

The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests

Jari Niemelä · Matti Koivula · D. Johan Kotze

Received: 18 November 2005 / Accepted: 20 March 2006 / Published online: 1 November 2006
© Springer Science+Business Media B.V. 2006

Abstract As compared to natural forests, managed boreal forests are younger, more homogeneous in terms of tree age and species composition, and consist of smaller fragments. Here we examine the effects of such characteristics caused by forestry on carabid beetles (Coleoptera, Carabidae) in the boreal region. The main results are the following. (1) Fragmentation of forests and the size of a fragment appear not to be crucial for the survival of the majority of forest carabids, as they tend to be distributed over various successional stages, but species requiring old-growth habitats suffer. (2) For carabids there appear to be no or very few edge specialist species, and forest-open land edges appear to be effective barriers for species associated with forest or open habitat. However, generalist species easily cross the edge, and edges of forest fragments may be invaded by species from the surrounding open habitat. (3) Habitat change following clear-cutting dramatically changes the composition of carabid assemblages: species restricted to mature forests disappear and open-habitat species invade, while habitat generalists survive at least in the short term. Carabid diversity can probably best be maintained if forest management mimics natural processes, maintains natural structures and includes the natural composition of vegetation and other structural elements

(such as dead wood) within the stands, provided that these forest features can be maintained and recreated through forest management practices. At a larger scale, the whole spectrum of forest types and ages (especially old-growth forests), and different successional processes (especially fire) should be maintained. These require the development and use of innovative logging methods, and the planning, implementation, and assessment of landscape-scale ecological management strategies.

Keywords Carabidae · Forest management · Boreal forests

Introduction

Forestry is simplifying tree species composition, homogenising tree age structure, and fragmenting forested landscapes in many parts of the vast boreal region (Bonan and Shugart 1989). As a consequence, managed forests are younger overall, consist of smaller fragments with more edge habitat, and are exposed to novel disturbance regimes. For example, the proportion of old-growth forest in state-owned land decreased from 44% to 7% between 1910 and 1990 in Sweden (Linder and Östlund 1992), and forestry rather than wildfire is the main stand-replacing factor initiating secondary succession (Esseen et al. 1997). Similar changes have occurred in many North American boreal forests (Loope 1991).

These changes have had clear impacts on the boreal biota. Managed forests host fewer forest-specialist species and lower abundances of many common species than do unmanaged old-growth forests (here,

J. Niemelä (✉) · D. J. Kotze
Department of Biological and Environmental Sciences,
University of Helsinki, P.O. Box 65, Viikinkaari 1,
FI-00014 University of Helsinki, Finland
e-mail: jari.niemela@helsinki.fi

M. Koivula
Department of Renewable Resources, University
of Alberta, 4-42 ESB, Edmonton, AB T6G 2E3, Canada

forests in which the dominant trees are older than 150 years and with no management for at least the past 100 years). Examples include, in addition to carabid beetles (Coleoptera, Carabidae) discussed here, bryophytes and epiphytic lichens (Andersson and Hytteborn 1991; Kuusinen 1994, 1996; Dettki and Esseen 1998), beetles living in and on dead wood (Väisänen et al. 1993; Siitonen and Martikainen 1994; Jonsell et al. 1998) and mycetophilid flies (Økland 1994).

Carabid beetles are among the best studied taxa regarding the effects of forest management on the boreal biota. Despite their general abundance it has often been difficult to model the habitat requirements of these beetles. Thus, in several studies cited in this paper carabids have been divided into “forest”, “generalist” and “open habitat” species. However, as is evident from Table 1 and the baseline literature (e.g. Lindroth 1985, 1986, 1992), such a classification is context specific. For instance, the term “forest” can be understood as meaning any area where trees grow, thus including e.g. clear-cuts, recent burns and other regenerating stands. Thus, a comparison between agricultural land and various treed areas (from clear-cuts to mature forest) may suggest that *Calathus micropterus* (Duftschmid) is a forest species, even a specialist, as in the data presented in Table 1 only 5% of the specimens were caught from agricultural habitat. However, in many studies “forest” is defined in a narrower sense: a treed area with a closed canopy and dominant trees being at least a few decades old. The younger regenerating phases, on the other hand, represent “open habitat”. From this perspective, *C. micropterus* is classified differently. Table 1 shows that this species is equally abundantly caught from clear-cuts (logged 1–3 years ago) and unlogged mature forests, suggesting a forest/open-habitat generalist life style. To conclude, species classifications according to their habitat associations should be done by carefully considering the nature of the compared habitats.

As the focus of this review is on forests, we use the term “forest” to indicate a treed area with closed canopy and (nearly) mature trees, whereas younger successional phases are referred to as “open” habitats. Accordingly, Table 1 shows a literature and field-data based classification of most of the abundant southern Finnish forest-associated carabid species to “forest”, “open habitat” and “generalist” species.

In this review we evaluate the effects of forestry on individual carabid species and communities in the boreal region. We will also identify threats, and propose ways to ameliorate the adverse effects of forestry on forest-dwelling carabid beetles.

Effects of forestry on carabids

Forestry practices often result in the fragmentation of the original forest landscape. Habitat fragmentation is the partitioning of continuous habitat into small remnants (e.g., Saunders et al. 1991; Hunter 1996; Haila 1999; Debinski and Holt 2000). Habitat loss is often included into the concept of fragmentation, and it is usually difficult to separate the effects of habitat loss from that of fragmentation per se on the biota. Here, we first focus on the effects of fragmentation, i.e. isolation, size, the configuration of the habitat remnants, and edge effects. Thereafter, we discuss the consequences of habitat loss on carabid beetles, and examine how species with different habitat affinities are affected.

Fragmentation

Forest fragmentation affects carabid assemblages in a myriad of ways (Niemelä 2001). For example, Niemelä et al. (1988) compared different-sized fragments of coniferous forest surrounded by clear-cut areas in Finland and found that although there were no differences in species richness, the abundance of many generalist and open habitat species was higher in small (<5 ha) than in large (>30 ha) forest remnants. In other studies, species richness increased with decreasing size of forest patches surrounded by agricultural land (Niemelä and Halme 1992; Halme and Niemelä 1993): small fragments (0.5–3.0 ha) had 18 species, larger ones (9.6–21.5 ha) had 13 species, while continuous, unfragmented forest had only 11 species. These differences are most likely attributed to the small fragments being more open and grassier, and thus more favourable for generalist and open habitat carabid species primarily residing in the surrounding agricultural grasslands or open clear-cut sites. Similar results have been reported from countries in other biogeographical regions, e.g. England (Usher et al. 1993), France (Fournier and Loreau 2001) and Hungary (Magura et al. 2001). In addition, Usher et al. (1993) noted that the number of species was affected by the shape of the forest patch so that remnants with high edge-to-area ratios contained more species, probably because of higher invasion rates from the matrix.

Contrary to the above studies, asphalt-isolated Finnish forest patches of 0.2–1.8 ha in size hosted fewer species than larger ones (0.5–37.4 ha) (Koivula and Vermeulen 2005). Similarly, a study in the Canadian temperate region showed that carabid species richness increased with increasing forest fragment size (Burke and Goulet 1998). The smallest fragment with a forest core area of 0.3 ha had only two carabid species,

Table 1 Literature and field-data based division of some Finnish boreal forest-associated carabids into habitat affinity groups

