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Distribution and occurrence of bark beetles and other forest insects in relation to environmental variation were analysed by multivariate methods. Eight different forest edges were studied using 10 × 10 m sample plots that formed 200 m linear transects perpendicular to the forest edge. Forest edge affected the distribution of insect species only in the edges between mature, non-managed spruce stands and clear cuts or young seedling stands, but not in the pine stands. The occurrence of the selected forest insects mainly depended on variables associated with the amount and quality of suitable woody material. The most significant environmental variables were forest site type, crown canopy coverage, tree species, number of stumps, number of dead spruce trunks and amount of logging waste at site. Quantitative classification of species and sample plots showed that some specialized species (*Xylechinus pilosus, Cryphalus saltuarius, Polygraphus poligraphus* and *P. subopacus*) adapted to mature spruce forests, tended to withdraw from the forest edge to interior stand sites. By contrast many generalized species (*Pityogenes chalcographus, P. quadridens, Pissodes* spp., *Hylurgops palliatus, Tomicus piniperda, Dryocoetes* spp. and *Trypodendron lineatum*) benefitted from cuttings and spread over stand borders into mature forest.

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1 Introduction

Intensive forest management and other human activities increase the fragmentation of forest landscape. As the landscape is composed of smaller and smaller compartments, the total amount of edges between different habitats increases rapidly. The juxtaposition of two structurally dissimilar landscape compartments, for example clear cut and forest, leads to ecological changes (e.g. microclimate, abundance and distribution of species, species interactions, behaviour of individuals) near the boundary of the adjacent habitats. These ecological phenomena have often been termed 'edge effects' (Ranney et al. 1981, Forman and Godron 1986, Lovejoy et al. 1986, Wilcove et al. 1986, for a review see Murcia 1995). As a result of the change in abiotic conditions, forest edge is, in general, warmer, drier, windier and lighter than deep forest sites (Matlack 1993, Williams-Linera 1990, Kapos 1989). Such deviate conditions lead to the development of shade-intolerant vegetation close to the forest edge (Palik and Murphy 1990, Saunders et al. 1991, Chen et al. 1992), which attracts generalized animal species (Helle and Muona 1985, Hansson 1994). Some species get significant benefit from man-made habitat edges (Punttila et al. 1994). On the other hand, forest-interior species may be very vulnerable to such ecological changes of environment (Helle 1985, Hansson 1994).

There are only few studies which have approached forest edges from an entomological point of view (Helle and Muona 1985, Bellinger et al. 1989, Halme and Niemelä 1993, Roland 1993, Punttila et al. 1994). Reliable information about the effect of forest edge on insects is needed for both conservation of rare species and careful forest management to avoid severe forest damage caused by insect pests. The aim of the present study is (1) to analyse the distribution pattern of bark beetles (and some other forest insect species) accross different kinds of man-made forest edges, (2) to classify the species according to their response to stand edges and (3) to explore how species community composition relates to environmental variables determined for the stand edges.

2 Material and Methods

2.1 Study Area

The data were collected in the surroundings of the Hyytiälä Forest Research Station (62°50' N, 24°19' E) in July–August, 1993. The study area belongs to the mid-boreal coniferous forests of southern Finland. The management of Hyytiälä forests has been relatively effective since the late 19th century. The average area of a managed stand in Hyytiälä forests is only a few hectares, as in managed forests of southern Finland in general. Because of topography and landscape features, the shapes of the stands are, to some extent, irregular.

2.2 Sampling Design and Studied Edges

The occurrence (presence/absence data) of bark beetles and a few other forest insect species and environmental variation were studied in 10×10 m quadrate sample plots that formed linear 200 m transects perpendicular to the stand edge. Each transect consisted of 20 plots. Five parallel transects were adjusted in each forest edge. The distance between transects varied from 0 to 20 m randomly (Fig. 1). Eight different forest edges were studied (Table 1). All studied edges were originally created by forest cutting and thus the changes between the adjacent stands were quite steep. The total number of sample plots was 800.
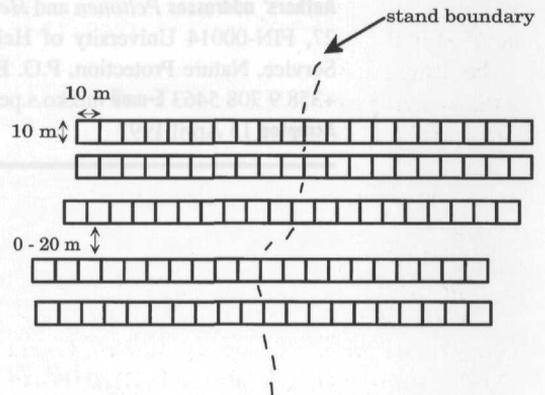

Fig. 1. The sampling design of the study.

