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KARI HELIÖVAARA, RAUNO VÄISÄNEN & AULI IMMONEN

QUANTITATIVE BIOGEOGRAPHY OF THE BARK  
BEETLES (COLEOPTERA, SCOLYTIDAE)  
IN NORTHERN EUROPE

POHJOIS-EUROOPAN KAARNAKUORIAISTEN  
KVANTITATIIVINEN ELIÖMAANTIETEELLINEN  
ANALYYSI

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ACTA FORESTALIA FENNICA 219

## QUANTITATIVE BIOGEOGRAPHY OF THE BARK BEETLES (COLEOPTERA, SCOLYTIDAE) IN NORTHERN EUROPE

Pohjois-Euroopan kaarnakuoriaisten kvantitatiivinen eliömaantieteellinen  
analyysi

Kari Heliövaara, Rauno Väisänen & Auli Immonen

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Biogeographical patterns of the Scolytidae in Fennoscandia and Denmark, based on species incidence data from the approximately 70 km × 70 km quadrats (n = 221) used by Lekander et al. (1977), were classified and related to environmental variables using multivariate methods (two-way indicator species analysis, detrended correspondence analysis, canonical correspondence analysis). The distributional patterns of scolytid species composition showed similar features to earlier presented zonations based on vegetation composition. One major difference, however, was that the region was more clearly divided in an east-west direction. Temperature variables associated with the location of the quadrats had the highest canonical coefficient values on the first axis of the CCA. Although these variables were the most important determinants of the biogeographical variation in the beetle species assemblages, annual precipitation and the distribution of *Picea abies* also improved the fit of the species data. Samples with the most deviant rarity and typicalness indices for the scolytid species assemblages in each quadrat were concentrated in several southern Scandinavian quadrats, in some quadrats in northern Sweden, and especially on the Swedish islands (Öland, Gotland, Gotska Sandön) in the Baltic Sea. The use of rarity indices which do not take the number of species per quadrat into account, also resulted in high values for areas near Stockholm and Helsinki with well-known faunas. Methodological tests in which the real changes in the distribution of *Ips acuminatus* and *I. amitinus* were used as indicators showed that the currently available multivariate methods are sensitive to small faunal shifts even, and thus permit analysis of the fauna in relation to environmental changes. However, this requires more detailed monitoring of the species' distributions over longer time spans. Distributions of seven species (*Scolytus intricatus*, *S. laevis*, *Hylurgops glabratus*, *Crypturgus cinereus*, *Pityogenes saalasi*, *Ips typographus* and *Xyleborus dispar*) were predicted by logistic regression models using climatic variables. In spite of the deficiencies in the data and the environmental variables selected, the models were relatively good for several but not for all species. The potential effects of climate change on bark beetles are discussed.

Keywords: Scolytids, biogeography, insect pests, boreal forests, biodiversity, faunal changes, climate change, multivariate methods, logistic regression models.  
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Fennoskandiassa ja Tanskassa esiintyvien kaarnakuoriaisten 70 × 70 km:n ruutuihin perustuvia Lekanderin ym. (1977) tutkimuksessa julkaistuja levinneisyyskarttoja (n=221) luokiteltiin ja analysoitiin ympäristömuuttujiin suhteutettujen monimuuttujamenetelmien avulla (TWINSPAN, DCA, CCA). Kaarnakuoriaiset muodostivat aiemmin esitettyjä kasvillisuusvyöhykkeitä muistuttavia lajistollisia vyöhykkeitä, jotka kuitenkin olivat selvemmin jakaantuneet lohkoiksi itä-länsi-suunnassa. CCA:n ensimmäisen akselin keskeisiä muuttujia olivat lämpötilamuuttujat ja ruudun maantieteellinen sijainti. Ne olivat tärkeimpiä muuttujia selitettäessä kaarnakuoriaislajiston eliömaantieteellistä vaihtelua, mutta myös vuotuisella sademäärällä ja kuusen levinneisyydellä oli merkitystä. Ruutukohtaisesti lasketut harvinaisuus- ja tyypillisyyksindeksit osoittivat lajistollisesti poikkeavimpien näytteiden sijaitsevan useissa Skandinavian eteläosien ruuduissa, eräissä Pohjois-Ruotsin sekä erityisesti eräillä Itämeren saarilla (Öölanti, Gotland, Gotska Sandön). Indeksit osoittivat myös Tukholman ja Helsingin ympäristöjen hyvin tunnetut kaarnakuoriaislajistot poikkeaviksi, mikäli ruudussa todettujen lajien lukumäärää ei otettu huomioon. Okakaarnakuoriaisen ja kiiltokirjanpainajan levinneisyysalueissa tapahtuneiden muutosten huomioonottaminen lajiston luokittelussa osoitti käytetyt monimuuttujamenetelmät herkiksi varsinkin vähäisille lajistollisille muutoksille. Kvantitatiivisten menetelmien käyttö on siten mahdollista analysoitaessa ympäristön muutosten aiheuttamia lajiston muutoksia. Tämä kuitenkin edellyttää lajien levinneisyyksien yksityiskohtaista ja pitkäjänteistä seurantaa. Tammenmantokuoriaisen, 'jalavanmantokuoriaisen' (*Scolytus laevis*), kaljunilurin, himmeäkääpiökirjaajan, tunturitähtikirjaajan, kirjanpainajan ja lustokuoriaisen levinneisyydet ennustettiin logististen regressiomallien avulla käyttäen ilmastollisia muuttujia. Huolimatta aineiston ja valittujen ympäristömuuttujien puutteista mallit olivat suhteellisen hyviä useille mutteivät kaikille lajeille. Ilmaston muutoksen mahdollisia vaikutuksia kaarnakuoriaisiin pohditaan.

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## Contents

1. INTRODUCTION .....	5
2. MATERIAL AND METHODS .....	6
21. Data .....	6
22. Classification and ordination .....	6
23. Rarity indices .....	7
24. Typicalness measurements .....	7
25. Polynomial regression analysis .....	7
26. Sensitivity of the multivariate methods .....	7
27. Logistic models .....	9
3. RESULTS .....	10
31. Biogeographical species grouping .....	10
32. Regional division .....	11
33. Environmental variation and species assemblages .....	15
34. Distribution of individual species .....	17
35. Rarity and typicalness .....	21
36. The effect of faunal change .....	24
4. DISCUSSION .....	27
41. The potential and constraints of the quantitative approach .....	27
42. Biogeographical classification of Fennoscandia and Denmark on the basis of bark beetles .....	27
43. Climate and bark beetle biogeography .....	28
44. Distribution of rarity and typicalness .....	31
5. CONCLUSIONS .....	32
REFERENCES .....	33
PÄÄTELMÄT .....	35

## Preface

Bark beetles (Scolytidae) are an insect group that is known to play a considerable role in boreal forest dynamics. They form a relatively coherent group of herbivorous insects. Some species (e.g. *Ips typographus*, *Tomicus piniperda*, *Trypodendron lineatum*) cause considerable economic losses in northern Europe. Although not all species of bark beetles have a pest status, it is difficult to predict which species are of potential economic significance in forest ecosystems modified by pollution, climate change and silvicultural techniques.

We try to summarize the biogeography of the bark beetles in northern Europe, and provide basic quantitative information on the family both for foresters and ecologists. We also hope that this work will remind forest researchers about the role of bark beetles and other forest insects during environmental changes. One alarming

aspect is that the abundance and high reproductive capacity of bark beetles may enable them to adapt more rapidly to new conditions than their host trees.

The present paper is a joint investigation carried out at the Finnish Forest Research Institute and the Water and Environment Research Institute (Nature Conservation). We are grateful to Professor E. Annala, Mr. J. Derome, Mr. B. Ehnström, Mr. I. Mannerkoski and two anonymous referees for commenting on the manuscript.

Vantaa, 11 March 1991

*Kari Heliövaara, Rauno Väisänen, Auli Immonen*

## 1. Introduction

Bark beetles (Scolytidae) are distributed worldwide and form many cosmopolitan genera. Scolytids occupy a wide range of niches on woody and herbaceous plants. Several species attack living trees when outbreaks occur and others bring about timber degradation by excavating galleries deep into the wood or by acting as vectors of blue stain fungi and diseases. Reliable information about the general distribution of bark beetles in northern Europe has long been available and maps for all 86 species recorded in Denmark and Fennoscandia have been published by Lekander et al. (1977).

Multivariate analysis techniques such as detrended correspondence analysis (DCA) have been used to determine the dominant pattern in community composition variation through ordination of the species data (Hill & Gauch 1980, Gauch 1982). Canonical correspondence analysis (CCA) has recently been developed to relate community composition directly to measured variation in environment (Ter Braak 1985b, 1986). Gradient analysis of this type can be applied to biogeographical data (Peet 1978, Luff et al. 1989, Eyre et al. 1990, Allen et al. 1991). The suitability of these analyses for provincial incidence data of some northern European insects has been tested in another article which shows that large areas can be covered by such analyses (Väisänen et al., in press). Quantitative indices of rarity and typicalness for certain sites have recently been developed (Dony & Denholm 1985, Minns 1987, Eyre & Rushton 1989). Multiple regression analysis has provided a useful approach in analysing species density gradients (Willig & Selcer 1989).

In the present study, these techniques are applied to incidence data of northern European bark beetles. The study area covers Fennoscandia (i.e. Norway, Sweden, Finland and some western parts of the U.S.S.R) and Denmark. The distribution of Scolytidae in this area is well documented as a result of their significance as forest pests. The distribution and abundance of bark beetles also change as a result of forest management and other environmental changes. The distribution of species has earlier been explained by factors such as climate, and the distribution, frequency and immigration history of the host trees (e.g. Lekander et al. 1977), but no quantitative biogeographical analyses have been presented.

Relatively large temperature increases are projected in temperate and arctic areas (e.g. Jäger 1990, Brouwer & Falkenmark 1990), and are expected to cause pronounced large-scale geographic shifts in species' ranges, changes in the species composition of biological communities and the extinction of certain species (Peters 1990). There has been a very gradual change in climate since the last ice age about 10 000 years ago, and organisms have had plenty of time to adapt to the new conditions. A climatic change of similar magnitude may now take place in perhaps two forest tree generations, leaving only limited time for genetic adaptation (Dahl 1990). The effect of higher winter temperatures will tend to be more pronounced in trees with an oceanic distribution like *Ulmus glabra* than in trees like *Picea abies* (Skre 1990).

The large fluctuation in minimum and maximum temperatures, the short growing season and the extreme cold during winter are factors limiting survival and growth in the region adjoining the northern timberline. Even without any human impact, summers in northern Fennoscandia have been characterized during the last millennium by alternating periods of generally cool and generally warm conditions (Briffa et al. 1990). Faunal analyses have shown, for instance, that the phases of extension and abundance in moth and butterfly fauna and other insects correspond accurately to the periods of warm summers (Kaisila 1962). However, it is possible that changes in moth and butterfly fauna are more abrupt than those in bark beetles. Logistic regression models provide one opportunity to predict distributions of species in relation to environmental variables and their changes.

Quantitative biogeographical information is a prerequisite of detecting and monitoring faunal changes effectively. This is one reason why the distribution of bark beetles in northern Europe is here quantitatively analysed. An attempt is made to identify biogeographical patterns by ordinating species and quadrats on the basis of these data and by relating them to some environmental variables. Regional comparison of the fauna may throw light on the local risk of pest damage. The analyses may also reveal areas of special entomological importance characterized by rare and non-typical fauna.

## 2. Material and methods

### 21. Data

The distribution maps of northern European bark beetles were obtained from volume 32 of *Acta Entomologica Fennica* (Lekander et al. 1977). These presence/absence data were used without taking species abundance into account. The study area was divided into 221 quadrats of approximately 70 × 70 km<sup>2</sup> according to Lekander et al. (1977). The number of species analysed was 86. The number of species per quadrat varied from 1 to 53 (Figs. 1 and 2) and the mean number was 21.9 (standard deviation 12.4) species per quadrat. The numbers of species per quadrat given by Lekander et al. (1977: map 2) differ considerably from those calculated directly from the species maps of the same paper. The latter numbers were used in the present analyses.

Abbreviated codes consisting of the first four letters of the generic name and four of the species name used by Lekander et al. (1977) are used in the figures of the present paper. The full names and the valid species names (see Silfverberg 1979) are given in full form in Table 1.

### 22. Classification and ordination

The major statistical programs used in the analyses were TWINSpan (Hill 1979a), DECORANA (Hill 1979b) and CANOCO (Ter Braak 1985a). In the two-way indicator species analyses the number of indicators was 13. The maximum level of divisions was 5, but the species were

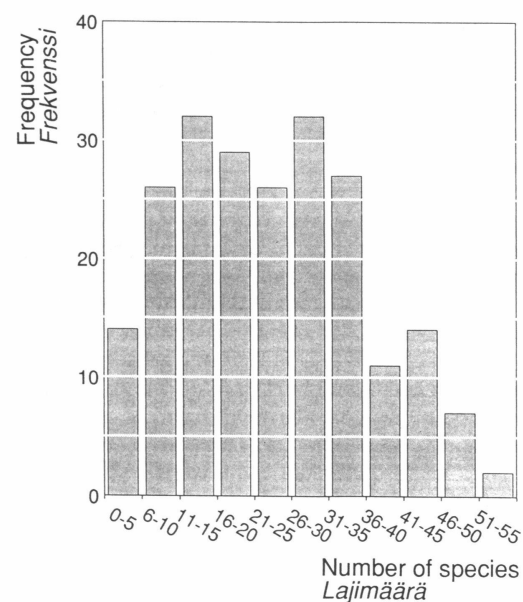


Fig. 1. Frequency distribution of bark beetle species per quadrat.  
Kuva 1. Kaarnakuoriaislajien esiintymisfrekvenssi ruudittain.

regrouped using four division levels in the final tabulation. Detrending by second-order polynomials was used in the DCAs. In the weighted averaging methods (DCA, CCA), the eigenvalue is a measure of the separation of the species' distributions along the ordination axis.

The following environmental variables were used in the CCAs:

- latitude (LAT) and longitude (LON);
- beginning of vegetative period (BVP), transformed to sea level in 1921–1950, and effective temperature sum of vegetative period (in ddu) (ETS) when absolute altitude has been taken into account (data derived from Laaksonen 1979);
- annual precipitation (PRE) using the scale: 1 = <500 mm, 2 = 500–600, 3 = 600–1000, 4 = 1000–2000 and 5 = >2000 mm (data from Hultén 1950), 0.5 was added to the lower value in borderline cases;
- vegetation zones (VEG): 1 = atlantic, 2 = subatlantic, 3 = hemiboreal, 4 = south-boreal, 5 = mid-boreal, 6 = north-boreal and 7 = arctic-alpine (data from Kalliola 1973);
- distribution of *Picea abies* (L.) Karst. (PIC) and *Pinus sylvestris* L. (PIN) using the scale: 0 = missing, 1 = scattered, 2 = intermediate and 3 = continuous (data from Hultén 1950).

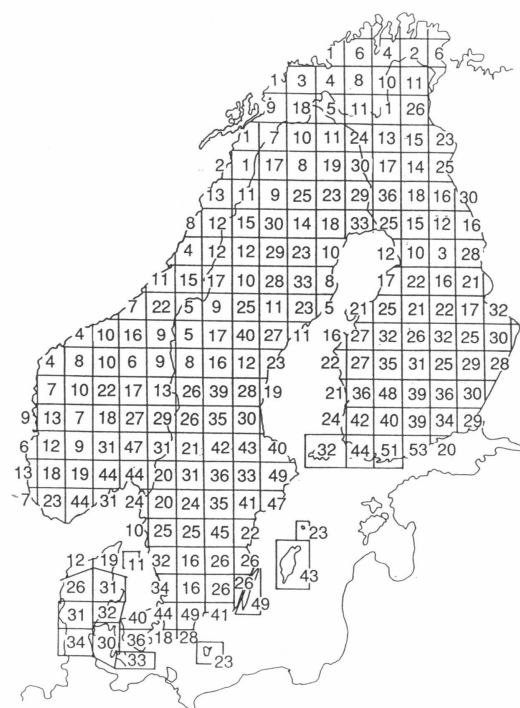


Fig. 2. Number of bark beetle species recorded in the quadrats according to the distribution maps 5–78 in Lekander et al. (1977).