Species	Habitat, literature		Habitat, field data (only for species with $n > 20$)			Habitat association	
	Forest	Open	Farmland vs. forest (% in forest)	Clear-cut vs. mature forest (% in mature)	Young vs. old regener. (% in older)	Literature assoc.	Field-data assoc.
<i>Agonum fuliginosum</i> (Panzer, 1809)	X	X	(98) 37.7	(326) 31.0	(114) 78.1	G	G
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)	–	X	–	(173) 1.7	–	O	O
<i>Amara brunnea</i> (Gyllenhal, 1810)	X	–	(27) 100.0	(51) 74.5	–	F	F (G)
<i>Amara communis</i> (Panzer, 1797)	X	X	(55) 58.8	–	–	(G) O	G (O)
<i>Amara eurynota</i> (Panzer, 1797)	–	X	(107) 4.3	–	–	O	O
<i>Amara lunicollis</i> (Schiöde, 1837)	–	X	(22) 8.1	(162) 0.6	(67) 1.5	O	O
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	–	X	–	–	–	O	–
<i>Badister bullatus</i> (Schrank, 1798)	X	X	–	–	–	G	–
<i>Bembidion bruxellense</i> Wesmaël, 1835	–	X	–	–	–	O	–
<i>Bembidion guttula</i> (Fabricius, 1792)	–	X	–	–	–	O	–
<i>Bembidion lampros</i> (Herbst, 1784)	–	X	–	–	–	O	–
<i>Bembidion quadrimaculatum</i> (Linnaeus, 1761)	–	X	–	–	–	O	–
<i>Bradycellus caucasicus</i> (Chaudoir, 1846)	–	X	–	–	–	O	–
<i>Calathus erratus</i> (Sahlberg, 1827)	–	X	–	–	–	O	–
<i>Calathus melanocephalus</i> (Linnaeus, 1758)	–	X	–	–	–	O	–
<i>Calathus micropterus</i> (Duftschmid, 1812)	X	–	(811) 95.1	(3313) 51.5	(634) 93.2	F	F (G)
<i>Carabus cancellatus</i> (Illiger, 1798)	–	X	–	(11) 9.1	–	O	O
<i>Carabus glabratus</i> (Paykull, 1790)	X	–	(38) 88.2	(218) 68.8	(72) 47.2	F	G (F)
<i>Carabus granulatus</i> (Linnaeus, 1758)	X	X	(140) 6.3	–	–	G	O
<i>Carabus hortensis</i> (Linnaeus, 1758)	X	–	(878) 91.3	(129) 95.3	(21) 90.5	F	F
<i>Carabus nemoralis</i> (Müller, 1764)	X	X	(122) 46.7	–	–	G	G
<i>Carabus nitens</i> (Linnaeus, 1758)	–	X	–	–	–	O	–
<i>Carabus violaceus</i> (Linnaeus, 1758)	X	–	–	–	–	F	–
<i>Cicindela campestris</i> (Linnaeus, 1758)	–	X	–	(55) 3.6	–	O	O
<i>Clivina fossor</i> (Linnaeus, 1758)	–	X	–	–	–	O	–
<i>Cychrus caraboides</i> (Linnaeus, 1758)	X	–	(43) 82.4	(98) 72.4	–	F	F (G)
<i>Dyschirius globosus</i> (Herbst, 1784)	–	X	–	–	–	O	–
<i>Harpalus affinis</i> (Schrank, 1781)	–	X	–	–	–	O	–
<i>Harpalus laevipes</i> Zetterstedt, 1828	X	X	(58) 86.4	(79) 19.0	–	G	G
<i>Harpalus latus</i> (Linnaeus, 1758)	–	X	–	–	–	O	–
<i>Harpalus rufibarbis</i> (Fabricius, 1792)	–	X	(119) 8.3	–	–	O	O
<i>Harpalus rufipes</i> (Degeer, 1774)	–	X	(409) 2.5	–	–	O	O
<i>Harpalus tardus</i> (Panzer, 1797)	–	X	–	–	–	O	–
<i>Leistus ferrugineus</i> (Linnaeus, 1758)	X	X	–	–	–	G	–
<i>Leistus terminatus</i> (Hellwig, 1793)	X	–	–	(20) 55.0	–	F	G
<i>Loricera pilicornis</i> (Fabricius, 1775)	X	X	–	–	–	G	–
<i>Notiophilus aquaticus</i> (Linnaeus, 1758)	–	X	–	–	–	O	–
<i>Notiophilus biguttatus</i> (Fabricius, 1779)	X	–	–	(126) 57.9	–	F	G
<i>Notiophilus germinyi</i> Fabricius, 1863	–	X	–	–	–	O	–
<i>Notiophilus palustris</i> (Duftschmid, 1812)	X	X	–	–	(20) 5.0	G	O
<i>Patrobis assimilis</i> (Chaudoir, 1844)	X	X	(122) 5.0	(49) 30.6	(35) 94.3	G	G (F)
<i>Patrobis atrorufus</i> (Ström, 1768)	X	X	(961) 29.6	–	–	G	G (O)
<i>Platynus mannerheimii</i> (Dejean, 1828)	X	–	–	–	–	F	–
<i>Platynus assimilis</i> (Paykull, 1790)	X	–	–	(20) 50.0	–	F	G
<i>Poecilus cupreus</i> (Linnaeus, 1758)	–	X	(402) 7.4	(29) 0.0	–	O	O
<i>Poecilus versicolor</i> (Sturm, 1824)	–	X	(69) 4.4	–	(27) 0.0	O	O
<i>Pterostichus adstrictus</i> Eschscholtz, 1823	–	X	–	(73) 0.0	–	O	O
<i>Pterostichus crenatus</i> (Duftschmid, 1812)	–	X	–	–	–	O	–
<i>Pterostichus diligens</i> (Sturm, 1824)	X	X	–	(24) 4.2	(65) 9.2	G	O
<i>Pterostichus melanarius</i> (Illiger, 1798)	X	X	(3453) 24.2	–	–	G	G (O)
<i>Pterostichus niger</i> (Schaller, 1783)	X	X	(1883) 39.7	(198) 36.4	(399) 6.3	G	G (O)
<i>Pterostichus nigrita</i> (Paykull, 1790) ^a	X	X	–	(22) 0.0	–	G	O
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	X	–	(352) 82.7	(2189) 34.9	(239) 35.6	F	G
<i>Pterostichus strenuus</i> (Panzer, 1797)	X	X	(26) 39.8	(34) 14.7	(30) 16.7	G	G (O)
<i>Synuchus vivalis</i> (Illiger, 1798)	X	X	–	–	–	G	–
<i>Trechus rivularis</i> (Gyllenhal, 1810)	X	–	–	–	–	F	–

Table 1 continued

Species	Habitat, literature		Habitat, field data (only for species with $n > 20$)			Habitat association	
	Forest	Open	Farmland vs. forest (% in forest)	Clear-cut vs. mature forest (% in mature)	Young vs. old regener. (% in older)	Literature assoc.	Field-data assoc.
<i>Trechus rubens</i> (Fabricius, 1792)	X	X	–	–	–	G	–
<i>Trechus secalis</i> (Paykull, 1790)	X	X	(466) 36.0	(374) 25.4	(118) 54.2	G	G
<i>Trichocellus placidus</i> (Gyllenhal, 1827)	–	X	–	(51) 0.0	–	O	O

“Forest” means treed areas with closed canopy except in farmland-forest comparison; “open habitat” refers to regenerating but not yet closed stands (unless otherwise specified). The first two columns show whether a given species is most often found in forests or in open phases of succession (a generalist is indicated with an “X” in both columns) based on Lindroth (1985, 1986, 1992) and Koivula (2001). The next three columns show results from three field data sets: (number of individuals in parentheses), % indicates proportion in closed canopy forests. The columns are (1) farmland vs. forested habitat, including clear-cuts (a total of 96 samples; percentages calculated from adjusted catch; data from Koivula, Niemelä & Kotze unpubl.); (2) mature spruce forest vs. recent clear-cuts (8 replicates for both habitat types; data from Koivula 2002a); and (3) young (5–10 years since clear-cutting) vs. old (30–60 years since clear-cutting) clear-cuts (8 replicates for both age classes; data from Koivula et al. 2002). The two last columns show habitat classifications based on the literature and on field data: F = species is associated with closed canopy forests; G = species is abundantly found in both open and closed phases of succession; O = species is associated with open phases of succession; letters in parentheses indicate alternative classifications for a few ambiguous cases

^aData include a possibility for *Pterostichus rhaeticus* Heer

while there were 16–17 species in fragments >30 ha, and 22 species in continuous forest. However, isolation confounded the results of Burke and Goulet (1998), as the lowest species richness was found in small, isolated fragments, while the species richness of less isolated small fragments was comparable to that of large fragments. Yet, some studies report no clear effects of fragmentation on carabids. Abildsnes and Tømmerås (2000) concluded that experimentally fragmented forests (40 m × 40 m and 150 m × 150 m clear-cut sites) did not result in clear area effects and that isolation affected forest-dwelling species only slightly. Time since fragmentation may be a possible reason for this apparent lack of response: sampling was done only one year after clearing the forest (Abildsnes and Tømmerås 2000).