Table 1. The main features of the different types of edges studied. OMT = *Oxalis-myrtillus* site type, MT = *Myrtillus* site type, VT = *Vaccinium* site type, CT = *Calluna* site type, ClT = *Cladonia* site type.

Stands		Age	Forest site type	Special features
Edge 1	Pine sapling	10	VT	Well grown, dense
	Spruce/mixed	120–150	MT/VT	Non-managed
Edge 2	Clear cut	2	MT	Efficiently burned
	Spruce	70	MT	Wind falls on the edge
Edge 3	Clear cut	1	MT	Lots of logging waste
	Spruce	30–70	OMT/MT	Partly thinned
Edge 4	Pine seed-tree	2	VT	Soil prepared
	Spruce	100	MT	Power line crosses the stand
Edge 5	Spruce/pine	30	MT	Tree species changes
	Spruce	120	OMT/MT	High volume, snow breaks
Edge 6	Pine seed-tree	2	CT/ClT	Soil prepared
	Pine	70	CT	Thinned
Edge 7	Pine	70	CT	Thinned, well-grown
	Pine	60	CT	Non-managed, poorly grown
Edge 8	Pine sapling	10	ClT	Poorly grown, thin
	Pine seed-tree	2	CT	Soil prepared

2.3 Insect Species and Environmental Variables

The insect species studied were mainly bark beetles but a few other easily recognizable and detectable forest insect species were included in the data. Because all insects or their markings could not be identified at the species level, four insect taxa were included as family (Diprionidae) or generic level (*Pissodes* spp., *Dryocoetes* spp. and *Crypturgus* spp). Thus, 27 taxa were included in the analyses.

The list of the insect taxa with their codes used in the analyses (printed in bold):

– *Retinia resinella* (Linnaeus, 1758). **Reti resi**
– Diprionidae. **Diprioni**
– *Hylobius abietis* (Linnaeus, 1758). **Hylo abie**
– *Pissodes* spp. **Pissodes**
– Scolytidae.
  – *Xylechinus pilosus* (Ratzeburg, 1837). **Xyle pilo**
  – *Tomicus piniperda* (Linnaeus, 1758). **Tomi pini**
  – *Hylurgops glabratus* (Zetterstedt, 1828). **Hylu glab**
  – *Hylurgops palliatus* (Gyllenhal, 1831). **Hylu pall**
  – *Hylastes brunneus* Erichson, 1836. **Hyla brun**
  – *Hylastes cunicularius* Erichson, 1836. **Hyla cuni**

  – *Polygraphus subopacus* Thomson, 1871. **Poly subo**
  – *Polygraphus poligraphus* (Linnaeus, 1758). **Poly poli**
  – *Crypturgus* spp. **Crypturg**
  – *Dryocoetes* spp. **Dryocoet**
  – *Cryphalus saltuarius* Weise, 1891. **Cryp salt**
  – *Pityophthorus micrographus* (Linnaeus, 1758). **Pity micr**
  – *Pityophthorus lichtensteinii* (Ratzeburg,1837). **Pity lich**
  – *Trypodendron lineatum* (Olivier, 1795). **Tryp line**
  – *Trypodendron signatum* (Fabricius, 1792). **Tryp sign**
  – *Pityogenes chalcographus* (Linnaeus, 1761). **Pity chal**
  – *Pityogenes quadridens* (Hartig, 1834). **Pity quad**
  – *Pityogenes bidentatus* (Herbst, 1783). **Pity bide**
  – *Ips typographus* (Linnaeus, 1758). **Ips typo**
  – *Ips amitinus* (Eichhoff, 1872). **Ips amit**
  – *Orthotomicus suturalis* (Gyllenhal, 1827). **Orth sutu**
  – *Orthotomicus laricis* (Fabricius, 1792). **Orth lari**
  – *Orthotomicus proximus* (Eichhoff, 1868). **Orth prox**

The measured environmental variables were forest site type, number of trees (for each tree species), crown canopy coverage, height of dominant trees, number of stumps, number of fallen or dead trunks, amount of logging waste (or similar material) and number of ant nests. The presence/absence data of the species were collected manually from the stumps, trunks, branches and other suitable habitats. The upper parts of trunks, tree-tops and roots were not included in this study. Both individuals and mother galleries were registered as species presences. Mother galleries were younger than 4 years and clearly identified.

The forest site type was classified according to the Cajanderian system (Cajander 1949). The number of trees (higher than 1 m) was counted for the pine (*Pinus sylvestris*), the spruce (*Picea abies*), the birch (*Betula* spp.) and collectively for other deciduous trees. The crown canopy coverage was estimated from the projection of the tree canopy in the middle of sample plot (scale: open = 0, 5, 10, 15,..., 100 = fully closed). The crown canopy coverage of a 2 m high sapling stand was 0.

