

Short-term effects of variable retention on epigaeic spiders and carabid beetles in Finland

Katja Matveinen-Huju

**Department of Biological and Environmental Sciences
P.O.Box 65
00014 University of Helsinki
Finland
katja.matveinen@helsinki.fi**

Academic dissertation

To be presented, with the permission of the Faculty of Biosciences of the University of Helsinki, for public criticism in Auditorium 1041 of Biocenter 2, Viikinkaari 5, Viikki, Helsinki, on May 11th, 2007, at 12 a.m.

Contributions

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

	I	II	III	IV
Original idea & design	KM-H	MK, JN	JN	JN
Materials	KM-H	MK	KM-H	KM-H, AMR
Analyses	-	KM-H, MK	KM-H, BO	KM-H
Manuscript preparation	KM-H	KM-H, MK	KM-H, JN, HR, BO	KM-H, JN

MK: Matti Koivula, KM-H: Katja Matveinen-Huju, JN: Jari Niemelä, BO: Bob O'Hara, AMR: Anna Maria Rauha, HR: Hannu Rita. The main effort in manuscript preparation for Papers III and IV was by KM-H. Other contributions are acknowledged in the relevant parts of the thesis.

Supervised by Prof. Jari Niemelä
University of Helsinki
Finland

Reviewed by Prof. Mikko Mönkkönen
University of Jyväskylä
Finland

Prof. John Spence
University of Alberta
Canada

Examined by Prof. Jari Kouki
University of Joensuu
Finland

- © Katja Matveinen-Huju (Introductory part, Paper IV)
- © Katja Matveinen-Huju and Matti Koivula (Paper II)
- © Entomologica Fennica (Paper I)
- © Elsevier Science Ltd (Paper III)

Papers I and III are reprinted with the permission of the publishers of the original articles.

ISBN 978-952-92-1984-1 (paperback)
ISBN 978-952-10-3894-5 (PDF)

Yliopistopaino
Helsinki 2007

Abstract

Forestry has influenced forest dwelling organisms for centuries in Fennoscandia. For example, in Finland ca. 30% of the threatened species are threatened because of forestry. Nowadays forest management recommendations include practices aimed at maintaining biodiversity in harvesting, such as green-tree retention. However, the effects of these practices have been little studied.

In variable retention, different numbers of trees are retained, varying from green-tree retention (at least a few live standing trees in clear-cuts) to thinning (only individual trees removed). I examined the responses of ground-dwelling spiders and carabid beetles to green-tree retention (with small and large tree groups), gap felling and thinning aimed at an uneven age structure of trees. The impacts of these alternative harvesting methods were compared to those of clear-cutting and uncut controls. I aimed to test the hypothesis that retaining more trees positively affects populations of those species of spiders and carabids that were present before harvesting.

The data come from two studies. First, spiders were collected with pitfall traps in south-central Finland in 1995 (pre-treatment) and 1998 (after-treatment) in order to examine the effects of clear-cutting, green-tree retention (with 0.01-0.02-ha sized tree groups), gap felling (with three 0.16-ha sized openings in a 1-ha stand), thinning aiming at an uneven age structure of trees and uncut control. Second, spiders and carabids were caught with pitfall traps in eastern Finland in 1998-2001 (pre-treatment and three post-treatment years) in eleven 0.09-0.55-ha sized retention-tree groups and clear-cuts adjacent to them.

It seems that original spider and carabid assemblages are better maintained after harvests that retain more trees. The thinning treatment maintained forest spiders well. However, gap felling maintained some forest spider species in the short-term, but seemed to negatively affect some species over time. This pattern was also observed in harvests leaving large retention-tree groups. However, use of small retention-tree groups was associated with negative effects on forest spider populations.

More studies are needed on the long-term effects of variable retention on terrestrial invertebrates; especially those directed at defining appropriate retention patch size and on the importance of structural diversity provided by variable retention for invertebrate populations. However, the aims of variable retention should be specified first. For example, are retention-tree groups planned to constitute 'life-boats', stepping-stones or to create structural diversity? Does it suffice that some species are maintained, or do we want to preserve the most sensitive ones, and if so, how are these best defined? Moreover, the ecological benefits and economic costs of modified logging methods should be compared to other approaches aimed at maintaining biodiversity.

Keywords: Araneae, Carabidae, forest management, gap felling, green-tree retention, ground beetles, life-boat, retention-tree group, spiders, thinning

List of original papers

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Matveinen-Huju, K. 2004: Habitat affinities of 228 boreal Finnish spiders: a literature review. – *Entomologica Fennica* 15: 149-192.
- II Matveinen-Huju, K. & Koivula, M. 2006: Effects of alternative harvesting methods on boreal forest spider assemblages. – Manuscript.
- III Matveinen-Huju, K., Niemelä, J., Rita, H. & O'Hara, R. B. 2006: Retention-tree groups in clear-cuts: do they constitute 'life-boats' for spiders and carabids? – *Forest Ecology and Management* 230: 119-135.
- IV Matveinen-Huju, K., Niemelä, J. & Rauha, A. M. 2006: Spider and carabid assemblages in retention-felled stands – short-term effects in Eastern Finland. – Manuscript.

1. Introduction

1.1. Forest management and biodiversity

For centuries forestry has changed the boreal landscape in Fennoscandia, and thus influenced the forest dwelling organisms (e.g. Esseen *et al.* 1997, Östlund *et al.* 1997, Larsson & Danell 2001). In recent decades, clear-cutting has dominated forest management practices around the world (e.g. McComb *et al.* 1993, Linder & Östlund 1998, Aubury *et al.* 1999). However, growing concern about the effects of large-scale clear-cutting on biodiversity led to gradual changes in silvicultural practices starting in 1970s (McComb *et al.* 1993, Aubury *et al.* 1999, Larsson & Danell 2001). Maintaining biodiversity became an explicit goal for forest management, in addition to timber production in 1990s (Larsson & Danell 2001, Raivio *et al.* 2001), and legislation changed in many countries reflecting the changed attitudes (Lance & Phinney 2001, Raivio *et al.* 2001, Emmingham 2002). Nowadays forest management recommendations include: 1) protection of certain habitats, 2) green-tree retention, and 3) dead-wood retention (Raivio *et al.* 2001, Mielikäinen & Hynynen 2003). Although such practices are in wide use (e.g. Bradshaw *et al.* 1994, Hallman *et al.* 1996), knowledge about their effects on biodiversity is limited (Niemelä *et al.* 2001).

The impact of forest management on biodiversity arises through forest fragmentation, changes in forest structure and dynamics (e.g. decline in the number of large diameter trees, deciduous trees and coarse woody debris), as well as changes in the dynamics of forests (e.g. fewer forest fires, shorter rotation lengths) (e.g. Haila & Kouki 1994, Linder & Östlund 1998, Kouki *et al.* 2001). In Finland, for example, about one third of the 1505 threatened species live in forests, and forestry has been designated as the main cause of threat for 30 % of the forest dwelling species (Rassi *et al.* 2001). In Norway, nearly half of the threatened beetle species are associated with forests (Hanssen *et al.* 1998). As only a small fraction of forests can be reserved from management, measures for the maintenance of biodiversity are needed in the managed forests (e.g. Mönkkönen 1999, Niemelä 1997). For example, in Finland only about 5% of forests are protected (Virkkala *et al.* 2000). Moreover, old forests cannot be maintained in a landscape only by preserving the current old forests, but old forests of the future must develop from the present young forests (DeBell & Curtis 1993). Thus, the quality of managed forests is of importance when planning for the old forests of the future.

Variable retention includes a wide range of intensity of tree removal (Drever & Lertzman 2003). In variable retention different numbers or volumes of trees are removed, varying from green-tree retention (at least a few standing trees are left in clear-cuts) to thinning (only some trees or a pre-defined volume of trees are removed). In this thesis, I examine and compare the effects of green-tree retention (**Papers II-IV**), gap felling, thinning aimed at an uneven age structure of trees, traditional clear-cutting (**Paper II**) in order to understand how these methods affect spider and carabid populations characteristic of uncut forests. The main thesis of this dissertation is that alternative approaches to forest harvest that leave residual live trees can have beneficial effects on terrestrial invertebrates, here modelled as spiders and carabids. I consider and compare three alternative approaches to harvest: 1) green-tree retention, which is defined as a forestry practice in which live trees are retained in clear-cuts either singly or in groups, 2) gap felling, where clear-cut size is reduced, and 3) thinning, achieved through removal of single trees to meet particular silvicultural objectives for post-thinning stands, perhaps in addition to removing some useful harvested volume (commercial thinnings).

Natural disturbance dynamics has been suggested as a good starting point for developing ecologically sustainable forest management practices (e.g. Hansen *et al.* 1991,

Attiwill 1994, Mönkkönen 1999, Niemelä 1999), although some authors suggest this view to be problematic (Spence 2001). Clear-cutting, as conducted more than a decade ago, was suggested to resemble massive fires, as both were thought to kill or remove most or all live trees. This view provided justification for clear-cutting, but has more recently faced criticism (e.g. Östlund *et al.* 1997, Simberloff 2001) because of huge differences in early successional communities that follow disturbance. For example, the ground-dwelling spider and carabid assemblages differ significantly between wildfire and clear-cut origin stands, although this difference seems to disappear in about 30 years after logging (Buddle *et al.* 2000, 2006, Larrivé *et al.* 2005).

Green-tree retention better resembles natural disturbance dynamics in one respect: even the most extensive forest fires often leave patches or single trees totally or partially unburned (e.g. Östlund *et al.* 1997, Simberloff 2001). Natural disturbance dynamics of boreal spruce forests might be driven by small-scale disturbances, such as gap formation (Kuuluvainen *et al.* 1998). Gap felling and thinning might mimic natural gap formation driven by small-scale natural disturbances (e.g. Guldin 1996). However, natural gap formation involves creation of structural heterogeneity, such as pit-and-mound topography and fallen logs (Ulanova 2000). Therefore, apart from creating a light-gap in the tree canopy, gap felling and thinning differ from natural gap formation. Although the metaphor of comparison between natural disturbance and harvesting is often weak, the question remains whether changes to harvesting inspired by natural disturbance can improve forest management with respect to conservation of biodiversity.

1.2. Green-tree retention

Green-tree retention (i.e. leaving live standing trees in clear-cuts) could potentially maintain biodiversity in at least three ways: 1) ‘life-boating’, i.e. enhancing survival of the original species over the regeneration phase, 2) acting as stepping-stones, i.e. enhancing dispersal and the associated re-colonisation of disturbed sites and 3) increasing structural diversity of the regenerated stands making them suitable as habitat for a wider range of organisms (Franklin *et al.* 1997). Green-tree retention differs from shelterwood or seed-tree systems, because the residual trees are not harvested later on (Vanha-Majamaa & Jalonen 2001). The terminology related to green-tree retention is still developing, and use of various terms may be confusing. For example, some terms used to designate green-tree retention also refer to other forest harvesting methods: retention felling (used in Jalonen & Vanha-Majamaa 2001), partial cutting (used e.g. in Barg & Edmonds 1999) and variable retention (used e.g. in Franklin *et al.* 1997, Tittler & Hannon 2000). In addition, different terminology is used of the trees that are not harvested: retention, residual, remnant, or legacy trees. I use the term retention, when trees are retained intentionally in order to improve biodiversity. Remnant is used of trees that are older than the prevailing tree generation. Residual trees can be either retention-trees or remnant trees.

Retention-trees can be left dispersed over the cut-block or in tree groups. The spatial pattern depends on management objectives (Schieck *et al.* 2000). Aggregated retention may be a better option for organisms demanding undisturbed ground, all canopy layers including understory vegetation or forest microclimate (Aubury *et al.* 1999). However, if the objectives demand uniformly distributed conditions or structures, dispersed retention may be the choice (Aubury *et al.* 1999). In this thesis, I examine the ecological function of aggregated retention, i.e. retention-tree groups. Retention-tree groups are sometimes referred to as retention patches or residual patches, which may also include larger patches than retention-tree groups.

Structural diversity of habitat is generally considered important for spiders and carabids (e.g. Uetz 1991, Rypstra *et al.* 1999, du Bus de Warnaffe & Dufrêne 2004, Langolletto & Denno 2004, Latty *et al.* 2006, Niemelä *et al.* 2007), although Langolletto & Denno (2004) failed to show any generally significant response of carabids to increased habitat complexity in a meta-analysis of existing literature. Clear-cutting reduces structural complexity of stands (Hansen *et al.* 1991). Structural complexity can be associated with variation in tree diameter, multi-layered canopy, tree species composition (especially deciduous trees), dead wood, continuity, spatial arrangement of trees, as well as micro-site variability (e.g. Hansen *et al.* 1991, Brunet 1993, Östlund *et al.* 1997, Fridman & Walheim 2000, Zenner 2000 and references therein, Rouvinen *et al.* 2002). For example, several taxa are known to profit from large old trees (bryophytes: Gustafsson & Hallingbäck 1988; lichens: Neitlich & McCune 1997, Peck & McCune 1997, Sillett & Goslin 1999; spotted owls: Moen & Gutiérrez 1997, North *et al.* 1999, Thome *et al.* 1999; vertebrates: Mazurek & Zielinski 2004), and a continuum of coarse woody debris is important not only for saproxylic species (e.g. Kolström & Lumatjärvi 2000, Martikainen 2001, Siitonen *et al.* 2000, Ehnström 2001, Hunter & Bond 2001), but spiders and carabids may also benefit from dead wood (e.g. Lowrie 1948, Buddle 2001, Pearce *et al.* 2003, Niemelä *et al.* 2007, Varady-Szabo & Buddle 2006; but see Martikainen *et al.* (2006) who did not find correlation between dead wood and carabid abundance). Such structural features could thus be produced by retaining trees in clear-cuts. However, although new dead wood can be produced, the dead wood that existed before treatment may be destroyed by uprooting of live trees (Hautala *et al.* 2004). The relationship of retention-trees and structural diversity seems to be corroborated by Zenner (2000) and Hansen *et al.* (1995), although information is lacking whether structural diversity helps conserve biodiversity (Lindenmayer *et al.* 2000). The usefulness of retention-tree groups as stepping stones has not been studied at all, and evidence for retention-tree groups acting as 'life-boats' is limited. In this thesis, I examined the usefulness of retention-tree groups as 'life-boats' for spiders and carabids (**Papers II-IV**).

