

Dissertationes Forestales 21

Green-tree retention and controlled burning in restoration
and conservation of beetle diversity in boreal forests

Esko Hyvärinen
Faculty of Forestry
University of Joensuu

Academic dissertation

To be presented, with the permission of the Faculty of Forestry of the University of Joensuu, for public criticism in auditorium C2 of the University of Joensuu, Yliopistonkatu 4, Joensuu, on 9th June 2006, at 12 o'clock noon.

Title: Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests

Author: Esko Hyvärinen

Dissertationes Forestales 21

Supervisors:

Prof. Jari Kouki, Faculty of Forestry, University of Joensuu, Finland

Docent Petri Martikainen, Faculty of Forestry, University of Joensuu, Finland

Pre-examiners:

Docent Jyrki Muona, Finnish Museum of Natural History, Zoological Museum, University of Helsinki, Helsinki, Finland

Docent Tomas Roslin, Department of Biological and Environmental Sciences, Division of Population Biology, University of Helsinki, Helsinki, Finland

Opponent:

Prof. Bengt Gunnar Jonsson, Department of Natural Sciences, Mid Sweden University, Sundsvall, Sweden

ISSN 1795-7389

ISBN-13: 978-951-651-130-9 (PDF)

ISBN-10: 951-651-130-9 (PDF)

Paper copy printed:

Joensuun yliopistopaino, 2006

Publishers:

The Finnish Society of Forest Science

Finnish Forest Research Institute

Faculty of Agriculture and Forestry of the University of Helsinki

Faculty of Forestry of the University of Joensuu

Editorial Office:

The Finnish Society of Forest Science

Unioninkatu 40A, 00170 Helsinki, Finland

<http://www.metla.fi/dissertationes>

Hyvärinen, Esko 2006. Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests. University of Joensuu, Faculty of Forestry.

ABSTRACT

The main aim of this thesis was to demonstrate the effects of green-tree retention and controlled burning on beetles (Coleoptera) in order to provide information applicable to the restoration and conservation of beetle species diversity in boreal forests. A methodological aspect was also included, in the form of an examination of the sampling of forest beetle communities. A large-scale field experiment involving 24 forest sites was established in eastern Finland, where harvesting intensity was manipulated together with burning treatments. The beetle data collected during one pre-treatment year and two post-treatment years covered altogether 201 501 individuals representing 1235 species. The main findings were: 1) Harvesting with or without burning increased the species richness, but it often began to decrease again in the second post-treatment year. 2) Many species of beetle colonized the sites effectively after the treatments, particularly the burned sites. 3) The richness of red-listed and rare saproxylic (deadwood-dependent) species was higher at burned than unburned sites, an effect which was not caused solely by pyrophilous species as many other species showed a similar pattern. 4) Higher levels of green-tree retention seemed to increase the richness of saproxylics, including red-listed and rare species, at burned sites in the second post-treatment year. 5) The abundance of red-listed and rare saproxylic species was higher at burned sites, and the pyrophilous species in particular showed population increases after fire. 6) Higher tree retention levels maintained the assemblages closer to the pre-treatment structure. The assemblages of saproxylic species were distinctly affected by the treatments and also differed between the two post-treatment years. 7) Harvesting with or without burning had a marked effect on herbivores, but they recovered by the second post-treatment year in burned areas. 8) Species dependent on ephemeral resources were the least affected by the treatments. 9) Burning and harvesting was detrimental for litter-dwelling species, but they seemed to recover quickly. 10) Ecological classification of the material collected in traps is important for revealing ecological patterns. 11) Large collections are needed to obtain representative samples of beetle communities in boreal forests.

The results show that the negative effects of timber harvesting on beetle diversity in boreal forests can be alleviated by increasing the green-tree retention volumes and by controlled burning. Many red-listed and rare saproxylic species seem to benefit particularly from the burning of harvested sites with retained trees. Unharvested burned sites seem to support rather different species assemblages from harvested ones, however, emphasizing the importance of fire as a restoration tool in conservation areas. Controlled burning and green-tree retention do not solve all the problems related to commercial forest management, but they will clearly benefit a significant part of the ecosystem, including perhaps the most species rich and one of the most endangered species groups, the saproxylic beetles.

Keywords: Biodiversity, Coleoptera, decaying wood, disturbance, forest management, saproxylic species

ACKNOWLEDGEMENTS

Over the past four years I have had a privilege to work and spent time with numerous colleagues and friends and it feels that all of you have affected to this thesis in a way or another. Many colleagues have already been mentioned in the original articles, so here I want to express my gratitude to other relevant persons. First of all, I thank Jari Kouki and Petri Martikainen for excellent supervision. You have arranged fruitful conditions for me to work and provided sound scientific advice when needed. There has also always been time for discussions and commenting of the manuscripts despite your other urgent matters. I hope you are pleased with the outcome, both the thesis and a researcher.

I want to thank the members of our diverse research team in Joensuu for many inspiring scientific as well as unscientific discussions both at group seminars and during lunch and coffee breaks, in particular Päivi Hokkanen, Kaisa Junninen & Harri Lappalainen, Jukka Kettunen, Atte Komonen, Kaisa Raitio and Olli-Pekka Tikkanen. It has been enjoyable to work with you. The King of “Nyppijät” Markku Karttunen, and during later years Osmo Heikkala have been of high value in the field and laboratory. I also thank the Mekrijärvi Research Station, especially Risto Ikonen, for taking care of arranging staff to sort the beetle material for identification. I have no records of all the people who have participated on the fieldwork and sorting of the material, but I sincerely thank you all for your work.

There are numbers of entomologists, whose enthusiastic and experienced company I have had a pleasure to enjoy in many memorable field trips to different parts of Finland (and I wish MANY more will come), and of course also in other events concerning beetles. I would particularly like to thank Tom Clayhills, Eero Helve, Seppo Karjalainen, Ilpo Mannerkoski, Jaakko Mattila, Jyrki Muona, Mikko Pentinsaari, Pertti Rassi, Ilpo Rutanen, Juha Salokannel and Juha Siitonen, I have learned a lot from and with you. The first important steps in the world of beetles I took in Jyväskylä, and I want to thank all the members of our young team there at that time (if not mentioned elsewhere), in particular Petri Ahlroth. I also wish to thank Docent Jari Haimi for being such an encouraging person in the field of insects during my M.Sc. studies.

I am grateful to have so many good friends sharing interests also on other forms of life than insects. Thanks for good company, excellent cuisine and lots of fun go to the “Taigan Pojat ry”: Ippu, Janne, Jokke, Jussi, Otso, Valtsu and Vesku, to other non-institutional friends Antti & Anna, Hemmo & Heidi, Jani & Päivi, Teukka & Suvi, Teija, and to many others I unfortunately too rarely get to meet.

The following institutions are thanked for financial support: the Academy of Finland, the Ministry of Agriculture and Forestry, the Ministry of Environment, the Finnish Forest Industries’ Association, the Finnish Forest Research Institute and the Metsähallitus (all these grants to J.K.), and the Graduate School in Forest Sciences and the Faculty of Forestry of the University of Joensuu.

I also want to express my gratitude to my parents Seija and Hannu for supporting my insect hobbies (among others), although butterflies and moths took most of my time (and ate some indoor plants) during my early years with insects. I also thank my sisters Pirjo (who has brought many larvae for me), and Sirpa and her family Leo, Iita & Azou for their interest to the diversity of nature and my work.

Finally, the dearest and most loving thanks are to Katja for being such a beautiful part of my life. It is sometimes hard to live with an entomologist, but as a biologist you fortunately understand.

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers referred to in the text by the Roman numerals I-IV:

- I** Hyvärinen, E., Kouki, J. and Martikainen, P. 2006. A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *European Journal of Entomology* 103:397-407.
- II** Hyvärinen E., Kouki, J. Martikainen P. and Lappalainen, H. 2005: Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management* 212:315-332.
- III** Hyvärinen, E., Kouki, J. and Martikainen, P. The response of beetle assemblages on green-tree retention and controlled burning in boreal forests: shared or idiosyncratic responses among four ecological groups? (Manuscript).
- IV** Hyvärinen, E., Kouki, J. and Martikainen, P. 2006. Fire and green-tree retention in conservation of red-listed and rare dead-wood dependent beetles in boreal forests. *Conservation Biology* (In press).

In all the studies E. Hyvärinen was responsible for identification (about 34% of the beetle material), preparation, classification, and analysing the data and writing the articles, and E.H. also participated the fieldwork. J. Kouki provided the idea of the study and designed the experiment. P. Martikainen participated in the study design, and he was specifically responsible in designing the beetle samplings. J. K. and P. M. participated also in the analyses and writing of the manuscripts together with E. H. H. Lappalainen participated on the identification of beetles and fieldwork.

TABLE OF CONTENTS

ABSTRACT.....	3
ACKNOWLEDGEMENTS.....	4
LIST OF ORIGINAL ARTICLES.....	5
TABLE OF CONTENTS.....	6
1 INTRODUCTION.....	7
1.1 Background.....	7
1.2 Study organisms – the beetles.....	9
1.3 Aims of the thesis.....	9
2 MATERIALS AND METHODS.....	10
2.1 Study area and experimental design.....	10
2.2 Sampling methods, data and analyses.....	12
3 MAIN RESULTS AND DISCUSSION.....	13
3.1 Sampling of forest-dwelling beetles (I).....	13
3.2 Effects of different levels of green-tree retention and controlled burning on the beetles in boreal forests (II, III, IV).....	15
3.2.1 <i>Species richness</i>	15
3.2.2 <i>Abundance of beetles</i>	17
3.2.3 <i>Changes in species assemblages</i>	18
3.2.4 <i>Methodological aspects</i>	19
4 IMPLICATIONS FOR FOREST MANAGEMENT AND SPECIES CONSERVATION.....	20
5 CONCLUDING REMARKS.....	22
REFERENCES.....	24
APPENDIX 1. Beetle species recorded at the study sites in 2000–2002. ...	30

1 INTRODUCTION

1.1 Background

For a long time disturbances were seen as events that interfere with the equilibrium of nature and shift climax communities away from near-equilibrium conditions (Clements 1936). Connell (1978) defined a disturbance briefly as an event that “regresses the succession”, while Sousa’s (1984) definition – “a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established” - adopts the paradigm shift from acknowledging “the equilibrium of nature” to understanding the dynamic character of all natural populations and communities, the fact that most communities exist in a state of non-equilibrium (Huston 1979). Nowadays a disturbance is simply regarded as a rapid release or reallocation of community resources (e.g. Sheil and Burslem 2003).

Natural disturbances of varying size, intensity and frequency create heterogeneity at the landscape and stand levels (Sousa 1984, Angelstam 1996, Kuuluvainen 2002). The classical intermediate disturbance hypothesis suggests that disturbances that are intermediate in frequency and size enable the coexistence of late-successional species and species adapted to younger sites, and thus maintain high species diversity (Connell 1978). Disturbances vary from small-scale (e.g. gap dynamics, small-scale flooding) to large-scale, stand-replacing disturbances (e.g. fires, windstorms, insect outbreaks) (Angelstam 1996). The most important large-scale disturbance factor in boreal forests is fire (e.g. Zackrisson 1977, Wein and MacLean 1983, Esseen et al. 1997, Niklasson and Granström 2001, Ryan 2002).

From the beginning of the 20th century in particular, natural disturbances have largely been replaced by stand-replacing disturbances of human origin, such as intensive forestry. This has taken place on a wide scale in Fennoscandia (e.g. Linder and Östlund 1998, Löfman and Kouki 2001) and is rapidly expanding eastwards in the boreal forests of Russia (Mayer et al. 2005). There is no doubt that disturbances, whether natural or not, have a major influence on many properties of these ecosystems. Disturbances caused by numerous agents on different temporal and spatial scales create a habitat mosaic for thousands of species. It is surprising to note, however, that the exact consequences of various disturbances for forest-dwelling species are still rather poorly understood. In particular, the similarities and differences between natural disturbances and those of human origin have remained unclear, although it is known that they differ notably in many critical aspects, such as in the amount of dead wood left behind (Angelstam 1996, Lindenmayer and Franklin 2002).

The importance of dead wood for species richness is well known (e.g. Harmon et al. 1986, Esseen et al. 1997, Siitonen 2001, Grove 2002, Jonsson et al. 2005). In boreal forests, where the tree species diversity is low, the role of decaying wood for biodiversity is even more pronounced. Dead trees provide microhabitats for numerous species during the decades of the decay succession. Natural stand-replacing disturbances create habitats with extensive biological legacies from the pre-disturbance forest (Lindenmayer and Franklin 2002), such as large living or dead trees. For saproxylic organisms, which in Speight’s (1989) definition are “species dependent upon dead or dying wood of moribund or dead trees (standing or fallen), or upon other such organisms”, these habitats provide an

abundance of resources. There are at least 5000 saproxylic species in Finland (Siitonen 2001). In Sweden, for example, it has been calculated that of the 380 beetle species living on Scots pine (*Pinus sylvestris* L.) only 6 % inhabit live trees and the remaining 94 % colonize dead trees in various phases of the decay process (Ehnström 1999). A considerable proportion of the saproxylic beetles inhabit dead trees situated in an open warm, environment (Ahnlund and Lindhe 1992, Kaila et al. 1997, Martikainen 2001, Sverdrup-Thygeson and Ims 2002), and species having similar habitat preferences can be expected to exist in many other taxa, too. Since natural early successional phases with plenty of dead wood are currently almost completely lacking from forest cycles, these species are restricted to the scarce and often small reserves, where dead wood is still available, although such habitats are not necessarily optimal for them (Martikainen 2001).

Habitat loss, fragmentation and declining habitat quality are driving numerous species worldwide towards extinction (Wilcox and Murphy 1985, Saunders et al. 1991, Myers et al. 2000, Brooks et al. 2002, Fahrig 2003). In the boreal forests of Fennoscandia these changes have largely been induced by forestry, and have already had substantial negative consequences on the biota of forests (Heliövaara and Väisänen 1984, Haila 1994, Berg et al. 1995, Hanski and Hammond 1995, Esseen et al. 1997, Linder and Östlund 1998, Rassi et al. 2001, Siitonen et al. 2001, Gärdenfors 2005). Due to the time delay in the response of species to habitat destruction – known as extinction debt (Tilman et al. 1994, Loehle and Li 1996) – species doomed to extinction in the prevailing state of habitats may still seem fairly abundant. The time delay before extinction occurs may be fairly long for some species, however (Komonen et al. 2000, Hanski and Ovaskainen 2002). Hanski (2000) has predicted the extinction of about 1000 species in Finnish forests in the near future. It is obvious that our current forests provide a rather different set of ecological niches from the forests that existed before modern, intensive forestry. Since it seems clear that natural disturbance regimes cannot and will not be restored on any large scale in managed forests so long as timber harvesting remains the main form of land use in these ecosystems (Brown et al. 2004, Kauffman 2004), we may have to focus on mimicking their effects on a smaller scale as far as possible in order to create important structural properties in the forest landscape for the benefit of certain focal species.

The role of the matrix outside nature reserves in the conservation of forest biota has been emphasized, in order to complement the traditional approach of conserving biodiversity by means of networks of reserves (Franklin 1993, Mönkkönen and Reunanen 1999, Kouki et al. 2001, Simberloff 2001, Lindenmayer and Franklin 2002). Unprotected areas may provide essential habitats for a number of species if their requirements are taken into account during management operations. By deliberately improving the occurrence of certain resources in the matrix outside the reserves, it may be possible to improve the quality of the environment sufficiently to benefit species for which unsuitable habitats do not so easily constitute dispersal barriers. Many insects and fungi are examples of such species. The use of controlled burning and green-tree retention has been under discussion lately as a possible means of improving the ecological quality of managed boreal forests (Niemelä 1996, Esseen et al. 1997, Franklin et al. 1997, Granström 2001, Ehnström 2001, Siitonen 2001, Vanha-Majamaa and Jalonen 2001, Penttilä et al. 2004). Conservation measures applicable on a smaller scale are realistic, but their consequences and effectiveness have remained somewhat ambiguous so far.

According to Franklin et al. (1997), retention trees have three major purposes: 1) “lifeboating” species and processes immediately after logging and before the forest cover is re-established, 2) “enriching” re-established forest stands with structural features that would

otherwise be absent, and 3) “enhancing connectivity” in the managed landscape. Trees can be retained in small groups or they may be dispersed throughout the logging area. Aggregated retention is currently favoured, because it is assumed to be more effective in maintaining the structural properties and species of the pre-harvest forest in undisturbed patches (Franklin et al. 1997).

Burning brings about major changes in environmental conditions, but controlled burning can create habitats and resources for species that are adapted to a burned forest environment. Pyrophilous species, those that conspicuously favour burned areas (Wikars 1997), are a distinct part of boreal forest ecosystems, but there are also many other species that benefit from fires but are not pyrophilous *sensu stricto* (Lundberg 1984, Muona and Rutanen 1994, II, III, IV). Moreover, forest fires affect the structure of regenerating stands, and consequently species communities, for several decades at least.

