Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient

MATTI KOIVULA*, JARNO KUKKONEN and JARI NIEMELÄ

*Department of Ecology and Systematics, Division of Population Biology, University of Helsinki, P.O. Box 17, FIN-00014 Helsinki, Finland; *Author for correspondence (e-mail: matti.koivula@helsinki.fi, jari.niemela@helsinki.fi)*

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Abstract. We examined the occurrence of carabid beetles along a forest succession gradient in central Finland (forest age classes: 5, 10, 20, 30 and 60 years since clear-cutting). Species richness of carabids was higher in the two youngest age classes, while no clear differences were detected in carabid abundance. The high species richness in the young, open sites was due to invasion of open-habitat species. Many forest species were absent from or scarce in the young sites and became gradually more abundant towards the older forest age classes. The catches indicated a drastic decrease and assemblage-level change in concert with canopy closure, i.e. 20–30 years after clear-cutting. Some forest specialists with poor dispersal ability may face local extinction, if the proportion of mature forest decreases further and the remaining mature stands become more isolated. We recommend that, while harvesting timber, connectivity between mature stands is ensured, mature stands are maintained close (a few tens of metres) to each other and the matrix quality is improved for forest species by green tree retention.

Introduction

Forestry has drastically changed the age structure of forest stands in Fennoscandia during recent centuries, and especially in the 1900s (Niemelä 1999). For example, in southern Finland, old (over 120–150 years) forests once covered more than half of the forested land area (Gyldén 1853), while today forests older than 150 years cover only approximately 2% of the forested land area (Sevola 1999; Virkkala et al. 2000). Concomitantly, young sapling stands with deciduous dominance have increased (Järvinen et al. 1977; Esseen et al. 1992, 1997). Forests younger than 100 years cover 80–90% of the forest area in southern Finland (Sevola 1999). The boreal forest landscape thus consists of a mosaic of varying successional stages created by forestry (Hansson 1992).

Forestry is evidently the major cause for population decline of approximately 35% of threatened Finnish species (Rassi et al. 2000). Large clear-cut areas, lack of old growth forests and lack of many elements of 'natural' forests (such as coarse woody debris) have resulted in population declines and extinctions of several forest-living taxa (Heliövaara and Väisänen 1984; Esseen et al. 1992, 1997; Berg et al. 1994; Haila 1994; Enoksson et al. 1995; Fries et al. 1997). The fragmentation of old-growth forests has created problems for many beetle species that are poor dispersers but demand old-growth conditions (Niemelä et al. 1987; Niemelä 1997, 1999; Siitonen and Saaristo 2000).

Forestry has replaced forest fire as the principal initiator of secondary succession. Plants are the driving force of succession (Finegan 1984) and changes in vegetation are reflected in animal communities (Siemann et al. 1998). For example, some oribatid mites were shown to be restricted to certain phases of pine-forest succession in Scotland (Horwood and Butt 2000), and the abundance and species richness of macroarthropod communities decreased along the succession gradient in Canadian boreal forests (Paquin and Coderre 1997). Similarly, carabid beetles (Coleoptera, Carabidae) are most species-rich in the early phases of clear-cut originated succession, mainly because of high abundance of open-habitat species and habitat generalists in recently cut sites (Niemelä et al. 1993a; Haila et al. 1994; Spence et al. 1996). Carabid assemblages associated with later phases of succession contain fewer species and are characterised by a peculiar abundance distribution: a few species are abundant and most are scarce, while intermediately common species may be lacking (Niemelä 1993). This contrasts with the common view that species' abundances are usually normally or log normally distributed (e.g. Magurran 1988; Begon et al. 1996). Indeed, in many Finnish spruce forests, *Calathus micropterus* (often with *Pterostichus oblongopunctatus*) strongly dominates carabid catch (e.g. Niemelä et al. 1992a; Niemelä and Halme 1992; Koivula et al. 1999; Koivula 2002a, b).

Clear-cutting affects species assemblages (Lenski 1982; Jennings et al. 1986; Niemelä et al. 1993a, b; Koivula 2002a, b), but a less studied question is whether species assemblages recover after the impact and, if they do, how rapidly (Niemelä 1999). Flightlessness is thought to be associated with stable environmental conditions (Darlington 1943), and many Fennoscandian forest carabid species are flightless (Lindroth 1985, 1986). They are, therefore, poor dispersers (Ranta and Ås 1982), often facing risk of local extinction in the managed landscape. The recovery of populations in clear-cut sites depends on the regeneration speed of their preferred sites, landscape structure (the amount, quality and spatial distribution of habitat patches) and on dispersal from nearby source habitats (den Boer 1990; Dunning et al. 1992; Taylor et al. 1993; Fahrig and Merriam 1994). In the recovery process, mature stands could possibly act as sources (Pulliam 1988) for forest-dwelling species, the sinks being clear-cuts and young sapling stands. Such knowledge is necessary for the development of rotation protocols and harvesting methods that ensure the long-term survival of species in the managed forests (Haila 1994).

Carabids are well suited for biodiversity studies, as they are easy to collect in numbers sufficient for statistical analyses, they are ecologically and taxonomically well known, and they consist of species with varying habitat demands and are therefore a good indicator group of environmental change (Thiele 1977; Langor et al. 1994; Lövei and Sunderland 1996; Niemelä et al. 2000). Additionally, the stand scale is appropriate for insect studies (e.g. Niemelä et al. 1992a; Koivula et al. 1999) and relevant for forestry in southern Finland, where the average size of a clear-cut is 2–3 ha.

In this paper, we study carabid assemblages along a successional gradient of boreal forest from 5 year-old stands to 60 year-old spruce-dominated stands. The objectives were to (1) evaluate the changes in carabid assemblages with vegetational succession, (2) evaluate abundance patterns of species along the succession gradient and determine if these species may be divided into ecological groups in relation to succession, (3) determine if variation exists among the stand-age classes in the species-abundance pattern (number of species distributed along an abundance gradient), how strongly the most abundant species dominate the catches of different-aged stands and are the dominant species different in different phases of succession, and (4) determine if surrounding old forest habitat affects the abundance patterns of forest carabids in the young sapling stands.

