JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE
220

Jonna Timonen

Woodland Key Habitats

A Key to Effective Conservation of Forest Biodiversity?

JYVÄSKYLÄN YLIOPISTO

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 220

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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Vanhassa juhlasalissa (S212)
huhtikuun 1. päivänä 2011 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2011

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URN:ISBN:978-951-39-4282-3
ISBN 978-951-39-4282-3 (PDF)

ISBN 978-951-39-4242-7 (nid.)
ISSN 1456-9701

Jyväskylä University Printing House, Jyväskylä 2011

ABSTRACT

Timonen, Jonna
Woodland key habitats – a key to effective conservation of forest biodiversity?
Jyväskylä: University of Jyväskylä, 2010, 33 p.
(Jyväskylä Studies in Biological and Environmental Science
ISSN 1456-9701; 220)
ISBN 978-951-39-4242-7 (nid.), 978-951-39-4282-3 (PDF)
Yhteenveto: Avainbiotooppien merkitys talousmetsien monimuotoisuuden säilymiselle
Diss.

Intensive forest management has fragmented the landscape and changed structural features of forests endangering many forest-dwelling species. Thus, conservation measures in production forests have become necessary in the maintenance of biodiversity. Today, woodland key habitats (WKH, small-scale presumed hotspots of biodiversity) constitute an essential conservation measure in the North European forests. In this thesis I studied the role of WKHs in the conservation of biodiversity in production forests. First, I compared the definitions, inventories and implementation processes of WKHs in Sweden, Finland, Norway, Latvia, Estonia and Lithuania. I found that even though the philosophy behind the WKH concept was the same in all of the countries the implementation varied nationally resulting in different sets of habitats being included in the WKH networks. Second, I systematically reviewed whether the WKH concept is an efficient conservation tool i.e. whether WKHs host more biodiversity qualities (e.g. dead wood and red-listed species), compared to production forests. WKHs seemed to be hotspots of dead wood, diversity of dead wood, species richness and red-listed species compared to the production forests but there were some differences among countries. Finally, I experimentally studied short-term effects of forest management practices on polypores and dead wood in WKHs. Dead wood volume, perennial, annual and red-listed polypores were not affected significantly by the management practices, but there were significant differences in the species turnover rates among the sites. My results suggest that protecting small-scale habitats in production forests could be a potential conservation tool. However, preserving solely WKHs is not enough to conserve biodiversity and thus other measures are also needed. Nowadays forest conservation has shifted its focus from a strong emphasis on protected areas towards conservation measures in production forests. From this perspective, WKHs could serve as a potential additional tool for sustaining forest biodiversity at the landscape scale.

Keywords: Biodiversity; conservation, forest management; red-listed species; woodland key habitats.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-III.

I Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A. & Mönkkönen, M. 2010. Woodland key habitats in northern Europe: concepts, inventory and protection. Scandinavian Journal of Forest Research 25: 309-324.

II a) Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. 2010. Review Protocol No. 81. Are Woodland Key Habitats Hotspots in Boreal Forests?
http://www.environmentalevidence.org/Documents/Protocol81.pdf
b) Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. 2010. Systematic Review No. 81 2010: Are Woodland Key Habitats Hotspots in Boreal Forests? http://www.environmentalevidence.org/SR81.html
c) Timonen, J., Gustafsson, L., Kotiaho, J.S. & Mönkkönen, M. 2010. Hotspots in cold climate: conservation value of woodland key habitats in boreal forests. Biological Conservation, in press.

III Timonen, J., Selonen, V.A.O., Halme, P., Mönkkönen, M., Peltonen, K, & Kotiaho, J.S. 2010. Short-term effects of experimental selective logging and buffer zone on dead wood and polypores in brook-side key habitats. Manuscript.

The table shows the contributions to the original papers. Smaller contributions are stated in the acknowledgements of the original papers. JT = Jonna Timonen, MM = Mikko Mönkkönen, JSK = Janne S. Kotiaho, LG = Lena Gustafsson, JS = Juha Siitonen, VS = Ville Selonen, KP = Katriina Peltonen, JNS = Jogeir N. Stokland, AST = Anne Sverdrup-Thygeson

	I	II	III
Original idea	MM, JT, JS	MM, JT, LG	JSK,VS
Data	JT	JT	VS, KP, JT
Analyses	JT, JS	JT, MM, JSK	JSK, JT, MM, VS
Writing	JT, JS, MM, LG, JSK, JNS, AST	JT, LG, MM, JSK	JT, JSK, PH, MM

1 FOREWORD

Conservation biology is not merely a scientific discipline. Conservation of biodiversity needs science but scientists in this field must carefully pay attention to society's values, take into account economics and most importantly, always communicate their findings to the practitioners. In my thesis I gathered all the available information about woodland key habitats (WKHs) in order to produce a comprehensive synthesis that would serve the scientific community with the recent knowledge and the society with practical guidelines concerning the conservation values of the woodland key habitats. First, I submerged myself in to the jungle of concepts, definitions and implementation of WKHs and produced a review in which the basic information of WKHs is organized and readily available. Second, I conducted a systematic review answering the question of whether WKHs are biodiversity hotspots or not. Systematic review provides a methodology to assess the effectiveness of policy and management interventions. Conducting a systematic review follows certain set of guidelines that include protocol formation, data search strategy, data inclusion, data extraction, and analysis. Starting from the protocol and leading to the finalized review the process is peer-reviewed and also open for a public consultation. All the stages of the review conduction are available to the public at www.environmentalevidence.org. Thus, the process is transparent and its main purpose is to communicate research findings to the practitioners. Finally, I left the office and went to the forest to conduct an experimental study of whether WKHs would be able to maintain forest biodiversity. To conclude, the aim of the thesis was to evaluate WKH's status as a conservation tool and produce a synthesis that could be valuable not only from the scientific but also from the practical point of view.