Simply counting the number of species, however, provides little information on the specific effects of fragmentation. Species richness used as a measure of conservation value may be misleading because disturbances may favour widespread and abundant generalists, leading to increased species richness as can be the case for carabids (e.g. Niemelä 1997). In contrast, analysing the responses of individual species is more likely to provide an understanding of the processes that lead to the extinction or persistence in fragmented landscapes (Davies and Margules 1998; Ewers and Didham 2006). For example, Koivula and Vermeulen (2005) showed that the response of *Pterostichus oblongopunctatus* (F.) to forest patch size in southern Finland depended on habitat quality that was indicated by tree-species composition and field-layer vegetation.

Based on current evidence, forest fragmentation and the size of a fragment appear not to be crucial for the survival of the majority of forest carabids, as they tend to be distributed over various successional stages (i.e. they are generalists; Ås 1993; Davies and Margules 1998; Gandhi et al. 2001). However, sensitive species requiring certain structural elements of old-growth forests, such as abundant large-sized dead wood, lush patches of mesic vegetation or wet spruce mires, or micro-climatic conditions created by closed canopy, suffer from forest fragmentation. In a Finnish study, many forest species were absent from small (0.5–3.0 ha) fragments, probably because of a lack of suitable habitat (Halme and Niemelä 1993). Similarly, Bauer (1989) and Usher et al. (1993) reported that individual specialist species responded positively to fragment size so that their species richness increased with increasing fragment size. Likewise, in Halme and Niemelä’s (1993) study the strictest of forest species, most notably *Carabus glabratus* Paykull and *C. violaceus* L., occurred only in continuous forests. These species are flightless, which probably hampers their movements across grassland surrounding the studied forest patches (see Riecken and Rath 1996).

Edge effects

Fragmentation leads to a decreasing proportion of interior and an increasing proportion of edge habitat (e.g., Murcia 1995; Haila 1999; Matlack and Litvaitis 1999). Changes in abiotic and biotic conditions at the edge are called ‘edge effects’. These include changes in

wind, humidity, radiation, predation, parasitism and species interactions (Saunders et al. 1991; Andr en 1995; Chen et al. 1995; Murcia 1995; Donovan et al. 1997; Laurance 2000). The extent of these effects is strongly influenced by edge structure. For example, Didham and Lawton (1999) showed that edge effect penetration distances of many variables of microclimate and vegetation structure can be as much as five times greater at open edges lacking sheltering vegetation than at closed, densely vegetated edges.

It has been shown that forest edges harbour a rich invertebrate fauna (e.g. Helle and Muona 1985; Jokim aki et al. 1998) that is a mixture of species found on either side of the edge zone (Kotze and Samways 1999). However, species requiring interior habitat suffer from edge effects (Stevens and Husband 1998) and, consequently, such species may be lost if fragments become too small and dominated by edge habitat (Haila 1999). To find ways to counteract the negative effects associated with edges it is important to understand how species respond to conditions at habitat edges (Haila et al. 1994).

For boreal carabids there appear to be no or very few edge specialist species (Spence et al. 1996; Abildnes and T ommer as 2000; Heli ol a et al. 2001; Koivula et al. 2004). Similar observations have been made in tropical systems (Didham 1997) and in the Mediterranean region (Taboada et al. 2004). Very small forest patches (a few tens of m², or 20–40 m wide forest strips) within clear-cuts have been shown to host a similar carabid fauna to clear-cuts (Koivula 2002a), i.e. such patches do not represent forest for carabids.

Some reports indicate that edges of forest fragments are easily invaded by species from the surrounding matrix, and some species may continue through the edge ‘filter’ into the forest interior (Spence et al. 1996; Koivula et al. 2004). Contrary to this, Heli ol a et al. (2001) found that carabid assemblages in mature spruce forests vs. clear-cuts were fairly clearly separated by the edge, with open-habitat species being restricted to the clear-cut.

As regards the distribution of forest species across edges, Koivula et al. (2004) showed that forest species rarely entered the field, and if they did, only to a maximum distance of 20 m. For farmland species the forest edge was even more abrupt, as very few individuals crossed the edge, and they tended to avoid the edge zone by decreasing in abundance 5–10 m from the forest patch.

For the conservation of intact forest habitat, a crucial question is how far into the forest interior the edge effects reach. Open-habitat carabids are reluctant to enter the forest (Heli ol a et al. 2001), and if they do,

they usually penetrate only tens of metres into the forest (Spence et al. 1996; Koivula et al. 2004). Thus, to the extent that it is possible to generalise from these studies, it appears that carabid communities of forest fragments of reasonable size (a few ha) remain more or less intact, and that the edge functions as an efficient barrier that stops open-habitat species from invading the fragment interior (see also H anggi and Baur 1998; Kotze and Samways 1999). Edge effects thus apparently do not make boreal forest fragments vulnerable to invasion by native open-habitat carabids.

Although native open-habitat carabids do not seem to penetrate forests, alien invasive species may be an exception, and therefore of concern for the conservation of native carabid assemblages. For example, Niemel a and Spence (1999) reported that the introduced *Pterostichus melanarius* Ill., an open-habitat to generalist species in Fennoscandia (Lindroth 1986), was spreading from road verges into mature forests in Canada.

Habitat loss and change

Carabid species richness and the abundances of generalist and open-habitat species usually increase following forest cutting (Niemel a et al. 1988, 1993a, b; Halme and Niemel a 1993; Haila et al. 1994; Spence et al. 1996; Beaudry et al. 1997; Heli ol a et al. 2001; Koivula 2002a, b; Sippola et al. 2002; Pearce et al. 2003; de Warnaffe and Lebrun 2004). The open, dry and warm clear-cuts are favoured by many carabid species usually found in grasslands and other similar habitats (e.g. genera *Harpalus* and *Amara*), while only a few species are associated with the dark and cool spruce forest (Niemel a 1993; see also Table 1). In addition to carabids, clear-cuts are also rich in species of spiders (Pajunen et al. 1995), ants (Punttila et al. 1991, 1994), butterflies (V ais anen 1995) and sun-loving dead-wood-dependent beetles (Martikainen 2001).

Clear-cutting affects the abundance of forest-associated species negatively (Niemel a et al. 1993a, b; Langor et al. 1994; Spence et al. 1996; Werner and Raffa 2000). However, such species may occur in recently clear-cut sites for a few years (Koivula 2002a, b). This observation has at least three explanations. First, individuals of forest species caught in the clear-cut may be wanderers from nearby mature stands (Spence et al. 1996). This may be the case, for example, in sites close to mature-stand edges (Koivula 2002b; Koivula et al. 2002). Second, catches of forest species may represent populations on their way to local extinction (or drastic decrease). Because some carabids may live for at least 2–3 years (van Dijk 1996), these species can persist for

some time in the clear-cuts. For example, populations of *Carabus hortensis* L., *Cychrus caraboides* L., *Platynus mannerheimii* Dej. and *Calathus micropterus* (Dft.) survived at least 2–3 years in Finnish clear-cuts (Koivula 2002a, b) but either decreased or disappeared later on (Niemelä et al. 1993a; Koivula et al. 2002; see also Abildsnes and Tømmerås 2000 and Table 1). Third, some species with a more generalist life style may be able to tolerate natural disturbances (e.g. windthrows and forest fires) better and may, therefore, survive in clear-cut sites.

In clear-cut sites, the ‘pioneer’ carabid assemblages gradually change as the succession of vegetation proceeds and the relict populations of forest species disappear. A drastic change usually occurs at canopy closure that takes place in the boreal region ca. 20–30 years after clear-cutting (Niemelä et al. 1996; Koivula et al. 2002; Koivula and Niemelä 2002; see also Table 1). After canopy closure, open-habitat species decline rapidly and species requiring mature forest become dominant.

Interestingly, the closed-canopy boreal forest appears to be a rather hostile environment for many carabid species, as only a few species are able to thrive (Koivula et al. 2002), resulting in peculiar species-abundance distributions in which there is a gap between the dominant species and the scarce ones (Niemelä 1993). For carabids, therefore, boreal forests may be an adversity or A-selected environment (Greenslade 1983) with low species richness (but not necessarily low densities). Such specialist species are rather few in the boreal forest making up <10% of the total forest carabid fauna (Niemelä 1997). Today, these species are in danger because of forestry.

Forest specialists are sensitive to habitat changes caused by forestry

Most forest-dwelling carabids require specific habitat elements (Niemelä et al. 1996; Koivula 2001; Koivula and Niemelä 2002; de Warnaffe and Lebrun 2004; Work et al. 2004), with many species showing associations with certain micro-site characteristics (Heliölä et al. 2001; Koivula 2002a, b; Koivula et al. 2002). These species can be considered forest-habitat specialists. For example, the circumboreal spruce-mire specialist *Platynus mannerheimii* Dej. requires wet sites dominated by *Sphagnum* mosses within mature coniferous forest (Niemelä et al. 1987).

