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Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland

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We compared beetle fauna among six types of forests: (1) old-growth pine, (2) old-growth spruce and (3) old-growth mixed forests; (4) 1-year-old and (5) 15-year-old seed-tree cut pine forests, and (6) 15-year-old clear-cut spruce forests using window trapping. In the old-growth forests, species richness was explained by site productivity, amount and quality of coarse woody debris (CWD), and tree species composition. Many of the explaining variables, e.g., site productivity, volume of living timber and volume of CWD were intercorrelated. Beetle assemblages varied according to the site fertility and successional stage. The species compositions of non-saproxylic species were rather similar in the seed-tree-cut areas and in the old-growth pine forests, but the species composition of saproxylics differed between the two forest types. On the contrary, the species compositions of both saproxylics and non-saproxylics differed distinctly between the old-growth spruce forest and clear-cut sites. Species colonising recently died trees, soil-dwelling open-habitat species and some polypore-living cisids were more abundant in regeneration areas than in old-growth forests, whereas species of many other mycetophagous beetle families were practically absent from the logged sites. Compared with old-growth forests, the proportion of nationally rare saproxylic species was high at the recently cut sites, but clearly lower at the old regeneration sites. This indicates that in the long run the changes in the amount and quality of CWD may have detrimental effects to rare saproxylic species in the regeneration areas.

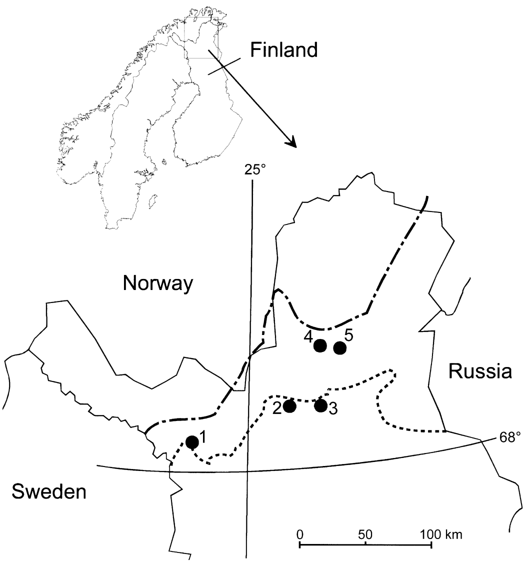

Fig. 1. Location of the study areas. 1 = Pallas-Ounastunturi, 2 = Härkäselkä, 3 = Sotajoki, 4 = Vaskojoki, 5 = Nukkumajoki. The northern limit of pine forest is indicated by the upper and that of spruce forest by the lower dashed line.

Introduction

Intensive forest management has been considered to be the main reason for the decrease of biodiversity in Fennoscandian forests (Esseen *et al.* 1992, 1997, Rassi *et al.* 1992, Ehnström *et al.* 1993). Especially many invertebrate, cryptogam and fungus species have declined (Heliövaara & Väisänen 1984, Rassi *et al.* 1992, Esseen *et al.* 1997). Many factors have simultaneously contributed to the decrease of species diversity in boreal forests: loss of old-growth forests, forest cutting and the consequent dominance of young age classes and even-aged stand structure, a decrease in the number of large deciduous trees and in the amount of decaying wood, and changes in disturbance dynamics, such as the elimination of forest fires (Berg *et al.* 1994, Angelstam 1996, Esseen *et al.* 1997, Niemelä 1997).

Beetles are a species-rich order with more than 3600 species known in Finland (Silfverberg 1992). They play an important ecological role in boreal forest ecosystems in initiating and promoting the decay process of trees, often acting as vectors of pathogenic or decomposer fungi (Crowson 1981). Forestry has particularly affected beetle species that are confined to primeval forests, sites subjected to forest fires and decaying wood (Heliövaara & Väisänen 1984, Niemelä 1997). The large number of threatened beetle species in Fennoscandia is an indication of environmental changes in forest ecosystems (Jonsell *et al.* 1998). In Finland, 332 species of beetles are considered as threatened, which is about 9% of the total beetle fauna (Rassi *et al.* 1992). The respective figures in Sweden are 1065 and 24% (Ehnström *et al.* 1993). About half of the threatened beetles, both in Finland and in Sweden, are confined to forest environments.

New forest management guidelines, which aim at maintaining biodiversity in managed forests, have been adopted in many Fennoscandian forestry organizations (Anon. 1990, 1994, 1995). Reference data from pristine forests are needed in order to develop the management methods. We should know which structures and processes are essential in maintaining the diversity of different organism groups, and how these features can be preserved in practical forestry operations.

Effects of forestry on beetle species diversity have mainly been studied in the southern and middle boreal zones of Fennoscandia. The studies cover, for instance, the influences of forest succession and fragmentation (Niemelä *et al.* 1988, 1996, Ås 1993, Halme & Niemelä 1993) and the effects of forest management on beetle fauna (Niemelä *et al.* 1993, Väisänen *et al.* 1993, Siitonen & Martikainen 1994, Martikainen *et al.* 1996, 1999, 2000, Økland *et al.* 1996, Kaila *et al.* 1997, Martikainen 2001). Information on invertebrate fauna in the northern boreal forests has been very scarce so far. In Finland, most of the remaining large and untouched continuous forests are located near the timberline in the northern part of the country. Some of these forests have been protected (Anon. 1991, 1997), but some will be used for timber production. The pristine timberline forests provide a good opportunity to compare species diversity between old-growth forests and areas that have been altered by regeneration cutting. In this study, we aim at answering the following questions: (1) What is the composition of beetle assemblages in different forest types in pristine northern boreal forests in Finnish Lapland? (2) How are different structural features of the forest related to species richness and species composition? (3) What are the effects of seed-tree and clear-cutting on beetle fauna in a 15-year perspective?

Material and methods

Study area and sample plots

The study was conducted in five areas in Finnish Lapland: one in western Lapland (68°N, 24°E), and four in central Lapland (between 68°25´N–26°35´E and 68°58´N–26°25´E) (Fig. 1). The region belongs to the northern boreal zone (*sensu* Ahti *et al.* 1968), and it is characterised by coniferous forests dominated by either Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) Karsten). Pubescent birch (*Betula pubescens* ssp. *czerepanovii* Orlova) grows commonly in all forest-site types as an admixture, and on fertile sites bird cherry *(Prunus padus* L.), rowan (*Sorbus aucuparia* L.), goat willow (*Salix caprea* L.) and aspen *(Populus tremula* L.) can be found occasionally. The study areas were located at altitudes of 175–380 m a.s.l.

A total of 19 sample plots were established in old-growth forests and nine in managed forests (Table 1). These represented a total of six forest site types or treatments. The size of the sample plots was one hectare, except in six stands where 0.5-hectare rectangular plots were established owing to restrictions set by the terrain. The sampling sites in old-growth forests represented the three main forest types to be found at these latitudes: (1) pine-dominated dry or subdry forests (nine stands) characterised by *Vaccinium myrtillus* L., *Empetrum hermaphroditum* L. (Hagerup)*, Calluna vulgaris* (L.) Hull and *Cladonia* species in the understorey vegetation; (2) spruce-dominated mesic forests (six stands) characterised by *Hylocomium splendens* (Hedw.) and *Vaccinium myrtillus*, and (3) mixed herb-rich forests (four stands) dominated by spruce and various deciduous tree species and characterised by *Geranium sylvaticum* L., *Dryopteris carthusiana* (Vill.) and, in some cases,

Table 1. Number of sample plots and average stand characteristics of the different forest type categories. The total volume and distribution of CWD in different categories and decay classes (Dec) are given. CWD pieces include fallen branches, stumps and logging residue.