Kuva 2. Lekander et al.:n (1977) levinneisyyskarttojen 5–78 perusteella lasketut ruudittaiset kaarnakuoriaisten lajimäärät.

Values for the variables PIC and PIN were determined according to the general distribution of these trees in a given quadrat, while the values of the other variables represent the mid-point ones. Comparing the arrow lengths in the CCA ordination diagrams indicates the importance of the environmental variables in question. The arrow roughly points in the direction of maximum variation of the corresponding variable. Monte Carlo permutation tests of the CCA were carried out by randomly permutating the sample numbers in the environmental data. If the observed value is among the 5% highest values, then the species are significantly related to the environmental variables. The first eigenvalue was used as test statistic.

The canonical coefficients in the CCA are the coefficients of a weighted multiple regression of the sample scores on the standardized environmental variables. The Student t-test is not appropriate for tests of significance of canonical coefficients. However, when the t-value of a variable is less than 2.1 in absolute terms, the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis. In such case the variable does not have an effect that is uniquely attributable to the specific variable and can be deleted without having any marked effect on the canonical eigenvalues (Ter Braak 1987).

The inter-set correlations of the environmental variables with the CCA axes are the correlation coefficients between the environmental variables and the species axes consisting of the sample scores. They do not become unstable when the environmental variables are intercorrelated. The fraction of total variance in the standardized environmental data that is extracted by each species axis is equal to the mean squared inter-set correlation. If the variance inflation factor (VIF) of a variable is large (>20), the variable is highly correlated with the other variables and therefore has no unique contribution to the regression equation. As a consequence its canonical coefficient is unstable and does not merit interpretation (Ter Braak 1986).

### 23. Rarity

Rarity indices were calculated using a three-step procedure as described by Eyre & Rushton (1989). Two scales of rarity based on the canonical (geometric) system were used. The indices were as follows:

- beetle rarity total (BRT): Species recorded in 1, 2–3, 4–7, 8–15, 16–31, 32–63, and 64 and more quadrats were given scores (Q) 7 to 1, respectively. A site score was the sum of the scores for each species:

$$BRT_i = \sum_{j=1}^m S_{ij} Q_j$$

where m = number of species,  $S_{ij}$  = presence (1) or absence (0) of species j at site i, and  $Q_j$  = conservation priority of species j;

- species rarity total (SRT): The scale was similar to that of BRT, except that scores corresponding to the number of quadrats counted were geometric values 64, 32, 16, 8, 4, 2 and 1, instead of 7 to 1. The index was the sum of these scores;
- rarity association total (RAT): This index was calculated in order to identify quadrats with several rare species. A value for a site was calculated using species that scored 2 or more in the geometric scale. The

highest score was reduced to that of the nearest score in order to eliminate bias caused by one very rare species in a list, where one score was far greater than the others (see Eyre & Rushton 1989). Thus, if a species list contained scores 64, 16, 8, 4, 2, 1 and 1, the 64 score would be reduced to 16 and all the scores of 2 or more would be summed. Finally, this score was added to the SRT to give the RAT index;

- beetle quality factor (BQF) was obtained by dividing BRT by the number of species in the quadrat;
- species quality factor (SQF) was obtained by dividing SRT by the number of species in the quadrat;
- rarity quality factor (RQF) was obtained by dividing RAT by the number of species in the quadrat.

The correlations between the first four canonical axes and the rarity indices were also calculated.

### 24. Typicalness

Typicalness indices were calculated using means and standard deviations of site ordination scores generated from an analysis of all the data (DCA) (cf. Eyre & Rushton 1989). The coordinates of each quadrat calculated in standard deviations of the ordination score for DCA axes 1 (TYP1) and 2 (TYP2) were interpreted as typicalness measurements. High absolute values of the measurements indicate deviant bark beetle fauna.

### 25. Polynomial regression analysis

Polynomial regression analysis was performed using the P5R BMDP program (Dixon & Braun 1979) in order to identify the strongest statistical relationship between bark beetle species richness and latitude from the multiple regressions (see Willig & Selcer 1989). In addition, the further statistical and appreciable criteria used for another polynomial model were that it was a statistical improvement over lower degree polynomials, and the next higher polynomial, if significant, must increase  $r^2$  by less than 0.05.

### 26. Sensitivity of the multivariate methods

In order to test the sensitivity of the multivariate methods to changes in the species distribution, the Finnish material was analysed using two different data sets. Two changes in species' ranges have been well documented during recent decades. *Ips amitinus* has expanded from the south-east to the north-west (Koponen 1975). During the same period, the range of *Ips acuminatus* has retracted northwards so that the species is today missing from southern Finland (Puukko 1981). *Ips sexdentatus* has also retracted to north both in Sweden (Lekander et al. 1977) and Finland (Löyttyniemi 1975), but the data are not accurate enough to permit quantitative analysis. First, we used a data set corresponding to the situation prior to these changes. Second, we used a data set corresponding to the situation after these documented changes. This analysis was performed only to test the sensitivity of the methods and it does not cover all faunal changes. However, it illustrates the effect of a realistic change in scale on the results obtained using these methods. Both the number of indicators and the maximum level of divisions was 4 in the TWINSpan.

Table 1. The percentage occurrence frequency of the scolytid species in the eight groups interpreted from the TWINSPAN analysis. Species order is as given by the TWINSPAN. Values greater than 70 are in bold type. The number of quadrats in each group is shown in parentheses.  
Taulukko 1. Kaarnakuoriaislajien esiintymisfrekvenssi TWINSPAN-analyysin ruuturyhmissä ohjelman antamassa järjestyksessä. Yli 70 %:n osuudet on lihavoitu. Ruutujen lukumäärä kussakin ryhmässä on esitetty sulkeissa.

Species	Quadrat group							
	1 (16)	2 (29)	3 (9)	4 (15)	5 (37)	6 (41)	7 (73)	8 (1)
<i>Xyleborus saxeseni</i> (Ratzeburg, 1837)	62	3	—	—	—	—	—	—
<i>Xyleborus monographus</i> (Fabricius, 1792)	12	7	—	—	—	—	—	—
<i>Dryocoetes villosus</i> (Fabricius, 1792)	<b>81</b>	31	33	—	—	—	—	—
<i>Phloeotribus rhododactylus</i> (Marshall, 1802) (= <i>Phloeophthorus rhododactylus</i> )	31	3	—	—	—	—	—	—
<i>Taphrorychus bicolor</i> (Herbst, 1793)	56	14	22	7	—	—	—	—
<i>Ernoporus fagi</i> (Fabricius, 1798)	62	3	—	—	—	—	—	—
<i>Hylastes ater</i> (Fabricius, 1792)	62	3	—	—	—	—	—	—
<i>Hylastes angustatus</i> (Herbst, 1793)	6	—	—	—	—	—	—	—
<i>Hylastinus obscurus</i> (Marshall, 1802)	19	3	—	—	—	—	—	—
<i>Hylurgus ligniperda</i> (Fabricius, 1787)	12	3	—	—	—	—	—	—
<i>Hylesinus oleiperda</i> (Fabricius, 1792)	56	14	33	—	—	—	—	—
<i>Scolytus scolytus</i> (Fabricius, 1775)	31	7	22	7	3	—	—	—
<i>Scolytus mali</i> (Bechstein & Scharfenberg, 1805)	50	7	33	13	—	—	—	—
<i>Scolytus laevis</i> Chapuis, 1873	<b>81</b>	10	44	7	—	—	3	—
<i>Scolytus pygmaeus</i> (Fabricius, 1787)	6	—	—	—	—	—	—	—
<i>Pityogenes trepanatus</i> (Nördlinger, 1848)	31	24	—	20	—	2	—	—
<i>Pityogenes monacensis</i> Fuchs, 1911	—	3	—	—	—	—	—	—
<i>Pityophthorus pubescens</i> (Marshall, 1802)	12	17	11	—	—	—	—	—
<i>Trypophloeus grothi</i> (Hagedorn, 1904)	19	7	—	—	—	—	—	—
<i>Hylesinus varius</i> (Fabricius, 1775) (= <i>Hylesinus orni</i> )	25	14	33	7	—	—	—	—
<i>Hylesinus fraxini</i> (Panzer, 1799)	<b>94</b>	69	<b>89</b>	40	—	—	3	—
<i>Scolytus carpini</i> (Ratzeburg, 1837)	6	3	—	—	—	—	—	—
<i>Pityophthorus glabratus</i> Eichhoff, 1879	25	7	33	13	3	—	—	—
<i>Lymantor coryli</i> (Perris, 1855)	37	14	67	7	3	—	—	—
<i>Ernoporus caucasicus</i> Lindemann, 1876	12	10	33	13	—	—	—	—
<i>Cryphalus abietis</i> (Ratzeburg, 1837)	<b>94</b>	55	<b>89</b>	67	3	5	—	—
<i>Hylastes attenuatus</i> Erichson, 1836	6	10	33	—	—	—	—	—
<i>Hylesinus crenatus</i> (Fabricius, 1787)	<b>75</b>	55	<b>89</b>	47	—	—	1	—
<i>Scolytus rugulosus</i> (Ratzeburg, 1837)	<b>81</b>	34	55	47	—	—	—	—
<i>Scolytus intricatus</i> (Ratzeburg, 1837)	<b>87</b>	55	<b>89</b>	40	—	2	—	—
<i>Xyleporus cryptographus</i> (Ratzeburg, 1837)	6	17	<b>78</b>	27	3	—	—	—
<i>Ernoporus tiliae</i> (Panzer, 1793)	18	17	<b>89</b>	33	3	—	—	—
<i>Scolytus multistriatus</i> (Marshall, 1802)	—	3	33	—	—	—	—	—
<i>Xyleborus dispar</i> (Fabricius, 1792)	<b>87</b>	65	<b>78</b>	67	51	—	—	—
<i>Orthotomicus longicollis</i> (Gyllenhal, 1827)	6	7	—	7	3	—	—	—
<i>Trypodendron domesticum</i> (Linnaeus, 1758)	<b>81</b>	65	<b>89</b>	<b>93</b>	8	17	8	—
<i>Hylastes opacus</i> Erichson, 1836	<b>81</b>	65	<b>100</b>	<b>73</b>	62	2	—	—
<i>Trypophloeus discedens</i> Palm, 1950 (= <i>Trypophloeus palmi</i> )	—	10	33	40	8	2	3	—
<i>Trypophloeus asperatus</i> (Gyllenhal, 1813)	6	21	55	40	5	5	1	—
<i>Trypodendron piceum</i> Strand, 1946	—	—	44	33	—	7	1	—
<i>Trypophloeus bispinulus</i> Eggers, 1927	—	3	55	67	24	10	—	—
<i>Crypturgus cinereus</i> (Herbst, 1793)	6	21	<b>89</b>	<b>80</b>	40	19	3	—
<i>Crypturgus subcribrosus</i> Eggers, 1933	56	14	<b>78</b>	67	38	17	3	—
<i>Orthotomicus laricis</i> (Fabricius, 1792)	69	65	<b>100</b>	<b>93</b>	<b>81</b>	39	5	—
<i>Crypturgus pusillus</i> (Gyllenhal, 1813)	<b>75</b>	52	<b>100</b>	<b>100</b>	<b>92</b>	22	4	—
<i>Dendroctonus micans</i> (Kugelann, 1794)	<b>94</b>	41	22	<b>100</b>	35	41	11	—
<i>Orthotomicus suturalis</i> (Gyllenhal, 1827)	<b>87</b>	59	<b>78</b>	<b>80</b>	<b>78</b>	63	10	—
<i>Crypturgus hispidulus</i> Thomson, 1870	44	38	<b>89</b>	<b>80</b>	68	51	5	—
<i>Polygraphus poligraphus</i> (Linnaeus, 1758)	<b>94</b>	48	<b>100</b>	<b>93</b>	62	66	14	—
<i>Dryocoetes alni</i> (Georg, 1856)	69	52	67	<b>80</b>	<b>78</b>	37	18	—

Species	Quadrat group							
	1 (16)	2 (29)	3 (9)	4 (15)	5 (37)	6 (41)	7 (73)	8 (1)
<i>Phloeotribus spinulosus</i> (Rey, 1883) (= <i>Phthorophloeus spinulosus</i> )	44	59	<b>89</b>	<b>100</b>	51	<b>76</b>	25	—
<i>Hylastes cunicularis</i> Erichson, 1836	<b>94</b>	<b>83</b>	<b>100</b>	<b>100</b>	<b>95</b>	<b>76</b>	26	—
<i>Tomicus minor</i> (Hartig, 1834) (= <i>Blastophagus minor</i> )	31	<b>76</b>	<b>100</b>	<b>100</b>	62	56	27	—
<i>Scolytus ratzeburgi</i> Janson, 1856	50	69	<b>100</b>	<b>100</b>	<b>86</b>	49	19	—
<i>Orthotomicus proximus</i> (Eichhoff, 1868)	31	69	<b>100</b>	<b>93</b>	<b>95</b>	63	15	—
<i>Ips sexdentatus</i> (Börner, 1776)	6	17	<b>78</b>	<b>93</b>	40	51	23	—
<i>Pityophthorus micrographus</i> (Linnaeus, 1758)	19	24	<b>100</b>	<b>100</b>	54	63	11	—
<i>Pityophthorus lichtensteini</i> (Ratzeburg, 1837)	19	14	55	<b>80</b>	40	29	14	—
<i>Trypodendron signatum</i> (Fabricius, 1787)	25	7	22	67	65	22	10	<b>100</b>
<i>Ips typographus</i> (Linnaeus, 1758)	<b>81</b>	65	<b>100</b>	<b>100</b>	<b>100</b>	<b>90</b>	45	—
<i>Pityogenes chalcographus</i> (Linnaeus, 1761)	<b>94</b>	<b>86</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>98</b>	51	—
<i>Pityogenes bidentatus</i> (Herbst, 1783)	<b>94</b>	<b>76</b>	<b>100</b>	<b>93</b>	<b>95</b>	<b>71</b>	42	—
<i>Trypodendron lineatum</i> (Olivier, 1795)	<b>94</b>	<b>83</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>76</b>	41	—
<i>Dryocoetes autographus</i> (Ratzeburg, 1837)	<b>100</b>	<b>83</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>90</b>	38	—
<i>Hylurgops palliatus</i> (Gyllenhal, 1813)	<b>100</b>	<b>90</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>76</b>	53	—
<i>Hylastes brunneus</i> Erichson, 1836	<b>100</b>	<b>90</b>	<b>100</b>	<b>100</b>	<b>97</b>	<b>78</b>	67	—
<i>Pityogenes quadridens</i> (Hartig, 1834)	44	<b>93</b>	<b>100</b>	<b>100</b>	<b>95</b>	<b>76</b>	56	—
<i>Tomicus piniperda</i> (Linnaeus, 1758) (= <i>Blastophagus piniperda</i> )	<b>94</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>90</b>	<b>85</b>	—
<i>Ips acuminatus</i> (Gyllenhal, 1827)	19	31	67	<b>93</b>	<b>89</b>	<b>83</b>	<b>77</b>	—
<i>Pityogenes saalasi</i> Eggers, 1914	—	—	—	—	3	17	3	—
<i>Pityogenes irkutensis</i> Eggers, 1910	—	—	—	7	5	12	5	—
<i>Carphoborus teplouchovi</i> Spessivtsev, 1916	—	—	—	—	—	2	1	—
<i>Pityophthorus morosovi</i> Spessivtseff, 1926	—	—	—	—	—	2	—	—
<i>Carphoborus minimus</i> (Fabricius, 1798)	—	—	—	—	3	—	—	—
<i>Carphoborus choldkovskiyi</i> Spessivtsev, 1916	—	—	—	—	—	15	—	—
<i>Dryocoetes hectographus</i> Reitter, 1913	6	28	<b>78</b>	<b>80</b>	<b>89</b>	66	15	—
<i>Cryphalus saltuarius</i> Weise, 1891	—	7	33	60	40	58	8	—
<i>Polygraphus subopacus</i> Thomson, 1871	—	3	33	53	43	58	7	—
<i>Polygraphus punctifrons</i> Thomson, 1886	—	—	33	<b>80</b>	59	<b>73</b>	14	—
<i>Hylurgops glabratus</i> (Zetterstedt, 1828)	—	10	44	<b>73</b>	<b>78</b>	<b>90</b>	23	—
<i>Xylechinus pilosus</i> (Ratzeburg, 1837)	31	3	—	<b>73</b>	49	46	12	—
<i>Ips amitinus</i> (Eichhoff, 1872)	—	7	—	40	54	—	—	—
<i>Trypophloeus alni</i> (Lindemann, 1875)	—	—	11	—	8	—	1	—
<i>Carphoborus rossicus</i> Semenov, 1902	—	—	—	13	19	12	—	—
<i>Ips duplicatus</i> (Sahlberg, 1836)	—	7	33	<b>87</b>	<b>70</b>	7	3	—
<i>Pityophthorus traegardhi</i> Spessivtseff, 1921	—	3	11	40	5	2	3	—

## 27. Logistic models

The distributions of seven individual species representing different distributional patterns in the area (see Table 4) were predicted by logistic regression models (stepwise logistic regression computer program, BMDPLR, Engelman 1988; see also Häkkinen & Linnilä 1987) using precipitation, beginning of the vegetative period and effective temperature sum, as well as the first four canonical axes of the CCA that included all species and environmental variables. This was done in order to determine the significance of the present environmental variables in the geographical distribution of the selected species. The model for three variables is as shown below:

$$W = \log \frac{P}{1-P} = a + bx_1 + cx_2 + dx_3$$

The log odds W is an increasing function of P and is equal to 0 for P = 0.5. Logistic regression assumes that W is a linear function of the covariates and estimates the coefficients of the linear function by maximum likelihood. The Hosmer-Lemeshow goodness of fit chi-square test divides the data into 10 cells and compares the observed and predicted frequencies for these cells. The cells are defined using the predicted frequencies.