Pine and spruce stumps (diameter > 10 cm) were counted separately. Stumps of deciduous trees were ignored. The fallen or dead trunks were counted if their maximum diameter was over 10 cm and length was over 100 cm. Pine and spruce trunks were classified separately. Dead standing conifers, windthrows and broken tops were all counted as pine or spruce trunks. Woody material over 4 cm and under 10 cm diameter was classified as logging waste. In recently managed sites, small tree tops and bigger branches were included, but in non-managed sites also dead conifer undergrowth and windthrown branches were counted. Over 4-year-old stumps, dead trunks and logging waste were ignored (visual estimation). The number of ant nests (*Formica rufa* coll.) was counted in each sample plot. Ant nests were used as an environmental variable in the analysis, because ants may fundamentally affect the habitat of other forest insects (Way and Khoo 1992).

2.4 Classification and Ordination

The presence/absence data were analyzed by two-way indicator species analysis (TWINSPAN computer program) (Hill 1979). The aim of this analysis was to classify the studied species as regards to their distribution pattern in the studied areas and to detect similarities and differences between the species' responces to the stand edges. The program first divides the sample plots into groups by repeated dichotomization, and then uses this classification to divide the species into groups. Sample plots in the same division group tend to have similar species assemblages. For species, being in the same division group indicates similar distribution patterns. The maximum number of indicator species was limited to 7 and the smallest divided group consisted of 3 sample plots/species at minimum.

Canonical correspondence analysis (CCA) (ter Braak and Prentice 1986, ter Braak 1986, 1987, Palmer 1993) is an ordination technique for multivariate direct gradient analysis. Here, CCA was used to relate the occurrence of the listed species to the environmental variables, that determine the structural boundaries between adjacent and differently managed stands. The distance from the stand border was included in the analysis as an environmental variable. The results are given as an ordination diagram, where species are points and environmental variables are vectors in the space determined by the ordination axes. The direction and length of the vectors indicate the influence of the environmental variables to the distribution of species. The importance of a single environmental variable is estimated on the basis of the values of canonical coefficient, correlation coefficient and Student's t-test for canonical coefficients. The use of Student's t-test is discussed in ter Braak (1987).

Classification and ordination techniques were used rather to reveal and describe the main patterns of species-environment relationships than to perform statistical tests of the effects of particular environmental variables on the species distribution. The species assemblage of a sample plot was presumed not to be affected by the neighbouring plots. All observed species have a good dispersal ability and their distribution is mainly directly associated with the distribution and availability of breeding material in suitable habitats. Thus, any similarities between adjacent sample plots were considered to result from the availability of suitable breeding material and other habitat qualities.

3 Results

3.1 Species

The highest number of insect species in a 10×10 m sample plot was eight. In 11 % (86) of the sample plots, none of the list species were found. The maximum number of species in a single stand edge was 20 and the minimum 11. The highest species richness was found in recently clear cut or thinned sites (Table 2). The most frequent taxa were *Tomicus piniperda, Pityogenes quadridens, P. chalcographus* and *Pissodes* spp. The least frequent species were *Orthotomicus proximus, Hylastes brunneus, Polygraphus subopacus, Trypodendron signa-*

tum, Pityophthorus lichtensteinii and *P. micrographus*.

3.2 Classification of Species and Sample Plots

The species data set was divided into 11 species groups and 15 sample plot groups by quantitative classification (Fig. 2, Fig. 3, Table 3). The distribution of sample plot groups in the edges is presented in coloured distribution maps (Fig. 4). The indicator species were *Xylechinus pilosus, Polygraphus poligraphus* and *Cryphalus saltuarius* in the first division. These species were typical for the 54 sample plots in groups H, I, J,

Table 2. List of the insect taxa in the edges. The values are frequencies of samples, where the species were present. Species total is the number of species found in each edge.