Forest category	*n*	Volume of living trees (m³ ha⁻¹)				Volume of CWD (m³ ha⁻¹)								
		Pine	Spruce	Decid.	Total	Logs	Snags	Pieces	Dec 1	Dec 2	Dec 3	Dec 4	Dec 5	Total
Old-growth forests														
Pine	9	78.8	1.2	2.6	82.6	9.5	5.8	0.5	0.8	5.1	3.7	3.3	2.9	15.8
Spruce	6	3.3	59.8	17.0	80.1	21.6	5.1	1.0	0.9	3.9	6.2	12.1	4.6	27.7
Mixed	4	0	111.8	40.0	151.8	47.2	10.8	1.9	1.1	15.1	14.8	18.4	10.5	59.9
Regeneration areas														
1-yr. seed tree cut	3	21.9	0	0.2	22.1	19.5	0.7	5.5	9.5	1.9	4.2	7.8	2.3	25.7
15-yr. seed tree cut	3	5.2	0	2.1	7.2	13.3	0.2	3.9	0	0.8	0.7	13.0	2.9	17.4
15-yr. clear-cut	3	3.6	0.4	0.5	4.5	6.6	0.4	1.3	0.1	0.4	0.5	5.2	2.1	8.3

Athyrium and *Matteuccia* species. Emphasis was laid on pine-dominated forests because they are the most common forest type at these latitudes, and also because forestry activities are mainly directed at pine forests in northernmost Lapland. The regeneration areas represented treatments of different age as follows (three sites in each treatment): (4) 1-year-old seed-tree cut pine forests, (5) 15-year-old seed-tree cut pine forests, and (6) 15-year-old clear-cut spruce forests (Table 1). The 15-year-old seed tree cut sites had regenerated naturally for pine and the seed-trees had been removed, whereas the 15-year-old clear-cut spruce forest sites had been planted with pine. When exploring the effects of regeneration cutting on beetle fauna, we compare the 1- and 15-year-old seed-tree cut pine forests with the old-growth pine forests, and the clear-cut spruce forests with the old-growth spruce forests.

Environmental variables and beetle sampling

The measured environmental variables included living trees and coarse woody debris (CWD; later referred to as stand variables), and the cover of understorey vegetation. Living trees were measured on five relascope plots in each sample plot. In the sapling stands, the saplings were measured on ten circular plots of 50 m^2 (radius = 3.99 m). All CWD with a minimum diameter of 1 cm at breast height (DBH = 1.3 m) (entire trees), or with a minimum mid-diameter of 5 cm and length of 1 m (snags, logs and branches) were measured. Five decay classes were distinguished:

1 = 1–2 years from death, bark and phloem still fresh,
2 = wood hard, most of the bark left in conifers, but no fresh phloem,
3 = wood partly decayed from the surface or in the centre (depending on tree species), usually at least part of the bark loosened or detached in conifers,
4 = most of the wood soft throughout, usually no bark left on conifers,
5 = wood almost completely decomposed and disintegrating when moved, forest-floor mosses and lichens covering the trunk.

The cover of the understorey vegetation was recorded on ten 1-m^2 squares in each sample plot by measuring the percentage cover of each species with the intervals < 1%, 1%, 3%, 5%, 7%, 10%, 15%, 20%, 25%, …, 100%. Vascular plants were identified to the species level. In the identification of lichens and mosses, the groups *Cladonia uncialis* coll., *Stereocaulon* spp., *Sphagnum* spp. and Hepaticae were used; otherwise the cryptogams were identified to species level. For the analyses, vascular plants were grouped into four groups indicating oligotrophy, mesotrophy, eutrophy and moisture availability. The plant grouping was based on Kalela (1961), Kaakinen (1982), and Eurola and Virtanen (1989). The thickness of the humus layer was measured using three classes (< 2 cm, 2–5 cm and > 5 cm).

The beetles were sampled by window-flight trapping during 1.VI.–15.IX.1993. The trap consisted of two crosswise, transparent acrylic panes of 40 × 60 cm, a funnel located below it, and a sampling bottle containing water, salt and detergent. Five traps were used in each sample plot, one at each corner and one in the middle. The traps were emptied every third week. The species were divided into saproxylic and non-saproxylic species, the first group consisting of species that are dependent on dead-wood habitats (including wood-decomposing fungi) during some stage of their life cycle (Speight 1989). For some comparisons, we also separated pyrophilous species, i.e. species that are known to strongly favour burnt areas. The main sources for the ecology of different species were Saalas (1917, 1923), Palm (1951) and Koch (1989a, 1989b), and for the pyrophilous species Lundberg (1984), Wikars (1992) and Muona and Rutanen (1994). The nomenclature follows Silfverberg (1992).

Statistical analyses

We used Mann-Whitney *U*-test and Kruskall-Wallis one-way analysis of variance with *a* *posteriori* comparisons of mean ranks in comparisons of the median numbers of species among the stand categories. The analyses were made separately for saproxylic and non-saproxylic species. To reduce the effect of sample size on species richness, we standardized the data using rarefaction (Simberloff 1978). The expected mean numbers of species for a given number of individuals were used in the statistical tests, except in the correlation analyses, where we used the original number of species caught.

Spearman rank correlation was used to study the correlations between species richness and environmental variables (Table 2). The risk level was adjusted with a Bonferroni correction (Rice 1989). Correspondence analysis was used to explore variation in the species composition of beetle samples among the stand categories, and the relationships between species composition and environmental variables (Ter Braak & Šmilauer 1998). We analysed saproxylic and non-saproxylic species separately because they are likely to be affected by different habitat characteristics (Martikainen *et al.* 2000). Only species occurring at more than one site were included in the analyses, and equal weight was applied to all the species. The beetle data were $\ln(x + 1)$-transformed. For both species groups,

Table 2. The environmental variables of the study sites included in the correlation and correspondence analyses. The variables indicating site fertility are marked with asterisks.