Material and methods

Study area, sampling design and the dataset

The study was carried out at the transition zone of the northern and southern boreal vegetation zones (Ahti et al. 1968), near the Hyytiälä Forestry Field Station in Häme, central Finland (61° N, 24° E). Within a 5-km radius, we chose 20 stands representing five age classes (four stands per age class): 5, 10, 20 (the accuracy was ±2 years in these three classes), 30 (±3 years) and 60 years (±10 years) since clear-cutting. The sizes of the stands varied from 0.7 to 7.7 ha, thus being large enough to host stand-age characteristic carabid assemblages (Mader 1984). For carabids, the stands were independent from each other, since the distances between them were at least 50 m (Digweed et al. 1995). Additionally, the stands were separated from each other by another forest type and/or a road. The stands of a given age class were also randomly distributed in the study area, thus not forming age-specific aggregates. The stands were *Myrtillus*-type, mesic spruce (*Picea abies*) dominated forests (see e.g. Cajander 1949). The studied stands were surrounded by recent clear-cuts, sapling stands and mature managed forests. Estimated from a randomly chosen 5-km^2 area, 27.9% of the forests in our study area were older than 60 years, 24.2% of them were younger than 15 years and the distance between isolated, over 60 year-old fragments was 30–220 m.

The stands originated from clear-cutting (databases of Finnish Forest and Park Service) and mostly with natural regeneration of trees (one 5-year old with planted pines). The exact harvesting year was confirmed by estimating the ages of 20–30 of the oldest saplings per stand. The two youngest age classes were dominated by deciduous trees, with plenty of birch (*Betula* spp.) saplings, and some saplings of spruce and pine (*Pinus sylvestris*). The 20 and 30 year-old stands represented a mixture of naturally established deciduous (birch, willow *Salix* spp. and aspen *Populus tremula*) and coniferous (spruce and pine) saplings. The stands of the oldest age class were spruce dominant, with some pines and birches as an admixture. The natural succession of Fennoscandian spruce forests begins with a deciduous phase and continues towards spruce dominance (e.g. Esseen et al. 1997).

As a sampling method we used pitfall traps with a depth of 68 mm and a diameter of 66 mm at the mouth. The traps were partly filled with 25% propylene glycol and detergent, and they were covered with 10 × 10 cm plexi roofs to protect them from litter and rain. In each study stand, 12 pitfall traps were placed in three groups of four traps as a 2 × 2 m square. The trap groups were 25 m apart and 25–50 m from the nearest stand edge. The trapping covered the whole growing season, i.e. from mid-May to early September, 1999. The traps were emptied once a month. The relatively long servicing interval did not result in decay of the captured beetles because of the cool climate. Shrews, mice and voles did not fall into the traps, and only occasional traps were otherwise disturbed during the study.

In order to study the distribution patterns of carabids in relation to the environment, the coverages of the common plant species were estimated from the central point of every trap group to a 2-m radius. Furthermore, red wood ants (*Formica rufa* group) and springtails (Collembola) were counted from the pitfall samples and used as environmental variables in the multivariate analyses. Ants correlate negatively with carabid catches (e.g. Koivula et al. 1999). Carabids use springtails as a food source (Hengeveld 1980; Lindroth 1985, 1986), their abundances correlating positively (Niemelä et al. 1986).

We also mapped the surrounding habitats of the 5, 10 and 20 year-old stands in order to examine the possible effects of the landscape structure on forest-carabid abundance in the young stands. The margin of each study stand and the proportions of different habitat types adjacent to the stand (age class of the dominant trees and forest type) were estimated from aerial photographs and field notes. Additionally, the size of these stands and the distance from the trap groups to the nearest older forest edge were measured. Due to earlier forestry activities, mature spruce-dominated stands edging the young study stands were not always available. Therefore, the distance and old-forest proportional measurements were restricted to the nearest over 40 year-old stand, which was the age of the oldest adjacent stand in five cases.

Statistical analyses

We first pooled the carabid catches of each stand (the three groups of four traps) and the study periods, because the catches from the same stands were interdependent and a separation of the trapping periods, in order to reach a repeated measures design, would have resulted in catches too small for reliable analyses. The carabid data were $\log(X+1)$ transformed.

In order to study whether the abundance and diversity of carabids varied along the succession gradient, we performed analyses of variance (ANOVA) by dividing the carabid species into three ecological groups: forest specialists, open-habitat species and habitat generalists (Table 1), according to the literature (Lindroth 1985, 1986; Kinnunen 1999). We also analysed those species that were found in at least 14 out of 20 sites, and the total catch and species richness. However, as the catchabilities of different species vary (Desender and Maelfait 1986), the two last-mentioned results should be interpreted cautiously.

As the open-phase stands often had very dense field-layer vegetation, which potentially correlates negatively with carabid catches (Honek 1988), we included

Table 1. The catches of red wood ants (*Formica rufa* group), springtails (Collembola) and carabid beetles. HAB = habitat preference of a given species: F = forest, O = open habitat and G = generalist species. n = number of individuals caught, (i) = incidence, i.e. in how many stands a given species occurred.