### 3. Results

#### 31. Biogeographical species grouping

The species were classified into 16 groups according to their distribution given by TWINSPAN (Fig. 3). Species occurring to the south of latitude 62° were grouped into the two uppermost branches. The only exceptions were *Hylesinus fraxini* (recorded in one quadrat in northern Sweden) and *Cryphalus abietis* (recorded in one quadrat in northern Finland and from two quadrats in Central Norway). The third branch consisted of species with a southwestern distribution (*Xyleborus dispar*, *Orthotomicus*

*longicollis*, *Trypodendron domesticum*, *Hylastes opacus*) and the fourth of species with a more or less western distribution (*Trypophloeus palmi*, *T. asperatus*, *Trypodendron piceum*).

Species occurring to the north of latitude 60° were grouped into the lower main branch. The only exceptions in this group were *Dryocoetes hectographus* and *Xylechinus pilosus* with a few additional recordings in the southern quadrats. *Ips sexdentatus* was grouped separately from other species with a northern distribution. The species clearly restricted to coastal areas in northern Europe (*Pityogenes trepanatus*, *Pityo-*

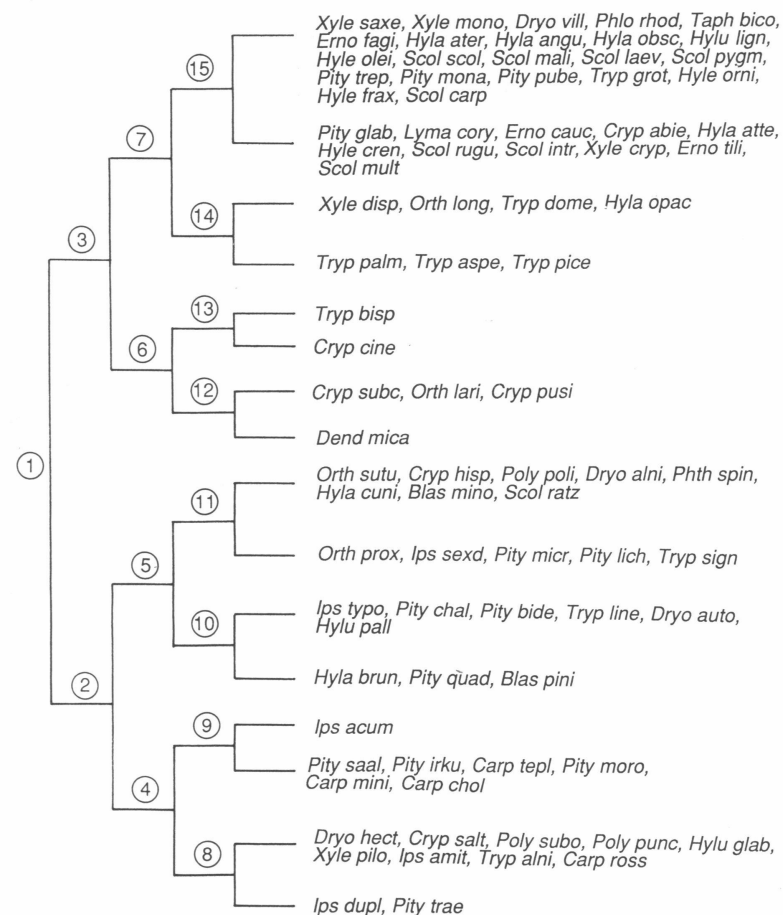


Fig. 3. A species dendrogram of a two-way indicator species analysis (TWINSPAN). The order of divisions is indicated by encircled numbers.  
 Kuva 3. Kaarnakuoriaislajien TWINSPAN-luokittelu. Jaon järjestyksenumeron merkityy ympyröitynä.

*phthorus glabratus*, *P. pubescens*) did not form a distinct group, but were classified together with other southern species.

The primary division was also associated with the total ranges of the species. Species with a Holarctic distribution were classified into the upper main branch (exception *Trypodendron lineatum*). Species with only European distribution records tended to occur in the upper main branch (exceptions *Pityophthorus lichtensteini*, *Hylastes brunneus*, *Pityogenes quadridens* and *Hylurgops glabratus*), while species with a known Eurosiberian distribution were more randomly distributed.

The primary division among the species was associated with the host tree distribution. All beetle species associated with deciduous trees with a southern distribution such as *Quercus*, *Fraxinus*, *Tilia*, *Fagus* etc. and some fruit trees were classified into the upper main branch. Species associated with *Alnus* (*Dryocoetes alni* and *Trypophloeus alni*), as well as species associated with *Betula* (*Scolytus ratzeburgi* and *Trypodendron signatum*), were classified in the lower branch of the first division together with most of the species associated with coniferous trees. It is noteworthy that *Ips duplicatus* and *Pityophthorus traegardhi* which have similar living habits (both attack withering but standing spruces), were classified in the same group.

The primary division is to some degree related to the duration of the life cycle and swarming period. Almost all species classified in the upper branch of the first division have a life-cycle of one year or shorter (exceptions: *Hylesinus oleiperda* and *Dendroctonus micans*), while 10 out of 12 species whose life-cycle is known (*Dryocoetes alni*, *Phloeotribus spinulosus*, *Hylastes cunicularis*, *Pityophthorus micrographus*, *Dryocoetes autographus*, *Hylastes brunneus*, *Carphoborus cholodkovskiyi*, *Cryphalus saltuarius*, *Hylurgops glabratus* and *Pityophthorus traegardhi*) in the lower main branch have a life-cycle of two years or longer. Late-swarming species are more numerous in the lower main branch: ten species out of 33 whose swarming time is known swarm in June-August (*Polygraphus poligraphus*, *Scolytus ratzeburgi*, *Pityophthorus micrographus*, *Dryocoetes autographus*, *Carphoborus cholodkovskiyi*, *Dryocoetes hectographus*, *Polygraphus subopacus*, *P. punctifrons*, *Hylurgops glabratus* and *Trypophloeus alni*), while only three out of 22 late-swarming species (*Scolytus mali*, *S. rugulosus* and *Trypophloeus asperatus*) occurred in the upper main branch. However, the biology of

several of these species is poorly known.

Bark beetles are known to form specific associations with each other. 26 different associations were interpreted from the source literature (Lekander et al. 1977), but the dendrogram could not be related to these associations. Only four of the associations occurred within the groups of the fourth division, and five within those of the third division.

#### 32. Regional division

A dendrogram showing the eight quadrat groups, as interpreted from TWINSPAN analysis of the scolytid data, is shown in Fig. 4. The number of quadrats in group 8 was only 1, while it varied between 9 and 73 in the others. The number of borderline and mis-classified quadrats was as high as 13 in the case of groups 5 and 6. The left branch of the primary division was characterized by *Hylesinus fraxini*, *Scolytus intricatus*, *Cryphalus abietis*, *Hylesinus crenatus*, *Trypodendron domesticum* and *Hylastes opacus*.

A map based on this TWINSPAN classification is shown in Fig. 5. Most of Denmark, southernmost Sweden (Scania) and Öland formed a group with a sister group in southern Sweden and Norway. Small areas in southern Finland, southeastern Sweden and Norway also formed a group. One group was concentrated in southern and Central Finland with a few quadrats in Central Sweden and southern Norway. Its sister group covered areas in northern Finland and Sweden and a few quadrats in Central Norway. The most scattered group occurred in Central Sweden and Norway, but one quadrat in southern Sweden also belonged to this group. Its sister group consisted of only one quadrat on the northwestern coast of Norway.

The frequency of occurrence of species in the quadrat groups interpreted from the TWINSPAN is shown in Table 1. Only one species (*Trypodendron signatum*) occurred in all eight quadrat groups, but 30 species were recorded in seven of the groups. The species richness was much higher in the first four groups representing the southern quadrats than in the others. *Tomicus piniperda* (*Blas pini*) was the only species whose frequency exceeded 70 % of the quadrats in every group where the species was recorded. 21 species occurred in at least one group in every quadrat, and three species (*Dryocoetes autographus*, *Hylurgops palliatus*, *Tomicus piniperda*) were recorded in every quadrat in four different groups. Seven species (*Carphoborus cholodkovskiyi*, *C.*

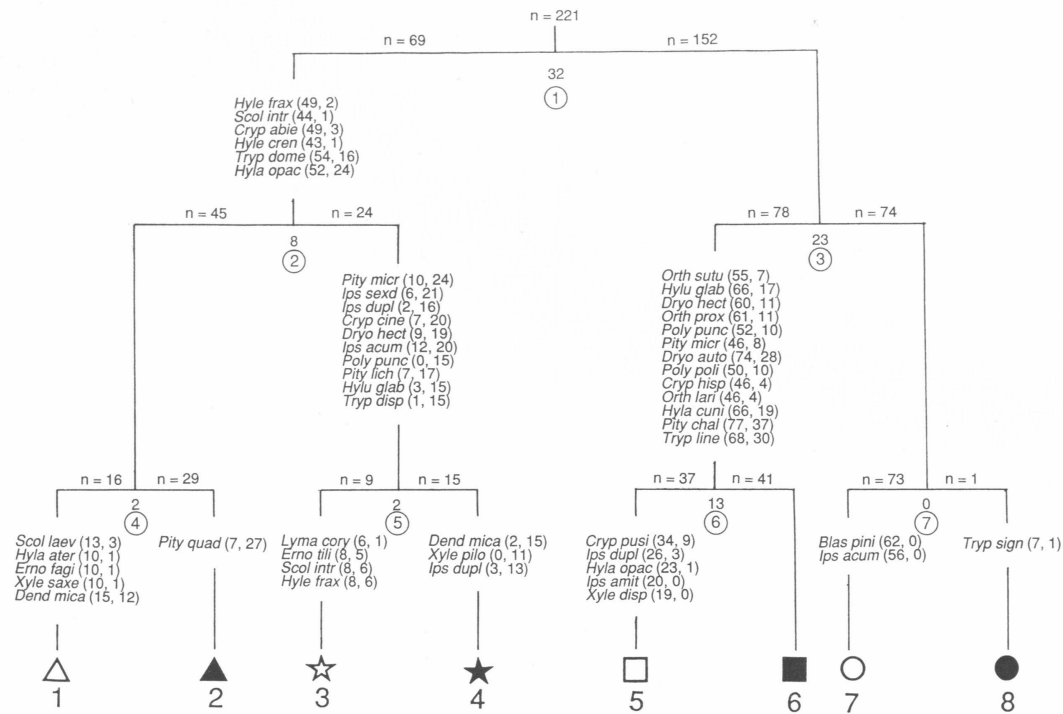
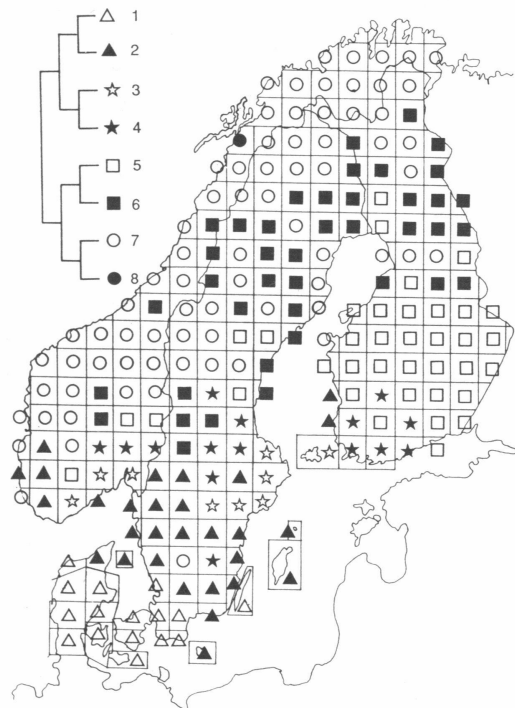


Fig. 4. A quadrat dendrogram of a two-way indicator species analysis (TWINSPAN) using the Scolytidae data. Numbers in parentheses are the frequencies of each species in the left and right hand cluster, respectively. The number of 'borderline and misclassified plots' is indicated at each division. The order of divisions is indicated by encircled numbers.

Kuva 4. Ruutujen TWINSPAN-luokittelu. Sulkeissa olevat numerot tarkoittavat lajin esiintymisfrekvenssiä jaossa syntyneissä ryhmissä. Vaikeasti luokiteltavien rajatapausten määrä on merkitty haaraumiin ja jaon järjestysnumero ympyröitynä näiden alle.



*minimus*, *Pityophthorus morosovi*, *C. teplouchovi*, *Hylastes angustatus*, *Scolytus pygmaeus* and *Pityogenes monacensis*) were recorded in one group only.

DCA ordination gives a similar picture (Fig. 6) and the province clusters corresponded well with those classified by TWINSPAN. Quadrats of group 7 (open circles) cover a relatively large space in the ordination. In contrast, quadrats of group 5 (open squares) and 6 (black squares) are densely packed in the middle of the picture. The deviating quadrat of group 8 (black circle) is isolated on the right.

Table 2 shows the mean values of the environmental variables analysed separately for each quadrat group. The mean difference between the groups in the beginning of the vegetative period is almost one month, ranging from April 13 to

Fig. 5. Distribution of the quadrats in the groups interpreted from the TWINSPAN analysis in northern Europe.

Kuva 5. TWINSPAN-analyysin perusteella tulkitettujen ruuturyhmien levinneisyys Pohjois-Euroopassa.

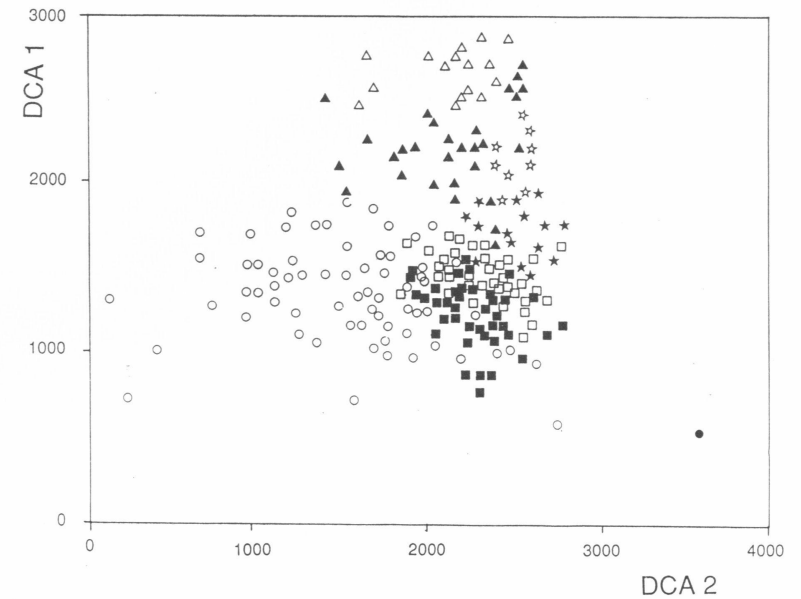


Fig. 6. The quadrats plotted on the 1st and 2nd axes (eigenvalues 0.27 and 0.11) of detrended correspondence analysis ordination (DCA).