Although evidence for the ability of green-tree retention in preserving biodiversity is limited, green-tree retention is a forestry practice that is currently in use. Retention trees are suggested to be useful for some species of epiphytic bryophytes and lichens (Hazell & Gustafsson 1999, Sillett & Goslin 1999, Keon & Muir 2002, Löhmus *et al.* 2006), vascular plants (North *et al.* 1996, Vanha-Majamaa & Jalonen 2001), small bats (Hogberg *et al.* 2002), small mammals (Hunter & Bond 2001), birds (Merrill *et al.* 1998, Schieck *et al.* 2000, Hunter & Bond 2001, Lance & Phinney 2001, Tittler *et al.* 2001), canopy arthropods (Schowalter 1995), saproxylic beetles (Kolström & Lumatjärvi 2000, Martikainen 2001, Hyvärinen *et al.* 2005, 2006, Hyvärinen 2006), and microbes (Barg & Edmonds 1999). However, in some studies green-tree retention was not useful for particular species of bryophytes and vascular plants (Jalonen & Vanha-Majamaa 2001, Löhmus *et al.* 2006), carabid beetles (Koivula 2002a), and soil arthropods (Siira-Pietikäinen *et al.* 2003). Lemieux and Lindgren (2004) and Martikainen *et al.* (2006) found carabid assemblages in retention-tree groups to be intermediate as compared to clear-cuts or uncut forests. Gandhi *et al.* (2004) showed that retention-tree groups had similar carabid and staphylinid assemblages to uncut forest, but that the assemblages of retention-tree groups differed from those of fire residuals.

Recommendations about the amount of retention-trees vary between countries. In Finland, Finnish Forest Certification System (FFCS) is applied, and the criterion is to leave five to eight green trees per hectare (Metsätalouden kehittämiskeskus Tapio 2001, Raivio *et al.* 2001, <http://www.ffcs-finland.org/>), although the amount left can be more. According to a follow-up study of the realization of the criteria, the total amount of green trees left in cut-blocks was 11.5 per hectare, but the number of large trees was only 5.9 trees per hectare (Kotiharju & Niemelä 2000). In Sweden, the recommended retention left is ten trees per

hectare (Raivio *et al.* 2001). In Northern America, the recommendations about appropriate retention-level vary from 0 to 18% (e.g. Aubury *et al.* 1999, Halpern & McKenzie 2001, Hunter & Bond 2001, Lance & Phinney 2001). After wildfire, the percentage of fire area covered by live trees varies considerably: mean from different studies was between 2% and 32% (range 0-98%; Smyth *et al.* 2005 and references therein). Thus, it seems that the amount of green trees left by wildfire may be clearly more than the recommended amount in green-tree retention. For example, in mixedwood forests in Canada, Smyth *et al.* (2005) estimated that existing harvesting practices result in less than a third of the live residual trees remaining and less variability in residual patch size, as compared to the amount of residual trees and patch size after wildfires.

1.3. Gap felling and thinning

Gap formation is an important natural disturbance in spruce forests (Kuuluvainen *et al.* 1998). Gap size in spruce (*Picea abies* (L.) Karst.) forest is usually small. For example, according to Liu and Hytteborn (1991) individual gaps were typically smaller than 150 m² (9-360 m²) in a primeval spruce forest, although there may be larger gaps as well (one gap was 2900 m² in size). Huggard and Vyse (2002) found that the effects of thinning and different sized clear-cuts on biodiversity depended on taxon studied. For example, pine marten (*Martes americana*) avoided all harvesting treatments, including thinning (20% removal, uniform thinning), but some voles used residual strips (30-m wide) adjacent to small (0.1 ha) clear-cuts. Slugs declined less in the small clear-cuts and in the thinned stands compared to larger clear-cuts (1 or 10 ha with residual strips; Huggard & Vyse 2002). For most ecological variables they studied, 10- and 1-ha clear-cuts did not differ from each other, but they were different from 0.1-ha clear-cuts (with 30-m wide residual strips) and thinning.

The impact of gap felling on spider and carabid populations has received attention in a small number of studies. Ulyshen *et al.* (2006) studied responses of carabids in different sized (0.13, 0.26 and 0.50 ha) young (1 year) and old (7 years, vegetation height 1-8 m) gaps, and found an effect of gap age. Open-habitat species were most abundant in the centres of young gaps, whereas for forest species young gaps did not differ from control forests. However, forest species were least abundant in old gaps. Therefore, the reason that Koivula and Niemelä (2003) did not find a response of forest carabid species for gap felling may be gap the young age. Klimaszewski *et al.* (2005) concluded that gap felling was more favourable for the maintenance of the original carabid assemblage than traditional clear-cutting, although in general, gap felling (with 0.25, 0.13 or 0.06 ha-sized gaps) produced carabid assemblages and catches of different habitat affinity groups similar to larger clear-cuts. Osawa *et al.* (2005) found that gap felling negatively influenced large-bodied carabid species, but small-bodied species were not influenced.

Jennings *et al.* (1986, 1988) studied carabids and spiders in strip clear-cut stands. The width of the residual strips (23.4-49.7 m) roughly corresponds to the width of the forested sections of the gap-felled stands in **Paper II**. They found that residual strips resembled uncut forest in their numbers of carabid and spider species and individuals. Huggard and Vyse (2002) studied different sized clear-cuts with residual strips and thinning. They found that the carabid *Scaphinotus angusticollis* Mannerheim, 1824 declined in the clear-cut micro-sites and thinned stands, but persisted in all-sized residual strips, whereas active hunters, such as spiders, increased in all harvesting treatments.

As regards the effects of thinning (selective cutting) on spiders and carabids, some studies reported that thinning well maintains 'original' spider and carabid fauna (Huhta 1965, Koivula 2002b, Vance & Nol 2003, Moore *et al.* 2004, Huber *et al.* 2006), but this was not

the case for all studies (Willett 2001). In addition, there may be some differences in spider and carabid fauna between uncut and thinned forests (Werner & Raffa 2000, Schowalter *et al.* 2003). Vance and Nol (2003) reported short-term effects (0.5-3 years after thinning), such as loss of the largest carabid species and reduction in overall numbers of individuals, but in older thinned stands (15-20 years after thinning), carabid assemblages resembled those of uncut forests. The negative effects of thinning on spiders in Willett (2001) may have been due to decreased structural diversity of the thinned stands.

1.4. Aims

The aim of this thesis was to find out, whether retaining larger numbers of trees uncut would maintain the original assemblages of spiders and carabid beetles better than retaining smaller amount of trees. Thus, I studied logging methods in which different numbers of trees were retained. In clear-cutting no trees were retained (**Paper II**). Green-tree retention was applied with small (0.01-0.02 ha; **Paper II**) and large (0.09-0.55 ha; **Papers III and IV**) retention-tree groups. In gap felling three 0.16-ha openings were logged in a 1-ha stand (**Paper II**), in thinning only single trees were removed (**Paper II**), and finally, in control stands no trees were removed (**Papers II and IV**). The data come from two studies. First, three methods of variable retention were studied in the project called 'Biodiversity in the regeneration of managed forests' (MONTA) (**Paper II**). The modified logging methods were green-tree retention, gap felling, and thinning aiming at an uneven age structure of trees. These logging methods were compared to traditional clear-cutting and uncut forests. Second, in the project called 'Effect of the size of retention tree groups on biodiversity in forest regeneration' (RETREE) different sized retention-tree groups were compared to find out whether increasing tree-group size has a positive effect on forest species, and whether retention-tree groups would constitute 'life-boats' for spiders and carabids (**Papers III-IV**). The second study was launched because the retention-tree groups in the first study appeared to be too small (Jalonen & Vanha-Majamaa 2001, Siira-Pietikäinen *et al.* 2001, 2003, Koivula 2002a). **Paper I** provides a background for the *a priori* hypotheses in **Papers II and III** (see Section 3).

2. Study organisms

Spiders and carabids were selected as study objects for the following reasons. First, these taxa and their ecology are well known in Finland. There is also information available on the effects of forestry on spiders and carabids (e.g. Huhta *et al.* 1967, Huhta 1971, 1976, Coyle 1981, Jennings *et al.* 1986, 1988, Niemelä *et al.* 1988, 1993, McIver *et al.* 1992, Haila *et al.* 1994, Atlegrim & Sjöberg 1995, Spence *et al.* 1996, Buddle *et al.* 2000, 2006, Koivula 2002a, 2002b, Siira-Pietikäinen *et al.* 2003, Larrivé *et al.* 2005, Huber *et al.* 2006, Martikainen *et al.* 2006). In addition, spiders and carabids have been promoted as useful ecological indicators (e.g. Churchill 1997, Rainio & Niemelä 2003, Pearce & Venier 2006). Second, invertebrates should play an important role in biodiversity assessment (e.g. Taylor & Doran 2001). They are among the most diverse and abundant groups of organisms (e.g. Churchill 1997, Nilsson *et al.* 2001). Invertebrates also respond quickly to the effects of forestry (e.g. Niemelä 1999). Third, spiders and carabids show pronounced reactions to habitat structure and/or microclimate (e.g. Thiele 1977, Hänggi *et al.* 1995, Churchill 1997, Pearce & Venier 2006). Fourth, spiders and carabid beetles are easy to catch by using pitfall traps, which is an important aspect for an indicator species (e.g. Churchill 1997).

3. Habitat affinity classification and hypotheses

Many studies dealing with habitat patch size often report that total numbers of species or individuals decrease with increasing patch size (e.g. Helle & Muona 1985, Didham 1997, Magura *et al.* 2001, Molnár *et al.* 2001). This was usually caused by open-habitat species invading the smallest patches (e.g. Didham 1997, Molnár *et al.* 2001). However, considering forest species, the interpretation changed. For example, Usher *et al.* (1993) and Magura *et al.* (2001) found that the number of forest carabid species increased with fragment size, and Ozanne *et al.* (2000) found higher abundances of forest interior species of canopy-dwelling spiders in larger forests. Therefore, it is important to separate species based on their habitat affinities. However, such classification was not available for most spider (and some carabid) species. **Paper I** presents such a classification for some Finnish spider species.

The habitat affinity classification for spiders (**Paper I**) and carabids followed the classification formulated by Huhta (1971). Light intensity (canopy cover) and moisture (i.e. moisture conditions at the ground level, where the studied spiders and carabids live) were assumed to be the most important abiotic factors that affect the occurrence of spiders and carabids (Thiele 1977, Huhta 1971). First, I classified different habitats, where spiders and carabids were caught in literature, into the following habitat classes:

Light intensity:

- A = open habitats (e.g. clear-cuts, meadows, fields, open bogs)
- B = semi-open habitats (e.g. open forests, forest edges)
- C = shady forests (spruce forests)

Moisture:

- 1 = dry habitats (e.g. clear-cuts, forests with ground layer of lichens)
- 2 = medium-moist habitats (e.g. groves, forests with forest mosses, such as *Hylocomium Schimper in B. S. G.*)
- 3 = moist habitats (e.g. forests with *Sphagnum* L. mosses, bogs, marshes)

Second, spider and carabid species were assigned to the above classes based on literature on their occurrences in different habitats (carabids: Lindroth 1985, 1986, Niemelä 1988, Niemelä *et al.* 1989, Niemelä & Halme 1992, Halme & Niemelä 1993, Kinnunen 1999, Grandchamp *et al.* 2000, Koivula 2002a, 2002b; spiders: see references in **Paper I**).

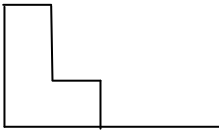
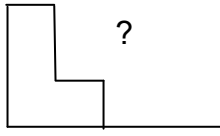
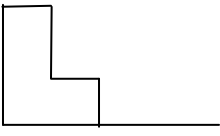
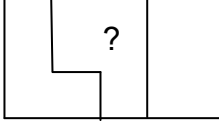
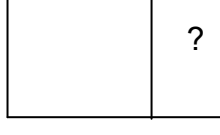

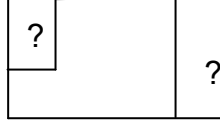
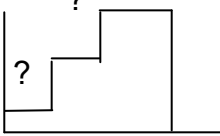
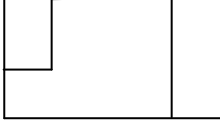
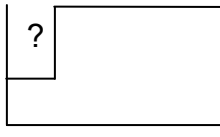
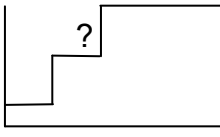
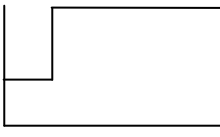
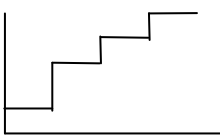
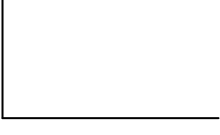
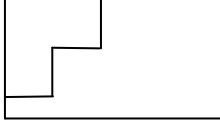
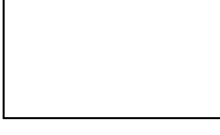
The above classes refer to species affinities towards the corresponding habitats. For example, A1 stands for species associated with open, dry habitat, such as clear-cuts or dry meadows, and C3 stands for species associated with shady, moist habitat, such as spruce mires. However, species may not follow strictly the above classification, and I use the following terms for species that are associated with more than one of the above habitat classes:

Light intensity:

- AB (or both A and B) = (semi-) open-habitat species
- BC = forest generalists
- ABC = species indifferent towards light intensity (or light-indifferent species)

Moisture:

- 12 (or both 1 and 2) = (medium-) dry-habitat species
- 23 (or both 2 and 3) = (medium-) moist-habitat species
- 123 = species indifferent towards moisture (or moisture-indifferent species)

a)	1	12	2, 23, or 3	123
A	 Re Ga Th Co	 Re Ga Th Co	Ambiguous hypotheses!	 Re Ga Th Co
AB	 Re Ga Th Co	 Re Ga Th Co	Ambiguous hypotheses!	 Re Ga Th Co
B	Ambiguous hypotheses!	 Re Ga Th Co	 Re Ga Th Co	 Re Ga Th Co
BC		 Re Ga Th Co	 Re Ga Th Co	 Re Ga Th Co
C			 Re Ga Th Co	
ABC		 Re Ga Th Co	 Re Ga Th Co	 Re Ga Th Co

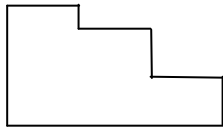
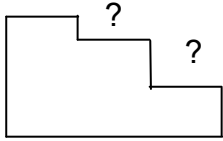
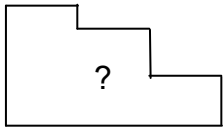
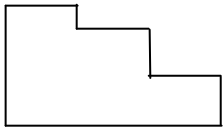
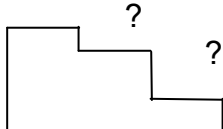
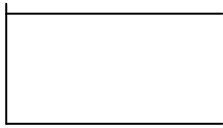
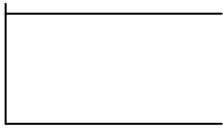
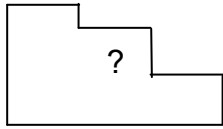





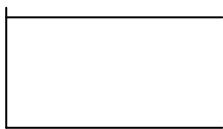

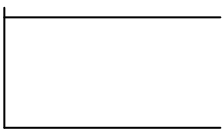
b)	1	12	2, 23, and 3	123
A	 Cl Re Ga	 Cl Re Ga	 Cl Re Ga	 Cl Re Ga
AB	 Cl Re Ga	 Cl Re Ga	Ambiguous hypotheses!	 Cl Re Ga
B	 Cl Re Ga	Ambiguous hypotheses!	 Cl Re Ga	 Cl Re Ga
BC		Ambiguous hypotheses!	 Cl Re Ga	 Cl Re Ga
C			 Cl Re Ga	
ABC		 Cl Re Ga	 Cl Re Ga	 Cl Re Ga

Figure 1. Hypotheses for **Paper II**. Habitat affinities: 'A' = open, 'B' = semi-open, 'C' = shady, '1' = dry, '2' = medium-moist and '3' = moist (see details in Section 3). Whenever two different hypotheses come from affinities for moisture and light intensity, hypotheses are ambiguous. Empty cells: habitat affinity combination does not exist. Treatments: 'Cl' = clear-cutting, 'Re' = retention felling, 'Ga' = gap felling, 'Th' = thinning and 'Co' = uncut control. a) Forested micro-sites of the treatments. b) Clear-cut micro-sites of the treatments.

