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Impacts of experimental habitat fragmentation on ground beetles (Coleoptera, Carabidae) in a boreal spruce forest

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A fine-scale fragmented area (twenty-two 40 × 40 m clear-cuts) and a coarse-scale fragmented area (three 150 × 150 m clear-cuts) were created in a spruce forest in Norway during 1995–1996. Before and after the logging, in 1994 and 1997 respectively, ground beetles were sampled in pitfall traps between the clear-cuts and from an untouched control area. Seven eurytopic forest species accounted for 99% of the catch. In the fine-scale fragmented area the abundance of *Leistus terminatus* was significantly negatively affected by fragmentation, whereas in the coarse-scale fragmented area *L. terminatus*, *Trechus obtusus* and *Calathus micropterus* were significantly negatively affected. No clear indications of area or edge effects were found. Isolation effects probably were minimal. The ambiguity in the explanation of the results is likely to be due to species-specific and complex responses to the different aspects of habitat fragmentation.

1. Introduction

In Fennoscandia, modern forestry practices, basically clear-cutting of large areas and subsequent planting, have turned most of the productive boreal coniferous forest into a patchwork of even-sized, even-aged monocultures with short rotation time (Esseen *et al.* 1997). Remaining virgin forest is mostly found as small, isolated fragments or in unproductive areas (Korsmo 1991, Hansson 1992, Esseen *et al.* 1997). In Norway, forest older than 160 years makes up only 0.8% of the productive forest area (Tomter 1994). Forest fragmentation and loss have had considerable negative effects on boreal insects (Heliövaara and Väisänen 1984, Hansen *et al.* 1991, Esseen *et al.* 1997). In Norway, forestry is the most important threat factor for 45% of the red-listed beetle species (Hanssen *et al.* 1997).

Fragmentation of habitats is one of the main threats to population survival and ecosystem function (UNEP 1995). The effects of habitat fragmentation may be divided into three groups (cf. Saunders *et al.* 1991): (i) Area effects — the total habitat area is reduced, possibly reducing population sizes, and thus increasing the risk of local extinctions (MacArthur and Wilson 1967); (ii) edge effects — the habitat becomes more exposed to the microclimate of the surrounding habitat because the perimeter to area ratio increases (Laurance and Yensen 1991), leading forest edges adjoining clear-cuts to be dryer, warmer and windier than forest interior (Ranney *et al.* 1981, Chen *et al.* 1995, Murcia 1995); and (iii) isolation effects — habitat patches become more-or-less isolated with reduced chances of being recolonised from other patches after local species extinction (Hanski 1991).

Ground beetles (Carabidae) are considered useful environmental indicators (e.g. Refseth 1980, Eyre and Rushton 1989, Butterfield *et al.* 1995), because of their sensitivity to environmental conditions (Thiele 1977) and rapid responses to habitat changes (e.g. Niemelä *et al.* 1993a, 1993b). Investigations in historically isolated habitat fragments indicate that stenotopic species with low dispersal abilities are vulnerable to habitat fragmentation, whereas eurytopic species and species with high dispersal abilities are less affected (e.g. Niemelä *et al.* 1988, Halme and Niemelä 1993, de Vries 1994, de Vries *et al.* 1996). However, eurytopic species associated with the habitat undergoing fragmentation are also likely to suffer from fragmentation effects (Niemelä 1997), but evidence for this is lacking.

In the present study the ground beetle fauna of an old-growth spruce forest in Central Norway was investigated before and after experimental habitat fragmentation. Responses to fragmentation were analysed by comparing catches of individual species before and after logging in fragmented areas and in a control area. To help the interpretation of fragmentation responses the habitat associations of the beetles were analysed by comparing pitfall catches to measured environmental variables.

