

Under which conditions does retention harvesting support ground beetles of boreal forests?

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Koivula M.J. 2012. Under which conditions does retention harvesting support ground beetles of boreal forests? *Baltic J. Coleopterol.*, 12(1): 7 – 26.

Forestry is currently undergoing a paradigm shift from the clear-cut, even-age timber-production model toward a model that is based on spatially and temporally complex natural disturbances and structures, i.e., the disturbance-based management model. This model involves a variety of logging methods, high level of green-tree retention, better consideration of legacy elements, and modifications of density, age, and species structure of harvested forests. Many characteristics of this model have been studied using boreal ground beetles (Coleoptera, Carabidae). These studies are mostly short term (up to 10 years after logging) and have been conducted at spatial scales of within or between stands. Compared to “classic” clear-cutting, modifications of it – green-tree retention and decreasing clear-cut size – positively affect closed-forest species and attenuate the increase of canopy-closure generalists and open-habitat species. Assuming a relatively even tree removal, thresholds in carabid response occur at 40-50% retention (trees/ha), below which closed-canopy specialists start to quickly decrease, and at 20-30%, below which open-habitat specialists drastically increase. Selective logging in principle creates gaps of up to ca. $r = 5$ m by removal of single trees and does not significantly affect forest carabids, assuming >60% retention. However, >0.1-ha clear-cut gaps (ca. $r > 10$ m) may face rapid changes in species composition: the larger the gap, the larger the change. Forest carabids also generally benefit from retention of patches of sub-dominant species and wet bogs, and increased downed dead wood. Notable knowledge gaps in carabid research in the boreal region exist particularly on large-scale responses of carabids to forestry, especially specific responses of arboreal species, and carabid responses to forestry in rare habitat types such as groves, pine heaths, and along forest streams. Long-term studies would be extremely valuable now, considering the many rapid global-scale climate and land-use changes.

Key words: clear-cutting, disturbance dynamics, green-tree retention, selective logging, restoration

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INTRODUCTION

Natural succession significantly contributes to the structural heterogeneity of forests. This characteristic manifests itself in varying density, age,

and species of trees in a given stand, and in varying sizes of pieces of a landscape mosaic consisting of such stands. Here, “stand” refers to a patch of forest with roughly homogeneous forest and soil type, as well as age, size, and species

composition of dominant canopy trees. The heterogeneity and patchiness are initiated, shaped, and driven by disturbances, which are sudden drastic alterations in tree structure so that new growth space appears and micro-climate changes (Esseen et al. 1997, Kuuluvainen 2002). In natural conditions, different disturbances take place at different spatial scales. Considering impacted areas, the largest of disturbances are wildfires and wind-caused tree falls, whereas insect outbreaks and deaths and falls of single trees usually affect considerably smaller areas (Kuuluvainen 2009). Forest fauna and flora respond to these changing conditions accordingly, including tree regrowth and vegetation succession. These responses are affected by, e.g., site heterogeneity, landscape characteristics, forest type, soil quality, and season (Barnes et al. 1999).

Man-made disturbances have largely replaced natural disturbances as initiators of secondary succession in North European forests (Esseen et al. 1997). In terms of affected area, forestry is the most important of these in this region: over 90% of merchantable forests are managed in Finland and Sweden (Anon. 2011, 2012a). Since the early 1950s, North European forestry has followed the so-called classic timber-production model (Hunter 1999; hereinafter “classic model” for brevity), i.e., maximizing economic benefit and tree growth while simultaneously minimizing timber losses caused by natural disturbances. This model relies on clear-cut harvesting and growing trees of even age and size in mostly one-dominant-species stands (e.g., Haila et al. 1994). In natural conditions such stand structure would result from a single disturbance event at the stand scale. In landscapes covered by such stands, habitat heterogeneity actualizes through a mosaic of distinctive stands of different ages and dominant tree species.

The classic model has long been justified through certain similarities between a clear-cut and a wildfire area (e.g., Parviainen & Seppänen 1994). Both have lost most if not all live trees, but the latter shows considerably more heterogeneous patterns of tree deaths and survivals, and impact severity on soil and biota (e.g., Esseen et al. 1997,

Fries et al. 1997). Also carabids respond differently to clear-cutting and wildfire (Beaudry et al. 1997, Gandhi et al. 2004), a pattern detectable for over 25 years post disturbance (Buddle et al. 2006). Another related belief is that wildfires initiate tree growth at a given site every 50-120 years, and hence clear-cutting could be applied in such rotation without large-scale effects on biodiversity. Large-scale forest fires are relatively common in North America (Bergeron et al. 2004), but in North Europe the commonness of large-scale fires has recently been questioned (Kuuluvainen 2009); other, smaller-scale disturbances appear more important in terms of frequency and impacted area, and many patches may not face a stand-replacing disturbance for several hundred years (Wallenius et al. 2007). A more recent dimension in the debate is that especially private forest owners increasingly often appreciate not just timber production but also biodiversity, ecosystem-service, and recreational and aesthetic values (Rämö & Toivonen 2009, Hänninen & Karppinen 2010). Thus, if forestry aimed at better emulating natural disturbances, and providing land owners with management alternatives that retain the many forest values, the so-called disturbance-based management model may be a viable solution (e.g., Hunter 1999, Lindenmayer & Franklin 2002, Kuuluvainen 2009).