Group/species	HAB	5(-y)		10(-y)		20(-y)		30(-y)		60(-y)		Total	
		n	(i)	n	(i)	n	(i)	n	(i)	n	(i)	n	(i)
Formica rufa group		12914	(4)	9812	(4)	7197	(4)	11414	(4)	4334	(4)	45671	(20)
Collembola		4595	(4)	2475	(4)	4521	(4)	12880	(4)	10330	(4)	34801	(20)
Calathus micropterus (Dft.)	F	30	(4)	13	(3)	123	(4)	355	(4)	236	(4)	757	(19)
Pterostichus niger (Schaller)	G	200	(3)	174	(4)	106	(4)	5	(2)	20	(2)	505	(16)
P. oblongopunctatus (F.)	G	107	(4)	47	(4)	10	(3)	27	(3)	58	(4)	249	(18)
Trechus secalis (Payk.)	G	26	(4)	28	(4)	49	(4)	25	(4)	39	(4)	167	(20)
Agonum fuliginosum (Pz.)	F	21	(3)	4	(3)	–	–	10	(2)	79	(2)	114	(10)
P. diligens (Sturm)	G	32	(4)	27	(4)	25	(3)	5	(2)	1	(1)	90	(14)
Carabus glabratus Payk.	F	17	(2)	21	(4)	3	(2)	14	(2)	20	(4)	75	(14)
Amara lunicollis (Schiødte)	O	32	(4)	34	(4)	6	(2)	–	–	1	(1)	73	(11)
Patrobus assimilis Chaud.	G	1	(1)	1	(1)	1	(1)	5	(1)	28	(3)	36	(7)
P. strenuus (Pz.)	G	13	(3)	12	(2)	3	(2)	5	(1)	–	–	33	(8)
P. versicolor (Sturm)	O	20	(3)	7	(3)	–	–	–	–	–	–	27	(6)
Carabus hortensis L.	F	1	(1)	1	(1)	2	(2)	6	(4)	13	(4)	23	(12)
Notiophilus palustris (Duft.)	O	12	(4)	7	(4)	3	(1)	1	(1)	–	–	23	(11)
Harpalus quadripunctatus Dej.	F	6	(3)	9	(3)	3	(1)	–	–	–	–	18	(7)
Leistus terminatus (Hellw. In Pz.)	F	3	(1)	–	–	–	–	9	(3)	3	(2)	15	(6)
P. adstrictus (Eschtz.)	O	13	(4)	–	–	–	–	–	–	–	–	13	(4)
Ag. mannerheimii (Dej.)	F	–	–	–	–	–	–	–	–	12	(1)	12	(1)
N. biguttatus (F.)	F	1	(1)	–	–	–	–	4	(4)	7	(4)	12	(9)
Cychrus caraboides (L.)	F	2	(2)	–	–	2	(1)	4	(3)	1	(1)	9	(7)
Bembidion lampros (Herbst)	O	8	(3)	–	–	–	–	–	–	–	–	8	(3)
P. nigrita (Payk.)	G	5	(1)	1	(1)	1	(1)	–	–	1	(1)	8	(4)
Cal. erratus (Sahlb.)	O	6	(1)	–	–	–	–	–	–	–	–	6	(1)
Car. cancellatus Ill.	O	3	(1)	2	(1)	–	–	1	(1)	–	–	6	(3)
Cymindis vaporariorum (L.)	O	3	(1)	3	(1)	–	–	–	–	–	–	6	(2)
Loricera pilicornis (F.)	G	–	–	–	–	–	–	2	(2)	3	(1)	5	(3)
Miscodera arctica (Payk.)	O	1	(1)	2	(1)	1	(1)	–	–	–	–	4	(3)
Ag. sexpunctatum (L.)	O	3	(2)	–	–	–	–	–	–	–	–	3	(2)
Am. brunnea (Gyll.)	F	2	(1)	–	–	–	–	–	–	1	(1)	3	(2)
Trichocellus placidus (Gyll.)	O	2	(2)	1	(1)	–	–	–	–	–	–	3	(3)
Bradycellus caucasicus Chaud.	O	2	(2)	–	–	–	–	–	–	–	–	2	(2)
L. ferrugineus (L.)	O	–	–	1	(1)	1	(1)	–	–	–	–	2	(2)
P. cupreus (L.)	O	2	(2)	–	–	–	–	–	–	–	–	2	(2)
Am. communis (Pz.)	O	1	(1)	–	–	–	–	–	–	–	–	1	(1)
Am. familiaris (Duft.)	O	1	(1)	–	–	–	–	–	–	–	–	1	(1)
Am. quenseli (Schönh.)	O	–	–	1	(1)	–	–	–	–	–	–	1	(1)
Car. nitens L.	O	1	(1)	–	–	–	–	–	–	–	–	1	(1)
N. aquaticus (L.)	O	–	–	–	–	1	(1)	–	–	–	–	1	(1)
N. germinyi Fauvel	O	1	(1)	–	–	–	–	–	–	–	–	1	(1)
Synuchus vivalis (Ill.)	G	1	(1)	–	–	–	–	–	–	–	–	1	(1)
Carabids, individuals		579		396		340		478		523		2316	
Carabids, spp.		34		21		17		16		17		39	

the percentage cover of the field-layer vegetation in the species-group ANOVAs. The data were analysed by performing a factorial ANOVA with stand-age class as a factor and the coverage of the vegetation as a covariate.

We studied whether the number of species differed among the age classes by calculating rarefaction-standardised number of species (for the calculations, see e.g. Magurran 1988). The catches were standardised to 38 individuals, which was the lowest total catch per stand. The species' dominance patterns among the age classes and among the dominant species were examined by plotting the number of species observed per abundance class ($\log_2$ of the number of individuals caught) for the treatments.

We used detrended correspondence analysis (DCA) (Jongman et al. 1995) to study carabid-community structure and how the species relate to different aged stands. The analysis was done by using CANOCO 4.0 software (ter Braak and Šmilauer 1998a). The 30 species occurring in two or more stands were included in the analysis, and Hill's scaling (e.g. Jongman et al. 1995; ter Braak and Šmilauer 1998b) was applied.

The relationship between the catches of species occurring in at least two stands and environmental structure of the stands was studied by canonical correspondence analysis (CCA) (ter Braak 1986; Jongman et al. 1995). Twenty-seven environmental variables, including vegetational data, wood-ant and springtail catches (Table 1), were included in the analysis. The importance of these variables in explaining the abundance and distribution patterns of carabids was studied by performing a partial CCA with Monte Carlo randomisations (ter Braak and Šmilauer 1998b). Variables were thus added one by one into the model, starting from the most important one until the subsequent variable was statistically non-significant.

We used linear regression to study whether the surrounding, older forest stands could act as sources of colonists for forest species in the 5, 10 and 20 year-old open-phase stands. We expected the forest species to occur in the sink habitat (young stand) with a higher probability and more abundantly if there was mature forest surrounding it. The likelihood of the occurrence in open stands would also increase with the closeness of the forest edge and decreasing size of the open-habitat patch.

Results

Invertebrate catches along the succession gradient

The carabid catches consisted of 39 species and 2316 individuals (Table 1). Total abundance of carabids peaked in the 5 and 60 year-old stands. Only *Trechus secalis* was caught from every stand. The most numerous species was *C. micropterus*, with 757 individuals (32.7% of the total carabid catch and 58.1% of the forest-species catch). The forest-species group consisted of 10 species, and 20 were open-habitat species. Red wood ants and springtails were also abundant in the catches (Table 1).