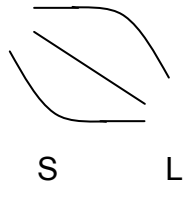
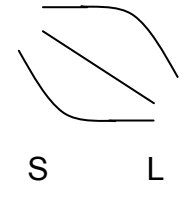
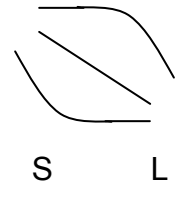
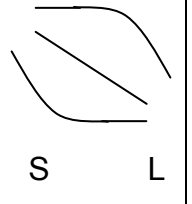
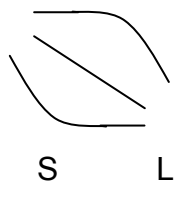
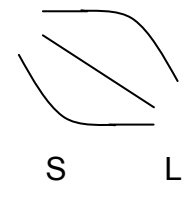
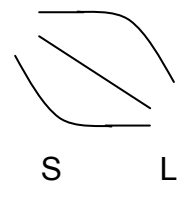
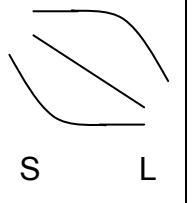
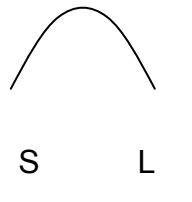
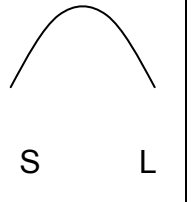
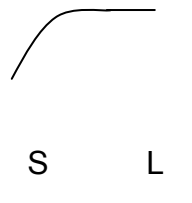
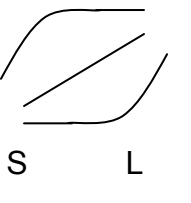
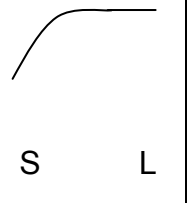
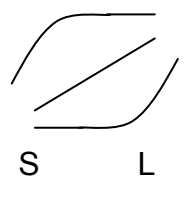
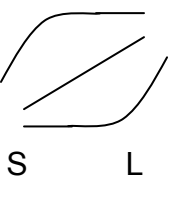
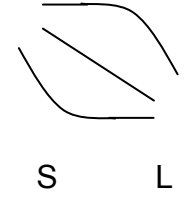
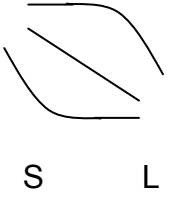
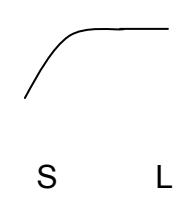
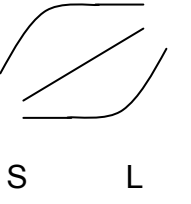
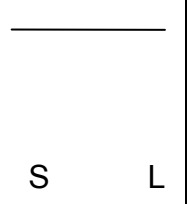
	1	12	2	23	3	123
A				Ambiguous hypotheses!	Ambiguous hypotheses!	
AB				Ambiguous hypotheses!	Ambiguous hypotheses!	
B	Ambiguous hypotheses!	Ambiguous hypotheses!	Ambiguous hypotheses!		Ambiguous hypotheses!	
BC		Ambiguous hypotheses!	Ambiguous hypotheses!			
C			Ambiguous hypotheses!			
ABC						

Figure 2. Hypotheses for **Paper III**. Habitat affinities: ‘A’ = open, ‘B’ = semi-open, ‘C’ = shady, ‘1’ = dry, ‘2’ = medium-moist and ‘3’ = moist (see details in Section 3). ‘S’ = small and ‘L’ = large represent hypothetical retention-tree group sizes. Linear relationships are hypothesised *a priori* and curvilinear shapes are exploratory (represented by the quadratic term in the GLMM models, see Section 4.3.1.). Whenever two different hypotheses come from affinities for moisture and light intensity, hypotheses are ambiguous. Empty cells: habitat affinity combination does not exist.

Note that (semi-) open (B) is used both in (semi-) open-habitat species and forest generalists, and medium-moist (2) is included in both (medium-) dry and (medium-) moist-habitat species.

I used the light intensity and moisture as a basis of my hypotheses (**Papers II-III**). Harvesting affects light intensity and moisture (Keenan & Kimmins 1993). I assumed that the smaller the forest patch, the edge effects become more intense (e.g. Matlack 1993). Thus, clear-cutting affects the adjacent forest patch in such a way that the edges of the forest patch become lighter and drier (e.g. Pearce *et al.* 2005).

The central question in **Paper II** was ‘are the original species maintained better with larger amounts of retention?’ In **Paper III** the central question was ‘do larger retention-tree groups maintain the original species better than the smaller ones?’. The aim of **Paper IV** was to study whether or not retention-tree groups enhance the survival of forest species in clear-cut dominated stands by examining changes in spider and carabid assemblages with respect to distance from the edge of a retention-tree group (i.e. from clear-cut into retention-tree group). I performed species-wise analyses for the *a priori* hypotheses, because erroneous habitat affinity classification could result in wrong interpretations (see discussion for errors in habitat affinity classification from **Papers I and III**). For example, if a species’ habitat affinity was suggested to be for forests, but actually was for open habitats, inclusion of such a species in the forest species group could have masked the possible response. Such a species could have been the spider *Alopecosa taeniata* (C. L. Koch, 1835) (see Results and Discussion in **Paper IV**). Thus, all analyses that were performed with species groups should be treated with caution (see Materials and methods in **Paper IV**). The more specific *a priori* hypotheses for species with different habitat affinities can be seen from Figures 1 and 2. More details are found in **Papers II and III**.

4. Materials and methods

4.1. Study areas and design

4.1.1. Alternative logging methods (Paper II)

Spiders were collected in south-central Finland in 1995 (pre-treatment) and in 1998 (the third summer after logging) (Figure 1 in **Paper II**). The study forests were Norway spruce (*P. abies*) dominated, *Myrtillus*-type (Cajander 1949), and 80-120 years of age. Each study stand consisted of a 1 ha core and its immediate surroundings, altogether ca. 2 ha. Each of the five studied treatments (control, thinning, gap felling, retention felling and clear-cutting) was replicated once in each of the four study areas (except that one gap felling was missing from the Keuruu study area). More details can be found in **Paper II**, and in Koivula (2002a, 2002b) and Koivula and Niemelä (2003).

The logging treatments formed a continuum from clear-cuts (all live trees were cut) to control (no trees removed) (Figure 1 in **Paper II**). In the retention-felled stands, 90.7-94.2% of trees were removed. Within each one-hectare core, 3-4 tree groups (0.01-0.02 ha each) were retained. In the gap-felled stands, 61.1-65.7% of the trees were removed. Within each one-hectare core, three 40 m x 40 m or 32 m x 50 m (i.e. 0.16 ha) clear-cut openings were logged. Thinning aimed at an uneven age structure of trees, and 10.9-33.7% of the trees were removed from each thinned stand.

Spiders were collected using pitfall traps. In each stand, the traps were placed into six groups, each group having four pitfall traps in a 4 m x 4 m square (4 areas x 5 treatments [~stands] x 24 traps – one stand = 456 traps) (Figure 1 in **Paper II**). In the retention-felled and gap-felled stands, three trap groups were situated in the forested sections (hereafter called forested micro-sites) and three trap groups were placed in the clear-cut sections (hereafter called clear-cut micro-sites). In 1995, the trapping was performed from 18 May to 27 June, and in 1998, the trapping period lasted from 14 May to 6 July.

4.1.2. Retention-tree groups (**Papers III and IV**)

Eleven retention-tree groups were established in three clear-cuts in Eastern Finland (Figure 1 in **Paper IV**). Hereafter, I call the clear-cuts with the retention-tree groups as retention-felled areas. In addition, one control site was established in uncut forest. Before logging the forest was of *Myrtillus*-type (Cajander 1949), dominated by Norway spruce (*P. abies*), and trees were 80-100 years of age. The retention-tree groups were established in small spruce mire patches within the forest. Size (0.09-0.55 ha) of the retention-tree groups varied according to the properties of the spruce mire patches (see Table 1 in **Paper III**). The size of the clear-cuts surrounding the retention-tree groups varied between ca. 8 and 14 ha (Table 1 in **Paper III**). The retention-level was 12.5% of the managed landscape (Hautala *et al.* 2004). More details are found in **Papers III and IV**.

Spiders and carabids were sampled with pitfall traps. Eight pitfalls were placed within the retention-tree groups, eight traps at the edges of the retention-tree groups and clear-cuts, and eight traps in the clear-cuts (Figure 1 in **Paper IV**), except for one retention-tree group where only seven traps were placed within. Hereafter, the within/edge/outside is referred to as location. In **Paper III** we used the data from within of retention-tree groups, i.e. the edges of the retention-tree groups, clear-cuts and control site were not included. In **Paper IV** we used all data.

Pre-treatment sampling was performed in the summer of 1998 (20 May- 3 September) and after-treatment sampling was performed during the summers of 1999 to 2001 (26 May-16 September 1999, 24 May-5 September 2000, and 23 May-4 September 2001). Hereafter, I call the years after logging the first year (1999), the second year (2000) and the third year (2001).

4.2. Nomenclature

The nomenclature of carabids follows Lindroth (1985, 1986) in **Paper III** and Silverberg (2004) in **Paper IV**. The differences in the nomenclature were as follows: *Pterostichus cupreus* (Linnaeus, 1758) equals *Poecilus cupreus* (Linnaeus, 1758), *Pterostichus versicolor* (Sturm, 1824) equals *Poecilus versicolor* (Sturm, 1824), *Pterostichus vernalis* (Panzer, 1796) equals *P. crenatus* (Duftschmid, 1812), *Agonum mannerheimii* (Dejean, 1828) equals *Platynus mannerheimii* (Dejean, 1828), and *Harpalus quadripunctatus* Dejean, 1829 equals *H. lavipes* Zetterstedt, 1828.

The nomenclature of spiders follows Platnick (2003) in **Papers I and III** and Platnick (2006) in **Papers II and IV**. The difference in nomenclature was as follows: *Lepthyphantes antroniensis* Schenkel, 1933 equals *Palliduphantes antroniensis* (Schenkel, 1933). The nomenclature was not rechecked for those spider species mentioned in **Paper I** that were not caught in papers **II-IV**.

Voucher specimens are deposited in the Finnish Museum of Natural History, Helsinki, Finland.

4.3. Statistical methods

4.3.1. Generalized linear mixed effects models (GLMM)

In **Papers II and III**, generalized linear mixed effects models (GLMM; McCullagh & Nelder 1989) were used to analyse the *a priori* hypotheses (see Section 3; in addition, some of the species-wise exploratory analyses were performed similarly in **Paper III**). The analyses were performed in the R software package (R Development Core Team 2004). Numbers of individuals in different spider and carabid species were used as response variables in the GLMMs. See details of the selection of analysed species and possible exclusions in **Papers II and III**. In addition, in **Paper II** we performed GLMMs for numbers of species in different habitat affinity groups.

For spiders, sex was included in the analyses because it was hypothesised that males and females might respond differently to harvesting (see details in **Paper III**). This hypothesis was an exploratory one. In **Paper II**, sex was initially included in the models, but the two sexes were ultimately combined, as there was no difference in their response. We omitted sex to shorten the text and to make the main message clearer.

The negative binomial distribution (White & Bennetts 1996) was applied as the error distribution for numbers of individuals (see **Papers II and III**) and Poisson distribution for numbers of species (see **Paper II**). Although the discovery that spiders and carabids are aggregated at the scale of sampling is not novel (e.g. Huhta 1971, Curry *et al.* 1985, Niemelä 1990, Niemelä *et al.* 1992), the negative binomial distribution has only rarely been used as the error distribution when studying spiders and carabids (e.g. Lehvävirta *et al.* 2006, Taboada *et al.* 2006). I agree with Lehvävirta *et al.* (2006), who recommend using negative binomial models when organisms are assumed to be aggregated.

Because trap losses were negligible in both studies, correcting for trap losses with a standardisation procedure was not used.

Because many species were tested simultaneously, the false discovery rate (FDR) was measured in **Paper III** (for **Paper II** the q-values were smaller than the p-values, and therefore were not used). The test gives q-values that measure the proportion of false positives. Both p-values and q-values were reported.

In addition to the above *a priori* analyses, we performed some exploratory GLMMs in **Paper IV**. As responses we had numbers individuals in different habitat affinity groups, in addition to total catch and some examples of individual species. Because we had lost some traps, we standardised catches by adding the log-transformed number of trapping days as an offset and sampling period as a ‘normal’ factor in the models (see details in **Paper IV**).

