between the occurrence of the flying squirrel and the existence of wood associated species representing polypores (Basidiomycetes), lichens (Lichenes) and beetles (Coleoptera). Many of these organisms typically use dead wood during their life. The hypothesis was that if stands occupied by the flying squirrel accommodate more species than random stands, the presence of the flying squirrel might be a sign to select species rich sites for conservation. The presence of the flying squirrel could thus be used as a shortcut tool to help in site-selection problems in northern boreal forests. As such, it could be a step towards the combination of species-oriented and ecosystem approaches. For the field surveys, I selected twenty mature spruce-dominated stands, of which twelve were occupied by the flying squirrel. The surveys for polypores, lichens and beetles in the stands were carried out in the year 2003 under average weather conditions. CWD was also measured.

I used general linear modeling (GLM; Quinn & Keough 2002) to model factors affecting the species richness. I also analyzed if the occupied stands had more species on average than randomly selected stands by using resampling (Blank *et al.* 2001). Finally, I addressed a site-selection problem by estimating the effect of available resources. This was carried out by defining a combination of stands that would cover the maximum number of species for a given level of protection using linear optimization analyses.

# 3 Results and discussion

## 3.1 Occupancy patterns (I, II, III)

Forests occupied by the flying squirrel, either defined as habitat patches based on MS-NFI data (I, II) or as forest stands based on forest stands data (III), were on average larger in size than the unoccupied forests. They also contained a higher proportion of spruce-deciduous rich sites (I, II) or higher volumes of spruce and birch (III). These findings were in line with earlier results (Reunanen *et al.* 2000, 2002c, Selonen & Hanski 2004), and show that important habitat characteristics for the flying squirrel can be recognized using both MS-NFI data and forest stand data.

Occupied habitat patches were situated below 300 m a.s.l. (I), which indicated a change in the forest structure with elevation. Therefore, forests above 300 m a.s.l. cannot be counted as suitable habitat for the flying squirrel. In this study landscape, forests below 300 m a.s.l. are prime commercial forests harvested mainly by clear cutting. If the amount of suitable habitat in the lowlands is decreased by assuming that ample suitable habitat remains at a higher elevation, conflicts between management for commercial forestry and flying squirrel persistence may increase. This highlights the importance of a proper habitat classification, because uncritical evaluation will overestimate the area of functional habitat. It also reveals some limitations of the forest estimates based on MS-NFI data and the habitat classification here, which were not entirely accurate to distinguish ecologically important differences in the forest structures at higher altitudes.

In addition, the configuration of the habitat patches in the study area was clustered (I). This was mainly due to the underlying topography and forest management history, but the configuration of occupied habitat patches seemed to be even more clustered than for the habitat patches in general. The distances between occupied patches were shorter than those from unoccupied patches to occupied patches (I). Within 500 m vicinity of the occupied forests, there was also more suitable habitat for the flying squirrel than around the unoccupied forests (I, III). A clustered arrangement of occupied forests may be related to population dynamics. If habitat patches are situated close to each other, the population processes may be more stable (McKelvey *et al.* 1993, Harrison & Fahrig 1995, Letcher *et al.* 1998). However, these data were limited to address the underlying processes for the aggregated pattern of occupied patches.

The distances between habitat patches were within the observed dispersal distances of the species (I), so all habitat patches in the study landscape were reachable. There were no clear effects of the potential dispersal areas in relation to occupancy. Only the habitat patches that were located far from other patches had more potential dispersal areas within their close surroundings (I). This suggests that flying squirrels seem to be able to move between habitat patches in this landscape. Matrix characteristics have been found to matter for species persistence (*e.g.* Selonen *et al.* 2001, Reunanen *et al.* 2002c, Selonen & Hanski 2004, Wiegand *et al.* 2005, Debinski 2006). It seems that the maintenance or regeneration of forests suitable for dispersal of the flying squirrel should be considered particularly among distantly situated habitat patches.