Forestry in the boreal region is currently facing a paradigm shift toward the disturbance-based management model (hereinafter “disturbance model” for brevity). The majority of peer-reviewed research papers on disturbance-model forestry is North American (Rosensvald & Löhms 2008), but interest in studying and applying this model is rapidly increasing in Europe, too (Nyland 2003, Kuuluvainen 2009). Based on this research, since the mid-1990s, clear-cutting has been commonly replaced by a variety of other logging methods that form the basis for the disturbance model (e.g., Valkonen et al. 2011). The use of these methods aims at an uneven age structure and often multiple dominant species of trees, and a maintenance of tree-canopy cover throughout the logging rotation in significant parts of harvested stands (Koivula et al. 2012). The paradigm shift is not abrupt, however, but is gradually taking place

through various modifications of management. For example, Metsähallitus (a state-owned company that manages most of the Finnish state forests) routinely retains approx. 5% of live trees in clear-cut plots, usually in 2-3 groups per 1-2 ha (Päivinen et al. 2011). Such modifications, and gradual changes in the public opinion on their importance, are small but crucial steps towards ecologically sustainable forest management.

This paper focuses on boreal forests only, and has three aims related to adaptive management within the disturbance-model paradigm. (1) I briefly summarize current knowledge about carabid responses to the classic model. A detailed evaluation can be found in Niemelä et al. (2007). (2) I summarize studies focusing on different elements of the disturbance model. I pay specific attention to logging methods with a relatively high level of retention. With retention percentages I refer to trees/ha unless otherwise stated. Questions of central importance from this point of view include the size of clear-cut plots and the density of retention trees. Other issues concern forest restoration (prescribed burning, creation of dead wood) and retention of so-called legacy elements (wet patches, tree diversity, and dead wood of natural origin). (3) Based on topics 1-2 I identify knowledge gaps and predict future issues related to the ecological effects of forestry.

CARABIDS AND THE CLASSIC TIMBER-PRODUCTION MODEL

The classic model relies on clear-cut harvesting as the main tree-regeneration method, top-soil preparation (ploughing or scarification, either patchy or in strips) and precommercial thinning to support tree regrowth, and – more recently – retention of some live trees to support forest biota (Hallman et al. 1996, Fries et al. 1997). Several studies have documented the impacts of these operations on forest-associated organisms, including carabids (Table 1).

Clear-cutting areas larger than one hectare profoundly impacts forest biota at the stand level.

This finding may presently sound trivial, but as late as in the 1980s ecologists were repeatedly questioned about the lack of experimental proof. The idea has since gained unquestionable support. Carabid beetles, e.g., commonly show the same short-term response: closed-canopy species decrease or even disappear from clear-cut plots, whereas open-area-associated species rapidly colonize them (Niemelä et al. 2007, Pohl et al. 2007). Carabids also reflect mature-forest/clear-cut edge gradients: open-habitat species occur almost exclusively in the clear-cut side and decrease rapidly toward the forest (e.g., Spence et al. 1996, Heliölä et al. 2001). In the longer term, the forest-carabid assemblage mostly recovers within 25-30 years, coinciding with canopy closure (e.g., Koivula et al. 2002, Niemelä et al. 2007). Some closed-canopy specialists, however, may require considerably longer periods and nearby source areas to recover (Niemelä et al. 1993a, 1993b, Spence et al. 1996, Paquin 2008).

Green-tree retention at clear-cut plots has become a common practice in Finland since the 1990s (Päivinen et al. 2011). Typically, the level of retention in Finland is modest: up to 5%. Koivula (2002a) studied such low retention in Norway spruce (*Picea abies*) forests three years post harvest, at 2-ha clear-cut plots with three retention plots of 10-20 trees (each up to ca. 10 x 20 m or 0.02 ha). He found that the carabid fauna had changed remarkably in the retention plots but, compared to clear-cut sections of the same stands, hosted significantly fewer open-habitat species individuals (see also Lemieux & Lindgren 2004). These findings suggest that such small tree groups retain at least some characteristics of the forest floor in the short term. The ability of these plots to function as refugia for closed-forest specialists over the open phase of clear-cut-initiated secondary succession remains questionable as these retention trees tend to fall down, which further alters the micro-climate.

The classic model also commonly applies precommercial thinning, i.e., mechanical or chemical removal of poor-quality trees (in regenerating stands) or unwanted tree saplings (in recent clear-cut plots), to release growth space for com-

Table 1. Aspects of the disturbance-based management model studied using ground beetles in the boreal region. - = aspect not yet studied; + = aspect studied in 1-3 papers; ++ = aspect studied in >3 papers. Evidence is presented according to spatial scale (variation within stands; comparisons between stands; landscape level) and to temporal scale (short-term, i.e., 1-4 years from initiation of the experiment; mid-term, i.e., 5-30 years; and long-term, i.e., >30 years, including chronosequences).

Aspect	Spatial scale			Temporal scale		
	Within stands	Between stands	Landscapes	Short-term	Mid-term	Long-term
<i>Logging techniques</i>						
Clear-cutting ^a	++	++	+	++	++	+
Clear-c with retention groups ^b	+	+	-	+	-	-
Clear-c with shelterbelts ^c	-	-	-	-	-	-
Gap felling ^d	++	++	+	++	-	-
Selective felling ^e	++	++	-	++	+	-
<i>Other management operations</i>						
Longer-than-usual rotation	-	-	-	-	-	-
Shorter-than-usual rotation	-	-	-	-	-	-
Clear-cut/mature-forest edges	++	-	-	++	-	-
Ploughing/scarification	++	+	-	++	-	-
Precommercial thinning	-	+	-	+	-	-
Logging residue	+	+	-	+	-	-
<i>Legacy elements</i>						
Downed dead wood	++	+	-	++	-	-
Subdominant tree species	++	-	-	+	+	+
Wet patches (mires)	++	++	-	++	+	+
<i>Restoration operations</i>						
Creation of dead wood	+	+	-	+	+	-
Prescribed burning	++	++	-	++	+	-
<i>Interactions between aspects</i>						
Logging tech x Other mgmt	++	++	-	++	-	-
Logging tech x Legacy	++	++	-	++	+	-
Logging tech x Restoration	-	-	-	-	-	-
Other mgmt x Legacy	-	-	-	-	-	-
Other mgmt x Restoration	-	-	-	-	-	-
Legacy x Restoration	+	+	-	+	+	-