4.3.1.1. Alternative logging methods (Paper II)

The following explanatory variables were used in the GLMM models for the forested (Type I models) and the clear-cut micro-sites (Type II models) of the treatments.

1. Treatment: four treatments for the forested micro-sites (control, thinning, gap felling, retention felling), and three treatments for the clear-cut micro-sites (clear-cutting, retention felling, gap felling).
2. Pre-treatment year 1995 as a covariate
3. Stand (to account for the correlated error structure)

The following explanatory variables were used in the GLMM models to compare the forested and the clear-cut micro-sites of the gap-felled and retention-felled stands (Type III models).

1. Treatment: two treatments (gap felling, retention felling)

2. Micro-site: two micro-sites (clear-cut, forested)
3. Interaction of treatment and micro-site
4. Pre-treatment year 1995 as a covariate
5. Stand (to account for the correlated error structure, as a random factor)

4.3.1.2. Retention-tree groups (Paper III)

The GLMM models were performed with the following explanatory variables.

1. Retention-tree group size (ha), i.e. size - mean of all sizes
2. Quadratic term for tree group size, i.e. (size - mean of all sizes)²
3. Year: three years (after-treatment years 1999-2001)
4. Sex (male, female) for spiders
5. Interactions between the above variables
6. Site (to account for the correlated error structure, as a random factor)
7. Pre-treatment year (1998; as a covariate with no interactions)
8. Number of wood ants (in the middle season of the year sampled; as a covariate with no interactions)

4.3.1.3. Retention-felled areas (Paper IV)

The GLMM models were performed with the following explanatory variables.

1. Location, i.e. within/edge/outside of a retention-tree group
2. Year (1998-2001)
3. Interaction of location and year
4. Log(trapdays) as an offset
5. Period (for standardisation purpose)
6. Site (to account for the correlated error structure, as a random factor)

4.3.2. Multivariate methods

4.3.2.1. Non-metric Multidimensional Scaling (NMDS)

Non-metric Multidimensional Scaling (NMDS) was used to explore the changes in species composition (and to check the habitat affinity classification), because it is a robust technique for indirect gradient analysis (Minchin 1987). In **Paper III**, the rankindex (Faith *et al.* 1987) was selected according to the instructions for the package ‘vegan’ of R (R Development Core Team 2004): the Gower metric for carabids, the Kulczynski index with Wisconsin double standardisation for spider males, and the Kulczynski index with square-root transformation for spider females. In **Paper II**, the NMDS was performed using Bray-Curtis distances (e.g. Krebs 1999) as the rankindex. The analyses were repeated until there were two similar solutions with the stress value as low as possible. The analyses were done in the R software package (R Development Core Team 2004) and PC-Ord (McCune & Mefford 1999). For spiders, males and females were kept separate in **Paper III**, but in **Paper II** sexes were pooled.

In **Paper II**, the significance of possible pair-wise differences between scores of different habitat types was tested by using multi-response permutation procedures (MRPP) for the Bray-Curtis distance matrix (Zimmerman *et al.* 1985) available in PC-Ord 4.0 (McCune & Mefford 1999).

4.3.2.2. Canonical Correspondence Analysis (CCA)

In **Paper IV**, Canonical Correspondence Analysis (CCA; Jongman *et al.* 1995) was used to explore the effects of some environmental variables on the spider and carabid assemblages in the three sampling locations (within tree groups, edge, clear-cut). For adult spiders, the ordinations were done separately for males and females. Permutation tests were performed for the environmental variables included in the CCAs (for each environmental variable separately, and for the whole set of environmental variables). The analyses were performed in the R software package (R Development Core Team 2004) with the following environmental variables:

1. Distance of the trap row from the edge of a retention-tree group (m)
2. Retention-tree group size, or forest size for the pre-treatment year and control (ha)
3. Number of standing trees per ha (zero for the clear-cuts)
4. Size of the clear-cut (ha)
5. Isolation of the retention-tree group (i.e. distance to the nearest continuous forest or forest fragment; m)
6. Number of wood ants (in the middle period of each season)

4.3.2.3. Multivariate Regression Trees (MRT) and Indicator Value calculations (IndVal)

In **Paper II**, Multivariate Regression Trees (MRT; De'ath 2002), combined with Indicator Value calculations (IndVal; Dufrêne & Legendre 1997) were performed. The MRT was done to study the significance of the GLMM variables (year, study area, treatment, micro-site) and some micro-site characteristics (number of spruce, pine and birch trees, % covers of bushes, shrubs and grasses, *Sphagnum* and 'forest' mosses, vascular plants associated with mesic micro-habitats, needle, leaf and mixed litter, drifted humus, bare soil, rocks and downed woody material) in determining spider assemblages.

4.3.3. Analysis of Similarities (ANOSIM)

Analysis of Similarities (ANOSIM; Chapman & Underwood 1999) was used in order to examine temporal changes in spider and carabid assemblages in the retention-felled areas (**Paper IV**). ANOSIM gives a value of R that lies between -1 and +1. No difference between assemblages is represented by zero.

5. Summary of the main results

In the alternative logging methods study, 8634 adult spiders representing 89 species or species groups were caught (Appendix 1 in **Paper II**). In the retention-tree group study, I caught a total of 24817 individuals of adult spiders representing 184 species in the retention-felled areas (Appendix 3 in **Paper IV**), and 1268 individuals representing 45 species in the control area (Appendix 4 in **Paper IV**). Of these, 5718 individuals representing 126 species were caught within the retention-tree groups (Appendix 1 in **Paper III**). In addition, I caught a total of 9968 carabid individuals representing 43 species in the retention-felled areas (Appendix 5 in **Paper IV**), and 725 individuals representing 13 species in the control area (Appendix 6 in **Paper IV**). Of these, 2319 individuals representing 25 species were caught within the retention-tree groups (Appendix 2 in **Paper III**). The main findings are summarised below.

Paper I: Habitat affinity classification of spiders

In **Paper I** I present the habitat affinity classification for spiders that was essential for the analyses of the *a priori* hypotheses in **Papers II and III**, the more exploratory analyses in **Paper IV**, and for the interpretation of the ordinations and multivariate regression trees in **Papers II-IV**.

Paper II: Alternative logging methods

1. As hypothesised, forest spiders responded negatively to logging. Thinning (aiming at an uneven age structure of trees) appeared to maintain forest spiders well. Following logging, forest species were virtually absent from the retention-tree groups and the clear-cut micro-sites. The responses of forest species to gap felling were not consistent. Two forest species were almost completely absent even from the forested micro-sites of the gap-felled stands; whereas two other forest species had similar catches in the forested micro-sites of the gap-felled stands compared to the control and thinned stands.

2. Surprisingly, most (semi-) open-habitat species (AB) responded to logging in a similar way as open-habitat species (A), although they were expected to be found also in semi-open habitats, such as forest edges (see **Paper I**). Most (semi-) open-habitat species (A and AB) were caught only after logging. For these species, clear-cutting did not differ from retention felling, but the gap-felled stands had fewer species and individuals. Many (semi-) open-habitat species were also caught within the retention-tree groups, but not as abundantly as in the large clear-cuts (with the exception of *P. lugubris*).

3. Species indifferent towards light intensity responded to logging in an inconsistent way. However, as hypothesised, the responses of the (medium-) moist-habitat species richness and the (medium-) moist-habitat species *Tenuiphantes alacris* (Blackwall, 1853) were similar to the forest species.

4. In the NMDS, the forested micro-sites grouped separately from the clear-cut micro-sites. The small retention-tree groups grouped with clear-cuts, whereas the forested micro-sites of the gap-felled stands grouped with the other forested micro-sites. Regarding species scores, forest species grouped together, and (semi-) open-habitat species grouped together. Similarly, species of different feeding guilds (hunters and web-builders, see Uetz 1977) formed distinctive clusters.

5. In the MRT, the clear-cut micro-sites differed from the forested ones and the retention-tree groups differed from the other forested micro-sites. The clear-cut micro-sites and retention-tree groups shared most of the indicator species, whereas the other forested micro-sites had different indicator species.

Paper III: Size of the retention-tree groups

1. There was no unambiguous support for the hypotheses that 1) species requiring forest and/or (medium-) moist habitat would be more abundant in larger retention-tree groups, 2) species requiring (semi-) open habitat would be more abundant in smaller retention-tree groups, and 3) species indifferent towards light intensity (excluding the (medium-) moist-habitat species) would be caught in equal numbers in all retention-tree groups irrespective of their size. Most species responded as expected only in some years or (for spiders) only one of the sexes responded. Furthermore, most responses were not statistically significant. Moreover, some species responded contrary to what was expected.

2. Within the retention-tree groups, numbers of individuals of many species requiring forest or (medium-) moist habitat decreased with time, and increased with time for many species requiring (semi-) open habitat.

3. In the NMDS graphs for spiders, the retention-tree groups moved with time. Forest species grouped separately from (semi-) open-habitat species. For carabids, there was no clear pattern in the NMDS graphs.

Paper IV: Retention-felled areas

1. Retention felling maintained some of the forest and/or (medium-) moist-habitat species in the short-term, but others seemed to disappear from the retention-tree groups.

2. Many forest species decreased with time in the retention-felled areas (i.e. retention-tree groups studied also in **Paper III** and adjacent clear-cuts), whereas (semi-) open-habitat species increased with time. The dominant spiders before logging were linyphiids (and other web-builders), but lycosids (and other hunters) became abundant after logging. The number of species of both spiders and carabids increased already in the first summer after logging.

3. The most abundant species of spiders changed over time, whereas the most abundant species of carabids remained the same. The change in the most abundant spiders took place also within the retention-tree groups, but it was greater in the clear-cuts. The ANOSIM revealed that the assemblages of spiders and carabids differed among the study years.

4. In the CCA, species assemblages in retention-tree groups separated from those in clear-cuts, and pre-treatment sites separated from after-treatment sites. In addition, forest and (semi-) open-habitat species formed distinctive scatters. Environmental variables connected with forest cover (i.e. retention-tree group size, number of standing trees, distance from the edge of a tree group) increased in different direction than environmental variables connected with clear-cuts (i.e. clear-cut size, isolation).

5. Although (semi-) open habitat spiders were collected fairly abundantly within the retention-tree groups after logging, they were more abundant in the clear-cuts.

6. Discussion

6.1. Forest species are maintained better when more trees are retained

The aim of this thesis was to examine if leaving trees in harvesting positively affects assemblages and individual species of forest spiders and carabid beetles. The more trees were retained, the better the original species were maintained in the study that compared alternative logging methods (**Paper II**). However, I discovered an increase or decrease in abundance with increasing size of retention-tree groups only for a few spider species, and not for any carabid species (size 0.09-0.55 ha; **Paper III**). Similarly, Gandhi *et al.* (2004) did not find relationships between retention-tree group size (<1 to 2 ha) and catches of the most abundant carabid species. In contrast, Gandhi *et al.* (2001) found an effect of patch size (0.012-10.8 ha) on a forest carabid species *Nebria crassicornis* Van Dyke in fire residuals. In larger forest fragments (43-2350 ha), Burke and Goulet (1998) discovered that species richness and abundance of forest carabids increased with increasing forest fragment size. Therefore, it may be that the size range was too small in **Paper III**. An important subject for future research, therefore, is determining a critical threshold for the amount or size of retention.

Thinning aiming at an uneven age structure of trees seemed to maintain the forest spider assemblage well (**Paper II**). This result is consistent with several studies, where thinning maintained forest spider and carabid assemblages well (Huhta 1965, Koivula 2002b, Vance & Nol 2003, Moore *et al.* 2004, Huber *et al.* 2006). However, this was not always the case (Willett 2001). In addition, in some studies there were differences between uncut and thinned forests (Werner & Raffa 2000, Schowalter *et al.* 2003). Furthermore, Vance and Nol (2003) found short-term effects, but 15-20 years after thinning, carabid assemblages resembled those of uncut forest. Moreover, it should be studied if thinning maintains forest fauna after the second regeneration (Vance & Nol 2003). Willett (2001) found that the more logging events there were the more the abundance and diversity of spiders were affected. Maintaining structural diversity with thinning may be crucial in maintaining the original spider (and carabid) assemblages (see Willett 2001).

Gap felling seems to better maintain forest spider assemblage than larger clear-cuts in the short-term, although some species may be lost (**Paper II**). As regards (semi-) open habitat spiders, gap felling (three 0.16 ha gaps) produced fewer individuals than larger (1 ha) clear-cuts. In the same study sites, Koivula and Niemelä (2003) found that catches of forest carabid species did not differ between gap-felled and control stands, and open-habitat species invaded the clear-cut micro-sites. Similarly, Jennings *et al.* (1986, 1988) found that 23.4-49.7 m wide (roughly the same width as the uncut sections of the gap-felled stands in **Paper II**) forested strips between clear-cuts resembled uncut forest in their numbers of spider and carabid species and individuals. However, Siira-Pietikäinen *et al.* (2003), also in the same sites as in **Paper II**, showed a negative effect of gap felling on the total numbers of predatory soil-dwelling arthropods, especially spiders. Also Osawa *et al.* (2005) found a negative effect of gap felling: large-bodied carabids decreased. On the other hand, Ulyshen *et al.* (2006) found differences in species composition between gaps (0.13, 0.26 and 0.50 ha in size) and uncut forests, but the abundance and richness of carabids in old gaps was similar to that of the surrounding forest. Therefore, gap age may be important; long-term studies should be conducted in order to determine if it is so.

Both the 0.16-ha and 1-ha sized clear-cut micro sites seemed to be as poor for forest spiders (Appendix 1 in **Paper II**: mean number of individuals less than one). (Semi-) open habitat spiders, on the other hand, responded to gap size, being more abundant in the larger clear-cuts. As regards open-habitat species, Oxbrough *et al.* (2006) concluded that open spaces should be at least 15 m wide (1-1.5 times tree height) to support open habitat spiders. They did not report if gaps narrower than 15 m supported forest species. However, Ulyshen *et al.* (2006) found that for carabids, gap edges were very similar in their assemblages to those of the surrounding forests. Therefore, if the aim is to conserve forest species, gaps smaller than 1-1.5 tree height may be suitable for them. The clear-cut micro-sites in **Paper II** were wider than this (40 m x 40 m or 32 m x 50 m). Shure and Phillips (1991) found fewer spiders in medium-sized (0.08-0.4 ha) than in smaller or larger clear-cuts (0.016 and 2-10 ha, respectively). Although they did not report the habitat affinities, it may be that forest species survived in the smallest clear-cuts, and (semi-) open-habitat species had an affinity for the largest clear-cuts, but intermediate-sized clear-cuts were not that suitable for either of these habitat affinity groups. Klimaszewski *et al.* (2005) found that small gaps (0.06 and 0.13 ha in size) differed from large gaps (0.25 ha) in their carabid assemblage composition, but all-sized gaps differed from controls. In conclusion, determining if small gaps maintain forest species of spiders and carabids is a question for future research.