Species	Edge							
	1	2	3	4	5	6	7	8
Retinia resinella	10						17	46
Diprionidae						71	91	53
Hylobius abietis		2					1	17
Pissodes spp.	19	47	7	30	19	26	3	22
Xylechinus pilosus	3	5	10	17	7			
Tomicus piniperda	47	26	15	23	20	98	84	92
Hylurgops glabratus	3	1	2		3			
Hylurgops palliatus	5	12	25	30	15	27	6	15
Hylastes brunneus							2	
Hylastes cunicularius		2	6	5				
Polygraphus subopacus		1			1			
Polygraphus poligraphus	7	10	1		1			
Crypturgus spp.	3	3	12	11	2			
Dryocoetes spp.	6	34	41	31	24	2		
Cryphalus saltuarius	1		4	12	2			
Pityophthorus micrographus	1	2		1	2			
Pityophthorus lichtensteinii	1					1	1	
Trypodendron lineatum	5	12	34	20	5	2	1	1
Trypodendron signatum				1				
Pityogenes chalcographus	11	50	58	56	30	11		4
Pityogenes quadridens	46	16	22	31		91	50	51
Pityogenes bidentatus	1		3	18	2	58	35	16
Ips typographus	2	3	2					
Ips amitinus		5		6	3			
Orthotomicus suturalis			13	6		6	6	1
Orthotomicus laricis			19	3			3	
Orthotomicus proximus				1				
Species total	17	20	18	18	14	11	13	11

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┌─ Tomi pini
│
│  ┌─ Reti resi
│  │  Diprioni
│  │  Hylo abie
│  │  Hyla brun
│  │  Pity quad
│  │  Pity bide
│
│  │  Hylu glab
│  │  Hyla cuni
│  │  Pity micr
│  │  Pity lich
│  │  Tryp sign
│  │  Ips typo
│  │  Orth sutu
│  │  Orth lari
│
│  │  Hylu pall
│
│  │  Pity chal
│
│  │  Pissodes
│
│  │  Crypturg
│  │  Dryocoet
│  │  Tryp line
│  │  Ips amit
│
│  │  Poly subo
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│  │  Orth prox
│  │  Xyle pilo
│  │  Cryp salt
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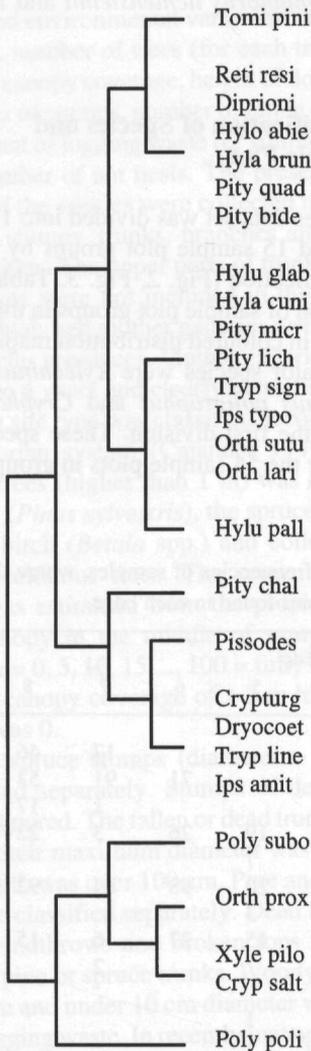
Fig. 2. The species dendrogram of a two-way indicator species analysis (TWINSPAN) using the species presence-absence data. The order of divisions is from left to right.

K, L, M, N and O, which seem to withdraw approximately 30–50 m from the stand border into the spruce forest interior (edges 1–5).

Sample plot groups A, B and C consisted of sample plots inhabited by taxa associated with the pine (*Tomicus piniperda, Retinia resinella,* Diprionidae, *Hylobius abietis, P. bidentatus* and *Pityogenes quadridens*). Groups A, B and C dom-

inated in plain pine stands (edges 6, 7 and 8). In edge 6, the thinned pine stand and the pine seed tree stand formed one continuous habitat for the studied insects. *Retinia resinella* (group B) was the indicator species (edges 7 and 8) that distinguished the adjacent pine stands (thinned–non-managed, seed tree–sapling) and its distribution followed the stand boundaries.

Groups D and E were composed of sample plots inhabited by numerous taxa living in recently cut or thinned pine or spruce stands (e.g. *Tomicus piniperda, Pityogenes chalcographus, P. quadridens, Pissodes* spp., *Hylurgops palliatus* and *Trypodendron lineatum*). Group E (226 sample plots) was especially typical in sites that contained plenty of fresh coniferous logging waste, but was also found in non-managed sites. In edges 2, 3 and 4 these sample plots seem to spread over the stand border at least 40 m into the non-managed stands. However, it is very difficult to estimate the approximate width of this penetration zone, probably because the species composition of group E was so varied. Only five sample plots were classified in groups F or G. These sample plots were inhabited by two species (*Trypodendron signatum, Pityophthorus micrographus*), which occured at very low frequencies.

3.3 Environmental Variables and Species Occurrence

The significance of the first canonical ordination axis was evaluated by the Monte Carlo permutation test. After 99 random permutations the first ordination axis was significant at the 1 % significance level. Thus, the effect of the environmental variables on the species distribution is significant. The eigenvalues, which measure the importance of an ordination axis, were 0.511 and 0.198 for the first two axes, respectively. The species-environment correlation is a measure of how well the extracted variation in community composition can be explained by the environmental variables. The species-environment correlation coefficient for the first axis was as high as 0.86 and for the second axis 0.57 (Table 4).