2. Material and methods

2.1. Study area

The study was carried out in Mosvik municipality, Central Norway, 63°47´N, 10°48´E (Fig. 1). The study area was a Norway spruce forest ca. 1 km^2 in size. The area was surrounded by extensive Norway spruce clear-cuts and bog woodland with Scots pine as the dominant tree species. The area was situated 6 km from Trondheimsfjord, and between 240 m and 300 m above sea level. Partial cutting was practised in the forest until 1910–1920. After this, forestry has had little effect on the forest except for the removal of some wind throws. The forest can be classified as old-growth, because it has numerous large and old trees (> 150 years), a multi-layered canopy, natural regeneration, dead trees in different stages of decomposition and numerous deciduous trees (Tømmerås *et al.* 1996). The vicinity to the coast is reflected by the occurrence of suboceanic plants, such as *Rhytidiadelphus loreus*, *Cornus suecica* and *Blechnum spicant*. Five main vegetation types classified according to Fremstad (1997) were distinguished in the area: (i) Fern — *C. suecica* woodland with *Gymnocarpium dryopteris*, *Phegopteris connectilis* and *Oxalis acetosella* was the most common vegetation type; (ii) Tall-fern woodland was also common, dominated by the ferns *Athyrium filix-femina* and *Dryopteris expansa*; (iii) Species poor *Vaccinium myrtillus–C. suecica* woodland was found in the driest parts of the forest; (iv) Poor swamp woodland characterised by *Equisetum pratense*, *Rubus chamaemorus* and *Sphagnum girgensohni*; and (v) Rich swamp woodland characterised by *Calamagrostris purpurea*, *Caltha palustris* and *Plagiomnium* spp were found in wet depressions.

2.2. Experimental design and sampling of ground beetles

The study site was divided into three areas, two of them chosen for fragmentation through logging, and the third a control area (Fig. 1). For practical reasons the entire area was marked off into a 50 ×

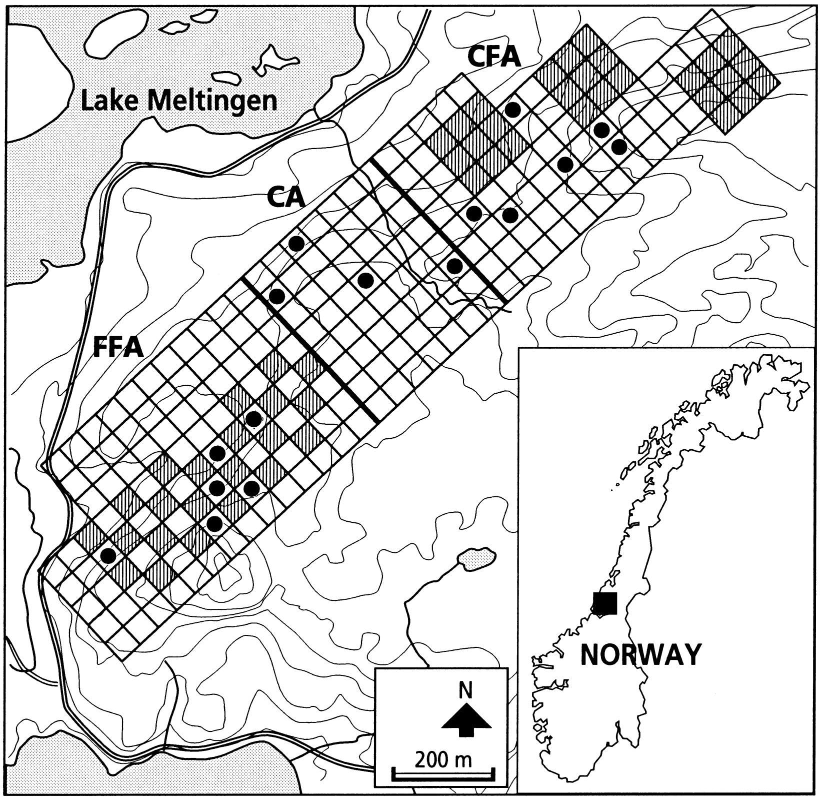

Fig. 1. Study site for a fragmentation experiment in a spruce forest, Central Norway. The study site was divided into three areas; a control area (CA), and two areas chosen for fragmentation of the tree layer; a fine-scale fragmented area (FFA) and a coarse-scale fragmented area (CFA). In the hatched squares, clear-cutting took place during the winter 1995–96. The clear-cut size was 40 × 40 m in the fine-scale fragmented area, and 150 × 150 m in the coarse-scale fragmented area. Filled circles show the position of the permanent pitfall trapping plots.