### 3.2 Predictability of the occurrence (I, II, III)

The occurrence of the flying squirrel in a forest was described and also predicted rather well. The models showed accuracy from about 70% in more applied approaches in papers II and III up to 88% in the descriptive model in paper I. In papers I and II the most important characteristics explaining the occurrence were related to habitat patch size, habitat patch quality and distances especially to the nearest occupied patches. Particularly in paper III, a model consisting of stand size and volumes of spruce and birch predicted occupancy of the majority of the stands correctly. As a conclusion, better forest patch quality in terms of larger size, a higher amount of deciduous trees, and shorter distances especially to other occupied forests, lead to a higher probability of the presence of the flying squirrel.

Evaluation of the models revealed that these findings were rather general. In paper I, the comparison between the five sub-models revealed similar characteristics that explained the occurrence of the flying squirrel. In paper II, one model was found rather transferable in time: the performance of the model from the year 2000 was similar also in the year 2004. The occurrence of the flying squirrel was mainly explained using patch size and distances to the nearest occupied patch in each year. Predictive models were similar between the years with only slight changes in their accuracy. In the year 2002, the proportion of core pixels describing the internal quality of a patch was included in the model. This may be related to a slightly lower prevalence of flying squirrels within variable-occupancy patches, and indirectly suggested a lower population density in the year 2002 in the study landscape.

In paper III, the models built in the Lakusuo area (in Taivalkoski) showed a relatively good transferability to the state-owned forests in the surrounding municipalities. In particular, a model based on stand size and volumes of spruce and birch predicted 68% of the occupied stands correctly in Pudasjärvi, 78% in Taivalkoski, and even 92% in Suomussalmi. However, within private-owned forests in a more southern study area of Kajaani, the Lakusuo models did not succeed better than a guess. Similarly, the model built in Kajaani did not perform well with data from other study areas and municipalities. This was most probably due to differences in vegetation zones and landscape structures of the areas as well as the forest ownership, which reflected the stand size and different forestry practices. In Lakusuo and in the surrounding municipalities the average stand size in state-owned forests corresponded well with the average home range size of a female flying squirrel. In Kajaani, the stand size in private forests was on average much smaller, and thus the habitat preferences of the species at the stand scale may not be so easy to detect.

In general, the absence of the species was better predicted than the presence in these studies (I, II, III). This was most likely due to the population dynamics, because at any time part of the patches will be unoccupied due to abandonments and mortality (see also II). It is also possible that some characteristics of the forests that are important for the flying squirrel were not recognized. For example, proper data on aspen, an important tree for food and cavities, was unavailable. Predicted probabilities for unoccupied stands may still be useful for landscape planning practices, if the absence is true. However, in these studies false predictions were found (I, II, III), which may affect the accuracy and performance of the models (Gu & Swihart 2004). In particular, false negative predictions for actually occupied forests must be taken into account in forest management, because destroying the occupied habitats of a protected species would be detrimental (Brito *et al.* 1999). In study III, it was found that the risk of falsely assigning an occupied stand as unoccupied can be decreased by lowering the cut point for the probability value, for example from 0.50 to 0.35, when the predicted presence is assigned for a stand.

Predictive models are not necessarily transferable to other geographical areas without carefully exploring the underlying landscape structure and land use history (Araújo & Guisan 2006). If the underlying uncertainties are kept in mind, the models built here (I, II, III) may help to locate potential habitats for the flying squirrel and be used to create thematic maps for landscape planning. The results in paper III especially encourage the application of predictive models in the Koillismaa region to predict the occurrence of the flying squirrel for forest management purposes. Careful considerations of model transferability between regions as well as field surveys to verify the occupancy are still needed. Based on the knowledge at hand and taking into account the availability of financial resources for field surveys in general, the pellets seem to be the best method to locate the used forest sites so far. This particularly concerns the habitats suitable for females to raise young, which should be the priority for population protection.

It appears that with additional data and further research, distribution models based on presence-absence data could be developed and used to estimate the abundance of the flying squirrel. It certainly would improve the ecological realism of the habitat models if occupancy data from several years could be included. Although abundance data, derived from the density of the species, has been thought to include more information for conservation purposes (Tosh *et al.* 2004), there seem to be a general relationship between abundance and presence of the species (Gaston *et al.* 2000, Nielsen *et al.* 2005, Pollock 2006). Pearce and Ferrier (2001) pointed out that appropriate use of models to predict species abundance must be based on a strong relationship between the true abundance and habitat quality, and especially between the measured species abundance. If so, predicted probabilities based on presence and absence as well as logistic regression models may suit the estimation of species abundance (Pearce & Ferrier 2001).