Although there was a negative correlation between stand age and the percentage cover of dwarf shrubs and grasses (Spearman rank correlation, df = 18, $r_s = -0.58$,

$P < 0.01$), neither stand age nor coverage correlated with the overall carabid catches (df $= 18$, and their $r_s = 0.15$ and 0.05, respectively).

The total carabid catches were similar among the age classes, but the catch of open-habitat species was highest in the 5 and 10 year-old stands (Table 2). Indeed, 165 of the 179 individuals of open-habitat species (92.2%) were caught from these stands and 16 species were caught exclusively from them. On the other hand, the catches of forest-species and generalist carabids, as well as those of wood ants and springtails, indicated neither differences among the catches of the age classes nor a correlation with the vegetation.

The rarefaction-standardised species richness was significantly higher in the two youngest age classes as compared to the older ones (Kruskal–Wallis ANOVA, $U = 10.53$, $P = 0.032$; Nemenyi test for the pairwise comparisons of the rank sums; see Zar 1999). The species richness was highest in the 5 year-old (11.88 ± 1.89 SD) and lowest in the 30 year-old (5.93 ± 2.53 SD) stands.

The species composition differed greatly among the age classes (Table 1). The catches of the age-classes were not even, since when plotting the total species numbers against the abundance classes (Figure 1), intermediately common species were lacking from the catches of some age classes of the young stands, though no such gap was detected in the oldest age class, where the abundance distribution was very even. In the 30 year-old class, the gap was widest and *C. micropterus* alone formed 74.3% of the total catch, while the rest of the species were rather scarce. The two next most common species (*P. oblongopunctatus* and *T. secalis*) together formed 10.8% of the total catch in that age class. In the other age classes, the most dominant species formed 34.5–45.1% of the total carabid catch. In the 5 year-old stands, the three most abundant species (*P. niger*, *P. oblongopunctatus* and *P. diligens*) made up 58.5%, and in 10 year-old ones *P. niger*, *P. oblongopunctatus* and *Amara lunicollis* made up 62.9% of the total catch. In the other age classes, the catches were more clearly dominated by the 1–3 most abundant species: in the 20 year-old stands, *C. micropterus*, *P. niger* and *T. secalis* formed 81.8%, and in the 60 year-old ones *C. micropterus*, *Agonum fuliginosum* and *P. oblongopunctatus* formed 71.3% of the total catch.

Carabids associated with the early phases of succession

Pterostichus strenuus was most often caught from the stands representing the three youngest age classes, in particular the 5 and 10 year-old stands (Table 1). Also *P. niger* and *P. diligens* showed a similar pattern, albeit statistically non-significant due to huge intersite variation (Figure 2). The latter species was relatively abundant in all of the stands under 30 years, except in one with a zero catch; that stand had slightly more fertile soil than the other stands, indicated by the abundance of *Oxalis acetocella*, and saplings strongly shaded the lower vegetation layers. Without this outlyer, *P. diligens* showed a statistically significant association with the three youngest age classes ($F = 5.63$, $P = 0.007$) and the effect of vegetation remained significant ($F = 23.95$, $P < 0.001$). *Amara lunicollis* was the most numerous open-habitat species, being represented in every open-stage stand (Table 1, Figure

Table 2. ANOVA results for the red wood ants (*Formica rufa* group), springtails (Collembola) and forest-specialist, open-habitat and generalist carabid groups, and six carabid species. Age class (Age class; 5, 10, 20, 30 and 60 year-old stands) as a factor, percentage cover of field-layer vegetation (Vegetation) as a covariate. *Post hoc* test (Scheffe) results indicate which age class(es) differ from the others, for example 60 > 5, 10, 20 indicates that there were more individuals in catches of the 60 year-old stands than in the 5, 10 or 20 year-old stands (the latter three thus being similar).

Group/species	Source	SS	df	MS	*F*	*P*	*Post hoc* test
Wood ants	Age class	1.466	4	0.366	0.479	0.751	
	Vegetation	0.545	1	0.545	0.712	0.413	
	Error	10.712	14	0.765			
Springtails	Age class	0.421	4	0.105	2.230	0.118	
	Vegetation	0.148	1	0.148	3.138	0.098	
	Error	0.661	14	0.047			
Carabids							
Carabids, total	Age class	0.134	4	0.034	0.368	0.828	
	Vegetation	0.094	1	0.094	1.026	0.328	
	Error	1.279	14	0.091			
Forest specialists	Age class	5.131	4	1.283	1.715	0.202	
	Vegetation	0.058	1	0.058	0.078	0.785	
	Error	10.469	14	0.748			
Open-habitat species	Age class	11.365	4	2.841	6.447	0.004	5, 10 > 20, 30, 60
	Vegetation	0.629	1	0.629	1.428	0.252	
	Error	6.170	14	0.441			
Generalists	Age class	0.080	4	0.020	1.358	0.295	
	Vegetation	0.019	1	0.019	1.299	0.273	
	Error	0.205	14	0.015			
Calathus micropterus	Age class	3.330	4	0.833	9.113	0.001	30, 60 > 5, 10, 20
	Vegetation	0.005	1	0.005	0.054	0.819	
	Error	1.279	14	0.091			
Carabus glabratus	Age class	0.841	4	0.210	1.269	0.328	
	Vegetation	0.010	1	0.010	0.062	0.806	
	Error	2.319	14	0.166			
Pterostichus diligens	Age class	0.567	4	0.142	2.235	0.118	
	Vegetation	0.886	1	0.886	13.954	0.002	
	Error	0.888	14	0.063			
P. oblongopunctatus	Age class	2.196	4	0.549	4.463	0.016	5 > 20
	Vegetation	0.032	1	0.032	0.261	0.617	
	Error	1.722	14	0.123			
P. niger	Age class	1.196	4	0.299	0.626	0.652	
	Vegetation	0.715	1	0.715	1.497	0.241	
	Error	6.688	14	0.478			
Trechus secalis	Age class	0.118	4	0.029	0.281	0.886	
	Vegetation	0.000	1	0.000	0.000	0.997	
	Error	1.470	14	0.105			

2). Sixty-six of the total of 73 individuals (90.4%) were caught from 5 and 10 year-old stands only. Also *P. versicolor* and *Notiophilus palustris* were restricted to the most open sites (Figure 2) and all of the 13 individuals of *P. adstrictus* were caught from the four 5 year-old stands. Surprisingly, a forest species (Lindroth 1986) *Harpalus quadripunctatus* was exclusively caught from the three youngest age classes (Table 1, Figure 2).