Small retention-tree groups (0.01-0.02 ha) did not well maintain forest spiders, although they differed to some extent from the clear-cut sections (**Paper II**). Large retention-tree groups (0.09-0.55 ha) maintained some forest spider and carabid species in the short term, but seemed to lose some (**Papers III and IV**). As in **Paper II**, retention-tree groups

also differed to some extent from the clear-cut sections in **Paper IV**. Koivula (2002a) showed that the small retention-tree groups (0.01-0.02 ha; the same study sites as in **Paper II**) did not well maintain carabid species present before harvesting. When comparing **Paper II** and Koivula (2002a) with **Papers III and IV**, it seems that the larger retention-tree groups better maintained the forest spiders and carabids than the smaller ones, although some species were probably lost. In addition, the spider and carabid assemblages in the larger retention-tree groups differed from clear-cuts (**Paper IV**: CCA), but the smaller ones were similar to clear-cuts (**Paper II**: NMDS and MRT). In contrast, Martikainen *et al.* (2006) found the carabid assemblages of retention-tree groups (three or five small tree groups with retention level of 10 m³/ha or 50 m³/ha, respectively) to be intermediate as compared to clear-cuts and uncut forests. In Lemieux and Lindgren (2004) retention-tree groups (typically 0.1-2 ha in size) were similar to uncut forests and forest edges in one year, but intermediate to clear-cuts and uncut forest in the other year. Similarly, Gandhi *et al.* (2004) showed that the carabid and staphylinid beetle assemblages of retention-tree groups (<1 to 2 ha in size) resembled those of uncut forest, but the assemblages of retention-tree groups differed from those of fire residuals.

6.2. Are forest species maintained in retention patches before forest grows back?

I examined the occurrences of (semi-) open-habitat species in order to determine if forest species are maintained in retention patches before forest grows back. I hypothesised that the occurrence of (semi-) open-habitat species in the forested micro-sites (e.g. retention-tree groups) indicates a change in the forest condition, and thus the harvested stands may not maintain forest species in the long term. Indeed, there was an increasing share of (semi-) open habitat spiders within the retention-tree groups over time (**Papers II-IV**), which may indicate that the retention-tree groups are not able to function as 'life-boats'. Also North *et al.* (1996; plants), Merrill *et al.* (1998; birds), Koivula (2002a; carabids), Gandhi *et al.* (2004; carabids and staphylinids) and Pearce *et al.* (2005; spiders, also some carabids) reported open-habitat species in retention-tree groups or small forest patches within clear-cuts. However, I did not catch many (semi-) open habitat carabids within the 0.09-0.55 ha sized retention-tree groups (**Papers III-IV**). In addition, I found that although (semi-) open habitat spiders invaded the retention-tree groups, their numbers were even higher in clear-cuts (**Papers II and IV**), possibly indicating that retention-tree groups may have a contribution in preserving forest species over the regeneration phase. Furthermore, in **Paper II** most (semi-) open habitat spiders did not invade the forested micro-sites of the gap-felled or thinned stands, indicating that if the retention level is high enough, at least some forest species may be preserved by variable retention. This viewpoint gets support from studies done in forest- clear-cut edges: open habitat spiders and carabids generally do not invade forest or move only a few meters into the forest (Heliölä *et al.* 2001, Oxbrough *et al.* 2006).

On the other hand, there were indications that some species might be lost already in the short-term. For example, the spruce mire carabid *Platynus mannerheimii* (Dejean, 1828) seemed to disappear from the 0,09-0,55 ha sized retention-tree groups in three years after logging (**Paper IV**), and the forest spiders *Microneta viaria* (Blackwall, 1841) and *Tenuiphantes tenebricola* (Wider, 1834) seemed to disappear from the forested micro-sites of the gap-felled stands, in addition to the small retention-tree groups (**Paper II**). Also Lance and Phinney (2001) found that some forest bird species were missing from the 2-5 ha sized retention-tree groups 2-4 years after logging. Similarly, Pearce *et al.* (2005), who studied forest patches (0.5-11.2 ha in size) within clear-cuts, found that small patches tended to maintain only common and abundant spider and carabid species. Therefore, it seems that the

retention-tree groups and even the forested parts of the gap-felled stands might lose the most sensitive species before forest grows back (or even in the short-term). It seems to take about 20-30 years until the clear-cut forest is regenerated into such a phase where it no longer is considered as matrix, but as habitat for a forest spider or carabid (McIver *et al.* 1992, Koivula *et al.* 2002, Buddle *et al.* 2006, Niemelä *et al.* 2007). The question is then, whether these species are able to re-colonise the harvested areas from the surrounding forests. There are implications that some forest carabid species may not re-colonise during this time (Niemelä *et al.* 1993, Spence *et al.* 1996). Long-term studies would be needed to determine for how long the fauna continues to develop, and if the retention patches would speed up the re-colonisation of the harvested areas by forest spiders and carabids. (See Discussion sections in **Papers II-IV.**)

6.3. How much should be retained?

What would be an appropriate level of retention? In particular, how large should the retention patches be? Even if the amount of green trees corresponded to the Fennoscandian recommendations (5-10 trees/ha; e.g. Raivio *et al.* 2001) in the alternative logging methods study, the retention-tree groups were too small for carabids (Koivula 2002a), soil arthropods (Siira-Pietikäinen *et al.* 2003), and vascular plants (Jalonen & Vanha-Majamaa 2001). The same seemed to apply for spiders (**Paper II**). This was because the spider assemblages of the small retention-tree groups were similar to the clear-cut micro-sites, i.e. (semi-) open-habitat species invaded the tree groups, and the numbers of individuals of forest species decreased there (some forest species were absent from the small retention-tree groups after logging). The amount of retention trees was higher in the retention-tree group study, but it appeared that retention-tree groups of 0.09-0.55-ha size might be too small to constitute 'life-boats', even if they maintained some forest species (**Papers III-IV**). I reached this conclusion because (semi-) open habitat spiders were fairly abundant within the tree groups irrespective of their size, the numbers of individuals of many forest species and (medium-) moist-habitat species decreased in the tree groups following logging, and some species seemed to disappear from the tree groups in three years following harvesting. Furthermore, even the forested micro-sites of the gap-felled stands seemed to be too small for some forest spider species (**Paper II**). This is consistent with Halpern *et al.* (1999) who stated that the retention-tree group size recommended in USA (from 0.2 to >1 ha) is too small to escape edge effects. Taking shape into account when establishing retention-tree groups could help in reducing edge effects. For example, Gandhi *et al.* (2004) found that shape of a retention-tree group affected carabids: total catches and species diversity were highest in round tree groups.

The appropriate size of a retention patch (e.g. retention-tree group) can be estimated by examining studies performed in forest fragments. In addition to the above studies, Mader (1984) estimated that forests smaller than 0.5 ha consist entirely of edge habitat. He also estimated that in order to have a larger proportion of forest-dwelling species than species of other habitats, the area needed for carabids would be 2-5 ha, and 10 ha for wandering spiders. Miyashita *et al.* (1998) found less web-building spiders in smaller forest fragments, and their density decreased considerably with fragment size less than 1 ha (web-builders are generally associated with forests, see e.g. Huhta 1971, Coyle 1981, Väisänen & Biström 1990, Pajunen *et al.* 1995, McIver *et al.* 1992, Buddle *et al.* 2000, Larrivéé *et al.* 2005). Halme & Niemelä (1993) found that open habitat carabid species were present in forest fragments smaller than three hectares, thus the assemblage structure differed from forest interior. Concerning both spiders and carabids, Pearce *et al.* (2005) estimated that patches smaller than three hectares may be too small to function effectively, unless very close to other forest patches.

Furthermore, Didham (1997) stated that even 100-ha-sized forest fragments might not be large enough to preserve an intact interior forest beetle fauna. When considering these estimates, it seems that the recommended retention-tree group sizes (e.g. from 0.2 to >1 ha in USA in Halpern *et al.* 1999; the Fennoscandian recommendations with 5-10 trees/ha also correspond to tree groups smaller than the small ones in **Paper II**) are not large enough for the maintenance of forest species of spiders and carabids, but the size of a retention patch should be at least a few hectares. In other words, retention-tree groups smaller than a few hectares probably do not constitute 'life-boats' for spiders and carabids. However, retaining patches that are that large may be impossible in Europe, as clear-cut areas are fairly small. For example, in Estonia the average clear-cut size is 2.3 ha (Lõhmus *et al.* 2006).

Before establishing the appropriate level of retention, the aims of retaining trees should be clarified. Is the goal to preserve an intact interior forest assemblage or to maintain a higher proportion of forest-dwelling species than that of species invading from the surrounding habitats? Or is the goal to preserve certain species, e.g. the most sensitive ones? As regards biodiversity, sustainable forest management is usually interpreted as preserving all species (Noss 1993 in Taylor & Doran 2001). However, the common forest species probably do not need modified logging methods, if there is enough forest habitat at the landscape level, so that these species can re-colonise the harvested areas. Potentially the most sensitive species are ones with poor dispersal ability, and strict habitat associations (e.g. den Boer 1990a, 1990b, de Vries & den Boer 1990). For example, Burke and Goulet (1998) discovered that decreasing forest fragment size especially affected forest specialist carabids with poor dispersal abilities. Taylor and Doran (2001) suggest that the focus should be on those species that are likely to be most adversely affected in the long term or that are associated with important microhabitats or structural components that could be affected by forest management. For example, Koivula (2002b) suggested that the most sensitive carabid species would be found amongst spruce mire specialists (e.g. *P. mannerheimii*). Such species of spiders and carabids that could benefit from retention patches should be specified (see Discussion in **Paper IV**).

6.4. Variable retention at the landscape-level

A consequence of providing recommendations of the number of green trees retained per hectare might lead to low number of retention-trees in every stand. However, biodiversity might benefit more if the amount of retention-trees is varied between stands, i.e. leaving a high amount of green trees in some stands, but none in others (Schieck *et al.* 2000, Raivio *et al.* 2001, Smyth *et al.* 2005). According to Hanski (2000) it would be more efficient to concentrate efforts to improve forest quality in certain areas, instead of spreading the same total effort evenly across the landscape. In a broader perspective, different harvesting methods should be applied varying from thinning to clear-cutting (and of course, reserving some areas totally from management). Implementing an array of management strategies may help in meeting the diverse requirements of different taxa (Lindenmayer *et al.* 2000, Werner & Raffa 2000, Huggard & Vyse 2002). Implementing several management strategies would also mimic natural disturbances better than applying the same amount and spatial pattern everywhere, because forest fires are heterogeneous and because there are different natural disturbances with different scales (Guldin 1996, Östlund *et al.* 1997, Schieck *et al.* 2000). For example, Smyth *et al.* (2005) recommended to incorporate the mean and range of live residual trees (which vary among forest types) observed after wildfire in landscape-level planning. This calls for studies determining if different amounts of residual trees in harvested areas correspond to those left by wildfire in their effects on biodiversity (Smyth *et al.* 2005).

Green-tree retention and gap felling may increase fragmentation. If a high amount of green trees is retained, timber companies must log more stands in order to obtain the same amount of timber, which also means constructing more roads and opening up the forests to human access (Tittler & Hannon 2000). In addition, a landscape with small clear-cuts and small forest fragments has a lot of edge habitat, but the amount of interior forest habitat is small (Swanson & Franklin 1992). Furthermore, at around 20% of original habitat in the landscape, habitat patches also start to be more isolated in addition to being smaller (Andrén 1994). Isolation of forest fragments may be important for spiders and carabids (Usher *et al.* 1993, Burke & Goulet 1998). Magura *et al.* (2001 and references therein) recommend the distance between forest patches (stepping stones) to be 500-600 m, because this is the distance that poorly colonising forest carabid species can move through matrix. Landscape-level planning would be important in order to insure sufficient amounts of interior habitat and structural features in a larger scale, in addition to avoiding isolation of forest patches.

6.5. Retention-tree group study

Although we took all the available patches that were similar enough in their vegetation, the number of retention-tree groups in the retention-tree group study design (**Papers III and IV**) may have been too small to detect statistically significant differences in responses for patch size (11, and one control area). The size of the retention-tree groups varied as well according to the original spruce mire patches (five of them about 0.1 ha, four about 0.2 ha, one about 0.3 ha, and one 0.6 ha). Thus, the replication of the largest sizes was especially few. The limited replication might be one reason why we detected ambiguous responses for the retention-tree group size in **Paper III**.

On the other hand, there were good reasons to harvest the sites the way they were logged. There was a need to perform the logging, as it would have been done in normal forestry (see **Paper III**). Therefore, the retention-tree groups were established in spruce mire patches. The retention-tree-groups-to-be differed from their surroundings in their vegetation, and had a higher amount of aspen (*Populus tremula* L.) and dead wood (Vanha-Majamaa & Jalonen 2001). In addition, spruce mires have been postulated as fire refugia, although only few of them seem to be such (Segerström *et al.* 1994, Hörnberg *et al.* 1998). Old-growth spruce mires are currently rare in Fennoscandia because of drainage of wetlands and short rotation periods (Hörnberg *et al.* 1998). Adding structural diversity with retention-tree groups might give a possibility of creating analogues for fire residuals in the long-term. Although retention-tree groups were not sufficient analogues for fire residuals for carabids and staphylinids in Canada (Gandhi *et al.* 2004), could they become such with time?

I considered a power analysis to figure out how many tree groups would have been needed if the experiment was redesigned, but the techniques for modelling the power of complex designs are not well developed, and there is little consensus regarding the appropriateness for those that do exist (Bausell & Li 2002). In addition, Muller *et al.* (1992) suggested that power should not be calculated if appropriate models were not available, as the estimated sample size might be too small or too large. In particular, power analysis for models using negative binomial as the error distribution seems not to be available. The power would probably have increased if traps were separated in the analyses, but they were pooled already in the field.

There was evidence that the number of standing trees may play a significant role for spiders and carabids (**Paper IV**: CCA). This may be another reason for not detecting the effect of patch size in **Paper III**, as a large amount of the retention-trees were wind blown. Hautala *et al.* (2004) estimated that by the end of the second year after logging, 40% of the

retention-trees were uprooted. However, the number of trees was not included in the GLMM analyses in **Paper III** because of limited replication, and therefore too many parameters could not be included in the models (we chose to perform the models with patch size, for which we had *a priori* hypotheses).