Variable	Registration
Living stand variables	
VLivTot	Total volume of living trees (m^3 ha^{-1})
VLivPin	Volume of living pine (m^3 ha^{-1})
VLivSpru	Volume of living spruce (m^3 ha^{-1})
VLivDec	Volume of living deciduous trees (m^3 ha^{-1})
CWD variables	
VDeadTot	Total volume of CWD (m^3 ha^{-1})
VDeadPin	Volume of pine CWD (m^3 ha^{-1})
VDeadSpr	Volume of spruce CWD (m^3 ha^{-1})
VDeadDec	Volume of deciduous CWD (m^3 ha^{-1})
VLog	Volume of logs (m^3 ha^{-1})
VSnag	Volume of snags (m^3 ha^{-1})
VStuBra	Volume of stumps and branches (m^3 ha^{-1})
VBigDead	Volume of entire dead trees with diameter at breast height over 30 cm (m^3 ha^{-1})
VBigLog	Volume of logs with mid diameter over 30 cm (m^3 ha^{-1})
Decay1	Volume of CWD in decay class 1 (m^3 ha^{-1})
Decay2	Volume of CWD in decay class 2 (m^3 ha^{-1})
Decay3	Volume of CWD in decay class 3 (m^3 ha^{-1})
Decay4	Volume of CWD in decay class e (m^3 ha^{-1})
Decay5	Volume of CWD in decay class 5 (m^3 ha^{-1})
Vegetation variables	
NVasc*	Number of vascular plant species
CovVasc*	Percentage cover of vascular plants
CovOlig	Percentage cover of oligotrophic plants
CovEutr*	Percentage cover of eutrophic plants
CovMeso	Percentage cover of mesotrophic plants
CovMoist	Percentage cover of plants preferring moist environment
CovShru	Percentage cover of shrubs (height < 1 m)
Site variables	
Humus*	Thickness of humus layer (cm)
CovLitter	Percentage cover of litter
Altitude	Altitude of the study site above sea level (m)

Table 3. Total and mean numbers of species and individuals in the different forest type categories.

	Pine		Spruce		Mixed		1-yr. seed tree cut		15-yr. seed tree cut		15-yr. clear-cut		Total	
	Species	Indiv.	Species	Indiv.	Species	Indiv.	Species	Indiv.	Species	Indiv.	Species	Indiv.	Species	Indiv.
Saproxylics														
Total	93	1709	107	1368	95	1153	87	635	80	944	54	448	180	6257
Mean/site	33	190	40	228	48	288	48	212	43	315	33	149	39	224
S.D.	±4.6	±78.1	±6.1	±86.4	±11.0	±169.5	±12.1	±89.9	±16.1	±181.2	±4.0	±14.2	±9.9	±109.5
Non-saproxylics														
Total	84	4042	78	2183	91	840	64	791	65	888	60	1021	182	9765
Mean/site	29	449	30	364	44	210	34	264	35	296	32	340	33	348
S.D.	±3.3	±155.0	±7.0	±155.5	±11.2	±34.8	±5.0	±139.7	±0.6	±150.6	±4.6	±5.5	±7.4	±149.1
All species														
Total mean/site	177	5751	185	3551	186	1993	151	1426	145	1832	114	1469	362	16022
	62	639	70	592	92	498	82	476	78	611	65	489	72	572
S.D.	±4.7	±138.2	±9.4	±183.0	±21.8	±201.9	±17.0	±203.2	±16.5	±331.7	±4.2	±11.4	±15.1	±178.7

we first applied detrended correspondence analysis (DCA; Ter Braak & Šmilauer 1998) in which we included the environmental variables (stand characteristics) by fitting them in the ordination as passive variables (McCune 1997). The passive fitting was done in order to aid interpretation of the main ecological gradients in the data, and in order to minimize the risk of irrelevant conclusions in the subsequent analyses. Secondly, we explored which minimum set of environmental variables best explained the compositional variation by using canonical correspondence analysis (CCA; Ter Braak & Šmilauer 1998). In the DCA's, detrending was performed by second order polynomials instead of segments because the number of samples was rather low. In the CCA's, the statistical significance of the environmental variables was tested with Monte Carlo permutations ($n = 999$). We applied forward selection of the environmental variables, and used the significance level of $p < 0.05$ to include a variable in the model. In all correspondence analyses, we restricted our interpretation to the ordination space determined by the first two axes.

Results

The pooled sample included 16 022 beetle individuals belonging to 362 species. The numbers of saproxylic (180) and non-saproxylic species (182) were about equal, whereas the majority of individuals (61%) were non-saproxylic (Table 3). The abundance distribution of the species was very skewed: the ten most abundant species comprised 62% of all the individuals, whereas 29% of the species were represented by only one individual. The most dominant species, *Anthophagus omalinus*, comprised almost 30% of the total catch. This staphylinid, which is a predator living in understorey vegetation, was the most abundant species in all the forest types except in the mixed forests (Appendix). Of the 100 most abundant species (min. 10 individuals in the pooled data), 37 species were found in all the old-growth forest types and in all the regeneration area types (Appendix). The complete list of species trapped in the study has been published in Sippola *et al*. (2000).

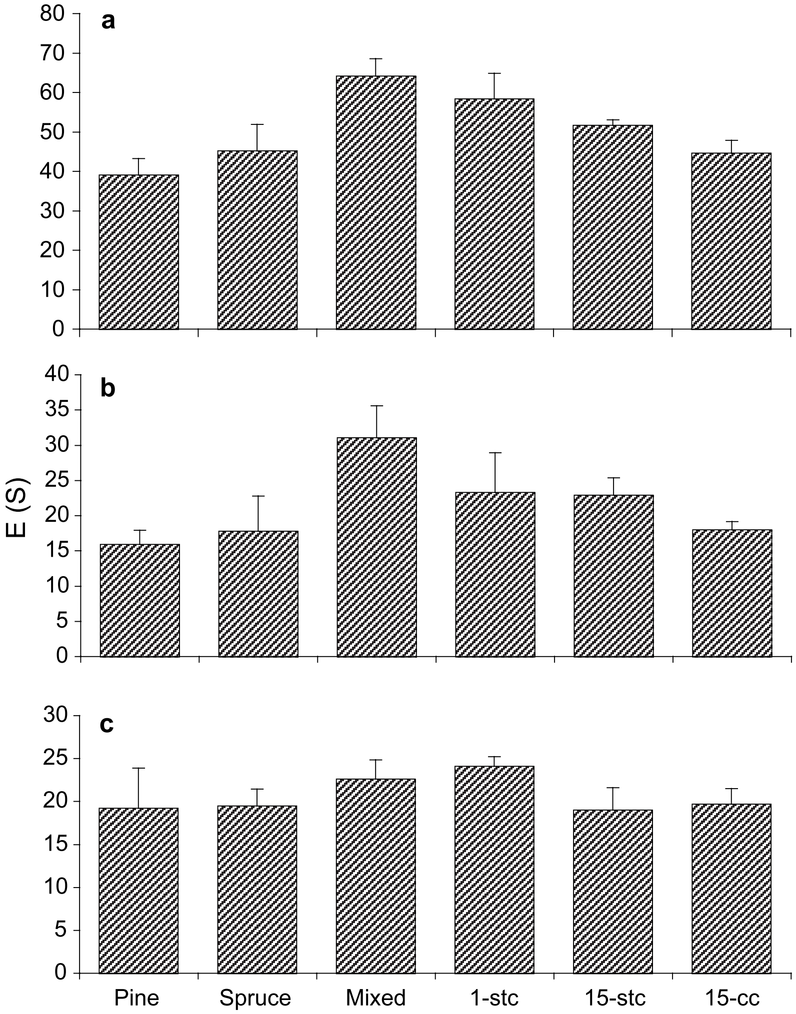

Fig. 2. The expected species numbers of all the species (**a**), non-saproxylic species (**b**) and saproxylic species (**c**) in the old-growth forests and regeneration areas. The standardized sample size for all the species is 240 individuals, for non-saproxylic species 110 individuals and for saproxylic species 60 individuals. Symbols for the regeneration areas: 1-stc = 1-year-old seed-tree cut pine forests, 15-stc = 15-year-old seed-tree cut pine forests, and 15-cc = 15-year-old clear-cut spruce forests.