2 INTRODUCTION

2.1 Biodiversity and boreal forest management policies

Biodiversity has been defined as "the totality of genes, species and ecosystems in a region" and it can be divided in to three hierarchical categories: genes, species and ecosystems (World Resources Institute, 1992). Today, we are losing biodiversity at a rapid rate and are on the verge of sixth known mass extinction of species. Globally, fragmentation and especially habitat loss are acknowledged as major threats to biodiversity. One of the most fundamental relationships in nature is the species-area relationship, or the increase in the number of species with area (Rosenzweig 1995). Thus, the loss of area decreases the number of species. Hanski (2005) defines four kinds of habitat loss: 1) loss of quality; 2) loss of quantity (area); 3) loss of connectivity and 4) loss of continuity. The first two refer to a one particular site and increase the risk of population extinction by decreasing population sizes. The loss of area of relatively small habitat patches may also increase edge effect that usually further reduces the area of the habitat. The latter two habitat loss types relate to spatial relationships among multiple habitats and increase the risk of metapopulation extinction by disrupting migration and dispersal of species.

Habitat loss and fragmentation are unquestionably threatening biodiversity also in Fennoscandian and Baltic forests (Hanski 2005; 2007). These forests have been heavily exploited in the past. Hence, there has been a dramatic transformation from the structurally diverse and multi-aged old-growth forests into young, even-sized, single-aged forest stands (Östlund et al. 1997, Löfman & Kouki 2001). Old-growth forests are primary habitats for a substantial number of threatened species and thus the loss of old-growth forests has caused the endangerment of many forest-dwelling species (Rassi et al. 2001).

The Convention on Biological Diversity (CBD), signed at the United Nations Conference on Environment and Development in Rio de Janeiro in 1992, launched a series of international and national initiatives, processes and resolutions in order to sustain biodiversity (.http://www.cbd.int/). The accepted principles were the bellwethers for European forest policy in 1990´s. In the Second Ministerial Conference held in Helsinki in 1993 the principles, criteria and indicators of sustainable forestry were established, and later they were reflected to national forest policies and legislation.

Since the 1990s, in Fennoscandian and Baltic countries the official objective of forest policy has been to practice forestry in a sustainable manner by taking conservation of biodiversity into account. Besides traditional conservation programmes, several conservation tools, such as controlled burning and leaving dead wood, were introduced (Larsson & Danell 2001, Vanha-Majamaa & Jalonen 2001). The most important and economically notable tools have been the retention tree approach, where individual trees or small groups of trees are retained on a cut area, and the conservation of woodland key habitats (WKH).

The term woodland key habitat was launched in Sweden in 1990 (see (Norén et al. 2002) and was introduced to a wider audience in 1992 in a special issue of Svensk Botanisk Tidskrift, which was dedicated to the preservation of boreal forest in Sweden. The WKH concept was subsequently adopted in other Fennoscandian countries (Finland, Norway) in the mid 1990s, and in Baltic countries (Latvia, Estonia, Lithuania) in late 1990s to early 2000s. The main idea behind the WKH concept is to conserve biodiversity in production forests by delineating and preserving small habitat patches that are supposed to be particularly valuable (of "key" importance; hence the term "key habitat") for maintaining landscape-level biodiversity. However, there are differences in the definitions and implementation of WKH concept among countries.

At present, all Fennoscandian and Baltic countries have national forest legislation, which sets certain minimum standards for conserving biodiversity in production forests, and several countries also have specific definitions and regulations concerning WKHs. More detailed standards for the identification, delimitation and management of WKHs have been included into forest management guidelines and into forest certification criteria. Large-scale inventories have been carried out by the forestry and nature conservation authorities to map and delimitate WKHs. On average, WKHs cover approximately 1% of the total forest area in Fennoscandian and Baltic countries. Put together, WKH inventories have probably been the most extensive habitat inventory effort in the world.

The WKH concept has been presented as a cost-efficient conservation method (Wikberg et al. 2009); it should be cost-efficient to conserve the maximum number of species with a minimum cost. In order to be an efficient conservation tool, WKHs should host more biodiversity qualities, such as red-listed species and dead wood, than typical production forests. Also, WKHs should be able to maintain these qualities in time, even if the surrounding forest would be heavily managed. The WKH concept has not gained unanimous support and it is based on several ecological assumptions which have been used to argue for and against the conservation status of WKHs (Hansson 2001, Hanski 2005).

2.2 Ecological questions of the WKH concept

2.2.1 Ecological assumptions behind the WKH concept

The idea that WKHs constitute a cost-efficient tool to sustain biodiversity in production forest landscapes hinges on several ecological assumptions. WKHs are assumed to represent natural hotspots in the landscape with concentrations of red-listed species (rarity hotspots). This assumption requires that red-listed species are clustered in space. WKHs should be identifiable on the basis of structural elements and/or the occurrence of indicator species. WKHs often represent extremities of main ecological gradients (moisture, productivity, topography, and disturbance), and therefore, they presumably host species assemblages that differ from those in typical forests in the region. Therefore there is supposedly also considerable complementarity among WKHs in their species assemblages.

Moreover, WKHs are assumed to represent high quality patches in the landscape fostering higher than average species numbers. Because of the general tendency for species assemblages to be nested (Wright et al. 1998), red-listed species are presumably over-represented in WKHs. Further, WKHs are assumed to constitute stepping stones enhancing connectivity and hence dispersal of species requiring unmanaged forests in the matrix of production forests.

In general, WKHs are small in size, and therefore the sizes of species populations are necessarily rather limited within a WKH. This may jeopardize the persistence of an individual population even if the site is set aside from forestry practices. The small size of WKHs may also result in isolation and strong edge effects further increasing the likelihood of population extinctions in small patches. Consequently, the small size of WKHs has been the main cause of criticism towards the use of WKHs as a conservation tool. One may argue that WKHs are useful only if they comprise a well-connected network and thus support a metapopulation. Next I will discuss the ecological assumptions concerning WKHs in more detail and finally I will address the size limitation of WKHs.