a. Includes clear-cutting with no retention, strip clear-cutting, and clear-cutting with shape and retention modifications (sometimes referred to as partial cutting); here, ≥ 0.5 ha in size. b. Groups of 10-30 trees within a clear-cut stand. c. Narrow (10-20 m wide) strips of uncut forest between a clear-cut plot and another habitat, e.g., farmland, bog, stream, or lake. d. Small clear-cut plots (gaps) logged within mature forest; here, >0.5 ha in size. e. Removal of part of the trees in a stand as to increase tree-age heterogeneity.

mercially valuable trees. (Growth release is often needed within disturbance-model management, too.) Thinning of regenerating stands, if applied at up to 25-30% removal intensity, does not much affect forest carabids (see below). If the stand was planted or seeded with conifers, which is a rather typical situation in Fennoscandian managed forests, deciduous trees, especially birch and aspen, are removed predominantly. Precommercial thinning, with the aim to release

space for conifers, was evaluated 7-9 years post clear-cutting and during the second growing season following thinning by Duchesne et al. (1999) in white and black spruce (*Picea glauca* and *P. mariana*) forests of northern Ontario, Canada. The authors observed that herbicide treatments and the use of a brush saw both increased carabid richness but not overall abundance; none of the studied species responded negatively to these treatments. However, if richness increased

and the total abundance did not change, this inevitably involves also negative responses. Cobb et al. (2007) studied carabid responses to combined effects of clear-cutting and herbicide use (chemical removal of deciduous saplings) two years post treatment in mixed white spruce and trembling aspen (*Populus tremuloides*) forests. The authors showed that *Scaphinotus marginatus* and *Platynus decentis* expectedly responded negatively to clear-cutting but were even more severely impacted when herbicide had been used in addition. In this study some open-habitat-associated species benefited from herbicide spraying, thus demonstrating that such combined treatments may also have positive effects.

Top-soil preparation to support sapling growth is a common practice in Fennoscandian management, both in the classic and disturbance models. Studies done in Central Europe suggest that extensive uncovering of mineral soil – which happens when ploughing is applied – fundamentally affects carabids (Mossakowski et al. 1990, Szyszko 1990, Desender et al. 1999, Skłodowski 1999). In many regions ploughing is considered an unnecessarily drastic operation even in the classic model, so lighter top-soil preparation techniques often dominate in forestry. Scarification (here, removal of humus layer in ca. 50-cm wide strips a few m apart) is one of such techniques and has been studied in Finland and in Canada. Koivula & Niemelä (2003) compared small clear-cut plots with scarified and unscarified Norway spruce forest floor and observed that the forest-succession generalist *Calathus micropterus* responded negatively to scarification; otherwise the operation had negligible impact on carabids. Similarly, a reanalysis of carabids collected at 60 within-stand plots (Koivula et al. 2002) revealed no significant effect of the percentage covered by visible sandy soil at this spatial scale on closed-forest, canopy-closure generalist, or open-habitat carabids (nested ANOVA with stands as blocks; results not shown). At the stand scale, however, bare soil significantly affected carabid assemblage composition (Koivula et al. 2002). Klimaszewski et al. (2005) in yellow birch (*Betula alleghaniensis*) and Pihlaja et al. (2006) in Norway spruce forest clear-cuts plots showed

that closed-forest carabids were more numerous in untreated forest floor but open-area-associated species were more abundant in bare-soil strips. Such light top-soil preparation thus varyingly affects carabids at the within-stand plot level, probably depending on the initial carabid composition and preparation technique *per se*, but this variation appears predictable at larger scales, i.e., between stands.

A recent approach within the classic model in Fennoscandia is the removal of logging residue and stumps for energy-production purposes. This removal has long-term impacts on soil nutrients and, in turn, tree-sapling growth, tree roots, and soil fauna (Helmisaari et al. 2011, Dighton et al. 2012). These play a role for carabids in providing shelter and food (e.g., Thiele 1977). Martikainen et al. (2006) found in harvested Scots pine (*Pinus sylvestris*) forests that logging residue did not significantly affect carabids in the short term. Similarly, Koivula & Niemelä (2003) evaluated the role of several stand-structural characteristics in determining carabid-assemblage structure and found that, although statistically significant, logging residue explained only 3% of variation in carabid data collected in Finnish Norway spruce forests. However, Nitterus et al. (2007) studied carabid responses to slash removal 5-7 years after harvesting in Swedish Norway spruce forests, and documented a structural shift in the carabid assemblage: closed-forest species decreased and canopy-closure generalists benefited from this operation. Although data originate from different parts of Fennoscandia and evidence is scarce, I believe that stump harvesting and removal of logging residue affect forest carabids after a few-year time lag, following alterations in field- and bottom-layer vegetation and soil fauna.