Another important factor affecting carabid distribution is the amount of leaf litter, indicating the importance of scattered deciduous trees within coniferous-dominated stands (Niemelä et al. 1992; Koivula

et al. 1999; Heliölä et al. 2001; Koivula et al. 2002; see also Poole et al. 2003; Magura et al. 2005). Deciduous-tree admixtures, together with spruce mires, are also important for epiphytic lichens, land snails and dead-wood-dependent beetles (Kuusinen 1996; Esseen et al. 1997; Niemelä 1997; Martikainen 2000; Siitonen and Saaristo 2000).

Due to their specialised habitat requirements, species associated with old-growth forests are at risk in the modern managed forest landscape. In the Palaearctic region, such carabid species are few but include, for example, *Carabus hortensis* L., *Cychrus caraboides* L. and *Platynus mannerheimii* that are typically found in mature coniferous forest (Koivula 2001, 2002a; see also Niemelä et al. 1993a and Table 1). To demonstrate the responses of such species to management, Koivula and Niemelä (2002) studied the responses of several species to micro-site variation, forest edges and logging, and presented a graphic representation depicting examples of the responses of a few forest carabid species to forestry (reproduced in Fig. 1; for a classification of these species, see Table 1). This model is rather similar to that of Spence et al. (1996) but with two major differences: firstly, open-habitat species do not colonise large forest stands (Heliölä et al. 2001), and secondly, the majority of forest species are assumed to survive in the clear-cut sites adjacent to mature forest stands.

According to this model some species, such as the forest species *Calathus micropterus*, suffer from clear-cutting and decrease in abundance (Fig. 1). Also the abundance of *Carabus hortensis* is lower in the clear-cut than in mature forest (Koivula 2002a), but individuals best persist in specific micro-sites, such as retained tree groups or in mesic and luxuriant clear-cut sites (not shown). These two species thus vary remarkably in abundance along the successional gradient but persist over the early open phases in low abundances (Koivula and Niemelä 2002). The latter species may demand lush vegetated patches to survive, however. The model also includes an effect of distance from mature forest. *Calathus micropterus* decreases in abundance toward clear-cut central areas (Fig. 1). Open-habitat species, such as *Pterostichus adstrictus* Eschz., on the other hand, show an opposite trend by increasing in abundance in the clear-cut with distance from mature forest edges (Heliölä et al. 2001; Koivula and Niemelä 2002; Fig. 1). Some species are forest generalists with varying degrees of micro-habitat requirements. For example, *Agonum fuliginosum* (Pz.) appears to be a generalist with respect to canopy closure, but is dependent on *Sphagnum* mires or other moist micro-sites (Fig. 1; see also discussion on *C. hortensis* above). Thus, if any mire habitat remains

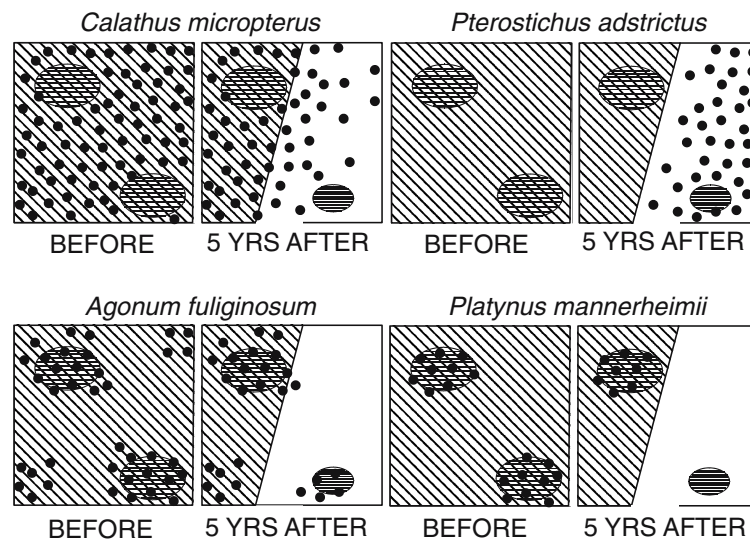


Fig. 1 Graphic model for four boreal forest carabid species showing their responses to micro-site characteristics (here, spruce mires), edge distance and clear-cutting within 1-ha forest blocks. The situations before and 5 years after partially clear-cutting are shown. Shaded sections are unlogged mature spruce

forest (*diagonal lines*) or spruce mires (*horizontal lines*), white areas are clear-cuts, and black dots indicate the presence of a given species (more densely placed dots indicate higher abundance). For species classification and model interpretation, see the text

in the clear-cut, *A. fuliginosum* will also persist there. Another mire specialist, *Platynus mannerheimii*, on the other hand, disappears from the clear-cut, as it seems to require closed canopy forest (Niemelä et al. 1987, 1993a, Fig. 1).

Modified harvesting methods have a lower impact on carabids

In recent years, harvesting practices have changed in the boreal forests of Fennoscandia and Canada (e.g. Hallman et al. 1996; Angelstam 1997; Schneider 2002). Various new practices intended to be environmentally sound have been developed (e.g. Vanha-Majamaa and Jalonen 2001), all with the intention of leaving more live and dead wood in the forest. The question is—do these practices better maintain the biota of mature forests than does clear-cutting?

One of the alternative logging methods in Fennoscandia is single-tree thinning and gap felling, mimicking wind-throws. In the short term, thinning and the creation of such small gaps (3 openings/ha, each 30–50 m in diameter) only moderately changed the forest carabid assemblage, while traditional clear-cutting and retention felling (2–3 groups of 10–30 retained trees/ha) caused more profound changes (Koivula 2002a, b; Koivula and Niemelä 2002, 2003; see also Atlegrim et al. 1997). The proportion of retained trees (70%–90%) in these thinned and gap-felled stands may provide enough canopy cover even for the more sen-

sitive forest species. From a longer-term study in the temperate forests of Oregon, Peck and Niwa (2004) reported that no differences in total abundance of carabids or species richness were found between stands thinned 16–41 years prior and unthinned stands, indicating that thinning has only minor effects on carabid communities. Overall, gap felling has been shown to maintain the original assemblages better than large clear-cuts (Koivula 2002a).

Logging methods form a continuum from clear-cutting and retaining small groups of trees (large changes in carabid assemblages) to thinning and gap felling (smaller changes in carabid assemblages). This pattern is highlighted by examining the response of open-habitat carabids to canopy cover (Fig. 2). Here, control (unlogged) and thinned stands (with ca. 400–1000 >1.3-m tall trees/ha) only rarely hosted open-habitat carabids, whereas gap felling (ca. 50% of trees removed in three 40 m × 40 m patches per ha) hosted considerably more individuals. Retention felling (with 10–30 trees in 3 groups/ha) and clear-cutting host these carabids abundantly (Fig. 2), indicating stronger changes compared to logging methods with more retention.

Moreover, Vance and Nol (2003) reported that carabid communities in stands harvested by single-tree-selection cutting 15–20 years previously contained a species composition similar to un-logged mature stands, suggesting few long-term effects on the carabid biota after the first rotation. Furthermore, Moore et al. (2004) showed that selective cutting and strip clear-cutting had no significant impacts on species diversity

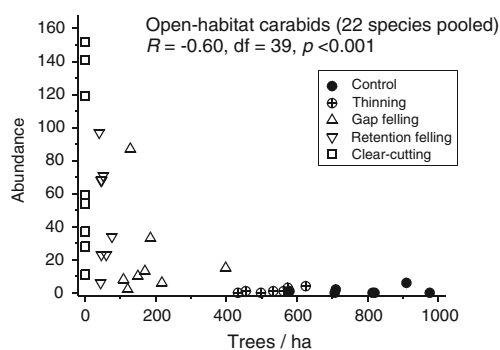


Fig. 2 The abundance of open-habitat carabids, plotted against a gradient of an increasing amount of retained trees (*horizontal axis*). Sampling was done in 40 differently logged spruce-forest stands in south-central Finland during second and third post-harvest summers. Logging methods were control (unlogged), thinning, gap and retention felling, and clear-cutting. Samples from the same stand over the 2 years were pooled. Data from Koivula (2002a, b)

and richness 6–13 years after treatment, yet some species were more abundant in either the managed forests or the control sites. Thus, retention of components that help sensitive species to persist in the managed landscape and avoiding homogenisation of stands are preferred management practices from the point of view of biodiversity (Law and Dickman 1998; Lindenmeyer and Franklin 2002). Preliminary estimates from Finland indicate that the harvesting costs per harvested timber unit in gap felling and retention felling are not much higher as compared to traditional clear-cutting.