## 3.3 Dynamics in the occupancy (II)

Temporal dynamics in the patch occupancy was characteristic of the study landscape. During the study period from 2000 to 2004, the proportion of patches occupied at least once was 57%. Therefore, more than half of mature spruce-dominated forest patches in this landscape were used by the flying squirrel when considering the time scale. Single-year and single survey estimates of the proportion of occupied habitat, for example 35% based on paper I (see also Reunanen *et al.* 2004) may severely underestimate the amount of suitable habitat (MacKenzie 2005).

The average characteristics of occupied and unoccupied habitat patches remained stable across the years. After the three surveys (2000–2004), there were 36 continuously occupied, 51 continuously unoccupied and 32 variable-occupancy habitat patches. Continuously occupied habitat patches were of the best quality, continuously unoccupied of the lowest while variable-occupancy patches were of intermediate quality. However, the differences between continuously unoccupied and variable-occupancy patches were not clear based on measured variables. Only repeated surveys revealed the changes in patch occupancy. For example, based on research of red squirrels (*Sciurus vulgaris*) van Apeldoorn *et al.* (1994) suggested that when population size is low fewer individuals would inhabit only the patches of better quality. It is also possible that patches of high quality function as source patches that support patches of lower habitat quality (*sensu* Pulliam 1988). Strayer (1999) noted that an apparent decline in patch occupancy may represent random variation or dynamics of a stable population. Habitat quality may still be more important for explaining turnover patterns than variables that just describe patch size and inter-patch distances (Fleishman *et al.* 2002). Selonen *et al.* (2007) found that dispersing flying squirrels tended to settle on patches lower in quality than the ones in which they were born. Therefore, since dispersal (but also density-dependent habitat selection) may affect the temporal dynamics and spatial distribution of populations, also seasonal and yearly variation in habitat selection should also be included in further analyses (Morris *et al.* 2004).

The number of habitat patches decreased due to harvesting during the study period. At the same time, the percentage of the habitat patches occupied by the flying squirrel increased from 36% in 2000, to 37% in 2002 and 52% in 2004. The year when data are gathered may affect the parameter estimation and model accuracy especially if the population demography patterns or the phase of population fluctuation is unknown. During 2000–2006 more patches were colonized than were abandoned. This suggests that the individuals can move regularly among habitat patches, that the landscape is functionally connected relatively well. An increase in the occupancy rate suggested a population increase or fluctuation in density. Unfortunately, there is no data to examine the processes behind this observed pattern. Information on the overall abundance of flying squirrels in Finland is also lacking. There may still be large regional differences in the species abundance. For example, due to weather conditions and food availability, density estimates from other populations would not necessarily hold true. In these data the changes in the patch occupancy were not related to cuttings in the vicinity of the patches. It is also possible that the time scale of this study has been too short to detect the effects of changes in landscape structure.

The results showed that a single year survey may reveal some of the major characteristics that explain the occurrence of the species, but does not necessarily identify the intermittently used habitats that are likely important for the local population. Ignoring seldom occupied habitats can also lead to the underestimation of a network of suitable habitats in landscape management. Thus, these results call for long-term follow-up studies to examine the species occurrence in a landscape. Increasing the number of years in the survey will likely increase our understanding of the variation in the ecological patterns and processes. In addition, surveys should probably also focus more on characteristics of a potential habitat such as sheltered core areas (characterized by deciduous trees for food and aspen for cavity trees), than only the presence or absence of pellets at the certain moment the forest is visited. The benefit of the habitat approach is that inventories of the forest structures are possible at almost any time of the year. The potential, but unoccupied habitats have been noticed in many surveys, but at the moment only the occupied sites are protected. Thus, many important forest sites that happen to be unoccupied may be lost simply due to mortality and the time lag before new colonization.