CARABIDS AND THE DISTURBANCE-BASED MANAGEMENT MODEL

The disturbance model maintains an uneven age structure or at least two tree-age cohorts within a stand, and is usually applied at smaller scale

than the classic model (Raymond et al. 2009). The philosophy with regard to the forest is fundamentally different between the two models: to put it simply, some trees are removed from the forest in the disturbance model, whereas some trees are (sometimes) retained in the clear-cut plot in the classic model. Logging regimes vary according to, e.g., the land owner's interests and forest type, but should be economically viable. The disturbance model essentially includes a variety of to-be-emulated stand dynamics (Table 2): even-aged, resulting from stand-replacing disturbances; cohort, originating from partial disturbances; and gap, which is driven by deaths of single or small groups of trees within stands. According to Kuuluvainen (2009) the latter two would dominate the Fennoscandian landscape under conditions without active forest management. The proportion of trees removed per harvesting event, and the size and shape of clear-cut gaps, vary with the use of multiple methods (Table 2, Koivula et al. 2012). Trees can also be retained at varying densities, depending on site characteristics, and already in precommercial thinning of regeneration phases (the "skips and gaps" principle; Harrington et al. 2009). Legacy elements – structures that are important for rare and threatened species or that significantly enrich the forest – are actively retained while harvesting (Lindenmayer & Franklin 2002). These elements include very large tree individuals, large-sized coarse woody debris, and sites with characteristics that make them special within a given stand, such as patches of large deciduous trees

within a pine or spruce stand (e.g., Päivinen et al. 2011).

Carabids have been used to evaluate biological responses to the above-listed logging regimes. They have also been sampled to model responses to clear-cut (gap) size and to certain legacy elements: coarse woody debris, patches of subdominant tree species, and so-called key biotopes such as forest bogs. Moreover, the introduction of certain processes that mimic natural disturbances into managed forests has been experimentally studied by using carabids; most notably is prescribed burning (Table 3).

In the short term and at the stand level assuming relatively even tree removal, the common fauna/flora of mature Norway spruce forest remains almost unchanged if up to 25-30% of tree individuals, or 33-50% of the total tree volume, are harvested. This pattern applies to a wide selection of taxa: spiders, soil invertebrates, lichens, vascular plants, blueberry and its herbivores, and carabids (Atlegrim et al. 1997, Jalonen & Vanhamajamaa 2001, Koivula 2002a, Hedenås & Erickson 2003, Siira-Pietikäinen et al. 2003, Matveinen-Huju & Koivula 2008). To avoid misinterpretation of this pattern, it is important to realize that carabid responses to logging generally vary according to forest type (Work et al. 2008, 2010) and that some closed-forest specialists – including certain epiphytic lichens and bryophytes – may negatively respond even to single-tree cutting (Esseen et al. 1996). Carabids have not been shown to be this sensitive, but there might be such among arboreal (tree-inhab-

Table 2. Example management techniques within the disturbance-based management model, and respective natural disturbances. Note that, in reality, these techniques are applied in a flexible way and rather form a continuum than strictly defined method categories. All methods include permanent retention of many trees, but this can be varied depending on conservation and forest owner's interests.

Technique	Disturbance	Applied spatial scale	Size class, ha	Removal/retention
Clear-cutting*	Wildfire	Stand to multiple stands	1-10	50-95/5-50 (1 visit/rotation)
Partial clear-cutting	Windthrow	Within stand	0.2-1	25-75/25-75 (1-2 visits/rotation)
Gap felling	Insect outbreak	Within stand	0.01-0.2	10-25/75-90 (multiple visits/rotation)
Selective felling	Tree deaths due to fungal infection	Stand to multiple stands	1-10	10-30 (multiple visits/rotation)

* Shape modifications and variable retention are applied.

iting) species, e.g., in the genera *Calosoma* and *Dromius*.

Selective logging, aiming at an uneven tree-age structure, appears to affect boreal carabids only if a relatively high amount of trees (more than 40-50% of merchantable-tree individuals) is removed and the forest consequently becomes very open and well-lit. In Finland, the first three post-logging years in Norway spruce forests were studied by Koivula (2002b). The results showed that the studied, up to 34% removal of trees did not significantly affect ground-dwelling carabids. However, removals of 56-57% of merchantable trees significantly increased the richness (but not abundance) of ground-dwelling beetles, including carabids, in mixed coniferous and deciduous forests of Quebec, Canada (Légaré et al. 2011). Such changes at least partly result from decreases of closed-canopy species and increases of canopy-closure generalist and open-habitat species (Peck & Niwa 2004, Niemelä et al. 2007). In accordance with these results, removals of over 50% of trees significantly altered the forest-carabid fauna five years post harvest in mixed aspen and spruce forests in Alberta, Canada (Work et al. 2010). The above studies thus suggest that low but even removal and high retention of trees retain the forest carabid assemblage almost unaltered. This might be independent of the tree-age structure of stands: Werner & Raffa (2000) compared mature managed uneven- and even-aged mixed-wood forests in northern USA but did not find significant differences in the abundance of 21 abundant carabid species.

A drastic threshold of tree density for carabids may exist in the lower part of the tree-density gradient. Open-habitat carabids remained very scarce in Finnish partially-logged Norway spruce forests until 20-30% of trees remained in harvested stands; below this threshold these carabids dramatically increased in abundance (Niemelä et al. 2007). As this analysis involved several logging methods, the result may be caused by the spatial arrangement and/or density of retained trees. I attempted to shed more light on this issue by examining four-year data collected from 8 selectively-logged and 8 gap-

felled Norway spruce stands (Koivula 2002a, 2002b): these methods essentially differ in the spatial arrangement of retained and logged trees. I modeled stand-specific catch rates and numbers of species of forest, generalist, and open-habitat carabids (GLM with Poisson error distribution, covariate = tree density [necessary because of the generally higher densities in thinned stands], blocks = study areas, factors = year + logging treatment + year × treatment). The analysis revealed no significant effects of treatment or interaction – which would have suggested some role of the spatial arrangement of trees – but detected a significant effect of tree density while the abundance and richness of open-habitat species increased through the four years of study (analysis not shown). Due to the covariation between tree density and treatment, this result should not be interpreted as to indicate that the spatial arrangement of trees would be unimportant for carabids. This aspect requires studies that are designed to test for the number and clustering of trees.