Kuva 6. Ruutujen luokittelu DCA-analyysin avulla ensimmäisen (ominaisarvo 0.27) ja toisen (ominaisarvo 0.11) akselin suhteen.

Table 2. Mean values and their standard deviations of the environmental variables for each quadrat group interpreted from the TWINSPAN. See the text for the full names of the variables.

Taulukko 2. TWINSPAN-analyysin ruuturyhmien ympäristömuuttujien keskiarvot ja keskihajonnat. Muuttujien täydelliset nimet tekstissä.

Group Ryhmä	LAT		LON		BVP		ETS	
	mean	SD	mean	SD	mean	SD	mean	SD
1	55°53'	0°42'	11°34'	2°16'	Apr 13	3	1515.6	87.0
2	58°22'	1°24'	13°28'	4°09'	Apr 18	5	1321.6	140.3
3	59°25'	0°36'	14°52'	4°18'	Apr 22	5	1277.8	53.7
4	60°24'	1°00'	17°49'	5°25'	Apr 24	4	1163.3	102.2
5	62°36'	1°30'	24°09'	5°30'	Apr 30	4	1068.2	94.6
6	64°56'	2°12'	20°30'	6°07'	May 5	7	829.9	139.3
7	65°13'	3°12'	16°34'	6°49'	May 4	12	777.7	214.8
8	68°12'	—	16°06'	—	May 8	—	825.0	—

	PRE		VEG		PIC		PIN	
	mean	SD	mean	SD	mean	SD	mean	SD
1	3.8	1.2	1.8	0.5	0.3	0.6	0.4	0.8
2	3.7	2.3	3.1	1.2	2.1	1.1	2.4	0.9
3	3.4	2.1	3.0	0.0	2.8	0.4	2.9	0.3
4	4.2	1.0	3.9	0.6	2.9	0.3	2.9	0.3
5	3.5	1.1	4.4	0.5	3.0	0.2	3.0	0.0
6	2.8	1.9	5.4	0.9	2.7	0.6	2.9	0.4
7	4.4	2.5	5.7	1.6	1.4	1.1	2.0	0.8
8	7.5	—	4.0	—	0.0	—	1.0	—



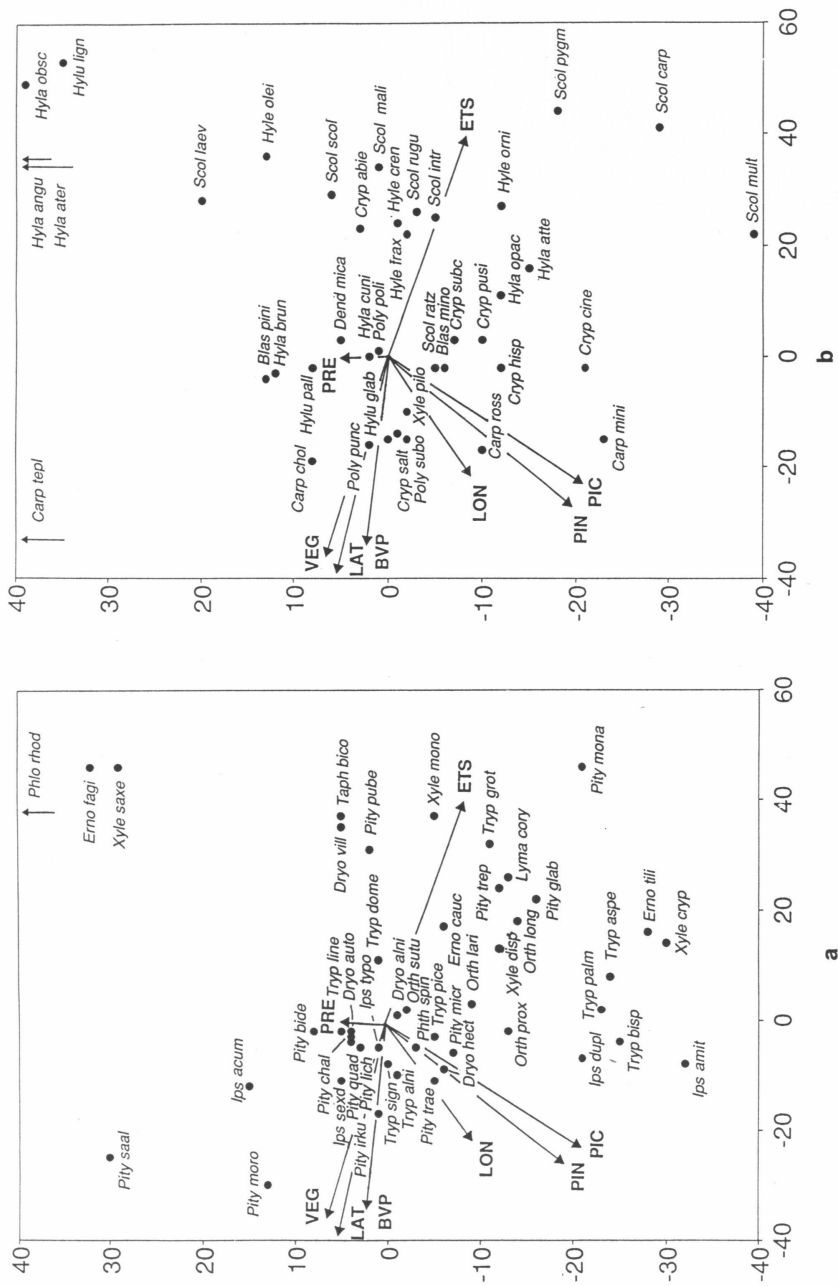


Fig. 7. Ordination diagram based on canonical correspondence analysis (CCA) of the distribution of Scolytidae in northern European quadrats with respect to eight environmental variables (arrows). The species are abbreviated as the first four letters of their generic and specific names (see Table 1 for full species names). The species have been divided into two groups (a and b) for practical reasons. The environmental variables are: latitude (LAT), longitude (LON), beginning of vegetative period (BVP), effective temperature sum (ETS), precipitation (PRE), vegetational zone (VEG), distribution of *Picea abies* (PIC) and distribution of *Pinus sylvestris* (PIN). The lengths of the arrows have been reduced by a factor of 10. Eigenvalue for the axis 1 is 0.24 and 0.07 for the axis 2.

Kuva 7. Pohjois-Euroopan kaarnakuoriaisten levinneisyksiin perustuva CCA-analyysin luokittelemalla kahdeksaan ympäristömuuttujan (nuolet). Lajien suku- ja lajinnimet on esitetty nelikirjaimisina lyhennyksinä (täydelliset lajinnimet taulukossa 1). Suuren lajimäärän vuoksi lajit on jaettu kahteen ryhmään (a ja b). Ympäristömuuttujat ovat: leveyspiiri (LAT), pituuspiiri (LON), kasvukauden alku (BVP), tehoisa lämpösusuma (ETS) sademäärä (PRE), kasvillisuusvyöhyke (VEG), kuusen levinneisyys (PIC) ja männyn levinneisyys (PIN). Nuolien pituudet on jaettu kymmenellä. Ensimmäisen akselin ominaisarvo on 0,24 ja toisen 0,07.

May 8. The mean effective temperature sum for the southernmost group is double that for the northernmost one, but the mean annual precipitation seems to be less related to latitude or longitude. The mean values of the indices depicting the distribution of *Pinus* and *Picea* were highest in the quadrat groups covering southern and Central Finland, Central Sweden and southern Norway.

### 33. Environmental variation and species assemblages

The faunistic data were related to variation in the environment. The CCA ordination diagram (Fig. 7 a and b) illustrates the Scolytidae fauna in relation to a number of environmental variables. The Monte Carlo permutation test showed that the species are related to these environmental variables (99 random permutations,  $p < 0.01$  for the first canonical axis).

The canonical coefficients for latitude (LAT), beginning of the vegetative period (BVP) and effective temperature sum (ETS) received the highest absolute value on the first axis, but also the distribution of *Picea abies* (PIC), longitude (LON) and precipitation (PRE) contributed to the fit of the species data (Table 3). However, the canonical coefficient for latitude is highly correlated with other environmental variables as

Table 3. Canonical coefficients, variance inflation factors (VIFs) and the inter-set correlations of environmental variables with the first four axes of canonical correspondence analysis (CCA) in Scolytidae. Canonical coefficients with a t-value  $> 2.0$  in absolute values are indicated by x.

Taulukko 3. Kanonisen korrespondenssianalyysin (CCA) kertoimet ja VIF:t sekä neljän ensimmäisen akselin ja ympäristömuuttujien korrelaatiot. Kertoimet, joiden t-arvo on suurempi kuin 2.0 on merkitty yläviiteellä x.

Axis Akseli	Canonical coefficients Kanoniset kertoimet				Correlation coefficients Korrelaatiokertoimet				VIFs
	1	2	3	4	1	2	3	4	
Variable Muuttuja									
LAT	-0.53 <sup>x</sup>	0.14 <sup>x</sup>	-0.46 <sup>x</sup>	-0.28 <sup>x</sup>	-0.85	0.18	-0.09	0.19	20.3
LON	-0.11 <sup>x</sup>	-0.03	-0.28 <sup>x</sup>	0.10 <sup>x</sup>	-0.47	-0.29	-0.20	0.51	3.7
BVP	0.36 <sup>x</sup>	-0.11 <sup>x</sup>	0.54 <sup>x</sup>	0.26 <sup>x</sup>	-0.74	0.08	0.15	0.38	19.3
ETS	0.22 <sup>x</sup>	-0.15 <sup>x</sup>	-0.02	-0.08	0.85	-0.27	-0.18	-0.08	12.8
PRE	-0.10 <sup>x</sup>	-0.04 <sup>x</sup>	-0.06 <sup>x</sup>	-0.06 <sup>x</sup>	-0.01	0.15	-0.20	-0.48	1.7
VEG	-0.02	-0.01	0.05	-0.02	-0.77	0.21	0.19	0.06	5.2
PIC	-0.18 <sup>x</sup>	-0.11 <sup>x</sup>	-0.15 <sup>x</sup>	0.00	-0.51	-0.67	0.05	0.05	8.1
PIN	0.02	-0.16 <sup>x</sup>	-0.24 <sup>x</sup>	-0.09 <sup>x</sup>	-0.57	-0.62	0.18	-0.02	7.9

indicated by its high value of VIF. The second axis was related to the distribution of *Pinus sylvestris* (PIN), effective temperature sum, beginning of the vegetative period, distribution of *Picea* the precipitation. The fraction of total variance of the species weighted averages represented by axis 1 was 42.2 %, 13.5 % by axis 2, and 8.5 % by axis 3. The effective temperature sum associated with the vegetation zone (VEG) and the beginning of the vegetative period, seem to be the major determinants of species composition along axis 1. This axis correlates positively (effective temperature sum) or negatively (vegetation zone, beginning of the vegetative period) relatively well with these variables (Table 3). Axis 2 was related to the distribution of the conifers, and, to some extent, the longitude. Precipitation was poorly related to the first two axes of CCA.

Species with a Holarctic or European distribution were concentrated on the right-hand side of the diagram (Fig. 7 a and b). *Phloeophthorus rhododactylus*, *Hylastes angustatus* and *H. ater* are known only from a few southernmost quadrats. Northern species lay in the upper left-hand corner of the diagram; *Carphoborus teplouchovi* is known only from northern Sweden. Eastern species tended to be concentrated on the lower left-hand side. In general, the species occurring to the south of latitude 62° lay on the right-hand side of the diagram, and species occurring to the

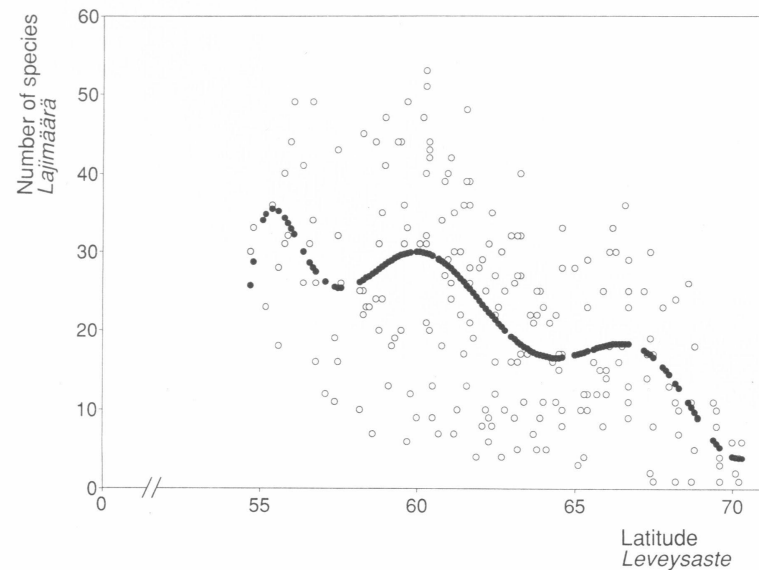


Fig. 8. The number of bark beetle species in a latitudinal direction. Polynomial regression using eighth degree equation was used to calculate predicted values (black dots) for each observed value (open circles).

Kuva 8. Kaarnakuoriaisten lajimäärä leveyspiirin suhteen. Kullekin havaitulle arvolle (valkea pallo) laskettu odotettu arvo (musta pallo) perustuu kahdeksannen asteen yhtälöstä laskettuun regressioon.

Table 4. Constants and terms with their coefficients used in the logistic regression models of distribution of the bark beetle species and the principal host tree species and characteristics of the distribution of the bark beetle species.  $X^2$  refers to Hosmer-Lemeshow test. D = Denmark, S = Sweden, N = Norway, F = Finland.

Taulukko 4. Logististen regressiomallien vakiot ja tekijät kertoimineen kaarnakuoriaislajeittain sekä näiden lajien isäntäpuulajit ja levinneisyyden luonnehdinta.  $X^2$  on Hosmer-Lemeshow -testin testisuure. D = Tanska, S = Ruotsi, N = Norja, F = Suomi.

Species	Principal host	Distribution		Term1	Coef.	Coef./SE	Term2	Coef.
<i>Scolytus intricatus</i>	<i>Quercus</i>	southern	D, S, N, F	ETS	0.011	6.50	PRE	-0.294
				CAN1	0.076	5.44	CAN2	-0.069
<i>Scolytus laevis</i>	<i>Ulmus</i>	southern	D, S, N	BVP	-0.259	-4.85	CAN4	-0.019
				CAN1	0.038	5.71		
<i>Hylurgops glabratus</i>	<i>Picea</i>	central	S, N, F	BVP	0.038	2.95	CAN2	-0.057
				CAN1	-0.057	-5.92		
<i>Crypturgus cinereus</i>	<i>Pinus</i>	central	S, N, F	ETS	0.002	3.46	PRE	-0.209
				CAN2	-0.076	-6.45		
<i>Pityogenes saalasi</i>	<i>Picea</i>	northern	S, F	BVP	0.109	3.17	CAN4	0.056
				CAN1	-0.048	-3.22		
<i>Ips typographus</i>	<i>Picea</i>	central	D, S, N, F	PRE	-0.475	-5.16	BVP	-0.077
				CAN2	-0.040	-6.60		
<i>Xyleborus dispar</i>	Deciduous trees	southern	D, S, N, F	ETS	0.008	7.06	PRE	-0.170
				CAN1	0.036	6.60	CAN2	-0.062

north of latitude 60° lay on the left-hand side of the diagram. Species associated with deciduous trees with a southern distribution were also concentrated on the right-hand side, but those associated with *Betula* and *Alnus* lay near the centre.