The most important environmental variable was the forest site type, but also the number of living
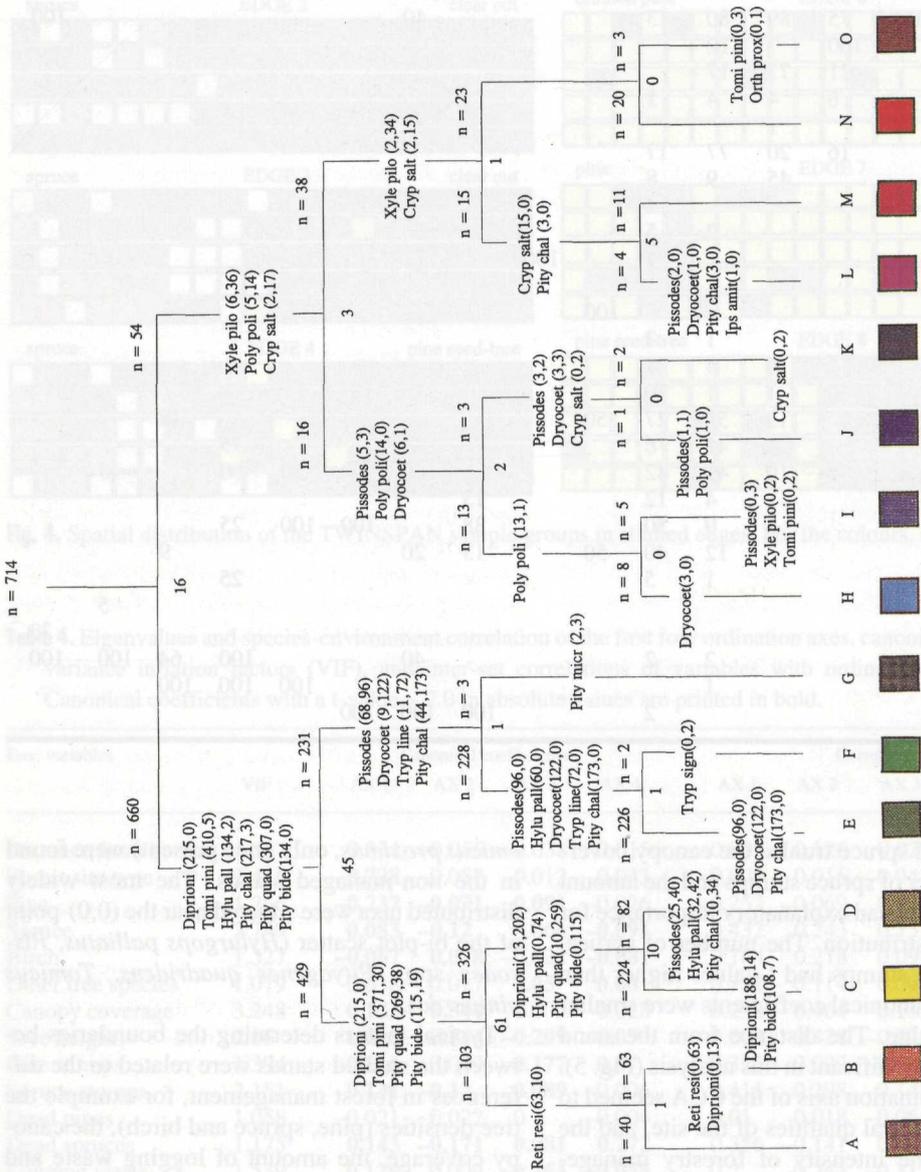
Fig. 3. The sample group dendrogram of a two-way indicator species analysis (TWINSPAN) using the species presence-absence data. Numbers in parentheses are the frequencies of each species in the left and right hand clusters, respectively. The number of "borderline and misclassified plots" is indicated for each division.

Table 3. The percentage occurrence frequency of the species in the 15 groups interpreted from the TWINSPAN. The number of sample plots in each group is shown under the group symbols (A–O).