Clear-cut plot size remarkably affects the carabid catch, and this effect may occur within months following logging, but very small gaps may change only little. Koivula (2002a) showed that up to three years post harvest, generalist carabids were more abundant in 2-ha clear-cut plots than in 0.16-ha gaps in Norway spruce forests. In accordance with this finding, Abildsnes & Tømmerås (2000) detected significant effects of logging of Norway spruce forests on carabids more frequently in landscapes characterized by large rather than by small clear-cut plots (150 x 150 m or 40 x 40 m). Variation in gap size while keeping the amount of retained trees constantly at 35% was studied in yellow birch forests a few months following logging in Quebec, Canada (Klimaszewski et al. 2005). The authors observed that logging two large gaps altered the carabid fauna more severely than the smaller (four- and eight-) gap alternatives; the latter closely resembled unharvested forest. Finally, Shields et al. (2008) compared ground-dwelling arthropod fauna between ca. 0.03 and 0.12 ha clear-cut gaps a few months after logging in yellow birch stands in northern Michigan, USA. Likewise, these au-

thors observed that the ground-dwelling beetle fauna (including carabids) of the smaller gaps closely resembled coenoses in unharvested forests while the larger-gap fauna had already begun to diverge.

Dead wood has become a scarce resource in Fennoscandian managed forests due to the application of forestry operations within the classic model since the 1950s (Siitonen 2001). The shortage of this resource has been identified as one of the most important reasons for hundreds of forest-associated species being threatened in Finland and in Sweden (Anon. 2010, Rassi et al. 2010, Siitonen 2012). Carabids are not considered dead-wood dependent, although many species benefit from dead wood (e.g., Cobb et al. 2007, Work et al. 2008), and *Tachyta nana* lives under the bark of dead trees (Lindroth 1985). Carabid individuals of several species frequently over-winter or lay eggs in decaying stumps or snags and under tree bark (Thiele 1977, Burakowski 1986, Lindroth 1985, 1986); the genus *Platynus* would deserve carabidologists' attention in this respect (J. Siitonen, Finnish Forest Research Institute, pers. comm.). Dead wood thus positively affects carabids by providing shelter, and other positive effects may concern food resources and micro-climate. A recent experiment tested an artificial creation of downed dead wood on carabids seven years after the creation (T. Toivanen, T. Heikkilä & M. Koivula, in prep.). Three levels of dead wood were applied: 5, 30, and 60 m³/ha, but this had no detectable effect on carabids. In summary, carabids benefit from dead wood, but the biological significance and determinants of this response should be experimentally evaluated.

Key biotopes are patches of habitat of high importance for species dependent on these habitats. Patches of deciduous trees within coniferous stands support certain carabid species (Niemelä et al. 1992, Bergeron et al. 2012), and leaf litter particularly contributes to this response (Koivula et al. 1999). Such patches of subdominant tree species are often retained within the disturbance model (see above). Also certain other within-stand micro-site types have been rou-

tinely retained in Fennoscandian forestry since the 1990s (Hallman et al. 1996, Angelstam & Pettersson 1997, Hansson 2001). For example, wet *Sphagnum* mires are usually not logged (e.g., Päivinen et al. 2011) as these host certain specialists not found elsewhere in the forest, such as *Platynus mannerheimii* (Niemelä et al. 1987, 2007). These patches are also preferred by certain other species, such as *Agonum fuliginosum* (e.g., Koivula 2002a, 2002b). Retention of 0.09-0.55 ha Norway spruce mire patches at clear-cut plots was recently studied in Finland by Matveinen-Huju et al. (2009). These patches supported *Patrobis assimilis*, a moisture-associated canopy-closure generalist, whereas *Cychnus caraboides*, a closed-canopy specialist, decreased in these patches and in adjacent clear-cut plots. The general decrease of *C. caraboides* may indicate conditions turned unfavorable in these mires following harvesting of the surrounding forest, and/or year-to-year population variation. Nevertheless, a recent study suggests that mires are important refugia for many closed-forest carabids, including the mire specialist *P. mannerheimii*, even if located within clear-cut plots of Norway spruce forest (T. Toivanen, T. Heikkilä & M. Koivula, in prep.).

Restoration aims at introducing structures and processes characteristic of pristine forests to managed forests; thus, many operations described above can be considered restoration. Prescribed burning is an increasingly often applied restoration operation in Fennoscandia (e.g., Päivinen et al. 2011). Due to the efficient fire suppression, North European forests generally lack fire, which has rendered many species rare. For example, the fire specialist *Sericoda bogemanni* may have become extinct in Western Europe for this reason (Siitonen 2012). Such carabids appear dependent on a landscape-scale continuity of fires that are suitable for only 1-2 years; Koivula et al. (2006) showed with multiple datasets that *Sericoda quadripunctata* and *S. bembidioides* occurred at fires abundantly only for the first two post-fire summers in mixed-wood forests in Alberta, Canada. Similarly, Paquin (2008) showed that, in black spruce forest succession in Canada, the first two post-fire summers are distinctive for

carabid assemblages. These patterns suggest that prescribed burning in managed forests would be beneficial for several specialist species, including many carabids.