## 3.4 Future scenarios (IV)

The objectives defined in the forest plans for future scenarios were well reflected in the results. During the planning period of 60 years, the amount of suitable habitat for the flying squirrel increased markedly: from about 9% to 25–34% depending on the plan. Suitable habitats also became better clustered in the area with time. This was likely related to the spatial habitat model, which took the closeness of neighboring habitats into account. These results suggest that habitat fragmentation in a landscape can be controlled if spatial goals are also used in forest planning.

The pure ecological plan "Max FSH" produced the highest amount of the habitat and as such, estimated the ecological potential of the area. Concurrently, it produced the lowest amount of timber flow. On the other hand, the pure economic plan "Max NPV" had the highest amount of timber which showed the economic potential of the area, but achieved the lowest amount of habitat. A comparison of the plans with the curve of theoretical production possibilities showed that ecological and economic targets were well achieved when both targets were simultaneously included in a plan. This was clear especially in the "FSH &

Timber" plan, but also in the "Forest Service" plan that represented the present planning strategy.

A new finding was related with the plan "Less Limits" that had both suitable habitat and timber as objectives but had a larger area for harvesting. This meant there were more possibilities for locating the timber harvest. The plan produced the largest amount of suitable habitat for the flying squirrel together with almost the largest amount of timber. This suggested some possibilities for dynamic forestry planning. Some other policies besides strict protection for species with less stringent habitat requirements can probably be considered. The same forests could produce several products or values in space and time simultaneously or separately. Stands could, for example, be used first partly for timber production and then for conservation purposes, or vice versa. Recreational or other social values could also be included into this kind of approach. However, not all ecological characteristics are compatible with timber production, and removing land use restrictions in real life requires careful consideration – if it even can be a realistic option.

This study showed that a predictive spatial habitat model based on forest stand data can be incorporated into forestry planning software. The structure of the spatial model was complex and its use rather time consuming, but at the same time it brought ecological realism into the planning procedure. According to the simulated scenarios, maintenance of suitable habitat does not necessarily mean there will be a considerable reduction in timber flow. Theoretically the most optimal scenarios had both ecological and economic targets, which suggested the importance of considering different targets simultaneously. Both a habitat model and future simulations of forest management still include uncertainties, for example, changes in forest structure, climate conditions, and timber price. When underlying uncertainties are kept in mind, a combination of ecological and economic goals in the planning process, both spatial and non-spatial, seem to be an encouraging way to learn more about the characteristics and long-term production potential of a landscape.

Incorporation of species distribution models into future management scenarios may also be an efficient way to combine ecological knowledge into the planning procedures. The scenarios can reflect interesting relationships and underlying processes in the landscapes, and may be useful to examine the importance of habitats outside of the protected areas. With a long time scale, some flexibility for the forest use and combination of different goals in space and time could be taken into account. Production of alternative landscape management scenarios should therefore thus be encouraged (see also Boutin & Hebert 2002).

### 3.5 The flying squirrel as an umbrella species (V)

The flying squirrel seemed to have the potential to be an umbrella species for some dead-wood associated species in the northern boreal forests of Finland. There was a tendency for a higher number of species or species records in stands occupied by the flying squirrel than in other stands. This relationship was mostly due to polypore species, which are an important part of the northern boreal forest ecosystem, but no co-occurrence was found between the flying squirrel and lichens or beetles.

The volume of CWD was higher in stands occupied by the flying squirrel than in unoccupied stands. Downed wood was the most important dead wood variable that explained the number of species and records. Stand size, downed spruce and the flying squirrel explained 69% of the number of polypore species, of which the flying squirrel explained 12%. A stand with a high amount of CWD and a flying squirrel present would therefore also likely foster a high number of polypore species. This is an interesting finding from a management perspective because CWD is currently a routine measurement in forestry planning, and the occupancy of the flying squirrel is also often checked. It is possible that the available forest stand data may already be used to indirectly estimate the stands with a high number of polypores.