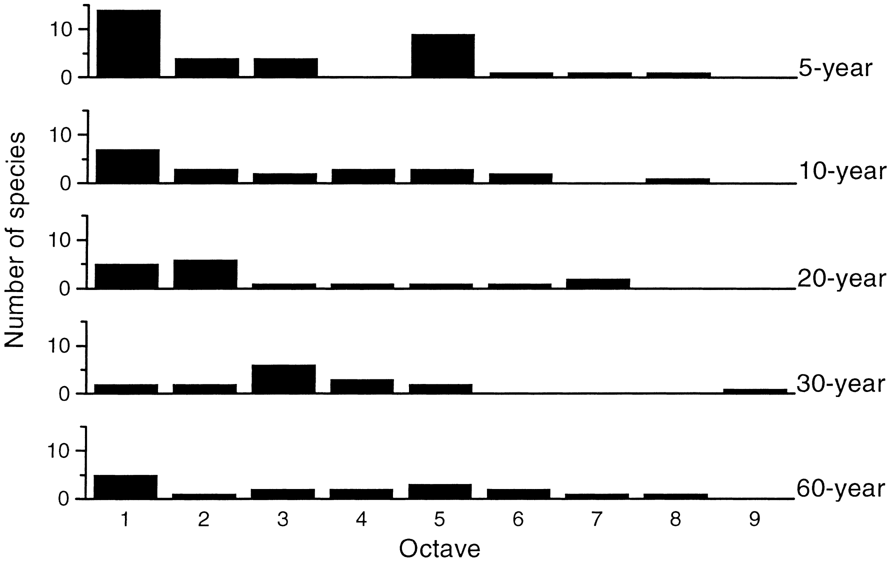

Figure 1. The number of species per abundance class (Octaves, $\log_2$ classes of the catches) for each stand-age class.

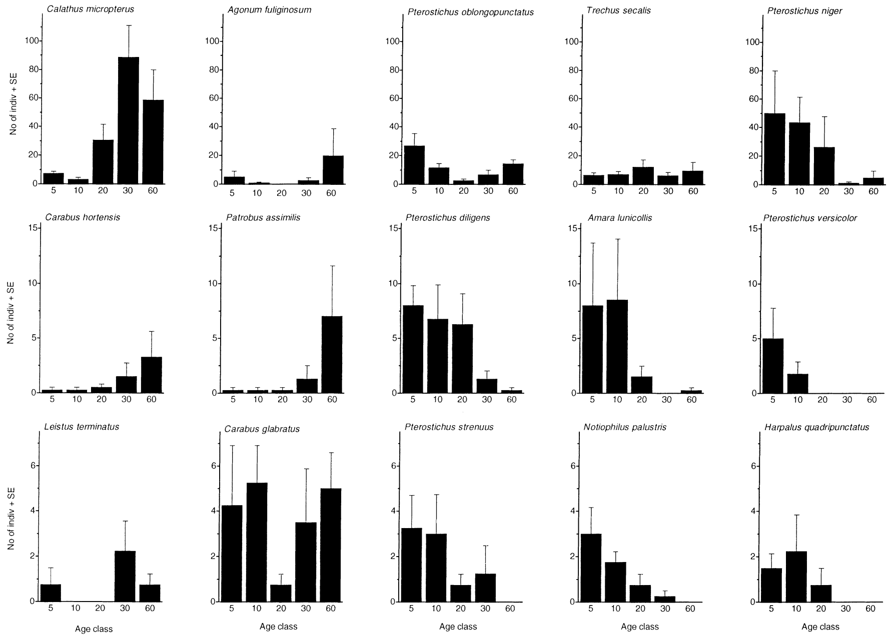

Figure 2. Fifteen carabid species, with total catches of at least 15 individuals and their mean catches along the stand-age gradient. The species are arranged from left to right to a gradient from closed-canopy to open-phase preference. Note different scales in the vertical axes of the three rows.

In the multivariate analyses (Figures 3 and 4), carabid catches indicated a gradual change from the early phases of succession to the oldest stands, and the species scatters also indicated the importance of site characteristics affecting the species abundances. In the DCA (Figure 3), carabid-beetle assemblages changed gradually from the oldest stands (near the origin) to the early stages of succession to the right (see also Figure 2). The first two axes together explained 33.0% of the total variance, their lengths being 2.23 and 1.50 SD units, respectively. The species compositions among the stands were thus relatively similar due to shared abundant species, e.g. *P. niger* and *C. micropterus*. Open-habitat species were clustered to the right side of the ordination: *P. versicolor*, *P. adstrictus*, *N. palustris*, *A. lunicollis*, *Carabus cancellatus* and *Bembidion lampros*.