Species richness in old-growth forests and regeneration areas

We first compared the overall species richness among the old-growth forest stands. A total of 299 species were trapped at the old-growth forest sites. The expected overall number of species per standardized sample size (240 individuals) was significantly higher in the mixed forests than in the pine forests ($H = 11.2$, df = 2, $p = 0.004$), whereas spruce forests did not differ in this respect from the other two old-growth forest types (Fig. 2a). We then analysed separately saproxylic and non-saproxylic species. The difference in the species richness between pine and mixed forests was statistically significant for non-saproxylic species ($H = 9.0$, df = 2, $p = 0.011$, standardized sample size of 110 individuals), but not for saproxylic species ($H = 5.0$, df = 2, $p = 0.081$, standardized sample size 60 of individuals) (Fig. 2b–c).

A total of 29 nationally rare species with less than 25 records in Finland between 1960 and 1990 (Rassi 1993) were found (Table 4). The number of rare saproxylic species was clearly higher in old-growth spruce forests than in the other forest types (Table 4). Two of the rare saproxylic species are included in the red data book of Finland: *Agathidium pallidum*, which was caught in a mixed forest, and *Pytho abieticola*, which was trapped in a spruce forest. Both species have declined as a result of the decrease of old-growth forests (Rassi *et al.* 1992).

Next we compared beetle species richness between old-growth and regeneration stands. A total of 258 species were found in the pooled data of old-growth pine forests and seed-tree cut sites. The expected overall number of species for the standardized sample size was significantly higher at the 1-year-old seed-tree cut sites than in the old-growth pine forests, whereas the 15-year-old seed-tree cut sites did not differ from the other two forest categories ($H = 10.5$, df = 2, $p = 0.005$, Fig. 2a). When saproxylic and non-saproxylic species were analysed separately, the expected number of non-saproxylic species was significantly higher at the 15-year-old seed-tree cut sites than in the old-growth pine forests ($H = 8.8$, df = 2, $p = 0.013$), whereas the differences in species richness of saproxylics were not significant ($H = 4.1$, df = 2, $p = 0.129$, Fig. 2b–c).

The pooled number of species in the old-growth spruce forests and clear-cuts was 216. No significant differences were detected in the rarefied number of species between old-growth and clear-cut sites ($U = 8$, $p = 0.905$ for all species, $U = 8$, $p = 0.905$ for saproxylics, and $U = 6$, $p = 0.548$ for non-saproxylics, Fig. 2a–c).

The number and proportion of nationally rare saproxylic species were higher at the 1-year-old seed-tree cut sites than in the old-growth pine forests, but lower at the 15-year-old seed-tree cut sites. At the clear-cut sites, the number and proportion of rare saproxylic species were clearly lower (1 vs. 12 species, and 1.9% vs. 11.2%) than in the old-growth spruce forests (Table 4). The number of rare non-saproxylic species did not show any clear trends among the forest categories.

Species richness and species composition in relation to environmental variables

Correlation analysis revealed three main groups of environmental variables that correlated positively with the overall species richness of beetles in the old-growth forests: site fertility and productivity (as indicated by the number of vascular plants, cover of eutrophic vegetation, thickness of humus layer and the total volume of living spruce), total amount of CWD, and volume of certain CWD types (CWD of spruce and deciduous trees, and decay classes 3 and 4) (Table 5). The correlations should be interpreted with caution since many of the environmental variables were intercorrelated.

As expected, the species richness of saproxylics correlated positively with most of the CWD variables. The highest correlations were found for the volume of CWD composed of deciduous trees, spruce and advanced decay classes (3 and 4), but also for the volume of living spruce. All these variables were positively correlated with site fertility. The negative correlation with the volume of dead pines was evidently a spurious one, and was due to the fact that the total volume and variation of CWD were, on the average, lower in the pine forests than in the spruce-dominated and mixed forests (*see* Sippola *et al.* 1998). The species richness of non-saproxylics correlated positively with the variables indicating fertility and productivity of the site, including the volume of the living stand and cover of eutrophic plants.

None of the environmental variables correlated significantly with the overall species richness of beetles at the regeneration sites, but the

Table 4. Numbers of rare species (less than 25 occurrences in Finland in 1960–1990) in different forest type categories. The figures in parentheses show the percentage proportion of rare species out of the total species number in each category.

	Pine	Spruce	Mixed	1-yr. seed tree cut	15-yr. seed tree cut	15-yr. clear-cut	Total
Saproxylic species	4 (4.3)	12 (11.2)	6 (6.3)	7 (8.0)	2 (2.5)	1 (1.9)	19 (10.6)
Non-saproxylic species	3 (3.6)	1 (1.3)	3 (3.3)	2 (3.1)	2 (3.1)	3 (5.0)	10 (5.5)
Total number of species	7 (4.0)	13 (7.0)	9 (4.8)	9 (6.0)	4 (2.8)	4 (3.5)	29 (8.0)

volume of CWD in decay class 2 showed the highest positive, and the cover of shrubs the highest negative correlation with the species richness of saproxylics.

The correspondence analyses on both saproxylic and non-saproxylic species assemblages revealed the same two, rather clear gradients in site fertility (or forest site type) and stand openness (or successional stage). The old-growth pine-dominated stands were separated from the old-growth spruce-dominated and mixed stands on the one hand, and the regeneration areas from the old-growth stands on the other. The longest gradients in the data were rather short, 1.64 and 2.08 SD units for the non-saproxylic and saproxylic species, respectively. The ordination space determined by the first and second axes in the non-restricted correspondence analysis (DCA) contained 21.2% and 27.0% of the variation in the non-saproxylic and saproxylic species data, respectively.

The main gradients in the DCA ordination of saproxylic species were the site-type transition from spruce and mixed stands to pine stands, which ran from top-left to bottom-right, and the openness transition from old-growth stands to

Table 5. Spearman rank correlation coefficients between environmental variables and species richnesses of beetles. Asterisks indicate statistically significant correlations (* = $p < 0.05$). The risk level was adjusted with a Bonferroni correction. $^+$ = variables indicating site fertility.