Site-selection analyses revealed that there was a larger number of species and records in stands occupied by the flying squirrel than in randomly selected stands. When the stand selection was optimized to maximize species number for a limited area, a majority of the selected stands were occupied by the flying squirrel. If only a small area can be protected, focusing first on stands occupied by the flying squirrel could be a useful strategy since they probably include more rare species than stands without the flying squirrel. The flying squirrel may thus, assist in site-selection and help define the spruce-dominated habitat network in a northern boreal forest landscape.

The positive relationship with the polypores may further suggest that the occurrence of the flying squirrel could reflect connected habitats for other species that have limited dispersal abilities. Angelstam (1992) has suggested that the existence of capercaillie (*Tetrao urogallus*), hazel grouse (*Bonasa bonasia*) and the white-backed (*Dendrocopos leucotos*) or three-toed woodpecker (*Picoides* *tridactylus*) could reflect sufficient resources for a typical bird species community in a boreal forest landscape. In Finland, there is some evidence supporting the use of the capercaillie (Pakkala *et al.* 2003) and white-backed woodpecker (Martikainen *et al.* 1998) as umbrella species. The capercaillie and white-backed woodpecker reflect the availability of large, pine-dominated forests with a closed canopy and old-growth birch forests, respectively. As an umbrella species for the richness of polypore species and mature spruce-dominated forests, the flying squirrel could complement this suggested set of umbrella species for biodiversity in boreal forests, and be used together with the capercaillie in forest management planning in northern Finland.

Monetary costs of the species survey also support the use of indirect methods to assist in the decision making. The cost for surveying the occurrence of the flying squirrel in study V was a fraction of the cost for surveying the dead wood dependent species: flying squirrel data from the 20 stands required two weeks of work but the field survey and species identification of the polypores, lichens and beetles required 14 months of work. Hence, surveying the occurrence of the flying squirrel is relatively easy and cheap compared to surveys of other species (see also Juutinen & Mönkkönen 2004).

The evidence from this study, however, did not suggest a strong, overall relationship between the flying squirrel and the other species in question. The observed relationship is most likely indirect. The occurrence of the flying squirrel probably indicates an overall forest structure and existing substrate for polypores, because mature and older boreal forests often have both downed wood and old deciduous trees for cavity trees (Esseen *et al.* 1997). Nevertheless, protected areas probably benefit a set of species simultaneously (Lindenmayer *et al.* 2002).

# 4 Conclusions

## 4.1 Occurrence of the flying squirrel in space and time

One of my central findings in this thesis was that the characteristics of mature spruce-dominated forests preferred by the flying squirrel can be expressed with forest variables currently in use (I, II, III). Both data types, MS-NFI data and forest stand data, can be used to illustrate potential habitats for the flying squirrel in northern Finland. I also found that temporal occupancy dynamics were typical in the boreal forest landscape studied here (II). A majority of the occupied forests were found by a single survey, but irregularly used sites were only recognized by repeated surveys. To locate the network of suitable habitats in the landscape, I recommend a follow-up study. In addition, a careful definition of suitable habitat is needed, so that the amount of functional habitat in a landscape is not severely overestimated.

Moreover, I found that at the landscape scale occupied forests were situated in clusters (I). It may be that a clustered arrangement of habitat patches of better quality enhances the occurrence of the flying squirrel at the local landscape scale. The high rate of colonization suggested that flying squirrels seemed to be able to move well in the landscape (II). Forested connections were characteristic only for the most distantly located habitat patches (I). When the purpose is to maintain the flying squirrel in boreal forest landscapes, a network idea with habitat patches as nodes and their clustered arrangement or forested connections as linkages (*sensu* Forman 1995) is worth considering.

Landscape level surveys call for data from a large area. Satellite-image based MS-NFI data do not have any limitations with respect to land ownership, and as such, they are suitable for classification of forested areas in large landscapes (I, II). Unfortunately, the availability of MS-NFI data for purposes other than research is limited. In addition, the databases are large and habitat classifications require expert skills that forest planners do not necessarily have. Therefore, the true application of the approaches or models built in papers I and II is not likely to happen in the near future. Forest stand data (III, IV) have better accuracy in smaller forest compartments and as such they are useful for daily forest planning practices. However, the availability of forest stand data from privately owned forests may also be limited or even restricted. This may diminish the possibilities for sustainable forest planning at the landscape level; however an increased understanding of the importance of the landscape scale in forest planning combined with good management skills would probably overcome this problem. Nevertheless, more accurate information on certain tree species (aspen in the case of flying squirrels) would improve the usefulness of forest stand data to locate preferred characteristics for forest dwelling species (III).