In the clear-cuts, the traps were placed fairly close to the retention-tree groups (Figure 1 in **Paper IV**). Thus, the two trap rows were situated 10 and 20 meters from the edge of a retention-tree group into the clear-cut. This is approximately 1-1.5 tree height, i.e. trees cast a shade this far into the clear-cut size (see Oxbrough *et al.* 2006). This may be one reason for finding forest species in the clear-cuts; they were shady enough close to the tree groups for the forest species to move around. This view is supported by Ulyshen *et al.* (2006) who found that the carabid assemblage at the gap edge was similar to that of the surrounding forest. Another explanation for finding forest species in clear-cuts is that they survive there for a few years (Huhta 1971, Niemelä *et al.* 1993, Koivula 2002a), but do not reproduce there (see Discussion in **Paper III**). This study does not allow for the evaluation of these rival explanations, as there were no traps further away in the clear-cut side to examine whether the number of individuals of forest species would be lower there.

6.6. Habitat affinity classification

Although Huhta's (1971) study emphasised both light intensity and moisture in the habitat affinity classification (see **Paper I**), it seems that, based on **Papers II-IV**, for most spiders and carabids it is sufficient to take only the affinity for light intensity into account when dealing with forest management. However, among the species indifferent towards light intensity, the (medium-) moist-habitat species (ABC23 and ABC3) were hypothesised to respond like forest species (see Huhta 1971), as they did. This is consistent with Koivula (2002b) who separated spruce mire carabid specialists as one habitat affinity group. Interestingly, (semi-) open-habitat species (AB) responded like open-habitat species (A), and the responses of forest generalists (BC) and shady forest species (C) were similar, although some differences were detected in **Paper IV**. Therefore, it seems that the classification into open habitat, forest and generalist species used in most papers (e.g. Koivula 2002a, Niemelä *et al.* 2007) is appropriate, except that the (medium-) moist-habitat species should be grouped with forest species when formulating hypotheses. In addition, I would like to know if the open-habitat species group contains species that also occur in semi-open habitats (AB), because there may be (semi-) open-habitat species that differ from the rest in their response. For example, in **Paper II**, *P. lugubris* responded differently than the other (semi-) open habitat spiders. *P. lugubris* is a species with a clear affinity for both open habitats and light forests (**Paper I**) because they use forests for over-wintering and openings for reproduction (Edgar 1971). Grouping such species together with open-habitat species in the analyses could hide a possible response. I did not have enough individuals of such species that would occur solely in semi-open habitats (B) to draw solid conclusions concerning them, although based on **Paper IV**, it seems that the semi-open habitat species responded like (semi-) open habitat species (A and AB).

In **Paper IV**, the mean number of spider individuals belonging to the habitat affinity class 'indifferent towards light intensity' (ABC) decreased after logging, and the same was true for the carabids in the third year (although for the carabids the total number of individuals decreased as well in the third year). This may be explained by the habitat affinity classification: the occurrence in clear-cuts in literature was taken into account in the classification (**Paper I**). Forest species of both spiders and carabids have been observed to survive in clear-cuts for a few years (e.g. Huhta 1971, McIver *et al.* 1992, Koivula 2002a), but

the occurrence in clear-cuts may not represent a ‘real’ affinity. If clear-cuts were not taken into account in the habitat affinity classification, most species now in the indifferent towards light intensity class would be either forest generalists (BC) or (medium-) moist-habitat species (ABC23 or ABC3). Both these groups should respond to logging exactly as I found them to respond (e.g. Huhta 1971, Koivula 2002a).

6.7. Occurrence of male and female spiders

Although previous literature (e.g. Heydemann 1960, Vlijm & Richter 1966, Vlijm & Kessler-Geschiere 1967, Edgar 1971) led me to hypothesise that male and female spiders might respond differently (or actually, that the response would be clearer for females than for males), there were no consistently different responses for males and females. This may be because sexes were not separated in the habitat affinity classification (**Paper I**).

Another possible reason may be that females were less numerous because I used pitfall traps for catching spiders. Therefore, I may not have detected the possible response. The highest abundances per species were found amongst lycosid males. Activity influences pitfall trap catches (e.g. Greenslade 1964). Male spiders move around actively when searching for mates, resulting in a higher probability in falling into pitfall traps (e.g. Tretzel 1954 in Huhta 1971). For example, in the retention-tree group study, I caught 2673 individuals (in 1999-2001) of the lycosid *Pardosa riparia* (C. L. Koch, 1833), 77% of which were males and 23% females (Appendix 3 in **Paper IV**). Another example from the same study is the linyphiid *Centromerus arcanus* (O. P.-Cambridge, 1873). I caught altogether 1674 individuals (in 1998-2001), 74% of which were males and 26% females (Appendix 3 in **Paper IV**). In addition, there is a nine-fold difference in activity for lycosids and linyphiids (Heydemann 1961 in Huhta 1971). The possible differences in responses of male and female spiders could be further explored with other sampling methods, such as soil/litter samples, but this can be done only after the habitat affinity is specified for each sex.

7. Conclusions

It seems that the more trees are retained the better the original spider and carabid assemblages are maintained in harvesting. Thinning aiming at uneven age structure seemed to be as good as uncut forest for ground-living spiders (**Paper II**). It should, however, be determined, if ‘normal’ thinning (with the aim of an even age structure or more space for ‘better-quality’ trees to grow) is as good as the thinning applied in this thesis (with the aim of an uneven age structure of trees), and the effects of the second regeneration should be studied. Small retention-tree groups (0.01-0.02 ha) did not well maintain forest spiders, although they differed to some extent from the clear-cuts (**Paper II**). Large retention-tree groups (0.09-0.55 ha) maintained some forest species of spiders and carabids in the short-term, but seemed to lose some (**Papers III and IV**). Also gap felling maintained some forest spider species in the short-term, but seemed to lose some (**Paper II**).

However, gap felling (**Paper II**) and green-tree retention (**Papers II-IV**) need to be studied more before final conclusions. Especially long-term studies are needed, along with studies determining appropriate patch size, and the importance of structural diversity provided by variable retention for spiders and carabids. However, before that can be done, aims of using modified logging methods should be specified carefully. The mechanisms of green-tree retention (i.e. ‘life-boating’, stepping-stones, or structural features; see Franklin *et al.* 1997) should be studied in order to decide about the aims of retaining green trees. More resources

should be allocated in determining those species that would benefit from variable retention. Moreover, as there are economic costs associated with modified logging methods, their ecological benefits as compared to other approaches aimed at maintaining biodiversity should be carefully assessed. Adaptive management, i.e. learning from management experiments, is imperative in order to develop better management strategies over time (e.g. Lindenmayer *et al.* 2000, Smyth *et al.* 2005).

Acknowledgements

Many people helped me with my thesis. My supervisor Jari Niemelä participated in all phases of both studies (MONTA and RETREE), allowing me also to develop independent thinking. Susanna Lehvävirta and Johan Kotze shared with me the enthusiasm of learning and trying to perform as good science as possible, as well as numerous academic discussions. Susanna also helped me to improve the introductory part considerably. The study circles by Hannu Rita and Timo Tuomivaara initiated a process of becoming an independent researcher. Besides being a co-author in one of the papers in my thesis, sharing my interest in forest management and arthropods, Matti Koivula participated in the design the alternative logging methods study and collected the data for it. I also want to thank Matti for being able to work intensively, especially when we revised Paper II. Bob O'Hara helped in performing the statistical analyses for the *a priori* hypotheses in retention-tree group study. We performed the habitat affinity classification of carabids together with Anna Ojala. Stephen Venn gave good comments for most papers of my thesis. Ilkka Vanha-Majamaa (FFRI) made a major contribution to the design of the retention-tree group study. The comments I got from the pre-examiners helped me to improve my thesis. Thus, I thank Mikko Mönkkönen for the comments on Papers II and IV and John Spence for the comments on the introductory part.

I also thank all the other members of the Urban Ecology Group that are not mentioned above and people from the Zoological Museum for discussions and company during lunch and coffee breaks: Heidi Björklund, Maria Heikkilä, Ville Heimala, Inari Helle, Pirjo Hätönen, Anne Koivunen, Meeri Mäki, Raisa Nikula, Katja Nylund, Anja Ouvinen, Sanna Saari, Jarmo Saarikivi, Ritva Talman, Juhani Terhivuo, Ilmari Valovirta, Salla Vehma, Risto Väinölä and Vesa Yli-Pelkonen.

There are also some practical issues that warrant thanking. The forest company Stora Enso (nowadays Tornator Oy) provided the study areas and performed logging in retention-tree group study. Land-owning companies in the alternative logging methods study were Finnish Forest and Park Services, Metsäliitto, StoraEnso and Yhtyneet Paperitehtaat. I was able to use a table at the Zoological Museum of Helsinki with the kind permission by Juhani Terhivuo. Timo Pajunen (Finnish Museum of Natural History, Helsinki, Finland) identified most of the spider material (for both alternative logging methods study and retention-tree group study), and Juhani Terhivuo helped me with spider identification when starting my thesis. Anna Maria Rauha identified all the carabids in the third study year of the retention-tree group study, and Matti Koivula as well as Olof Biström helped me with the most difficult carabid specimens. The following people helped in the fieldwork of the retention-tree group study: Anita Etholén, Ann-Catherine Grandchamp, Mikko Huju, Mervi Koskela, Johan Kotze, Jari Niemelä, Johanna Nikolov and Anna Maria Rauha. I also thank The Finnish Biodiversity Research Programme (FIBRE), Maj and Tor Nessling foundation and University of Helsinki for funding my thesis. Tree data were provided by the Finnish Forest Research Institute (FFRI; Harri Hautala, Marja-Leena Heinilehto, Ilkka Vanha-Majamaa).

And last, but not least, I thank my family and all my friends for support.

References:

- Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – *Oikos* 71: 355-366.
- Atlegrim, O. & Sjöberg, K. 1995: Effects of clear-cutting and selective felling in Swedish boreal coniferous forest: response of invertebrate taxa eaten by birds. – *Entomologica Fennica* 6(2-3): 79-90.
- Attiwill, P. M. 1994: The disturbance of forest ecosystems: the ecological basis for conservative management. – *Forest Ecology and Management* 63: 247-300.
- Aubury, K. B., Amaranthus, M. P., Halpern, C. B., White, J. D., Woodard, B. L., Peterson, C. E., Lagoudakis, C. A. & Horton, A. J. 1999: Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. – *Northwest Science* 73 (Special issue): 12-26.
- Barg, A. K. & Edmonds, R. L. 1999: Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Oregon. – *Canadian Journal of Forest Research* 29: 705-713.
- Bausell, R. B. & Li, Y-F. 2002: Power analysis for experimental research. A practical guide for the biological, medical and social sciences. – Cambridge University Press, Cambridge. 363 pp.
- Bradshaw, R., Gemmel, P. & Björkman, L. 1994: Development of nature-based silvicultural models in Southern Sweden: the scientific background. – *Forest & Landscape Research* 1: 95-110.
- Brunet, J. 1993: Environmental and historical factors limiting the distribution of rare forest grasses in south Sweden. – *Forest Ecology and Management* 61: 263-275.
- Buddle, C. M. 2001: Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. – *Agricultural and Forest Entomology* 3: 241-251.
- Buddle, C. M., Langor, D. W., Pohl, G. R. & Spence, J. R. 2006: Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbances in forest management. – *Biological Conservation* 128: 346-357.
- Buddle, C. M., Spence, J. R. & Langor, D. W. 2000: Succession of boreal forest spider assemblages following wildfire and harvesting. – *Ecography* 23 (4): 424-436.
- Burke, D. & Goulet, H. 1998: Landscape and area effects on beetle assemblages in Ontario. – *Ecography* 21: 472-479.
- Cajander, A. K. 1949: Forest types and their significance. – *Acta Forestalia Fennica* 56: 1-71.
- Chapman, M. G. & Underwood, A. J. 1999: Ecological patterns in multivariate assemblages: information and interpretation of negative values in ANOSIM tests. – *Marine Ecology Progress Series* 180: 257-265.
- Churchill, T. B. 1997: Spiders as ecological indicators: an overview for Australia. – *Memoirs of the Museum of Victoria* 56(2): 331-337.
- Coyle, F. A. 1981: Effects of clearcutting on the spider community of a southern Appalachian forest. – *Journal of Arachnology* 9: 285-298.
- Curry, S. J., Humphreys, W. F., Koch, L. E. & Main, B. Y. 1985: Changes in arachnid communities resulting from forestry practices in karri forest, south-west Western Australia. – *Australian Forest Research* 15: 469-480.
- de Vries, H. H. & den Boer, P. J. 1990: Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. – *Netherlands Journal of Zoology* 40: 484-498.
- de Vries, H. H., den Boer, P. J. & van Dijk, T. S. 1996: Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. – *Oecologia* 107: 332-342.
- De'ath, G. 2002: Multivariate regression trees: a new technique for modeling species-environment relationships. – *Ecology* 83(4): 1105-1117.
- DeBell, D. S. & Curtis, R. O. 1993: Silviculture and new forestry in the Pacific Northwest. – *Journal of Forestry* 91(12): 25-30.
- den Boer, P. J. 1990a: The survival value of dispersal in terrestrial arthropods. – *Biological Conservation* 54: 175-192.
- den Boer, P. J. 1990b: Density limits and survival of local populations in 64 carabid species with different powers of dispersal. – *Journal of Evolutionary Biology* 3: 19-48.