	Old-growth forests ($n = 19$)			Regeneration areas ($n = 9$)		
Variable	Saproxylics	Non-saproxylics	**All species**	Saproxylics	Non-saproxylics	**All species**
Living stand variables						
VLivTot	0.247	0.885*	0.629	0.544	0.359	0.525
VLivPin	–0.562	–0.294	–0.486	0.636	0.287	0.555
VLivSpru	0.646	0.550	0.719*	–0.478	–0.301	–0.40
VLivDec	0.585	0.285	0.604	–0.477	–0.099	–0.239
CWD variables						
VDeadTot	0.561	0.497	0.698*	0.333	0.353	0.444
VDeadPin	–0.393	–0.352	–0.365	0.383	0.445	0.477
VDeadSpru	0.673	0.384	0.694*	–0.037	–0.083	–0.018
VDeadDec	0.683*	0.493	0.753*	0.083	–0.151	0.084
VLog	0.563	0.448	0.639	0.350	0.370	0.485
VSnag	0.318	0.453	0.602	0.20	0.513	0.494
VStuBra	0.570	0.346	0.593	0.350	0.252	0.360
VBigDead	0.377	0.498	0.484	0.233	0.546	0.594
Decay 1	0.422	0.235	0.580	0.417	0.176	0.485
Decay 2	0.446	0.533	0.618	0.867	0.504	0.870
Decay 3	0.617	0.523	0.774*	0.383	0.521	0.536
Decay 4	0.632	0.365	0.679*	0.233	0.487	0.360
Decay 5	0.347	0.411	0.469	–0.083	0.210	0.134
Vegetation variables						
Nvasc$^+$	0.743*	.389	0.796*	–0.271	0.111	–0.077
CovVasc$^+$	–0.155	0.292	–0.170	–0.452	–0.325	–0.420
CovOlig	–0.539	–0.385	–0.653	0.150	0.076	0.226
CovEutr$^+$	0.541	0.787*	0.749*	–0.174	–0.305	–0.392
CovMeso	0.334	0.103	0.411	–0.167	0.235	0.059
CovMoist	0.307	–0.049	0.296	–0.351	0.038	–0.076
CovShru	0.209	0.108	0.115	–0.844	–0.237	–0.651
Site variables						
Humus$^+$	0.773*	0.197	0.764*	0.267	0.606	0.617
CovLitter	–0.187	0.292	–0.023	0.350	0.134	0.234
Altitude	–0.332	0.265	–0.237	–0.169	0.430	0.102

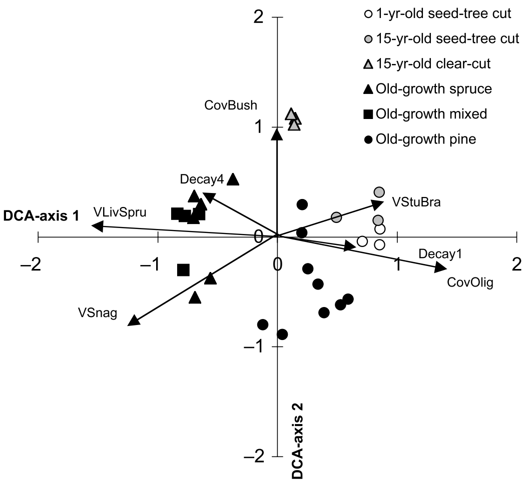

Fig. 3. The DCA-ordination of saproxylic species. Environmental variables are fitted into the ordination as passive variables. Acronyms of the environmental variables: VLivSpru = volume of living spruce, VSnag = volume of snags, VStuBra = volume of stumps and branches, Decay 1 = volume of CWD in decay class 1, Decay 4 = volume of CWD in decay class 4, CovShru = cover of shrubs, and CovOlig = cover of oligotrophic vegetation.

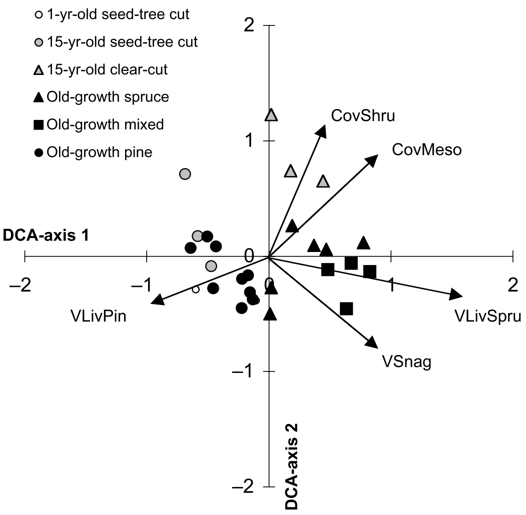

Fig. 4. The DCA-ordination of non-saproxylic species. Environmental variables are fitted into the ordination as passive variables. Acronyms of the environmental variables: VLivSpru = volume of living spruce, VLivPine = volume of living pine, VSnag = volume of snags, CovShru = cover of shrubs, and CovMeso = cover of mesotrophic vegetation.

regeneration areas which ran from bottom-left to top-right (Fig. 3). In saproxylic species, the managed and old-growth stands were clearly separated from each other in both the pine-dominated and spruce-dominated forests. The same main gradients were also revealed in the direct gradient analysis (CCA). The stand characteristics best explaining the species variation (in the order in which they were included in the model) were the volume of living spruce, volume of stumps and branches, volume of CWD in decay class 1, cover of shrubs, cover of oligotrophic vegetation, volume of snags, and volume of CWD in decay class 4 (Fig. 3). Altogether, these seven environmental variables explained 48.1% of the variation in the saproxylic species data (Monte Carlo permutation test for the overall fit, $F = 2.6$, $p = 0.001$).

The main gradients in the DCA ordination of non-saproxylic species were also rather clear. Site-type transition from pine stands to spruce and mixed stands ran from bottom-left to top-right in the ordination (Fig. 4). The openness transition (from top-left to bottom-right in the ordination) was clear in the spruce-dominated sites, but much less evident in the pine-dominated sites, where openness is also characteristic of old-growth stands. The overlap of regeneration areas and old-growth stands was considerable in the pine-dominated forests. The same main gradients were also revealed in the direct gradient analysis (CCA), and forward selection of environmental variables identified (in this order) the volume of living spruce, cover of mesotrophic vegetation, volume of living pines, volume of snags and cover of shrubs as the best variables explaining the variation in the assemblages of non-saproxylic beetles among the stands. Altogether, these five environmental variables explained 31.8% of the variation in the non-saproxylic species data (Monte Carlo permutation test for the overall fit, $F = 2.0$, $p = 0.001$).

Effects of forest cutting on the beetle fauna

There were several faunal differences between the old-growth forests and regeneration areas. Many scolytid species and other saproxylic species which breed in recently died trees occurred only at the 1-year-old sites (e.g. *Pityogenes chalcographus*, *Acanthocinus aedilis* and *Asemum striatum*) or were more abundant there than at the old-growth sites (e.g. *Hylastes brunneus*, *Tomicus piniperda* and *Hylobius abietis*) (Appendix). On the other hand, the most abundant scolytid species in the old-growth pine forests, *Pityopthorus lichtensteinii*, which breeds in dying branches of living pines, was less abundant in the regeneration areas than in the old-growth forests. Other saproxylic species that were more abundant at the seed-tree cut sites include *Anaspis bohemica* and *Xylita laevigata*, and the elaterids *Ampedus nigrinus* and *A. tristis* (which was also abundant at the clear-cut sites). All these species evidently favour decaying wood in open conditions. Two pyrophilous species, *Cryptophagus corticinus* and *Acmaeops pratensis*, were also caught in the recently seed-tree cut sites. However, we also caught several other species that are considered to be pyrophilous in the older logged sites and old-growth forests (*Denticollis borealis, Stagetus borealis, Laemophloeus muticus, Pediaceus fuscus, Henoticus serratus* and *Stenotrachelus aeneus*). *Rhagonycha elongata,* which is a predatory species climbing in vegetation (larvae ground-living), was abundant at the 15-year-old seed-tree cut sites. Two very abundant saproxylic species in old-growth forests, *Hylecoetus dermestoides* and *H. flabellicornis*, were less abundant at or absent from the logged sites; both species breed on recently died trees and are dependent on ambrosia fungi. *Epuraea* spp. were less abundant and less species rich at the seed-tree cut sites than in the old-growth forests, and were practically absent from the clear-cut sites. Several cryptophagid and latridiid species in the genera *Atomaria*, *Caenoscelis, Corticaria* and *Enicmus* were similarly less abundant at the seed-tree cut sites than in the old-growth forest, and were practically absent from the clear-cut sites. All these species are mycetophagous and are known or assumed to depend on different kinds of microfungi (molds, fungi imperfecti, myxomycetes, etc.). On the other hand, the number of species and abundance of cisids, which live in polyporous fungi, were conspicuously higher at the 15-year-old seed-tree cut sites. Species that were more abundant at the clear-cut sites than in the old-growth forests include the saproxylic species *Trichius fasciatus* and *Judolia sexmaculata*, and several elaterids developing in soil as larvae (*Orithalis serraticornis, Selatosomus melancholicus* and *Sericus brunneus*). A number of species confined to pine occurred at the clear-cut sites planted with pine, including *Dasytes obscurus* which is a predatory species on pine saplings, and species living in the phloem of recently died trees (*Magdalis phlegmatica*, scolytids *Pityogenes bidentatus, Pityopthorus lichtensteinii* and *Tomicus piniperda*). The dominating scolytids in the old-growth spruce forest, *Hylastes cunicularius* and *Hylurgops glabratus*, were practically absent from the clear-cut sites.