Based on the results of multiple regression analysis, latitude was used as the independent variable in polynomial analysis. Although the statistically appropriate polynomial relation was an eighth degree equation with  $r^2 = 0.328$ , the simple polynomial based on the statistical and appreciable (see 2.5.) criteria was a first degree equation with  $r^2 = 0.273$  (Fig. 8). Species richness decreased northwards, but the relation was not very convincing, suggesting that more specific factors may affect diversity in the Scolytidae.

### 34. Distribution of individual species

Three environmental variables (ETS, PRE, BVP) were used in the logistic regression models to predict the ranges of seven bark beetle species (Table 4). The models best predicted the distributions of *Scolytus laevis* and *Pityogenes saalasi* and worst those of *Hylurgops glabratus*, *Ips typographus* and *Crypturgus cinereus*. There were differences between the species in the terms (variables) entered in the equations. The best predictor was the effective temperature sum (ETS) in three species (*Scolytus intricatus*, *Crypturgus cinereus*, *Xyleborus dispar*) and the beginning of the vegetative period (BVP) in

three species (*Scolytus laevis*, *Hylurgops glabratus*, *Pityogenes saalasi*). For example, according to the model, with a standard error of 0.053 a BVP difference of + 1 unit decreases the odds ( $W = P/1-P$ ) of a quadrat being occupied by 0.772. Other terms did not contribute significantly to the fit of the model for those species best predicted by the beginning of the vegetative period, but precipitation contributed significantly to the fit in those species best predicted by the effective temperature sum. The annual precipitation was the best predictor only in *Ips typographus*.

Predictions for each species were better when their distributions were predicted by logistic regression on the four major canonical axes of the CCA, except for *Scolytus* spp. The models based on CCAs (whole data) best predicted the distributions of *Pityogenes saalasi* and *Xyleborus dispar*. The best term was CAN1 in five species and CAN2 in two species.

Next, the predicted probability of species occurrence in a quadrat was plotted against the best predictor term of the logistic regression model (Fig. 9). Distinct sigmoidal curves emerged in the cases of *Scolytus intricatus* and *Xyleborus dispar*. The curves of *Pityogenes saalasi* and *Scolytus laevis* were exponential with different signs of the coefficient. In *Hylurgops glabratus* there was a linear relation between the probability and the beginning of the vegetative period. In *Crypturgus cinereus* and *Ips typographus* the relationship was less stable.

The predicted probabilities (based on the lo-

Coef./SE	Term3	Coef.	Coef./SE	Term4	Coef.	Coef./SE	Const.	Const./SE	$X^2$	P
-2.03							-12.65	-6.29	11.546	0.173
-4.05							-2.680	-4.62	15.566	0.049
							1.780	2.73	4.378	0.821
-2.02							-3.424	-6.22	19.637	0.012
							-1.058	-3.19	53.397	0.000
-6.47	CAN4	-0.017	-2.21				-0.998	-3.17	6.962	0.541
-2.32							-2.597	-3.73	22.414	0.004
							-1.374	-5.48	5.814	0.668
							-6.180	-5.11	7.732	0.460
4.01	CAN3	0.029	2.92				-6.515	-5.00	3.231	0.919
-4.19							4.770	6.36	27.296	0.001
							2.107	7.76	7.532	0.480
-1.67							-8.620	-6.95	14.581	0.068
-5.85	CAN3	-0.034	-4.02	CAN4	-0.028	-3.16	-0.876	-3.23	4.330	0.826

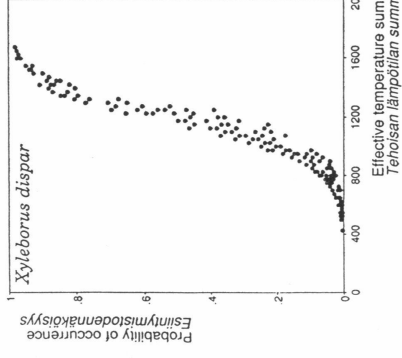
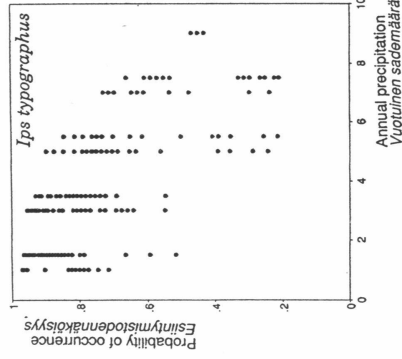
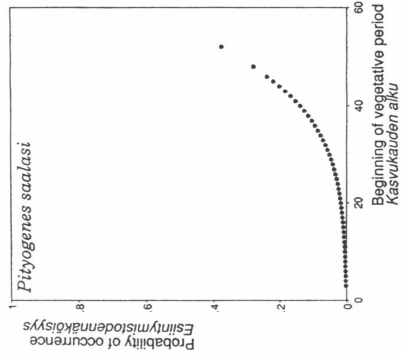
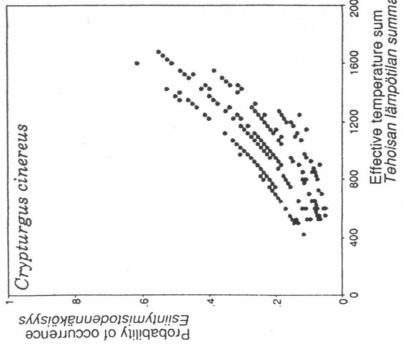
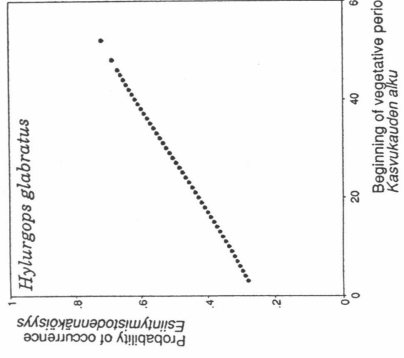
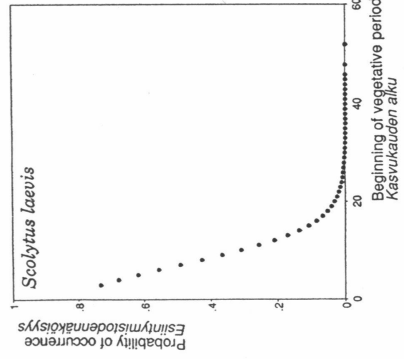
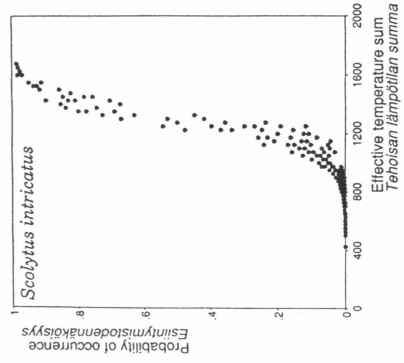


Fig. 9. Relationship between the best predictor term of the logistic regression model and the predicted probability of a species' occurrence in a quadrat.

Kuva 9. Logistisen regressiomallin parhaan selittävän muuttujan ja lajin ruuduttaisen ennustetun esiintymistodennäköisyyden välinen suhde seuraaville lajeille: tammennantokoirainen (*Scolytus intricatus*), jalavanmantokoirainen (*Scolytus laevis*), kaljuliluri (*Hylurgops glabratus*), himmekkäpiökirjaaja (*Crypturgus cinereus*), tunturihäikiriijaaja (*Ips typographus*) ja lustokoirainen (*Xyleborus dispar*).

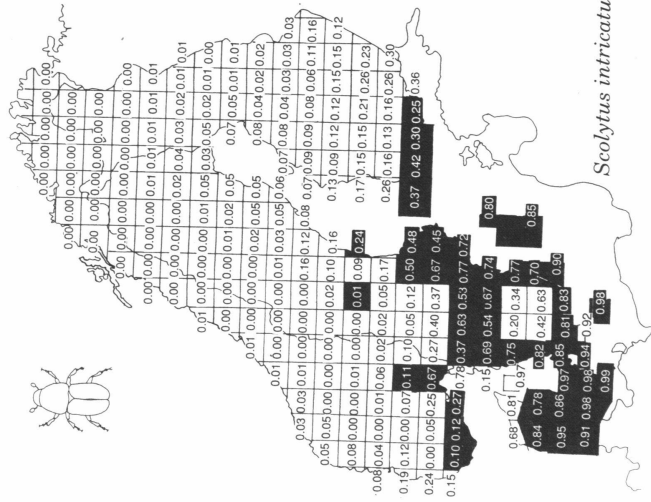


Fig. 10. Predicted probabilities for *Scolytus intricatus* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 10. Kasvukauden alkamiseen, vuotuisen sademäärän ja tehoisan lämpösummaan perustuvan logistisen mallin antama tammennantokoiraisen ruuduttaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

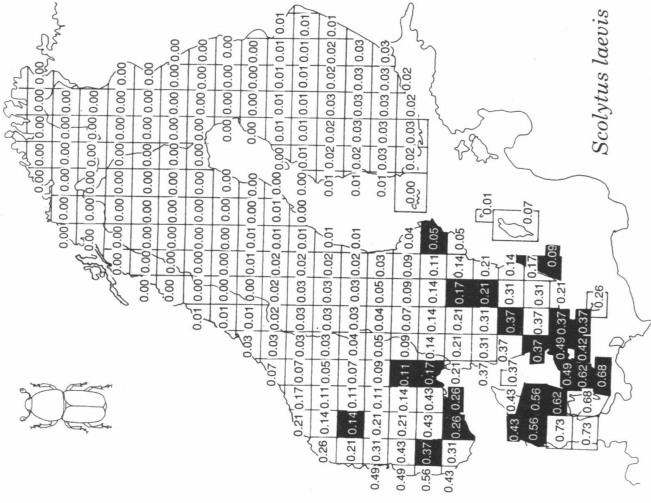


Fig. 11. Predicted probabilities for *Scolytus laevis* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 11. Kasvukauden alkamiseen, vuotuisen sademäärän ja tehoisan lämpösummaan perustuvan logistisen mallin antama *Scolytus laevis* -mantokoiraisen ruuduttaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

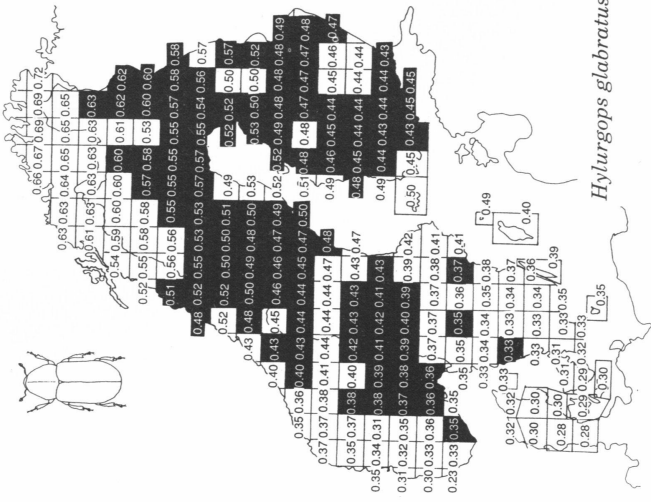


Fig. 12. Predicted probabilities for *Hylurgops glabratus* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 12. Kasvukauden alkamiseen, vuotuisen sademäärän ja tehoisan lämpösummaan perustuvan logistisen mallin antama kaljulilurin ruuduttaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

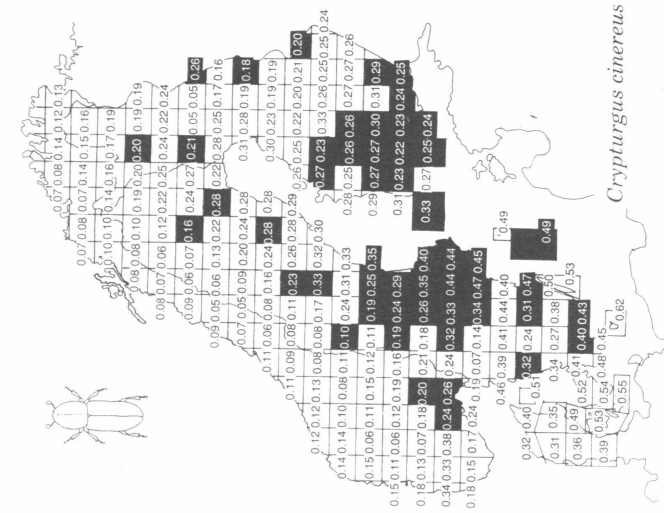


Fig. 13. Predicted probabilities for *Crypturgus cinereus* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 13. Kasvukauden alkamisen, vuotuisen sademäärän ja tehoisan lämpösomaan perustuvan logistisen mallin antama himmeäkääpiökirjaajan ruuduittaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

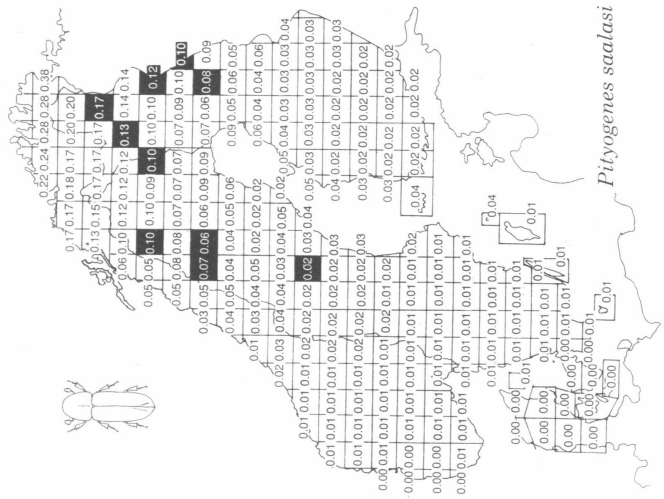


Fig. 14. Predicted probabilities for *Pityogenes saalasi* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 14. Kasvukauden alkamisen, vuotuisen sademäärän ja tehoisan lämpösomaan perustuvan logistisen mallin antama tunturihämähäkikirjaajan ruuduittaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.



Fig. 15. Predicted probabilities for *Ips typographus* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 15. Kasvukauden alkamisen, vuotuisen sademäärän ja tehoisan lämpösomaan perustuvan logistisen mallin antama kirjainpöytäkirjaajan ruuduittaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

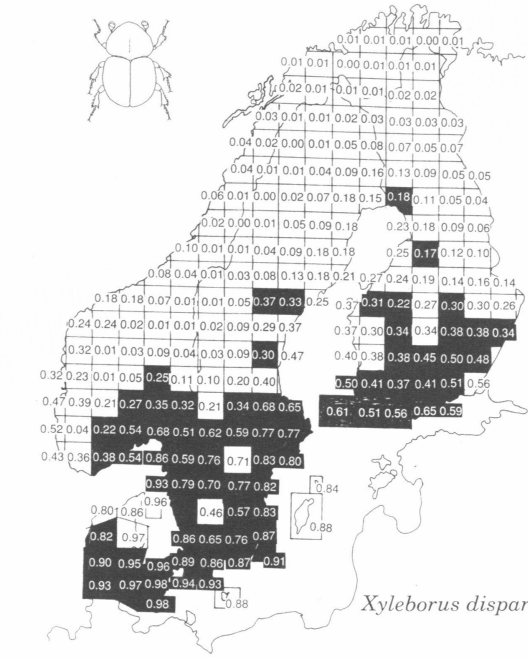


Fig. 16. Predicted probabilities for *Xyleborus dispar* to occur in the quadrats according to the logistic regression model calculated using the beginning of the vegetative period, the annual precipitation and the effective temperature sum. The observed distribution is indicated by blackened areas.

Kuva 16. Kasvukauden alkamisen, vuotuisen sademäärän ja tehoisan lämpösomaan perustuvan logistisen mallin antama luskokuoriaisen ruuduittaisen esiintymisen todennäköisyys. Havaittu levinneisyys on osoitettu mustalla.

gistic regression models using the three environmental variables) of the species occurrence in each quadrat are shown on maps (Figs. 10–16). The models suggest that the highest probabilities for the two *Scolytus* species and *Xyleborus dispar* to be found in unoccupied quadrats are in Denmark and southern Sweden. The highest probabilities for *Hylurgops glabratus* and *Pityogenes saalasi* are in the northern regions, respectively, and those for *Crypturgus cinereus* in southern Scandinavia. The lowest probabilities of occurrence for *Ips typographus* are in northern Norway.