In the CCA (Figure 4), the sum of all the unconstrained eigenvalues was 1.30 and

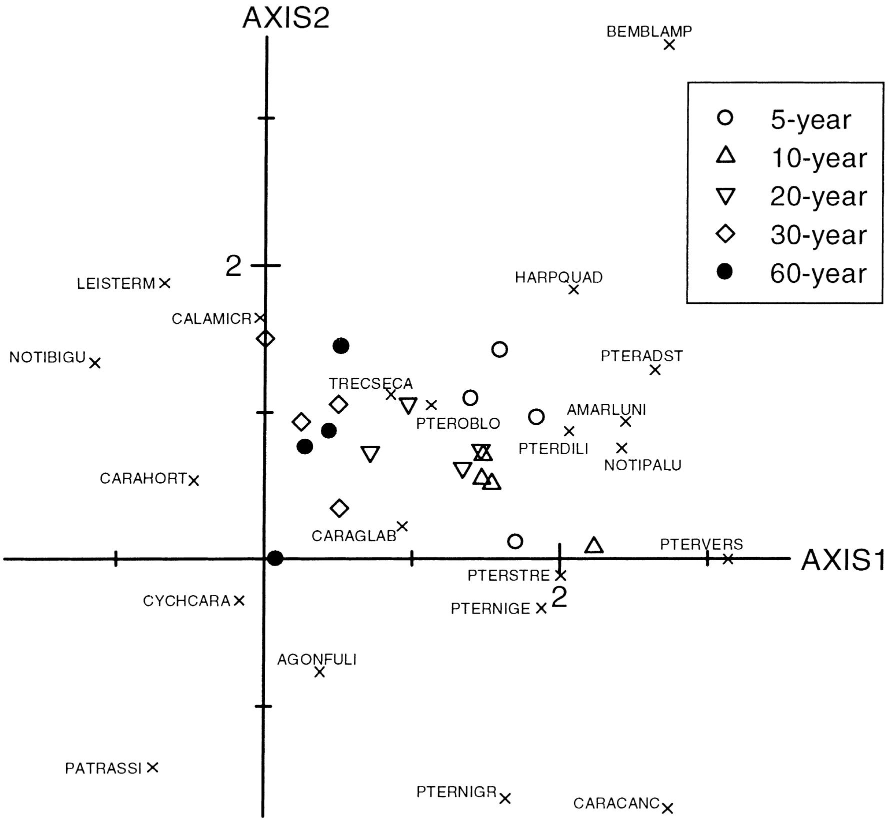

Figure 3. DCA biplot for carabid-beetle and sample (the stands) scores. Only species with at least five individuals are presented. The stands of different age classes are shown as different symbols (for the key, see legend box). The carabid species are marked with 4 + 4 letter abbreviations, e.g. *C. micropterus* = calamicr.

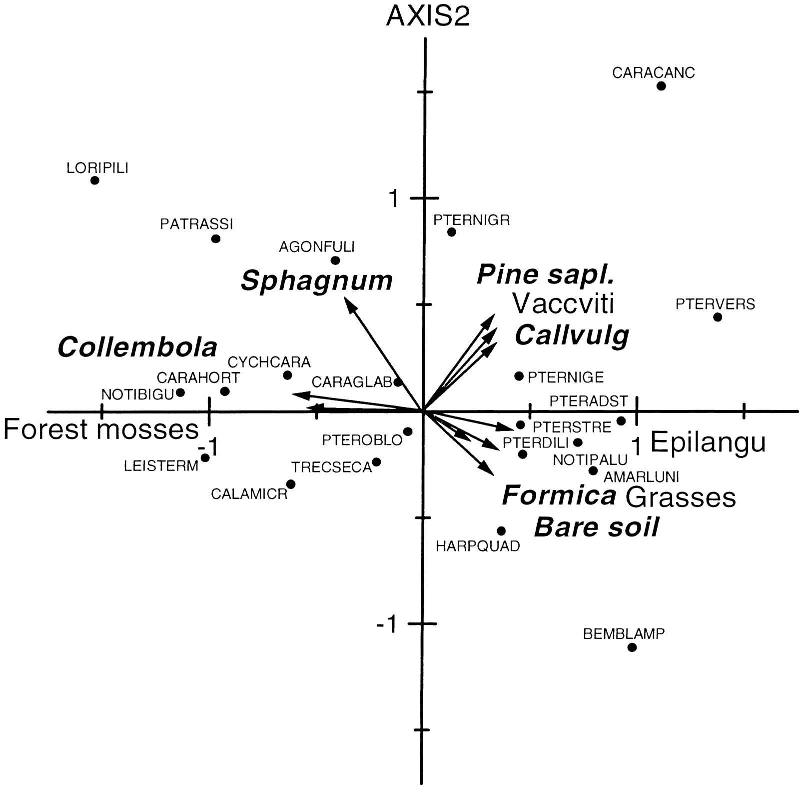

Figure 4. CCA for carabid species and 10 environmental variables which were the most important in shaping the carabid-abundance patterns. Only species with at least five individuals are presented. The environmental variables are given in italics, if statistically significant. The carabid and plant species are marked with 4 + 4 letter abbreviations, e.g. *C. micropterus* = calamicr.

the eigenvalues of the first two gradients were 0.30 and 0.18, respectively. These axes explained 37.7% of the cumulative variance of the species dataset and 50.2% of the species–environment relationship. Some factors reflecting openness and indicating young successional stages were at their optimum downwards and to the right from the origin in the ordination, namely bare soil ($F = 1.88$, $P = 0.045$), grasses (not significant) and *Epilobium angustifolium* (not significant) (Figure 4). *Pterostichus adstrictus*, *P. diligens*, *P. strenuus* and *H. quadripunctatus* clustered in the same direction, where wood ants (*Formica*) ($F = 1.70$, $P = 0.030$) were also at their optimum. Finally, the environmental variables indicating somewhat drier and well-lit conditions were located upwards and to the right from the origin. The occurrence of pine saplings and *Calluna vulgaris* were statistically significant with *F*- and *P*-values of 2.57 and 0.040 and 2.41 and 0.035, respectively, whereas *Vaccinium vitis-idaea* did not explain the patterns significantly. The occurrence of *Ca. vulgaris* indicates dry conditions, possibly due to drought caused by logging. In that direction, *P. niger* and *P. versicolor* were at their optimum, as was, surprisingly, *P. nigrita*, which is a moist-loving species (Lindroth 1986).

Carabids associated with closed canopy

Catches of *C. micropterus* were highest in the 30 and 60 year-old stands (78.1% of the total catch) and the species clearly dominated these catches (Figure 2). However, only 43 individuals (5.7%) of *C. micropterus* were caught from the 5 and 10 year-old stands (Table 1) and the catch was zero in one 10 year-old stand, where the percentage covers of *Ca. vulgaris*, *V. vitis-idaea* and *Cladina* lichens were higher than in any other stand, reflecting a drier vegetation type (Cajander 1949). When re-analysed without this outlyer, the observed differences in the abundances among the age classes became clearer ($F = 6.52$, $P = 0.004$). Despite a much lower total catch, *Car. hortensis* and *Patrobus assimilis* showed a similar abundance pattern along the succession gradient as *C. micropterus* (Figure 2).