- Didham, R. K. 1997: An overview of invertebrate responses to forest fragmentation. – In: Watt, A. D., Stork, N. E. & Hunter, M. D. (eds.), *Forests and insects*: 303-320. Chapman & Hall, London.
- Drever, C. R. & Lertzman, K. P. 2003: Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. – *Canadian Journal of Forest Research* 33(1): 137-146.
- du Bus de Warnaffe, G. & Dufrêne, M. 2004: To what extent can management variables explain species assemblages? A study of carabid beetles in forests. – *Ecography* 27: 701-714.
- Dufrêne, M. & Legendre, P. 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. – *Ecological Monographs* 67(3): 345-366.
- Edgar, W. D. 1971: The life-cycle, abundance and seasonal movement of the wolf spider *Lycosa (Pardosa) lugubris* in Central Scotland. – *Journal of Animal Ecology* 40: 303-322.
- Ehnström, B. 2001: Leaving dead wood for insects in boreal forests – suggestions for the future. – *Scandinavian Journal of Forest Research Supplementum* 3: 91-98.
- Emmingham, W. H. 2002: Status of uneven-aged management in the Pacific Northwest, USA. – *Forestry* 75(4): 433-436.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997: Boreal forests. – *Ecological Bulletins* 46: 16-47.
- Faith, D. P., Minchin, P. R. & Belbin, L. 1987: Compositional dissimilarity as a robust measure of ecological distance. – *Vegetatio* 69: 57-68.
- Franklin, J. F., Berg, D. R., Thornburgh, D. A. & Tappeiner, J. C. 1997: Alternative silvicultural practices to timber harvesting: variable retention harvesting systems. – In: Kohm, K. A. & Franklin, J. F. (eds.), *Creating forestry for the 21st century. The science of ecosystem management*: 11-14. Island Press, Washington, D.C.
- Fridman, J. & Walheim, M. 2000: Amount, structure, and dynamics of dead wood on managed forestland in Sweden. – *Forest Ecology and Management* 131: 23-36.
- Gandhi, K. J. K., Spence, J. R., Langor, D. W. & Morgantini, L. E. 2001: Fire residuals as habitat reserves for epigeic beetles (Coleoptera: Carabidae and Staphylinidae). – *Biological Conservation* 102: 131-141.
- Gandhi, K. J. K., Spence, J. R., Langor, D. W., Morgantini, L. E. & Cryer, K. J. 2004: Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. – *Canadian Journal of Forest Research* 34: 1319-1331.
- Grandchamp, A.-C., Niemelä, J. & Kotze, J. 2000: The effects of trampling on assemblages of ground beetles (Coleoptera, Carabidae) in urban forests in Helsinki, Finland. – *Urban Ecosystems* 4(4): 323-334.
- Greenslade, P. J. M. 1964: Pitfall trapping as a method for studying populations of carabidae (Coleoptera). – *Journal of Animal Ecology* 33: 301-310.
- Guldin, J. M. 1996: The role of uneven-aged silviculture in the context of ecosystem management. – *Western Journal of Applied Forestry* 11(1): 4-12.
- Gustafsson, L. & Hallingbäck, T. 1988: Bryophyte flora and vegetation of managed and virgin coniferous forests in south-west Sweden. – *Biological Conservation* 44: 283-300.
- Haila, Y. & Kouki, J. 1994: The phenomenon of biodiversity in conservation biology. – *Annales Zoologici Fennici* 31: 5-18.
- Haila, Y., Hanski, I. K., Niemelä, J., Punttila, P., Raivio, S. & Tukia, H. 1994: Forestry and the boreal fauna: matching management with natural forest dynamics. – *Annales Zoologici Fennici* 31: 187-202.
- Hallman, E., Hokkanen, M., Juntunen, H., Korhonen, K.-M., Raivio, S., Savela, O., Siitonen, P., Tolonen, A. & Vainio, M. 1996: Alue-ekologinen suunnittelu. – *Metsähallituksen metsätalouden julkaisu* 3/1996. Vantaa. (In Finnish.)
- Halme, E. & Niemelä, J. 1993: Carabid beetles in fragments of coniferous forest. – *Annales Zoologici Fennici* 30: 17-30.
- Halpern, C. B. & McKenzie, D. 2001: Disturbance and post-harvest ground conditions in a structural retention experiment. – *Forest Ecology and Management* 154: 215-225.
- Halpern, C. B., Evans, S. A., Nelson, C. R., McKenzie, D., Liguori, D. A., Hibbs, D. E. & Halaj, M. G. 1999: Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. – *Northwest Science* 73 (Special issue): 27-44.

- Hänggi, A., Stöckli, E. & Nentwig, W. 1995: Habitats of Central European Spiders – Characterisation of the habitats of the most abundant spider species of Central Europe and associated species. – *Miscellanea Faunistica Helvetiae* 4: 1-459.
- Hansen, A. J., Garman, S. L., Weigand, J. F., Urban, D. L., McComb, W. C. & Raphael, M. G. 1995: Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. – *Ecological Applications* 5(3): 535-554.
- Hansen, A. J., Spies, T. A., Swanson, F. J. & Ohmann, J. L. 1991: Conserving biodiversity in managed forests: lessons from natural forests. – *BioScience* 41(6): 382-392.
- 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.
- Hanssen, O., Ødegaard, F. & Kvamme, T. 1998: Proposal to red list for Norwegian insects. Part 1. Beetles (Coleoptera). – NINA Fagrappport 031: 1-31. (In Norwegian with English summary.)
- Hautala, H., Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2004: Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. – *Biodiversity and Conservation* 13: 1541-1554.
- Hazell, P. & Gustafsson, L. 1999: Retention of trees at final harvest – evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. – *Biological Conservation* 90: 133-142.
- Heliölä, J., Koivula, M. & Niemelä, J. 2001: Distribution of carabid beetles (Coleoptera, Carabidae) across boreal forest – clearcut ecotone. – *Conservation Biology* 15(2): 370-377.
- Helle, P. & Muona, J. 1985: Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. – *Silva Fennica* 19: 281-294.
- Heydemann, B. 1960: Die biozönotische Entwicklung vom Vorland zum Koog. Vergleichend-ökologische Untersuchungen an der Nordseeküste. I. Teil: Spinnen (Araneae). – *Academie der Wissenschaften und der Literatur. Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse* 11: 747-913. (In German.)
- Heydemann, B. 1961: Untersuchungen über die aktivitäts- und besiedlungsdichte bei epigäischen spinnen. – *Verhandlungen der Deutschen zoologischen Gesellschaft Saarbrücken 1961*: 538-556. (In German.)
- Hogberg, L. K., Patriquin, K. J. & Barclay, R. M. R. 2002: Use by bats of patches of residual trees in logged areas of the boreal forest. – *American Midland Naturalist* 148: 282-288.
- Hörnberg, G., Zackrisson, O., Segerström, U., Svensson, B. W., Ohlson, M. & Bradshaw, R. H. W. 1998: Boreal swamp forests. Biodiversity “hotspots” in an impoverished forest landscape. – *BioScience* 48(10): 795-802.
- Huber, C., Schulze, C. & Baumgarten, M. 2006: The effect of femel- and small scale clear-cutting on ground dwelling spider communities in a Norway spruce forest in Southern Germany. – *Biodiversity and Conservation* (in press).
- Huggard, D. J. & Vyse, A. 2002: Comparing clearcutting and alternatives in a high-elevation forest: early results from Sicamous Creek. – *Extension Note* 63: 1-10.
- Huhta, V. 1965: Ecology of spiders in the soil and litter of Finnish forests. – *Annales Zoologici Fennici* 2: 260-308.
- Huhta, V. 1971: Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. – *Annales Zoologici Fennici* 8. 483-542.
- Huhta, V. 1976: Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. – *Annales Zoologici Fennici* 13: 63-80.
- Huhta, V., Karppinen, E., Nurminen, M. & Valpas, A. 1967: Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. – *Annales Zoologici Fennici* 4: 87-143.
- Hunter, J. E. & Bond, M. L. 2001: Residual trees: wildlife associations and recommendations. – *Wildlife Society Bulletin* 29(3): 995-999.
- Hyvärinen, E. 2006: Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests. – *Dissertationes Forestales* 21: 1-55. Academic dissertation, University of Joensuu.
- Hyvärinen, E., Kouki, J. & Martikainen, P. 2006: Fire and green-tree retention in conservation of red-

- listed and rare deadwood-dependent beetles in Finnish boreal forests. – *Conservation Biology* 20(6): 1711-1719.
- Hyvärinen, E., Kouki, J., Martikainen, P. & 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.
- Jalonen, J. & Vanha-Majamaa, I. 2001: Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. – *Forest Ecology and Management* 146: 25-34.
- Jennings, D. T., Houseweart, M. W., Dondale, C. D. & Redner, J. H. 1988: Spiders (Aranae) associated with strip-clearcut and dense spruce-fir forests of Maine. – *Journal of Arachnology* 16: 55-70.
- Jennings, D. T., Houseweart, M. W. & Dunn, G. A. 1986: Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. – *Coleopterists Bulletin* 40(3): 251-263.
- Jongman, R. H. G., Ter Braak, C. J. F. & Van Tongeren, O. F. R. (eds.) 1995: *Data analysis in community and landscape ecology*. – Cambridge University Press, Cambridge.
- Keenan, R. J. & Kimmins, J. P. 1993: The ecological effects of clear-cutting. – *Environmental Review* 1: 121-144.
- Keon, D. B. & Muir, P. S. 2002: Growth of *Usnea longissima* across a variety of habitats in the Oregon Coast Range. – *Bryologist* 105: 233-242.
- Kinnunen, H. 1999: In search of spatial scale – carabid beetle communities in agricultural landscapes. – Academic Dissertation. Department of Ecology and Systematics, University of Helsinki.
- Klimaszewski, J., Langor, D. W., Work, T. T., Pelletier, G., Hammond, H. E. J. & Germain, C. 2005: The effects of patch harvesting and site preparation on ground beetles (Coleoptera, Carabidae) in yellow birch dominated forests of southeastern Quebec. – *Canadian Journal of Forest Research* 35: 2616-2628.
- Koivula, M. 2002a: Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). – *Forest Ecology and Management* 167: 103-121.
- Koivula, M. 2002b: Boreal carabid-beetle (Coleoptera, Carabidae) assemblages in thinned uneven-aged and clear-cut spruce stands. – *Annales Zoologici Fennici* 39: 131-149.
- Koivula, M. & Niemelä, J. 2003: Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera: Carabidae). – *Ecography* 26: 179-187.
- Koivula, M., Kukkonen, J. & Niemelä, J. 2002: Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. – *Biodiversity and Conservation* 11(7): 1269-1288.
- Kolström, M. & Lumatjärvi, J. 2000: Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. – *Forest Ecology and Management* 126: 113-120.
- Kotiharju, S. & Niemelä, H. 2000: Talousmetsien luonnonhoidon laadun arviointi. Seurantaportti. – Metsätalouden kehittämiskeskus Tapio, Porvoo.
- 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 Supplementum* 3: 27-37.
- Krebs, C.J. 1999: *Ecological Methodology*. 2nd Edition. – Benjamin/Cummings, Addison-Welsey Educational Publishers, Menlo Park, California, USA. 620 pp.
- Kuuluvainen, T., Syrjänen, K. & Kalliola, R. 1998: Structure of a pristine *Picea abies* forest in northeastern Europe. – *Journal of Vegetation Science* 9: 563-574.
- Lance, A. N. & Phinney, M. 2001: Bird responses to partial retention timber harvesting in central interior British Columbia. – *Forest Ecology and Management* 142: 267-280.
- Langellotto, G. A. & Denno, R. F. 2004: Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. – *Oecologia* 139(1): 1-10.
- Larrivé, M., Fahrig, L. & Drapeau, P. 2005: Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. – *Canadian Journal of Forest Research* 35: 2575-2588.
- Larsson, S. & Danell, K. 2001: Science and the management of boreal forest biodiversity. – *Scandinavian Journal of Forest Research Supplementum* 3: 5-9.

- Latty, E. F., Werner, S. M., Mladenoff, D. J., Raffa, K. F. & Sickley, T. A. 2006: Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. – *Forest Ecology and Management* 222: 335-347.
- Lehvävirta, S., Kotze, D. J., Niemelä, J., Mäntysaari, M. & O'Hara, B. 2006: Effects of fragmentation and trampling on carabid beetle assemblages in urban woodlands in Helsinki, Finland. – *Urban Ecosystems* 9: 13-26.
- Lemieux, J. P. & Lindgren, B. S. 2004: Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia. – *Ecography* 27: 557-566.
- Lindenmayer, D. B., Margules, C. R. & Botkin, D. B. 2000: Indicators of biodiversity for ecologically sustainable forest management. – *Conservation Biology* 14(4): 941-950.
- Linder, P. & Östlund, L. 1988: Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. – *Biological Conservation* 85: 9-19.
- Lindroth, C. H. 1985: The Carabidae (Coleoptera) of Fennoscandia and Denmark. Part 1. – *Fauna Entomologica Scandinavica* 15: 1-225.
- Lindroth, C. H. 1986: The Carabidae (Coleoptera) of Fennoscandia and Denmark. Part 2. – *Fauna Entomologica Scandinavica* 15: 231-497.
- Liu, Q. & Hytteborn, H. 1991: Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. – *Journal of Vegetation Science* 2: 391-402.
- Löhmus, P., Rosenvald, R. & Löhmus, A. 2006: Effectiveness of solitary retention trees for conserving epiphytes: differential short-term responses of bryophytes and lichens. – *Canadian Journal of Forest Research* 36: 1319-1330.
- Lowrie, D. C. 1948: The ecological succession of spiders of the Chicago area dunes. – *Ecology* 29: 334-351.
- Mader, H.-J. 1984: Animal habitat isolation by roads and agricultural fields. – *Biological Conservation* 29: 81-96.
- Magura, T., Ködöböcz, V. & Tóthmérész, B. 2001: Effects of habitat fragmentation on carabids in forest patches. – *Journal of Biogeography* 28: 129-138.
- Martikainen, P. 2001: Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. – *Ecological Bulletins* 49: 205-218.
- Martikainen, P., Kouki, J. & Heikkala, O. 2006: The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests. – *Ecography* 29: 659-670.
- Matlack, G. R. 1993: Microenvironment variation within and among forest edge sites in the eastern United States. – *Biological Conservation* 66: 185-194.
- Mazurek, M. J. & Zielinski, W. J. 2004: Individual legacy trees influence vertebrate wildlife diversity in commercial forests. – *Forest Ecology and Management* 193: 321-334.
- McComb, W. C., Spies, T. A. & Emmingham, W. H. 1993: Douglas-fir forests. Managing for timber and mature-forest habitat. – *Journal of Forestry* 91: 31-42.
- McCullagh, P. & Nelder, J.A., 1989: *Generalized linear models*. – 2nd Edition. Chapman & Hall, London.
- McCune, B. & Mefford, M.J. 1999: *Multivariate Analysis of Ecological Data*. – Version 4.14. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McIver, J. D., Parsons, G. L. & Moldenke, A. R. 1992: Litter spider succession after clear-cutting in a western coniferous forest. – *Canadian Journal of Forest Research* 22: 984-992.
- Merrill, S. B., Cuthbert, F. J. & Oehlert, G. 1998: Residual patches and their contribution to forest-bird diversity on northern Minnesota aspen clearcuts. – *Conservation Biology* 12(1): 190-199.
- Metsätalouden kehittämiskeskus Tapio 2001: Hyvän metsänhoidon suositukset. – Metsätalouden kehittämiskeskus Tapio, Helsinki. (In Finnish.)
- Mielikäinen, K. & Hynynen, J. 2003: Silvicultural management in maintaining biodiversity and resistance of forests in Europe – boreal zone: case Finland. – *Journal of Environmental Management* 67: 47-54.
- Minchin, P. R. 1987: An evaluation of the relative robustness of techniques for ecological ordination. – *Vegetatio* 69: 89-107.
- Miyashita, T., Shikai, A. & Chida, T. 1988: The effects of forest fragmentation on web spider communities in urban areas. – *Biological Conservation* 86: 357-364.