### 35. Rarity and typicalness

The six different rarity indices calculated for the scolytid data are presented in Figs. 17–22. There was wide variation between beetle rarity totals

(BRT) in the quadrats (Fig. 17). The highest BRT value (116) was obtained for Öland. High values (84–95) were also obtained for two quadrats in southernmost Sweden, two near Stockholm, two near Helsinki, and the one in Gotland. The lowest values were obtained for quadrats situated in western and northern Norway and for northern parts of Sweden and Finland. This variation was more or less related to the number of species, since differences in the beetle quality factor (BQF) were reduced (Fig. 18). The highest BQF values were obtained for Öland (2.37) and Gotska Sandön (2.22). The values near Stockholm and Helsinki were relatively lower and those of Denmark higher compared to the BRTs.

The use of a geometric scale amplified the rarity value of the quadrats. When the species rarity totals (SRT) were calculated (Fig. 19), roughly the same quadrats received the highest values as in BRT. The SRT of Öland was as high as 288. As was the case with BRT, the SRTs were related to the number of species in the quadrat. Differences in the SQFs (Fig. 20) were higher than those for the BQFs and the use of the geometric scale also caused changes in the ranking of the highest-quality quadrats. Öland (5.9) and Gotska Sandön (5.8) still had the highest SQF values, followed by two quadrats in northern Sweden (4.7, 4.3) and one in southwestern Denmark (4.4).

The rarity association totals (RAT) gave very similar results to SRTs, although the values were higher (Fig. 21). The highest RATs were found on Öland (520), Gotland (272) and in southernmost Sweden (259). As with the SRT, the RATs were related to the number of species in the quadrat. There was some re-ordering of the highest-quality quadrats in RQFs (Fig. 22) compared to RATs. Öland (10.6) and Gotska Sandön (9.0) had the highest values. In addition to Denmark (up to 6.8) and Gotland (6.3), high RQFs were also found in three northern Swedish quadrats (5.1–5.6).

The rarity indices and the number of species correlated positively with canonical axes 1 and 4, and negatively with 3 (Table 5). The number of species and BRT correlated best with CCA axis 2, while the other indices correlated best with CCA axis 1. BQF, SQF, RAT and RQF correlated second best with CCA axis 4.

The typicalness measurements for the quadrats are shown in Figs. 23–24. The highest absolute values of TYP1 were found for Öland (2.5), for most of the Danish quadrats (7 values > 2.0), and for two quadrats in northern Norway (–3.0,

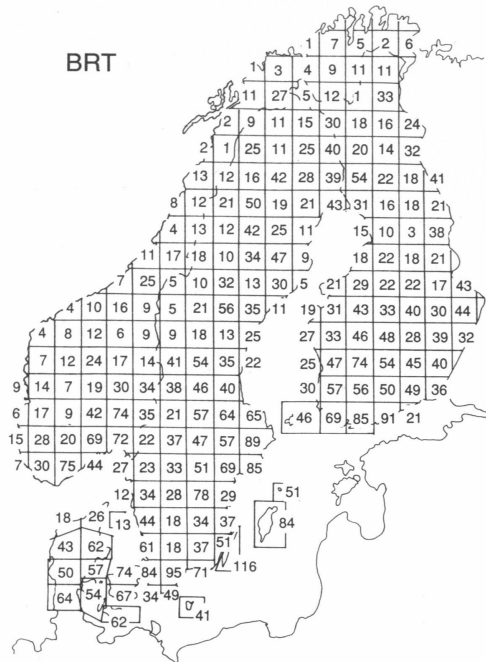


Fig. 17. The beetle rarity total (BRT) calculated for each quadrat.  
 Kuva 17. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi BRT.

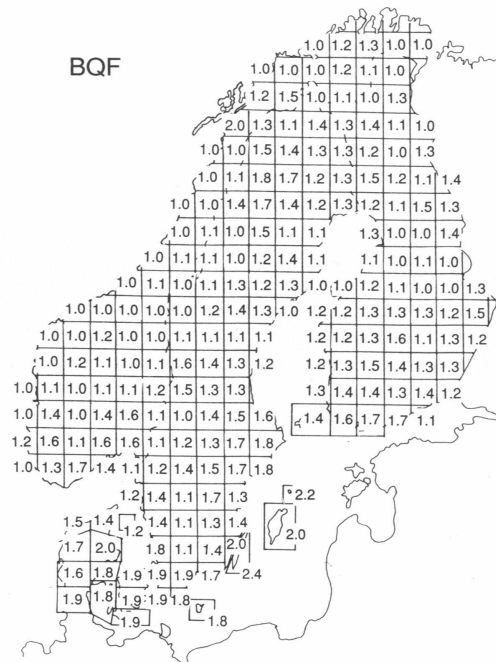


Fig. 18. The beetle quality factor (BQF) calculated for each quadrat.  
 Kuva 18. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi BQF.

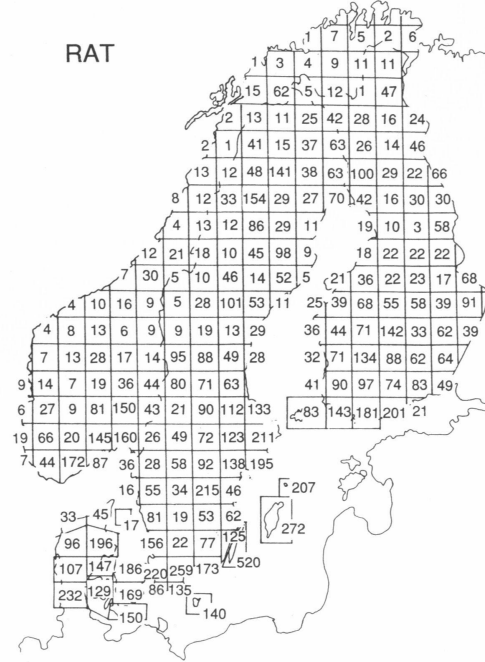


Fig. 21. The rarity association total (RAT) calculated for each quadrat.  
 Kuva 21. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi RAT.



Fig. 22. The rarity quality factor (RQF) calculated for each quadrat.  
 Kuva 22. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi RQF.

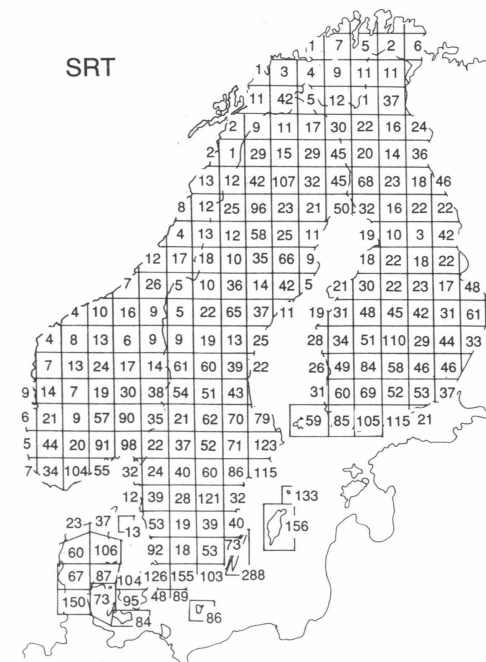


Fig. 19. The species rarity total (SRT) calculated for each quadrat.  
 Kuva 19. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi SRT.

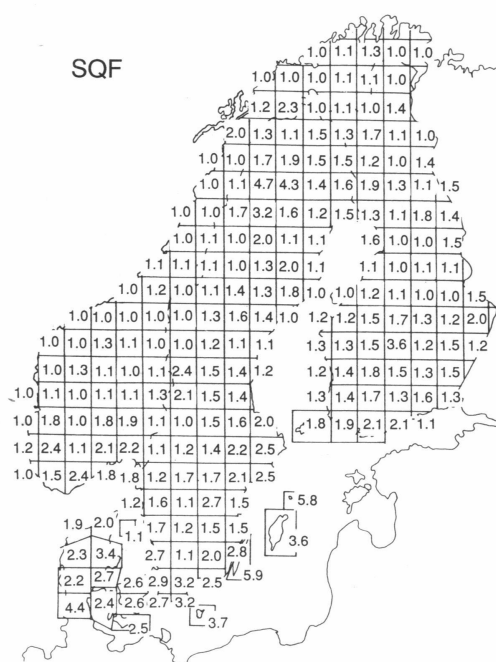


Fig. 20. The species quality factor (SQF) calculated for each quadrat.  
 Kuva 20. Kaarnakuoriaislajistolle laskettu ruuduittainen harvinaisuusindeksi SQF.

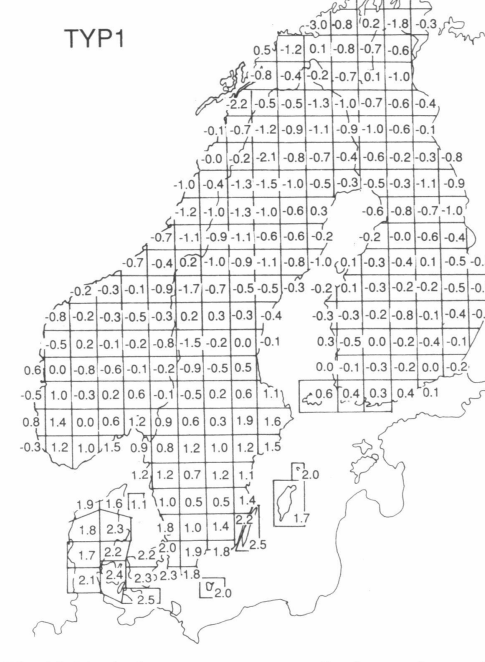


Fig. 23. Typicalness measurements for the quadrats calculated separately for DCA axis 1 (TYP1).  
 Kuva 23. Kaarnakuoriaislajiston DCA-analyysin ensimmäisen akselin suhteen laskettu ruuduittainen tyypillisyyssindeksi (TYP1).

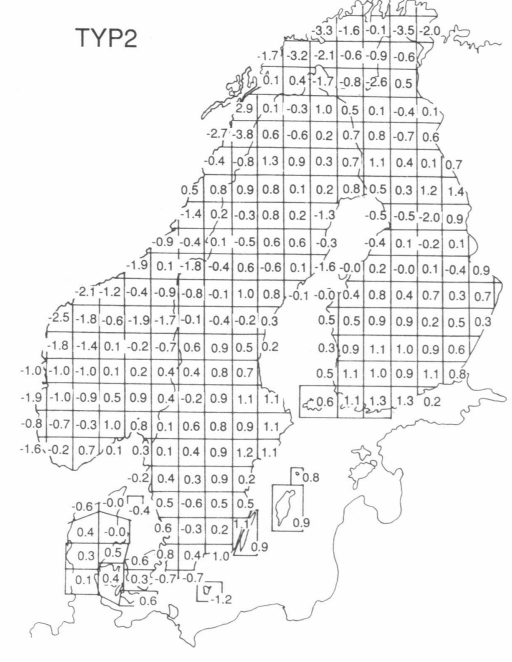


Fig. 24. Typicalness measurements for the quadrats calculated separately for DCA axis 2 (TYP2).  
 Kuva 24. Kaarnakuoriaislajiston DCA-analyysin toisen akselin suhteen laskettu ruuduittainen tyypillisyyssindeksi (TYP2).

Table 5. Correlations between the canonical variables of the CCA and the rarity indices. \*\* =  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Taulukko 5. CCA-analyysin kanonisten muuttujien ja harvinaisuusindeksien väliset korrelaatiot. \*\* =  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Index	CCA 1	CCA 2	CCA 3	CCA 4
Number of species	0.477***	-0.752***	-0.185**	0.252***
BRT	0.608***	-0.635***	-0.093	0.286***
BQF	0.679***	-0.369***	-0.078	0.473***
SRT	0.642***	-0.475***	0.017	0.326***
SQF	0.581***	-0.217**	0.092	0.417***
RAT	0.670***	-0.530***	0.038	0.312***
RQF	0.677***	-0.276***	0.074	0.401***

-2.2) indicating deviating species assemblages (Fig. 23). Small absolute values occurred in most quadrats in Finland, Central Sweden and Norway. The deviation from the mean in 156 quadrats out of 221 (70.6 %) was less than one standard deviation, i.e.  $-1 < TYP1 < 1$ . Quadrats with the highest negative TYP2 values were mainly restricted to the northern parts of the area, and the highest positive values to southern Finland and the surroundings of Stockholm in Sweden (Fig. 24). The measurements of 168 quadrats (76.0 %) deviated by less than one standard deviation in TYP2.

### 36. The effect of faunal changes

In order to test the sensitivity of the present multivariate methods to faunal changes, the Finnish scolytid material comprising 63 species was analysed using data sets before (old data) and after (new data) the documented changes in the distribution of *Ips acuminatus* and *I. amitinus*

(Fig. 25). Major changes were observed in the species classification in the TWINSpan species dendrogram. The species were classified into 15 groups according to their distribution using the old data, and into 16 groups using the new data. 30 species were classified to the same branch in the final (fourth) division in both data sets. Of the rest, 11 species (including *I. acuminatus*) changed their position in the final division, but remained in the same branch of the third division. 12 species (including *I. amitinus*) changed their position in the third division, and 6 species changed their position in the second division. The position of four species changed in the primary division: *Hylesinus crenatus* moved from the lower main branch to the upper one, and *Dendroctonus micans*, *Hylurgops glabratus*, and *Orthotomicus proximus* moved from the upper main branch to the lower one.

The actual changes in the distribution of the two species considerably affected the Finnish quadrat groups interpreted from TWINSpan (Fig. 26). Classification of 57 quadrats out of 73 remained unchanged. These quadrats were mostly situated in parts of southern and Central Finland where faunal changes had actually taken place. Of the changed quadrats, seven quadrats were classified into their sister groups in the TWINSpan quadrat dendrogram. Six quadrats changed their position in the second division, and three quadrats were classified into the other main branch of the primary division. In the DCA analyses, the main pattern remained rather similar (Fig. 27). However, there were considerable differences in details (e.g. black squares). It should be stressed that this analysis only takes into account the changes in the distribution of *Ips acuminatus* and *I. amitinus*. If the less clearly documented changes in the range of other species had also been analysed, both the species and quadrat classification would probably have been different.

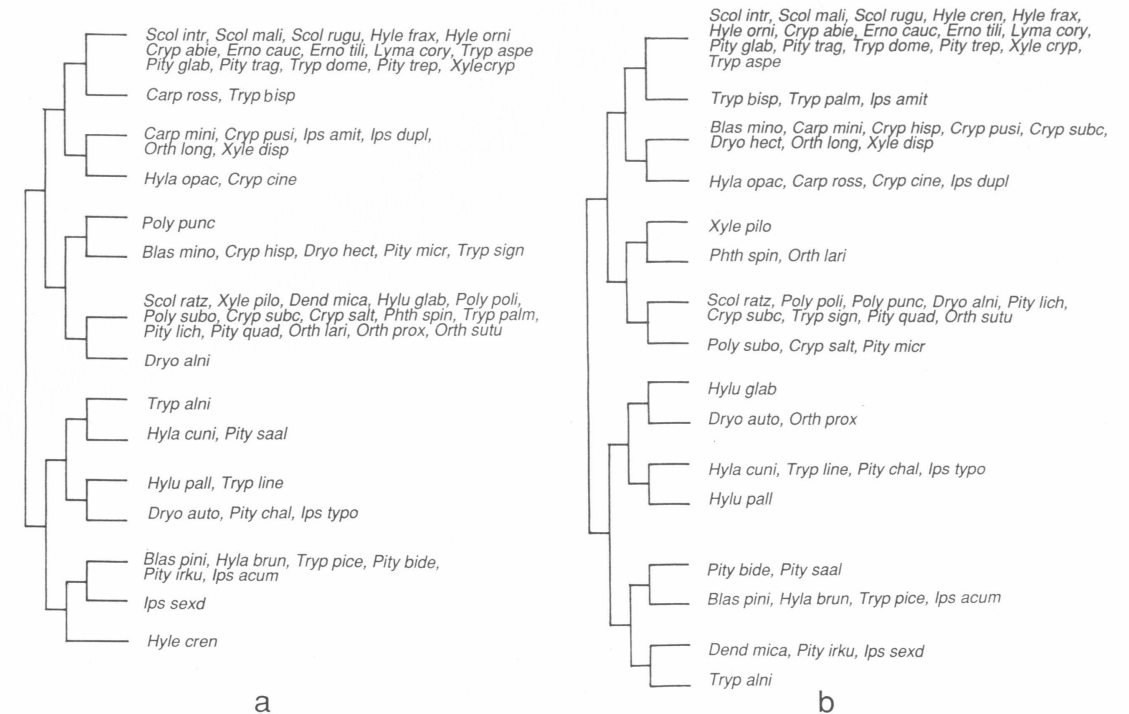


Fig. 25. Species dendrograms of a two-way indicator species analysis (TWINSpan) using the Finnish Scolytidae data before (a) and after (b) the change in the distribution of *Ips acuminatus* and *I. amitinus*.  
Kuva 25. Suomessa esiintyvien kaarnakuoriaisten TWINSpan -luokittelu a) ennen okakaarnakuoriaisen ja kiiltokirjanpajan levinneisyysalueissa tapahtuneita muutoksia ja b) niiden jälkeen.