Prescribed burning expectedly supports *S. quadripunctata* and *Pterostichus adstrictus*, but as with wildfire, this effect appears short-lived (Koivula et al. 2006, Martikainen et al. 2006; see also Gongalsky et al. 2006). Similar findings for several beetle groups – including carabids – were reported in eastern Finnish Scots pine forests (Hyvärinen et al. 2009). Accordingly, seven years after prescribed burning in southern Finland, the Norway spruce forest-carabid fauna had recovered quite well, and fire-specialist carabids were not caught (T. Toivanen, T. Heikkilä & M. Koivula, in prep.). Factors positively affecting the abundance of *S. quadripunctata* are increases in the amount of burned wood (Wikars 1995) and in burn severity (Koivula et al. 2006). The ecological effect of prescribed burning also generally depends on topography, forest type, soil moisture, weather, and season (cf. Zackrisson 1977, Wallenius et al. 2004), but carabid responses to interactions between fire and these factors have not yet been evaluated.

DISCUSSION

1. Variable retention, critical thresholds, and carabids

Evidence summarized above expectedly suggests that, in boreal forests, closed-forest carabids benefit from decreasing clear-cut size and an increasing level of green-tree retention, and open-habitat-associated carabids show an opposite response. These may sound like circular arguments, but habitat associations were initially derived from habitats of natural origin, such as mature forests and meadows; they have now been used to examine species responses in a man-modified environment, i.e., managed forests. Similar results concerning clear-cut size have been reported, e.g., in German temperate forests by Huber & Baumgarten (2005). Accordingly, Pawson et al. (2006) reviewed studies on clear-cut size and

concluded that (a) different groups of organisms show varying responses, e.g., considering species richness, and (b) not all responses are linear and hence threshold conditions may exist for clear-cut size.

Two thresholds along the tree-density gradient can be detected concerning selective logging applied relatively evenly spread over the to-be-harvested stand. In spruce forests, closed-canopy species show a critical retention level at 40-50% (trees/ha or m³/ha), under which they start to decrease. This threshold may possibly be independent of forest type, as studies in different regions and both coniferous and deciduous forests point to the same direction (Table 3). Similarly, in temperate forests of Washington and Oregon, USA, Halaj et al. (2008) compared harvested Douglas fir (*Pseudotsuga mentziesii*) stands with 15-40% of retention to unharvested mature forest five years post harvest, and reported a 60% abundance decrease of forest carabids due to logging. Moreover, selective logging with 20% tree removal maintained the carabid assemblage unaltered in German temperate forests (Huber & Baumgarten 2005). Regarding open-habitat carabids, on the contrary, retention of less than 20-30% makes them increase rapidly in Norway spruce forests (Niemelä et al. 2007). However, abundance and richness comparisons between unharvested and clear-cut sections of partially-harvested stands (cf. Koivula 2002a) suggest that the spatial arrangement of retained (or logged) trees plays a highly important role here (see Section 2).

Succession is a key driver of the carabid-assemblage structure (Niemelä et al. 1996). Open-habitat species are common at spruce-forest clear-cut plots only until the aggressive invasion of tall grasses, i.e., 5-15 years following logging, but on drier soils (pine forests) the habitat may longer remain suitable. The most notable temporal threshold for carabid-assemblage structure along the secondary spruce-forest succession coincides with canopy closure, i.e., 20-30 years post disturbance (clear-cutting or wildfire; see above). These patterns may appear very general as similar results have been reported in the tem-

perate region (e.g., Szujewski et al. 1977, Butterfield 1997, Pawson et al. 2011, Vele et al. 2011). However, work by Jan Szyszko and colleagues (e.g., Szyszko 1990, Szyszko et al. 2000, Schwerk & Szyszko 2011) suggest that the carabid assemblage might continue to change considerably longer. Different successional stages are indeed characterized by deciduous or coniferous trees, hosting different carabid assemblages (Work et al. 2010). Of these stages, mature conifer-dominated stands have reached the end of logging rotation and will thus normally be harvested, but they also host the least logging-tolerant carabid assemblage (Work et al. 2010). Mature-forest and open-habitat specialists both inhabit successional stages that are short-lived in landscapes managed according to the classic timber-production model. The disturbance-based management model would probably better support both species groups through various management modifications.

Species associated with old-growth forests (here, age of dominant trees >120 years and no management activity for several decades) have long been of conservation concern (e.g., Spence et al. 1996). Work et al. (2010) showed that carabid response to retention felling was more pronounced in advanced than in younger successional stages. This finding suggests a distinctive old-growth assemblage that cannot emerge unless logging rotation is sufficiently long. Protection of very large parts of old-growth forest would be the most efficient way to support these species, but in managed forests longer-than-average logging rotation and various retention-logging techniques should be applied to improve conditions at the forest-landscape scale and to secure the ecological connectivity of forest reserves.

Also earlier successional stages host many threatened species, including carabids (e.g., Rassi et al. 2010). These species are usually highly specialized to certain structures, such as sun-exposed dead trees, sandy heaths, or post-fire habitat. Such specialists can be supported through restoration that often involves logging. Three Finnish examples serve here. First, boreal sandy-heath specialists – such as the threatened

Carabus convexus – may be supported by selection logging that returns the well-lit conditions of dry pine heaths. Second, selection felling targeted to conifers improves lighting, micro-climatic, and soil quality of lush deciduous forests and hence supports grove specialists such as the threatened *Badister sodalis*. Third, fire-specialist carabids of the genus *Sericoda* can be supported by introducing fire into logged stands (Wikars 1995, Toivanen & Kotiaho 2007). This operation also drastically increases dead wood, so conditions improve for dead-wood dependent (non-carabid) species, too.