2.2.2 Role of WKHs as hotspots for red-listed species

Hotspots are defined as sites particularly rich in species, rare species, threatened species, or some combination of these attributes (Reid 1998). WKHs should represent hotspots in the landscape with concentrations of rare specialist species (rarity hotspots). WKHs could be ‘natural’ hotspots of rare species for example due to special structural factors or soil properties. WKHs could also be remnants of natural forests and thus host species that are extinct or rare in the surrounding forests. Empirical evidence for the hotspot status of WKHs is inconclusive. Some studies have shown that WKHs indeed foster high numbers of red-listed species (Gustafsson et al. 1999; Gustafsson 2002; Perhans et al.

2007) but other studies have failed to unequivocally support the hotspot status of WKHs (Gustafsson 2000; Johansson & Gustafsson 2001; Gustafsson et al. 2004; Sverdrup-Thygeson 2002; Pykälä et al. 2006).

The hotspot status of WKHs has been criticized mostly due to their small size (Hanski 2005). Gjerde et al. (2004) concluded that WKHs ability to capture red-listed species is scale-dependent. When WKHs constitute 5% of the landscape, only 20-25% of red-listed species populations may be located within WKHs when red-listed species are mapped at the scale of 1 ha. Therefore, most of the red-listed species are not captured in small-scaled habitats.

2.2.3 Red-listed species are clustered in space

The efficiency of WKHs for conservation depends on the degree of clustering in space of red-listed species. Nitare and Norén (1992) list six possible explanations for the spatial aggregation of rare and endangered species: 1) age and degree of continuity of the sites, 2) continuous occurrence of the habitat in the nearby area, 3) previous land use or occurrence of natural disturbance, 4) the present age and condition of the stand, 5) particular edaphic and climatic factors and 6) abundance of important key elements.

Gjerde et al. (2004) did not find strong clustering patterns of red-listed species and suggest that many of the red-listed species would be consistently found outside defined hotspots. Thus, in landscapes dominated by mature forests, selection of rarity hotspots would be more challenging. However, Gjerde et al. (2004) also suggested that in forest landscapes highly dominated by clearcuts and young plantations red-listed species would more likely be clustered rendering WKH concept applicable.

2.2.4 Use of indicator species

Indicator species have been used in the identification of WKHs. In the WKH context, the term indicator species has been used for more or less specialized species, which have rather strict habitat requirements. The presence of indicator species should indicate high probability of occurrence of red-listed species. Gustafsson (2000) sets two criteria for a good indicator of WKHs: a good indicator should correlate with the red-listed species in WKHs and it should also be more common in WKHs that in production forests.

Indicator vascular plants, however, did not fulfill both of these criteria in Swedish WKHs (Gustafsson 2000) and neither did lichen species, although some of the indicator lichens did correlate with red-listed species (Johansson & Gustafsson 2001). Nordén et al. (2007) found that the number of indicator species indicated the number of red-listed species in lichens but not in bryophytes or wood-inhabiting fungi. Sverdrup-Thygeson (2001) found no association between fungal indicator species and red-listed saproxylic beetles. However, Jonsson and Jonsell (1999) found a significant correlation between indicator wood-living fungi and vascular plants but not between other species groups (vascular plants, bryophytes, epiphytic lichens, wood-inhabiting fungi).

In sum, the empirical studies have not consistently supported the applicability of the indicator species approach, and nicely exemplify the complexity and difficulty of using indicator species. Different species groups correlate with different species or factors. Therefore Jonsson and Jonsell (1999) suggest the inclusion of a wide range of indicators. Nordén et al. (2007) suggest that perhaps one alternative to indicator species inventories could be to focus more directly on red-listed species.

2.2.5 Complementarity of key habitats

One strategy used to maximize species diversity in sites is based on complementarity (Vane-Wright et al. 1991). Complementarity strategy involves selecting a set of sites so that each newly selected site captures new species that were not present in the previously selected sites (Pressey et al. 1993). Lewandowski et al. (2010) suggest that conservation planning should emphasize complementarity rather than the hotspot approach when using surrogate taxa. However, only the Norwegian WKH policy incorporates both hotspot and complementarity components (Baumann et al. 2002a, Baumann et al. 2002b, Baumann et al. 2002c). Sætersdal et al. (2003) showed that environmental variables associated with site productivity and humidity explained most of the differences in species assemblages. If the sites for conservation were selected purely on the basis of their species richness sites, then sites with fewer red-listed species would not be selected (Gjerde et al. 2007) and a considerable proportion of species may fall short of adequate protection (see also Similä et al. 2006).

2.2.6 Nestedness

A set of species is said to be nested if the species present in species-poor sites are subsets of the species present at richer sites (Patterson and Atmar 1986). If species are highly nested, rare species are only found in species rich sites (Gustafsson 1999). Thus, in case of high nestedness, species conservation should focus on richness hotspots in order to capture the maximum number of red-listed species.

Several studies have measured the nestedness of different boreal species groups and the results are variable and even contradictory. Jonsson and Jonsell (1999) found that among 10 boreal spruce forest stands only lichens and vascular plants showed significant nestedness, while bryophytes and wood-inhabiting fungi did not. Also Gustafsson (2000) found significant nestedness in vascular plants. Berglund and Jonsson (2003) found significant nestedness in all the studied taxa (vascular plants, mosses, liverworts, crustose lichens, polypores and corticoids). However, in this study nestedness was dependent on area and quality of sites, i.e., in larger and higher quality patches red-listed species were over-represented given the overall level of nestedness. Berglund and Jonsson (2003) conclude that small habitats of high quality should not be neglected in conservation. WKHs are assumed to represent high quality patches and therefore over-representation of red-listed species could be expected. Nestedness analysis can also be used to discern indicators of rare species and thus many red-listed species. Species with intermediate occurrence and high degree of nestedness can indicate species rich communities and thus rare species (Jonsson & Jonsell 1999, Gustafsson 2000, Halme et al. 2009).