Species	A 40	B 63	C 244	D 82	E 226	F 2	G 3	H 8	I 5	J 1	K 2	L 4	M 11	N 20	O 3
Tomi pini	100	75	89	80	13			40							100
Reti resi		100		12											
Diprioni		21	77	17											
Hylo abie	3	6	4	4	1										
Hyla brun			1												
Pity quad		16	20	77	17										
Pity bide			45	9	8										
Hylu glab					4										
Hyla cuni				2	5										
Pity micr					1	100									
Pity lich															
Tryp sign						100									
Ips typo				1	3										
Orth sutu			6	4	7										
Orth lari			1	1	10										
Hylu pall			13	51	27	50							18		
Pity chal			4	41	76							75			
Pissodes		5	10	49	42				60	100	50	50		5	
Crypturg				4	12		13								
Dryocoet			1	9	50		38		100	100	25				
Tryp line			12	40		50	13	20					9		
Ips amit			1	5							25				
Poly subo														5	
Orth prox															33
Xyle pilo			2	2				40				100	64	100	100
Cryp salt			1							100	100	100			
Poly poli				2			100	100	100						

pines and dead spruce trunks, the canopy coverage, the number of spruce stumps and the amount of logging waste had explanatory importance for the species distribution. The number of spruce, birch and pine stumps had t-values higher than 2.1, but their canonical coefficients were smaller in absolute value. The distance from the stand edge was non-significant in this analysis (Fig. 5).

The first ordination axis of the CCA seemed to measure the natural qualities of the site, and the second axis the intensity of forestry management. Taxa found in the poorest pine dominated sites (*Hylastes brunneus*, *Retinia resinella*, Diprionidae) were situated on the left in the bi-plot scatter and the uppermost species *Xylechinus pilosus, Cryphalus saltuarius, Pityogenes micrographus, Polygraphus subopacus* (and *Orthot-*

omicus proximus, only once present) were found in the non-managed stands. The most widely distributed taxa were situated near the (0,0)-point of the bi-plot scatter (*Hylurgops palliatus, Pissodes* spp., *Pityogenes quadridens, Tomicus piniperda*).

Typical factors determing the boundaries between the studied stands were related to the differences in forest management, for example the tree densities (pine, spruce and birch), the canopy coverage, the amount of logging waste and the number of stumps. These variables had also explanatory importance for the spatial distribution of species. However, the distribution patterns of species, according to the quantitative classification, did not usually follow the stand boundaries.
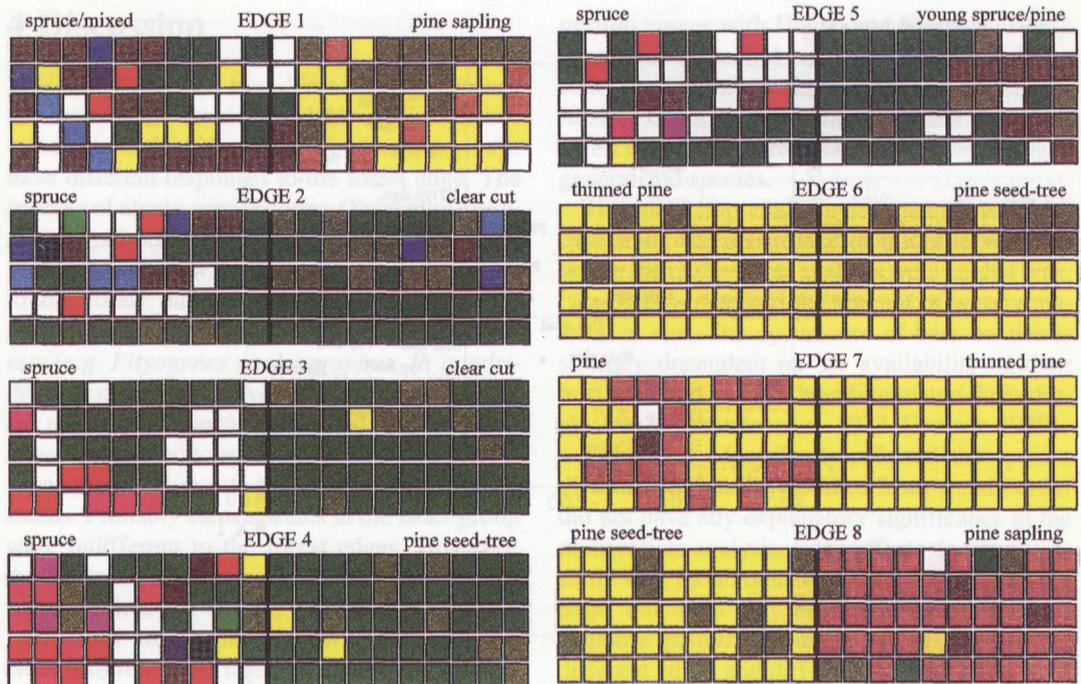
Fig. 4. Spatial distribution of the TWINSPAN sample groups in studied edges. For the colours, see Fig. 3.

Table 4. Eigenvalues and species-environment correlation of the first four ordination axes, canonical coefficients, variance inflation factors (VIF), and inter-set correlations of variables with ordination axes of CCA. Canonical coefficients with a t-value > 2.0 in absolute values are printed in bold.