1.2 Study organisms – the beetles

Insects numerically make up a major part of biodiversity (e.g. Erwin 1982, May 1988, Wilson 1992). The beetles (Coleoptera) is worldwide the most species rich order with at least 250000 species described so far (Capinera 2004). The use of beetles in ecological studies of community level is very laborious due to often large samples and many difficulties in identifying the specimens. In tropical forests huge number of species, of which many are undescribed, makes the situation even more difficult (Lawton et al. 1998). This frequently leads ecologists to use morphospecies (Oliver and Beattie 1996) or higher taxa when analyzing the samples, which prevents detailed community level analyses. On the other hand, high number of species together with their species specific requirements make beetles exceptionally well applicable group for ecological studies. Changes in beetle communities can reflect wide variety of changes occurring in the environment.

There are 3670 beetle species recorded from Finland based on Silfverberg (2004) and a few new unpublished records. Of these, 54 are classified as regionally extinct (RE), 347 are threatened (CR, EN, VU) and 196 near threatened (NT) (Rassi et al. 2001). About 2000 species of beetle can be found from forests, and 800 of these are obligatorily saproxylic (Siitonen 2001). Due to the long entomological tradition the fauna of Fennoscandia is exceptionally well known compared to most other areas and provides sound basis for using beetles as study objects. Also, the habitat preferences of species are well known, particularly those of saproxylics, thanks to pioneering works of, e.g., Saalas (1917, 1923) and Palm (1951, 1959), and more recent authors, e.g., Ehnström and Axelsson (2002).

1.3 Aims of the thesis

This thesis aims to demonstrate the effects of green-tree retention and controlled burning on beetles, and to provide information applicable to the restoration and maintenance of beetle species diversity in boreal forests. It also incorporates a methodological aspect, as there are many difficulties involved in insect sampling which also relate to the interpretation of the results. More specifically, the questions addressed here are:

- 1) How do different trapping methods perform when sampling communities of forest beetles, and how do the method chosen, the sampling scheme, sample size and ecological classification of the species affect the results and their interpretation? (I)

- 2) How do different post-harvest green-tree retention volumes with or without controlled burning affect local beetle assemblages in the short-term, including destructive effects, and what are their consequences for early colonization? (II)
- 3) How do beetle assemblages respond to different levels of post-harvest green-tree retention with or without controlled burning during the first two years of the post-disturbance succession? (III)
- 4) Can populations of red-listed and rare saproxylic beetle species be restored and maintained by post-harvest green-tree retention and controlled burning in managed forests, and consequently, can the current extinction debt be reversed at least partly to a species credit situation by these methods? (IV)

2 MATERIALS AND METHODS

Here I only briefly overview the materials and methods. For details refer to the original papers (I, II, III, IV).

2.1 Study area and experimental design

The data for this thesis come from a large-scale field experiment carried out in eastern Finland in the municipalities of Lieksa and Ilomantsi (approx. 63° N, 30° E) (Fig. 1). The area falls into the transition zone between the south and middle boreal vegetation zones (Ahti et al. 1968). All the study sites were located in state-owned land and within an area of 20 km × 30 km. The study area lies close to Russian border and remained outside intensive forestry until early 1900s. Due to the rather short management history and closeness of near natural forests in Russia the species pool in the area is still very representative when compared to more southerly and westerly parts of Finland. This makes the area exceptionally suitable for studying the effects of different forest management methods on the diverse beetle assemblages, in particular on more demanding forest-dwelling species, such as many saproxylic and red-listed species.

The 24 forest sites used for the experiment covered an area of 3–5 ha each, and were initially mature 150-year-old forests dominated by Scots pine, which comprised on average 72 % of the volume of trees. Other tree species in the sites were Norway spruce (*Picea abies* [L.] Karst.), birch (*Betula* spp.) and other deciduous trees such as aspen (*Populus tremula* L.) and grey alder (*Alnus incana* [L.] Moench). Altogether deciduous trees comprised an average of 6 % of the volume of trees. The mean volume of living trees was 287.9 m³/ha (S.D.=71.1) and that of the decaying wood 40.8 m³/ha (S.D.=17.5) of which 36% was in downed logs. Selective harvesting had taken place in all of the study sites dating back to 1950s and before, but intensive modern forestry was not yet practiced at the sites. Signs of previous forest fires were found at all of the study sites (Kaipainen 2001). Eighteen of the sites had burned during the 19th century, when slash-and-burn cultivation was common in the area (Lehtonen et al. 1996). There were no statistically significant differences between the sites assigned to eight treatment categories in the volume of living trees, snags, or logs before the treatments.

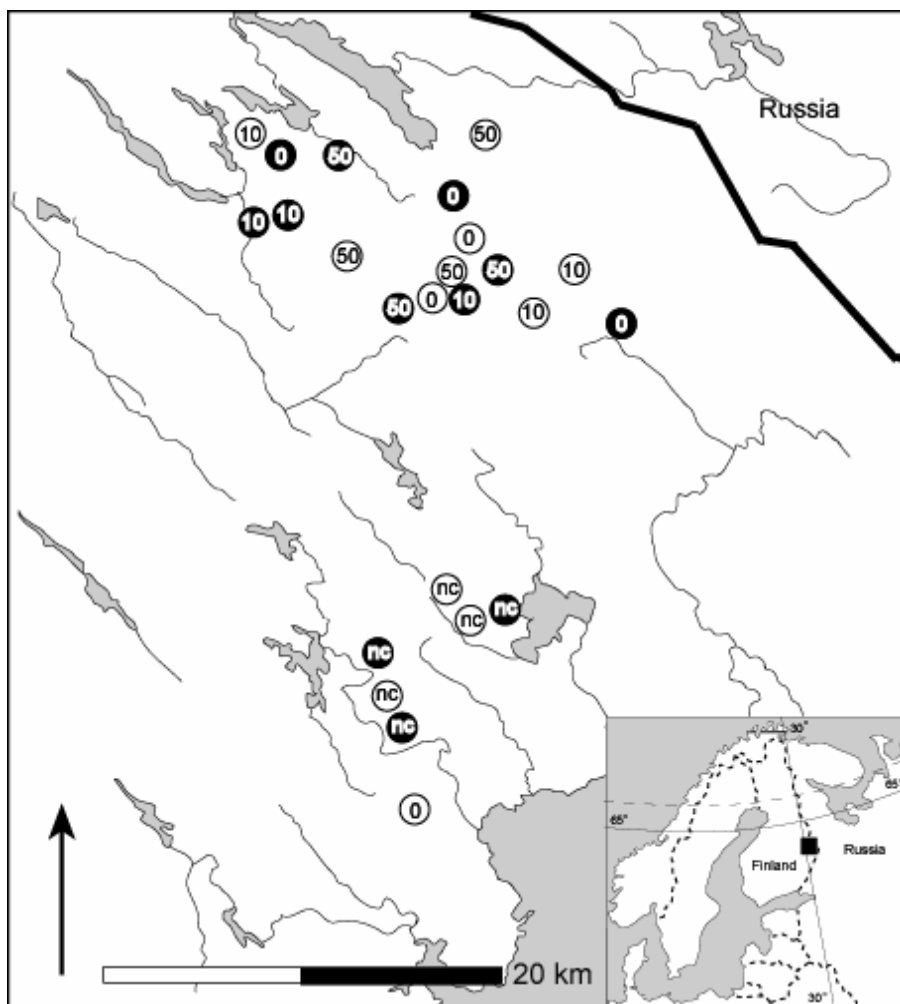


Figure 1. Map of the experimental area and treatments on study sites. The volume of green-tree retention is given within symbols: 0, 10, 50 m³/ha and nc (no cuttings). Black circles represent burned study sites and white circles unburned sites.

The experiment focused on two factors: the volume of green-tree retention and the burning, and the study applied the before-after-control-impact (BACI) principle (Green 1979). Post-harvest green-tree retention had three volumes, 0, 10 and 50 m³ trees/ha, in addition to the unharvested sites (Fig. 1). Trees were principally retained in small groups (Fig. 2). The harvesting treatments were implemented during the winter 2000/2001, and twelve of the study sites were burned on 27–28 June 2001. The burning procedure is described in detail in paper II. The experimental treatments resulted in three replicates of each treatment combination. The treatments were assigned to the study sites in random, except for the unharvested sites, which were situated within the Patvinsuo National Park. The study sites were similar to those outside the park in terms of tree species and volume, forest site type, and management history, despite their national park status.



Figure 2. A group of retention trees and a freely-hanging window trap in a burned study site. The volume of green-tree retention is $10 \text{ m}^3/\text{ha}$ at the site.

The intensity of fire was recorded by measuring the average flame height and changes in the thickness of humus layer. In harvested sites the humus layer became on average 27 %, and in unharvested sites 8 % thinner as a result of burning, but there was considerable small-scale variation within sites (Laamanen 2002). The scorch height was measured by estimating the height of charred bark from the retained trees (Sidoroff 2001). On unharvested sites the mean height of flames was 2.2 m, on sites with 50 m^3 retention trees/ha 3.9 m, and on sites with 10 m^3 retention trees/ha 5.8 m. Naturally on the sites where no trees were retained this method could not be applied.

2.2 Sampling methods, data and analyses

The beetles were sampled with three trapping methods: freely hanging window (flight-interception) traps (Fig. 2), trunk window traps, and pitfall traps (I). Freely hanging window traps were used as a primary source of data (Table 1), due to many benefits of that method in comparison with the other two (I). The beetles were sampled with 240 freely hanging window traps during three growing seasons 2000–2002, i.e. in one pre-treatment year and two post-treatment years (II, III, IV). From other two types of trap the beetle material was used only from one one-month period in 2002 in order to compare the performance of different types of trap (I).

Table 1. Sampling years and proximate duration of sampling, types of trap used, and data used for papers I, II, III and IV. FWT: freely hanging window trap; TWT: trunk window trap; PFT: pitfall trap.

	I	II	III	IV
Sampling years	2002	2000-2001	2000-2002	2000-2002
Sampling duration/year	1 month	1 month	4 months	4 months
Trap type	FWT, TWT, PFT	FWT	FWT	FWT
Number of individuals	59760	34175	153334	2107
Number of species	814	740	1142	84

Almost all individuals were identified to species level except for a small number of deteriorated specimens, which were excluded from the data. For practical reasons also a few species difficult to identify to species level were treated as species pairs, or in one case as a triplet, but were counted as one species in the analyses. Species were classified into ecological groups on the basis of several published sources (e.g. Saalas 1917, 1923, Palm 1948-1972, 1951, 1959, Koch 1989-1992, Ehnström and Axelsson 2002) and unpublished empirical information.

Factorial analysis of variance (ANOVA) was used as primary statistical testing tool to study main effects and interactions of green-tree retention and burning on beetles. Changes in species assemblages induced by the treatments were examined with detrended correspondence analysis (DCA), non-metric multidimensional scaling (NMDS), and Bray-Curtis similarity index.

3 MAIN RESULTS AND DISCUSSION

The results of this thesis are based on a total material of 201 501 individuals representing 1235 beetle species collected over a period of three years (Appendix 1), including 18 095 individuals of 572 species recorded in the pre-treatment year and altogether 120 074 individuals of 1030 species at burned sites and 63 332 individuals of 963 species at unburned sites in the two post-treatment years. Of these latter species, 231 were recorded exclusively on burned sites and 166 on unburned sites.

The first results I present will apply to a comparison of three methods commonly used for sampling forest-dwelling species and an examination of the effects of varying sample sizes and the importance of ecological classification of the beetle material for interpretation of results (I). This will be followed by a summary of the results of three papers (II, III, IV) concerned with the effects of post-harvest green-tree retention volume and controlled burning on beetles in boreal forests.

3.1 Sampling of forest-dwelling beetles (I)

Boreal forests are often considered to be relatively species-poor, suggesting that representative sampling of their insect fauna might be fairly easy. This is clearly not the case, however, since boreal forests harbour a surprisingly high number of species, reaching

a level of one thousand beetle species per stand, for example (Hanski and Hammond 1995, Muona 1999, Martikainen and Kouki 2003). Such a high species richness is quite amazing, because there are only a few tree species and the forests in Fennoscandia, for example, are composed mainly of pine, spruce and birch with some aspen and other deciduous trees.

Several methods have been developed for sampling forest-dwelling insects (Southwood 1978, Leather 2005), such as interception traps, malaise traps, pitfall traps, canopy fogging, sieving and direct searching, but only a few of them are considered to be quantitative or semi-quantitative and thus suitable for numerical comparisons between areas or treatments. Flight-intercept traps and pitfall traps have been widely employed in many other recent studies in boreal forests (Muona and Rutanen 1994, Siitonen 1994, Spence and Niemelä 1994, Niemelä et al. 1996, Økland et al. 1996, Martikainen 2001, Koivula et al. 2002, Similä et al. 2002, Lindhe and Lindelöw 2004).

Insect communities are very difficult to sample, and the effects of different sampling protocols and data processing methods on the results need to be fully understood in order to achieve reliable interpretations. Three methods commonly used for sampling forest-dwelling beetles were compared here: freely hanging flight-intercept (window) traps (FWT), flight-intercept traps attached to trunks (TWT) and pitfall traps placed on the ground (PFT). Four partly overlapping groups of beetles were used in the analyses: all species and saproxylic, rare, and red-listed species.

In terms of the number of species collected, the TWTs were the most effective for all these groups, and the rarer the species in the species group the larger were the differences between the types of trap. In particular, the TWTs caught the most red-listed species. However, when the sample sizes were standardized by resampling the data, the FWTs and TWTs caught the same number of species in all the species groups, while the PFTs caught fewer species in all the groups, regardless of whether the sample sizes were standardized or not and seem in general to be unsuitable for the representative sampling of saproxylic, rare and red-listed species in boreal forests. However, the PFTs clearly sampled different parts of the species assemblages from the window traps. The distribution of the abundance of all species recorded took the form of the right tail of a lognormal or logseries distribution with the mode in the first octave. When an ecologically well-defined group of forest-dwelling species – the saproxylics – was investigated, the abundance distribution revealed a clear mode in the TWT and pooled material, which had a lognormal distribution, despite the fact, that the limited trapping period of one month obviously increased the number of temporal edge species occurring in low numbers. These differences in abundance distributions indicate that when studying material collected by means of traps, classification of the species into ecologically relevant groups is important for revealing the underlying ecological patterns. This, of course, requires a good knowledge of the biology of the species concerned.

The present results clearly confirmed that even in boreal forests local beetle species richness can be so high that sample sizes of at least several thousand individuals, preferably tens of thousands, are needed in order to obtain a representative sample of a local community (see also, Muona 1999, Martikainen and Kouki 2003) and to perform reliable community-level analyses. The results also indicate that figures and generalizations based on small samples collected using a few traps of one type and consisting of diverse species groups such as beetles are likely to be unreliable. Moreover, relevant ecological classification of the material is also very important for the achieving of reliable comparisons. Differences in performance between the types of trap should be considered when designing a study, and in particular when evaluating the results.

In short, the main results related to the sampling of forest-dwelling beetles were:

- 1) Window traps attached to trunks were the most effective for all species groups in terms of the number of species collected. The rarer the species in the group the larger were the differences between the types of trap in the number of species caught.
- 2) Freely-hanging window traps were equally as effective as trunk-window traps after standardization for sample size.
- 3) Pitfall traps caught fewer species of all groups, but they clearly sampled different parts of the species assemblages from the window traps.
- 4) Ecological classification of the material collected using traps is important for revealing ecological patterns.
- 5) Large collections are needed to obtain representative samples of beetle communities in boreal forests.

3.2 Effects of different levels of green-tree retention and controlled burning on the beetles in boreal forests (II, III, IV)

Different ecological groups of beetles showed variable responses to harvesting and controlled burning with different levels of green-tree retention. Here I summarize the patterns of species richness, abundance and composition of the assemblages induced by the harvesting and burning treatments.

3.2.1 Species richness

Biodiversity is most commonly measured in terms of species richness (Gaston and Spicer 2004). This is a basic measure which is often readily available in community-level data and the present work is no exception in this sense.

Species richness at the sites increased almost without exception immediately after harvesting irrespective of whether the site was burned or not (II). Not only pyrophilous species but also many other boreal forest beetle species, including saproxylic and rare ones, were among the first colonizers and displayed an ability to locate newly formed resources even in managed forests. It is also significant, that the number of red-listed species was already higher on the burned sites than on the unburned ones during the first few weeks after burning (II). This effect was partly caused by the pyrophilous species, many of which are endangered species in Finland. The patterns reported in paper II, however, may have partly been distorted by the fact that the data contain only the first colonizers, those attracted by the odours and warmth of the recently logged and burned sites. The results should be considered primarily as an evidence of good colonization ability on the part of many beetle species, particularly saproxylics, which is the first important requirement that must be met before the restoration of beetle assemblages becomes possible. In order to complete the colonization successfully, however, the individuals of a species must be able to reproduce at the site.