Discussion

Beetle diversity in old-growth forests

The main environmental factors which contributed to the species richness of flying beetles in the old-growth forests were site productivity, tree species composition and the amount and variation of CWD. Thus, species richness increased with increasing productivity and structural heterogeneity of the stands (cf. Rosenzweig & Abramsky 1993).

The variables related to site productivity and the volumes of CWD and living timber are usually intercorrelated (Harmon *et al.* 1986, Sippola *et al.* 1998). This probably explains why the volume of living trees and many variables indicating site productivity were among the best explanatory variables for beetle-species richness. Tree species composition is also related to site fertility, the poorest sites in our study area being dominated by pine, and the more fertile ones by spruce and deciduous species. In our data, most of the variables related to CWD, particularly the volumes of spruce and deciduous CWD, correlated positively with the number of beetle species. Both spruce and deciduous trees host more invertebrate species than pine (Esseen *et al.* 1992, Rassi *et al.* 1992). According to Esseen *et al.* (1992), a higher invertebrate diversity in spruce is due to the more rapid decay process and more diverse fungal flora in spruce than in pine, which creates microhabitats for fungus-living species. A number of beetle species are confined to the woody debris of deciduous trees. Also the presence of fungal flora may play a crucial role in the correlation between deciduous CWD and saproxylic species, since e.g. the fruit bodies of some birch-inhabiting polypores such as *Fomes fomentarius* are known to host a high number of beetle species (Kaila *et al.* 1994, Økland 1995).

The amount of CWD was found to be an important factor contributing to the species richness of the beetle fauna. Saproxylic species comprised more than half of all the species in the old-growth forests. Even higher proportions of saproxylic beetles have been recorded for hemiboreal spruce forests in southern Norway, where saproxylics comprised about two thirds of the species in window flight trapping (Stokland 1994). CWD in the advanced decay classes (3 and 4) had high positive correlations with the species richness of saproxylic species (and consequently with the overall species richness). In boreal forests, the peak of beetle diversity occurs in dead spruce trunks 5–20 years after the death of a tree, corresponding approximately to CWD in decay classes 2 and 3. The beetle fauna of these decay classes comprise many cambial-eaters, fungal consumers and their associates (Esseen *et al.* 1992). Decay classes 3 and 4 host the highest diversity of species associated with wood-decomposing fungi, and a large number of threatened saproxylic species (Esseen *et al.* 1992, Jonsell *et al.* 1998). However, the high correlations between beetle diversity and CWD in decay classes 3 and 4 may be partly due to the fact that the amount of CWD belonging to these classes increased towards the more productive sites, being the highest in mixed forests.

If the conservation value of old-growth boreal timberline forests is measured in terms of the species richness of beetles, the most valuable habitats are spruce-dominated forests containing several admixed deciduous tree species and a rich undergrowth vegetation. Spruce-dominated forests especially host more rare saproxylic species than pine-dominated forests. This does not mean that the old-growth pine forests would not have conservational value. In our data, many species found in pine forests did not occur in spruce-dominated forests, and many of them did not occur at any of the regeneration sites either.

The influence of regeneration cutting on beetle diversity

The species composition of the seed-tree cut and clear-cut sites differed from that of the respective old-growth forests. Both the correspondence analysis and comparison of the species lists showed that the difference in the species composition was more distinct between old-growth spruce forests and clear-cuts than between old-growth pine forests and seed-tree cut sites. A significantly higher number of species was trapped in the recently seed-tree cut sites than in the old-growth pine forests. The increase in species richness in the seed-tree cut sites is probably a consequence of several factors:

1. Species that are primary colonisers of CWD, e.g. cambial-feeders, increase at recently cut sites (*see* Nuorteva 1956, Väisänen *et al.* 1993). In our data, many of the scolytids, curculionids and cerambycids which were not present in the old-growth pine forests were trapped in the recently cut sites. Some of these species also occurred at the 15-year-old seed-tree cut sites.
2. Many beetle species of pine forests, especially non-saproxylics, are able to inhabit both old-growth and seed-tree cut areas. This may be due to the fact that old-growth pine forests are relatively open even before cutting, and the environmental change from old-growth to seed-tree cut stand is relatively small.
3. Species that prefer open habitats and young successional stages benefit from logging. Their increase was obvious at both the seed-tree cut and clear-cut sites. However, the species composition after these two regeneration methods was different, probably as a consequence of differences in stand characteristics (tree-species composition, CWD, vegetation) between both the pre- and post-harvest sites.
4. Colonisation of logging waste by wood-decomposing fungi increases the abundance

of some groups of mycetophagous species. The abundance of cisid species, which mainly inhabit the basidiocarps of wood-decaying fungi, was high in the 15-year-old seed-tree cut areas. The number of species and number of records of wood-decomposing fungi at these sites were also relatively high, and species of mid-decayed trees predominated (cf. Sippola & Renvall 1999).
5. Other factors that may affect the species richness of logging areas are landscape-scale distribution of forest patches and the edge effect. Many groups of forest arthropods disperse actively into the open young stands (Niemelä *et al.* 1996). As suggested by Spence *et al.* (1996), forest specialists may regularly colonise open areas which are small islands in a landscape comprised mainly of older age classes. The forests surrounding our regeneration sites were mainly old-growth forests, which probably act as sources of colonisers for the regeneration areas. In addition, the mean size of 1-year-old seed-tree cut sites was only about 10 ha. In such small patches, most of the cut area may represent more an edge habitat than an open stand for many flying invertebrates (cf. Helle & Muona 1985, Jokimäki *et al.* 1998).