Above we have demonstrated that forestry practices indeed affect carabid assemblages, but that the intensity of these practices determines the rate of change. A critical question remains: how persistent are these changes following forestry practices (Niemelä 1999)? More specifically, do carabid assemblages recover after timber harvesting? If they do, and all species re-colonise the harvested sites some time during succession, we may be able to maintain carabid assemblages of natural forest by long enough rotations and by leaving source areas for colonisation. If, however, recovery does not take place, forest tracts close by and of reasonable size (at least a few ha) should be left intact to provide habitat for forest-dwelling carabids. What evidence is there to illuminate this question?

A Canadian study supports the recovery view by showing that carabid assemblages in stands selectively logged 15–20 years prior to the study had started to recover towards assemblages in mature stands (Vance and Nol 2003). Also, Heyborne et al. (2003) reported indications of recovery, as beetle assemblages (including carabids) paralleled changes in plant communities from young herb-stage regrowth to

mature forest during a 17-year study. Evidence is, however, equivocal as Niemelä et al. (1993a, b) reported that carabid assemblages did not recover even after 25–30 years post-harvest in western Canada. However, Koivula et al. (2002) showed that the carabid assemblages changed drastically 20–30 years since clear-cutting in Finland. Stands 60 years of age hosted virtually no open-habitat carabids, and the carabid assemblage closely resembled faunas reported from mature forests. Thus, it remains unclear whether Niemelä et al. (1993a) studied the carabid assemblages over a long enough chronosequence to document recovery. Furthermore, differences between the studies may be due to the history of forestry activities in these regions. Heavy forest use over a long period of time (e.g. in Finland) may have resulted in the most sensitive forest species having disappeared (see Kotze and O'Hara 2003), causing less changes and a rapid recovery in carabid assemblages after current harvesting as compared to sites where pristine forest in being logged, e.g. western Canada (Niemelä et al. 1993a).

The role of spatial scale for forest carabids

The maintenance and recovery of mature-forest species in the managed forest landscape requires attention at two interlinked spatial scales, viz. landscape and stand scale (Work et al. 2004). At the landscape level, conservation of a range of forest types and age classes is required to maintain the diversity of ground-dwelling beetles (Werner and Raffa 2000). For strict old-growth species, such as *Platynus mannerheimii*, reasonable amounts of old-growth stands should be retained to act as reservoirs and sources of colonists (Spence et al. 1996; Niemelä 1997, 1999; Werner and Raffa 2000). Also, several other species associated with mature forests benefit from retaining intact closed-canopy forests, e.g. *Carabus hortensis* and *Cychrus caraboides*. Thus, such habitats must be present in the landscape.

The spacing of suitable habitat patches in the landscape is crucial for species with limited dispersal powers (Desender et al. 1999), such as *Carabus hortensis* and *Cychrus caraboides* (Lindroth 1985, 1986). Within a fragmented landscape, the dispersal abilities of species and the distance between favoured habitat patches are critical for their survival (den Boer 1990a, b; Fahrig and Merriam 1994; With et al. 1997; Hanski 1999; Niemelä 2001). Flightless carabids may move up to a few hundred metres by foot (Mascanzoni and Wallin 1986), but these movements are seldom target-oriented at the scale of tens of metres (Wallin 1986). Koivula (2001) and Koivula et al. (2002) reported that

the abundance of forest-dwelling carabids decreased in clear-cuts and sapling stands as the size of the clear-cuts and its distance from adjacent over 40-year-old stands increased. These findings indicate that the spatial configuration of mature and maturing stands in the managed forest landscape is of great importance to forest-dwelling carabids.

The retained old forest stands should include specific structural features (Werner and Raffa 2000). These include coarse woody debris (Work et al. 2004) that is an important habitat for many carabids (Pearce et al. 2003; Koivula et al. 2005). Moreover, *Platynus mannerheimii* requires *Sphagnum*-covered patches within mature spruce forest to survive (Niemelä et al. 1987; Liebherr and Song 2002). At the stand level, the new logging methods that leave more trees in the harvested stands may favour some forest species because retained trees shelter the ground layer from direct sunlight and, to some extent, from microclimatic alterations (Jalonen and Vanha-Majamaa 2001). However, the sheltering efficiency depends on the number of trees retained, as indicated by the negative relationship between the abundance of generalist carabids and increasing tree density (Koivula 2002b), and the degree of exposure and geographical location of the site. The most sensitive sites in spruce forests, such as spruce mires, should be left intact or managed carefully. Forest management should also aim at minimising the adverse effects of edges on forest specialist species, for example by leaving large enough fragments for forest-interior specialists to persist (Spence et al. 1996; Burke and Goulet 1998).

Those open-habitat carabid species that thrive in forest openings, on the other hand, are not at risk in the boreal forests of today, as the large areas of clear-cut habitat and young sapling stands function as source habitats for them (e.g. Spence et al. 1996; Koivula 2006). In Finland, such species are commonly found even in isolated clear-cuts (over 200 m from the nearest clear-cut; Koivula 2002b). In addition to dispersal by flight, the dense forest-road network in Finland (Västilä and Herrala-Ylinen 1999; Martikainen 2000) enhances the colonisation of recent clear-cuts by open-habitat species by offering dispersal corridors (Koivula 2003, 2006).

Changing forestry to become compatible with the maintenance of carabid diversity

In this review we showed that there are, broadly speaking, three types of carabid beetle responses to forestry practices. In strongly managed stands, such as

clear-cuts, (1) open-habitat species appear and increase in abundance (but disappear when the canopy closes ca. 20–30 years later); (2) forest generalists persist throughout the clear-cut originated succession; and (3) species requiring mature closed-canopy forests are affected negatively by management and may not recover within several decades. The latter group further seems to consist of two recovery types: (a) the majority of forest-specialist species tend to recover following logging. This view is supported by the low forest carabid abundances during the first ca. 20–30 years of clear-cut originated succession followed by an increase later on (30–60 years; Koivula et al. 2002), but (b) several species show poor or no re-colonisation even after tens of years after the harvesting event (Niemelä et al. 1993a).

As there are more open-habitat species that colonise clear-cuts than there are forest species disappearing from them (Niemelä et al. 1988, 1993a, b; Koivula 2002a, b), species richness tends to increase following clear-cutting or other major forestry practices. Modern forestry creates clear-cuts suitable for open-habitat and disturbance-tolerant species, and consequently these are the ‘winners’ in intensively managed forest landscapes today. Also forest-habitat generalists (species found in different types and ages of forest) appear to be thriving. From a conservation point of view, species requiring mature closed-canopy forest are of concern. Their habitat continues to become fragmented and lost.

What can be done to maintain populations and assemblages of mature forest carabids and other forest taxa in the managed forest landscape? Obvious approaches include the decrease of clear-cut size, adoption of logging methods other than clear-cutting, and retention of certain “key” biotopes. Swedish and Finnish management guidelines and forestry laws have recently changed towards an ecologically more sustainable direction (Angelstam and Pettersson 1997; Savolainen 1997; Karvonen 2000). In Finland, for example, clear-cut size is usually less than 3–4 ha (Parviainen and Seppänen 1994), above which the economical benefit/cost relationship does not increase markedly (Imponen and Kaila 1988). Management guidelines also include the retention of ecological corridors, the maintenance of certain key habitats, and the use of modified logging methods (Karvonen 2000).

Natural forest dynamics is increasingly used as a guideline when practicing forestry (Angelstam 1998). However, this approach relies on the assumption that natural variation in stand structure and composition can be adequately maintained and recreated through forest management practices (Work et al. 2004). This

matching is a challenge as there are several critical differences between natural disturbances and timber harvesting (Niemelä 1999). For example, in the boreal region, it has been suggested that clear-cutting mimics wildfire as a stand-replacing disturbance. According to this logic, species adapted to wildfire would also be adapted to clear-cutting. However, this is only partly true in carabids because assemblages in recently burned stands include fire-dependent species that are lacking from or are scarce in harvested unburned stands (Holliday 1984, 1991, 1992; Wikars 1992, 1995; Beaudry et al. 1997; Niwa and Peck 2002; Koivula et al. 2005; Saint-Germain et al. 2005). Overall, McCullough et al. (1998) concluded that studies examining the effects of forest fire on boreal carabid beetles suggest that the effects of fire on species diversity are small, but species composition may change (see Wikars and Schimmel 2001). However, these effects may depend on fire characteristics: Koivula et al. (2005) showed that the abundance of the fire specialist carabid *Sericoda quadripunctata* (DeGeer) within burns of a post-fire mixed-wood forest in Canada is determined by fire severity (measured using tree survival and scorch in the studied stands).