### 4.2 Predictive models as tools

I had encouraging results from building and using predictive habitat models in the case of the flying squirrel (I, II, III). The occurrence of the flying squirrel could be predicted rather accurately, and particularly models based on forest stand data could be applied within the same region. The models were found suitable to estimate the distribution of flying squirrel habitats within the study landscapes (I, II, III, see also IV), and also in time (II). The models in paper I (and II) were still rather complicated and mainly descriptive, mostly due to the characteristics of MS-NFI data and habitat classification. More understandable and testable models in paper III were closer to the needs of forest practices. Even though there was some variation in the habitat models, I found the basic models similar enough to highlight the most important patterns in the occupancy. As such, these robust models can illustrate the majority of the flying squirrel distribution in the boreal forest landscape. This suggests that with further research it could be possible to build ecological tools that are widely applicable in space and time.

The models are always tied to the built-in settings and data limitations. Models that are built with different data or applied to different areas, for example, are not necessarily congruent (Araújo & Guisan 2006, but see Menendez & Thomas 2006). The user of predictive models always has to cope with a trade-off between accuracy and usability (Randin *et al.* 2006), and the uncertainties in predictions must be interpreted for the management purposes (Pollock 2006). The model accuracy can be increased by including more variables, but this happens at the expense of simplicity and usability of the model. As such, a model is also always a compromise between accuracy and transferability: a model with a perfect fit with certain data may not explain patterns in other data, whereas a relatively robust model may also find the most important patterns in other systems (Araújo & Guisan 2006).

As a conclusion, models I particularly built in paper III with the use of forest stand data can be used in forestry practices to point out important forest characteristics for the flying squirrel. Since these parsimonious models are relatively robust, I also found them useful from the perspective of landscape management. However, I emphasize that field surveys cannot be totally dismissed, and the model performance should be estimated before applying models to a new area. The characteristics of known flying squirrel forests in the region can be the start. The habitat estimation in the landscape can also be done by first locating potential habitat stands from the forest stand data using rather broad criteria, then producing a thematic map of them, and finally surveying a part of those stands in the field. The findings will give some insight for the occupancy pattern of flying squirrels there and help in modifying the area-specific habitat criteria for further management purposes.

## 4.3 Perspectives for landscape management planning

Even though this thesis consisted of studies concerning only one species in a relatively limited geographical area, I found several results that provide applications for conservation and forest management. First of all, MS-NFI data and forest stand data, as well as predictive habitat models can be used to locate habitat characteristics of the flying squirrel in northern Finland (I, II, III). The habitat models performed rather effectively within the region, so they can also be used to illustrate potential habitats at the landscape level. However, access to both types of forest data should be provided to improve effective forest planning at the landscape scale.

Second, the integration of a spatial habitat model into long-term forest planning calculations turned out to be a very interesting and encouraging exploration. Future scenarios revealed that the maintenance of suitable habitat for the flying squirrel is possible and it does not necessarily require a considerable loss of timber during the planning period (IV). Thus, I can recommend the consideration of different targets simultaneously as an alternative for forest management planning. These are combinations of ecological and economic goals, both spatial and temporal. A comparison of different scenarios may enhance learning about the characteristics and possibilities of the area in question (Keeney 1982, Fries *et al.* 1998, IV). While being aware of the underlying uncertainties, the produced scenarios may further help the decision making in complex planning situations. However, the quality of future forests grown by today's forest practices remains a question. Especially concerning flying squirrels and other forest dwelling species, variation in the forest structure is essential. This requires inclusion of more information concerning the economically invaluable but ecologically valuable forest characteristics to the databases, as well as repeated surveys in time for focal species and their habitats.