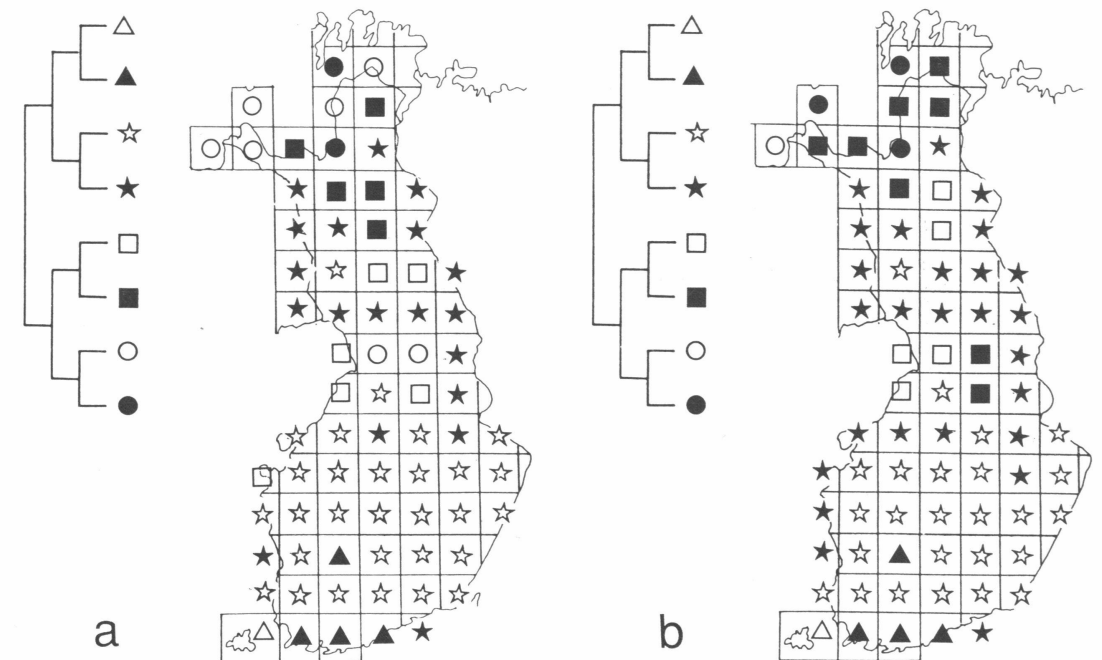


Fig. 26. Distribution of the Finnish quadrats in the groups interpreted from the TWINSpan analysis before (a) and after (b) the change in the distribution of *Ips acuminatus* and *I. amitinus*.  
Kuva 26. TWINSpan-analyysiin perustuva Suomen ruutujen luokittelu ryhmiin a) ennen okakaarnakuoriaisen ja kiiltokirjanpajan levinneisyysalueissa tapahtuneita muutoksia ja b) niiden jälkeen.

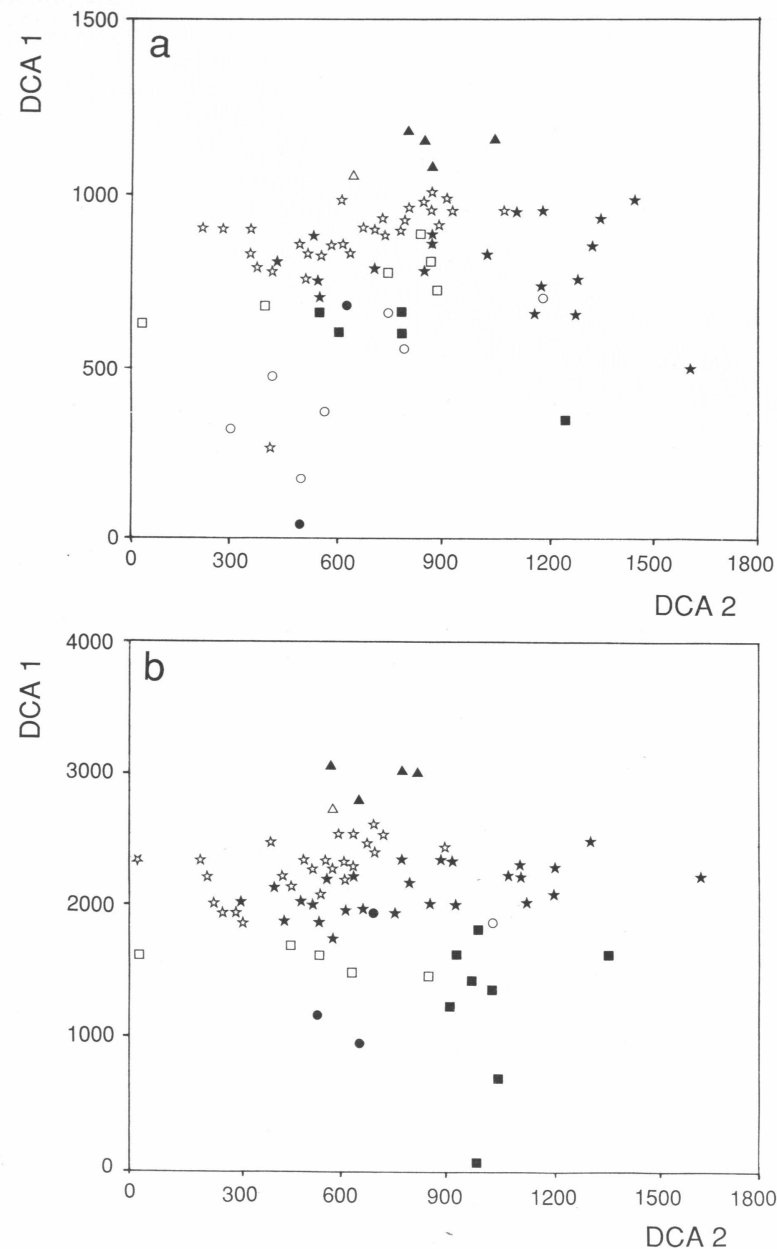


Fig. 27. The quadrats plotted on the 1st and 2nd axes of detrended correspondence analysis ordination (DCA) using the Finnish Scolytidae data before (a; eigenvalues 0.16 and 0.08) and after (b; eigenvalues 0.18 and 0.09) the change of the distribution of *Ips acuminatus* and *I. amitinus*.

Kuva 27. Suomessa esiintyvien kaarnakuoriaisten luokittelu DCA-analyysin avulla ensimmäisen ja toisen akselin suhteen a) ennen okakaarnakuoriaisen ja kiiltokirjanpajan levinneisyysalueissa tapahtuneita muutoksia (ominaisarvot 0.16 ja 0.08) ja b) niiden jälkeen (ominaisarvot 0.18 ja 0.09).

## 4. Discussion

### 41. The potential and constraints of the quantitative approach

Modern quantitative biogeography provides effective tools for analysing existing data sets of the distributions of species in different groups of organisms. Although comprehensive and detailed qualitative analyses have been carried out on distributional patterns, their results are difficult to use for comparative purposes with respect to faunal changes, different areas or environmental changes such as climate change or acidification. In entomology, the possibilities of utilizing distributional maps in more detailed investigations have often been underestimated. Multivariate methods can reveal patterns in species assemblages that are impossible to recognize when the sequential single species approach is used. They also provide the possibility to relate objectively the faunal characteristics to environmental variables. Data can be easily included in up-dated reanalyses as they accumulate.

The state of knowledge and the size of the areal sampling unit are the main constraints in all biogeographical studies. The distribution of *Trypodendron piceum* is poorly known due to the problems in species identification. It is a typical taiga-species, whose range cannot be concentrated only in the western part of the region. *Ips sexdentatus*, which has disappeared from the southern parts of the area, was grouped apart from the other species with a northern distribution, since older records were also used in the analysis. The classification of *Orthotomicus longicollis* may be misleading, since the distribution of the species has a relic character and is probably affected by factors different to those for other bark beetles. In northern Europe the species now definitely occurs only on Gotska Sandön, in the Pyhä-Häkki National Park in Central Finland, and in Białowieża forest in Poland (Lekander et al. 1977). *Carphoborus minimus* is probably another relic in the area. It is only known from Pyhä-Häkki. Some species are intensively investigated in certain areas, thus giving a biased total distribution pattern (e.g. *Dendroctonus micans* in Denmark; Bejer-Petersen 1952, 1976).

The present results based on 70 × 70 km<sup>2</sup> quadrats and an intensively collected material comprising a well-known group of insect pests show that these constraints are not too difficult

to overcome. Smaller quadrats would increase the accuracy of the results, since the variation of environmental variables in a given quadrat would then be smaller. However, smaller quadrats could lead to a higher number of quadrats if the study area was constant which, in turn, presupposes more detailed and laborious faunal analyses. The present methods are, however, sensitive even to small changes in the data set. Although faunal changes are easy to demonstrate, changes in the state of knowledge are also reflected in the results (e.g. BRTs). Thus, special care is needed when interpreting the biogeographical patterns that emerge.

### 42. Biogeographical classification of Fennoscandia and Denmark on the basis of bark beetles

The highest number of bark beetle species per quadrat, 53 species, was recorded in one quadrat in southern Finland. Quadrats lying near Stockholm, Oslo and southern Sweden, as well as Öland and Gotland, also had a high number of species. This may show higher species richness in these areas, but it also reflects a higher collecting activity. The number of species is low in western and northern Norway, which is mainly due to the lack of suitable host trees and climatic factors and also to a lower collecting activity. Several common species (e.g. *Hylastes brunneus*, *Hylurgops palliatus*, *Tomicus piniperda* (*Blas pini*)) are missing from a large number of quadrats. There are also considerable variations in topography within small areas in Norway. The climate varies according to the elevation and thus affects bark beetle species assemblage (Bakke 1968).

As a whole, bark beetle species richness decreases northwards as shown by the multiple regression analysis. However, the relationship between latitude and the number of species was not unambiguous in the polynomial analysis. For instance, climatic factors associated with continentality, the shape of peninsular landmasses, local research activity and latitude may all be important determinants of the species assemblage.

The distribution of bark beetles is largely determined by the distribution and abundance of their host tree species (Lekander et al. 1977). In addition, most bark beetles are very sensitive to

the size, age and resistance of the host tree, and the site conditions and previous forest management. On the basis of scolytid distribution the study area can be classified into relatively distinctive quadrat groups. These groups resemble vegetational classifications but differ in details (cf. Ahti et al. 1968). The major difference is that the area is more clearly divided in an east-west direction according to continentality. Furthermore, the extension of southern vegetational zones cannot be distinguished along the western coast of Norway in the bark beetle maps.

The transition of one quadrat group to another was usually complex. This may reflect the real situation in nature, but more detailed faunal analyses could clarify the boundaries of the zones. The differences in the bark beetle fauna in an east-west direction may be partly due to the short post-glacial period during which the bark beetles have expanded to the area. Since the spreading of herbivores may sometimes be slower than that of their host trees, it is possible that all species have not had enough time to occupy fully their potential ranges.

An interesting detail in the classification was the deviating quadrat in southern Sweden (open circle in Fig. 5). More northern characteristics (southern boreal among hemiboreal) in the same area have also been observed in vegetational studies (Ahti et al. 1968). Only 16 species have been recorded in this quadrat. The faunal deviation from the surrounding areas was mainly caused by such species as *Tomicus minor*, *Hylastes cunicularius*, *Dryocoetes autographus*, *Pityogenes bidentatus* and *Orthotomicus proximus*. These species are missing in the adjacent quadrats, where southern species such as *Scolytus rugulosus*, *Hylesinus fraxini*, *Hylastes opacus*, *Ernoporus fagi* and *Xyleborus dispar* occur instead.

The range of the bark beetle species associated with Scots pine has a northern boundary but no southern one, while the range of the species associated with Norway spruce has a southern boundary but no northern one (Lekander et al. 1977). The northern borderlines of deciduous trees are key factors in determining the distribution of several bark beetle species associated with these trees. This is especially true for the fauna of *Quercus robur*, *Fagus silvatica*, *Tilia cordata*, *Fraxinus excelsior*, *Ulmus* species, *Acer platanoides* and *Corylus avellana*. The bark beetle fauna associated principally with these tree species includes e.g. *Scolytus laevis*, *S. intricatus*, *S. multistriatus*, *S. pygmaeus*, *S. scolytus*, *Hylesinus crenatus*, *H. fraxini*, *H.*

*oleiperda*, *H. orni*, *Ernoporus caucasicus*, *E. tiliae*, *E. fagi*, *Lymantria coryli*, *Dryocoetes villosus* and *Xyleborus monographus*. The general distribution of their host tree species comprises Denmark, southern Sweden, southern Norway and southern Finland including the Åland archipelago approximately up to latitude 60°N (Hultén 1950). *Fagus silvatica* does not occur naturally in Finland. The present classification of quadrats in Fig. 5 (triangles and stars) is largely associated with the present distribution of these tree species.

### 43. Climate and bark beetle biogeography

A wide variety of factors, both abiotic (e.g. temperature, precipitation) and biotic (e.g. predation, competition) have been recognized as being important in limiting species distributions (for a review, see Gaston 1990). The results of the present study show that environmental variables associated with temperature conditions apparently play a major role in shaping the scolytid species assemblage, as well limiting the range of individual species. The availability of *Pinus* and *Picea* is another decisive factor in this respect. Climatological variables such as temperature have formerly been widely used in forecasting the potential distribution of insect pests into uninfested areas (Uvarov 1931, Messenger 1959). In the huge number of investigations dealing with bark beetles, special attention has traditionally been paid to the role of temperature in relation to the timing of swarming (e.g. Annila & Perttunen 1964, Bakke 1968, Annila 1969, Führer & Chen 1979, Långström et al. 1984, Saarenmaa 1983, 1985). The present results show that latitude and associated temperature variables were the most significant determinants of biogeographical variation in the Scolytidae. The canonical coefficients of latitude, beginning of the vegetative period and effective temperature sum were the highest.

The beginning of the vegetative period is an important determinant of biogeographical variation in the Scolytidae (cf. Väisänen et al. in press). This variable is likely to be associated with swarming, a typical behaviour of matured individuals attacking new host trees. The onset of swarming affects the length of the developmental period of larvae. This may be a significant factor affecting the distribution of bark beetles. The onset of swarming in spring depends on temperature, and many bark beetles do not take flight until the air temperature has reached a

certain level. The spontaneous take-off rate of *Tomicus piniperda* has been shown to be extremely low at 15°C, much higher at 20°C, and maximal at 25°C (see Lekander 1984). At higher temperatures it gradually decreased, being very low at 35°C and totally absent at 40°C (Perttunen & Häyrinen 1969).

Human activities, including forest management and possibly increased acidic deposition and climate change, shape the distribution of bark beetle species. Changes in host distribution and quality, be they the result of a major ecological host shift, or of human activities, evidently provide sufficient impetus for major population increases. These conditions may also contribute to the success of insects introduced into new areas. Furthermore, short-time changes in food quality, often the result of climatic changes, and subsequently the insect's utilization abilities have often been implicated in insect outbreaks (Scriber & Hainze 1987). An epidemic of *Ips typographus*, originally caused by heavy storm and snow damage at the end of the 1960s, broke out spontaneously over an area of 6000 hectares after the warm summers in the early 1970s in the Nordic Countries (Löytyniemi et al. 1979). The level of the bark beetle population also increased after the warm summer 1976, but the following cooler summers decreased the population level. The decline of the outbreak in southern Scandinavia has been partially attributed to cool and wet summers (Bakke 1983).