50-m grid with corner stakes. In the area fragmented on a fine scale, the logging pattern consisted of 22 clear-cuts in a chess-board pattern 40 × 40 m each, whereas in the coarse-scale fragmented area, 3 clear-cuts of 150 × 150 m were laid out (Fig. 1). Permanent pitfall trapping plots were placed in the centre of 16 randomly selected 50 × 50-m squares that were not to be logged: 6 each in the fine-scale and coarse-scale fragmented areas, and 4 in the control area (Fig. 1). The pitfall trapping plots consisted of a 5 × 10-m area divided into 1 × 1-m squares. Pairs of pitfall traps were placed at the left and right margin of five randomly selected 1 × 1-m squares in each trapping plot. Thus there were 10 traps per plot and 160 traps in all. Logging took place on snow-covered ground during the winter 1995–1996. Ground beetles were collected before and after logging in 1994 and 1997, respectively. Pitfall traps consisted of 9.5-cm deep plastic cups, 6.5 cm in diameter. Ethylene glycol was used as preservative. To prevent flooding during rain, transparent plastic roofs (10 × 10 cm) were mounted above each trap. The traps were activated as soon as possible after snow melt and emptied on a three-week basis. The trapping period in 1994 was 19 May–7 September, except for the coarse-scale fragmented area where the trapping period was 27 May–7 September. The trapping period in 1997 was 2 June–15 September. Beetles were identified according to Lindroth (1985, 1986).

2.3. Environmental variables

The following environmental variables were measured at the pitfall traps to investigate their possible association with the occurrence of ground beetles:

— Coverage of bare ground, spruce needles, twigs, other dead plant material, mosses, hepaticas, bottom layer, heather, field layer, herbs and grass.

— Vegetation type.
— Relative solar radiation.
— Canopy cover.
— Number of trees taller than 2 m, grouped as spruce trees, deciduous trees (birch, rowan and sallow) and total (spruce + deciduous trees)
— Mean height of the five tallest spruce trees.

Coverage of bare ground, spruce needles, etc. were registered in a 0.5 × 0.5-m square around each trap by assessing cover to the nearest 10 percent. Vegetation type was identified at each trapping plot (5 × 10 m) based on a survey of vegetation types in five 1 × 1-m squares at each trapping plot. A vegetation type occurring in at least four of these squares was considered the main vegetation type of the trapping plot; if less dominance, mixed vegetation types were identified. Relative solar radiation was calculated at each trapping plot using the formula

$$RS = \cos\left(90 - h_{opt} - h\cos\left(e_{opt} - e\right)\right) \qquad (1)$$

(Myklebost 1996), where RS = relative solar radiation, h = slope of the ground, h_{opt} = optimal slope (45°; Dargie 1984), e = exposition of the ground, e_{opt} = optimal exposition (205°; Dargie 1984). Slope and exposition were measured with a clinometer compass. The remaining variables were measured at each trapping plot, including a 2-m wide zone surrounding the plot (9 × 14 m). Canopy cover percentage was calculated by drawing the canopies onto a millimetre sheet.

2.4. Occurrence of ground beetles in relation to environmental variables

The occurrence of ground beetles was analysed in relation to environmental variables by subjecting the 1994-ground-beetle data to Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980). To perfom the DCA we used the data program CANOCO (ter Braak 1987). DCA ordination has proved useful in extracting environmental factors important for the distribution pattern of ground beetles (e.g. Niemelä *et al.* 1988, Luff *et al.* 1989, Butterfield *et al.* 1995). We used the options for detrending by segments and non-linear rescaling recommended by Eilertsen *et al.* (1990). Down-weighing of rare species by median down-weighing with the data program BDP/PC (Pedersen 1988) was performed to reduce the influence of rare species (Eilertsen *et al.* 1990). Two of the 160 pitfall traps were excluded from the ordination; one because it occurred as an extreme outlier and the other because of zero catch. To help in the interpretation of the ordination axes, pair-wise Spearman rank correlation tests between trap-score along each ordination axis and the values of measured environmental variables at the traps were performed.

2.5. Changes in abundance of individual ground beetle species after fragmentation

To separate changes in abundance caused by fragmentation from natural year to year variation, species-specific changes in catch per pair of pitfall traps from 1994 to 1997 in the fragmented areas were compared with the corresponding changes in the control area. This was carried out for the seven most common species only, due to very low catches of the remaining species. The null-hypothesis that changes in catch in the fragmented areas and the control area were equal was tested with the Mann-Whitney U-test. This test assumes equal distribution in the compared groups, or more precisely, under the null-hypothesis the ranking of all observations are assumed to have the same probability (Sokal and Rohlf 1995). As this assumption was not fulfilled, the changes in catch in each pair of pitfall traps were standardised with the transformation

$$X_i = \frac{\left[a_i - \left(\frac{ab_i}{2}\right)\right]}{0.5\sqrt{ab_i}} \qquad (2)$$

where X_i = standardised change in catch for species i between year A and year B, a_i = the number of individuals of species i caught in year A, ab_i = the total number of individuals of species i caught in year A and B. The transformation is based on the a_i conditional on the ab_i being approximately binomially distributed with parameters $(ab_i, 1/2)$. This test design requires that the habitat quality of the fragmented areas before fragmentation was similar to the habitat quality of the control area. If not, possible changes in ground beetle abundance patterns may be due to habitat heterogeneity. To check for this, the DCA ordination scores of the traps in the fragmented areas along ordination axes 1 and 2 were compared to the scores of the traps in the control area with the Mann-Whitney *U*-test.