2.2.7 Connectivity

Connectivity can be divided to structural and functional connectivity (Baudry & Merriam 1988; Mönkkönen 1999). Structural connectivity refers to the physical pattern of the habitat and possible connections between habitats in the landscape. Functional connectivity refers to the actual movement of individual organisms between habitats and its associated responses to the matrix. Therefore, connectivity depends also on the condition of the matrix and even relatively minor changes may substantially enhance connectivity for many taxa (Lindenmayer & Franklin 2002). WKHs could constitute stepping stones enhancing connectivity and hence dispersal of species in the matrix. Laita et al. (2010) concluded that WKHs are important from the connectivity perspective, especially in case of rare and scattered habitat types. However, connectivity is highly species-specific and the critical distance between habitats varies between and within organism groups (Lindenmayer & Franklin 2002). Species with poor dispersal abilities are not likely to benefit greatly from WKHs in the connectivity perspective. Good dispersers, on the other hand, benefit from WKHs also as bridging habitats in reserves that would otherwise remain unconnected (Laita et al. 2010). Species dispersal abilities are generally poorly known, and thus the importance of WKHs as stepping stones for red-listed species is difficult to evaluate.

2.2.8 Metapopulation

A metapopulation consists of spatially separated populations of one species that interact with each other (Hanski 2005). In a fragmented forest matrix WKHs can be seen as patches separated by production forests where populations exist. Some of the patches may encounter extinctions of local populations and some unoccupied patches may become occupied by immigrants from other patches. Immigrants may also emigrate to patches occupied by small population and decrease the extinction risk. A sufficiently dense network of even small habitat patches could possibly sustain a metapopulation. However, WHKs form such a sparse network that it is unlikely that they would support viable metapopulations (Hanski 2005). Small habitat patches, such as WKHs, can support only small local populations of threatened and specialist species which have a high extinction risk in the long term. According to source-sink population dynamics, large habitats are more likely to act as a source of individuals than smaller habitats. Small habitats could actually become a sink for the species due to edge effect (Hansson 2001). Consequently, WKH networks are likely to host non-equilibrium metapopulations where local extinctions far outweigh the recolonization rate of empty patches.

The contribution of WKHs to metapopulation persistence depends not only on WKHs themselves but also on the protected areas network and the quality of the production forest landscape matrix surrounding WKHs and protected areas. The metapopulation approach usually considers landscape as consisting of suitable habitat patches embedded in the matrix of hostile landscape of non-habitat and thus ignores the dynamics in the matrix. Yet, the matrix quality may have important effects on metapopulation dynamics (Vandermeer & Carvajal 2001). The quality of the matrix depends on the species experiencing it. Many red-listed species that are habitat specialists may experience the production forest (matrix) as a hostile and uninhabitable environment, but for some species production forests provide resources and habitats and thus increases, for example, species dispersal abilities. The efficiency WKHs should be evaluated in concert with other measures taken to sustain biodiversity in production forests (Mönkkönen et al. 2010) and they may in some cases support the existing protected areas network (Laita et al. 2010).

2.2.9 Isolation and edge effects

Fragmentation of the forest landscape causes isolation of suitable habitats. The degree of isolation depends on the quality of the habitats and how they are situated in the landscape (Aune et al. 2005). If the WKHs are scattered in the landscape without connectivity to other WKHs or reserves, it is unlikely that particular species will be able to persist. Also, the species composition will possibly become more like the composition in the matrix.

The sizes of WKHs vary (on average 0.7 ha in Finland to 4.6 ha in Sweden) but often they are relatively small and thus prone to edge effects. Edge effect may cause changes in the microclimatic conditions due to increased exposure to sunlight and wind. The physical damage caused by wind has been shown to reduce lichen abundance (Esseen 1998}. The core area analysis done by Aune et al. (2005) suggests that edges do have a strong impact in the WKHs. Given a 25m edge influence, only half of the total area could be considered as core area of WKH. WKHs in the study area of Aune et al. (2005) were on average 8.6 ha whereas in general WKHs are much smaller. Thus most of the habitats do not have core area at all but are entirely under the edge influence. For some species the edge effect could extend up to even 50m but the response of species is species-specific and context-dependent (Moen 2003).

Altogether, there is no consistent evidence that the ecological assumptions behind the WKH concept are fulfilled. First of all, empirical evidence for the hotspot status of WKHs is inconclusive. Also, it is unclear whether red-listed species are clustered in WKHs or whether the use of indicator species is more applicable in the selection of WKHs. The complementarity approach could perhaps enhance the capture of red-listed species but in relation to WKHs it has only been used in Norway. The results of measuring nestedness of different boreal species groups have also been variable and even contradictory. The complexity of the assumptions behind the WKH concept increases because several assumptions are intertwined. Isolation and edge effect affect the lack of connectivity that hinders the dispersal of species and thus the function of metapopulations. The role of WKHs as stepping stones enhancing metapopulation persistence in the matrix could be important but there are currently too few studies to fully evaluate this.

3 AIMS OF THIS THESIS

Woodland key habitats constitute an essential instrument in the conservation of biodiversity in production forests in Fennoscandia and Baltic countries. Yet, a comprehensive view of the WKH concept and its implication is missing. To be a successful conservation tool, the WKH concept should first fulfil the ecological assumption behind the concept. Secondly, the concept should be properly implemented. Thirdly, if the implementation has been successful, WKHs should host more biodiversity qualities than production forest. Finally, WKHs should be able to maintain their species composition in time, also under the forest management practices conducted in the vicinity or even in the habitats themselves. Based on these themes the specific objectives of my thesis were to:

1) Introduce the ecological assumptions behind the WKH concept
2) Compare the definitions, inventories and implementation processes of WKHs in Sweden, Finland, Norway, Latvia, Estonia and Lithuania
3) Systematically review whether the WKH concept is an efficient conservation tool, i.e., whether WKHs host more biodiversity qualities compared to the production forest, and also whether WKHs would be able to maintain biodiversity qualities even when surrounded by clear cuts
4) Experimentally study short-term effects of forest management practices on polypores and dead wood in WKHs

4 MATERIAL AND METHODS

4.1 Review of the WKH concepts and policy (I)

In order to study the WKH concept thoroughly, it is necessary to get a clear and comprehensive picture of the subject. Hence, I conducted a review of the definitions, inventories and implementation processes of WKHs in Sweden, Finland, Norway, Latvia, Estonia and Lithuania. The potential differences in WKH definitions and terminologies may cause confusion and misinterpretation when statistics or research results about WKHs are compared, for instance, among countries. The material for the review consisted of official inventory reports, inventory handbooks and information found from the internet. We also consulted several experts who had been participating concretely in the planning of WKH inventories.