In the longer term, i.e. over the two-post treatment years, the different ecological groups – saproxylics, herbivores, species dependent on ephemeral resources and litter-dwelling species – showed variable responses to the experimental treatments (III). Harvesting with or without burning increased the richness of all these groups in the first post-treatment year, but the richness decreased in the second year in many cases. One notable pattern was for

the richness of saproxylic species to continue to increase on the burned sites in the second post-treatment year, indicating successful reproduction and ongoing colonization, whereas the numbers decreased on the unburned sites (III), suggesting that many of the species that had come there initially after harvesting had most probably been unable to find suitable resources for reproduction, so that colonization was unsuccessful. The results can be explained by the fact that burning of the sites killed or weakened many of the trees that had been retained and thus rapidly created suitable resources for saproxylic species, whereas only occasional tree deaths occurred on the unburned sites during the first two years after harvesting. The rather high occurrence of saproxylic species on the unburned harvested sites in the first post-treatment year can be explained by olfactory stimuli from the recently cut stumps and logging waste, which evidently attracted large numbers of species to the areas (Brattli et al. 1998).

The richness of herbivores continued to increase on burned harvested sites in the second post-treatment year, particularly on those with lower green-tree retention volumes, whereas on the unburned sites the species richness remained fairly similar (III). The richness of litter-dwelling species on the harvested sites increased in the first post-treatment year regardless of whether burning took place, but often decreased in the following year. The richness of the species dependent on ephemeral resources did not change markedly as a result of the treatments.

The responses of the red-listed and rare saproxylic species to the treatments were rather similar to those of the saproxylics in general, the highest mean number of species being observed on the burned sites with 10 m³ tree retention/ha in the first year and increasing still further in the second year (IV). The results nevertheless showed a trend toward a greater increase in the richness of red-listed and rare saproxylic species at the higher tree-retention levels in the second year, an effect that was particularly notable at the uncut burned sites. The difference between the burned and unburned sites in the richness of these species showed an increase in the second post-treatment year, so that as there was on average 2.71 red-listed and rare saproxylic species more on the burned than the unburned sites in the first year, the difference had increased to an average of 3.91 species in the second year. This indicates that burned areas are very important for conservation of the rarest portion of the forest beetle fauna. The differences between the burned and unburned sites were not caused by pyrophilous species alone, as other species followed a similar pattern. The higher richness of red-listed and rare saproxylic species observed on the burned sites can be explained by the combined effects of fire *per se* (smoke, heat, a burned environment) and of the consequent increase in the availability of free resources (trees killed by the fire).

The differences in species richness between the harvested sites with different levels of tree retention were generally fairly small, although lower numbers of saproxylic species were generally recorded at sites where no trees were retained (II, III, IV). The unharvested sites usually showed the lowest richness of beetle species (II, III, IV). It may be concluded that although there were differences in fire intensity among the harvested sites, the fires were intense enough everywhere to induce largely parallel changes in the environment.

In short, the main results related to species richness were:

- 1) Harvesting with or without burning increased the species richness (II, III, IV), but the richness had often already decreased by the second post-treatment year (III, IV).
- 2) Colonization after the treatments was particularly active at the burned sites (II, III, IV).

- 3) The richness of red-listed and rare saproxylic species was higher on the burned than unburned sites, not entirely by virtue of the pyrophilous species (II, IV).
- 4) Higher levels of green-tree retention promoted an increase in the richness of saproxylics, including red-listed and rare species, on the burned sites in the second post-treatment year. No clear patterns were observed in this respect on the unburned sites (III, IV).
- 5) The number of red-listed and rare species on the unburned sites had already declined by the second post-treatment year (IV).
- 6) Different ecological groups among the beetles showed different responses to harvesting at different levels of green-tree retention and burning (III).

3.2.2 Abundance of beetles

The abundance of species in trapping material is rather an unreliable measure, particularly when used in comparisons between years, because differences in weather conditions, for example, affect the activity of insects considerably. Differences in the abundance of a focal group of species, such as red-listed and rare species, between treatments may provide valuable information, however, and can reflect successful conservation action if the abundance has been increased through measures such as green-tree retention and burning.

One notable result obtained here was that red-listed and rare saproxylic species were much more abundant on burned than unburned sites, and that the abundance of many such species increased on the burned sites with higher levels of green-tree retention in the second post-treatment year indicating successful reproduction there (IV). As the increase in the numbers of individuals was clearly smaller or negative on the harvested sites with or without burning, it may be concluded that reproduction was not so successful there. Pyrophilous species dominated the samples of red-listed and rare saproxylic species in terms of the numbers of individuals in the first post-treatment year, but their proportion decreased in the following year, especially at the unburned sites. Their dominance was even more striking among the red-listed species alone, but this was largely caused by the high abundance of just a few species, in particular *Sphaeriestes stockmanni* (Biström). Pyrophilous species accounted for 98.6% of the abundance of red-listed species on the burned sites in the first post-treatment year and 72.6% in the second, whereas the proportions on the unburned sites were 72.6% and 32.4%, respectively. *Sphaeriestes stockmanni* and *Clypastraea pusilla* (Gyllenhal) were the most abundant species, particularly on the burned sites, while most of the other red-listed species were observed in smaller numbers, although many of them increased in abundance in the second post-treatment year.

Many of the pyrophilous species were also observed at the unburned sites, some of them in considerable abundance. It is thus possible that some of them can at least occasionally make use of dead trees situated in unburned, open environments as a breeding substrate (Wikars 2002), although suitable resources are probably very scarce in such areas. If some of these species can persist in the forest landscape in low numbers or reasonable lengths of time without regular fires, their population levels could easily be enhanced by controlled burning, because they could be expected to colonize the burned areas effectively.

In short, the main results related to the abundance of beetles were:

- 1) Abundance increased due to the treatments, this being more pronounced at the burned than unburned sites (II, III, IV).

- 2) Colonization after the treatments was particularly active at the burned sites (II, III, IV).
- 3) The abundance of red-listed and rare saproxylic species was higher at the burned sites, and particularly the pyrophilous species showed population increases after fire (II, IV).

3.2.3 Changes in species assemblages

Changes in the composition of assemblages are often much more interesting and informative than changes in overall species richness, for example. Species richness may remain unchanged in situations where the composition of the assemblages is altered as a result of environmental change. Thus the latter may serve better to reveal underlying ecological processes.

Although the harvesting and burning treatments induced profound changes in the beetle assemblages (II, III, IV), there were considerable differences in response between the four ecological groups of beetle over the two post-treatment years (III). The assemblages of saproxylics, species dependent on ephemeral resources, and litter-dwelling species were greatly affected by the harvesting and burning treatments, whereas the assemblages of herbivores were originally more heterogeneous between the sites and did not show such a marked change in response to the treatments as did the other three species groups. The treatments had the strongest impact on the saproxylic and litter-dwelling species, and there was also a clear difference in the assemblages of these species between the first and second post-treatment years (III).

The assemblages of saproxylic species were distinctly affected by the treatments and differed between the two years (III). In the first year the burned and unburned sites supported different assemblages, particularly when tree retention levels were also taken into account, whereas in the second year the difference between the burned and unburned sites remained fairly similar but the assemblages showed a clear change from the first year. This probably reflects the rather rapid decay succession after tree death. The first phase lasts only 1–2 years and is dominated by bark beetles, other phloem feeders and their associated species, which rapidly colonize the dead trees (e.g., Esseen et al. 1997, Siitonen 2001). The second phase is characterized by secondary phloem feeders, detritivores, species associated with mycelia growing under the bark and their associates. It is likely that many of the trees that died as a result of burning, and also logging waste at the unburned sites, had already proceeded to the second decay phase by the second post-treatment year.

Although most of the deciduous trees, on which many forest-dwelling herbivores are dependent, were killed by the fire, fire is also known to create favourable conditions for the regeneration of deciduous trees (Esseen et al. 1997). This explains the rapid recovery of the herbivores, particularly at the burned sites, as indicated by the increased similarities in the second post-treatment year (III). The ordinations nevertheless suggested that the assemblages of herbivores were fairly heterogeneous among the sites both before and after the treatments, which makes it difficult to interpret the results. The species dependent on ephemeral resources were the least affected by the treatments, presumably because of their high mobility in the forest landscape. Suitable resources such as elk dung and rotten fungi were also readily available at and around the sites concerned.

Burning seemed to be detrimental to the litter-dwelling species. The low similarity between the first post-treatment year assemblages and the pre-treatment assemblages indicated a very high species turnover in response to the pronounced alteration in the habitat on account of burning. It is likely that burning also caused direct mortality among

these species (Paquin and Coderre 1997, Wikars and Schimmel 2001). Nevertheless, the assemblages seemed to recover fairly quickly, as indicated by the similarity indices. Species living on the soil surface in boreal forests probably have good opportunities to colonize disturbed areas rapidly from the surroundings. A parallel pattern was also seen at the unburned harvested sites, which indicates that harvesting operations without burning also had a powerful, although transient, impact on these species, in spite of the fact that no post-harvesting soil preparation work intended to improve the regeneration of a new stand was carried out here.

Higher tree-retention levels generally maintained the assemblages closer to the pre-treatment structure at both the burned and unburned sites. Groups of trees may provide refugia for some species from the effects of harvesting and burning, although there are indications that small groups of trees cannot maintain the original assemblages of forest carabids (Koivula 2002, Martikainen et al. unpubl.). It is obvious that retained trees affect different species through different mechanisms. For saproxylic species the additional presence of dead wood resources is relevant, and they colonize the newly formed substrate after the trees have died as a result of burning or for some other reason. For many other species, such as litter-dwelling ones, the tree retention volume may not be important *per se*, but it can affect such factors as the size of the area not disturbed by cutting, the degree of shading, or the result of burning (e.g. fire intensity), thus having indirect consequences on these.

In short, the main results related to species assemblages were:

- 1) Higher tree retention levels maintained the assemblages closer to the pre-treatment structure (II, III).
- 2) The assemblages were greatly affected by harvesting and burning, but different ecological groups showed different responses to burning (II, III, IV).
 - the assemblages of *saproxylic species* were distinctly affected by the treatments, and also differed between the two post-treatment years (III).
 - harvesting with or without burning had a marked effect on *herbivores*, but they had recovered by the second post-treatment year in the burned areas (III).
 - the *species dependent on ephemeral resources* were affected least by the treatments (III).
 - burning and harvesting was detrimental to the *litter-dwelling species*, but they seemed to recover quickly (III).

3.2.4 Methodological aspects

The traps used in this work can be expected to have been of fairly similar efficiency at the harvested sites, but less so at the more shaded unharvested ones. Moreover, the beetles may have been more active at the burned sites than at the unburned ones due to the higher temperatures caused by the charred environment which absorbs solar radiation more efficiently. The bias can be partly corrected by resampling the data, or by calculating species accumulation curves. These tend to underestimate the species richness, however, if there is even one very abundant species in the sample (Magurran 2004), so that a comparison between two otherwise similar samples where only one contains an abundant species will result in two rather differently shaped curves. The use of such methods here would have greatly underestimated the species richness at the burned sites by comparison with the unburned ones, due to high abundance of several species at the former. Thus standardization of the samples was avoided, on the assumption that the results for species

richness based on unstandardized samples are reasonably reliable in the current case and more justified than to those based on species accumulation curves.

The classification of beetle material collected with traps into ecological groups is important for revealing underlying ecological patterns (I). Material of this kind is nevertheless apt to contain beetle individuals that occur as “tourists” at a particular site (only crossing the area), even though the habitat may seem suitable for the species. Particularly in the first post-treatment year the assemblages consisted mostly of colonizing species and individuals, as was seen especially at the sites where no trees were retained. Many species which obviously were unable to find suitable resources for reproduction were recorded at that stage (II, III, IV). By the second year, however, the assemblages included the progeny of the first-year colonizers, and thus these results can be considered to be more important for evaluating the effects of green-tree retention and burning, although colonization was presumably still active in that year. The results would probably have been even clearer, however, particularly concerning the saproxylic species, if it had been possible to eliminate the “tourists” from the data.

4 IMPLICATIONS FOR FOREST MANAGEMENT AND SPECIES CONSERVATION

The conservation of biodiversity is a fundamental component of ecologically sustainable forestry (Hunter 1999, Maa- ja metsätalousministeriö 1999, Lindenmayer and Franklin 2002). In addition to the maintenance of ecosystem functions, for example, the definition of ecological sustainability includes the maintenance of species diversity in the long-term. There are clearly a lot of improvements that modern forestry still has to make in this field. The biological legacies left from preceding forests through natural disturbances are significant aspects of newly developing stands, for example, but they have been largely ignored in forestry (Franklin et al. 2002).

Fire and timber harvesting share some of their effects on boreal forest ecosystems, and it may be tempting for this reason to assume that their effects on forest-dwelling biota are also similar, and consequently to argue that clear-cutting, perhaps with some retention trees, mimics natural disturbances. Several recent studies have shown that this is not the case, however, and that natural disturbances and timber harvesting have substantially different effects on the ecological properties of forests (Bergeron et al. 1999, Kouki et al. 2001, Siitonen 2001, Uotila et al. 2001, Franklin et al. 2002, Similä et al. 2003). Forest fires, for example, typically consume less than 10% of the wood, whereas 95–98% of the wood is removed in normal final harvesting (Angelstam 1996). The results presented in this thesis confirm that burning has a rapid and profound effect on beetle assemblages both in harvested areas and in uncut forests, and that the resulting species compositions are quite different from those in unburned areas. The differences arose not only through colonization by pyrophilous species but also because of the behaviour of a large number of other species that either increased or decreased as a result of burning and logging.

It is shown here that the living conditions of many red-listed and rare saproxylic species can be significantly improved by making certain fairly simple alterations to existing forest management methods. Then current extinction debt (Hanski 2000) could consequently be partly reversed to a species credit situation, although this would require some reduction in

timber production. Current forest management recommendations in Finland (Hyvän metsänhoidon suosituksset, 2001) suggest that at least an average of 5 trees/ha should be retained in final harvesting operations. These trees may be small (dbh >10 cm) (Metsäsertifiointin standardityöryhmä, 2003) and of low economic value, which usually results in retention volumes of only few cubic metres per hectare, a level of little significance for the diversity of saproxylic species. The recently revised recommendations for state-owned forests nevertheless suggest that 5–10 m³ of trees should be retained in final harvesting operations, and volumes could be even higher than that, up to 20–50 m³/ha, close to reserves and other areas of special importance (Heinonen 2004). No general recommendations for critical thresholds regarding dead wood volumes can be given on the basis of the present results, because every saproxylic species has its own requirements with respect to deadwood quality, its temporal and spatial availability and other biotic and abiotic factors in the environment. It is clear, however, that any addition to deadwood volumes will be beneficial, and 10 m³/ha could already induce distinct positive effects, particularly in the presence of controlled burning. In any case, retention volumes should be increased from the current average of 3.4 m³/ha (Hänninen 2001). In addition to the burning of harvested areas, more unharvested forests should be burned as a part of forest restoration activities as they differ in many respects from harvested areas.

Controlled burning with reasonable green-tree retention is an effective method for the conservation of many saproxylic species, since deadwood resources are created rapidly and effectively (II, III, IV). Further regional extinctions of species of this kind could most likely be prevented if burning were used more frequently. Although burning has major and sometimes negative effects on other forest-dwelling species, fire is a natural part of the boreal forest succession, so that species in general are adapted to such disturbances and able to recover from them. Burned trees host different assemblages of species than trees that have died for other reasons (Wikars 2002), which further emphasizes the importance of fire for forest biodiversity.

Species that have adapted to taking advantage of sudden disturbances such as forest fires, apparently have good dispersal abilities. These species are quite easy to maintain in a forest landscape if suitable habitats are adequately formed both spatially and temporally. Jonsson (2002) found that insects inhabiting wood-decaying fungi may fly distances of several kilometres, although there are species-specific differences. Pyrophilous species have even better dispersal abilities than that (Evans 1964, 1966, Schutz et al. 1999). In order to gain the most benefit from controlled burning with respect to forest biota, it should be implemented at the time of the year when the natural ignition probability is highest, from late May to early July in the case of Finland (Larjavaara et al. 2004). Saproxylic species inhabiting stable, long continuity habitats are expected to be poorer dispersers and to have a continuous need for large amounts of suitable substrate within short distances in order to maintain their populations (e.g. Siitonen and Saaristo 2000). Such species may only be expected to persist where there are large enough reserves of old-growth forest.

The eventual effects of different levels of green-tree retention on saproxylic species at unburned sites can be evaluated only after the retained trees begin to die. At this point of time it can only be concluded that harvesting operations have marked effects on beetle assemblages, as observed in several previous studies dealing with litter-dwelling beetles (Niemelä et al. 1993, Spence et al. 1996, Koivula 2002), and that there are major differences in response between the ecological groups. The increasing of green-tree retention volumes in unburned areas is probably beneficial, although the formation of resources for saproxylic species may be postponed for years or decades. The fact that beetle

assemblages remained closer to the pre-treatment structure in areas where higher volumes of green trees were retained (II, III) indicates that some properties of a pre-harvest forest can be maintained by green-tree retention, at least for a few years. Thus sufficient retention may also be important in maintaining the functional properties of ecosystems.