3. Results

In 1994, 5 315 individuals belonging to 18 ground beetle species were captured, and in 1997, 7 076 individuals belonging to 17 species (Table 1). Seven species amounted to more than 99% of the total catch: *P. atrorufus* (52%), *T. obtusus* (24%), *C. micropterus* (11%), *P. assimilis* (4%), *L. terminatus* (3%), *N. biguttatus* (3%) and *N. reitteri* (2%).

3.1. Occurrence of ground beetles in relation to environmental variables

In the DCA ordination of the 1994 ground beetle catch (Fig. 2), ordination axis 1 and ordination axis 2 explained 33.5% and 12.6% of the variation in the material, respectively. Ordination axis 1 was significantly positively correlated with coverage of spruce needles, mean height of the five tallest spruce trees, canopy cover, number of spruce trees, total number of trees and coverage of hepaticas (Table 2). Relative solar radiation, number of deciduous trees and coverage of mosses were sig-

Table 1. Number of individuals of different ground beetles species captured in pitfall traps in a spruce forest, Central Norway, in 1994 and 1997. In a fine-scale fragmented area and a coarse-scale fragmented area (60 traps each), the tree layer was fragmented by logging during the winter 1995–1996. A control area (40 traps) was left untouched.

Species	Fine-scale fragmented		Coarse-scale fragmented		Control		Total	
	1994	1997	1994	1997	1994	1997	1994	1997
Leistus terminatus	122	55	128	42	29	25	279	122
L. ferrugineus	–	3	3	2	–	2	3	7
Notiophilus reitteri	22	24	74	67	21	25	117	116
N. biguttatus	37	27	87	102	49	52	173	181
Loricera pilicornis	–	6	2	1	1	–	3	7
Carabus violaceus	1	5	4	7	1	6	6	18
C. coriaceus	1	–	4	2	–	4	5	6
Cychrus caraboides	2	4	6	10	2	3	10	17
Clivina fossor	–	–	–	–	1	–	1	–
Patrobus assimilis	74	95	56	98	40	99	170	292
P. atrorufus	515	656	1 529	1 804	654	1 313	2 698	3 773
Trechus rubens	–	1	1	–	–	–	1	1
T. obtusus	498	629	551	557	284	480	1 333	1 666
Bembidion grapii	–	–	–	–	1	–	1	–
B. bruxellense	–	–	1	–	–	–	1	–
Pterostichus oblongopunctatus	1	–	1	1	5	–	7	1
Calathus micropterus	115	237	261	345	119	279	495	861
Agonum fuliginosum	–	1	–	–	–	–	–	1
Amara brunnea	3	3	4	–	5	2	12	5
Harpalus quadripunctatus	–	2	–	–	–	–	–	2
Total	1 391	1 748	2 712	3 038	1 212	2 290	5 315	7 076