The multivariate analyses showed the existence of distinctive forest-species groups. In the DCA, many forest species – *Car. hortensis*, *N. biguttatus*, *Leistus terminatus* and *Cychrus caraboides* – were at the left side of the ordination space, near the origin, together with stands with closed canopy (Figure 3). Species preferring moist conditions were downwards and to the left (*Cy. caraboides*, *P. assimilis* and *A. fuliginosum*). This was also the direction towards stands with moist and wet microsites. However, the two last-mentioned species were scattered relatively far away from the stand scatter, indicating that their optimal microhabitat conditions were not met among the stands or, perhaps more likely, that the pooling masked the microsite variation. In the CCA (Figure 4), *Sphagnum* mosses ($F = 2.61$, $P = 0.03$), indicating moist microsites and spruce mires, were at their optimum upwards and to the left from the origin, and the optimum of *A. fuliginosum*, a species of moist and shady sites (Lindroth 1986), was almost the same. Several other species were at the left side of the ordination, namely *Carabus glabratus*, *Car. hortensis*, *Cy. caraboides* and *P. assimilis*. Forest mosses (not significant) were at their optimum on the left-hand side of the ordination, near the optimum of springtails (Collembola) ($F = 3.17$, $P = 0.005$), where *N. biguttatus*, *L. terminatus* and *C. micropterus* also scattered.

Succession generalists in the stand-age gradient

Six species were more or less generalists with respect to stand openness (Figures 2–4). In the DCA (Figure 3), these species – e.g. *T. secalis*, *P. oblongopunctatus* and *Car. glabratus*, a forest species (Lindroth 1985) – were near the centre of the stand cluster. These species showed a relatively even abundance pattern along the succession gradient (Figure 2, Table 2), but *C. glabratus* had a much lower total catch in the 20 year-old sites. *Pterostichus oblongopunctatus* had a slight preference for the youngest age class, with lowest catches in the 20 and 30 year-old stands, where only 14.9% of the species' total catch was caught. Additionally, *P. oblon-*

gopunctatus had a zero catch in one 30 year-old, slightly dry and wood-ant rich stand. In fact, there was a negative correlation between the total catches of carabids and the catches of wood ants in our samples, too (Pearson's correlation; df = 18, $r = -0.48$, $P = 0.030$) and, although not analysed, this species showed the same tendency. When re-analysed without the outlyer stand, *P. oblongopunctatus* still showed a preference for the youngest age class ($F = 5.91$, $P = 0.006$). *Agonum fuliginosum* was caught in young and old sites, having in common the occurrence of *Sphagnum* indicating mire conditions (see also Figure 4). *Leistus terminatus* (Table 1, Figure 2) was most often caught in certain sites of 30 year-old stands, with shadiness, plenty of field-layer vegetation and much litter.

Effects of surrounding habitat on forest-carabid abundance in young stands

The possible source-sink or edge effect between the open-phase stands and the surrounding forest habitat was studied by examining the distribution of the forest carabids caught in the 5, 10 and 20 year-old stands. These catches were higher the closer the adjacent old stand was ($R^2 = 0.53$, $F = 12.30$, $P = 0.007$). Additionally, the increasing amount of over 40 year-old forest surrounding the studied stand had a slight positive effect on the forest-species catch ($R^2 = 0.18$, $F = 3.44$, $P = 0.093$), but the size of the stand had no discernible relationship with the catches ($R^2 = 0.01$, $F = 0.69$). Because of poor catches, the analyses were not performed at the species level but *C. micropterus* showed the above tendencies when plotted against the mentioned three stand measurements. Since its catch formed 37.9% of the total forest-species catch of these age classes, it potentially had a strong effect on the regression results. *Cyn. glabratus*, *A. fuliginosum*, *Cy. caraboides* and *Car. hortensis* showed no indications of such a dependence.

Discussion

The carabid catches from the five age classes demonstrated a succession of carabid assemblages along the stand age-class gradient. The canopy closure distinguished the open phases from the closed ones: the highest species richness was detected in the former, while there was a lower overall carabid diversity in the 20 and 30 year-old stands with closed canopy. Similar results have been reported by Szyszko (1990), Niemelä et al. (1996) and Kinnunen (1999). In our study, the species abundance distribution was uneven in the 30 year-old stands but was remarkably even in the 60 year-old stands. This is in contrast with Niemelä (1993), who has shown that Finnish spruce forests host a few abundant and many scarce species but no intermediately common ones. In Niemelä's (1993) study, *C. micropterus* was always the dominant species. However, we demonstrated that the dominant species may change as the succession proceeds, which corroborates the results of Ings and Hartley (1999). The difference between Niemelä's (1993) and our results may be due to a too coarse division of the study sites into mature and young sites in the former.

The present results indicate that when forests form a heterogeneous mosaic of differently aged stands, the majority of forest species thrives well (Haila et al. 1987; Niemelä et al. 1988). Also, the landscape hosts a more diverse carabid assemblage than either a clear-cut or a closed-stand monoculture (Niemelä et al. 1993b), which supports the intermediate disturbance hypothesis (Connell 1978). However, because of intensive forest management specialist species are lost, as shown by Desender et al. (1999). Such species, often strict habitat specialists with poor dispersal ability, should thus determine the appropriate conservation actions.

Carabids in the managed forest landscape

The richness of the carabid assemblages in young, open stands, compared to the closed 30 and 60 year-old ones, was mostly due to richness of open-habitat species. Open-habitat species are abundant only 20–30 years after clear-cutting, i.e. until canopy closure, as earlier studies have demonstrated (Szyszko 1990; Niemelä et al. 1993a, 1996; Haila et al. 1994; Butterfield 1997; Ings and Hartley 1999). Intensive forest management has created ample habitat for these species, from which to disperse to new clear-cut sites (Spence et al. 1996). Approximately 20% of the southern Finnish forests are younger than 30 years (Sevola 1999). Furthermore, the rapid increase of Finnish forest roads since the 1950s (Västilä and Herrala-Ylinen 1999; Martikainen 2000) has created road margins that are used as dispersal corridors or habitat by open-habitat species (M. Koivula, unpublished data). Open-habitat species are well adapted to temporary habitats (den Boer 1990), the majority being either macropterous or wing dimorphic (Thiele 1977; Lindroth 1985, 1986).