With the exception of polypore-feeding cisids, the species that were absent from or less abundant in the regeneration areas than in the old-growth forests were mainly species associated with fungi. Their low abundance was especially pronounced in the clear-cuts. The absence of these species is probably related to the changes in microclimatic conditions of the regeneration areas, since most fungi are sensitive to drought. Also, the low volume of CWD at the clear-cut sites may have affected the number of wood-inhabiting fungi and, consequently, the number of fungal consumers. The characteristic scolytids of old-growth spruce forests were mostly absent from the clear-cut sites, whereas some pine-inhabiting species, mainly species living in saplings, were trapped there.

As compared with respective old-growth stands, the proportion of nationally rare saproxylic species was higher at the recently seed-tree cut sites, but lower both at the 15-year old seed-tree and clear-cut sites. This is probably a result of both changes in the variation of CWD, and the disrupted recruitment of CWD at the older sites. There are many rare saproxylic species that are specialized either to open, sun-exposed habitats, or closed, shady forests (Kaila *et al.* 1997, Jonsell *et al.* 1998, Martikainen 2001). It is probable that the recently seed-tree cut areas provide substrate for the former group. However, recruitment of new CWD in the both types of regeneration areas is very slow (Sippola *et al.* 1998). The CWD in the regeneration areas is also substantially different from the CWD in the old-growth forests. Except for of some residual CWD from pre-logging time, the majority of CWD in the regeneration areas is small-diameter logging waste, whereas CWD in advanced decay classes in old-growth forests consists mainly of large-diameter trunks. It is likely that, over the course of time, species which prefer large-diameter logs, CWD in advanced decay classes or relatively moist CWD, will decline or disappear from the regeneration areas. However, more studies are needed on the requirements of individual species to evaluate what is the role of the substrate decline *per se*, and how much the microclimatic factors affect the survival of species. The 15-year time span of the present study is a relatively short period of time, and many changes in the composition of saproxylic species can be delayed because of the slow decay process in northern latitudes. Thus, the possible loss of species is likely to be detected only in the long run ("extinction debt", *see* e.g. Hanski 1998, 2000).

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Appendix

The mean numbers of abundant species (min. 10 individuals in the pooled catch) per study site in different forest type categories. S = saproxylic species, N = non-saproxylic species. Total number of individuals in the pooled catch in parenthesis.

	Status	Pine	Spruce	Mixed	1-yr. seed tree cut	15-yr. seed tree cut	15-yr. clear-cut	Total mean per site
Carabidae								
Dromius agilis (F.)	S	2.6	8.0	2.8	0.7	0.5		3.5 (99)
Leiodidae								
Agathidium rotundatum (Gyllenhal)	S	0.1	0.5	0.3	1.0	0.7	0.7	0.4 (12)
Anisotoma glabra (Kugelann)	S		0.3	1.3	1.0	0.7	3.0	0.8 (21)
Cholevidae								
Catops alpinus Gyllenhal	N	0.2	0.8	0.5	0.3		0.3	0.4 (11)
Staphylinidae								
Acidota crenata (F.)	N	0.3	0.2	0.5	0.3	1.3	0.3	0.4 (12)
Acrostiba borealis Thomson	N	0.1	1.0	2.5		0.3	0.3	0.7 (19)
Anthophagus omalinus Zetterstedt	N	208.7	216.2	54.8	123.3	147.3	173.0	168.8 (4725)
Atheta laevicauda J. Sahlberg	N	0.6	0.8		1.3	1.0	2.3	0.9 (24)
Atheta myrmecobia (Kraatz)	N	0.1	1.5	1.0		0.3	0.7	0.6 (17)
Atheta procera (Kraatz)	N	2.1	2.3	1.5	3.0	3.0		2.0 (57)
Atrecus pilicornis (Paycull)	S	0.1	2.2	1.5		0.3	3.7	1.1 (32)
Bryoporus punctipennis Thomson	N	1.1	0.8	1.8	1.0			0.8 (23)
Bryoporus rugipennis (Pandelle)	N	3.6	1.2	1.5	5.3	5.3	0.7	2.8 (79)
Coryphium angusticolle Stephens	N	5.0	0.3	0.3		5.0	0.3	2.3 (64)
Dimetrota aeneipennis (Thomson)	N	0.7	0.3	1.0	0.3			0.5 (13)
Eusphalerum sorbicola (Y. Kangas)	N	0.1	0.3	2.3				0.4 (12)
Haploglossa marginalis (Gravenhorst)	S				11.3			1.2 (34)
Mycetoporus lepidus (Gravenhorst)	N	0.6	1.5	1.5	3.7	2.3	1.7	2.2 (61)
Olisthaerus megacephalus (Zetterstedt)	S	0.2	0.3	1.3	0.3	0.7	1.3	0.6 (16)
Oxypoda skalitzkyi Bernhauer	N	1.2	0.3	1.3	0.7			0.7 (20)
Oxytelus laqueatus (Marsham)	N	0.1	0.2	2.0			1.0	0.5 (13)
Phloeonomus lapponicus (Zetterstedt)	S	0.9		0.3	1.7	1.0		0.6 (17)
Quedius plagiatus (Mannerheim)	S	1.0	3.5	7.0	1.0	0.7	2.7	2.5 (71)
Tachinus elongatus Gyllenhal	N	3.6	12.8	18.0	1.3	3.7	6.7	7.7 (216)
Tachinus pallipes (Gravenhorst)	N	0.2	0.7	1.0		0.3	0.7	0.5 (13)
Scirtidae								
Cyphon variabilis (Thunberg)	N	3.7	3.8	5.6	0.7	5.0	8.7	4.4 (122)
Scarabaeidae								
Aphodius lapponum Gyllenhal	N	4.2	5.2	14.0	4.0	0.7	5.3	5.5 (155)
Aphodius piceus Gyllenhal	N	0.7	0.5	1.5	0.3		0.3	0.6 (17)
Aphodius tenellus Say	N	1.0	0.3	0.3	0.3	0.3	0.3	0.5 (15)
Trichius fasciatus (L.)	S	0.4	1.0	0.3		0.7	38.7	4.6 (129)
Lycidae								
Dictyoptera aurora (Herbst)	S	0.1	0.5	0.8	1.3	1.7	0.7	0.6 (18)
Cantharidae								
Absidia schoenherri (Dejean)	N	5.0	11.8	9.3	1.0	5.3	11.7	7.4 (207)
Malthodes guttifer Kiesenwetter	N	83.6	7.8	3.5	5.8	5.7	8.7	31.4 (879)
Rhagonycha atra (L.)	N		3.5	3.0			1.3	1.3 (37)
Rhagonycha elongata (Fallén)	N	1.3	0.2			13.0		1.9 (52)
Elateridae								
Ampedus nigrinus (Herbst)	S	5.0	0.8	1.0	19.3	41.0	8.0	9.3 (259)
Ampedus tristis (L.)	S	0.1	0.2		0.7	5.7	3.3	1.1 (31)
Eanus costalis (Paykull)	N	7.1	39.3	16.5	53.0	43.0	22.7	38.6 (1082)
Liotrichus affinis (Paykull)	N	6.1	13.5	16.3	11.7	10.7	23.0	12.0 (337)
Orithalis serraticornis (Paykull)	N	1.2	0.5	0.3	0.3	0.3	31.3	4.0 (111)
Selatosomus impressus (F.)	N	2.0		0.8	4.3	2.7	0.3	1.5 (43)
Selatosomus melancholicus (Fabricius)	N	1.1	0.3				11.3	1.6 (46)
Sericus brunneus (L.)	N	1.1	1.0	0.5	1.3	4.7	8.3	2.2 (61)

Continued

Appendix. Continued.