2. Within-stand management and carabids

The spatial distribution of retained trees appears crucial for the carabid response to logging: at the stand level, both closed-forest and open-habitat species generally benefit from clustered retention, as patches of their preferred habitat become larger and hence micro-climatically more favorable (Table 3). I believe the lower the retention level the more important this clustering appears in this respect. For closed-canopy specialist carabids, up to 0.05-ha retention plots within clear cuts are too small (Koivula 2002a), so the clustering concerns larger areas for a positive impact. Niemelä et al. (2007) suggested that “a few ha” would be sufficient for a mature-forest carabid assemblage to occur within the focal patch, but positive impact for many if not most of these species probably occurs in considerably smaller patches unless they become very open and well-lit. Changes in micro-climatic conditions in retention patches could be softened by retaining single or small groups of trees near edges of clear-cut plots and unlogged forest, and/or by carrying out the harvesting in very narrow or amoeba-shaped clear-cut plots that account for, e.g., topography.

Even very small retention-tree plots might be important for non-carabid taxa and/or for protecting certain rare or sensitive habitat types such as forest bogs (cf. Matveinen-Huju et al. 2009, Päävinen et al. 2011). Shelterbelt retention along clear-cut edges is a common practice in North European forestry, and a general rule of thumb is

Table 3. Summary of responses of carabids associated with closed tree canopy (closed-canopy species) and those associated with no or little tree-canopy cover (open-hab. species) to aspects of forest management in the boreal region. Note that these are coarse generalizations and results vary according to, e.g., geographic region, species, and forest type. Logging-regime abbreviations are CTR = unlogged mature forest (“control”), CC = clear-cutting (>0.5 ha), GF = gap felling, and SF = selective felling. Studies are divided into short-, mid- and long-term; na = not yet assessed. For more information, see text and Table 1.

Aspect	Closed canopy			Open hab.		
	Short-term	Mid-term	Long-term	Short-term	Mid-term	Long-term
<i>Logging-regime comparisons</i>						
CTR vs CC	CTR>CC	CTR>CC	CTR=CC	CTR<CC	CTR=CC	CTR=CC
CTR vs CC vs GF	CTR>(CC=GF)	na	na	CTR<(CC>GF)na	na	na
CTR vs CC vs SF	CTR>(CC<SF)	na	na	CTR<(CC>GF)na	na	na
CTR vs GF vs SF	CTR>(GF=SF)	na	na	CTR<(GF>SF)na	na	na
<i>Other management operations</i>						
Small retention groups*	±	na	na	+	na	na
Ploughing/scarification	–	na	na	+	na	na
Precommercial thinning	–	±	na	+	–	na
Removal of logging residue	–	na	na	+	na	na
Increase in tree-age variation	na	na	na	na	na	na
Increase in tree-density variation	na	na	na	na	na	na
Protected old-growth forests	na	na	na	na	na	na
<i>Legacy elements and restoration</i>						
Increase of dead wood	± (+)	na	na	±	na	na
Clusters of subdominant tree spp.	+ (–)	na	na	na	na	na
Wet patches (mires, bogs)	+	+	+	–	na	na
Prescribed fire	–	±	±	+	±	–

* Groups of 10-30 trees within a clear-cut stand.

that their minimum width should correspond to the height of trees. Such retention has not been studied using carabids in the boreal region, but edge-associated micro-climatic alterations may occur over considerably longer distances within the retention forest (Harper et al. 2005), so these strips may largely represent open habitat for carabids (see Koivula 2002a). Thus, such strips will not retain the to-be-sheltered habitat completely unchanged, but they are certainly better than no shelter: even very narrow strips of trees bear some significance for carabids. For example, rows of trees at temperate-region farmland edges support some forest-associated carabids (e.g., Trnka et al. 1990, Nemtsev et al. 2000). Moreover, 10-20 m wide retention-tree strips within clear-cut plots or at their edges might serve as movement corridors for such species (cf. Niemelä 2001). However, the significance of

such corridors or very small patches of retained trees as stepping stones for carabid movements between mature-forest patches remains to be evaluated (see Sklodowski 1999).

Based on green-tree retention studies (e.g., Koivula 2002a, 2002b, Work et al. 2010), increasing structural variation raises carabid diversity at the stand level during the first few post-logging years. In the mid and long term, the structural evenness of trees as such may not be important for carabids (Werner & Raffa 2000). However, Lassau et al. (2005) collected several structural variables, calculated an index reflecting structural complexity, and found that beetle catches – including carabids – were more speciose at structurally complex than at simpler forest sites near Sydney, Australia. Also, patches

of subdominant trees within stands appear important (Table 3). Moreover, at the landscape level, patches of the natural spectrum of successional stages and associated dominant trees are important for the maintenance of full boreal-forest carabid fauna (cf. Work et al. 2010). Thus, two cautious conclusions regarding the importance of structural within-stand heterogeneity can be drawn. First, assuming a constant tree-species composition, structural variation may appear important for boreal carabids only if a stand includes strongly contrasting patches (Peck & Niwa 2004) of mature trees and of very recent small-scale disturbances (such as gap-felled openings; Table 3), but this effect may be difficult to detect after the canopy has recovered in the disturbed patches. Second, other elements of structural heterogeneity – particularly variation in tree-species composition – are crucial for the spatio-temporal distribution of carabid diversity at the within-stand and landscape scales (see above).

Logging not only removes merchantable trees but mechanically affects tree saplings, soil, and litter, alters micro-climate, and adds organic material to the forest floor (Niwa et al. 2001). Forest managers also actively carry out post-harvest operations that contribute to these impacts. Although evidence as summarized above is scarce, precommercial thinning, top-soil scarification, and removal of logging residue apparently affect forest carabids only little. Perhaps the most significant of these impacts is the positive response of open-habitat associated species.