4.2 Systematic review (II)

To be a cost-efficient tool for sustaining biodiversity in managed forest landscapes WKHs should contain a higher number of biodiversity qualities, such as dead wood and red-listed species, than the surrounding production forests of similar age, and these qualities should persist even if surrounding forests were clear cut. Many forest-dwelling species are dependent on dead wood: thus, dead wood is an important biodiversity quality that should be abundant in WKHs. I conducted a systematic review to detect whether WKHs are biodiversity hotspots. Conducting a systematic review follows a certain set of guidelines that include protocol formation, data search strategy, data inclusion, data extraction, and analysis (Pullin & Steward 2006). First, I formulated a protocol which I then followed when I conducted the literature searches. I then extracted the data from the relevant studies that I found during the searches. For the statistical analysis of the data I used MetaWin 2.0, (Rosenberg et al. 2000) to conduct a meta-analysis. The chief purpose of a meta-analysis is to provide an estimate of the true effect based on all studies that are available. To obtain this estimate, different test statistics, means and variances or simple significance levels are first transformed into a common currency called effect size and then combined (Rosenthal 1991; Gurevitch & Hedges 1993; Cooper & Hedges 1994).

4.3 Experimental study (III)

In Finland, low-intensity management is permitted in WKHs if their characteristic features, for example their natural species composition and community structure, is not altered. It is unclear, however, by which management methods the maintenance of habitat characteristic features can be guaranteed. In our experimental study I explored how buffer zones and selective logging affect the dead wood volume and polypore species in brook-side forests. This study is a part of a follow-up study established in 2004 and the before treatment data was collected in October 2004 and 2005. Treatments were conducted in January 2006 and after treatment data was collected during the October 2007.

The study sites are situated in Central Finland, North Savonia and North Karelia. Twelve of the sites are situated in the southern boreal vegetation zone and 31 in the middle boreal vegetation zone (Ahti et al. 1968). The studied brook-side forests are mesic Norway spruce dominated forests. We established a two-by-two factorial experiment supplemented with controls. Our focal area in each of the experimental sites was the immediate surroundings of the brook (within 15m). We considered the immediate surroundings to be 15m from the brook. We had two manipulated factors in the experiment: the existence of a buffer zone (with or without) and selective logging (logged or not). The control sites were left outside any forest management actions. Thus, control sites are surrounded by a minimum of 80m of continuous forest cover in which no logging has taken place. Adjacent to treatment sites we conducted a minimum of 0.8 ha clear cut. In pursuance of the clear cutting, a 15 meter buffer zone or no buffer zone was left. In addition to the clear cutting, we applied selective logging on some of the sites by harvesting 30% of the basal area of the stand. In treatments without a buffer zone, the selective logging was conducted on the focal area whereas in treatments with the buffer zone, the selective logging was conducted on both the focal area and the buffer zone. Altogether there were 4 different treatments: 1) no buffer zone, no selective logging, 2) no buffer zone but selective logging in the habitat, 3) buffer zone, no selective logging on the brook habitat, 4) buffer zone and selective logging on both the buffer zone and the habitat and control. Control sites were left outside of all the cutting activities. At each site, I measured the dead wood from 30m x 15m plots and polypores from 0.2ha (66.66m x 30m) plots.

To determine the effects of selective logging and buffer zone on dead wood and perennial, annual, and red-listed species number and records, I analyzed the data with repeated measures ANOVA. It could be expected that if the treatments did not have an effect, both the dead wood volume and the polypore diversity increase slowly in all treatments.

I calculated the number of species that went extinct and the number of species that colonized each of the sites between 2004 and 2007. I calculated these separately for perennial, annual and red-listed polypores. First, I analyzed the overall trends in extinctions and colonizations with a one-sample t-test against zero and then by an ANOVA testing for the treatment effects and their interactions.

To see whether annual and perennial polypores behave the same way or whether changes in annuals are more pronounced, I analyzed the differences in the number of extinct and colonized species between annual and perennial polypores. First, I analyzed the overall trends in the difference in extinctions and colonizations between perennials and annuals with a paired sample t-test followed by repeated measures ANOVA where I entered colonization or extinction of perennials and annuals as the repeated measure and buffer zone and selective legging and their interaction as independent factors.

I also wanted to test for the possible changes in the polypore community caused by the treatments. Therefore, I employed a non-metric multidimensional scaling (NMDS). In NMDS, I used species abundance data and ordination was calculated by using relative Sørensen distance measure. Species occurring only once in the data were excluded from the final ordination. I conducted the ordination analysis with PC-Ord version 4.41 (MJM Software Design).

Finally, I analyzed the effect of the treatments on the most abundant species. The analyses were conducted with repeated measures ANOVA.

5 RESULTS AND DISCUSSION

5.1 Woodland key habitats - concept, implementation and protection (I)

The philosophy behind the WKH concept is basically the same in all of the countries: to protect biodiversity in production forests. Sweden and the Baltic countries have similar WKH models, while the models in Finland and Norway are clearly different. Depending on the country, the definitions emphasize different factors, such as soil and bedrock properties, stand structure and occurrence of indicator species.

The mean size of the WKHs varied considerably, from 0.7ha (Finland) to 4.6ha (Sweden). The degree of formal protection also differs. Preservation of WKHs is primarily based on forest legislation in Finland, Estonia and Latvia, and on forest certification in the other countries.

The implementation of the WKH concept is nationally and regionally variable and susceptible to personal and communal subjectivity, resulting in different sets of habitats being included in the WKH networks. The control surveys revealed that the identification and delineation of WKHs has not been very comprehensive. According to control surveys this underestimation is most severe in Finland and Sweden, where majority of WKHs may have gone unnoticed.