	Status	Pine	Spruce	Mixed	1-yr. seed tree cut	15-yr. seed tree cut	15-yr. clear-cut	Total mean per site
Lymexylidae								
Hylecoetus dermestoides (L.)	S	41.4	24.3	12.0	26.7	6.0	1.3	23.9 (669)
Hylecoetus flabellicornis (Schneider)	S	21.1	52.2	23.5				21.3 (597)
Melyridae								
Aplocnemus tarsalis (Sahlberg)	S	3.7	0.2		9.3	10.0		3.3 (92)
Dasytes obscurus Gyllenhal	S	0.1					49.0	5.3 (148)
Nitidulidae								
Epuraea aestiva (L.)	N	1.8	2.5	4.3	2.3	1.0	2.7	2.4 (66)
Epuraea angustula Sturm	S	1.9	0.8	1.3	0.7			1.0 (29)
Epuraea biguttata (Thunberg)	S	0.8	0.3	1.5		0.7		0.4 (12)
Epuraea boreella (Zetterstedt)	S	2.7	1.3	4.5	1.0			1.9 (54)
Epuraea pygmaea (Gyllenhal)	S	0.2	1.5	2.3				0.8 (22)
Epuraea rufomarginata (Stephens)	S	1.0	1.3	4.8	0.3	0.7		1.4 (39)
Rhizophagidae								
Rhizophagus ferrugineus (Paykull)	S	1.4	0.5	3.5	7.0	0.3		1.9 (52)
Cryptophagidae								
Atomaria pulchra Erichson	N	0.1	0.3	1.3	0.7			0.4 (10)
Cryptophagus dorsalis Sahlberg	N	2.7			1.0	1.3	0.3	1.1 (32)
Cryptophagus lapponicus Gyllenhal	N	37.1	8.5	7.8	8.0	3.0	0.3	16.1 (450)
Erotylidae								
Triplax russica (L.)	S	0.7	2.0	1.0	0.3	0.3		0.9 (24)
Triplax scutellaris Charpentier	S	1.0	1.3	0.3	0.3	0.7	0.3	0.8 (22)
Cerylonidae								
Cerylon ferrugineum Stephens	S	1.0	1.5	1.0	1.0	9.3	4.3	2.4 (66)
Latridiidae								
Corticaria ferruginea Marsham	N	2.8	1.5	3.3	2.7	1.3		2.1 (59)
Corticaria orbicollis Mannerheim	N	2.6	2.3	2.0	3.0	1.3	0.7	2.1 (60)
Corticaria rubribes Mannerheim	N	0.9	1.0	0.8	3.7		0.3	1.0 (60)
Enicmus fungicola Thomson	S	3.7	2.7	4.0	1.0	1.0	0.7	2.6 (29)
Latridius consimilis Mannerheim	S	1.0	1.5	1.5	2.0	0.7	1.0	1.3 (35)
Stephostethus rugicollis (Olivier)	N		0.3	2.0				0.4 (10)
Cisidae								
Cis boleti (Scopoli)	S	0.2	0.7	1.3	0.7	63.0	0.3	7.3 (203)
Cis comptus Gyllenhal	S	0.2				7.0		0.8 (23)
Orthocis alni (Gyllenhal)	S	0.9	0.7		0.7	9.0	1.7	1.7 (46)
Pythidae								
Pytho depressus (L.)	S	1.4		0.5	0.3			0.6 (16)
Salpingidae								
Rabocerus foveolatus (Ljungh)	S	2.9	2.0	3.5	0.3	4.7	0.6	2.4 (68)
Salpingus ruficollis (L.)	S	9.3	3.2	1.5		1.7		4.1 (114)
Anaspidae								
Anaspis arctica Zetterstedt	S	12.1	10.3	8.0	10.3	5.0	26.3	11.7 (328)
Anaspis bohemica Schilsky	S	0.1			2.7	9.7		1.4 (38)
Anaspis rufilabris (Gyllenhal)	S	1.9	0.3	1.0	5.3		1.0	1.4 (39)
Tetratomidae								
Tetratoma ancora F.	S	1.8	0.3	1.0	0.3	1.0	0.3	1.0 (27)
Melandryidae								
Orchesia micans (Panzer)	S	0.7	0.8	0.5	0.3	0.7		0.6 (16)
Xylita laevigata (Hellenius)	S	2.3	0.5	0.3	3.3	21.0	0.3	3.5 (99)
Cerambycidae								
Judolia sexmaculata (L.)	S	2.9	1.3	0.5	1.7	8.0	18.3	4.3 (120)
Pogonocherus fasciculatus (Degeer)	S	0.3	0.3	0.2	0.7	0.7	0.3	0.4 (11)
Nemonychidae								
Cimberis attelaboides (F.)	N	2.7				1.0		1.0 (27)
Attelabidae								
Deporaus betulae (L.)	N	1.6	1.0	0.5	0.3	2.3	1.7	1.3 (35)

Continued

Appendix. Continued.

	Status	Pine	Spruce	Mixed	1-yr. seed tree cut	15-yr. seed tree cut	15-yr. clear-cut	Total mean per site
Curculionidae								
Hylobius abietis (L.)	S	0.9			10.0	1.0		1.5 (41)
Magdalis duplicata Germar	S		0.2		3.7	0.3	0.3	0.5 (14)
Magdalis phlegmatica (Herbst)	S	0.3			0.7	0.3	3.7	0.6 (17)
Polydrosus ruficornis (Bonsdorff)	N	0.6	4.5	1.3		2.0	0.3	1.6 (44)
Scolytidae								
Crypturgus hispidulus Thomson	S		0.3	2.0				0.4 (10)
Cryphalus saltuarius Weise	S		0.7	6.3		4.3		1.5 (42)
Dryocoetes autographus (Ratzeburg)	S	0.2	8.2	11.5	0.3	0.7	2.3	3.8 (107)
Hylastes brunneus Erichson	S	7.2	0.2		21.7	3.3	0.7	5.1 (143)
Hylastes cunicularius Erichson	S	1.8	19.8	29.8	0.7	0.7	1.7	9.4 (263)
Hylurgops glabratus (Zetterstedt)	S	1.9	38.5	56.0	0.3		1.0	17.0 (476)
Phloeotribus spinulosus (Rey)	S		2.0	2.8				0.8 (23)
Pityogenes bidentatus (Herbst)	S	0.3			7.3	2.7	0.3	1.2 (34)
Pityogenes chalcographus (L.)	S		0.2	2.3	0.7	0.7	0.3	0.5 (15)
Pityophthorus lichtensteinii (Ratzeburg)	S	31.9		0.3	5.3	9.0	1.0	11.9 (334)
Polygraphus punctifrons Thomson	S		0.7	12.5		0.3	0.3	2.0 (56)
Tomicus piniperda (L.)	S	0.9			14.0		1.3	1.9 (54)
Trypodendron lineatum (Olivier)	S	7.3	2.5	10.0	8.7	0.7		5.3 (149)
Xylechinus pilosus (Ratzeburg)	S		6.2	30.8		1.0		5.8 (163)