5 CONCLUDING REMARKS

The results of this thesis are likely to be applicable over the whole boreal forest region, where fire has previously been the major natural disturbance factor, and has been superseded in recent times by stand-replacing disturbances of human origin. In areas where the forest fauna has become impoverished due to modern forestry, as in Fennoscandia, controlled burning with reasonable green-tree retention should be applied in everyday forestry to improve the quality of managed forests for forest-dwelling species. The ecological significance of these measures, however, is highly dependent on the spatial and temporal scale upon which they are implemented.

The effects of green-tree retention without controlled burning could not be fully assessed here because its relevance to the focal group, saproxylics, is seen only after the trees have died, implying a longer time-span than that employed here. Nevertheless, other studies have already demonstrated that retention trees can provide resources for many saproxylic species (Kaila et al. 1997, Martikainen 2001). It was demonstrated here, however, that higher volumes of green-tree retention seem to reduce the impact of timber harvesting on many other species in the short-term.

The characteristics and location of the area used in this work should be taken into account when interpreting the results. The forests in many parts of eastern Finland have maintained most of their natural diversity until now due to the rather short management history and the vicinity of large, almost natural forests on the Russian side of the border. This is probably one explanation for the rich beetle assemblages recorded here. In more westerly and southerly parts of Finland, data on red-listed and rare species in particular would have been much more difficult or even impossible to obtain to this extent. Consequently, the positive effects of green-tree retention and controlled burning on the rarer portion of the forest-dwelling species will probably not be seen everywhere in such magnitude or over such a short period of time as in the present data, because the role of spatial and temporal factors – such as isolation effects – are likely to be more influential.

Green-tree retention and controlled burning naturally do not solve all the problems related to commercial forest management, but they will clearly benefit a significant part of perhaps the most species-rich and most seriously endangered group, the saproxylic beetles. Some of the species that are currently largely restricted to nature reserves could probably be induced to return to managed forests provided that suitable resources are retained or created there. These are mainly species confined to natural young forests, where the availability of dead wood, for example, is high after disturbances. It seems that species of this kind may be more common among the beetles and other insects (Jonsell et al. 1998), than among many other taxa (Tikkanen et al. in press), and hence the present results cannot directly be generalized to other groups of species inhabiting forests. It should also be emphasized, that there still remain a large number of species which can probably thrive only in representative networks of strictly protected forests. Further research would be needed to

fully reveal the effects of green-tree retention and controlled burning on forest biota. The observations made in this thesis, however, help to fill in some of the gaps in our understanding of the effects of these methods on the diverse beetle assemblages in boreal forests.

REFERENCES

- Ahnlund, H. & Lindhe, A.. 1992. Hotade vedinsekter i barrskogslandskapet - några synpunkter utifrån studier av sömländska brandfält, hållmarker och hyggen. *Entomologisk Tidskrift* 113:13-23.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation Zones and Their Sections in Northwestern Europe. *Annales Botanici Fennici* 5:169-211.
- Angelstam, P. 1996. The ghost of forest past - natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. In: DeGraaf, R. M. & Miller, R. I. (eds.) *Conservation of Faunal Diversity in Forested Landscapes*. Chapman & Hall, London. P. 287-337.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1995. Threat levels and threats to red-listed species in Swedish forests. *Conservation Biology* 9:1629-1633.
- Bergeron, Y., Harvey, B., Leduc, A. & Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. *The Forestry Chronicle* 75:49-54.
- Brattli, J. G., Andersen, J. & Nilssen, A. C. 1998. Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. *Journal of Applied Entomology* 122:345-352.
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16:909-923.
- Brown, R. T., Agee, J. K. & Franklin, J. F. 2004. Forest restoration and fire: Principles in the context of place. *Conservation Biology* 18:903-912.
- Capinera, J. L. (ed.) 2004. *Encyclopedia of Entomology*. Kluwer Academic Publishers, Dordrecht.
- Clements, F. E. 1936. Nature and structure of the climax. *The Journal of Ecology* 24:252-284.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Ehnström, B. 1999. Red listed beetles on Scots pine (*Pinus sylvestris*) in Sweden. *Proceedings of the XXIV Nordic Congress of Entomology*:55-61.
- 2001. Leaving dead wood for insects in boreal forests - Suggestions for the future. *Scandinavian Journal of Forest Research Supplement* 3:91-98.
- & Axelsson, R. 2002. *Insektsnag i bark och ved*. ArtDatabanken, SLU, Uppsala.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* 36:74-75.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46:16-47.
- Evans, W. G. 1964. Infra-red receptors in *Melanophila acuminata* DeGeer. *Nature* 202:211.
- 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). *Ecology* 47:1061-1065.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34:487-515.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes. *Ecological Applications* 3:202-205.

- , Berg, D. R., Thornburgh, D. A. & Tappeiner, J. C. 1997. Alternative Silvicultural Approaches to Timber Harvesting: Variable Retention Harvest Systems. In: Kohm, K. A. & Franklin, J. F. (eds.). *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*. Island Press, Washington DC. p. 111-139.
- , Spies, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K. & Chen, J. Q. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155:399-423.
- Gaston, K. J. & Spicer, J. I. 2004. *Biodiversity: An Introduction*. Blackwell Science Ltd, Malden, USA.
- Granström, A. 2001. Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research Supplement* 3:62-69.
- Green, R. H. 1979. *Sampling Design and Statistical Methods for Environmental Biologists*. Wiley, New York, USA.
- Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33:1-23.
- Gärdenfors, U. (ed.) 2005. Rödlistade arter i Sverige 2005 – The 2005 redlist of Swedish species. ArtDatabanken, SLU, Uppsala.
- Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Annales Zoologici Fennici* 31:203-217.
- Hänninen, H. 2001. Luontokohteet ja säästöpuusto talousmetsien hakkuissa - seurantatulokset vuosilta 1996-99. In: Siitonen, J. (ed.). *Monimuotoinen metsä. Metsäluonnon monimuotoisuuden tutkimusohjelman loppuraportti*. Metsäntutkimuslaitoksen tiedonantoja 812. Metsäntutkimuslaitos, Vantaan tutkimuskeskus, Vantaa. p. 81-95.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37:271-280.
- & Hammond, P. 1995. Biodiversity in boreal forests. *TREE* 10:5-6.
- & O. Ovaskainen. 2002. Extinction debt at extinction threshold. *Conservation Biology* 16:666-673.
- Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. J. & Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Heinonen, P. (ed.) 2004. *Metsätalouden ympäristöopas*. Metsähallitus. Vantaa.
- Heliövaara, K. & Väisänen, R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennica* 189:1-29.
- Hunter, M. L., Jr. (ed.) 1999. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge.
- Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113:81-101.
- Hyvän metsänhoidon suositukset 2001. Metsätalouden kehittämiskeskus Tapio, Helsinki.
- Jonsell, M., Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation* 7:749-764.
- Jonsson, B. G., Krüys, N. & Ranius, T. 2005. Ecology of species living on dead wood - lessons for dead wood management. *Silva Fennica* 39:289-309.
- Jonsson, M. 2002. *Dispersal Ecology of Insects Inhabiting Wood-Decaying Fungi*. PhD thesis. Swedish University of Agricultural Sciences, Uppsala.

- Kaila, L., Martikainen, P. & Punttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation* 6:1-18.
- Kaipainen, T. 2001. Metsäpalohistoria Lieksan alueella. MSc.-thesis. University of Joensuu, Joensuu.
- Kauffman, J. B. 2004. Death rides the forest: Perceptions of fire, land use, and ecological restoration of western forests. *Conservation Biology* 18:878-882.
- Koch, K. 1989-1992. Die Käfer Mitteleuropas. Ökologie Bds. 1-3. Goecke & Evers Verlag, Krefeld, Germany.
- Koivula, M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management* 167:103-121.
- , Kukkonen, J. & Niemelä, J. 2002. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation* 11:1269-1288.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90:119-126.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research Supplement* 3:27-37.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36:97-125.
- Laamanen, J. 2002. Tulen voimakkuuden vaikutus metsikön pienialaiseen vaihteluun. MSc. thesis. University of Joensuu, Joensuu.
- Larjavaara, M., Kuuluvainen, T., Tanskanen, H. & Venäläinen, A. 2004. Variation in forest fire ignition probability in Finland. *Silva Fennica* 38:253-266.
- Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdsley, N. A., Stork, N. E., Srivastava, D. S. & Watt, A. D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391:72-76.
- Leather, S. 2005. *Insect Sampling in Forest Ecosystems*. Blackwell Science Ltd, a Blackwell Publishing Company.
- Lehtonen, H., Huttunen, P. & Zetterberg, P. 1996. Influence of man on forest fire frequency in North Karelia, Finland, as evidenced by fire scars on Scots pines. *Annales Botanici Fennici* 33:257-263.
- Lindenmayer, D. B. & Franklin, J. E. 2002. *Conserving Forest Biodiversity: a Comprehensive Multiscaled Approach*. Island Press, Washington, DC.
- Linder, P. & Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation* 85:9-19.
- Lindhe, A. & Lindelöw, A. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management* 203:1-20.
- Loehle, C. & Li, B.-L. 1996. Habitat destruction and the extinction debt revisited. *Ecological Applications* 6:784-789.
- Lundberg, S. 1984. Den brända skogens skalbaggsfauna i Sverige. *Entomologisk Tidskrift* 105:129-141.
- Löfman, S. & Kouki, J. 2001. Fifty years of landscape transformation in managed forests of southern Finland. *Scandinavian Journal of Forest Research* 16:44-53.
- Magurran, A. E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Malden, USA.

- Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecological Bulletins* 49:205-218.
- & J. Kouki. 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodiversity and Conservation* 12:1815-1831.
- May, R. M. 1988. How many species are there on Earth? *Science* 241:1441-1449.
- Mayer, A. L., Kauppi, P. E., Angelstam, P., Zhang, Y. & Tikka, P. M. 2005. Importing timber, exporting ecological impact. *Science* 308:359-360.
- Maa- ja metsätalousministeriö 1999. Kansallinen metsäohjelma 2010. Maa- ja metsätalousministeriö, Helsinki.
- Metsäsertifiointin standardityöryhmä 2003. FFCS 1002-1:2003, Ryhmäsertifiointin kriteerit metsäkeskuksen toimialueen tasolla. http://www.ffcs-finland.org/media/Standardit/suomeksi/FFCS_1002_1_2003SU.pdf.
- Mönkkönen, M. & Reunanen, P. 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84:302-305.
- Muona, J. 1999. Trapping beetles in boreal coniferous forest - how many species do we miss? *Fennia* 177:11-16.
- & I. Rutanen. 1994. The Short-Term Impact of Fire on the Beetle Fauna in Boreal Coniferous Forest. *Annales Zoologici Fennici* 31:109-121.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- Niklasson, M. & Granström, A. 2001. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81:1484-1499.
- Niemelä, J. 1996. Invertebrates and boreal forest management. *Conservation Biology* 11:601-610.
- , Haila, Y. & Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352-368.
- , Langor, D. & Spence, J. R. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera, Carabidae) in western Canada. *Conservation Biology* 7:551-561.
- Økland, B., Bakke, A., Hagvar, S. & Kvamme, T. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation* 5:75-100.
- Oliver, I. & Beattie, A. J. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* 6:594-607.
- Palm, T. 1948-1972. Svensk Insektfauna 9. Skalbaggar. Coleoptera. Kortvingar: Fam. Staphylinidae 1-7. Entomologiska Föreningen i Stockholm, Stockholm.
- 1951. Die Holz- und Rinden-Käfer der nordschwedischen Laubbäume. *Meddelanden från statens skogsforskningsinstitut* 40.
- 1959. Die Holz- und Rinden-Käfer der süd- und mittelschwedischen Laubbäume, Lund, Sweden.
- Paquin, P. & Coderre, D. 1997. Deforestation and fire impact on edaphic insect larvae and other macroarthropods. *Environmental Entomology* 26:21-30.
- Penttilä, R., Siitonen, J. & Kuusinen, M. 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation* 117:271-283.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. 2001. The 2000 Red List of Finnish Species. Edita Plc, Helsinki.
- Ryan, K. C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* 36:13-39.

- Saalas, U. 1917. Die Fichtenkäfer Finnlands. I. *Annales Academiae Scientiarum Fennicae*, Series A 8:1-547.
- 1923. Die Fichtenkäfer Finnlands. II. *Annales Academiae Scientiarum Fennicae*, Series A 22:1-746.
- Saunders, D. A., Hobbs, R. J. & Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32.
- Schutz, S., Weissbecker, B., Hummel, H. E., Apel, K. H., Schmitz, H. & Bleckmann, H. 1999. Insect antenna as a smoke detector. *Nature* 398:298-299.
- Sheil, D. & Burslem, D. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution* 18:18-26.
- Sidoroff, K. 2001. Metsäpallon vaikutus puuston kuolleisuuteen ja lahoppun määrään, kokeellinen tutkimus Lieksassa. MSc. thesis. University of Joensuu, Joensuu.
- Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests - a comparison based on two sampling methods. *Annales Zoologici Fennici* 31:89-95.
- 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49:11-41.
- , Penttilä, R. & Kotiranta, H. 2001. Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russian Karelia. *Ecological Bulletins*:231-242.
- & Saaristo, L. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biological Conservation* 94:211-220.
- Silfverberg, H. 2004. *Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae*. *Sahlbergia* 9:1-111.
- Simberloff, D. 2001. Management of boreal forest biodiversity – a view from the outside. *Scandinavian Journal of Forest Research Supplement* 3:105-118.
- Similä, M., Kouki, J. & Martikainen, P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. *Forest Ecology and Management* 174:365-381.
- , Kouki, J., Martikainen, P. & Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biological Conservation* 106:19-27.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Southwood, T. R. E. 1978. *Ecological methods*. Chapman and Hall, London.
- Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg.
- Spence, J. R., Langor, D. W., Niemelä, J., Carcamo, H. A. & Currie, C. R. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici* 33:173-184.
- & Niemelä, J. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist* 126:881-894.
- Sverdrup-Thygeson, A. & Ims, R. A. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biological Conservation* 106:347-357.
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K. & Kouki, J. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici* (in press).
- Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994. Habitat destruction and the extinction debt. *Nature* 371:65-66.

- Uotila, A., Maltamo, M., Uutera, J. & Isomäki, A. 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological Bulletins* 49:149-158.
- Vanha-Majamaa, I. & Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. *Scandinavian Journal of Forest Research Supplement* 3:79-90.
- Wein, R. W. & MacLean, D. A. (eds.) 1983. *The role of fire in northern circumpolar ecosystems*. John Wiley & Sons Ltd.
- Wikars, L.-O. 1997. *Effects of Forest Fire and the Ecology of Fire-Adapted Insects*. PhD thesis. Uppsala University, Uppsala.
- 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation* 6:1-12.
- & Schimmel, J. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *Forest Ecology and Management* 141:189-200.
- Wilcox, B. A. & Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist* 125:879-887.
- Wilson, E. O. 1992. *The diversity of life*. Allen Lane The Penguin Press, Massachusetts.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29:22-32.

APPENDIX 1. Beetle species recorded at the study sites in 2000–2002.

Beetle species recorded at the study sites in Lieksa and Ilomantsi in 2000–2002. The nomenclature follows Silfverberg (2004). If red-listed, the category (Rassi et al. 2001) is given after the species. Group refers to the ecological group of species as used primarily in the paper IV; S: obligatorily saproxylic; H: herbivore; E: species dependent on ephemeral resources, such as rotten fungi, dung and carrion; N: other non-saproxylic species. The latter group (N) contains mainly litter-dwelling species, but also other species not clearly belonging to the first three groups or having wider requirements for substrate. Records are specified in 10 km × 10 km Finnish grids, number of study sites within each grid is shown at the end of the table. Sampling methods or experimental treatments are not specified. The total number of individuals is given for each species. Five red-listed species that are not included in the thesis, but have been observed during the study are marked with an asterisk.