Env. variables	VIF	Canonical coefficients				Correlation			
		AX 1	AX 2	AX 3	AX 4	AX 1	AX 2	AX 3	AX 4
Distance from border	1.087	0.034	0.056	0.038	–0.015	–0.005	0.126	0.028	–0.031
Forest site type	2.415	**–0.728**	–0.057	0.012	0.043	–0.805	0.016	–0.041	0.102
Pine	1.266	**–0.237**	–0.071	**0.091**	–0.026	–0.252	–0.069	0.212	–0.154
Spruce	2.749	**0.083**	–0.12	0.064	**–0.091**	0.432	0.243	0.152	–0.1
Birch	1.327	–0.067	0.078	–0.022	**–0.081**	0.164	0.218	0.098	–0.185
Other tree species	1.079	0.038	0.017	**0.05**	**0.08**	0.151	0.114	0.094	0.072
Canopy coverage	3.248	**0.133**	**0.344**	0.003	0.028	0.294	0.464	0.119	0.062
Tree height	2.16	0.026	**0.144**	**–0.209**	**0.09**	–0.008	0.428	–0.023	0.221
Pine stumps	1.394	**–0.116**	0.049	**–0.177**	**0.07**	–0.325	0.022	–0.34	0.105
Spruce stumps	2.151	**0.131**	**–0.12**	–0.089	–0.006	0.411	–0.298	–0.142	–0.109
Dead pines	1.058	–0.021	–0.022	0	–0.004	0.01	0.018	–0.065	–0.004
Dead spruces	1.175	**0.143**	**–0.171**	**0.081**	**0.272**	0.356	–0.141	0.095	0.425
Logging waste	1.539	**0.129**	0.009	**–0.254**	–0.055	0.2	–0.243	–0.317	–0.129
Ant nests	1.044	–0.029	–0.047	0.004	–0.001	0.059	–0.067	0.004	–0.011
		AX 1	AX 2	AX 3	AX 4				
Eigenvalues		0.511	0.198	0.126	0.102				
Species-environment correlation		0.86	0.57	0.52	0.57				
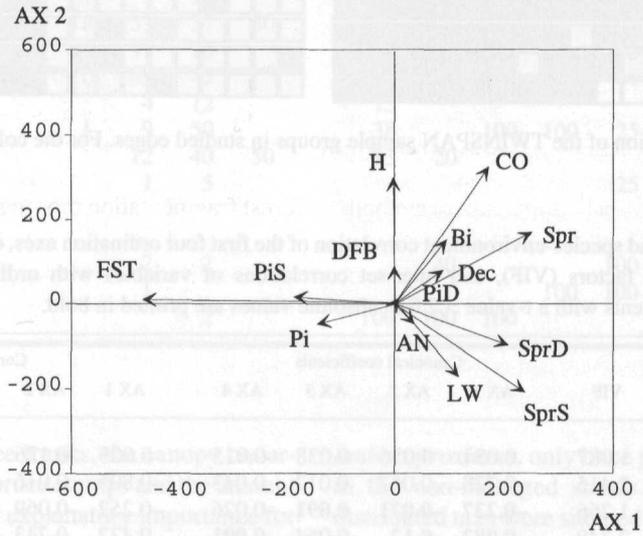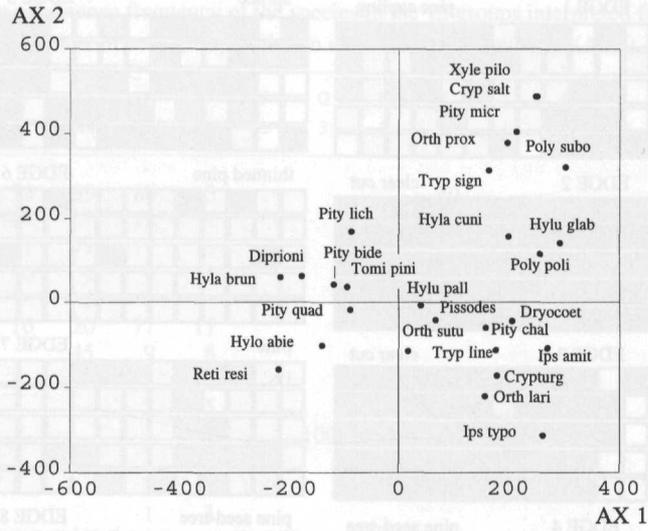
Fig. 5. Ordination diagram of species-environment relations based on canonical correspondence analysis. The environmental variables (arrows) are: distance from stand border (DFB), forest site type (FST), pines (Pi), spruces (Spr), birches (Bi), other deciduous trees (Dec), crown canopy coverage (CC), height of dominant trees (H), pine stumps (PiS), spruce stumps (SprS), dead pine trunks (PiD), dead spruce trunks (SprD), logging waste (LW) and ant nests (AN). For full names of the insect taxa, see the text. The lenghts of arrows have been divided by a factor of 10. Eigenvalues: axis 1: 0.511, axis 2: 0.198.