In order to improve the efficacy of the WKH concept more emphasis should be placed on the precision of implementation, including the training of the inventory personnel. Also, the protection of WKHs should be controlled so that the logging of WKHs would be subject to penalty. Clearly, WKHs are not able to conserve the biodiversity of production forests alone because their total area is limited in all the countries, all the habitat types are not adequately covered by WKHs and the persistence of species in WKHs is uncertain. However, WKHs may improve the spatial connectivity of naturally rare and scattered habitat types, although the functional connectivity for any particular species is dependent on the dispersal abilities of the species (Laita et al. 2010).

5.2 Hotspot or not? (II)

In total, we included 18 relevant studies in our review, of which only two studied whether WKHs are able to maintain their biodiversity qualities when surrounded by clear cuts. Sixteen studies compared the biodiversity qualities between WKHs and production forests. Based on those studies, WKHs seem to be relative hotspots for dead wood volume, diversity of dead wood, number of species and number of red-listed species. Dead wood volume was significantly higher in WKHs (mean 19m^3 ha^{-1}) than production forests (11m^3 ha^{-1}). In general, the dead wood volume in production forests varies between 2 and 10 m^3 ha^{-1} but in old-growth forests it could be 60-90 m^3 ha^{-1} on average (Siitonen, 2001). Even though WKHs do have more dead wood compared to production forests in general, the volume of dead wood in WKHs is still rather scant when compared to the old-growth forests. The diversity of dead wood was 1.7 times higher in WKHs than production forests. In general, WKHs should represent remnants of old-growth forests and this could reflect the diversity of dead wood. Old-growth forests are structurally more diverse compared to the production forests, and thus the source of dead wood in WKHs has been more diverse.

WKHs hosted 1.5 times more species than production forests. The difference was most pronounced in vascular plants and least pronounced in saproxylic beetles. This is quite surprising since saproxylic beetles are dependent on dead wood and there was significantly more dead wood in WKHs that in production forests. Although, saproxylic beetles may be difficult to sample extensively and therefore their detectability may be low.

Significantly more red-listed species in WKHs than in production forests were found in Sweden and Norway but this difference between WKHs and production forests was not significant in Finland. However, the only red-listed species group studied in Finland was the polypores. According to the Swedish definition red-listed species are likely to occur in WKHs and the Norwegian definition emphasizes habitat elements that are important for species. The sample size from Norway was low and thus results should be interpreted with caution.

In general, the lack of data is a common problem in systematic reviews (Steward et al. 2005) and this was also the case in our review, especially with studies comparing WKHs surrounded by clear cuts or production forests. It is also problematic to extract relevant data for meta-analysis because many of the studies do not report all the information needed. Further, the variable methodologies used in different studies complicate the interpretation of results. Whittaker (2010) criticized ecological meta-analyses of this reason and called for more rigorous and critical attitudes toward the use of meta-analyses.

5.3 The effects of forest management (III)

The volume of dead wood did not differ between study sites with or without buffer zones even though it could have been expected due to the increased windthrows. It may be that during the time between the logging and the dead wood inventory the wind was simply not strong enough to cause windthrows. Also, the volume of dead wood did not differ between selectively logged habitats and habitats that were not selectively logged. Sippola et al. (1998) also concluded that the volume of dead wood did not change remarkably 2 years after selective logging.

The species richness of perennial and red-listed polypores was not significantly affected by the treatments but the abundance of perennial polypores tended to increase when there was selective logging. Considering the number of annual species and records, a positive change took place when there was a buffer zone and no selective logging was done. Thus, if a brook-side key-habitat is not selectively logged and it is surrounded by buffer zone diversity and abundance of fungal assemblages can be maintained or even increased. Effects of selective logging on annual species tended to be slightly negative and strongest in sites with buffer zones.

There were significant differences in species turnover rates among the sites; in comparison to the controls, the number of extinctions was reduced in both perennial and annual species and there was a simultaneous reduction in the number of colonization in annual species. This result may seem unexpected since one could assume that forest management actions should increase turnover rate in polypore species assemblages. The presence of the buffer zone seemed to buffer the local fungal assemblages particularly well against logging effects on species turn-over.

Even though we did not detect strong overall change in the number of polypore species, our results indicate that the community turnover rate, in terms of extinctions and colonizations, is reduced in the treatment sites. Responses of fungal species to changes in environmental conditions and true extinctions and colonizations may be more profound over longer time periods and the extinction debt may occur only after decades. Therefore, it is important to conduct long-term follow-up studies.

5.4 The role of WKHs in the conservation of forest biodiversity

WKHs seemed to host more biodiversity qualities than production forests (II) and thus may have potential to function as a conservation tool. However, protecting only small-scale habitats in production forests is not enough to conserve biodiversity. My review revealed (I) that WKHs seem to be too small and too scattered in the production forest landscape to be able to sustain species persistence, especially if the quality of the matrix is poor. In small habitat patches the risk of extinction of populations is increased due to small population sizes and edge effect. The lack of connectivity disrupts dispersal and migration and thus increases the risk of extinction. Therefore, more conservation measures are needed if the goal is to maintain a full array of species in boreal landscapes.

Forest conservation has shifted its focus from a strong emphasis on protected areas to conservation measures in the matrix (Lindenmayer & Franklin, 2002). From this perspective, WKHs could serve as a potential tool for the conservation of forest biodiversity. However, there are several aspects that should be taken into account when implementing the WKH concept. First, the quality of the inventories should be improved so that WKH identification would be more thorough and efficient. The control inventories revealed (I) that the percentage of all assumed WKHs found during the original inventory was only 20 - 70% depending on the country. This may seriously undermine the ecological efficiency of the WKH policy. WKH based conservation should be considered an experiment and its effects should be systematically monitored. Systematic monitoring of ecological benefits and economic costs of WKHs would provide a solid basis for adaptive management of biodiversity in the boreal forest landscapes. The delimitation of the habitats should not have upper size limits, as is the case in Finland, where the upper size limit of a WKH is 1 ha in practice. This size limitation has resulted in very small WKHs in Finland, with the mean size of habitats being only 0.7 ha (I). The protection of WKHs should be emphasized so that they would not be destroyed by logging. Buffer zones should be left around WKHs in order to counterbalance edge effects. In my study (III), the buffer zone protected polypores from the edge effect when WKHs were adjacent to clear cuts. Also, connectivity to other protected areas in the landscape should be enhanced so that WKHs could operate as a part of a larger conservation network and not as separate network of small and scattered habitats (I).