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
TRACHYPACHIDAE									
<i>Trachypachus zetterstedtii</i>	N	X				X			3
DYTISCIDAE									
<i>Hydroporus nigrita</i>	N				X		X		3
<i>Hydroporus morio</i>	N	X		X	X		X		8
<i>Hydroporus incognitus</i>	N	X		X	X	X	X	X	63
<i>Hydroporus palustris</i>	N			X	X	X	X	X	18
<i>Hydroporus melanarius</i>	N				X				1
<i>Agabus melanarius</i>	N	X							1
<i>Agabus congener</i>	N					X			1
<i>Ilybius opacus</i>	N	X							1
<i>Ilybius guttiger</i>	N	X							3
<i>Ilybius aenescens</i>	N	X							1
<i>Ilybius fuliginosus</i>	N	X		X					2
<i>Rhantus notaticollis</i>	N				X				1
CARABIDAE									
<i>Notiophilus aquaticus</i>	N			X	X		X		9
<i>Notiophilus palustris</i>	N	X		X	X	X	X		21
<i>Notiophilus germinyi</i>	N	X		X	X	X	X	X	34
<i>Notiophilus biguttatus</i>	N	X	X	X	X	X	X		51
<i>Carabus glabratus</i>	N	X	X	X	X			X	42
<i>Carabus violaceus</i>	N				X				1
<i>Cychrus caraboides</i>	N	X			X		X		10
<i>Cicindela sylvatica</i>	N				X	X	X		18
<i>Cicindela campestris</i>	N				X		X	X	11
<i>Loricera pilicornis</i>	N					X	X		2
<i>Clivina fossor</i>	N	X		X	X	X	X		44
<i>Miscodera arctica</i>	N			X	X	X	X		25
<i>Patrobus assimilis</i>	N			X	X				3
<i>Trechus rubens</i>	N	X		X	X	X	X		21
<i>Trechus quadristriatus</i>	N	X		X	X				3
<i>Blemus discus</i>	N			X					1
<i>Bembidion lampros</i>	N	X		X	X	X	X		86

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Bembidion grapii</i>	N	X	X	X	X	X	X	X	47
<i>Bembidion bruxellense</i>	N	X		X	X	X	X		23
<i>Bembidion obliquum</i>	N				X				1
<i>Bembidion doris</i>	N					X			1
<i>Bembidion gilvipes</i>	N			X		X	X		4
<i>Bembidion quadrimaculatum</i>	N	X		X	X	X	X		48
<i>Bembidion guttula</i>	N			X	X				4
<i>Bembidion mannerheimii</i>	N			X					1
<i>Porotachys bisulcatus</i>	N			X			X		2
<i>Tachyta nana</i>	S	X		X	X	X	X		18
<i>Poecilus cupreus</i>	N						X		1
<i>Poecilus versicolor</i>	N				X	X	X		7
<i>Pterostichus crenatus</i>	N			X	X		X		7
<i>Pterostichus oblongopunctatus</i>	N	X	X	X	X	X	X		152
<i>Pterostichus adstrictus</i>	N	X		X	X	X	X	X	639
* <i>Pterostichus quadrifoveolatus</i> VU	N						X		1
<i>Pterostichus melanarius</i>	N	X		X					2
<i>Pterostichus rhaeticus</i>	N	X			X	X	X		8
<i>Pterostichus strenuus</i>	N	X		X	X		X	X	12
<i>Pterostichus diligens</i>	N					X	X		2
<i>Calathus melanocephalus</i>	N				X		X		3
<i>Calathus micropterus</i>	N	X	X	X	X	X	X	X	203
<i>Sericoda quadripunctata</i>	N	X		X	X		X		34
<i>Platynus mannerheimii</i>	N			X		X			2
<i>Agonum gracile</i>	N	X		X			X		5
<i>Agonum fuliginosum</i>	N			X					7
<i>Agonum thoreyi</i>	N						X		1
<i>Agonum sexpunctatum</i>	N			X	X	X	X	X	24
<i>Amara plebeja</i>	N			X	X		X		5
<i>Amara ovata</i>	N			X	X	X			12
<i>Amara montivaga</i>	N				X				1
<i>Amara nitida</i>	N				X		X		2
<i>Amara communis</i>	N			X	X		X		5
<i>Amara nigricornis</i>	N			X	X	X	X	X	72
<i>Amara lunicollis</i>	N	X		X	X	X	X	X	289
<i>Amara famelica</i>	N			X	X				2
<i>Amara familiaris</i>	N	X		X	X	X	X	X	17
<i>Amara tibialis</i>	N				X	X	X	X	8
<i>Amara erratica</i>	N						X		1
<i>Amara interstitialis</i>	N						X		2
<i>Amara bifrons</i>	N	X			X	X			11
<i>Amara praetermissa</i>	N			X	X	X	X	X	24
<i>Amara brunnea</i>	N				X	X			4
<i>Amara quenseli</i>	N			X	X	X	X		13
<i>Amara apricaria</i>	N	X		X	X	X	X		12
<i>Harpalus griseus</i>	N				X	X			3
<i>Harpalus affinis</i>	N				X				4
<i>Harpalus solitarius</i>	N				X	X	X		26
<i>Harpalus latus</i>	N	X		X		X	X		5
<i>Harpalus laevipes</i>	N	X		X	X	X	X	X	165
<i>Harpalus tardus</i>	N				X	X			2
<i>Anisodactylus binotatus</i>	N			X			X		2

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Bradycellus caucasicus</i>	N	X		X	X	X	X	X	410
<i>Trichocellus cognatus</i>	N				X		X	X	14
<i>Trichocellus placidus</i>	N	X		X	X	X	X	X	151
<i>Acupalpus flavicollis</i>	N						X		1
<i>Acupalpus parvulus</i>	N				X		X		3
<i>Dromius agilis</i>	N	X	X	X	X	X	X	X	51
<i>Dromius schneideri</i>	N	X		X	X	X	X	X	25
<i>Cymindis vaporariorum</i>	N				X				3
HYDROPHILIDAE									
<i>Helophorus flavipes</i>	N					X	X		2
<i>Anacaena lutescens</i>	N	X			X				4
<i>Enochrus affinis</i>	N	X		X	X			X	7
<i>Hydrobius fuscipes</i>	N	X		X	X	X			11
<i>Cercyon impressus</i>	E	X				X	X		3
<i>Cercyon melanocephalus</i>	E				X				1
<i>Cercyon emarginatus</i> NT	E	X							2
<i>Cercyon borealis</i>	E	X		X	X		X		10
<i>Cercyon lateralis</i>	E	X			X		X		8
<i>Megasternum concinnum</i>	E	X	X	X	X	X	X	X	67
<i>Cryptopleurum subtile</i>	E			X	X	X	X		4
<i>Cryptopleurum minutum</i>	E			X		X	X		3
<i>Cryptopleurum crenatum</i>	E					X	X		2
SPHAERITIDAE									
<i>Sphaerites glabratus</i>	E	X			X	X	X		6
HISTERIDAE									
<i>Plegaderus saucius</i>	S			X	X				5
<i>Plegaderus vulneratus</i>	S	X		X	X		X	X	178
<i>Gnathoncus buyssoni</i>	N		X		X				5
<i>Myrmetes paykulli</i>	N	X			X		X	X	13
<i>Dendrophilus pygmaeus</i>	N				X				2
<i>Paromalus parallelepipedus</i>	S	X							5
<i>Margarinotus ventralis</i>	E	X							1
<i>Platysoma minus</i>	S	X		X	X		X	X	6
<i>Platysoma deplanatum</i>	S	X		X	X		X		15
<i>Platysoma angustatum</i>	S	X		X	X	X	X		28
<i>Platysoma lineare</i>	S	X		X	X		X		6
PTILIIDAE									
<i>Ptenidium formicetorum</i>	N	X							1
<i>Ptenidium pusillum</i>	N				X				1
<i>Ptenidium nitidum</i>	N				X				1
<i>Ptilium exaratum</i>	N				X				1
<i>Euryptilium saxonicum</i>	E	X			X	X	X		4
<i>Ptiliola kunzei</i>	E	X			X				2
<i>Ptiliolium caledonicum</i> NT	S	X							2
<i>Ptinella limbata</i>	S	X	X	X	X		X		9
<i>Ptinella johnsoni</i>	S				X				1
<i>Pteryx suturalis</i>	S	X		X	X	X	X		9
<i>Pteryx splendens</i>	S		X						1
<i>Nephanes titan</i>	E						X		1
<i>Smicrus filicornis</i>	N	X					X		2
<i>Baeocrara variolosa</i>	N	X		X	X		X		6
<i>Acrotrichis grandicollis</i>	N			X	X		X		6

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Acrotrichis sericans</i>	N			X	X	X		X	5
<i>Acrotrichis dispar</i>	E				X		X		2
<i>Acrotrichis silvatica</i>	N			X	X	X	X		17
<i>Acrotrichis cognata</i>	N				X				2
<i>Acrotrichis insularis</i>	N	X	X	X	X	X	X	X	180
<i>Acrotrichis intermedia</i>	N	X	X	X	X	X	X	X	934
<i>Acrotrichis rugulosa</i>	N	X	X	X	X	X	X	X	25
AGYRTIDAE									
<i>Pteroloma forstromii</i>	N			X			X		4
LEIODIDAE									
<i>Triarthron maerkelii</i>	N				X			X	3
<i>Sogda suturalis</i>	N					X	X		2
<i>Hydnobius spinipes</i>	N	X		X	X	X	X	X	43
<i>Leiodes punctulata</i>	N							X	1
<i>Leiodes silesiaca</i>	N	X		X	X	X	X	X	46
<i>Leiodes hybrida</i>	N				X				1
<i>Leiodes lucens</i>	N				X				1
<i>Leiodes picea</i>	N	X		X	X	X	X	X	66
<i>Leiodes ruficollis</i>	N	X		X	X	X	X	X	44
<i>Leiodes obesa</i>	N	X		X	X	X	X	X	186
<i>Leiodes ferruginea</i>	N			X					2
<i>Leiodes puncticollis</i>	N	X			X				2
<i>Anisotoma humeralis</i>	S	X	X	X	X	X	X		111
<i>Anisotoma axillaris</i>	S	X	X	X	X	X	X	X	167
<i>Anisotoma castanea</i>	S	X	X	X	X	X	X	X	267
<i>Anisotoma glabra</i>	S	X	X	X	X	X	X	X	1339
<i>Anisotoma orbicularis</i>	S	X	X	X					3
<i>Amphicyllis globus</i>	N	X	X		X	X	X		25
<i>Agathidium pulchellum</i> EN	S				X				1
<i>Agathidium pallidum</i> NT	S	X							1
<i>Agathidium rotundatum</i>	N	X	X	X	X	X	X	X	44
<i>Agathidium confusum</i>	N	X	X	X	X	X	X	X	96
<i>Agathidium arcticum</i>	N			X	X	X			3
<i>Agathidium discoideum</i>	S	X			X				6
<i>Agathidium nigripenne</i>	S	X		X	X	X			14
<i>Agathidium atrum</i>	N	X		X	X	X	X	X	54
<i>Agathidium seminulum</i>	N	X	X	X	X	X	X	X	1345
<i>Agathidium laevigatum</i>	N	X	X	X	X	X	X	X	229
<i>Agathidium pisanum</i>	S	X	X	X	X	X	X		119
<i>Colon latum</i>	N				X				1
<i>Colon serripes</i>	N	X		X			X		4
<i>Colon bidentatum</i>	N			X					1
<i>Nargus velox</i>	N		X		X				3
<i>Choleva lederiana</i>	N				X				1
<i>Choleva glauca</i>	N			X	X	X			9
<i>Choleva sturmii</i>	N		X		X		X		6
<i>Sciodrepoides watsoni</i>	E	X	X	X	X	X	X	X	206
<i>Sciodrepoides fumatus</i>	E	X	X	X	X	X			82
<i>Sciodrepoides alpestris</i>	E		X		X				14
<i>Catops subfuscus</i>	E		X						4
<i>Catops alpinus</i>	E	X	X		X		X		16
<i>Catops coracinus</i>	E	X							1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Catops tristis</i>	E			X	X	X			11
<i>Catops morio</i>	E			X	X				2
<i>Catops nigrita</i>	E	X	X	X	X	X		X	55
SCYDMAENIDAE									
<i>Eutheia linearis</i>	N	X					X		7
<i>NevrAPHES coronatus</i>	N				X	X		X	3
<i>ScydmorePHES minutus</i>	S	X			X				4
<i>Stenichnus collaris</i>	N	X	X	X	X	X	X	X	99
<i>Stenichnus bicolor</i>	N	X	X	X	X	X	X	X	101
<i>Microscydmus nanus</i>	S	X	X	X	X		X	X	63
<i>Microscydmus minimus</i>	S	X	X		X		X		16
<i>Euconnus claviger</i>	N	X							1
<i>Scydmaenus hellwigii</i>	N		X						5
SILPHIDAE									
<i>Oiceoptoma thoracica</i>	E	X		X	X		X		4
<i>Phosphuga atrata</i>	E	X	X		X	X			31
<i>Nicrophorus investigator</i>	E		X		X				2
<i>Nicrophorus vespilloides</i>	E	X	X	X	X	X	X	X	260
<i>Nicrophorus vespillo</i>	E	X							1
STAPHYLINIDAE									
<i>Eusphalerum minutum</i>	N	X			X				2
<i>Eusphalerum lapponicum</i>	N	X		X	X				3
<i>Acrulia inflata</i>	S	X			X	X	X		8
<i>Phyllodrepa melanocephala</i>	S	X	X						2
<i>Phyllodrepa linearis</i>	S	X	X	X	X				17
<i>Phyllodrepa clavigera</i>	S	X		X	X	X	X	X	99
<i>Omalium rivulare</i>	E						X		1
<i>Omalium strigicolle</i>	E		X						1
<i>Omalium caesum</i>	E	X		X	X		X	X	16
<i>Omalium rugatum</i>	E	X		X	X	X	X	X	47
<i>Phloeostiba plana</i>	S	X		X	X		X		30
<i>Phloeostiba lapponica</i>	S	X		X	X	X	X	X	278
<i>Phloeonomus pusillus</i>	S	X		X	X		X	X	36
<i>Phloeonomus sjobergi</i>	S	X		X	X	X	X	X	182
<i>Phloeonomus punctipennis</i>	S						X		3
<i>Xylodromus depressus</i>	N				X		X		2
<i>Porrhodites fenestralis</i>	N			X	X		X		6
<i>Deliphrum tectum</i>	E	X	X	X	X	X	X		14
<i>Olophrum fuscum</i>	N			X					2
<i>Olophrum consimile</i>	N	X		X	X	X	X	X	72
<i>Arpedium quadrum</i>	N			X	X	X			4
<i>Eucnecosum brachypterum</i>	N	X	X	X	X	X	X	X	104
<i>Eucnecosum brunnescens</i>	N						X		1
<i>Acidota crenata</i>	N	X	X	X	X	X	X	X	104
<i>Acidota quadrata</i>	N			X	X	X	X		15
<i>Geodromicus plagiatus</i>	N				X				2
<i>Anthophagus omalinus</i>	N	X	X	X	X	X	X	X	1058
<i>Anthophagus caraboides</i>	N			X	X	X	X	X	125
<i>Coryphium angusticolle</i>	N						X		1
<i>Megarthritis strandi</i>	E	X					X		3
<i>Megarthritis depressus</i>	E	X	X	X	X	X	X	X	81
<i>Megarthritis fennicus</i>	E	X			X				3

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Proteinus brachypterus</i>	E	X	X		X	X	X	X	19
<i>Proteinus atomarius</i>	E	X	X						3
<i>Arrhenopeplus tessera</i>	N	X		X	X	X			6
<i>Bibloporus bicolor</i>	S	X	X		X	X	X		24
<i>Bibloporus minutus</i>	S	X	X	X	X	X	X	X	38
<i>Biblopectus ambiguus</i>	N	X		X	X		X		12
<i>Euplectus kirbii</i>	S	X							1
<i>Euplectus piceus</i>	S	X			X		X		6
<i>Euplectus decipiens</i>	S		X		X	X	X		9
<i>Euplectus signatus</i>	N	X							1
<i>Euplectus punctatus</i>	S	X	X		X	X	X	X	117
<i>Euplectus karstenii</i>	N	X	X	X	X	X	X	X	43
<i>Euplectus mutator</i>	S	X	X	X	X	X	X	X	44
<i>Trimium brevicorne</i>	N	X	X	X	X	X	X	X	49
<i>Batrisesodes hubenthalii</i>	S	X			X				5
<i>Bryaxis puncticollis</i>	N	X		X	X		X	X	12
<i>Bryaxis bulbifer</i>	N	X		X	X	X	X	X	73
<i>Rybaxis longicornis</i>	N		X		X				2
<i>Pselaphaulax dresdensis</i>	N				X				2
<i>Pselaphus heisei</i>	N				X		X		2
<i>Tyrus mucronatus</i>	S	X		X	X	X	X		16
<i>Phloeocharis subtilissima</i>	S	X					X		2
<i>Olisthaerus substriatus</i>	S	X	X	X	X			X	11
<i>Mycetoporus tenuis</i>	N			X	X				2
<i>Mycetoporus monticola</i>	N				X				1
<i>Mycetoporus lepidus</i>	N	X	X	X	X	X	X	X	1030
<i>Mycetoporus glaber</i>	N				X				1
<i>Mycetoporus clavicornis</i>	N	X		X	X		X		10
<i>Mycetoporus maerkeli</i>	N	X		X	X	X	X		12
<i>Mycetoporus punctus</i>	N	X	X	X	X	X	X	X	37
<i>Ischnosoma bergrothi</i>	N	X		X	X	X	X	X	41
<i>Ischnosoma longicorne</i>	N	X	X	X	X	X	X	X	28
<i>Ischnosoma splendidum</i>	N	X	X	X	X	X	X	X	830
<i>Bryoporus ceruus</i>	N	X	X	X	X	X	X	X	67
<i>Bryoporus crassicornis</i>	N				X				1
<i>Lordithon thoracicus</i>	E	X	X	X	X	X	X	X	36
<i>Lordithon exoletus</i>	E	X	X				X		3
<i>Lordithon trimaculatus</i>	S	X			X		X		8
<i>Lordithon lunulatus</i>	E	X	X	X	X	X	X	X	204
<i>Lordithon speciosus</i>	E	X	X	X	X				7
<i>Bolitobius cingulatus</i>	N	X			X	X	X		13
<i>Bolitobius castaneus</i>	N					X			2
<i>Bolitobius formosus</i>	N	X	X	X	X	X	X	X	16
<i>Sepedophilus littoreus</i>	E	X	X	X	X	X	X	X	424
<i>Sepedophilus testaceus</i>	E	X	X	X	X	X	X	X	48
<i>Sepedophilus marshami</i>	E	X			X				4
<i>Sepedophilus constans</i>	E	X		X	X	X	X		27
<i>Sepedophilus immaculatus</i>	E	X				X	X	X	9
<i>Sepedophilus pedicularius</i>	N	X		X	X	X	X	X	28
<i>Tachyporus nitidulus</i>	N	X		X	X		X		7
<i>Tachyporus obscurellus</i>	N	X		X	X	X	X		21
<i>Tachyporus abdominalis</i>	N	X			X				5