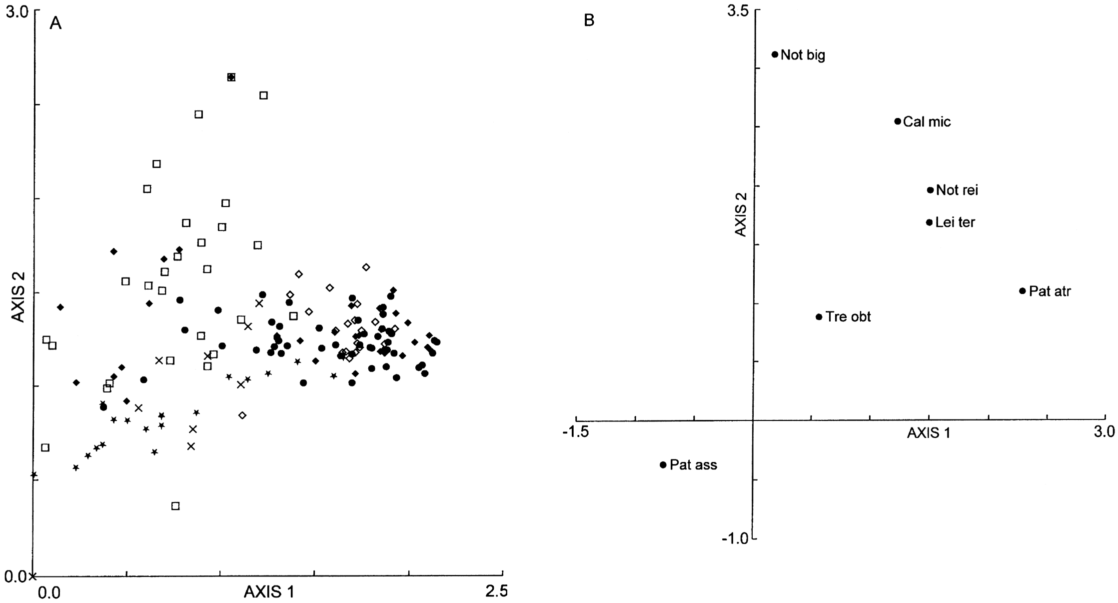

Fig. 2. DCA ordination of 18 ground beetle species captured in 158 pitfall traps in a spruce forest, Central Norway, in 1994. Total inertia = 0.848. — A: Trap plot. Traps are given symbols according to their vegetation type; □ = *V. myrtillus –C. suecica* woodland, ● = fern–*C. suecica* woodland, ◇ = tall-fern woodland, ◆ = tall-fern woodland/fern–*C. suecica* woodland, **x** = rich swamp woodland / tall-fern woodland, ★ = poor swamp woodland. — B: Species plot. Only the seven most common species are shown (circles and codes consisting of the first three letters in the genus and species names).

Table 2. Spearman rank correlation between the axis-scores of pitfall traps in a DCA ordination of 18 ground beetle species captured in a spruce forest, Central Norway, in 1994, and 17 environmental variables measured at the traps. Significant *p*-values after sequentially rejective Bonferroni correction (Holm 1979) and corresponding correlation coefficients are shown in bold types.

Environmental variable	Axis 1		Axis 2	
	r	*p*	*r*	*p*
Bare ground	0.211	0.450	–0.197	0.481
Spruce needles	**0.418**	**0.000**	**0.348**	**0.000**
Twigs	0.136	0.093	**0.506**	**0.000**
Other dead plant material	–0.022	0.785	–0.077	0.341
Mosses	**–0.242**	**0.002**	–0.178	0.025
Hepaticas	**0.290**	**0.000**	–0.174	0.029
Bottom layer	–0.120	0.134	**–0.297**	**0.000**
Heather	–0.154	0.068	0.206	0.014
Herbs	0.087	0.276	–0.214	0.007
Grass	–0.087	0.355	–0.104	0.264
Field layer	–0.102	0.201	–0.115	0.152
Relative solar radiation	**–0.437**	**0.000**	**0.255**	**0.000**
Number of spruce trees	**0.379**	**0.000**	0.189	0.017
Number of deciduous trees	**–0.268**	**0.001**	–0.212	0.008
Total number of trees	**0.350**	**0.000**	0.124	0.121
Mean height of five tallest spruce trees	**0.400**	**0.000**	**0.257**	**0.001**
Canopy cover	**0.394**	**0.000**	**0.375**	**0.000**

nificantly negatively correlated with axis 1. When the traps' vegetation types were plotted in the ordination diagram (Fig. 2a), swamp woodland and *V. myrtillus–C. suecica* woodland had their centres of gravity to the left of axis 1, while the fern types had their centres of gravity to the right of the axis. From this, axis 1 is interpreted as a gradient of light with relatively thin and sun-exposed forest to the left and relatively dense, shady and large-grown forest to the right. Ordination axis 2 was significantly positively correlated with coverage of twigs, canopy cover, coverage of spruce needles, mean height of the five tallest spruce trees and relative sun radiation (Table 2). Coverage of the bottom layer was negatively correlated with axis 2. Traps in swamp woodland had their centre of gravity on the lower part of axis 2, whereas the driest vegetation type, *V. myrtillus–C. suecica* woodland, had its centre of gravity on the upper part (Fig. 2a). The fern types occur between the swamp woodland and *V. myrtillus–C. suecica* woodland. From this, axis 2 is interpreted as a moisture gradient, with wet swamp woodland on the lower part and relatively dry *V. myrtillus–C. suecica* woodland on the upper part of the axis.