- Moen, C. A. & Gutiérrez, R. J. 1997: California spotted owl habitat selection in the Central Sierra Nevada. – *Journal of Wildlife Management* 61(4): 1281-1287.
- Molnár, T., Magura, T., Tóthmérész, B. & Elek, Z. 2001: Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. – *European Journal of Soil Biology* 37: 297-300.
- Mönkkönen, M. 1999: Managing Nordic boreal forest landscapes for biodiversity: ecological and economic perspectives. – *Biodiversity and Conservation* 8: 85-99.
- Moore, J-D., Ouimet, R., Houle, D. & Camiré, C. 2004: Effects of two silvicultural practices on ground beetles (Coleoptera: Carabidae) in a northern hardwood forest, Quebec, Canada. – *Canadian Journal of Forest Research* 34: 959-968.
- Muller, K. E., LaVange, L. M., Landesman Ramey, S. & Ramey, C. T. 1992: Power calculations for general linear multivariate models including repeated measures applications. – *Journal of the American Statistical Association* 87(420): 1209-1226.
- Neitlich, P. N. & McCune, B. 1997: Hotspots of epiphytic lichen diversity in two young managed forests. – *Conservation Biol.* 11: 172-182.
- Niemelä, J. 1988: Habitat occupancy of carabid beetles on small islands and the adjacent Åland mainland, SW Finland. – *Annales Zoologici Fennici* 25: 121-131.
- Niemelä, J. 1990: Spatial distribution of carabid beetles in the southern Finnish taiga: a question of scale. – In: Stork, N. (ed.), *Ground beetles: their role in ecological and environmental studies*: 143-155. Intercept Publ. Andover.
- Niemelä, J. 1997: Invertebrates and boreal forest management. – *Conservation Biology* 11(3): 601-610.
- Niemelä, J. 1999: Management in relation to disturbance in the boreal forest. – *Forest Ecology and Management* 115: 127-134.
- Niemelä, J. & Halme, E. 1992: Habitat associations of carabid beetles in fields and forests on the Åland Islands, SW Finland. – *Ecography* 15: 3-11.
- Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. 1988: The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. – *Annales Zoologici Fennici* 25:107-119.
- Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1989: The annual activity cycle of carabid beetles in the southern Finnish taiga. – *Annales Zoologici Fennici* 26: 35-41.
- Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1992: Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. – *Journal of Biogeography* 19: 173-181.
- Niemelä, J., Koivula, M. & Kotze, D. J. 2007: The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. – *Journal of Insect Conservation* 11(1): 5-18.
- Niemelä, J., Langor, D. & Spence, J. 1993: Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. – *Conservation Biology* 7(3): 551-561.
- Niemelä, J., Larsson, S. & Simberloff, D. 2001: Concluding remarks – finding ways to integrate timber production and biodiversity in Fennoscandian forestry. – *Scandinavian Journal of Forest Research Supplementum* 3: 119-123.
- Nilsson, S. G., Hedin, J., Niklasson, M. 2001: Biodiversity and its assessment in boreal and nemoral forests. – *Scandinavian Journal of Forest Research Supplementum* 3: 10-26.
- North, M. P., Franklin, J. F., Carey, A. B., Forsman, E. D. & Hamer, T. 1999: Forest stand structure of the northern spotted owl's foraging habitat. – *Forest Science* 45: 520-527.
- North, M., Chen, J., Smith, G., Krakowiak, L. & Franklin, J. 1996: Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. – *Northwest Science* 70(1): 24-35.
- Noss, R. F. 1993: Sustainable forestry or sustainable forests? – In: Aplet, G. H., Johnson, N., Olson, J. T. & Sample, V. A. (eds.), *Defining sustainable forestry*: 17-43. Washington, DC, Island Press.
- Osawa, N., Terai, A., Hirata, K., Nakanishi, A., Makino, A., Sakai, S. & Sibata, S. 2005: Logging impacts on forest carabid assemblages in Japan. – *Canadian Journal of Forest Research* 35: 2698-2708.

- Östlund, L., Zackrisson, O. & Axelsson, A.-L. 1997: The history and transformation of a Scandinavian boreal forest landscape since the 19th century. – *Canadian Journal of Forest Research* 27: 1198-1206.
- Oxbrough, A. G., Gittings, T., O'Halloran, J., Giller, P. S. & Kelly, T. C. 2006: The influence of open space on ground-dwelling spider assemblages within plantation forests. – *Forest Ecology and Management* 237: 404-417.
- Ozanne, C. M. P., Speight, M. R., Hambler, C. & Evans, H. F. 2000: Isolated trees and forest patches: patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots Pine). – *Forest Ecology and Management* 137: 53-63.
- Pajunen, T., Haila, Y., Halme, E., Niemelä, J. & Punttila, P. 1995: Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. – *Ecography* 18: 62-72.
- Pearce, J. L. & Venier, L. A. 2006: The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. – *Ecological Indicators* 6: 780-793.
- Pearce, J. L., Venier, L. A., Eccles, G., Pedlar, J. & McKenney, D. 2005: Habitat islands, forest edge and spring-active invertebrate assemblages. – *Biodiversity and Conservation* 14: 2949-2969.
- Pearce, J. L., Venier, L. A., McKee, J., Pedlar, J. & McKenney, D. 2003: Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. – *Canadian Entomologist* 135: 337-357.
- Peck, J. E. & McCune, B. 1997: Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. – *Ecological Applications* 7: 1181-1187.
- Platnick, N.I., 2003. The world spider catalog, version 4.0. American Museum of Natural History, online at <http://research.amnh.org/entomology/spiders/catalog/index.html>.
- Platnick, N. I. 2006. The world spider catalog, version 7.0. – American Museum of Natural History, online at <http://research.amnh.org/entomology/spiders/catalog/index.html>. (Accessed in Oct 6th 2006.)
- R Development Core Team 2004: R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org>.
- Rainio, J. & Niemelä, J. 2003: Ground beetles (Coleoptera: Carabidae) as bioindicators. – *Biodiversity and Conservation* 12: 487-506.
- Raivio, S., Normark, E., Pettersson, B. & Salpakivi-Salomaa, P. 2001: Science and the management of boreal forest biodiversity – forest industries' views. – *Scandinavian Journal of Forest Research Supplementum* 3: 99-104.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. (eds.) 2001: Suomen lajien uhanalaisuus 2000. – Ministry of the Environment and Finnish Environment Institute, Helsinki. 432 p. (In Finnish with English summary.)
- Rouvinen, S., Kuuluvainen, T. & Karjalainen, L. 2002: Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. – *Canadian Journal of Forest Research* 32: 2184-2200.
- Rypstra, A. L., Carter, P. E., Balfour, R. A. & Marshall, S. D. 1999: Architectural features of agricultural habitats and their impact on the spider inhabitants. – *Journal of Arachnology* 27: 371-377.
- Schieck, J., Stuart-Smith, K. & Norton, M. 2000: Bird communities are affected by amount and dispersion of vegetation retained in mixedwood boreal forest harvest areas. – *Forest Ecology and Management* 126: 239-254.
- Schwalter, T. D. 1995: Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. – *Forest Ecology and Management* 78: 115-125.
- Schwalter, T. D., Zhang, Y. L. & Rykken, J. J. 2003: Litter invertebrate responses to variable density thinning in Western Washington forest. – *Ecological Applications* 13(5): 1204-1211.
- Seegerström, U., Bradshaw, R., Hörnberg, G. & Bohlin, E. 1994: Disturbance history of a swamp forest refuge in Northern Sweden. – *Biological Conservation* 68: 189-196.
- Shure, D. J. & Phillips, D. L. 1991: Patch size of forest openings and arthropod populations. – *Oecologia* 86: 325-334.
- Siira-Pietikäinen, A., Haimi, J. & Siitonen, J. 2003: Short-term responses of soil macroarthropod

- community to clear felling and alternative forest regeneration methods. – *Forest Ecology and Management* 172: 339-353.
- Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H. & Haimi, J. 2001: Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. – *Canadian Journal of Forest Research* 31: 88-99.
- Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. 2000: Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. – *Forest Ecology and Management* 128: 211-225.
- Silfverberg, H. 2004: *Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae*. – *Sahlbergia* 9(1): 1-111.
- Sillett, S. C. & Goslin, M. N. 1999: Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. – *Canadian Journal of Forest Research* 29: 1204-1215.
- Simberloff, D. 2001: Management of boreal forest biodiversity – a view from the outside. – *Scandinavian Journal of Forest Research Supplementum* 3: 105-118.
- Smyth, C., Schieck, J., Boutin, S. & Wasel, S. 2005: Influence of stand size on pattern of live trees in mixedwood landscapes following fire. – *Forestry Chronicle* 81(1): 125-132.
- Spence, J. R. 2001: The new boreal forestry: adjusting timber management to accommodate biodiversity. – *Trends in Ecology and Evolution* 16(11): 591-593.
- Spence, J. R., Langor, D. W., Niemelä, J., Cárcamo, H. A. & Currie, C. R. 1996: Northern forestry and carabids: the case for concern about old-growth species. – *Annales Zoologici Fennici* 33: 173-184.
- Swanson, F. J. & Franklin, J. F. 1992: New forestry principles from ecosystem analysis of Pacific Northwest forests. – *Ecological Applications* 2: 262-274.
- Taboada, A., Kotze, D. J., Tárrega, R. & Salgado, J. M. 2006: Traditional forest management: do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? – *Forest Ecology and Management* 237: 436-449.
- Taylor, R. J. & Doran, N. 2001: Use of terrestrial invertebrates as indicators of the ecological sustainability of forest management under the Montreal Process. – *Journal of Insect Conservation* 5: 221-231.
- Thiele, H.-U. 1977: *Carabid beetles in their environments*. – Springer-Verlag, Berlin.
- Thome, D. M., Zabel, C. J. & Diller, L. V. 1999: Forest stand characteristics and reproduction of Northern spotted owls in managed north-coastal California forests. – *Journal of Wildlife Management* 63(1): 44-59.
- Tittler, R. & Hannon, S. J. 2000: Nest predation in and adjacent to cutblocks with variable tree retention. – *Forest Ecology and Management* 136: 147-157.
- Tittler, R., Hannon, S. J. & Norton, M. R. 2001: Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. – *Ecological Applications* 11(6): 1656-1666.
- Tretzel, E. 1954: Reife- und Fortpflanzungszeit bei Spinnen. – *Zeitschrift für Morphologie und Ökologie der Tiere* 42: 634-691. (In German.)
- Uetz, G. W. 1991: Habitat structure and spider foraging. – In: Bell, S. S., McCoy, E. D. & Mushinsky, H. R. (eds.), *Habitat structure. The physical arrangement of objects in space*: 325-348. Chapman & Hall, London.
- Uetz, G. W. 1977: Coexistence in a guild of wandering spiders. – *Journal of Animal Ecology* 46: 531-541.
- Ulanova, N. G. 2000: The effects of windthrow on forests at different spatial scales: a review. – *Forest Ecology and Management* 135: 155-167.
- Ulyshen, M. D., Hanula, J. L., Horn, S., Kilgo, J. C. & Moorman, C. E. 2006: The response of ground beetle (Coleoptera: Carabidae) to selection cutting in a South Carolina bottomland hardwood forest. – *Biodiversity and Conservation* 15: 261-274.
- Usher, M. B., Field, J. P. & Bedford, S. E. 1993: Biogeography and diversity of ground-dwelling arthropods in farm woodlands. – *Biodiversity Letters* 1: 54-62.
- Väisänen, R. & Biström, O. 1990: Boreal forest spiders and the preservation of biotic diversity: results from Finnish primeval forests. – *Acta Zoologica Fennica* 190: 373-378.
- Vance, C. C. & Nol, E. 2003: Temporal effects of selection logging on ground beetle communities in northern hardwood forests of eastern Canada. – *Écoscience* 10(1): 49-56.

- Vanha-Majamaa, I. & Jalonen, J. 2001: Green tree retention in Fennoscandian forestry. – Scandinavian Journal of Forest Research Supplementum 3: 79-90.
- Varady-Szabo, H. & Buddle, C. M. 2006: On the relationship between ground-dwelling spider (Araneae) assemblages and dead wood in a northern sugar maple forest. – Biodiversity and Conservation 15(13): 4119-4141.
- Virkkala, R., Korhonen, K. T., Haapanen, R. & Aapala, K. 2000: Metsien ja soiden suojelutilanne metsä- ja suokasvillisuusvyöhykkeittäin valtakunnan metsien 8. inventoinnin perusteella. – Suomen ympäristö 395. Suomen ympäristökeskus, Metsäntutkimuslaitos. (In Finnish.)
- Vlijm, L. & Kessler-Geschiere, M. 1967: The phenology and habitat of *Pardosa monticola*, *P. nigripes* and *P. pullata* (Araneae, Lycosidae). – The Journal of Animal Ecology 36(1): 31-56.
- Vlijm, L. & Richter, C. J. J. 1966: Activity fluctuations of *Pardosa lugubris* (Walckenaer), Araneae Lycosidae, during the breeding-season. – Entomologische Berichten 26: 222-230.
- Werner, S. H. & Raffa, K. F. 2000: Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. – Forest Ecology and Management 139: 135-155.
- White, G.C. & Bennets, R.E. 1996: Analysis of frequency count data using the negative binomial distribution. – Ecology 77(8): 2549-2557.
- Willett, T. R. 2001: Spiders and other arthropods as indicators in old-growth versus logged Redwood stands. – Restoration Ecology 9(4): 410-420.
- Zenner, E. K. 2000: Do residual trees increase structural complexity in Pacific Northwest coniferous forests? – Ecological Applications 10(3): 800-810.
- Zimmerman, G.M., Goetz, H. & Mielke Jr., P.W. 1985: Use of an improved statistical method for group comparisons to study effects of prairie fire. – Ecology 66: 606-611.