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Tachyporus pallidus</i>	N			X	X		X		5
<i>Tachyporus hypnorum</i>	N	X		X	X		X		17
<i>Tachyporus chrysomelinus</i>	N	X		X	X	X	X	X	297
<i>Tachyporus dispar</i>	N	X		X			X		7
<i>Tachyporus transversalis</i>	N	X		X	X	X	X		13
<i>Tachyporus pulchellus</i>	N	X		X	X		X		15
<i>Tachyporus scitulus</i>	N	X		X	X				3
<i>Tachyporus corpulentus</i>	N	X			X		X		7
<i>Tachinus signatus</i>	E		X	X					3
<i>Tachinus elegans</i>	E	X	X	X	X	X	X		54
<i>Tachinus pallipes</i>	E	X	X	X	X	X	X		124
<i>Tachinus proximus</i>	E	X	X	X	X	X	X	X	49
<i>Tachinus atripes</i>	E				X				1
<i>Tachinus subterraneus</i>	E	X			X				3
<i>Tachinus basalis</i>	E	X	X						2
<i>Tachinus corticinus</i>	E			X	X				2
<i>Tachinus laticollis</i>	E	X	X	X	X	X	X	X	141
<i>Tachinus marginellus</i>	E	X		X					2
<i>Tachinus elongatus</i>	E	X		X	X	X	X	X	21
<i>Trichophya pilicornis</i>	N	X		X	X	X	X		59
<i>Aleochara brevipennis</i>	E				X	X	X		5
<i>Aleochara inconspicua</i>	E				X	X	X		3
<i>Aleochara fumata</i>	E	X	X	X	X	X	X		34
<i>Aleochara moerens</i>	E	X	X	X	X	X	X	X	117
<i>Aleochara bilineata</i>	E					X			1
<i>Aleochara binotata</i>	E						X		1
<i>Aleochara bipustulata</i>	E				X	X			2
<i>Tinotus morion</i>	E	X		X	X	X	X		10
<i>Oxypoda lugubris</i>	N	X							1
<i>Oxypoda elongatula</i>	N			X			X		7
<i>Oxypoda procerula</i>	N	X	X	X	X	X	X	X	24
<i>Oxypoda opaca</i>	N				X	X			2
<i>Oxypoda nigricornis</i>	N			X	X				2
<i>Oxypoda operata</i>	N	X		X	X	X	X		11
<i>Oxypoda spectabilis</i>	N	X			X				3
<i>Oxypoda skalitzkyi</i>	N	X	X	X	X	X	X	X	472
<i>Oxypoda brevicornis</i>	N	X		X	X	X	X	X	102
<i>Oxypoda doderoi</i>	N					X			1
<i>Oxypoda hansseni</i>	N		X		X				3
<i>Oxypoda vicina</i>	N			X	X	X	X		7
<i>Oxypoda exoleta</i>	N					X			1
<i>Oxypoda alternans</i>	E	X	X	X	X	X	X	X	78
<i>Oxypoda annularis</i>	N	X	X	X	X	X	X	X	294
<i>Oxypoda flavicornis</i>	N	X			X				4
<i>Oxypoda formiceticola</i>	N	X		X	X			X	8
<i>Oxypoda haemorrhhoa</i>	N	X	X	X	X		X		10
<i>Hygropora cunctans</i>	N	X							1
<i>Acrostiba borealis</i>	N	X		X	X		X		12
<i>Ocyusa maura</i>	N			X	X				3
<i>Chilomorpha longitarsis</i>	N	X	X	X	X	X	X	X	22
<i>Calodera aethiops</i>	N	X		X	X	X	X		15
<i>Parocyusa rubicunda</i>	N					X			1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Atheta nesslingi</i>	E					X	X		3
<i>Atheta liliputana</i>	E					X			1
<i>Atheta boreella</i>	E	X							1
<i>Atheta nigra</i>	E					X			1
<i>Atheta dadopora</i>	E	X		X	X				4
<i>Atheta canescens</i>	E				X				1
<i>Atheta sordidula</i>	E				X				1
<i>Atheta celata</i>	E	X		X	X	X	X		19
<i>Atheta myrmecobia</i>	N	X	X	X	X	X	X	X	1438
<i>Atheta laticollis</i>	N	X							1
<i>Atheta orbata</i>	N				X	X			3
<i>Atheta fungi</i>	N	X	X	X	X	X	X	X	678
<i>Atheta amplicollis</i>	N	X			X		X		5
<i>Atheta lateralis</i>	N	X	X	X	X	X	X	X	166
<i>Atheta scapularis</i>	N	X	X	X	X		X		16
<i>Atheta sodalis</i>	N	X	X	X	X	X	X	X	171
<i>Atheta gagatina</i>	E	X		X	X	X	X		59
<i>Atheta flavipes</i>	N	X	X	X	X	X	X		77
<i>Atheta subterranea</i>	N	X							1
<i>Atheta macrocera</i>	E			X	X				6
<i>Atheta longicornis</i>	E				X		X		4
<i>Atheta cribripennis</i>	E				X	X			2
<i>Atheta eremita</i>	N	X		X	X		X		21
<i>Atheta nigripes</i>	E			X	X		X		3
<i>Atheta cinnamoptera</i>	E					X			1
<i>Atheta aeneipennis</i>	E	X	X	X	X	X	X	X	44
<i>Atheta picipennis</i>	E						X		1
<i>Atheta lapponica</i>	E					X			1
<i>Atheta intermedia</i>	E				X				1
<i>Atheta cauta</i>	E			X					1
<i>Atheta atramentaria</i>	E				X				1
<i>Atheta hypnorum</i>	N	X	X	X	X	X	X	X	149
<i>Atheta graminicola</i>	N			X	X		X		3
<i>Atheta incognita</i>	N	X		X	X	X	X	X	35
<i>Atheta procera</i>	E	X			X				5
<i>Atheta nidicola</i>	N				X				1
<i>Atheta allocera</i>	E							X	1
<i>Atheta boletophila</i>	S					X			1
<i>Atheta diversa</i>	E	X			X	X			4
<i>Atheta strandiella</i>	E				X				1
<i>Atheta pilicornis</i>	E	X		X	X	X	X	X	40
<i>Atheta acutangula</i>	E				X				1
<i>Atheta boleticola</i>	E	X	X		X	X	X		7
<i>Atheta crassicornis</i>	E	X			X				2
<i>Atheta paracrassicornis</i>	E			X	X	X	X	X	10
<i>Atheta crassic./paracrassic.</i>	E	X		X	X	X	X	X	41
<i>Atheta euryptera</i>	E			X	X		X		6
<i>Atheta nigricornis</i>	E	X		X			X		5
<i>Atheta coriaria</i>	N			X	X				3
<i>Atheta nigrifula</i>	E	X			X		X		4
<i>Atheta excellens</i>	E	X		X	X				4
<i>Anopleta corvina</i>	E				X				1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Autalia rivularis</i>	E						X		1
<i>Autalia puncticollis</i>	E			X					1
<i>Holobus apicatus</i>	E			X	X		X		3
<i>Holobus flavicornis</i>	E	X	X	X	X		X		7
<i>Oligota parva</i>	N	X					X		2
<i>Myllaena intermedia</i>	N	X		X	X	X	X	X	54
<i>Myllaena gracilis</i>	N				X				1
<i>Myllaena minuta</i>	N	X	X	X	X	X	X	X	50
<i>Gymnusa brevicollis</i>	N						X		1
<i>Scaphidium quadrimaculatum</i>	S	X							2
<i>Scaphisoma agaricinum</i>	N	X	X	X	X	X	X	X	602
<i>Scaphisoma inopinatum</i>	S	X		X	X	X			22
<i>Scaphisoma boleti</i>	S				X			X	2
<i>Scaphisoma subalpinum</i>	S	X	X		X	X	X	X	71
<i>Scaphisoma boreale</i>	S	X	X	X	X	X	X	X	55
<i>Scaphisoma assimile</i>	S				X				1
<i>Syntomium aeneum</i>	N	X		X	X	X	X	X	33
<i>Deleaster dichrous</i>	N						X		1
<i>Coprophilus striatulus</i>	E	X							1
<i>Thinobius flagellatus</i>	N				X				2
<i>Carpelimus bilineatus</i>	N			X			X		4
<i>Carpelimus lindrothi</i>	N					X			1
<i>Carpelimus corticinus</i>	N	X		X	X	X	X		120
<i>Carpelimus subtilicornis</i>	N	X			X				2
<i>Carpelimus pusillus</i>	N						X		3
<i>Carpelimus gracilis</i>	N			X	X		X		6
<i>Aploderus caelatus</i>	E	X			X	X			4
<i>Bledius gallicus</i>	N			X	X				2
<i>Oxytelus sculptus</i>	E			X	X		X		8
<i>Oxytelus migrator</i>	N						X		1
<i>Anotylus rugosus</i>	E	X		X	X	X	X	X	67
<i>Anotylus nitidulus</i>	E	X			X				3
<i>Anotylus clavatus</i>	E				X	X			7
<i>Platystethus arenarius</i>	E	X			X	X	X	X	23
<i>Platystethus nodifrons</i>	E					X			2
<i>Oxyporus maxillosus</i>	E	X	X		X		X		52
<i>Stenus biguttatus</i>	N			X					2
<i>Stenus fossulatus</i>	N	X			X				2
<i>Stenus juno</i>	N				X	X	X		5
<i>Stenus bilineatus</i>	N	X			X				3
<i>Stenus fasciculatus</i>	N						X		1
<i>Stenus clavicornis</i>	N	X	X	X	X	X	X	X	107
<i>Stenus morio</i>	N	X		X	X	X	X		25
<i>Stenus excubitor</i>	N						X		1
<i>Stenus canaliculatus</i>	N			X	X	X	X		11
<i>Stenus argus</i>	N					X			1
<i>Stenus nanus</i>	N			X					1
<i>Stenus humilis</i>	N				X		X		2
<i>Stenus carbonarius</i>	N			X					1
<i>Stenus scabriculus</i>	N	X		X	X	X	X		85
<i>Stenus opticus</i>	N	X				X			2
<i>Stenus crassus</i>	N						X		1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Stenus intermedius</i>	N	X		X	X	X	X		23
<i>Stenus fulvicornis</i>	N	X							1
<i>Stenus tarsalis</i>	N	X						X	2
<i>Stenus bohemicus</i>	N							X	1
<i>Stenus tarsalis/bohemicus</i>	N				X		X		5
<i>Stenus flavipes</i>	N				X				1
<i>Stenus bifoveolatus</i>	N	X			X				3
<i>Stenus palustris</i>	N	X			X	X			10
<i>Stenus geniculatus</i>	N		X		X		X		3
<i>Astenus pulchellus</i>	N				X				1
<i>Astenus gracilis</i>	N			X	X		X		7
<i>Medon apicalis</i>	N				X				3
<i>Pseudomedon obscurellus</i>	N	X		X					2
<i>Lithocharis nigriceps</i>	N	X			X	X			9
<i>Lathrobium zetterstedti</i>	N	X		X					2
<i>Lathrobium terminatum</i>	N			X	X	X	X		29
<i>Lathrobium quadratum</i>	N			X			X	X	5
<i>Lathrobium elongatum</i>	N			X	X		X		3
<i>Lathrobium rufipenne</i>	N				X	X			2
<i>Lathrobium geminum</i>	N				X		X		3
<i>Lathrobium fulvipenne</i>	N	X		X		X	X	X	21
<i>Lathrobium brunnipes</i>	N	X	X	X	X	X	X	X	69
<i>Lathrobium longulum</i>	N	X		X	X	X	X		40
<i>Ochtheophilum fracticorne</i>	N				X	X	X	X	17
<i>Leptacinus formicetorum</i>	N	X			X				4
<i>Leptacinus intermedius</i>	N					X	X		2
<i>Gyrophypnus punctulatus</i>	N	X							1
<i>Gyrophypnus angustatus</i>	N			X	X		X		4
<i>Gyrophypnus atratus</i>	N						X		1
<i>Nudobius lentus</i>	S	X		X	X	X	X	X	137
<i>Xantholinus linearis</i>	N	X		X	X	X	X	X	282
<i>Xantholinus tricolor</i>	N	X			X	X	X	X	99
<i>Xantholinus laevigatus</i>	N	X			X		X		4
<i>Othius punctulatus</i>	N	X			X	X			21
<i>Othius lapidicola</i>	N	X		X	X	X	X		29
<i>Othius subuliformis</i>	N	X		X	X	X	X		79
<i>Atrecus pilicornis</i>	S	X	X	X	X	X	X	X	117
<i>Atrecus affinis</i>	S	X	X	X	X	X	X	X	67
<i>Atrecus longiceps</i> NT	S	X			X			X	4
<i>Erichsonius cinerascens</i>	N				X		X		2
<i>Gabrius appendiculatus</i>	N	X		X	X	X	X	X	45
<i>Gabrius sphagnicola</i>	N						X		1
<i>Gabrius austriacus</i>	N			X	X	X			6
<i>Gabrius breviventer</i>	N			X	X	X	X		18
<i>Gabrius expectatus</i>	S	X	X	X	X	X	X	X	75
<i>Gabrius astutoides</i>	N			X	X		X		5
<i>Gabrius trossulus</i>	N	X	X	X	X	X	X	X	337
<i>Bisnius scoticus</i>	N		X						1
<i>Bisnius fimetarius</i>	E				X				1
<i>Bisnius puella</i>	E	X			X				6
<i>Bisnius nigriventris</i>	E	X		X	X	X	X		10
<i>Bisnius cephalotes</i>	E	X							1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Philonthus rectangulus</i>	N	X					X		4
<i>Philonthus laminatus</i>	E	X							1
<i>Philonthus politus</i>	E	X			X	X	X		6
<i>Philonthus succicola</i>	E	X		X	X		X		8
<i>Philonthus addendus</i>	E	X			X				2
<i>Philonthus tenuicornis</i>	E	X			X				2
<i>Philonthus decorus</i>	E		X		X	X			3
<i>Philonthus cognatus</i>	E				X				1
<i>Philonthus cruentatus</i>	E			X					1
<i>Philonthus varians</i>	E	X		X	X				7
<i>Philonthus marginatus</i>	E	X							1
<i>Philonthus lederi</i>	E	X	X	X	X	X		X	12
<i>Philonthus carbonarius</i>	E	X		X			X		4
<i>Philonthus albipes</i>	E			X	X		X		5
<i>Philonthus concinnus</i>	E	X		X	X	X	X		26
<i>Philonthus debilis</i>	E	X			X				3
<i>Philonthus nigrata</i>	N	X		X	X	X	X	X	101
<i>Platydracus fulvipes</i>	N	X		X	X		X		21
<i>Staphylinus erythropterus</i>	N	X		X				X	41
<i>Heterothops stiglundbergi</i>	N						X		1
<i>Heterothops quadripunctulus</i>	N	X		X	X	X	X	X	132
<i>Quedius mesomelinus</i>	N	X	X					X	5
<i>Quedius maurus</i>	N		X						1
<i>Quedius brevis</i>	N	X		X	X		X		18
<i>Quedius tenellus</i>	N	X	X	X	X	X	X	X	398
<i>Quedius xanthopus</i>	S	X	X	X	X	X	X	X	442
<i>Quedius plagiatus</i>	S	X	X	X	X	X	X	X	162
<i>Quedius fuliginosus</i>	N	X		X	X		X	X	17
<i>Quedius subunicolor</i>	N	X		X	X		X		5
<i>Quedius molochinus</i>	N	X	X	X	X	X	X	X	122
<i>Quedius lucidulus</i>	N	X			X	X	X		11
<i>Quedius limbatus</i>	N	X		X	X	X	X		11
<i>Quedius nitipennis</i>	N			X	X	X	X	X	14
<i>Quedius fulvicollis</i>	N	X	X	X	X	X	X	X	39
<i>Quedius boops</i>	N	X		X	X	X	X	X	53
LUCANIDAE									
<i>Platycerus caprea</i>	S	X	X	X	X	X	X	X	177
GEOTRUPIDAE									
<i>Geotrupes stercorosus</i>	E	X	X	X	X				32
SCARABAEIDAE									
<i>Aphodius brevis</i>	E						X		1
<i>Aphodius rufipes</i>	E	X	X	X	X	X	X	X	427
<i>Aphodius depressus</i>	E	X	X	X	X	X	X	X	194
<i>Aphodius fimetarius</i>	E				X	X			5
<i>Aphodius borealis</i>	E	X		X	X		X	X	21
<i>Aphodius nemoralis</i>	E	X	X	X	X	X	X	X	13
<i>Aphodius lapponum</i>	E	X	X	X	X	X	X	X	35
<i>Aphodius piceus</i>	E	X	X	X	X	X	X		15
<i>Serica brunnea</i>	H		X		X		X		5
<i>Potosia cuprea</i>	N	X			X	X	X	X	11
<i>Trichius fasciatus</i>	S	X		X	X	X	X	X	520