Although all forestry practices apparently result in changes in carabid assemblages, maintaining patches of closed canopy of a minimum of a few ares per hectare retains mature-forest carabid assemblages better than traditional clear-cuts (Koivula 2002a, b; Koivula and Niemelä 2002, 2003). However, this practice increases the amount of edge habitat in the stand (and at larger spatial scales; see below). Also, uncut strips between small clear-cut openings represent edge habitat for species requiring forest interior habitat. Therefore, in addition to invading the small openings, open-habitat carabids also invade the uncut strips between the openings (Koivula 2002a; Koivula and Niemelä 2003). Retained trees and vegetation in logged sites may nevertheless act as a buffer for adjacent forest reserves by decreasing edge effects and increasing the effective area of interior reserves (Lindenmeyer and Franklin 2002).

Modifications of the gap felling method are worthy of further study. For example, how does the spatial arrangement of retention patches or cuts affect the carabid fauna? Moreover, strip clear-cutting might maintain forest species assemblages better than traditional clear-cutting, but we are not aware of carabid studies that compare these logging methods. Nevertheless, Moore et al. (2004) showed that 60-m wide uncut strips host different assemblages than adjacent 60-m wide harvested strips. Increasing the logging rotation considerably from the current 80–120 years

may have positive consequences on the forest fauna. Some important old-growth structures, such as decaying wood, large trees and trees with cavities, may need 200 years or longer to develop after harvesting (Siitonen 2001). Furthermore, a central European study indicated that populations of forest-specialist carabids may need centuries to return after strong forest-habitat alteration activities (Desender et al. 1999).

At the larger spatial scale, i.e. up to hundreds of hectares, forest biodiversity can probably best be maintained if forest management mimics natural processes of regeneration, such as fire-initiated succession, and maintains the natural age and tree-species composition (Fries et al. 1997). These views are supported by studies on carabids. Forest management should clearly aim at maintaining natural landscape structure and processes, including the availability of old-growth forests (see above). The key here is to maintain large-scale stand variation together with careful management at the smaller spatial scales (within stands). Moreover, Beaudry et al. (1997) suggested that the presence of regenerating sites with and without prescribed burning, in addition to preserved mature forest, could contribute to the maintenance of carabid diversity and to the avoidance of the extermination of some sensitive old-growth species. A challenge for forest managers is the introduction of fire to the North European boreal forests. This is imperative based on the current rarity of several fire specialists, such as the carabid *Sericoda bogemanni* Gyllenhal that is threatened in Finland and in Sweden (Rassi et al. 2000, Anon 2005). Also, little is known on the impact of fire on ecosystem processes (e.g. fire dependence) and the consequent long-term persistence of many forest species. Earlier Spence et al. (1999) underlined the importance of accommodating complex stand structures associated with gap-dynamic processes characteristic of post-rotational forests to conserve the biota and the processes that ensure the maintenance of site productivity.

One of the most pressing problems of applying smaller clear-cuts is the increasing amount of edges at the landscape level, as well as the total area that has to be managed to gain the same economic benefits as if clear-cuts were fewer in number but larger in size. Therefore, in the highly altered Fennoscandian forested landscape, restoration efforts should perhaps be focused on forests adjacent to existing reserves for the maximum benefit for threatened forest species, rather than spreading these activities evenly (and thinly) over large areas (Hanski 2000). However, in those parts of the North American and Russian boreal forest, where the history of intensive management is shorter and,

thus, large-scale losses of forest specialist species are less likely yet to have taken place, the development and use of logging methods and landscape-scale ecological assessment of management strategies may still be a more efficient way to conserve forest diversity.

Needs for future research on carabids and forest management

This review has shown that most boreal forest carabids can survive in the forested landscape modified by forestry practices. However, the value of using carabids in forest research comes from the assumption that the management practices least affecting carabids are also those that have less of an impact on other forest taxa. Whether carabids truly act as indicators of the well-being of intact forests (and other habitats), including their most sensitive fauna and flora, should be evaluated. Among carabids there are sensitive species requiring old-growth conditions or other aspects of natural dynamics (such as fire) that are at risk in the managed forest landscape. Modern forestry practices aim at retaining certain key biotopes (such as riparian forest strips) and leaving more dead and live trees in the forest after harvest in order to enhance the survival of such old-growth species. However, the efficiency of these practices in maintaining forest species communities and especially in enhancing the survival of endangered species is currently poorly understood. Thus, the question to be answered by scientists remains: do these practices work, i.e. do they guarantee the survival of sensitive forest species?

Finally, we would like to point out a few other knowledge gaps on the relationship between carabids and forestry. First, the large-scale effects of landscape structure and processes on the distribution and abundance of boreal carabids have been little studied so far. Second, it is largely unknown how climate change will affect carabids and their biotopes in the near future, and whether these changes interact with the effects of forestry. Third, different large-scale management and conservation strategies should be experimentally evaluated. At a smaller scale, additional issues arise. First, certain forest types have been little studied; these include, for example, coastal North European pine forests. Second, we lack specific information on critical amounts of (micro-) habitat and forest characteristics, such as downed dead wood, on carabids. Third, despite the remarkable contributions of many great carabidologists—most notably Carl Lindroth—on species ecology, we still know very

little on the dispersal abilities of carabid beetles, i.e. distances covered by foot and by flying, and how frequently carabids actually rely on these abilities and under which conditions. Also carabid behaviour in habitats other than their preferred ones is largely unknown. Clearly, we need to understand the importance of these aspects better than we currently do, as they affect carabid survival in the managed forested landscapes and, more generally, in the rapidly changing world.

Acknowledgments MK thanks the University of Alberta for funding (Izaak Walton Killam Postdoctoral Fellowship).

References

- Abildsnes J, Tømmerås BÅ (2000) Impacts of experimental habitat fragmentation on ground beetles (Coleoptera, Carabidae) in a boreal spruce forest. *Ann Zool Fenn* 37:201–212
- Andersson LI, Hytteborn H (1991) Bryophytes and decaying wood: a comparison between managed and natural forest. *Holarct Ecol* 14:121–130
- Andrén H (1995) Effects of landscape composition on predation rates at habitat edges. In: Hansson L, Fahrig L, Merriam G (eds) *Mosaic landscapes and ecological processes*. London, Chapman & Hall, pp 225–255
- Angelstam P (1997) Landscape analysis as a tool for the scientific management of biodiversity. *Ecol Bull* 46:140–170
- Angelstam P (1998) Maintaining and restoring biodiversity by developing natural disturbance regimes in European boreal forest. *J Veget Sci* 9:593–602
- Angelstam P, Pettersson B (1997) Principles of present Swedish forest biodiversity management. *Ecol Bull* 46:191–203
- Anon (2005) Official Swedish red lists. SLU ArtDatabanken, Sweden; <http://www.artdata.slu.se/rodlista> (Accessed date 27 February 2006)
- Atlegrim O, Sjöberg K, Ball JP (1997) Forestry effects on a boreal ground beetle community in spring: selective logging and clear-cutting compared. *Entomol Fenn* 8:19–26
- Ås S (1993) Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography* 16:219–228
- Bauer LC (1989) Moorland beetle communities on limestone ‘habitat islands’. I. Isolation, invasion and local species diversity in carabids and staphylinids. *J Anim Ecol* 58:1077–1098
- Beaudry S, Duchesne LC, Cote B (1997) Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Can J For Res* 27:2065–2071
- Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annu Rev Ecol Syst* 20:1–28
- Burke D, Goulet H (1998) Landscape and area effects on beetle assemblages in Ontario. *Ecography* 21:472–479
- Chen J, Franklin JF, Spies TA (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol Appl* 5:74–86
- Davies KE, Margules CR (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. *J Anim Ecol* 67:460–471
- de Warnaffe GDB, Lebrun P (2004) Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. *Biol Conserv* 118:219–234

- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355
- den Boer PJ (1990a) Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *J Evol Ecol* 3:19–48
- den Boer PJ (1990b) The survival value of dispersal in terrestrial arthropods. *Biol Conserv* 54:175–192
- Desender K, Ervynck A, Tack G (1999). Beetle diversity and historical ecology of woodlands in Flanders. *Belg J Zool* 129:139–155
- Dettki H, Esseen P-A (1998) Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography* 21:613–624
- Didham RK (1997) The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. In: Laurance WF, Bierregaard RO Jr (eds) *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. Chicago & London, The University of Chicago Press, pp 55–70
- Didham RK, Lawton JH (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30
- Donovan TM, Jones PW, Annand EM, Thompson FR III (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075
- Esseen P-A, Ehnström B, Ericson L, Sjöberg K (1997) Boreal forests. *Ecol Bull* 46:16–47
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142
- Fahrig L, Merriam G (1994) Conservation of fragmented populations. *Conserv Biol* 8:50–59
- Fournier E, Loreau M (2001) Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetles (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecol* 16:17–32
- Fries C, Johansson O, Pettersson B, Simonsson P (1997) Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *For Ecol Manage* 94:89–103
- Gandhi KJK, Spence JR, Langor DW, Morgantini LE (2001) Fire residuals as habitat reserves for epigeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biol Conserv* 102:131–141
- Greenslade PJM (1983) Adversity selection and the habitat templet. *Am Nat* 122:352–365
- Haila Y (1999) Islands and fragments. In: Hunter ML Jr (ed) *Maintaining biodiversity in forest ecosystems*. Cambridge, Cambridge University Press, pp 234–264
- Haila Y, Hanski IK, Niemelä J, Punttila P, Raivio S, Tukiä H (1994) Forestry and the boreal fauna: matching management with natural forest dynamics. *Ann Zool Fenn* 31:187–202
- Hallman E, Hokkanen M, Juntunen H, Korhonen KM, Raivio S, Savela O, Siitonen P, Tolonen A, Vainio M (1996) Alueekologinen suunnittelu. *Vantaa, Finnish Forest and Park Service* [In Finnish]
- Halme E, Niemelä J (1993) Carabid beetles in fragments of coniferous forest. *Ann Zool Fenn* 30:17–30
- Hanski I (1999) *Metapopulation ecology*. Oxford, Oxford University Press
- Hanski I (2000) Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann Zool Fenn* 37:271–280
- Heliölä J, Koivula M, Niemelä J (2001) Distribution of carabid beetles (Coleoptera, Carabidae) across boreal forest – clear-cut ecotone. *Conserv Biol* 15:370–377
- Helle P, Muona J (1985) Invertebrate numbers in edges between clear-fellings and mature forests in Northern Finland. *Silva Fenn* 19:281–294
- Heyborne WH, Miller JC, Parsons GL (2003) Ground-dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *For Ecol Manage* 179:123–134
- Holliday NJ (1984) Carabid beetles (Coleoptera, Carabidae) from burned spruce forest (*Picea* spp.). *Can Entomol* 116:919–922
- Holliday NJ (1991) Species responses of carabid beetles (Coleoptera, Carabidae) during post-fire regeneration of boreal forest. *Can Entomol* 123:1369–1389
- Holliday NJ (1992) The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. *Can J Zool* 70:440–452
- Hunter ML (1996) *Fundamentals of conservation biology*. Blackwell Science Inc
- Hänggi A, Baur B (1998) The effect of forest edge on ground-living arthropods in a remnant of unfertilized calcareous grassland in the Swiss Jura mountains. *Mitt Schw Entomol Gesell Bul Soc Entomol Suisse* 71:343–354
- Imponen V, Kaila S (1988) Uudistusalan koon vaikutus metsän uudistamiskustannuksiin Etelä-Suomen oloissa. *Metsätieteellinen Katsaus* 18:1–6 [In Finnish]
- Jalonen J, Vanha-Majamaa I (2001) Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *For Ecol Manage* 146:25–34
- Jokimäki J, Huhta E, Itämies J, Rahko P (1998) Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Can J For Res* 28:1068–1072
- Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Conserv* 7:749–764
- Karvonen L (2000) *Guidelines for landscape ecological planning*. Forestry Publications of Metsähallitus 36
- Koivula M (2001) Carabid beetles (Coleoptera, Carabidae) in boreal managed forests – meso-scale ecological patterns in relation to modern forestry. PhD thesis, University of Helsinki, 120 pp
- Koivula M (2002a) Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *For Ecol Manage* 167:103–121
- Koivula M (2002b) Carabid beetles (Coleoptera, Carabidae) in thinned uneven-aged and clear-cut spruce stands. *Ann Zool Fenn* 39:131–149
- Koivula M (2003) The forest road network – a landscape element affecting the spatial distribution of boreal carabid beetles (Coleoptera, Carabidae). In: Szyszko J et al (eds) *How to protect or what we know about Carabid beetles*. Warsaw Agricultural University Press, Warsaw, pp 287–299
- Koivula M (2006) Effects of forest roads on spatial distribution of boreal Carabid beetles (Coleoptera: Carabidae). *Coleopt Bull* 59(4/2005):465–487
- Koivula M, Niemelä J (2002) Boreal carabid beetles (Coleoptera, Carabidae) in managed spruce forests – a summary of Finnish case studies. *Silva Fenn* 36:423–436
- 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 MJ, Vermeulen HJW (2005) Highways and forest fragmentation – effects on carabid beetles (Coleoptera, Carabidae). *Landscape Ecol* 20:911–926
- Koivula M, Haila Y, Niemelä J, Punttila P (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22:424–435