In the future, we need more information on how species are able to persist in WKHs if the surrounding forest is clear cut. Besides studying WKHs on the patch scale, considering WHKs and the conservation of forest biodiversity in the future should focus on the landscape scale. We should consider all the available conservation tools together and combine them optimally so that they would complement each other.

Acknowledgements

First of all, I would like to express my gratitude to my supervisors Mikko Mönkkönen and Janne Kotiaho. Mikko, you are the man of solutions. You have the enviable skill to resolve problems in your dreams but unfortunately it has not passed on me, yet. Your optimism has helped me many times when I have been in doubt. You have believed in me even though sometimes I did not believe in me myself. Janne, your door has always been open and I could just walk in and have a melt down. Quite many times I have rushed in to you office and said 'Houston, we have a problem'. You have always listened patiently. You have an amazing skill of making things look better and building one's confidence when needed.

Lena, although you have not been my official supervisor, I felt like you were one. I feel very privileged being able to work with you. The time I spent in Uppsala was a healing time for me in so many ways. Thank you for having me! Huge thanks also to all the people at SLU, I had great fika with you.

I am deeply grateful to all my co-authors whom without it would have been impossible to get this thesis done. My dear Master's student Katriina, without you I would not have been able to conduct the polypore study. We had some memorable moments in Egyptinkorpi and elsewhere. Thank you for holding on. Ville, I also want to thank you for sharing your research sites and thank you for your help in the field.

Thank you, Eco section people! It has always been pleasure to come to work. I cannot imagine a better working environment than this. I could count on you all whenever I needed help. Special thanks to our Sauna & Support group, I really enjoyed our moments together! Marko, Heikki, Carita, Santtu, Aapo, Inka, Tuomas, Nina, Saana, Mika, Veronica, Gaia, Robert, Venera, and all the other PhD students, thank you for the good times, I hope that we'll have plenty of more of them. Monday Coffee Club people, we have had many good discussions and I value you not only as scientists but also as friends. Katja and Elisa, you have been extra helpful with so many things. I admire you and your amazing skills.

I have had the best time with my officemates. Merja, we have experienced so many things together and I could not have had a better friend to go through the whole PhD-business. We have laughed and cried together. We have also ended up in very odd situations together. Thank you for everything! Panu, you genuinely are one of the kindest persons I have met. You have helped me tremendously even when you have been extremely busy. Thank you! Tero, you are the encyclopaedia of knowledge. Thank you for helping me in numerous occasions and being my Excel-support person.

I am probably the luckiest person in this planet to have so many loving and caring friends. Thank you all for being my friends! You mean the world to me. Jani, you have supported me and reminded me about things that really matter in this life. Maria, you are my angel. You have stood up for me when I have been putting myself down. Riikka, you are my non-biological sister. We have our ups and downs, but most of all we have fun. Thank you for letting me be 'kireä kotka' and supporting me. I am looking forward to our 'ponivaellus Pohjanmaalla'. Jenni, I want to thank you for all the tea and therapy sessions, they have been priceless. Yinka, you are my salsa-buddy and dear friend. With you I have so much fun! Yo no se mañana, but I know we will have lots of salsa in the future. Niina and Virpi, you are about to finish your theses too. I wish all the luck for that. Thank you so much for countless conversation about the PhD-student life and life in general. Maarit, Mika, Mikko, Merja and Emma, thank you for your friendship that has lasted for decades. Lahti people, you have stepped in my life during the undergraduate years. Thank you for bringing so much joy in my life! Pia, Tiina, Katsu and Piia, with you I have started my university 'career' as trainees at the university. We have all come a long way. I'm privileged to be your friend.

My family, I thank you deeply. Äiti ja isä, kiitos että olette tukeneet minua kaikessa, mitä olen halunnut tehdä. Hanna and Robert, I always feel at home when I'm in Kirkkonummi, thank you so much for that. Tobias ja Matilda, te olette ihania! Puss och kram!

Finally, I want to thank Jackson Jennings for correcting the language. This study has been financed by the Academy of Finland (proj # 115560), the Finnish Ministry of the Environment (Ympäristöklusterin tutkimusohjelma) and Finnish Cultural Foundation (North Karelia Regional Fund).

YHTEENVETO (RÉSUMÉ IN FINNISH)

Avainbiotooppien merkitys talousmetsien monimuotoisuuden säilymiselle

Arviolta 95 - 99 % koskaan eläneistä lajeista on kuollut sukupuuttoon maapallomme historian aikana. Sukupuutot kuuluvat osana elämän kiertokulkuun, mutta niin sanottujen sukupuuttoaaltojen aikana huomattava osa lajeista kuolee sukupuuttoon suhteellisen lyhyessä ajassa. Yleisimmin sukupuuttoaaltojen syynä ovat olleet luonnonkatastrofit. Ihmisen toiminta on kiihdyttänyt monimuotoisuuden häviämistä niin kovaa vauhtia, että nykytilanteen voidaan sanoa vastaavan sukupuuttoaaltoa. Suurin syy monimuotoisuuden häviämiselle on elinympäristöjen pirstoutuminen ja häviäminen. Boreaalisissa metsissä suurimpana ongelmana ei ole pinta-alan vaan elinympäristöjen laadun huonontuminen ja sitä kautta myös elinympäristöjen väheneminen. Intensiivinen metsätalous on muuttanut metsien rakennepiirteitä monille lajeille epäedulliseen suuntaan. Fennoskandiassa vanhat metsät ovatkin ensisijaisia elinympäristöjä uhanalaisille lajeille. Arviolta noin viidennes Suomen metsälajeista on arvioitu hävinneiksi, uhanalaisiksi tai silmälläpidettäviksi. Monimuotoisuuden vähenemisen hidastamiseksi on metsätalouden toimenpiteitä muutettu osittain pehmeämmiksi, ja useita eri keinoja on otettu käyttöön monimuotoisuuden suojelemiseksi. Tällaisia keinoja ovat muun muassa kontrolloitu metsänpoltto, säästöpuiden jättäminen sekä erityisten arvokkaiden elinympäristöjen (tästä eteenpäin avainbiotooppien) suojeleminen. Avainbiotooppi-käsitteen käyttö sai alkunsa Ruotsista 90-luvun alussa ja sitä on sovellettu Ruotsin lisäksi Suomessa, Norjassa, Latviassa, Virossa ja Liettuassa. Avainbiotooppien perusajatuksena on toimia monimuotoisuuden keskittyminä eli uhanalaisten ja harvinaisten lajien elinympäristöinä.