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
EUCINETIDAE									
<i>Eucinetus haemorrhoidalis</i> NT	N				X				1
<i>Euclodes caucasicus</i> VU	S		X		X	X			4
CLAMBIDAE									
<i>Clambus pubescens</i>	N	X			X		X		5
<i>Clambus punctulum</i>	N	X	X		X	X	X		17
<i>Clambus gibbulus</i>	N				X		X		2
<i>Clambus armadillo</i>	N	X	X	X	X	X	X	X	56
SCIRTIDAE									
<i>Microcara testacea</i>	N			X					1
<i>Cyphon coarctatus</i>	N	X		X	X	X	X		493
<i>Cyphon palustris</i>	N		X	X	X		X		22
<i>Cyphon kongsbergensis</i>	N	X		X	X		X		25
<i>Cyphon ochraceus</i>	N	X		X			X		8
<i>Cyphon variabilis</i>	N	X	X	X	X	X	X	X	435
<i>Cyphon punctipennis</i>	N	X	X	X	X	X	X	X	226
<i>Cyphon padi</i>	N	X	X	X	X	X	X	X	1602
BUPRESTIDAE									
<i>Buprestis rustica</i>	S	X		X	X		X	X	20
<i>Melanophila acuminata</i> NT	S	X			X	X	X		16
<i>Phaenops formaneki</i>	S			X					1
<i>Anthaxia quadripunctata</i>	S				X		X	X	8
<i>Chrysobothris chrysostigma</i>	S				X	X			4
<i>Agrilus betuleti</i>	S						X		1
<i>Agrilus viridis</i>	S						X		1
BYRRHIDAE									
<i>Simpliocaria semistriata</i>	H				X		X		5
<i>Cytilus sericeus</i>	H	X		X	X	X	X	X	184
<i>Cytilus auricomus</i>	H	X					X		2
<i>Byrrhus fasciatus</i>	H	X		X	X	X	X	X	647
<i>Byrrhus arietinus</i>	H	X	X	X	X	X	X		85
<i>Byrrhus pustulatus</i>	H	X		X	X	X	X	X	57
<i>Curimopsis paleata</i>	H				X	X	X		17
ELMIDAE									
<i>Oulimnius tuberculatus</i>	N						X		1
DRYOPIDAE									
<i>Dryops anglicanus</i>	N			X					1
THROSCIDAE									
<i>Trixagus carinifrons</i>	H	X	X	X	X	X	X	X	38
ELATERIDAE									
<i>Lacon conspersus</i> NT	S	X		X	X	X	X	X	44
<i>Lacon fasciatus</i> NT	S	X		X	X	X	X	X	132
<i>Athous subfuscus</i>	H	X	X	X	X	X	X	X	3024
<i>Limonium aeneoniger</i>	H				X	X	X		7
<i>Harminius undulatus</i>	S	X		X	X		X	X	9
<i>Denticollis linearis</i>	S	X		X	X	X	X	X	41
<i>Denticollis borealis</i>	S	X			X		X	X	7
<i>Hypnoidus riparius</i>	H			X	X				3
<i>Ctenicera pectinicornis</i>	H			X	X	X	X		16
<i>Ctenicera cuprea</i>	H			X	X	X	X	X	12
<i>Liotrichus affinis</i>	H	X		X	X	X		X	25
<i>Orithales serraticornis</i>	H	X		X	X	X	X	X	12518

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Epuraea laeviuscula</i>	S	X		X	X		X		90
<i>Epuraea rufobrunnea</i> NT	S	X							2
<i>Epuraea deubeli</i>	S	X		X	X	X	X		41
<i>Epuraea thoracica</i>	S	X		X	X	X			31
<i>Epuraea angustula</i>	S	X		X	X	X	X	X	47
<i>Epuraea oblonga</i>	S	X	X	X	X		X		26
<i>Epuraea longipennis</i>	N	X			X	X	X		8
<i>Epuraea fussii</i>	S	X							4
<i>Epuraea boreella</i>	S	X	X	X	X	X	X		60
<i>Epuraea opalizans</i>	N	X		X	X		X		5
<i>Epuraea marseuli</i>	S	X	X	X	X	X	X	X	915
<i>Epuraea pygmaea</i>	S	X	X	X	X	X	X	X	1198
<i>Epuraea binotata</i>	N	X	X	X	X	X	X	X	1080
<i>Epuraea terminalis</i>	N	X		X	X	X	X		14
<i>Epuraea biguttata</i>	S	X		X	X	X	X		24
<i>Epuraea unicolor</i>	N			X		X			6
<i>Epuraea variegata</i>	S	X	X		X	X	X		20
<i>Epuraea muehli</i>	S	X			X	X			41
<i>Epuraea silacea</i>	S	X		X	X		X		5
<i>Epuraea aestiva</i>	N	X	X	X	X	X	X	X	257
<i>Epuraea rufomarginata</i>	S	X	X	X	X	X	X	X	140
<i>Epuraea contractula</i>	S	X		X		X			5
<i>Epuraea silesiaca</i> EN	S				X				1
<i>Meligethes denticulatus</i>	H						X		1
<i>Meligethes aeneus</i>	H	X							1
<i>Meligethes viridescens</i>	H						X		1
<i>Omosita depressa</i>	N	X							1
<i>Nitidula bipunctata</i>	E						X		1
<i>Ipidia binotata</i>	S	X		X	X	X	X	X	65
<i>Pocadius ferrugineus</i>	E				X				1
<i>Thalycra fervida</i>	E				X	X			2
<i>Cychramus variegatus</i>	E					X			1
<i>Cychramus luteus</i>	E	X			X				4
<i>Glischrochilus hortensis</i>	S	X		X	X	X	X		25
<i>Glischrochilus quadripunctatus</i>	S	X		X	X	X	X	X	200
<i>Pityophagus ferrugineus</i>	S	X	X	X	X	X	X	X	780
<i>Cybocephalus politus</i>	N	X	X	X	X	X	X	X	21
MONOTOMIDAE									
<i>Rhizophagus grandis</i>	S	X					X		2
<i>Rhizophagus depressus</i>	S	X		X	X	X	X		41
<i>Rhizophagus ferrugineus</i>	S	X	X	X	X	X	X	X	3995
<i>Rhizophagus dispar</i>	E	X	X	X	X	X	X	X	52
<i>Rhizophagus bipustulatus</i>	S	X					X		8
<i>Rhizophagus nitidulus</i>	S	X		X	X	X	X		27
<i>Rhizophagus parvulus</i>	S	X	X	X	X	X	X		115
<i>Rhizophagus cribratus</i>	S	X	X		X	X			46
<i>Monotoma conicicollis</i>	N	X							5
<i>Monotoma angusticollis</i>	N	X							1
<i>Monotoma picipes</i>	N	X		X	X	X	X		7
<i>Monotoma longicollis</i>	N				X				1
SILVANIDAE									
<i>Dendrophagus crenatus</i>	S	X	X	X	X		X	X	39

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Ahasverus advena</i>	N	X							1
<i>Silvanus bidentatus</i>	S						X		2
<i>Silvanoprus fagi</i>	S	X	X	X	X	X	X	X	395
CUCUJIDAE									
<i>Pediacus fuscus</i>	S	X		X	X	X	X	X	969
LAEMOPHLOEIDAE									
<i>Laemophloeus muticus</i>	S	X		X	X	X	X		14
<i>Cryptolestes abietis</i>	S	X		X	X		X		20
<i>Cryptolestes weisei</i>	S	X							8
<i>Cryptolestes alternans</i>	S	X		X	X		X		23
<i>Cryptolestes corticinus</i>	S	X		X	X	X			8
PHALACRIDAE									
<i>Phalacrus substriatus</i>	H	X					X		3
<i>Olibrus norvegicus</i>	H				X				1
CRYPTOPHAGIDAE									
<i>Telmatophilus typhae</i>	H	X			X				2
<i>Henoticus serratus</i>	S	X		X	X	X	X		138
<i>Pteryngium crenatum</i>	S	X			X	X	X		5
<i>Micrambe abietis</i>	N	X	X	X	X	X	X	X	340
<i>Micrambe longitarsis</i>	S	X	X	X	X	X	X	X	50
<i>Cryptophagus acutangulus</i>	N	X					X		2
<i>Cryptophagus parallelus</i>	S	X		X	X		X		7
<i>Cryptophagus fallax</i>	N						X	X	2
<i>Cryptophagus badius</i>	N	X			X	X			8
<i>Cryptophagus quadrihamatus</i>	S	X		X					2
<i>Cryptophagus sp. cf. confertus</i>	N	X		X	X				5
<i>Cryptophagus lapponicus</i>	N	X	X	X	X	X	X	X	245
<i>Cryptophagus subdepressus</i>	N	X		X	X	X	X		8
<i>Cryptophagus dorsalis</i>	N	X	X	X	X	X	X	X	117
<i>Cryptophagus corticinus</i>	S			X	X	X	X		21
<i>Cryptophagus setulosus</i>	N	X	X	X	X	X	X	X	43
<i>Spavius glaber</i>	N	X		X	X	X			51
<i>Antherophagus nigricornis</i>	N	X	X	X	X	X	X	X	85
<i>Antherophagus pallens</i>	N	X		X	X		X		8
<i>Caenoscelis subdeplanata</i>	N	X		X	X	X	X		38
<i>Caenoscelis ferruginea</i>	N	X	X	X	X	X	X	X	458
<i>Caenoscelis sibirica</i>	N	X		X					2
<i>Atomaria impressa</i>	N			X			X		4
<i>Atomaria ornata</i>	N	X			X	X			8
<i>Atomaria peltata</i>	E	X	X	X	X	X	X	X	395
<i>Atomaria peltataeformis</i>	E	X			X	X		X	18
<i>Atomaria pusilla</i>	N			X					1
<i>Atomaria sodermani</i>	N				X	X			3
<i>Atomaria lundbergi</i>	N				X				1
<i>Atomaria clavigera</i> NT	N	X							1
<i>Atomaria fuscata</i>	N	X		X	X	X	X		9
<i>Atomaria lewisi</i>	N	X		X	X	X	X		89
<i>Atomaria rubella</i>	N		X		X	X			3
<i>Atomaria hislopi</i>	E	X			X	X	X		7
<i>Atomaria turgida</i>	N	X	X		X	X			17
<i>Atomaria apicalis</i>	N			X	X		X	X	10
<i>Atomaria testacea</i>	E	X		X	X		X		28

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Atomaria umbrina</i>	S	X	X	X	X	X	X	X	22
<i>Atomaria nigrirostris</i>	N	X		X	X	X	X		39
<i>Atomaria subangulata</i>	S	X	X	X	X	X	X		30
<i>Atomaria abietina</i> NT	S				X				1
<i>Atomaria badia</i>	S	X			X	X	X		8
<i>Atomaria elongatula</i> NT	S	X				X	X		4
<i>Atomaria affinis</i>	S		X		X				2
<i>Atomaria bella</i>	S	X	X	X	X	X	X	X	594
<i>Atomaria pulchra</i>	N	X	X	X	X	X	X	X	3589
<i>Atomaria atrata</i>	N	X		X	X	X	X	X	37
<i>Atomaria procerula</i>	N	X		X					3
<i>Atomaria ihsseni</i>	N	X					X		2
EROTYLIDAE									
<i>Zavaljus brunneus</i> VU	S			X					3
<i>Dacne bipustulata</i>	S	X		X	X	X	X	X	138
<i>Triplax aenea</i>	S				X	X	X		11
<i>Triplax russica</i>	S	X	X	X	X	X	X	X	615
<i>Triplax scutellaris</i>	S	X	X		X	X	X		20
<i>Triplax rufipes</i>	S	X		X	X	X	X		10
BYTURIDAE									
<i>Byturus tomentosus</i>	H			X			X		3
CERYLONIDAE									
<i>Cerylon fagi</i>	S	X	X	X	X		X		14
<i>Cerylon histeroides</i>	S	X	X	X	X	X	X	X	150
<i>Cerylon ferrugineum</i>	S	X	X	X	X	X	X	X	187
<i>Cerylon impressum</i> VU	S	X		X			X		13
<i>Cerylon deplanatum</i>	S	X	X	X	X	X		X	23
ENDOMYCHIDAE									
<i>Leiestes seminigra</i>	S	X							3
COCCINELLIDAE									
<i>Scymnus nigrinus</i>	N					X			1
<i>Scymnus frontalis</i>	N				X	X			3
<i>Scymnus suturalis</i>	N				X				1
<i>Scymnus haemorrhoidalis</i>	N	X			X	X			4
<i>Scymnus fennicus</i>	N						X		1
<i>Nephus redtenbacheri</i>	N	X			X		X		5
<i>Nephus bisignatus</i>	N	X		X	X	X	X		50
<i>Chilocorus renipustulatus</i>	N	X			X	X	X		9
<i>Exochomus quadripustulatus</i>	N						X		2
<i>Coccinula quatuordecimpustulata</i>	N	X		X	X	X	X	X	62
<i>Anisosticta novemdecimpunctata</i>	N			X					3
<i>Myzia oblongoguttata</i>	N	X			X		X		4
<i>Myrrha octodecimguttata</i>	N	X						X	2
<i>Calvia quatuordecimguttata</i>	N		X						1
<i>Anatis ocellata</i>	N	X	X	X	X			X	6
<i>Hippodamia tredecimpunctata</i>	N				X		X	X	3
<i>Hippodamia septemmaculata</i>	N				X				1
<i>Hippodamia variegata</i>	N					X	X		3
<i>Hippodamia notata</i>	N						X		1
<i>Coccinella trifasciata</i>	N						X		2
<i>Coccinella septempunctata</i>	N	X		X	X	X	X	X	104
<i>Coccinella magnifica</i>	N	X			X	X			10

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Coccinella hieroglyphica</i>	N	X		X	X	X	X	X	28
<i>Adalia bipunctata</i>	N			X					1
CORYLOPHIDAE									
<i>Clypastraea pusilla</i> VU	S	X		X	X	X	X	X	210
<i>Orthoperus brunripes</i>	N	X						X	8
<i>Orthoperus nigrescens</i>	S	X				X	X		16
<i>Orthoperus punctatus</i>	N	X				X			2
<i>Orthoperus rogeri</i>	N	X	X		X		X	X	23
<i>Orthoperus atomus</i>	N	X	X						6
LATRIDIIDAE									
<i>Latridius hirtus</i>	S	X	X	X	X	X	X		216
<i>Latridius consimilis</i>	N	X	X	X	X	X	X		17
<i>Latridius minutus</i>	N	X	X	X	X		X		23
<i>Latridius nidicola</i>	N	X							1
<i>Enicmus fungicola</i>	S	X	X	X	X	X	X	X	510
<i>Enicmus planipennis</i>	S	X	X	X	X	X	X	X	116
<i>Enicmus rugosus</i>	S	X	X	X	X	X	X	X	1658
<i>Enicmus transversus</i>	N	X		X	X		X		7
<i>Enicmus histrio</i> NT	N	X		X	X	X			5
<i>Stephostethus pandellei</i>	N	X							2
<i>Stephostethus rugicollis</i>	N	X	X	X	X	X	X	X	493
<i>Cartodere constricta</i>	N	X		X	X	X	X	X	842
<i>Corticaria pubescens</i>	N	X		X	X	X	X	X	37
<i>Corticaria umbilicata</i>	N	X		X	X	X	X		15
<i>Corticaria impressa</i>	N	X		X	X	X	X	X	54
<i>Corticaria lapponica</i>	S	X	X	X	X	X	X	X	59
<i>Corticaria saginata</i>	N			X	X				2
<i>Corticaria orbicollis</i>	S	X		X	X	X	X	X	45
<i>Corticaria abietorum</i>	N	X			X				3
<i>Corticaria interstitialis</i>	N	X		X	X	X	X	X	93
<i>Corticaria foveola</i> VU	S				X				1
<i>Corticaria rubripes</i>	N	X	X	X	X	X	X	X	10568
<i>Corticaria polypori</i>	S		X		X		X		4
<i>Corticaria crenicollis</i>	S				X		X		5
<i>Corticaria fennica</i> NT	S	X							1
<i>Corticaria lateritia</i>	S	X		X	X	X	X		25
<i>Corticaria longicollis</i>	N	X	X		X	X			18
<i>Corticaria elongata</i>	N	X			X		X		3
<i>Corticaria obsoleta</i>	S	X			X				8
<i>Corticaria ferruginea</i>	N	X	X	X	X	X	X	X	20445
<i>Cortimicara gibbosa</i>	N	X	X	X	X	X	X	X	232
<i>Corticarina obfuscata</i>	N	X	X	X	X	X	X	X	128
<i>Corticarina fuscula</i>	N	X	X	X	X	X	X	X	636
<i>Corticarina latipennis</i>	N	X		X	X	X	X	X	43
<i>Melanophthalma curticollis</i>	N				X				1
MYCETOPHAGIDAE									
<i>Litargus connexus</i>	S	X		X	X	X	X	X	100
<i>Mycetophagus quadripustulatus</i>	S						X		3
<i>Mycetophagus piceus</i>	S	X		X	X	X	X	X	128
<i>Mycetophagus decempunctatus</i>	S	X							1
<i>Mycetophagus multipunctatus</i>	S	X	X		X	X	X		11
<i>Mycetophagus fulvicollis</i>	S	X			X	X			9