4 Discussion

This study revealed two distinct groups among the species: the species of shady spruce forests, and the species of clear cut areas. The two groups have different responses to the forest edge. The species of shady spruce forest (*Xylechinus pilosus, Cryphalus saltuarius* and *Polygraphus poligraphus*) withdrew 30–50 m from the stand edge to the forest interior. On the other hand, the species of clear cut areas or luminous pine forests (e.g. *Pityogenes chalcographus, P. quadridens, Pissodes* spp., *Hylurgops palliatus, Tomicus piniperda, Dryocoetes* spp. and *Trypodendron lineatum*) tended to spread from the recently cut sites at least 40 m into the non-managed spruce stands. Probably some species in the latter group were indifferent to the forest edges. However, the present analyses were not able to identify these species.

Previous studies have shown that there are clear differences in insect (Punttila et al. 1994, Haila et al. 1994) and spider (Pajunen et al. 1995) species assemblages between clear cuts and mature forests. Previously it has also been shown, that among breeding birds, there are both forest edge and interior favouring species (Kroodsma 1982, Helle 1985, see also Harris 1988). Forest fragmentation is evidently one reason for the decrease of old forest interior favouring bird species in northern Finland during the last few decades (Helle and Järvinen 1986). In our data, the insect species of shady spruce forests were proportionally less frequent than the species of clear cut areas, probably because the stand edges had reduced the share of forest interior habitats.

Forest edge affected the distribution of species only in the edges between mature, non-managed spruce stands and clear cuts or young seedling stands. We could not find such effect in luminous and recently thinned pine stands, where the edge contrast (Kotliar and Wiens 1990, Wiens et al. 1993) was weak and the microclimatical changes were not as significant as in the case of shady spruce stands. The species related to clear cut areas and pine stands are probably more generalized as to their habitat requirements than those living in shady spruce forests, which are more sensitive to environmental changes. This suggestion agrees with Halme and Niemelä (1993), who studied carabid beetles in fragmented forests. They found specialized species only in the interior of large forest fragments but the small forest fragments were inhabited only by the most generalized species.

The most important environmental variables explaining the occurrence of the observed species in the multivariate analysis were habitat type, canopy coverage and the amount of woody material at site. The occurrence of bark beetles is strongly dependent on the availability of their host trees and suitable breeding material (Rudinsky 1962, Lekander et al. 1977, Coulson 1979).

The forest edge clearly affected the species distribution, but the distance from stand border did not have any explanatory significance in the multivariate analysis. Edge effects do not necessarily vary monotonically with distance from the edge, but there may be, for instance, bimodal response patterns (Murcia 1995). Pooling the different edges and diffenrently responding species in the same data masked the importance of the distance variable in our analyses. This is not, however, in contradiction to our conclusion, that forest fragmentation thoroughly changes the distribution patterns of forest insect species.

In the present study, some of the species living in clear cut areas and pine dominated forests are potential or economically important forest pests, e.g. *Tomicus piniperda* (Långström and Hellqvist 1990). Forest edges may be attractive habitats for such harmful insects, and in this respect forest edges can have economical importance. Studies on the effect of forest edge on the distribution and impact of defoliating Lepidoptera (Bellinger et al. 1989, Roland 1992) support this conclusion.

Mathematical models have been designed for predicting the impacts of fragmentation and 'edge effects' (Patton 1975, Laurance 1991, Laurance and Yensen 1991, Malcolm 1994). The essential factors determing the total amount of habitat edge in a landscape matrix are the relation between fragment perimeter and area, and the width of the edge zone. The geometric shape with the greatest area and the least perimeter or edge is a circle. When the fragment size decreases and the geometric shape gets more complicated the share of edge increases. If we assume that edge pene-

trates 30 m (which seems to be realistic minimum edge width according to the present results) into the non-managed forest, in a square shaped 8 ha stand, 38 % of the total stand area is edge. Respectively, in a 4 ha square shaped stand, the share of edge is 51 % of the total stand area. In the southern Finnish managed forests, the shapes of the stands are far more complicated and irregular than circles or squares. The power of a particular 'edge effect' is dependent on several factors, such as edge contrast, disturbance history and orientation (Palik and Murphy 1990, Chen et al. 1992, Matlack 1993). Still, a managed forest landscape includes much more edge than one might generally expect, and the effect of habitat edges should be taken into consideration in practical nature conservation, forestry and landscape ecological planning.

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