Väitöskirjassani tutkin sitä, mikä on avainbiotooppien merkitys talousmetsien monimuotoisuuden säilymiselle. Ensimmäisenä selvitin kirjallisuuskatsauksen muodossa, kuinka avainbiotoopit määritellään ja suojellaan eri maissa ja kuinka avainbiotooppi-käsitteeseen pohjautuvaa suojelumenetelmää on toteutettu käytännössä. Aineistona käytin julkaistuja tutkimuksia ja raportteja sekä internetistä löytyvää tietoa. Jotta käytännöntoteutus olisi onnistunut, avainbiotooppien tulisi olla lajistoltaan ja rakennepiirteiltään monimuotoisempia kuin talousmetsän. Selvitin meta-analyysin avulla onko avainbiotoopeilla enemmän lahopuuta, lajeja ja uhanalaisia lajeja kuin talousmetsässä. Lisäksi pyrin selvittämään, pystyvätkö avainbiotoopit ylläpitämään monimuotoisuutta mikäli ne sijaitsevat avohakkuiden ympäröiminä. Aineistona tässä tutkimuksessa käytin myös julkaistuja tutkimuksia. Lopuksi tutkin kokeellisesti, kuinka metsätaloustoimenpiteet vaikuttavat lyhyellä aikavälillä avainbiotooppien kääpien ja uhanalaisten kääpien lajimäärään sekä lahopuun tilavuuteen. Koe toteutettiin Suomessa runsaslukuisimmilla avainbiotooppityypeillä eli purojen lähiympäristöillä. Koealueiden lähiympäristöt avohakattiin ja joidenkin avainbiotooppien ja avohakkuiden välille jätettiin suojavyöhyke. Lisäksi osalla avainbiotoopeista ja suojavyöhykkeistä suoritettiin poimintahakkuu.

Havaitsin, että avainbiotooppien määritelmät ovat lähtökohtaisesti samanlaisia kaikissa maissa, mutta eroja löytyi maiden käytännöntoteutuksessa ja suojelussa. Avainbiotooppi-käsitteen alla suojeltavat elinympäristötyypit vaihtelivat maiden välillä. Myös avainbiotooppien keskikoko vaihteli Suomen 0,7 hehtaarista Ruotsin 4,6 hehtaariin. Avainbiotoopit olivat lailla suojeltuja Suomessa, Virossa ja Latviassa, kun taas muissa maissa suojelu toteutui lähinnä metsäsertifioinnin avulla. Avainbiotooppien inventoinneissa oli selviä puutteita varsinkin Suomessa ja Ruotsissa, joissa suurin osa potentiaalisista avainbiotoopeista jäi rajausten ulkopuolelle. Käytännön toteutuksen eroista johtuen avainbiotooppiverkostostot muodostuvat erilaisista elinympäristö-tyypeistä maasta riippuen.

Meta-analyysin perusteella voidaan sanoa, että avainbiotoopeilla oli merkitsevästi enemmän lahopuuta, lajeja ja uhanalaisia lajeja kuin talousmetsissä. Myös erilaisten lahopuulajien ja lahoasteiden määrä oli avainbiotoopeilla korkeampi. Aineiston vähäisyyden vuoksi en voinut vastata kysymykseen, pystyvätkö avainbiotoopit säilyttämään monimuotoisuutta avohakkuiden keskellä. Tähän kysymykseen vastaavia tutkimuksia löytyi vain kaksi, mikä ei ole riittävä määrä meta-analyysin tekemiseen.

Havaitsin, että lyhyellä aikavälillä metsätoimenpiteillä ei ollut suurta vaikutusta monivuotisten, yksivuotisten ja uhanalaisten kääpien tai lahopuun määrään. Suojavyöhyke kuitenkin suojasi lajistoa silloin, kun kohteella ei ollut poimintahakkuuta. Kääpäyhteisössä tapahtui muutoksia siten, että sukupuuttojen ja kolonisaatioiden määrä laski käsittelyiden myötä.

Tulosten perusteella voidaan sanoa, että avainbiotooppien rooli talousmetsien monimuotoisuuden säilyttämiselle voi olla huomionarvoinen, mikäli ne nähdään osana suurempaa, maisematason suojelualueverkostoa. Itsessään avainbiotoopit voivat olla liian pieniä ja liian hajanaisesti esiintyviä pystyäkseen säilyttämään monimuotoisuutta pitkällä tähtäimellä. Avainbiotooppien inventoinnin laatuun tulisi kiinnittää enemmän huomiota ja avainbiotooppien koolle ei tulisi laittaa ylärajaa. Lisäksi avainbiotooppien ympärille olisi suositeltavaa jättää suojavyöhykkeet ja niitä tulisi suojella tehokkaammin hakkuilta. Ennen kuin avainbiotooppien merkitystä monimuotoisuuden ylläpitäjänä voidaan arvioida kokonaisvaltaisemmin, tarvitaan lisää tutkimusta avainbiotooppien kyvystä turvata monimuotoisuutta pidemmällä aikavälillä.

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