Habitat associations of the seven most common species were interpreted from the species' positions along ordination axes 1 and 2 (Fig. 2b). *N. biguttatus* was associated with the driest and most sun-exposed localities in the forest (low score on axis 1 and high score on axis 2). *C. micropterus* was associated with relatively dry and modestly sun-exposed localities (intermediate score on axis 1 and relatively high score on axis 2). *N. reitteri* was associated with modestly moist and modestly light open localities (intermediate score on both axes). *L. terminatus* showed similar association with light as the former species, but was associated with somewhat moister localities (intermediate score on both axes). *P. atrorufus* was associated with shaded and moist localities (high score on axis 1 and relatively low score on axis 2). *T. obtusus* was associated with light open and moist localities (low score on axis 1 and relatively low score on axis 2). *P. assimilis* was associated with the combination of high moisture and much light (low score on both axes).

3.2. Comparison of habitat quality in the fragmented areas with the control area

There were no significant differences between the DCA ordination axis scores of the traps in the fragmented areas and the traps in the control area after sequentially rejective Bonferroni correction of the significance level (Holm 1979) (Mann-Whitney U-test, fine-scale fragmented area versus control area: axis 1, $U = 970.5$, $p = 0.14$, axis 2, $U = 886.5$, $p = 0.036$, coarse-scale fragmented area versus control area: axis 1, $U = 1\,055.5$, $p = 0.38$, axis 2, $U = 1\,148.5$, $p = 0.82$). This suggests that the habitat quality did not differ significantly between the control area and the fragmented areas before the fragmentation took place. Thus, testing changes in ground beetle abundance caused by fragmentation by comparing changes in catches from 1994 to 1997 in the fragmented areas to the corresponding changes in the control area is justified.

3.3. Changes in abundance of individual ground beetle species after fragmentation

The mean number of individuals of the seven most common species captured per pair of pitfall traps in each area in 1994 and 1997 are shown in Fig. 3. Three of the seven species showed significant negative responses to habitat fragmentation. Standardised catches of *T. obtusus* and *C. micropterus* increased significantly less in the coarse-scale fragmented area than in the control area (Table 3). *L. terminatus* showed a significantly larger reduction in standardised catch in both the fine-scale and coarse-scale fragmented areas than in the control area (Table 3).

4. Discussion

The present study shows that the fragmentation of a spruce forest significantly and negatively affected the abundance of three of the seven most common ground beetle species in the forest remnants during the two first breeding seasons after logging. Captures of *T. obtusus* and *C. micropterus*