Restoration of boreal-forest habitats varyingly affects carabids. Artificial addition of dead wood by cutting live trees may affect carabids only little (T. Toivanen, T. Heikkilä & M. Koivula, in prep.) or even have a positive impact on carabids, as was shown for temperate forests of North Carolina, USA (Ulyshen & Hanula 2009). At a larger scale, prescribed burning positively affects certain specialist carabids (Table 3; see above). Some species thus benefit from combinations of logging and fire, such as *Sericoda quadripunctata* (Koivula et al. 2006). However, as such operation is a “disturbance on top of a disturbance” it could lead to a large-scale simpli-

fication of the carabid assemblage. Indeed, Cobb et al. (2007) experimented with a set of man-made and natural disturbances and showed that the compositional variability was higher in single than in combinations of disturbances. Fire should therefore be applied with caution and for explicitly-set conservation targets, e.g., to support threatened dead-wood- or fire-dependent species.

3. Changing conditions and knowledge gaps

Retention of multiple tree species is not just beneficial for forest organisms (see above) but also potentially retains the resilience of the forest ecosystem in changing conditions (Campbell et al. 2009). Large-scale application of single-species forestry, which may currently be economically advantageous, can suddenly turn to an economic disaster: due to monoculture and several subsequent warm winters, the mountain pine beetle (*Dendroctonus ponderosae*) managed to kill over 17.5 million ha of lodgepole pine (*Pinus contorta*) forests in barely over one decade in British Columbia, Canada (Anon. 2012b). This also exemplifies that climate change may alter the relative importance of different disturbances (mountain pine beetles used to be non-epidemic for several decades in British Columbia), and hence also the disturbance-model forestry must maintain flexibility in the future. Regarding carabids, the structure of assemblages is difficult to predict when conditions change at a global scale, as several characteristics of the environment probably change in concert. A large-scale application of forestry characterized by continuous-canopy, multiple-species, and uneven-age stands of managed forests presumably supports the maintenance of most carabid populations, but the speed of environmental change makes long-term follow-up studies extremely important. In the worst case, data collected 10-20 years ago might become irrelevant in just a few decades.

Long-term carabid data are rare, but also certain other knowledge gaps should be closed (Table 1). Most aspects of management listed in Table 1 have been fairly well studied at the spatial scales of within and between stands using boreal

carabids. However, comparisons of different logging regimes in wet alder forests, rocky pine forests, and groves using carabids are lacking in the boreal region. Other knowledge gaps include clear-cut-edge shelterbelts (10-30 m wide retention-tree buffers between clear-cut plots and any other habitat type such as stream, lake, or bog), variation in logging rotation, and precommercial thinning (Table 1). The landscape level appears extremely poorly studied, which probably results from the requirement for extensive sampling. Based on the above text and Tables 1 and 3, I suggest the following topics for future carabid research:

- Study the importance of trees *per se* for carabids: study arboreal carabids, i.e., species living on and in live and dead wood, as these potentially suffer most from forestry.
- Study interactions between different management operations and forest structure (see gaps in Table 1).
- Carry out long-term follow-up studies but also retrospective studies; repeat sampling at your old study sites if possible.
- Initiate experiments on the role of legacy elements for carabids.
- Study certain within-stand aspects linked to the disturbance model: the roles of edge softening, permanent retention of key habitats, and succession in stands managed according to the disturbance model.

4. Conclusions

Despite political initiatives on conservation, such as the Countdown 2010 declaration of the European Union, the general trend of biodiversity decline will continue in the near future. Remarkable improvements in this sense require drastic changes in managing habitats outside existing reserves. The above-described, ongoing paradigm shift in forestry probably supports the resilience of forest ecosystems. But even if the disturbance model is applied throughout the boreal region, extensive parts of old-growth forests should be excluded from forestry.

Three points of view have to be kept in mind while considering the disturbance model. First,

clear-cutting is not “bad” or retention logging “good”; both can be justified for certain situations, based on ecology, economics, aesthetics, and other reasons. Second, clear-cutting as such is not the reason for most threatened species being so rare, but the associated management operations causing scarcity of legacy elements and old-growth forests, lower heterogeneity of trees, and alterations in ecological conditions at sensitive micro-habitats. Third, in a North European situation where most forests have been clear-cut at least once and consist of even-aged monoculture stands, a sudden large-scale replacement of clear-cutting with retention-logging regimes will lead to an increase of managed-forest area. If gap and selection logging are applied, the amount of new edge habitat may be of minor concern: old-growth forests, for example, are characterized by various-sized gaps (Esseen et al. 1997, Kuuluvainen 2009). But theoretically this might make it more difficult to justify new forest reserves, as the timber needs of the forest industry will not automatically adjust to the paradigm but rather to the markets. Perhaps the improvement of the ecological quality of managed forests will compensate for this and transcend this obstacle.

Descriptive and experimental studies at a very large spatial scale (landscape) and long duration (several decades) would be extremely valuable for justifying the functioning of different management techniques in supporting forest organisms, especially threatened and rare species. Even more value and expectations can and should be imposed on such studies now, considering the speed and magnitude of global changes in land use and climate, and their many predicted ecological consequences.

ACKNOWLEDGEMENTS

I would like to thank the organizers of the XV ECM for inviting me as a plenary speaker; this paper is based on my congress presentation. I also thank Hanna Koivula and two anonymous

reviewers for commenting an earlier draft of the manuscript.

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- Received: 21.07.2012.*
Accepted: 25.08.2012.