- Koivula M, Kukkonen J, Niemelä J (2002) Carabid-beetle (Coleoptera, Carabidae) assemblages in the boreal forest succession. *Biodivers Conserv* 11:1269–1288
- Koivula M, Hyyryläinen V, Soinen E (2004) Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. *J Insect Conserv* 8:297–309
- Koivula M, Cobb T, Déchéne A, Jacobs J, Spence JR (2005) *Sericoda* Kirby, 1837 (Coleoptera: Carabidae) responses to time since fire, fire severity, post-fire logging, and smoke and charcoal stimuli. In: Serrano J, Gomez-Zurita J, Ruiz C (eds) XII European carabidologists meeting, Murcia, September 19–22, 2005. Ground beetles as a key group for biodiversity conservation studies in Europe. University of Murcia & David Mayntz, Murcia, pp 153–159
- Kotze DJ, O'Hara RB (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135:138–148
- Kotze DJ, Samways MJ (1999) Invertebrate conservation at the interface between the grassland matrix and natural Afro-montane forest fragments. *Biodivers Conserv* 8:1339–1363
- Kuusinen M (1994) Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. *Ann Bot Fenn* 31:245–260
- Kuusinen M (1996) Importance of spruce swamp-forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. *Ecography* 19:41–51
- Langor D, Spence J, Niemelä J, Carcamo H (1994) Insect biodiversity in the boreal forests of Alberta, Canada. In: Haila Y, Niemelä P, Kouki J (eds) Effects of management on the ecological diversity of boreal forests. *Metsäntutkimuslaitoksen tiedonantoja* 482. Finnish Forest Research Institute, pp 25–31
- Laurance WF (2000) Do edge effects occur over large spatial scales? *Trends Ecol Evol* 15:134–135
- Law BS, Dickman CR (1998) The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodivers Conserv* 7:323–333
- Liebherr JK, Song HJ (2002) Distinct ground beetle (Coleoptera: Carabidae) assemblages within a New York State wetland complex. *J N Y Entomol Soc* 110:127–141
- Lindenmeyer DB, Franklin JF (2002) Conserving forest biodiversity. A comprehensive multiscaled approach. Washington DC, Island Press
- Linder P, Östlund L (1992) Förändringar i norra Sveriges skogar 1870–1991 (Changes in the boreal forests of Sweden 1870–1991). *Svensk Bot Tidskrift* 86:199–215
- Lindroth CH (1985) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomol Scand* 15:1–225
- Lindroth CH (1986) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomol Scand* 15:233–497
- Lindroth CH (1992) Ground beetles (Carabidae) of Fennoscandia. A zoogeographic study. Part I. Specific knowledge regarding the species. Washington D.C., Smithsonian Institution Libraries and the National Science Foundation. xxviii + 630 pp
- Loope WL (1991) Interrelationships of fire history, land use history, and landscape pattern within Pictured Rocks National Lakeshore, Michigan. *Can Field-Nat* 105:18–28
- Magura T, Kodobocz V, Tothmeresz B (2001) Effects of habitat fragmentation on carabids in forest patches. *J Biogeogr* 28:129–138
- Magura T, Tothmeresz B, Elek Z (2005) Impacts of leaf-litter addition on carabids in a coniferous plantation. *Biodivers Conserv* 14:475–491
- Martikainen P (2000) Effects of forest management on beetle diversity, with implications for species conservation and forest protection. PhD thesis, University of Joensuu
- Martikainen P (2001) Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecol Bull* 49:205–218
- Mascanzoni D, Wallin H (1986) The harmonic radar: a new method of tracing insects in the field. *Ecol Entomol* 11:387–390
- Matlack GR, Litvaitis JA (1999) Forest edges. In: Hunter ML Jr (ed) Maintaining biodiversity in forest ecosystems. Cambridge, Cambridge University Press, pp 210–233
- McCullough DG, Werner RA, Nuemann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. *Annu Rev Entomol* 43:107–127
- Moore JD, Ouimet R, Houle D, Camire C (2004) Effects of two silvicultural practices on ground beetles (Coleoptera: Carabidae) in a northern hardwood forest, Quebec, Canada. *Can J For Res* 34:959–968
- Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol Evol* 10:58–62
- Niemelä J (1993) Mystery of the missing species: species-abundance distribution of boreal ground beetles. *Ann Zool Fenn* 30:169–172
- Niemelä J (1997) Invertebrates and boreal forest management. *Conserv Biol* 11:601–610
- Niemelä J (1999) Management in relation to disturbance in the boreal forest. *For Ecol Manage* 115:127–134
- Niemelä J (2001) Carabid beetles (Coleoptera, Carabidae) indicating habitat fragmentation: a review. *Eur J Entomol* 98:127–132
- 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, Spence J (1999) Dynamics of local expansion by an introduced species: *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) in Alberta, Canada. *Divers Distrib* 5:121–127
- Niemelä J, Haila Y, Halme E, Pajunen T, Punttila P, Tukia H (1987) Habitat preferences and conservation status of *Agonum mannerheimii* Dej. in Häme, southern Finland. *Notulae Entomol* 67:175–179
- 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. *Ann Zool Fenn* 25:107–119
- 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. *J Biogeogr* 19:173–181
- Niemelä J, Spence JR, Langor DW, Haila Y, Tukia H (1993a) Logging and boreal ground beetle assemblages on two continents: implications for conservation. In: Gaston KJ, New TR, Samways MJ (eds) Perspectives in insect conservation. Intercept Publishers Ltd, Andover, Hampshire, pp 29–50
- Niemelä J, Langor DW, Spence JR (1993b) Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv Biol* 7:551–561
- Niemelä J, Haila Y, Punttila P (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19:352–368
- Niwa CG, Peck RW (2002) Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. *Environ Entomol* 31:785–796
- Økland B (1994) Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biodivers Conserv* 3:68–85

- Pajunen T, Haila Y, Halme E, Niemelä J, Punttila P (1995) Ground-dwelling spiders (Arachnida, Araneae) in fragments of old forest and surrounding managed forests in southern Finland. *Ecography* 18:62–72
- Parviainen J, Seppänen P (1994) Metsien ekologinen kestävyys ja metsänkasvatusvaihtoehdot. Metsäntutkimuslaitoksen tiedonantoja 511. Finnish Forest Research Institute [In Finnish]
- Pearce JL, Venier LA, McKee J, Pedlar J, McKenney D (2003) Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *Can Entomol* 135:337–357
- Peck R, Niwa CG (2004) Longer-term effects of selective thinning on carabid beetles and spiders in the Cascade Mountains of southern Oregon. *Northwest Sci* 78:267–277
- Poole A, Gormally A, Skeffington MS (2003) The flora and carabid fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. *For Ecol Manage* 177:207–220
- Punttila P, Haila Y, Pajunen T, Tukka H (1991) Colonisation of clearcut forests by ants in the southern Finnish taiga: a quantitative survey. *Oikos* 61:250–262
- Punttila P, Haila Y, Niemelä J, Pajunen T (1994) Ant communities in fragments of old-growth taiga and managed surroundings. *Ann Zool Fenn* 31:131–144
- Rassi P, Alanen A, Hakalisto S, Hanski I, Lehtikainen E, Oheñoja E, Siitonen J, Suvantola L, Vitikainen O, Väisänen R, Kanerva T, Mannerkoski I (2000) Suomen lajien uhanalaisuus 2000. Uhanalaisten lajien II seurantatyöryhmä. Finnish Ministry of Environment, 432 pp [In Finnish]
- Riecken U, Raths U (1996) Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. *Ann Zool Fenn* 33:109–116
- Saint-Germain M, Larrivé M, Drapeau P, Fahrig L, Buddle C (2005) Short-term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape. *For Ecol Manage* 212: 118–126.
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32
- Savolainen J (ed) (1997) Metsälaki perusteluineen. Edita, Helsinki [In Finnish]
- Schneider RR (2002) Alternative futures. Alberta's boreal forest at the crossroads. The Federation of Alberta Naturalists and the Alberta Centre for Boreal Research, Edmonton, 152 pp
- Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol Bull* 49:11–42
- Siitonen J, Martikainen P (1994) Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scand J For Res* 9:185–191
- Siitonen J, Saaristo L (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol Conserv* 94:211–220
- Sippola A-L, Siitonen J, Punttila P (2002) Beetle diversity in timberline forests: a comparison between old-growth and regenerating areas in Finnish Lapland. *Ann Zool Fenn* 39:69–86
- Spence JR, Langor DW, Niemelä J, Cárcamo HA, Currie CR (1996) Northern forestry and carabids: the case for concern about old-growth species. *Ann Zool Fenn* 33:173–184
- Spence JR, Buddle CM, Gandhi KJK, Langor DW, Volney WJA, Hammond HEJ, Pohl GR (1999) Invertebrate biodiversity, forestry and emulation of natural disturbance: a down-to-earth perspective. In: Meurisse RT, Ypsilantis WG, Seybold C (eds) Proceedings: Pacific northwest forest and rangeland soil organism symposium 461, pp 80–90
- Stevens SM, Husband TP (1998) The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. *Biol Conserv* 85:1–8
- Taboada A, Kotze DJ, Salgado JM (2004) Carabid beetle occurrence at the edges of oak and beech forests in NW Spain. *Eur J Entomol* 101:555–563
- Usher MB, Field JP, Bedford SE (1993) Biogeography and diversity of ground-dwelling arthropods in farm woodlands. *Biodivers Lett* 1:54–62
- Vance CC, Nol E (2003) Temporal effects of selection logging on ground beetle communities in northern hardwood forests of eastern Canada. *EcoScience* 10:49–56
- van Dijk TS (1996) The influence of environmental factors and food on life cycle, ageing and survival of some carabid beetles. *Acta Jutland* 71:11–24
- Vanha-Majamaa I, Jalonen J (2001) Green tree retention in Fennoscandian forestry. *Scand J For Res* 3(Suppl.):79–90
- Väisänen R (1995) Perhosen. In: Raivio S (ed) Talousmetsien luonnonsuojelu – yhteistutkimushankkeen väliraportti. Metsähallinnon luonnonsuojelujulkaisuja, Sarja A, 43, pp 103–108 [In Finnish]
- Väisänen R, Biström O, Heliövaara K (1993) Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? *Biodivers Conserv* 2:95–113
- Västilä S, Herrala-Ylinen H (1999) Silviculture. In: Sevola Y (ed) Finnish statistical yearbook of forestry. Finnish Forest Research Institute, pp 101–148
- Wallin H (1986) Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. *Ecol Entomol* 11:457–466
- Werner SM, Raffa KF (2000) Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *For Ecol Manage* 139:135–155
- Wikars L-O (1992) Skogsbränder och insekter. *Entomol Tidskrift* 113:1–11 [In Swedish with English summary]
- Wikars L-O (1995) Clear-cutting before burning prevent establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Ann Zool Fenn* 32:375–384
- Wikars L-O, Schimmel J (2001) Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *For Ecol Manage* 141:189–200
- With KA, Gardner RH, Turner MG (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151–169
- Work TT, Shorthouse DP, Spence JR, Volney WJA, Langor D (2004) Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwest Alberta. *Can J For Res* 34:417–430