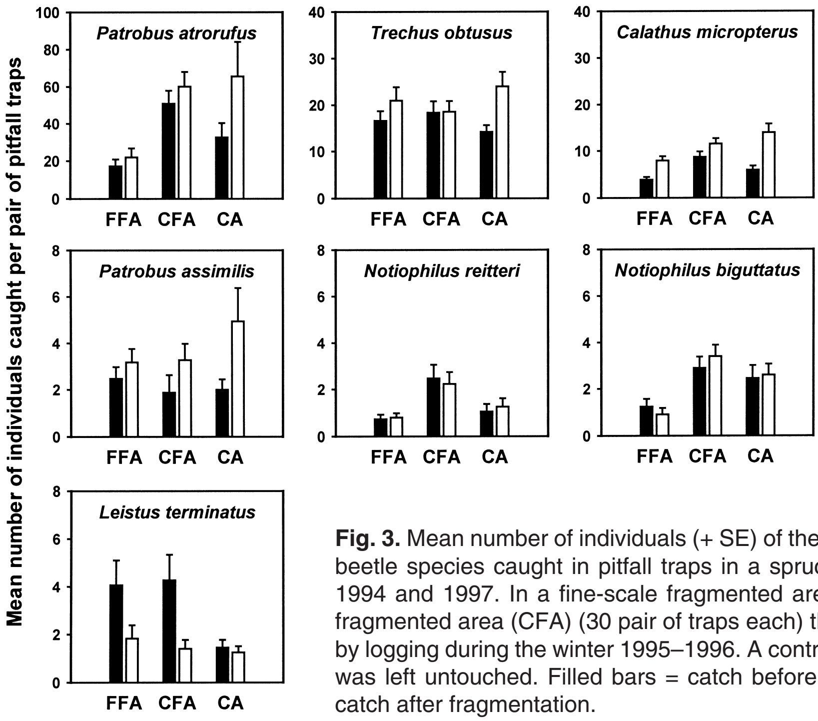

Fig. 3. Mean number of individuals (+ SE) of the seven most common ground beetle species caught in pitfall traps in a spruce forest, Central Norway, in 1994 and 1997. In a fine-scale fragmented area (FFA) and a coarse-scale fragmented area (CFA) (30 pair of traps each) the tree layer was fragmented by logging during the winter 1995–1996. A control area (CA) (20 pair of traps) was left untouched. Filled bars = catch before fragmentation. Open bars = catch after fragmentation.

were reduced in the coarse-scale fragmented area, whereas those of *L. terminatus* were reduced in both the fine-scale and coarse-scale fragmented areas relative to the unlogged control area.

The seven investigated ground beetle species occur as eurytopic forest species in the region of the study, that is, they mainly occur in forested habitats, but show little specialisation with regard to forest types (Lindroth 1985, 1986). Thus, the present study shows that not only stenotopic carabids with low dispersal abilities are vulnerable to fragmentation effects (e.g. Niemelä *et al.* 1988, Halme & Niemelä 1993, de Vries 1994, de Vries *et al.* 1996), but also abundant and rather eurytopic species. However, the effect of fragmentation in these species did not seem to be dramatic; *T. obtusus* and *C. micropterus* were captured in higher numbers after fragmentation than before fragmentation both in the fragmented and in the control areas (Table 1). Furthermore, *L. terminatus* decreased in the fragmented areas after fragmentation, but its abundance was still higher in the fragmented areas than in the control area.

The generally higher pitfall trap catches of ground beetles in 1997 as compared with 1994 (Table 1) was probably due to the weather being far warmer in 1997 than in 1994 (cf. Briggs 1961).

4.1. Area effects

Newly established clear-cuts seem to represent an unsuitable habitat for eurytopic forest ground beetle species (*see* Niemelä *et al.* 1993a). Thus in the present study, if the area requirements of individuals of the investigated species exceeded the size of the forest remnants, area effects may have contributed to fragmentation responses. However, information on the actual occupation of space by ground beetles is limited. Mean individual "home ranges" of the ground beetle species *Abax ater* was estimated at 660 m^2 in a Belgian beechwood (Loreau & Nolf 1994). However, since spatial behaviour in ground beetles is prone to vary between species as well as between habitats (Baars 1979), this estimate may not be transferred to the boreal forest species in the present study.

4.2. Edge effects

Clear-cuts in the coarse scale were much larger than clear-cuts in the fine-scale fragmented area (150 × 150 m vs. 40 × 40 m). This may have produced steeper microclimatic gradients between clear-cuts and forest remnants in the coarse-scale than in the fine-scale fragmented area (*see* Odin 1976, Peltola 1996), possibly creating a strongest edge effect intensity in the coarse-scale fragmented area. However, in the fine-scale fragmented area the logging created more edge, measured in metres, than in the coarse-scale fragmented area. It, therefore, is uncertain in which of the fragmented areas the impact of edge effects was strongest.

As forest edges adjoining clear-cuts generally have more intense solar radiation, higher air temperature, higher wind speed and lower air humidity than forest interiors (e.g. Chen *et al.* 1995), shade- and moisture-preferring species can be

Table 3. Comparison of catches of 7 ground beetle species in a spruce forest, Central Norway, in 1994 and 1997. In a fine-scale fragmented area and a coarse-scale fragmented area (30 pairs of pitfall traps each) the tree layer was fragmented by logging during the winter 1995–1996. A control area (20 pairs of traps) was left untouched. Standardised change in catch per pair of pitfall traps in the fine-scale and coarse-scale fragmented areas from 1994 to 1997 versus corresponding changes in the control area was statistically tested using the Mann-Whitney *U*-test. Significant *p*-values after sequentially rejective Bonferroni-correction (Holm 1979) are shown in bold types. Fr = mean standardised change in catch from 1994 to 1997 in the fragmented areas. Co = mean standardised change in catch from 1994 to 1997 in the control area, *n* = the actual number of trap-pairs compared.