Finally, support for the role of the flying squirrel as an umbrella species was found. The support was based on the co-occurrence of the flying squirrel and dead wood dependent polypores as well as the monetary costs of the species survey. Costs for surveying the occurrence of the flying squirrel were a fraction of the costs for surveying the dead wood dependent species (V). Limited funding often requires the use of indirect methods, such as the occupancy of the flying squirrel to assist in decision making. However, replacing intensive species surveys with other alternatives due to a lack of financial resources must be considered carefully since improper knowledge of ecological patterns may have negative consequences for landscape management (MacKenzie 2005). Earlier, flying squirrels have been found to prefer more continuous forests (Reunanen *et al.* 2000), and inhabit relatively large home ranges (Hanski 1998, Hanski *et al.* 2000). The occupied sites also seem to situate close to each other (I). While occupying relatively clustered mature spruce-dominated forests, the flying squirrel could complement a set of surrogate species suggested for boreal forest management (*sensu* Angelstam 1992). Based on these findings, I propose the use of the flying squirrel as one of the target species in research and especially in forest management planning in northern Finland. This also takes into consideration the important structural elements (*e.g.* dead wood, large aspen) in future mature forests.

Conservation goals are just one piece in the big picture of landscape planning (Margules & Pressey 2000). A wider perspective in landscape planning includes the participation of many professionals and different interest groups. Further challenges in landscape management include the examination of habitat thresholds and the production of future scenarios to help complex decision making processes (Boutin & Hebert 2002). These scenarios will need combinations of ecological, economic as well as social aspects. To conclude, I believe that multi-scaled spatial and temporal approaches are future challenges that will help us to understand the structure and changes in a heterogeneous mosaic of landscapes, as well as deal with complex systems and problems within large areas. Forman (1995) has described the ideal practice of landscape planning well: “Think globally, plan regionally, and then act locally”.

### 4.4 Future research questions

Even though the findings in this thesis were encouraging for applications in forest planning and other land use, some questions need further inspection. The examination of population processes of the flying squirrel across Finland could be carried out. An emphasis should be placed on habitat threshold effects based on a landscape continuum approach. This approach could include research on species diversity within the core areas of the home ranges of flying squirrels. These core areas are rich in deciduous trees and typically include aspen, which is considered a key species in the boreal forest. Core areas could be small hot spots for biodiversity.

Research considering ecological, economic and sociological aspects of the flying squirrel habitats would increase our knowledge of multi-purpose land use. In particular, research on the relationship between the flying squirrel habitats, recreational values and game species survival would be interesting. Exploration of these aspects would need expert knowledge at a multi-disciplinary level, but despite of the complexity, this research might provide important insights for sustainable landscape management planning.

Besides multi-species approaches, MS-NFI data and forest stand data could be further combined with more detailed aerial photographs. Lindenmayer & Franklin (2002) pointed out that the diversity of landscape management questions needs a diversity of management strategies. The locating of important biological characteristics probably also needs a diversity of data. Landscape heterogeneity could probably be better studied with multi-scale data, preferably both in space and time, which would be beneficial for further research concerning habitat thresholds and management scenarios. However, there may be a considerable challenge to applying multi-scaled habitat mapping approaches in operational forestry.

Finally, the extent to which ecological understanding is incorporated into forest management practices in the long term should be studied. This would help not only future research in conservation biology and the ecology of different species, but also the landscape and forest managers in their work. In addition, estimating the effectiveness of legislation to maintain biodiversity is essential for the development of future legislation in which will successfully reach these goals. This includes research into the roles of different forest owners as well as their understanding and willingness to follow the policies in actual landscapes.

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# Original articles

I Hurme E, Reunanen P, Mönkkönen M, Nikula A, Nivala V & Oksanen J (2007) Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. Ecography 30: 277–287.

II Hurme E, Mönkkönen M, Reunanen P, Nikula A & Nivala V (2008) Temporal patch occupancy dynamics of the Siberian flying squirrel in a boreal forest landscape. Ecography 31: 469–476.

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ISBN 978-951-42-8938-5 (Paperback)
ISBN 978-951-42-8939-2 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)

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