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Mycetophagus populi</i>	S	X			X	X			5
CIIDAE									
<i>Cis lineatocribratus</i>	S	X	X	X	X	X	X	X	62
<i>Cis jacquemartii</i>	S	X	X	X	X	X	X	X	54
<i>Cis glabratus</i>	S	X		X	X		X		14
<i>Cis comptus</i>	S	X		X	X	X	X		19
<i>Cis hispidus</i>	S	X	X	X	X	X	X	X	46
<i>Cis boleti</i>	S	X	X	X	X	X	X	X	115
<i>Cis quadridens</i>	S				X				1
<i>Cis punctulatus</i>	S	X	X	X	X	X	X	X	67
<i>Cis dentatus</i>	S				X				1
<i>Cis bidentatus</i>	S	X							1
<i>Ennearthron cornutum</i>	S	X	X	X	X				8
<i>Ennearthron laricinum</i>	S	X	X	X	X				16
<i>Orthocis alni</i>	S	X	X	X	X	X	X		47
<i>Hadreule elongatula</i>	S	X	X	X	X	X	X	X	15
<i>Sulcacis affinis</i>	S	X		X	X	X	X	X	22
<i>Ropalodontus strandi</i>	S	X	X		X	X	X	X	32
<i>Octotemnus glabriculus</i>	S				X	X			6
TETRATOMIDAE									
<i>Tetratoma ancora</i>	S	X	X		X	X	X		7
MELANDRYIDAE									
<i>Hallomenus binotatus</i>	S	X	X	X	X	X	X		30
<i>Hallomenus axillaris</i>	S	X	X	X	X	X	X	X	36
<i>Orchesia micans</i>	S	X			X	X	X	X	42
<i>Orchesia minor</i>	S					X			1
<i>Orchesia fasciata</i>	S	X			X	X			3
<i>Abdera affinis</i>	S	X			X	X	X	X	14
<i>Abdera flexuosa</i>	S							X	1
<i>Abdera triguttata</i>	S	X	X	X	X	X	X	X	71
<i>Xylita laevigata</i>	S	X	X	X	X	X	X	X	702
<i>Xylita livida</i>	S		X			X		X	6
<i>Serropalpus barbatus</i>	S	X				X			3
* <i>Melandrya dubia</i> NT	S				X				1
MORDELLIDAE									
<i>Tomoxia bucephala</i> NT	S	X		X	X	X	X		41
<i>Mordella aculeata</i>	N	X		X	X	X	X		65
<i>Mordella holomelaena</i>	N	X		X	X	X	X	X	238
<i>Curtimorda maculosa</i>	S	X		X	X		X	X	26
<i>Mordellistena connata</i>	H				X				1
<i>Mordellistena humeralis</i>	S				X				1
ZOPHERIDAE									
<i>Synchita humeralis</i>	S	X	X	X	X		X	X	21
<i>Bitoma crenata</i>	S	X			X		X		9
<i>Lasconotus jelskii</i>	S			X	X				9
TENEBRIONIDAE									
<i>Lagria hirta</i>	N	X		X	X		X		9
<i>Bius thoracicus</i>	S			X	X		X		7
<i>Pseudocistela ceramboides</i>	S	X			X				3
<i>Mycetochara flavipes</i>	S	X	X	X	X	X	X	X	106
<i>Mycetochara obscura</i>	S	X	X	X	X	X	X	X	91
<i>Corticeus longulus</i> VU	S	X		X	X	X			6

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Corticeus fraxini</i> VU	S				X			X	2
<i>Corticeus suturalis</i>	S	X		X	X		X		15
<i>Corticeus linearis</i>	S	X		X	X	X	X	X	98
<i>Bolitophagus reticulatus</i>	S	X	X	X	X	X	X	X	87
<i>Alphitophagus bifasciatus</i>	N						X		2
<i>Diaperis boleti</i>	S		X		X		X		6
<i>Myrmechixenus vaporariorum</i>	N			X					1
<i>Upis ceramboides</i>	S			X	X	X			3
OEDEMERIDAE									
<i>Calopus serraticornis</i>	S	X		X	X	X	X		15
<i>Chrysanthia geniculata</i>	S	X		X	X	X	X	X	60
<i>Oedemera virescens</i>	H	X			X	X	X	X	8
STENOTRACHELIDAE									
<i>Stenotrachelus aeneus</i>	S			X	X	X	X		10
BORIDAE									
<i>Boros schneideri</i> VU	S				X		X		3
PYTHIDAE									
<i>Pytho depressus</i>	S			X	X	X	X	X	22
<i>Pytho abieticola</i> VU	S			X					2
PYROCHROIDAE									
<i>Schizotus pectinicornis</i>	S	X		X	X	X	X	X	38
SALPINGIDAE									
<i>Rabocerus foveolatus</i>	S	X	X	X	X	X	X	X	43
<i>Rabocerus gabrieli</i>	S	X							1
<i>Sphaeriestes bimaculatus</i>	S	X			X		X	X	17
<i>Sphaeriestes stockmanni</i> NT	S	X		X	X	X	X	X	1354
<i>Salpingus planirostris</i>	S				X				1
<i>Salpingus ruficollis</i>	S	X	X	X	X	X	X		41
ANTHICIDAE									
<i>Omonadus floralis</i>	N					X		X	3
<i>Omonadus formicarius</i>	N					X			1
<i>Anthicus ater</i>	N	X		X	X	X	X	X	183
ADERIDAE									
<i>Euglenes pygmaeus</i>	S	X		X	X	X	X	X	42
<i>Euglenes sp. cf. nitidifrons</i>	S				X		X	X	5
<i>Anidorus nigrinus</i>	S			X					1
SCRAPTIIDAE									
<i>Anaspis bohemica</i>	S	X		X	X	X	X	X	51
<i>Anaspis frontalis</i>	S	X			X	X	X		22
<i>Anaspis marginicollis</i>	S	X	X	X	X	X	X	X	1289
<i>Anaspis arctica</i>	S	X	X	X	X	X	X	X	119
<i>Anaspis rufilabris</i>	S			X		X	X		3
CERAMBYCIDAE									
<i>*Tragosoma depsarius</i> VU	S	X			X				2
<i>Spondylis buprestoides</i>	S			X	X				2
<i>Arhopalus rusticus</i>	S	X		X	X	X	X	X	50
<i>Asemum striatum</i>	S	X		X	X	X	X	X	174
<i>Tetropium castaneum</i>	S	X		X	X	X	X	X	66
<i>Rhagium mordax</i>	S	X	X	X	X	X	X	X	416
<i>Rhagium inquisitor</i>	S	X		X	X	X	X	X	355
<i>Oxymirus cursor</i>	S	X	X	X	X	X	X	X	70
<i>Pachyta quadrimaculata</i>	S				X				1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Pachyta lamed</i>	S	X		X	X	X	X	X	678
<i>Brachyta interrogationis</i>	H		X		X				3
<i>Gaurotes virginea</i>	S	X			X	X	X		20
<i>Acmaeops septentrionis</i> VU	S	X		X	X	X	X		67
<i>Acmaeops marginata</i> VU	S			X	X	X	X	X	33
<i>Acmaeops pratensis</i>	S	X		X	X	X	X	X	1837
<i>Alosterna tabacicolor</i>	S	X	X	X	X	X	X		27
<i>Anoplodera maculicornis</i>	S			X					1
<i>Anoplodera rubra</i>	S	X							2
<i>Anoplodera sanguinolenta</i>	S	X		X	X	X	X	X	322
<i>Anoplodera reyi</i>	S	X		X	X	X	X	X	70
<i>Anoplodera virens</i>	S	X		X	X	X	X	X	618
<i>Judolia sexmaculata</i>	S	X		X	X	X	X	X	327
<i>Leptura quadrifasciata</i>	S	X		X	X	X	X		113
<i>Leptura melanura</i>	S	X		X	X	X	X	X	204
<i>Obrium cantharinum</i> VU	S						X		1
<i>Molorchus minor</i>	S	X		X	X		X		32
<i>Callidium coriaceum</i>	S						X	X	2
<i>Callidium violaceum</i>	S			X	X		X	X	8
<i>Xylotrechus rusticus</i> NT	S				X				1
* <i>Monochamus urussovii</i> VU	S	X							1
<i>Monochamus sutor</i>	S	X		X	X	X	X		94
<i>Monochamus galloprovincialis</i>	S					X			1
<i>Pogonocherus fasciculatus</i>	S	X	X	X	X	X	X	X	240
<i>Pogonocherus decoratus</i>	S				X				2
<i>Acanthocinus aedilis</i>	S	X		X	X	X		X	19
<i>Acanthocinus griseus</i>	S	X		X	X		X		7
<i>Saperda carcharias</i>	S				X				1
<i>Saperda scalaris</i>	S						X		1
<i>Saperda perforata</i> NT	S				X				1
CHRYSOMELIDAE									
<i>Donacia obscura</i>	H						X		1
<i>Plateumaris discolor</i>	H	X	X				X		9
<i>Plateumaris sericea</i>	H			X			X		2
<i>Lilioceris merdiger</i>	H			X		X			2
<i>Clytra quadripunctata</i>	N	X	X	X	X				13
<i>Cryptocephalus quadripustulatus</i>	H				X		X		3
<i>Cryptocephalus pini</i>	H	X			X	X	X		21
<i>Cryptocephalus punctiger</i>	H	X				X			2
<i>Cryptocephalus labiatus</i>	H	X							3
<i>Syneta betulae</i>	H	X		X	X	X		X	25
<i>Bromius obscurus</i>	H	X		X	X	X	X	X	465
<i>Chrysolina marginata</i>	H				X				1
<i>Plagioderia versicolora</i>	H			X					1
<i>Chrysomela populi</i>	H				X	X	X		3
<i>Chrysomela tremula</i>	H					X	X		2
<i>Gonioctena viminalis</i>	H	X							4
<i>Gonioctena decemnotata</i>	H						X		1
<i>Gonioctena quinquepunctata</i>	H				X				1
<i>Phratra vulgarissima</i>	H			X					1
<i>Phratra polaris</i>	H			X					32
<i>Phratra vitellinae</i>	H	X		X	X	X	X		9

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>Galerucella sagittariae</i>	H	X							1
<i>Galerucella griseescens</i> VU	H		X						1
<i>Galerucella lineola</i>	H	X				X	X		3
<i>Lochmaea caprea</i>	H	X			X	X	X	X	11
<i>Lochmaea suturalis</i>	H	X	X	X	X	X	X		9
<i>Galeruca pomonae</i>	H				X				1
<i>Agelastica alni</i>	H	X							1
<i>Phyllotreta quadrimaculata</i>	H			X					2
<i>Calomicrus pinicola</i>	H			X	X	X	X		17
<i>Luperus flavipes</i>	H				X				2
<i>Phyllotreta vittula</i>	H	X			X				3
<i>Phyllotreta undulata</i>	H			X	X		X		5
<i>Phyllotreta striolata</i>	H			X	X	X			3
<i>Longitarsus melanocephalus</i>	H						X		1
<i>Longitarsus suturellus</i>	H	X		X			X		3
<i>Longitarsus luridus</i>	H						X		1
<i>Altica chamaenerii</i>	H	X			X		X		4
<i>Altica longicollis</i>	H						X		1
<i>Lythriaria salicariae</i>	H			X	X	X	X		15
<i>Neocrepidodera motschulskii</i>	H						X		1
<i>Crepidodera fulvicornis</i>	H				X		X		2
<i>Chaetocnema concinna</i>	H				X				2
<i>Chaetocnema laevicollis</i>	H			X	X	X	X		4
<i>Chaetocnema aridula</i>	H				X				1
<i>Chaetocnema mannerheimii</i>	H			X					1
<i>Chaetocnema hortensis</i>	H				X	X			2
NEMONYCHIDAE									
<i>Cimberis attelaboides</i>	H	X	X	X	X	X	X	X	51
ANTHRIBIDAE									
<i>Tropideres dorsalis</i> VU	S	X			X				3
<i>Allandrus undulatus</i> VU	S			X	X		X		5
* <i>Platyrrhinus resinosus</i> VU	S				X		X		2
<i>Platystomos albinus</i>	S			X	X	X	X		14
<i>Anthribus scapularis</i>	N				X		X	X	10
<i>Anthribus nebulosus</i>	N				X		X		3
ATTELABIDAE									
<i>Temnocerus nanus</i>	H	X		X	X	X	X		14
<i>Temnocerus tomentosus</i>	H				X		X		6
<i>Byctiscus betulae</i>	H					X			2
<i>Byctiscus populi</i>	H	X			X		X		7
<i>Deporaus betulae</i>	H	X		X				X	8
APIONIDAE									
<i>Apion simile</i>	H	X	X		X	X	X		42
<i>Apion cerdo</i>	H				X	X			2
<i>Apion viciae</i>	H			X			X		2
CURCULIONIDAE									
<i>Otiorhynchus nodosus</i>	H	X	X	X	X	X	X	X	1971
<i>Otiorhynchus scaber</i>	H	X	X	X	X	X	X	X	1515
<i>Otiorhynchus ovatus</i>	H			X					1
<i>Phyllobius viridicollis</i>	H			X					1
<i>Phyllobius pyri</i>	H			X	X				3
<i>Phyllobius maculicornis</i>	H						X		1

Species	Group	700:(3)68	701:(3)68	702:(3)67	702:(3)68	702:(3)69	703:(3)67	703:(3)68	Total
<i>H. brunneus/cunicularius</i>	S	X	X	X	X	X	X	X	2309
<i>Hylastes opacus</i>	S	X		X	X	X	X	X	686
<i>Xylechinus pilosus</i>	S	X	X	X	X	X	X	X	213
<i>Tomicus minor</i>	S		X	X	X		X		19
<i>Tomicus piniperda</i>	S	X		X	X	X	X	X	141
<i>Dendroctonus micans</i>	S				X				1
<i>Phloeotribus spinulosus</i>	S	X	X	X	X	X	X	X	95
<i>Polygraphus subopacus</i>	S	X	X	X	X		X	X	146
<i>Polygraphus poligraphus</i>	S	X		X	X	X	X	X	2235
<i>Polygraphus punctifrons</i>	S	X		X	X	X	X		24
<i>Carphoborus rossicus</i>	S	X		X			X		3
<i>Scolytus ratzeburgi</i>	S	X		X	X	X	X		31
<i>Pityogenes chalcographus</i>	S	X	X	X	X	X	X	X	8068
<i>Pityogenes quadridens</i>	S	X		X	X	X	X	X	165
<i>Pityogenes bidentatus</i>	S	X		X	X	X	X	X	449
<i>Orthotomicus proximus</i>	S	X		X	X	X	X	X	36
<i>Orthotomicus suturalis</i>	S	X		X	X	X	X	X	1198
<i>Orthotomicus laricis</i>	S	X		X	X		X	X	74
<i>Ips acuminatus</i>	S				X				1
<i>Ips duplicatus</i>	S			X	X				3
<i>Ips typographus</i>	S	X		X	X	X	X	X	143
<i>Ips amitinus</i>	S	X		X	X	X	X	X	308
<i>Dryocoetes autographus</i>	S	X	X	X	X	X	X	X	3954
<i>Dryocoetes hectographus</i>	S	X	X	X	X	X	X	X	216
<i>D. autographus/hectographus</i>	S	X	X	X	X	X	X	X	1066
<i>Crypturgus subcribrosus</i>	S	X		X	X	X	X	X	334
<i>Crypturgus cinereus</i>	S	X		X	X		X		32
<i>Crypturgus pusillus</i>	S	X	X	X	X	X	X		31
<i>Crypturgus hispidulus</i>	S	X	X	X	X	X	X	X	104
<i>Trypodendron laeve</i>	S	X	X	X	X		X		37
<i>Trypodendron lineatum</i>	S	X	X	X	X	X	X	X	737
<i>Trypodendron signatum</i>	S	X	X	X	X	X	X	X	144
<i>Xyleborus dispar</i>	S	X			X		X		11
<i>Trypophloeus asperatus</i> EN	S				X		X		2
<i>Cryphalus saltuarius</i>	S	X			X	X	X		19
<i>Pityophthorus micrographus</i>	S	X		X	X	X	X	X	35
<i>Pityophthorus lichtensteinii</i>	S	X		X	X	X	X	X	183
<i>Pityophthorus tragardhi</i>	S	X			X				2
Number of species		792	326	704	939	656	797	419	1241
Number of study sites		6	1	2	8	2	4	1	24