Species	Fine-scale fragmented		Coarse-scale fragmented	
Leistus terminatus	U = 148.0		U = 137.5	
	$\mathbf{p = 0.022}$		$\mathbf{p = 0.026}$	
	Fr = –0.85	n = 26	Fr = –1.08	n = 24
	Co = 0.01	n = 19	Co = 0.01	n = 19
Notiophilus reitteri	U = 138.5		U = 136.5	
	p = 0.88		p = 0.66	
	Fr = 0.11	n = 22	Fr = –0.10	n = 23
	Co = 0.17	n = 13	Co = 0.17	n = 13
N. biguttatus	U = 127.5		U = 236.5	
	p = 0.13		p = 0.82	
	Fr = –0.28	n = 21	Fr = 0.20	n = 29
	Co = 0.21	n = 17	Co = 0.21	n = 17
Patrobus assimilis	U = 220.0		U = 245.0	
	p = 0.28		p = 0.91	
	Fr = 0.29	n = 27	Fr = 0.80	n = 25
	Co = 0.82	n = 20	Co = 0.82	n = 20
P. atrorufus	U = 191.5		U = 211.5	
	p = 0.21		p = 0.43	
	Fr = 0.58	n = 29	Fr = 1.07	n = 29
	Co = 2.35	n = 17	Co = 2.35	n = 17
Trechus obtusus	U = 232.5		U = 164.0	
	p = 0.18		$\mathbf{p = 0.007}$	
	Fr = 0.57	n = 30	Fr = 0.11	n = 30
	Co = 1.38	n = 20	Co = 1.38	n = 20
Calathus micropterus	U = 223.0		U = 159.5	
	p = 0.17		$\mathbf{p = 0.008}$	
	Fr = 1.20	n = 29	Fr = 0.68	n = 29
	Co = 1.71	n = 20	Co = 1.71	n = 20

expected to suffer more from edge effects than species that are associated with less shady and moist conditions. However in the present study, the relation between the light and moisture preference of the species analysed and their responses to fragmentation were ambiguous. There were no significant changes in abundances of *P. atrorufus,* presumably the most shade- and moisture-preferring species, after fragmentation. *L. terminatus*, that was found to be associated with modestly shady and modestly moist conditions as compared with the other species, was negatively affected by fragmentation in the both fragmented areas. *N. reitteri* showed similar habitat associations, but no significant changes after fragmentation. Furthermore, *C. micropterus*, that was found to be associated with modestly shade and relatively dry conditions, was negatively affected by fragmentation in the coarse-scale fragmented area.

Spence *et al.* (1996) studied edge effects in ground beetles in a Canadian pine forest by sampling beetles at different distances from forest edges adjoining clear-cuts. They found that two species were clearly limited with respect to habitat use on one side of the edge, while the remaining species were captured on both sides of the edge. Several old-growth forest species did not show any trend to increase towards the forest interior. Thus, their results suggest that edge effects exist, but that they are variable and difficult to interpret generally for ground beetles.

4.3. Isolation effects

Poorly dispersing stenotopic ground beetle species living in widely isolated habitat fragments surrounded by habitats strongly modified by man, may become regionally extinct because individuals are unable to spread between the fragments (den Boer 1990, de Vries & den Boer 1990). In the present study, however, fragments were not isolated; even in the fine-scale fragmented area the "forest squares" had 15 m wide connections in the corners. Furthermore, the analysed species were eurytopic, and it is doubtful that the relatively small clear-cuts represented significant barriers to their dispersal. Therefore, it seems unlikely that isolation could affect the ground beetles' observed responses to fragmentation.

5. Conclusion

Fragmentation of the spruce forest caused significant, but not dramatic, negative effects on the abundance of three of the seven investigated eurytopic forest ground beetle species. However, it proved difficult to point out the causal connection to the species' responses to forest fragmentation. Isolation effects probably were minimal, whereas no clear indications of area or edge effects were found. A better knowledge of area requirements in ground beetles is needed to improve the assessment of area effects. Furthermore, the ambiguity in the explanation of the results is likely to be due to species-specific and complex responses to the different aspects of habitat fragmentation. For example, fragmentation responses in organisms interacting with the different ground beetle species, such as their prey, predators or parasites will indirectly influence the ground beetles' responses, and thus, complicate the picture.

Nonetheless, this study shows that certain eurytopic forest carabids may be negatively affected by fragmentation effects after partial clear-cutting. If forest regeneration on the clear-cuts is allowed, these common species will probably recover (cf. Niemelä 1993a). However, if habitat loss becomes permanent, such species may in the long run face increased risk of local extinction due to fragmentation effects.

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