In this study, some occasional open-habitat dwellers were caught from the 30 and 60 year-old stands, exclusively in sites with greater-than-average openness or sparsity of trees. These individuals can either represent relict populations of previous open phases or, perhaps more likely, dispersing individuals searching for suitable habitats. Species may penetrate the forest interior from the surrounding matrix (Murcia 1995), which was demonstrated with carabids by Spence et al. (1996) and Magura et al. (2001). However, in a Finnish mature-forest and clear-cut edge study, open-habitat species did not disperse into the forest interior (Heliölä et al. 2001).

As indicated by our catches, the majority of the forest species maintained relatively large populations throughout the clear-cut originated succession. This is probably due to the ecological flexibility of several common forest dwellers. However, some poor dispersers were scarce in, or absent from, the youngest phases of the succession. Possibly this is a result of changes in the landscape (reduced forest area, isolation of the forest patches) or, alternatively, the open sites simply differed too much from those that are used by these species.

Four forest dwellers showed an association with closed stands. Of these, *C. micropterus* had low catches in the 5 and 10 year-old stands. Similarly, after logging in Norwegian spruce forests, the abundance of *C. micropterus* decreased drastically (Abildsnes and Tømmerås 2000). The species probably survives through the open phases of the succession by maintaining viable, albeit strongly decreased, populations (sinks or relics) in the young stands. A similar pattern, indicating a decrease of local populations after logging, was detected with *Car. hortensis*, too. Also seven out of nine individuals of *Cy. caraboides* and all 12 individuals of *Ag. mannerheimii* were caught from the closed stands.

Biotic and abiotic factors explaining carabid abundances

The species fell into three groups according to their abundance in the differently aged stands: closed-canopy specialists (true forest species), succession generalists, and open-phase specialists. The trapping sites were determined by varying biotic (food, competitors) and abiotic (moisture, wind, temperature) factors.

Some carabids showed indications of responses to red wood ant and springtail abundances. Three species (*A. lunicollis*, *N. palustris* and *P. diligens*) aggregated close to the wood-ant optimum in the CCA, indicating that they tolerate ants. The first two are diurnal and *N. palustris* is also rapidly moving (Lindroth 1985, 1986), and may be capable of avoiding diurnal ants, which possibly interfere with nocturnal carabids in their resting places. The abundances of some forest carabids correlated positively with that of springtails. Pitfall catches reflect the activity density of species living on the top of the litter (Berbiers et al. 1989): abundant springtails at the litter surface provide abundant food for carabids (Hengeveld 1980).

Some carabids require conditions that are more commonly met in closed stands than in clear-cuts or young stands, e.g. shady mesic sites and spruce mires. At the scale of metres, forest is a patchy environment for carabids (Niemelä et al. 1992a, b), explaining the small-scale abundance variation of carabids. For example, *P. assimilis* was caught in moist sites with canopy closure, often together with *A. fuliginosum*. In our study, wet *Sphagnum* moss bogs hosted distinctive carabid assemblages, and have been shown to be crucial for the persistence of *Ag. mannerheimii* (Niemelä et al. 1987, 1988, 1992b, 1993a), a species with no flight ability (Lindroth 1986). These sites are key habitats also for other forest organisms (Niemelä 1999; Siitonen and Saaristo 2000). It probably takes 50–60 years for a spruce mire and its assemblage to recover after logging. Therefore, mire sites should be managed with methods other than clear-cutting, and leaving plenty of trees in these sites in order to protect the ground from microclimatic factors that lead to drainage. Also soil preparation may have strong effects on carabids and their recovery. The recovery of stenotopic forest carabids may take hundreds of years if the soil is strongly altered and if large-scale logging is practiced (Desender et al. 1999).

Can stenotopic forest carabids thrive in the managed forests?

The surrounding older stands had a positive effect on the forest-carabid catches in the young stands, demonstrating the importance of landscape-level forestry planning. The adjacent older stands may act as sources of individuals or shelters against some environmental factors such as wind and direct sunlight. This implies that small clear-cuts may enable forest species to maintain populations in the managed landscape better than if the clear-cuts were large (Koivula 2002a). Although many forest species have a good ability to re-establish after logging, certain mature-forest specialists probably need a long time to recover, and the elements of the landscape (nearby source habitats and matrix quality) play an important role in this process (Spence et al. 1996; Niemelä 1997, 1999; Desender et al. 1999).

Poorly dispersing species may encounter two kinds of problems in the managed landscape (Niemelä 2002). Firstly, population size may decrease in the small patches because of area effects and low rate of immigration. This was reported from Australia, where Davies and Margules (1998) showed that the abundances of some carabids decreased in small fragments of their preferred forest habitat. Secondly, mature-forest patches may disappear unpredictably through logging, which destroys populations and increases the isolation of the remaining patches. Thus, the availability of mature stands sufficiently close to each other is crucial in the managed landscape (see also de Vries and den Boer 1990; de Vries et al. 1996). The quality of the matrix can be improved for forest species through silvicultural practices, e.g. leaving single trees and patches of trees in the clear-cuts or wide enough movement corridors. However, more research is needed about the utility of movement corridors in forested landscapes (Niemelä 2001), but creating patches of deciduous trees is a useful practice in helping the maintenance and re-establishment of carabids (Magura et al. 2000). Possibly also strip management, with very narrow clear-cuts within stands, may be efficient in trying to incorporate forest-species conservation into forest management, but this question remains to be studied. Additionally, not all potentially suitable patches within a hostile matrix are always occupied. Survival in such a patchy metapopulation environment is dependent on dispersal between the patches (Hanski 1999).

Since isolation of suitable habitats may cause a serious threat for some species, it is crucial to find out whether or not species demanding mature stands are able to disperse from one patch to another. Flightless carabids move up to some hundreds of metres by foot (Thiele 1977; Mascanzoni and Wallin 1986; den Boer 1990). Taking this ability as the only restriction, the majority of forest carabids can probably survive in the studied landscape with relatively short distances between mature stands and small clear-cuts. However, some forest species are reluctant to cross open habitat (Riecken and Raths 1996), in which case a clear-cut of only a few tens of metres can be unsurpassable. Therefore, old and mature stands should always form a spatio-temporal continuum at the landscape level. If this is not possible, our study indicates that the maximum distance between such stands should not exceed a few hundred metres. However, Hanski (2000) showed that it is more effective to focus conservation efforts on forests adjacent to existing reserves than to spread the same efforts thinly over the whole landscape.

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