The influence of climate change on fauna can be examined, for instance, using available multivariate methods. Long-term monitoring will accumulate and update biogeographical data that can be utilized in evaluating the significance of different environmental variables. Even these preliminarily selected environmental variables seemed to be determinants of the species composition of bark beetles in different areas. The logistic models obviously are useful tools for future investigations on bark beetles. The models predicted relatively well the ranges of several individual bark beetle species, though there were considerable difference between species. However, the present data were not very good. The selection of the environmental variables can be further developed for specific purposes. For example, it is known that the northern border of the distribution of *Xyleborus dispar* correlates well with the areas with the maximum temperature of July more than +16°C (Lekander et al. 1977). Tree species distribution should also be included in the models to obtain a better fit. *Hylurgops glabratus* and *Pityogenes saalasi* apparently do

not occur in northernmost Norway where the spruce is absent.

It is difficult to assess the effects of climate change on the scolytids on the basis of currently available data. Relative changes in temperature, precipitation and habitat characteristics increase uncertainty in forecasting potential changes in species' ranges. High degrees of interaction between temperature and humidity are especially crucial for bark beetles, which are commonly, perhaps generally, associated with fungi (Beaver 1989). The symbiotic fungi are poorly known, not to speak of the regional variation in beetle-fungus interactions. Bark beetle populations spreading from different directions may have different symbiotic fungus species which, in turn, may affect the survival of the beetles in a number of ways. Nevertheless, annual precipitation contributed significantly to the fit of the scolytid data in the present analysis. This may be explained by the fact that the symbiotic relationship between beetles and fungi requires a certain humidity level to operate effectively (see Crowson 1981). The general environmental requirements of the fungi have been almost completely ignored. Ambrosia beetles can only reproduce in logs with a sufficiently high moisture content, although attack density is primarily governed by other factors (Annila 1975).

In addition to blue stain and ambrosia fungi, climatic changes can also affect the more virulent fungi associated with bark beetles. The so-called Dutch elm disease (*Ceratostomella ulmi*) has caused catastrophic losses of elms (*Ulmus*) in the USA (Berryman 1982) and in Europe (Crowson 1981). In Denmark, the spread of the disease is associated with *Scolytus scolytus* and *S. laevis* but hardly ever with *S. multistriatus* (Harding & Ravn 1982). It is possible that climatic conditions have prevented these elm bark beetles from becoming effective as vectors of the disease in Denmark (Harding & Ravn 1982). A potential increase in temperature may widen the range of the beetles, thus putting elms growing in even more northern conditions at risk. On the other hand, *Scolytus triarmatus* and *S. laevis* are at present distributed over the whole distribution area of *Ulmus* in Sweden, except for its relic distribution in Lapland. It has also been suggested that higher temperatures may favour *Ips typographus* which, in turn, may threaten plantations of *Pinus contorta* in northern Sweden (Larsen 1990).

Local abundance and the size of the geographic range of a species are interdependent (Gaston 1990). The most widely distributed species in



the study area also seem to be the most abundant ones (e.g. *Ips typographus*, *Pityogenes chalcographus*, *Tomicus piniperda*). The abundance of a species is associated with the number of generations and offspring produced. An outbreak of a forest pest is often associated with a dramatic increase in its geographic area. Temperature not only affects the geographic and local distribution of insects, but also regulates the rate of insect development. The number of generations produced by bark beetles is highly dependent on environmental conditions and latitude (see Postner 1974, Austarå et al. 1977, Zurr & Soldan 1981, Anderbrant 1986, Forsse 1989). In extreme cases, univoltine bark beetles may accelerate their development so that two generations emerge during a single growing season. This does not necessarily favour the beetle population since all individuals of the second generation may not have enough time to develop to the normal overwintering stage. In addition, biennial bark beetles may become univoltine. The rate of developmental increase varies somewhat at different temperatures and in different species. In general, however, an increase of 10°C between the lowest effective temperature and the optimum point doubles the rate of development (Knight & Heikkinen 1980).

The distribution of the bark beetles analysed in this study is based on maps showing the total distribution of the species from the middle of the 19th century up to the year 1975 (Lekander et al. 1977). However, the species distributions are rarely constant in either time or space. Consequently, the ranges of individual bark beetle species are likely to change due to climatic, historical (dispersal), silvicultural or unknown reasons, but the period of observation largely affects the behaviour recorded. It may be possible to include some of these variables in the regression models, for example, by using data from remote sensing studies. It is likely that modern silvicultural practices have changed the between-species competition of bark beetles. The increased area of cultivated forests has made the forest area too one-sided to maintain the high natural diversity of bark beetles (Eidmann 1985). In general, the removal of dying standing trees has decreased the availability of suitable breeding material of several specialized species such as *Ips acuminatus* and *I. duplicatus*. On the other hand, increased amounts of logging waste have benefitted *Pityogenes chalcographus*, *P. bidentatus* and *P. quadridens*. Wood stacks have provided new breeding sites for some species. *Tomicus piniperda* and *Ips typographus* have

greatly benefitted from this practice, and in the north *Trypodendron lineatum*, *Hylurgops palliatus*, *Orthotomicus laricis*, *Pityogenes quadridens* and *Ips acuminatus* breed abundantly in wood stacks (Skogsskyddsutredning 1977, Heliövaara & Väisänen 1984).

The ranges of organisms have been broadly grouped according to their dynamic behaviour, i.e. whether the ranges are constant, expanding or contracting (for a review, see Gaston 1990). Bark beetle literature has documented only a few changes in species' distribution. This observation is largely due to the time scale used and does not imply that the ranges of most species are of constant size. There are examples of bark beetle species probably filling an empty niche and thus expanding their range in size. *Ips amitinus* has spread through Finland at a rate of about 20 km per year (Koponen 1980) and may fall into this category. Another candidate is *Xylechinus pilosus*, which has expanded its range in the Scandinavian peninsula both from the north via Finland and from the south via Denmark (Lekander et al. 1977). However, the possibility of environmental change favouring expansion into new areas is not excluded. *Cryphalus abietis* has immigrated northwards to Sweden and Finland probably only after spruce started to be regenerated artificially in Denmark (Lekander et al. 1977). This species falls into the category of species penetrating new areas as a result of environmental changes. Species exploiting new areas after having overcome barriers or other limits are typically introduced species or exotic pests. However, there is no evidence of this happening in northern Europe.

No examples of bark beetle species showing a simultaneous expansion in one direction and a contraction in another direction are known. Some species are clearly contracting. Such changes in the distribution of *Ips acuminatus* (Nuorteva 1968, Puukko 1981) and *Ips sexdentatus* (Löyttyniemi 1975) are well documented. Both species have retracted northwards, but the reasons are unclear. It has been hypothesized that increased acidic deposition may inhibit the growth of the blue stain fungi essential for both species, but the abundance of these species in Central Europe does not support this view (Heliövaara & Puukko 1986, see also Heliövaara & Väisänen 1991). In contrast, *Tomicus minor* has retracted southwards. This species has previously also been common in the northern parts of the area, but is now extremely rare or totally absent north of latitude 62°N (Lekander et al. 1977). There is also some unpublished evidence

that *Ips duplicatus* is declining in abundance and possibly in distribution, but the species is difficult to detect in the crowns of withering spruces. It is also possible that *I. amitinus* has replaced *I. duplicatus* during its expansion from the south-east to the northwest. Better knowledge of their living habits has led to the detection of *Carphoborus teplouchovi* and *Hylesinus oleiperda* in several new localities.

As a whole, the changes in species' ranges, especially contractions, are difficult to detect without thorough faunal monitoring. The most distinctive or northern species are the easiest ones to monitor. If updated data sets had been used in the statistical analyses, a different picture would probably have emerged. The present results give, however, a basis for future quantitative analyses and ecological modelling when more precise knowledge of the distribution of the species has accumulated.

#### 44. Distribution of rarity and typicalness

The distribution of bark beetles in most areas is rather well known. The most thoroughly surveyed areas are those most centrally placed in the region, i.e. the southern parts of Finland and the Åland archipelago, central and southern Sweden including the islands of Öland and Gotland, southern Norway, especially along the coast and near Oslo, and Sjaelland and some other islands in Denmark (Lekander et al. 1977). The high faunal diversity in the Pyhä-Häkki National Park and the Pisavaara strict nature reserve in Finland increased the indices of the respective quadrats. There are several very rare species (e.g. *Orthotomicus longicollis*, *Carphoborus minimus*) in Pyhä-Häkki especially. In addition, the faunas of both areas have been very thoroughly investigated (e.g. Lindberg & Saris 1952, Biström & Väisänen 1988). Information from the northernmost quadrats especially is less reliable, but the small number of species in these quadrats (see Fig. 2) is also explained by climatic factors and the scarcity of suitable host trees.

The areal distribution of rarity or commonness has seldom been investigated in insects (e.g. Eyre & Rushton 1989, Baz 1991). The present results show that the selection of rarity index is crucial since different indices give quite different results. Although specific aims require different measures of rarity, the simultaneous use of several indices gives analytical depth for comparative evaluations.

Simple rarity indices emphasized the quadrats near the capitals, where the collecting activity can be assumed to be the highest. More effective indices, which also take into account the number of recorded species and set less weight on sporadic species, gave a more realistic picture of the existing diversity. Irrespective of the index, the fauna of Öland seemed to be the most diverse one.

The number of scolytid species increased from north to south, thus following the general pattern recognized for a large number of species (Fisher 1960). The most plausible explanation for this trivial finding is that the number of tree species is higher and the climate milder in the southern parts of the region. The area of managed forests is now extremely large and this also affects the faunal diversity. For example, bark beetles associated with conifers have expanded their ranges in Denmark. One of the reasons may be the intensified use of conifers in forestry and gardens (Bejer-Petersen & Jorum 1977). Some species (e.g. *Carphoborus minimus*, *C. choldkovskiy*, *Orthotomicus longicollis*) are associated with virgin forests (Butovitsch & Heqvist 1947, Biström & Väisänen 1988). However, the high number of scolytid species on the islands of Öland, Gotland and Gotska Sandön, as well as their reputation as 'rarity centres', cannot be explained by the number of tree species alone. This also concerns some quadrats near Kiruna in northern Sweden where the calculated rarity indices indicated a rare bark beetle assemblage. The special character of the northern rarity centre is largely due to a few eastern species such as *Carphoborus choldkovskiy*, *C. teplouchovi* and *Pityogenes saalasi*. The climate in the area east of the mountain ridge has a continental character and the insect fauna is known to include some rare noctuid moth species such as *Polia lamuta* (Hertz) and *Xestia borealis* (Nordström). The special character of the Baltic islands is probably largely due to their history (e.g. Coulianos & Sylvén 1983). The presence of primeval pine forests on Gotska Sandön also probably contributes to its characteristic fauna (e.g. *Pityogenes monacensis*, *Orthotomicus longicollis*, *Pityophthorus pubescens*; Butovitsch 1963), as well as the presence of old stands of deciduous trees on the large islands. Gaston (1990) suggested that species occurring at a faunistically diverse site have, on the average, smaller ranges than those occurring at a faunistically poor site. The present results seem to support this idea.

The bark beetle fauna throughout the Nordic Countries is rather similar, at least in areas be-

longing to the southern and central boreal zones. This indicates that similar control measures can be used against the pest species and that results obtained about the fauna in one region can be fairly well generalized to the other respective

areas. The present biogeographical classification can also be used in the design of studies when wide-scale biogeographical investigations on the Scolytidae are planned.

## 5. Conclusions

1. Biogeographical patterns of the Scolytidae in Fennoscandia and Denmark were classified using two-way indicator species analysis and ordinated by detrended correspondence analysis and canonical correspondence analysis. Multivariate methods reveal patterns of species assemblages that are impossible to recognize using ordinary qualitative methods. Faunal characteristics can also be related to environmental variables, and accumulated data can be easily re-analysed.
2. The present multivariate methods are sensitive to faunal changes. When the state of knowledge is good, changes in the distribution of species make accurate biogeographical analyses possible. In the opposite case, a lack of knowledge is reflected in the results and make the interpretations more uncertain.
3. The biogeographical patterns of the Scolytidae that emerged roughly resembled the zones previously presented for vegetation. Temperature variables associated with the locality were the most important determinants of the biogeographical variation, but annual precipitation and the distribution of *Picea abies* also contributed to the fit of the species data.
4. Multivariate methods and logistic regression models provide tools for analysing the influence of climate change on individual species and species assemblages, assuming that biogeographical data are accumulated in continuous faunal surveys. It is obvious that higher temperatures favour both southern tree and scolytid species. The rates of expansion may be related to the duration of life cycles. Insect-tree-pathogen relationships may change so that new vectors emerge. Dutch elm disease of *Ulmus* will probably spread northwards more easily. Associations between blue stain fungi and bark beetles are so poorly known that any forecasting is premature.
5. Rarity and typicalness indices can be used when additional criteria are needed for biogeographic classification of regions. Such information can be used in the planning of control measures against pests, in planning research projects on scolytids and in land-use planning that takes into account nature conservation values associated with biological diversity.

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Total of 80 references

## Päätelmät

- Fennoskandiassa ja Tanskassa esiintyvien kaarnakuoriaislajien levinneisyyskarttoja analysoitiin monimuuttujamenetelmien (TWINSPAN, DCA, CCA) avulla. Käytetyt monimuuttujamenetelmät voivat paljastaa lajistossa sellaisia ominaisuuksia, joita tavannaomaisin kvalitatiivisin menetelmin ei voi havaita. Eläimistön paikalliset erityispiirteet voidaan kytkeä ympäristömuuttujiin, ja kertyvää aineistoa on helppo käsitellä tarvittaessa uudelleen.
- Käytetyt monimuuttujamenetelmät osoittautuivat suhteellisen herkiksi eläimistössä tapahtuville muutoksille. Tarkat eliömaantieteelliset analyysit ovat mahdollisia vain, jos lajien levinneisyydet tunnetaan hyvin. Tulokset muuttuvat epävarmemmiksi ja tulosten tulkinnassa on oltava varovainen, mikäli lajien levinneisyydet tunnetaan huonosti.
- Kaarnakuoriaisten levinneisyyksiin perustuvat eliömaantieteelliset alueet muistuttivat aiemmin esitettyjä kasvillisuusvyöhykkeitä. Lämpötilamuuttujat sekä ruudun sijainti olivat tärkeimpiä kaarnakuoriaisten eliömaantieteellisen vaihtelun selittäjiä, mutta myös vuotuisella sademäärällä ja kuusen levinneisyydellä oli merkitystä.
- Monimuuttujamenetelmät ja logistiset regressiomallit tarjoavat mahdollisuuksia ilmastoon muutoksen tutkimiseksi edellyttäen, että eliömaantieteellisiä aineistoja jatkuvasti kartutetaan faunistisilla tutkimuksilla. On selvää, että lämpötilan noustessa sekä eteläiset puulajit että eteläiset kaarnakuoriaislajit levittäytyvät pohjoisemmaksi. Hyönteisillä levittämisen nopeus riippuu mm. elämäntien nopeudesta. Hyönteisen, isäntäpuun ja kasvitaudin väliset suhteet voivat muuttua niin, että uusia taudinsiirtäjiä ilmaantuu. Hollannin jalavatauti saattaa levitä pohjoisemmaksi. Sinistäjäsiemien ja kaarnakuoriaisten välinen suhde on niin puutteellisesti tunnettu, että lämpenemisen vaikutusta ei voi ennakoita.
- Lajiston harvinaisuus- ja tyypillisuusindeksejä voidaan käyttää lisätietona alueiden eliömaantieteellisessä luokittelussa. Niillä on merkitystä myös tuholaisten torjunnan suunnittelussa, kaarnakuoriaisiin liittyvien tutkimusprojektien valmistelussa tai maankäytön suunnittelussa erityisesti määriteltäessä alueen lajistollista monimuotoisuutta ja luonnonsuojellusta arvoa.

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